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## Sequential Radiation through Host-Race Formation: Herbivore Diversity Leads to Diversity in Natural Enemies

WARREN G. ABRAHAMSON AND CATHERINE P. BLAIR

Biologists have long sought an answer to the question, "What determines species diversity?" Indeed, this question is one of only 25 key questions featured in the 125th anniversary issue of *Science* that were intended to expose critical gaps in scientific knowledge (Pennisi 2005). A *Nature* article by Emerson and Kolm (2005a; but see also Cadena et al. 2005; Emerson and Kolm 2005b) suggests that species diversity itself might help to promote speciation. Put another way, these authors argue that species cause species.

Emerson and Kolm (2005a) used species lists of the plants and arthropods from the Canary and Hawaiian islands to address whether there is a positive relationship between species diversity and the rate of diversification (measured as the proportion of endemic species). Species richness was a strong predictor of the rate of diversification even after controlling for important biogeographical features such as island age, area, altitude, and proximity to the nearest neighboring island.

Given this finding, one crucial question is what factors could drive the positive feedback between species diversity and speciation rates. A number of authors (e.g., Dawkins 1982; Jones et al. 1997; Odling-Smee et al. 2003; Erwin 2005) have suggested processes that could enhance the number of species in an area, including that new species may continue to subdivide resources via specialization as part of an adaptive radiation, "niche construction," in which an organism modifies its own niche and thus occupies formerly unoccupied niche space, and "ecosystem engineering," in which one species modifies the environment and in so doing facilitates the production of niches for other species. As a consequence of niche construction and ecosystem engineering, many organisms provide habitat and thus new niche opportunities for other species (Erwin 2005).

### **Species Cause Species: Sympatric Speciation through Host-Race Formation**

Sympatric speciation through host-race formation may present a situation where specialization and resultant diversification in one species cause diversification in another. Speciation is typically envisioned as a multiple-step process in which populations of a species first become geographically isolated, then undergo divergence, and finally reproductive isolation occurs. This classical view holds that isolation and divergence come about over time and arise only when populations are located in separate geographic areas. Without geographic separation, gene flow between populations is expected to swamp any differences that may arise between populations. However, studies involving a number of taxa including fish (e.g., cichlids), birds (e.g., crossbills), crustaceans (e.g., parasitic copepods), mollusks (e.g., pulmonate snails), mites (e.g., hummingbird flower mites), and herbivorous insects (e.g., aphids, apple maggots, goldenrod gall flies, treehoppers) indicate that reproductive isolation and divergence can take place sympatrically (Wood 1980, 1993; Strong et al. 1984; Tauber and Tauber 1989; Bush 1994; Abrahamson and Weis 1997; Berlocher and Feder 2002).

Most of the insect examples of sympatric speciation involve host-race formation. Under a scenario of sympatric speciation, an herbivorous insect initially shifts to a closely related or chemically similar host-plant species and changes its preferences for mating and/or oviposition. As a consequence, at least partial reproductive isolation of the host-associated populations occurs. Isolation enables selection, drift, and mutation to produce additional differences between host-associated populations and facilitates differentiation between populations (Abrahamson et al. 2003). Host-race formation may be one of the primary reasons that

clades of herbivores undergo speciation more rapidly than their nonherbivore counterparts (Mitter et al. 1988). The bottom line is that herbivore biology strongly promotes evolutionary diversification (Funk et al. 2002).

## Sequential Radiation

What has been little explored is whether diversification of herbivores in response to their host plants causes differentiation of their natural enemies. Does the genetic differentiation of an herbivorous insect create a new resource that when exploited by a natural enemy causes that natural enemy to undergo genetic and/or behavioral differentiation itself? In this chapter, we explore five examples in which the genetic diversification of herbivores has created new resource opportunities that have been exploited by natural enemies, which subsequently have undergone differentiation via host-race formation themselves.

We have previously termed the process of herbivore differentiation causing natural-enemy divergence “sequential radiation” (Abrahamson et al. 2003). In this sense, sequential radiation is characterized by a diversification of taxa (e.g., natural enemies) farther up a trophic web in response to diversification of their hosts (in this case, of herbivorous insects), which differentiated as a consequence of shifts to novel host plants.

However, sequential radiation could also be used to identify instances in which the diversification of an organism at one trophic level results in diversification of organisms that are lower in a trophic web (e.g., endosymbionts of herbivores or mycorrhizae of host plants). For example, sequential radiation could conceivably describe the reasonably well-understood process of cospeciation (e.g., Clayton et al. 2003; Hafner et al. 2003; Page 2003), such as with the vertically transmitted endosymbiont *Buchnera aphidicola*, which is differentiating in response to its pea aphid (*Acyrtosiphon pisum*) host’s specialization (Baumann et al. 1995; Via 1999, 2001; Shigonebu et al. 2000; Simon et al. 2003). The pea aphid has formed genotypic races, which attack different host plants (e.g., pea, alfalfa, clover) (Via 1999; Simon et al. 2003). In response to the aphid’s host-race formation, *B. aphidicola* is differentiating in parallel. The evolution of these organisms is linked by their mutualistic association, as neither can reproduce in the absence of the other (Baumann et al. 1995). *Buchnera aphidicola* is so specialized that it cannot survive outside the eukaryotic cell; it resembles an organelle. As a consequence of the tight mutualism, which includes both vertical transmission and obligate endosymbiosis, cospeciation results (Shigonebu et al. 2000).

The situation is quite different for free-living organisms, where the influence of the host is less overwhelming. The parthenogenetic pea aphids are not known to cross-infect each other with *Buchnera*, so there is no option for host shifting. However, the radiation of differences up the trophic levels in free-living organisms is more complex and less inevitable.

In this chapter, we focus on sequential radiation as it describes an escalation of biodiversity up a trophic system based on differentiation of an herbivore via host shifts among host plants and subsequent differentiation by a natural enemy. Hence, the examples that we present are not simply cases of cospeciation in which the speciation process occurs in two interacting species in parallel. Each example involves a three-trophic-level interaction, and in all but one example, one of the trophic levels (herbivore) has constructed a new niche and/or “engineered its ecosystem” with subsequent exploitation of created resources and host-race formation.

In addition to examining five examples of natural-enemy differentiation in response to the diversification of their host herbivore, we also explore one example that appears similar, yet no differentiation farther up the trophic web has occurred. Comparison of cases where sequential radiation is present versus absent should shed light on the conditions necessary for escalation of biodiversity. Unfortunately, we have few examples at this point to draw upon, and as a result our ability to determine the conditions that promote reproductive isolation, host-race formation, and speciation are limited. As a consequence, the conclusions we reach must be viewed as tentative as they require testing in additional studies. Nonetheless, our exploration will illustrate a potentially common source of biodiversity and will emphasize the contribution that evolutionary ecologists and population biologists can make to explain “what determines species diversity.” Our goals in reviewing these examples are (1) to illustrate a potentially common source of biodiversity among insects and (2) to identify the conditions that promote sequential radiation.

## Conditions for Host-Race Formation

The circumstances that are probably relevant to host-race formation in natural enemies are likely to be the conditions that apply to host-race formation in general. Studies of sympatric speciation among insects have examined the setting of host-race formation. Jaenike (1981), Diehl and Bush (1984), Tauber and Tauber (1989), Bush (1993), Itami et al. (1997), and Abrahamson et al. (2001) have summarized a number of conditions that are often present in host races:

1. Host-race formation and speciation involve a shift to a new habitat or resource. In moving to a new host, species can modify their own niche and occupy formerly unoccupied niche space (niche construction) or, alternatively, modify the environment (“ecosystem engineering”), unintentionally facilitating the production of niches for other species. When host races form via shifts to new resources, gene flow among host-associated populations can be reduced, and genetic differentiation between sympatric, host-associated populations becomes more likely.

2. Habitat selection and fidelity to a host are under genetic control, although in some examples, host fidelity is subject to modification through conditioning to the host.
3. Females determine the larval host and discriminate among hosts for oviposition. Preferences in oviposition on different hosts by host races are essential to a successful host shift and subsequent host-race formation.
4. Insect phenology is related to host-plant phenology. Differences in the phenologies of hosts can promote reproductive isolation among organisms associated with different hosts. Host-associated emergence differences of only a few days can dramatically affect the availability of mates from the same or alternative hosts because many adult insects are short-lived.
5. Fitness is related to differences in host-associated traits. For example, individuals in a population on a derived host may have a fitness advantage over individuals on the ancestral host in spite of poor adaptation to the new host if individuals on the derived host have shifted into enemy-reduced space or to a better-quality resource.
6. Mate choice is dependent on habitat or resource selection. Specifically, insect males and females use their hosts as a rendezvous for courtship and mating. The coupling of mating and habitat or host choice facilitates assortative mating via host selection and can rapidly establish ecological isolation between the ancestral and the derived populations. Herbivorous insects in which mate choice is directly dependent on habitat or resource choice represent some of the best-documented cases of evolutionary diversification and sympatric speciation.

In the following section, we explore five cases of natural-enemy differentiation and one case of no differentiation to identify which, if any, of the above conditions, determined from studies of herbivores, are also present during the differentiation of natural enemies.

## Cases of Sequential Radiation via Host-Race Formation

### Case 1: Host-Habitat Fidelity

*Herbivore Radiation* *Rhagoletis pomonella* (Diptera: Tephritidae) and its sibling species, *R. mendax*, *R. zephyria*, and *R. cornivora*, are morphologically similar yet they exhibit strong association with different host plants (Frey et al. 1992; Feder et al. 1994; Berlocher 2000; Linn et al. 2003, 2004; Schwarz et al. 2005). For example, the blueberry maggot *R. mendax* attacks the fruits of ericaceous shrubs such as highbush blueberry (*Vaccinium corymbosum*), while the apple maggot *R. pomonella* attacks hawthorn (*Crataegus* spp.) and

apples (*Malus pumila*) (Table 14.1). The most-often cited example of sympatric speciation via host shifts involves host-race formation within the apple maggot. During the past 150 years, this fly has formed genetically divergent host races as a consequence of a host-plant shift from its ancestral hawthorn host to introduced, domestic apples (Bush 1969, 1994; Feder et al. 1993). The entire *Rhagoletis* species complex is believed to have diversified in sympatry through shifts to new hosts. This diversification has been facilitated by their striking host fidelity, which produces premating reproductive isolation among diverging and existing species. Host fidelity in *Rhagoletis* is based on the fly's strong host-associated mating and oviposition behaviors, both of which occur on unabsorbed host fruits (Feder et al. 1994).

*The Natural Enemy* The wasp *Diachasma alloenum* (Hymenoptera: Braconidae) is a specialist endoparasitoid that is known to attack only the third-instar larvae of the apple maggot (Glas and Vet 1983) and second-instar larvae of the blueberry maggot (Stelinski et al. 2004). *Diachasma alloenum* seems to be tracking both the herbivore and its host fruit. Experimental studies using hawthorn fruits suggest that *D. alloenum* finds its host by locating unabsorbed fruit and that visual cues are important to the process (Glas and Vet 1983). However, cues from the host insect are also important. Studies using apple maggot-infested as well as uninfested hawthorn fruits show that the time spent on a fruit and the level of fruit-probing activity by mated *D. alloenum* females are strongly affected by the presence of an apple maggot larva within the fruit. *Diachasma alloenum* females exhibited nonrandom probing when they explored hawthorn fruits containing actively gnawing apple maggot larvae; in contrast, *D. alloenum* females showed random probing on fruits that contained parasitized and hence paralyzed apple maggot larvae (Glas and Vet 1983). Similarly, field observations of host foraging by *D. alloenum* on highbush blueberry fruits showed that this endoparasitoid alighted more frequently on clusters of fruits infested with blueberry maggot larvae than on uninfested clusters or mechanically damaged fruit (Stelinski et al. 2004).

Stelinski et al. (2004) posited that ovipositing *D. alloenum* females are attracted by either plant volatile compounds released by blueberry maggot-infested blueberries but not mechanically damaged fruits, or acoustic signals given off by larvae as they gnaw and tunnel through infested fruits. The timing of the host was also important. The majority of *D. alloenum* females were attracted to host-infested blueberries 15 to 21 days after *R. mendax* females had oviposited into fruit. Such natural-enemy attentiveness to plant cues, alteration of host-plant traits, or host resources is likely a frequent correlate of differentiation of natural enemies in response to their host's differentiation.

*Sequential Radiation* *Diachasma alloenum* wasps appear to have formed host races by tracking the speciation of their hosts, apple maggots on one hand or blueberry maggots on the other. Conditions that might lead to assortative mating

TABLE 14.1

## Traits Relevant to Host-race Formation Demonstrated in Natural Enemies of Differentiating Herbivores

<i>Natural Enemy</i>	<i>Diachasma alloecum</i>	<i>Koptothrips dyskritus</i> and <i>K. flavicornis</i>	<i>Mordellistena convicta</i>	<i>Platygaster variabilis</i>	<i>Copidosoma gelechia</i>	<i>Eurytoma gigantea</i>
Order	Hymenoptera	Thysanoptera	Coleoptera	Hymenoptera	Hymenoptera	Hymenoptera
Family	Braconidae	Phlaeothripidae	Mordellidae	Platygasteridae	Encyrtidae	Eurytomidae
Niche	Parasitoid	Herbivore, kleptoparasite, predator	Herbivore, inquiline, predator	Parasitoid	Parasitoid	Parasitoid
Herbivore	<i>Rhagoletis pomonella</i> , <i>R. mendax</i>	<i>Kladothrips habrus</i> , <i>K. rugosus</i> , <i>K. waterhousei</i>	<i>Eurosta solidaginis</i>	<i>Rhopalomyia solidaginis</i> , <i>R. capitata</i>	<i>Gnorimoschema gallaesolidaginis</i>	<i>Eurosta solidaginis</i>
Host plant	<i>Crataegus</i> spp., <i>Malus pumila</i> , and <i>Vaccinium corymbosum</i>	<i>Acacia</i> spp.	<i>Solidago altissima</i> and <i>S. gigantea</i>	<i>Solidago altissima</i> and <i>S. gigantea</i>	<i>Solidago altissima</i> and <i>S. gigantea</i>	<i>Solidago altissima</i> and <i>S. gigantea</i>
<b>Natural-enemy Traits</b>						
Host-related genetic difference	?	Yes	Yes	Yes	Yes (local)	?
Eats plant tissue	No	Yes	Yes	No	No	Yes
Orients to herbivore's host plant	Yes	?	?	?	?	?
Female determines larval host	Yes	Yes	Yes	Yes	Yes	Yes
Female discriminates among hosts	Yes	?	Probably	?	?	No
Phenology constrained by herbivore and/or host-plant phenology	Yes	Yes	Yes	Yes	Yes	Yes
Phenology differs between hosts	?	?	Yes	?	?	Yes
Fitness differences between hosts	?	?	Yes	?	?	Yes
Mates on herbivore's host plant	Yes	?	?	?	?	?
Assortative mating	Yes (on host plant)	?	Yes (without host plant)	?	?	No (without host plant)
<b>Herbivore Traits</b>						
Radiates to another habitat	Yes	Yes	Yes	Yes	Yes	Yes
Niche construction	No	Yes	Yes	Yes	Yes	Yes
Ecosystem engineering	No	Yes	Yes	Yes	Yes	Yes

NOTE: Yes, demonstrated trait; no, demonstrated absence of trait; probably, likelihood of trait demonstrated; ?, trait not determined.

and host-race formation are present in *D. alloeum*. Stelinski and Liburd (2005) performed a series of no-choice and choice behavioral experiments to explore (1) male responses to female pheromones and (2) male and female responses to fruit odors. In the absence of a host plant, male *D. alloeum* did not discriminate between females from their natal host and other hosts. However, male *D. alloeum* did respond to female pheromones in no-choice experiments as more male wasps of either hawthorn origin or blueberry origin reached females in one arm of a Y tube than reached the empty, control arm. But since courtship and mating occur on or near the host fruit, host fidelity plays a part in mating. Male and female wasps of both origins responded to the odors of their natal fruits given that more blueberry-origin *D. alloeum* males and females contacted fresh blueberry fruit compared to the control, and more hawthorn-origin *D. alloeum* males and females contacted fresh hawthorn fruit compared to the control. Notably, male wasps of neither origin responded to nonnatal fruit. Such fidelity to the host fruit in both males and females would lead to assortative mating.

Although genetic studies of the putative *D. alloeum* host races are necessary to confirm the existence of genetic divergence, the parasitoid's behavioral discrimination in response to its insect host's speciation raises the question of what factors have facilitated the wasp's differentiation. *Diachasma alloeum* exhibits several traits common to host races. Mate choice for this narrow specialist parasitoid is dependent on habitat, since courtship and mating occur on foliage of the herbivore's host plant. This coupling of mating and habitat facilitates assortative mating via host selection and should help generate ecological isolation between ancestral and derived populations. In addition, females determine the larval host and discriminate among hosts for oviposition. This establishes fidelity, which enables isolation. Finally, the apparent differentiation of *D. alloeum* involves a shift to a new habitat (i.e., herbivore and host plant). As a consequence, gene flow among host-associated populations is reduced and genetic differentiation between sympatrically occurring, host-associated populations becomes more likely. As has been argued for other host-associated populations, such differentiation can eventually isolate the host races to the extent that they become distinct species (Waring et al. 1990; Craig et al. 1993; Feder et al. 1994).

*Diachasma alloeum* appears to differentiate in the same way its host herbivore does—by orienting to the host plant. We might expect host-race formation in any natural enemy that behaves as its differentiated host herbivore does in relation to the host plant.

### Case 2: Plant-Mediated Host Shifts and Competition for a Desirable Niche

*The Herbivore* Australian thrips in the genus *Kladothrips* (Thysanoptera: Phlaeothripidae) engage in niche construction by inducing galls on *Acacia* species (Table 14.1). Three

nominal species—*Kladothrips rugosus* (14 recorded hosts), *K.* (formerly *Oncothrips*) *habrus* (2 hosts), and *K.* (formerly *Oncothrips*) *waterhousei* (9 hosts)—are each a suite of morphocryptic sibling species or host races attacking related *Acacia* hosts (Crespi and Mound 1997; Crespi et al. 1998; Kranz et al. 2000; Crespi et al. 2004). Each member taxon in a suite attacks a different *Acacia* host, and several *Acacia* species are galled by two *Kladothrips* cryptic species/host races: one *K. rugosus* and one *K. waterhousei* or *K. habrus*.

The gall niche is important enough to be the object of acute competition. The galls are formed in *Acacia* phyllodes, flattened expansions of the petiole, by a female (or in *K. rugosus* often by a male and female) (Crespi and Mound 1997). The founding thrips feeds on a petiole, enlarging the feeding site until the petiole tissue grows over and encloses her. She lays eggs inside the gall, and her larvae feed and develop there. In the arid and semiarid climates of Australia in which these gall thrips occur, galls offer not only food and sites for reproduction but also protection from predation, including the remarkably high level of ant predation common to these areas, and probably also protection from desiccation that can result from the intense insolation, high temperatures, and low humidity (Crespi 1992; Morris and Mound 2002). In many gall thrips species, while the female is inducing the gall, she must defend the site against conspecifics who attempt to usurp the gall. Such battles have been described for *K. rugosus* on *A. pendula* where attacks are common: the female employs her enlarged forelegs to lift her opponents off the plant surface while she pierces their cuticles with her foretarsal teeth, inflicting injuries that result in eventual death (Crespi 1992). Another defense adaptation occurs in *K. habrus* and *K. waterhousei*, where the first offspring to develop are a "soldier" morph with reduced wings and enlarged forelegs, who remain within the gall and defend against invaders (Crespi and Mound 1997).

*The Natural Enemy* The competition for the gall niche is not limited to gall-inducers. Gall founders of the three nominal species are also attacked by kleptoparasitic thrips of the genus *Koptothrips* (Phlaeothripidae); the invading female parasitic thrips attempt to kill the gall-inducers and use the galls for breeding. Like the gall-inducers, the kleptoparasites lay their eggs in the gall and feed by inserting their stylets into individual modified cells in the gall inner wall (Geyer and Chapman, unpublished). *Koptothrips* species that attack the gall-thrips cryptic complexes are *K. dyskritus*, which assault various sibling species/host races in *Kladothrips rugosus*, and *Koptothrips flavicornis*, which besides attacking several other species, assaults the sibling taxa in *Kladothrips rugosus*, *K. habrus*, and *K. waterhousei* (Crespi and Abbot 1999).

*Koptothrips* species seem adapted to compete for the gall: although they do not have the enlarged forelegs of the gall-inducing thrips, a stab with their foretarsal teeth kills very quickly, possibly with venom (Crespi and Mound 1997). *Koptothrips* also have dorsoventrally flattened heads that

appear to be an adaptation for squeezing into galls where the sides meet in narrow lips. The gall thrips in turn may have developed techniques for evading or resisting the *Koptothrips*. *Koptothrips* attack has probably contributed to the selection for female gall thrips armament and pugnacity as well as the development of the soldier morph (Crespi and Abbot 1999; Perry 2004). In addition, *Kladothrips rugosus* larvae spend only a brief time in the gall before pupating in the soil, a trait that may be useful in evading *Koptothrips* attack (Crespi and Abbot 1999).

**Sequential Radiation** Both *Koptothrips dyskritus* and *K. flavicornis* are diversifying along with gall thrips diversification on *Acacia* hosts. A phylogeny developed from mtDNA sequences from the COI and 16S rDNA genes, adult morphological characters, and gall morphology characters reveals that the *Koptothrips* attacking gall thrips species complexes are themselves a suite of host races or sibling species (Crespi and Abbot 1999). The levels of mtDNA sequence divergence found between specimens of *K. flavicornis* and *K. dyskritus* collected from different species of host thrips on different *Acacia* species range up to 7% and average about 3%. These values suggest reduced gene flow consistent with sibling species or host races (Crespi and Abbot 1999).

Patterns of diversification in *K. flavicornis* suggest a combination of cospeciation with gall-inducing thrips and, of interest here, recent shifting to new thrips hosts. The lowest divergence values, suggesting two pairs of newly forming host races, were exhibited by specimens of *K. flavicornis* collected from host thrips in *Kladothrips rugosus* and *K. waterhousei*. In both of these cases, the host shifting appears to have been mediated by the host plant: the two species of gall-inducers are on the same host-plant species (either *A. loderi* or *A. ammophila*) suggesting that the kleptoparasite simply shifted to a new gall on the same *Acacia* (Crespi and Abbot 1999). Such a shift may be easier than moving to a new thrips host on a new *Acacia* species. Remaining on the same *Acacia* species would probably mean that although the new thrips and the new gall would present novel problems of behavior, phenology, and morphology, some of the underlying plant chemistry and phenology would be the same. Differentiation through plant-mediated host shifting suggests that along with adapting to a particular gall-inducing thrips species, adapting to an *Acacia* species can be an important factor in *Koptothrips* speciation.

Patterns in *Koptothrips dyskritus* suggest either cospeciation or host shifting (Crespi and Abbot 1999). The *K. dyskritus* complex primarily attacks the *Kladothrips rugosus* sibling species, whose ancestor was probably attacked by the ancestor of *K. dyskritus*. However, an enhanced phylogeny is needed to further elucidate the relationship.

Diversification through host shifting may be at the root of *Koptothrips* phylogeny. Evidence suggests that *Koptothrips* became kleptoparasites when they shifted to *Acacia*, where the advantage of living in galls outweighed the problems of adapting to a new host (Morris et al. 1999). The gall thrips'

construction of a niche for themselves engineered the ecosystem for the *Koptothrips* by modifying the *Acacia* environment to include the gall niche.

Conditions that might lead to host-race formation are present in *Koptothrips*. The larvae must develop in the gall chosen by the mother; therefore a simple change in a female's gall preference is enough to move her progeny to a new habitat. Additionally, phenology is important: host-plant phenology influences both gall thrips and their kleptoparasites. Galls are produced on young, developing phyllodes that are available on *Acacia* in a narrow window either in the spring or after a heavy rain. Analysis of gall contents suggests that *Koptothrips* phenology is closely tied to gall thrips and *Acacia* phenology (Crespi 1992; Crespi and Mound 1997).

*Koptothrips* host-race formation involves complex demands to adapt timing and skills to both the host thrips and the host plant (Crespi et al. 2004). For instance, gall morphology is a function of both the herbivore and plant genome (Weis and Abrahamson 1986), with different host thrips producing different galls on the same plant and plants producing, of course, different phyllodes out of which galls are formed (Crespi et al. 1998). In addition, defense behaviors of the gall thrips species differ: invading *Koptothrips* may face a large founding female or several soldiers. Thus, *Koptothrips* speciation may be a response to some of the same forces driving gall thrips speciation in addition to new forces produced by the gall thrips themselves. Finally, the necessity of success in invading and occupying this very desirable niche could result in a high level of selection. The intense competition for galls, played out in mortal combat, might add to the selection pressure for traits adapted to the individual gall type and the host thrips species or host race (Crespi et al. 2004).

### Case 3: Niche Construction and Niche-Related Selection

**The Herbivore** The univoltine North American native gall fly *Eurosta solidaginis* (Diptera: Tephritidae) induces galls on the stems of *Solidago altissima* and *S. gigantea*, closely related members of the *S. canadensis* species complex (Abrahamson and Weis 1997) (Table 14.1). The distributions of both host plants broadly overlap through eastern and central North America, from southern Canada to Florida and Texas, and they frequently co-occur in old fields, disturbed areas, and roadsides (Abrahamson et al. 2005). Although the gall fly attacks *S. altissima* throughout the host-plant's range, this gall-inducer infests *S. gigantea* only in southern Canada and the northern tier of the United States (Abrahamson et al. 1989, 1994, 2001; Abrahamson and Weis 1997).

The sympatric gall fly populations associated with *S. altissima* and *S. gigantea* in the northern United States and southern Canada are distinct host races that show reproductive isolation as a result of allochronic emergence, assortative mating, and strong female oviposition preferences for their

natal host-plant species (Craig et al. 1993, 1994). For example, *S. gigantea* gall flies emerge on average 10 to 13 days earlier than *S. altissima* gall flies. Because gall flies strongly associate with their natal host-plant species, they exhibit strong assortative mating in the presence of host plants, and adult females demonstrate a striking preference to oviposit in their natal host-plant species. In addition, hybridization experiments demonstrate that hybrids of the gall fly host races, as well as backcross progeny from crosses between  $F_1$  hybrids and *S. altissima* or *S. gigantea* gall flies, are less able to induce galls on their host plant relative to *S. altissima* and *S. gigantea* goldenrod gall flies (Craig et al. 1997, 2001). This finding indicates that disruptive selection is operating to maintain the reproductive isolation of host races.

Allozyme and mtDNA studies (Waring et al. 1990; Brown et al. 1996; Itami et al. 1997; Craig et al. 2001; Smith et al. 2002, 2003) show marked genetic differentiation of the *S. altissima* and *S. gigantea* gall flies. The patterns of clade formation and the greater heterozygosity of loci in *S. altissima* gall flies indicate that *S. altissima* is the ancestral host plant and that the host shift took place in the northeastern United States (Waring et al. 1990; Brown et al. 1996). The survivorship of the derived *S. gigantea* host race is enhanced in at least some populations by reduced natural-enemy attack and diminished competition. A survey of New England old fields that included sites with sympatric host-race populations found higher survival of the *S. gigantea* host race compared with the *S. altissima* host race (36% vs. 21%, respectively), primarily due to reduced attack by the parasitoid wasp *Eurytoma obtusiventris* and downy woodpeckers on the *S. gigantea* host race (Abrahamson et al. 1994; Brown et al. 1995; but see Poff et al. 2002). Behavioral studies with *E. obtusiventris* suggest that this early-attacking parasitoid uses host-plant cues to locate its prey (Brown et al. 1995). Thus, the gall-inducer's shift to *S. gigantea* effectively reduces the incidence of parasitism by *E. obtusiventris*. Furthermore, because of higher levels of gall-inducer attack on *S. altissima* and the lack of an oviposition deterrent in female gall flies, competition among larvae on the ancestral host *S. altissima* is likely more severe than on *S. gigantea* (Abrahamson et al. 1994; Hess et al. 1996; Craig et al. 2000).

*The Natural Enemy Mordellistena convicta* (Coleoptera: Mordellidae), a tumbling flower beetle, is a complex of at least 7 sympatric cryptomorphic sibling species whose larvae bore stems of 10 species of the Asteraceae including 5 species of goldenrod (Ford and Jackman 1996; Blair et al. 2005; C.P.B., unpublished). One of the *M. convicta* cryptic species is an inquiline in the *E. solidaginis* galls induced on both hosts where it lives by consuming the gall tissue. It is also an important predator of the gall fly. In a 14-year study, 73.2% of the beetles managed to tunnel into the central chamber of the gall and consume the fly (Uhler 1961).

By inducing galls on goldenrod, the fly has provided a new and superior niche for the beetles that could facilitate survival after a host shift. The galls seem to be a better

niche than the stem environment from which the gall beetles shifted. Mean gall beetle mass at emergence is significantly larger than stem beetle mass (Blair et al. 2005). Gall tissue is richer in resources than stem pith (Stinner and Abrahamson 1979; Abrahamson and McCrea 1986), and the gall-inducer is a meal rich in proteins and fats (Abrahamson and Weis 1997). *Mordellistena convicta* generally consumes the last instar of the *E. solidaginis* larva when the fly reaches a mean dry mass of approximately 17 mg (*S. altissima* galls in PA [Stinner and Abrahamson 1979])—a highly beneficial meal to a beetle with a mean adult dry mass of approximately 0.5 mg (*S. altissima* galls in PA [Blair et al. 2005]). The stem and gall beetles have become genetically differentiated (Blair et al. 2005). Like *Koptothrips* becoming kleptoparasites by shifting to *Acacia* and discovering galls, the beetles have become a natural enemy of the gall fly by shifting to galls. In both cases, the desirability of the resource has created a predator.

*Sequential Radiation* In addition, like the gall fly, the gall beetle is differentiating between the two goldenrod hosts. The *M. convicta* gall beetle cryptic species has formed sympatric host races in response to the *Eurosta* host shift, one race in the galls on each of the host plants (Abrahamson et al. 2001, 2003; Eubanks et al. 2003; Blair et al. 2005). Exact tests for allozyme allele frequency difference showed the sympatric gall samples from *S. altissima* and *S. gigantea* to be significantly different from one another, although the  $F_{ST}$  between the two gall populations is quite small ( $F_{ST} = 0.021$ ), similar to the very recent host races of *Rhagoletis pomonella* ( $F_{ST} = 0.012$ ) (McPheron et al. 1988) and on the low side of the host-race range (Blair et al. 2005).

Beetle samples from the two host galls collected from the New Hampshire and Vermont portion of their sympatric range showed evidence of host-related selection. Beetles exhibited host-related differences in phenology. They emerged as adults from the galls at significantly different times at ambient temperatures, emerging an average of 1.1 days from the earlier-formed gall, *S. gigantea*, than from the later gall on *S. altissima* (Blair et al. 2005). This allochronic difference was also tested in growth chambers at five temperature regimes (18, 20, 22, 24, or 26°C), where beetles consistently emerged from *S. gigantea* galls before *S. altissima* galls (Eubanks et al. 2003). Since the beetles can live for more than a month, the ambient-temperature emergence difference is not enough to prevent mating between beetles from the two galls but is an indicator of plant-related selection that has resulted in genetic differences in phenology.

There are indications of other selective trade-offs related to fitness between the two gall niches that could promote differentiation. *Gigantea* gall beetles weighed more than adults emerging from *S. altissima* galls, but, on the other hand, selective pressure from parasitoids was greater on *S. gigantea* (Blair et al. 2005). A parasitoid that caused a mortality rate in *S. gigantea* gall beetles that was at least 42.3% of

live beetle emergence hardly occurred in the gall beetles on sympatric *S. altissima* host plants.

Beetles from the two hosts have shown behavioral evidence of reproductive isolation (Eubanks et al. 2003). In no-choice experiments, pairs of beetles reared from different host plants were significantly less likely to mate than pairs reared from the same host. In choice experiments, beetles preferred mates from their own host. These experiments were conducted in the absence of the host plants and thus lead to no conclusions about one of the traits expected to lead to host-race formation: the linking of mate choice and host choice through mating on the host. Where the beetles mate in nature is unknown. Assortative mating in the absence of the host is a surprising finding in host races whose slight genetic differentiation suggests that their impediments to gene flow are recent.

*Mordellistena convicta* females choose the oviposition site, a trait common to insects that form host races. There are suggestions that females prefer their natal host for egg laying. When beetles of both sexes were caged on galls of either their host or nonhost and allowed to mate and lay eggs, offspring were recovered the following spring only from host galls. When beetles were allowed to mate and oviposit while caged with both host and nonhost plants, significantly more beetles were produced from host-plant galls: 84% of the *S. altissima* beetle cages and 82% of the *S. gigantea* cages produced offspring only from the host galls (Eubanks et al. 2003). These experiments likely indicate ovipositional host preference, although host-related offspring performance may also be involved.

Ecosystem engineering by the gall flies provided new niches for two rounds of beetle differentiation: between the stem beetles and a subset of that population that shifted to galls and also between the populations in the two host galls. Differentiation between the gall fly host races has radiated up the trophic web to the beetles that have also formed host races in the *Eurosta* galls. Gall-niche-related selection seems to be the driving force behind gall-beetle differentiation on *S. altissima* and *S. gigantea*: beetle phenology is related to host-gall phenology, and fitness is related to differences in host-gall-influenced traits such as final beetle mass. Similar to the situation with the kleptoparasitic *Koptothrips* who also inhabit another's gall, the same host-related selection that drives gall-inducer host-race formation drives the process in the beetle. Once the gall-inducer alters the plant environment, others are attracted to the new niches and differentiate as the result of the niches being on separate plants.

#### Case 4: A More Distant Relationship with the Host Gall

*The Herbivore* *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae) and its closely related sister species *R. capitata* form galls on *S. altissima* and *S. gigantea*, respectively, as do the host races of *Eurosta solidaginis* (McEvoy 1988; Stireman

et al. 2005) (Table 14.1). Analysis of mtDNA sequences from several sympatric populations of *Rhopalomyia* on the two goldenrods in the Upper Midwest of the United States revealed host-related differentiation at the COI locus consistent with cryptic sibling species (10.2% net sequence divergence) (Stireman et al. 2005). As in *Eurosta*, the *S. gigantea* host form seems to be the derived one because it exhibits far less genetic variation. Although female *Rhopalomyia* from the two host species are indistinguishable, there are interspecific differences in male genitalia and gall morphology. On both plant species, there are two generations of *Rhopalomyia*, one emerging in spring and one in late summer (McEvoy 1988; Netta Dorchin, 2005, personal communication). Adults of the spring-emerging generation lay their eggs in the apical meristem of the host plants to induce the summer galls, whereas adults of the late-summer generation lay their eggs in the ground near the plant (McEvoy 1988).

*The Natural Enemy* On both host plants, eggs laid by the spring generation in the apical meristems are attacked by *Platygaster variabilis* (Hymenoptera: Platygastridae), a polyembryonic egg parasitoid. Whether *P. variabilis* attacks the eggs of the following generation is yet to be determined (Netta Dorchin, 2005, personal communication). Not much is known about *P. variabilis* behavior, including whether this species mates on the herbivore's host plant. Since *P. variabilis* is an egg parasitoid, the ovipositing females need to orient to midge eggs in the apical meristem prior to the formation of the gall.

*Sequential Radiation* *Platygaster variabilis* appears to be differentiating along the same lines as *Rhopalomyia*. Maximum likelihood analysis of mtDNA from wasp broods collected from *Rhopalomyia* apical galls in Minnesota, Iowa, Nebraska, and South Dakota indicate that *P. variabilis* is divided into two clades, one attacking *Rhopalomyia* on *S. altissima* and one on *S. gigantea* (Stireman et al. 2006). As is the case with its midge host, within-clade genetic diversity is much higher for the *S. altissima* clade of *P. variabilis* than for the *S. gigantea* clade. Likewise, the degree of differentiation suggests morphologically cryptic sibling species. Stireman et al. (2006) describe the differentiation of the *P. variabilis* parasitoid in response to the differentiation of its host *Rhopalomyia* as "cascading host-associated differentiation." Although these authors restrict cascading host-associated differentiation to the host-related diversification of parasitoids, the pattern depicted is the same pattern we describe as sequential radiation.

Little is known about factors in *P. variabilis* that might lead to host-race formation. The species does have at least one known host-race related trait: the ovipositing female chooses the host egg so that a genetic change in the female's host preference would be sufficient to initiate a host shift. Similar to *Diachasma alloeum*, the female *P. variabilis* must orient to the correct host plant to find her prey. Thus, chemical differences between the host-plant species could influence host-race formation in this parasitoid. *Platygaster*

*variabilis* phenology is likely influenced by the timing of egg laying in *Rhopalomyia*, but how narrowly constrained *Rhopalomyia* egg laying is by plant phenology is unknown.

Unlike *M. convicta* and *Koptothrips* species, which also attack gall-inducers, *P. variabilis* larvae do not consume gall tissue. As an endoparasitoid, *P. variabilis* contacts the host gall only indirectly through the herbivorous *Rhopalomyia* larva that is eating the plant as it is itself being eaten. Thus it need not adapt to eating tissue from two different hosts. Although it does not eat the gall, *P. variabilis* benefits from niche construction and ecosystem engineering by the gall midge. As an endoparasitoid of the midge larva, it needs the gall for development of its prey and therefore itself. But unlike the inquiline *M. convicta* and the kleptoparasite *Koptothrips* species, this parasitoid is not attracted by the gall itself, and gall features are unlikely to affect its differentiation.

### Case 5: Recurring Local Sequential Radiation

**The Herbivore** The moth *Gnorimoschema gallaesolidaginis* (Lepidoptera: Gelechidae) also forms galls on both *S. altissima* and *S. gigantea* (Table 14.1). Females lay eggs in the autumn on the underside of goldenrod leaves, and larvae overwinter in the eggs from which they hatch in the spring. They crawl to a new goldenrod shoot and burrow laterally into the terminal bud and down into the stem where their feeding stimulates gall formation (Leiby 1922a). Analysis of 12 allozyme loci from six sites in the Midwest revealed host-associated differentiation consistent with reduced gene flow between the moth populations on *S. altissima* and *S. gigantea* (Nason et al. 2002). An  $F_{ST}$  estimate of 0.16 between the two host-associated populations lies within the range common to insect herbivore host races. Nason et al. (2002) speculate that the two populations are either well-established host races or young cryptic species.

**The Natural Enemy** *Gnorimoschema gallaesolidaginis* is parasitized on both goldenrod plants by *Copidosoma gelechiae* (Hymenoptera: Encyrtidae), a polyembryonic parasitoid wasp that attacks the moth eggs in the autumn (Leiby 1922a). Multiple *C. gelechiae* larvae (about 165 per moth larva) develop within the overwintering moth larva and remain within it when it forms its gall. Larval development and pupation in the parasitoid is closely aligned to development in the moth (Leiby 1922b). When the moth dies in its final instar, *C. gelechiae* larvae pupate in the moth mummy until late summer, when they emerge as adults and gnaw through the gall to parasitize the new generation of moth eggs (Patterson 1915; Leiby 1922b).

**Sequential Radiation** Analysis of nine polymorphic enzyme loci revealed host-associated genetic differentiation in large samples of *C. gelechiae* from *Gnorimoschema* galls in intermixed stands of *S. altissima* and *S. gigantea* from three geographically distant areas: New Brunswick, Ontario, and Minnesota (Stireman et al. 2006). Within

each of the sympatric sites, the wasp exhibited host-related genetic differentiation. However, the divergence was caused by a different group of allozyme loci at each site, suggesting that differentiation was local and developed independently in each area. Also, the differentiation at each site was minor ( $F_{ST\ site} = 0.002-0.05$ ), which indicates recent divergence. So although the herbivore has only two host forms spread throughout the sampled area, sequential radiation, or as termed by Stireman et al. (2006), cascading host-associated differentiation, in *C. gelechiae* seems to have produced multiple local host-related forms in the recent past. Repeated local host differentiation that affects allozymes suggests an almost inevitable process; rather than occurring only once and spreading, differentiation seems to occur repeatedly.

Like *P. variabilis*, *C. gelechiae*, except when chewing its way out as a newly emerged adult, is not required to digest plant tissue from two divergent herbivore hosts. And the emergence chewing is brief because *C. gelechiae* adults use the exit tunnel created by the gall moth larva and are merely required to nibble through the final tissue layer to the outside (Leiby 1922b). Thus, again like *P. variabilis*, *C. gelechiae* benefits from environmental engineering only insofar as the gall offers it protection during development. But *C. gelechiae* does have a relationship to the herbivore's host plant. Like *P. variabilis*, it must find the host plants on which the gall moth has laid its eggs, most likely through chemical tracking, a process requiring plant recognition. The *C. gelechiae* female, like the *D. allozum* parasitoid that attacks the apple and blueberry maggots, has considerable contact with the herbivore's host plant, crawling about the goldenrod leaves and stems, searching assiduously until her antennae contact an egg (Leiby 1922b). The need to find and search the correct plant may lead to the host fidelity characteristic of differentiating host races. But determination of the mechanisms of divergence require behavioral and ecological data not yet available (Stireman et al. 2006).

### Example Showing No Differentiation

#### Case 6: Goldenrod Gall Flies and a Parasitoid Wasp—Probably No Host-Race Formation

The parasitoid *Eurytoma gigantea* (Hymenoptera: Eurytomidae) oviposits into the central chambers of fully grown galls induced by the goldenrod gall fly *Eurosta solidaginis* (Weis and Abrahamson 1985) (Table 14.1). As described above, the gall fly has formed genetically and behaviorally distinct races on its host plants *S. altissima* and *S. gigantea*. Cronin and Abrahamson (2001) tested the hypothesis that *E. gigantea* has formed host races in direct response to the host shift and subsequent host-race formation of *E. solidaginis* by determining emergence times, mating preference, and female oviposition preference for parasitoids derived from galls of each gall fly host race.

Even though the wasps emerged earlier from *S. gigantea* than *S. altissima*, male and female *E. gigantea* from each gall fly host race broadly overlapped in their emergence times, indicating that there was at least no phenological barrier to gene flow. Furthermore, female parasitoids did not assortatively mate in choice experiments. Females that emerged from one gall fly host race were as likely to mate, in the absence of host plants, with males from their natal gall fly host race as they were with males of the other gall fly host race. Finally, female parasitoids exhibited no preference to oviposit on their natal gall fly host race or any overall preference for one host race, even though fitness was higher when parasitoids came from galls of the *S. gigantea* host race than when they were reared from galls of the *S. altissima* host race (Cronin and Abrahamson 2001). Taken together, these results suggest that *E. gigantea* has not diverged in parallel with its host as its host herbivore shifted from *S. altissima* to *S. gigantea*. Genetic evidence would be necessary to confirm such a conclusion.

Nevertheless, *Eurytoma gigantea* has traits consistent with host-race formation. The female chooses the larval host. She seeks out a gall, pierces it with her ovipositor, and lays an egg on the fly larva in the central chamber. The females show an adaptation to a particular host: the ovipositor of females from *S. gigantea*, the plant that produces larger galls, is on average significantly longer than the ovipositor of females from *S. altissima* (Cronin and Abrahamson 2001). Furthermore, the wasp is the beneficiary of the ecosystem engineering of the gall fly. Once it consumes the fly larva, the wasp larva lives free in the central chamber of the gall, consuming gall tissue, pupating, and becoming an adult. Furthermore, it appears to be constrained by herbivore and host-plant phenology, attacking galls in their sixth and seventh weeks when they are fully developed (Weis and Abrahamson 1985; Cronin and Abrahamson 2001). Although the emergence times of adult wasps from *S. altissima* and *S. gigantea* broadly overlap, the wasps emerge earlier from the earlier-galled *S. gigantea*, reflecting plant and gall fly phenology. Finally, assortative mating remains a possibility if *Eurytoma* mate on their prey's host plant. But the exhibition of no plant preference by the mated *Eurytoma* females is a strong indication of high gene flow between the populations on the two host plants.

Is there anything about *E. gigantea*'s biology that might suggest why this parasitoid has not differentiated in response to the divergence of its host? *Eurytoma gigantea* may be a visually orienting parasitoid given that it attacks fully developed galls (Weis and Abrahamson 1985), unlike the other two gall-inducer parasitoids *P. variabilis* and *C. gelechiae*. If visual cues rather than host-plant volatile compounds are key to this parasitoid finding its host, it would be likely that *E. gigantea* females are just as apt to find the galls of their gall fly hosts on *S. gigantea* as on *S. altissima*, especially given that these two host plants frequently occur sympatrically (Abrahamson and Weis 1997). So in spite of the fact that this parasitoid consumes plant tissues as well as

its prey's tissues, it may not use host-plant chemicals to locate its hosts. Such a search strategy could be a barrier to host-race formation. Female oviposition preference for the natal plant must occur for differentiation to take place. It is a key step in the host-race scenario. If that fails to develop in a species where the female chooses the larval host, then no differentiation is possible.

## Conclusions

In order to better understand the conditions that promote sequential radiation, we have presented five examples of sequential radiation that involve two species of kleptoparasites, three species of parasitoid wasps, and a gall inquiline that acts as a facultative predator. For comparison, we have included an additional case involving a parasitoid wasp that shows no host-associated differentiation. Although the number of examples available for this initial evaluation of the conditions associated with sequential radiation is small, our examination of these cases suggests several preliminary conclusions.

### How Common Is Sequential Radiation?

The variety of guilds that exhibit sequential radiation and the high proportion of examples that display sequential differentiation (of those available for review) imply that the pattern of sequential differentiation may be common. Of course, there is the possibility that unreported negative results exist. Nevertheless, we suspect that sequential radiation will eventually account for a sizeable number of herbivore natural-enemy species radiations. The examples that we have reviewed suggest that existing species are a source of diversity, supporting the notion that species beget species (Emerson and Kolm 2005a; Erwin 2005). If so, then the study of sequential radiation in plant-herbivore-natural-enemy systems will offer valuable information about speciation and the origin of biodiversity.

### When Does It Happen?

#### EXISTENCE OF A NEW NICHE

What conditions promote or prevent the spread of differentiation up the trophic levels of host-plant, herbivore, and natural-enemy systems? In each of the cases of sequential radiation reported here, an herbivore has differentiated after taking advantage of host-plant diversity by shifting host plants and, in all but one case (that of *D. alloenum*), constructing a new niche. These herbivores are attacked by other insects including kleptoparasites, parasitoids, or inquiline/facultative predators, which have in turn differentiated along the lines of the herbivores' differentiation. Ecosystem engineering may have been central to the conditions that facilitated sequential radiation in the case of the kleptoparasites *Koptothrips dyskritus* and *K. flavicornis* and the

gall inquiline/facultative predator *M. convicta*. The construction of a new resource, which in these examples is a gall, by the herbivore created a new niche that was exploited by the kleptoparasites or inquiline/facultative predator.

Galls provide better nutrition than the ungalled plant organs from which they are derived (Abrahamson and Weis 1987, 1997), and hence the resources provided via the gall may help offset negative fitness consequences when the gall-inducer's natural enemies shift to the new resource. This could certainly be the case for both the kleptoparasites and gall inquiline/facultative predator, which consume plant tissues. Furthermore, in many cases galls can afford protection from the environment and natural enemies, and consequently galls present gall-inducer natural enemies with a highly desirable niche.

Ecosystem engineering such as the stimulation of a gall is not involved in the case of the apple and blueberry maggot. In this case a new, empty niche is available to *D. alloeum* parasitoids via the host shift of its host herbivore into a new fruit. *Diachasm alloeum* has followed its herbivorous host into a new niche using altered cues for tracking and infesting its host. This situation also occurs for *P. variabilis* and *C. gelechiae* parasitoids of the midge and moth gall-inducers on *S. altissima* and *S. gigantea*. The availability of a new resource is necessary for the subsequent exploitation of that resource by natural enemies.

#### INFLUENCE OF THE PLANT

A critical driving force in the formation of host races within an herbivore species is its host plant. Likewise, the herbivore's host plant can play a large role in the sequential radiation of natural enemies. Three of the natural enemies, *M. convicta*, *Koptothrips dyskritus*, and *K. flavicornis*, are herbivores themselves and hence are subject to the same host-switching constraints and consequent selection as the gall-inducing herbivores that they follow. Such natural enemies must adapt to new host-plant chemicals, morphologies, and phenologies and must develop a preference for ovipositing in the new plant, although the two *Koptothrips* species sidestep some of these challenges when they switch to a new gall thrips host on the same *Acacia* species.

Similarly, the plant also affects the differentiation of the *D. alloeum* parasitoid of the apple and blueberry maggot system. In this example, the parasitoid orients to the herbivore's host plant for mating, prey location, and oviposition. Mating on its prey's host plant is likely central to reducing gene flow among differentiating host-associated parasitoid populations. The two egg parasitoids, *P. variabilis* and *C. gelechiae*, must also orient to the correct species of host plant in order to infest an egg of the correct insect host. Selection for plant preference must be part of their differentiation process.

#### CONDITIONS FOR HOST-RACE FORMATION

Several of the conditions that commonly appear among the known instances of host-race formation may be fundamental

to the sequential radiation of natural enemies. The following conditions should serve as a guide for future studies that examine sequential radiation. In order to more fully understand sequential radiation, we need to better evaluate the roles of each of these conditions in the differentiation process.

1. *Host-race formation involves a shift to a new habitat or resource and genetic differentiation.* A host shift by the herbivore in each of our examples appears to be fundamental to its differentiation. With the exception of *D. alloeum*, the subsequent differentiation of the natural enemy may be facilitated by the construction of a new niche and/or ecosystem engineering of a new resource by a host herbivore. Genetic differentiation has been demonstrated in each of our examples with the exception of *D. alloeum*, where the genetics have yet to be examined. Yet this parasitoid's behavioral discrimination in response to its prey's speciation strongly suggests that genetic differentiation is developing, given the potential of behavioral preferences to restrict gene flow among host-associated populations.
2. *Host races exhibit strong habitat selection and fidelity to their host.* Because natural enemies need to locate their hosts, it is no surprise that the examples we have reviewed show indications of host fidelity and habitat-selection ability. Examples such as *M. convicta* reveal an exceptional degree of behavioral specificity that may occur in sequentially radiated natural enemies (Eubanks et al. 2003; Blair et al. 2005). While it is yet undetermined if there is a genetic basis to these behavioral preferences, it is apparent that habitat selection and host fidelity are well developed.
3. *Females determine the larval host and discriminate among hosts for oviposition.* In each of our positive examples, the accuracy and specificity of the oviposition choices of the female are essential for natural-enemy differentiation. If females were unable to choose the appropriate host for their offspring, gene flow could prevent differentiation of host-associated populations. Strict oviposition preferences on different hosts by host races are critical to successful host shifts and subsequent host-race formation. Furthermore, a simple change in female oviposition preference would be enough to initiate a host shift since in all of these systems larvae must grow where the egg is placed.
4. *Natural-enemy phenology is related to its host's phenology.* In all the cases, the herbivore's phenology is constrained by the host-plant's phenology and in turn influences the phenology of the natural enemy. In the case of the two *Koptothrips* kleptoparasites, young, developing *Acacia* phyllodes are available to the gall thrips and kleptoparasites for only a narrow window of time (Crespi 1992; Crespi and Mound 1997). Likewise, adult *M. convicta* emerge from the previous

year's galls just as galls become visible on the current year's goldenrod (Weis and Abrahamson 1985). The slightly different timing of the host plants and of the gall fly emergence is reflected in the timing of the beetle emergence (Blair et al. 2005). Similarly, the egg parasitoids *P. variabilis* and *C. gelechiae* must synchronize oviposition with the availability of gall moth or gall midge eggs. The restricted host phenology in these systems is a selective force on the natural enemy. Furthermore, shifts in natural-enemy phenology due to differences in host insect phenologies can promote reproductive isolation, especially when the adult phases of the herbivore are short lived, as in *Rhopalomyia* gall midges. In such cases, emergence differences of only a few days could dramatically affect the availability of mates from the same or alternative hosts.

5. *Fitness is related to differences in host-associated traits.* While fitness information is not available for most of the cases detailed here, *M. convicta* offers an example of remarkable fitness differences on alternate hosts (Blair et al. 2005). Fitness advantages in derived host races compared to ancestral host races are essential as a means of overcoming poor adaptation to the new host. Selective differences between hosts promote differentiation between the host races.
6. *Mate choice is dependent on habitat or resource selection.* While we might expect this to be the case for sequentially radiating natural enemies, information about the association of mate and habitat choice is available only for *D. alloeum* among our examples. As noted above, *D. alloeum* orients to its prey's host plant for both mating and oviposition, and part of its host-location process involves responses to the host plant. It certainly makes sense that differentiation would be promoted if mate choice is coupled with host choice. Such coupling could quickly create ecological isolation between ancestral and derived populations.

#### When Does It Not Happen?

Why has *Eurytoma gigantea*, a parasitoid of the goldenrod ball gall fly, not formed host races, given the clear host-related differentiation of its herbivore host? If indeed it has not, the answer may lie in the possibility that in its search for fully developed galls, visual cues may be far more important to *E. gigantea* than plant and/or host-chemical cues (Cronin and Abrahamson 2001). That *E. gigantea* has not differentiated in response to its herbivore host's differentiation may indicate that plant chemical location is a key factor in host-race formation. Certainly in the scenario suggested by Bush (1993, 1994) for host-race formation, a change in an herbivore's plant preference, usually in its orientation to that plant's chemistry, leads the herbivore to mate and oviposit on a new plant. Perhaps host-plant pref-

erence cannot develop without such genetically based chemical orientation. Of course, the fact that *E. gigantea* shares some of the traits considered vital to host-race formation raises the question of whether there are key factors that research on host-race formation has so far failed to investigate.

#### Sympatric Speciation Studies

Most of the examples of the secondary host-race formation that have resulted in species begetting species have come from studies of sympatric speciation. Because these systems are well studied at the level of plant-herbivore interactions, they have clearly established the conditions in the relationship between the host plant and herbivore necessary to produce the formation of host races. It is from these well-established foundations that we can expect the most information about the spread of differentiation up the trophic levels, and it is here that population biologists can make a highly valuable contribution to the study of evolutionary diversity.

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