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Host races in plant-feeding insects and their importance in sympatric speciation

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The existence of a continuous array of sympatric biotypes—from polymorphisms, through ecological or host races with increasing reproductive isolation, to good species—can provide strong evidence for a continuous route to sympatric speciation via natural selection. Host races in plant-feeding insects, in particular, have often been used as evidence for the probability of sympatric speciation. Here, we provide verifiable criteria to distinguish host races from other biotypes: in brief, host races are genetically differentiated, sympatric populations of parasites that use different hosts and between which there is appreciable gene flow. We recognize host races as kinds of species that regularly exchange genes with other species at a rate of more than *ca.* 1% per generation, rather than as fundamentally distinct taxa. Host races provide a convenient, although admittedly somewhat arbitrary intermediate stage along the speciation continuum. They are a heuristic device to aid in evaluating the probability of speciation by natural selection, particularly in sympatry. Speciation is thereby envisaged as having two phases: (i) the evolution of host races from within polymorphic, panmictic populations; and (ii) further reduction of gene flow between host races until the diverging populations can become generally accepted as species. We apply this criterion to 21 putative host race systems. Of these, only three are unambiguously classified as host races, but a further eight are strong candidates that merely lack accurate information on rates of hybridization or gene flow. Thus, over one-half of the cases that we review are probably or certainly host races, under our definition.

Our review of the data favours the idea of sympatric speciation via host shift for three major reasons: (i) the evolution of assortative mating as a pleiotropic by-product of adaptation to a new host seems likely, even in cases where mating occurs away from the host; (ii) stable genetic differences in half of the cases attest to the power of natural selection to maintain multilocus polymorphisms with substantial linkage disequilibrium, in spite of probable gene flow; and (iii) this linkage disequilibrium should permit additional host adaptation, leading to further reproductive isolation via pleiotropy, and also provides conditions suitable for adaptive evolution of mate choice (reinforcement) to cause still further reductions in gene flow. Current data are too sparse to rule out a cryptic discontinuity in the apparently stable sympatric route from host-associated polymorphism to host-associated species, but such a hiatus seems unlikely on present evidence. Finally, we discuss applications of an understanding of host races in conservation and in managing adaptation by pests to control strategies, including those involving biological control or transgenic parasite-resistant plants.

Keywords: biotypes; ecological speciation; parasitism; gene flow; species concepts; hybridization

1. HOST RACES AS A FORM OF ECOLOGICAL DIFFERENTIATION

Most biologists accept that speciation is a more or less continuous process in which genetic variation becomes segregated between populations, but the exact route to speciation remains contested (Turelli *et al.* 2001). Host races, as treated here, are just one of a number of intermediates in the continuum between polymorphisms and full species: other intermediate stages are often referred to as 'biotypes' or 'ecological races'. In this discussion, we will use the term 'biotype' in an unspecialized way to mean a population that has some genetic or phenotypic differences from another population, but which may fall anywhere in the taxonomic spectrum from polymorphisms within species up to the level of species. Typical examples are biotypes resistant to various chemicals or biotic stresses in insects or plants (Gallun *et al.* 1975; Macnair 1989; Gould 1991; McKenzie & Batterham 1994; Macnair & Gardner 1998) and ecologically specialized morphs of animals as diverse as sea anemones (Quicke *et al.* 1983), fish (Bell & Foster 1994; Schluter & Nagel 1995; Lu & Bernatchez 1999; Taylor & McPhail 1999; Jonsson & Jonsson 2001) and marine mammals (Ford *et al.* 1998; Wang *et al.* 1999).

In most of these examples (see also a review of such cases in Kondrashov & Mina (1986)), adaptive differentiation to ecological conditions occurs at or below the taxonomic level considered to represent species. Perhaps because it is a particularly specialized mode of life, parasitism provides excellent conditions for the evolution of biotypes. Host-associated biotypes (including host races) are known in a variety of parasitisms and commensalisms: for

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example, in Batesian mimicry of butterflies (Turner 1984), sponge-dwelling snapping shrimps (Duffy 1996), nest parasitism of the common cuckoo (where biotypes are known as 'gentes' (see Marchetti *et al.* 1998; Gibbs *et al.* 2000)), schistosome worms (Theron & Combes 1995), mistletoes (Clay *et al.* 1985; Glazner *et al.* 1988; Nickrent & Stell 1990; Zuber & Widmer 2000) and fungi (e.g. Bucheli *et al.* 2000).

Insect biotypes feeding on different species of host plants are particularly well documented and are also the category most strongly associated with controversial theories of sympatric speciation (Bush 1969; Diehl & Bush 1984; Via 2001). The literature has been reviewed several times, both by authors who argue that sympatric speciation is common (Diehl & Bush 1984; Strong *et al.* 1984; Tauber & Tauber 1989; Via 2001; see also Mopper & Strauss 1998) and by those who argue the reverse (Futuyma & Mayer 1980; Jaenike 1981; Claridge 1988). Recently, there has been renewed interest in the possibility of sympatric speciation (Schilthuizen 2000; Mallet 2001*a*; Via 2001), and many new empirical studies of host races in phytophagous insects have been published in the last 10 years. It therefore seems timely to review host-associated biotypes from a modern evolutionary perspective.

We here:

(i) operationally define the term 'host race' by a set of empirically testable criteria;
(ii) identify some well-studied biotypes that meet our criteria, and some that do not;
(iii) outline recent developments in the theoretical study of sympatric speciation;
(iv) summarize evidence for speciation via host shift; and
(v) discuss possible practical applications in conservation and pest control.

2. DEFINING HOST RACES

(a) *Previous definitions of host races and difficulties in their use*

New models of sympatric speciation have largely overcome objections to the possibility of sympatric speciation via host shift (Via 2001); however, differing opinions about the existence and meaning of host races continue to cloud the literature. Populations described as host races by some biologists are regarded as polymorphisms or sibling species by others. Here, we examine some of the most common definitions and present an operational definition of host races that refines and clarifies what appears to us to be a consensus running through previous literature.

The first definition of a host race in the recent literature of which we are aware is from Bush (1969, p. 237):

> a population of a species living on and showing a preference for a host which is different from the host or hosts of other populations of the same species. Host races represent a continuum between forms that freely interbreed to those that rarely exchange genes. The latter may approach the status of a species, generally regarded as an interbreeding population reproductively isolated from all other such populations.

This definition, which emphazises the relationship between host races and other taxa (discussed in the next section) rather than their practical identification, has been echoed in several others.

Mayr (1942, p. 208 and subsequently) defines host races using Thorpe's (1930) definition of biological races, as follows:

> A biological race may be said to exist where the individuals of a species can be divided up into groups usually isolated to some extent by food preferences occurring in the same locality and showing definite differences in biology, but with corresponding structural differences few or inconsistent or completely absent.

Like the previous definition, Mayr's is not tailored for use in empirical studies. It does not, for example, suggest how biotypes isolated due to differences in plant preferences are detected, or what degree of morphological differentiation can be considered 'few'. More importantly, under the widely used biological species concept, the requirement that the biotypes be reproductively isolated (and lacking in morphological differentiation) in fact describes host-associated sibling species (Diehl & Bush 1984).

Jaenike (1981) was the first to propose a definition of host races consisting of a set of experimentally verifiable criteria, abbreviated here from pp. 830–831:

> 1. [The populations are] sympatric, so that individuals in breeding condition in one population are within normal cruising range of those in another.
> 2. There must be a statistically significant genetic difference between the populations, suggesting, though not proving, that gene flow between them is not extensive.
> 3. The genetic difference (2) under consideration cannot be one that is directly related to host selection … [unless] both males and females manifest genetic differentiation in host preference, and … mating takes place on or near the host plant.
> 4. It must be shown that the genetic difference (2) is not solely the result of natural selection acting on the current generation of individuals.
> 5. Finally, if the above conditions are met it should be shown, if experimentally feasible, that the genetic difference between the two populations disappears over a period of generations when they are confined to breed on a single food type … If the genetic differences between the two groups do not disappear …, or if they do so initially only to reappear in subsequent generations … then reproductive isolation between them in the field cannot be ascribed to differences in host preference. In this case the two groups represent distinct species, not host races.

Criteria 1, 2, and 4 of Jaenike's definition have been incorporated into the operational definition that we propose below. However, we argue that the main distinction between host races and host-associated species is the occurrence of appreciable gene flow between the host races. While Jaenike's definition does not exclude the possibility of gene flow between host races, neither does it explicitly require it, suggesting only that it is 'not extensive' (criterion 2). Host race collapsibility, Jaenike's criterion 5 (also echoed by Berlocher 1999, p. 661), would presumably require replicated observations of the extinction of a host race; it seems unnecessarily stringent (see also Diehl & Bush 1984) and difficult to test in real systems. In our definition below, we argue that gene flow between host races, which may also cause extinction (Rhymer & Simberloff 1996), is a more relevant feature that has the virtue of being easier to investigate.

The need for a consistent definition of host races was raised by Diehl & Bush (1984), who discussed several alternatives before proposing what is now perhaps the most widely quoted:

> a population of a species that is partially reproductively isolated from other conspecific populations as a direct consequence of adaptation to a specific host. (p. 472)

This definition concisely conveys several features of a host race but it still does not clearly state a set of properties required of candidate biotypes. For example, it is not obvious what would constitute adaptation to a specific host, given that in order for a host shift to occur, the only change necessary may be a preference for a new host. 'Partial reproductive isolation' is also open to interpretation: it could include a variety of types of 'post-mating isolation' (hybrid unfitness, or any ecological trait under disruptive selection; Diehl & Bush 1984, p. 472) or 'pre-mating isolation' (i.e. affecting mate choice). Conversely, in other ways the definition seems too strict: reproductive barriers between host races could be strengthened by indirect as well as direct consequences of adaptation to different hosts.

Another set of criteria, incorporating some of Jaenike's ideas, was proposed by Bush (1992, p. 342):

1. Individuals of different host-associated populations in breeding condition must be sympatric.
2. Statistically significant genetic differences exist between these sympatric populations that are not directly related to host selection or solely the result of natural selection acting on a single generation.
3. Males and females exhibit genetic variation in host preference that results in assortative mating, i.e. mating occurs on the preferred host plant and host preference is under genetic control.
4. Males and females show host-associated tradeoffs in fitness.
5. There is no evidence of post-mating reproductive incompatibility. Hybrid incompatibility between host-associated populations indicates that they are sibling species, not host races.

Again, there is no direct requirement for gene flow between the races in the wild. Bush's criterion 5 seems unnecessary for the same reason as Jaenike's criterion 5; host races (provided at least, that there is gene flow (see below) and especially those in later stages of divergence) need not lack post-mating reproductive incompatibility completely. Another reason why we ignore post-mating incompatibility below is that there is no clear distinction between 'post-mating' incompatibility and incompatibilities that are an inevitable, pleiotropic result of host adaptation. Hybrid inviability might be due to faulty host choice, faulty detoxification of host-chemistry, or even asynchrony with host phenology. Similarly, it is unclear why the second part of criterion 3, 'mating occurs on the host', is stipulated, as we see no reason to exclude a less direct means of reduction in gene flow.

Building on the ideas above, particularly Jaenike's (1981) critera 1, 2 and 4 and Bush's (1992) criteria 1–3, we present here an updated definition.

Host races are sets of populations that are defined as follows:

1*a*. *They use different host taxa in the wild.*

1*b*. *They consist of individuals that exhibit 'host fidelity', i.e. are associated with particular hosts.* Host fidelity is necessary so that a correlation between host use and genetic differentiation (1*a*, 3*a*) is not solely the result of host-associated selection within a single generation. Normally, this host fidelity will not be due to conditioning alone, since similar genetic differentiation must be seen in multiple areas (3*b*). Thus, either conditioning must be strongly associated with genetic differences, without recombinational leakage, or else, more probably, the host fidelity itself will be genetically determined.

2. *They coexist in sympatry in at least part of their range.* Completely allopatric or parapatric populations would simply be classical geographic races. By 'sympatry', we mean that infested hosts occur together within the dispersal radius of the insects, but we do not exclude local clustering of co-occurring hosts. Some have argued that host fidelity constitutes a kind of 'micro-allopatry', but this seems qualitatively distinct from true allopatry caused by geographic barriers across which dispersal is virtually impossible. Similarly, we do not regard use of different, locally clustered hosts as a kind of 'parapatry', because classical parapatry implies a very limited overlap zone between two major geographic regions, as in hybrid zones (Barton & Hewitt 1981). Our use of the term 'sympatry' is therefore less idealized than that of Kondrashov & Mina (1986), who require complete and somewhat unrealistic spatially homogenised environments.

3*a*. *They are genetically differentiated at more than one locus.* Unlike members of a polymorphic population, host races must consistently maintain correlated allelic differences at multiple loci that are not just due to selection within a single generation. If only a single differentiated locus is found, it would instead be regarded as a normal polymorphism (which may of course be under host-related selection). In mixed samples of host races, there should thus be strong linkage disequilibria between unlinked divergent genes or, equivalently, correlations between heritable quantitative traits. (By contrast, for disequilibria to be used as evidence for reduced gene flow in 4*b*, disequilibria must also be present within each host-associated population). The loci involved may be at putatively neutral marker loci, but any inherited differences may be used, including those under selection. Indeed, if it can be shown that multiple inherited genetic differences exist for morphology, mate choice (see also 4*a*), and/or adaptation to the host (but this latter is not required, see also 5*a* below), such that intermediate multi-trait phenotypes are rarer than more extreme forms, a host race designation may be hypothesized.

3*b*. *They are spatially and temporally replicable, i.e. are more genetically differentiated from populations on another host in sympatry (and at the same time) than at least some geographically distant populations on the* *same host*. When populations have been shown to meet criteria 1, 2 and 3*a*, there is evidence of at least a fleeting correlation of host use genetics and other genetic differences in sympatry. In populations also showing a degree of assortative mating (criterion 4*a*), these correlations are very likely to persist in the face of gene flow. Direct evidence for the stability of these correlations should, whenever possible, be obtained by showing that genetic differentiation between host races in sympatry is greater than in at least some distant (and, if possible, also temporally separated) populations on the same host.

4*a*. *They display a correlation between host choice and mate choice*. Populations on different hosts can only maintain genetic differences (criterion 3) across generations if mating is somewhat assortative relative to host use. Thus, this assortative mating criterion is not strictly required, although a demonstration of assortative mating will be extremely helpful, particularly when it is unclear whether genetic differences are due to selection within a single generation.

4*b*. *They undergo actual gene flow (hybridization and backcrossing) at an appreciable rate (roughly* $m \geqslant 1\%$ *per generation)*. This is the criterion that we regard as important for distinguishing host races from host-associated species. Evidence for this gene flow may be obtained directly, via mark–recapture studies and observation of mating behaviour, or indirectly, perhaps via detection of linkage disequilibria between host-associated marker loci in populations on a single host (Barton *et al.* 1988; Feder & Bush 1991). However, a common estimate of 'gene flow', Nm, estimated from studies of genetic markers, is not suitable either here or in other studies of speciation (Mallet 2001*b*; *contra* Porter 1990; Via 1999). In an island model of population structure where divergent genetic drift in local populations is balanced by gene flow between them, levels of genetic differentiation (F_{ST}) can be used to obtain a combined estimate of population size (N) multiplied by a gene flow parameter (m), $Nm \approx (F_{ST}^{-1} - 1)/4$. However, Nm estimates between host-associated biotypes, or where reproductive isolation is likely, are not valid as measures of gene flow for several reasons: (i) selection, rather than genetic drift, is the probable cause of genetic difference, so an assumption of a drift-gene flow equilibrium is clearly invalid. A high F_{ST} (or low Nm) may be due to strong selection rather than low rates of actual gene flow (m); (ii) conversely, completely isolated species that have diverged very recently will typically retain many alleles in common as they slowly diverge, giving values of $F_{ST} \ll 1$, and estimated 'gene flow,' $Nm \gg 0$ even though actual gene flow, m, may be zero (see also Via 1999); and (iii) the combined parameter estimated, Nm, is not the same as actual gene flow, m is the fraction of the population exchanged. Nm is merely a transformation of a measure of genetic differentiation (criterion 3 above) and cannot logically be used as separate evidence for host race status.

Finally, members of different host races are likely to:

5*a*. *have higher fitness on natal than alternative hosts*; and

5*b*. *produce hybrids that are less fit than parental forms*. If genetic differentiation is consistently maintained in the face of gene flow, there must usually be some selection against moving to the other host and/or breeding with native populations on that host. However, genetic differences in host choice or phenology might be all that is required initially to separate two genetically distinct forms onto different hosts (Butlin 1990). In addition, host races in the earliest stages of divergence could be under only weak disruptive selection, which would be hard to detect. Strong host associations and host-associated assortative mating might even evolve entirely via sexual selection, rather than natural selection necessitated by the host environment, as suggested for hummingbird flower mites (Colwell 1986). Thus, criteria 5*a*,*b* are, in our view, suggestive rather than diagnostic of host races and may generally be harder to elucidate than criteria 1–4. For this reason, we do not regard criteria 5*a*,*b* as absolute requirements for host race identification.

It may be convenient to use a much shorter form of our definition: host races are genetically differentiated, sympatric populations of parasites that use different hosts, and between which there is appreciable gene flow.

This shortened definition emphasizes the four criteria that we consider the most important in distinguishing host races from other forms of variation: (1) host association and fidelity (both are implied by the word 'use'); (2) sympatry; (3) genetic differentiation; and (4) some gene flow (but not total panmixia, which would obliterate genetic differences).

(b) *Host races in the continuum from polymorphism to species*

Sympatric host races form an intermediate stage between polymorphic populations and full species; they are difficult to define, in part because definitions of species themselves are still contested. The most widely quoted idea of species in evolutionary biology is the biological or isolation species concept (Mayr 1963, 1970), which describes species as reproductively isolated populations. However, the continued usefulness of this concept has become somewhat uncertain because many sister taxa that are normally considered to be species are now known to undergo gene flow and hybridize at measurable rates (e.g. Grant & Grant 1992; Wang *et al.* 1997). A number of alternative species definitions, including the ecological, mate recognition, cohesion and phylogenetic concepts have also been proposed (Van Valen 1976; Paterson 1985; Cracraft 1989; Templeton 1989) but this debate is not yet resolved (see Mallet 1995, 2001*c*). However, most species concepts can be viewed as ideas for the mechanisms by which separate clusters of genotypes originate or are maintained. Ecological concepts, for example, highlight the role of disruptive selection, while the biological concept emphasizes the role of pre- and post-mating isolation and phylogenetic concepts are concerned more with the history of origination. Here, we employ a 'genotypic cluster' criterion of species, which specifically allows for gene flow, non-monophyly and genetic differences at loci that are not necessarily fixed. Under this criterion, species are genotypic clusters distinguishable in sympatry by actual correlated genetic differences at multiple loci rather than by inferences about process (Mallet 1995, 2001*c*; Feder 1998). Correlations between loci should be sufficient to cause a bimodal genotypic distribution such that two groups or 'clusters' of genotypes are identifiable, separated by intermediates rarer than more extreme genotypes (Jiggins & Mallet 2000). Genotypic bimodality in the face of gene flow has also been termed 'dumbbell structure' by Kondrashov & Mina (1986). However, our argument here is independent of any particular species concept: almost all taxonomically recognized species occurring in sympatry will also be separate sympatric genotypic clusters.

Correlations between alleles at different polymorphic loci (linkage disequilibria) can only be maintained between populations when disruptive selection is strong relative to interpopulation gene flow and recombination of population-specific alleles. However, provided countervailing selection is strong enough, movement of genes from one population to another via hybridization and backcrossing may occur without obliterating genetic differences. Thus, unlike the isolation concept, the genotypic cluster definition allows for incomplete reproductive isolation between species.

Like species, host races defined as above are clusters of genotypes separated by gaps. The only difference between genotypic cluster species and host races lies in the extent of 'actual gene flow'—the exchange of migrants and hybridization that they undergo (Mallet 2001*b*). Between host races, actual gene flow is appreciable, but between most pairs of species it occurs rarely or not at all. Distinguishing taxa on the basis of the level of gene flow is, of course, arbitrary because species and host races defined in this way are part of a continuum, but we believe that a reasonable minimal probability of hybridization between host races for practical purposes is 1% per generation, at least an order of magnitude higher than rates of hybridization between taxa normally recognized as 'good' species (Grant & Grant 1992; Mallet *et al.* 1998).

Host races and genotypic cluster species differ from polymorphic populations in the pattern, and often the number, of their differences. Host races differ at multiple loci, while morphs within a polymorphic population may differ at only a single locus (e.g. in polymorphic Batesian mimicry; see Turner (1984)). If more loci are involved, the polymorphisms within a species may be more or less uncorrelated, so that individuals are placed in different groups depending upon which phenotype or locus is examined. By contrast, when members of two host races or species are placed in groups according to multiple criteria, a bimodal distribution of genotypes occurs (Mallet 1995, 2001*c*; Feder 1998; see also Jiggins & Mallet 2000).

Our definition of host races is close to that used implicitly by Feder (1998), who would agree with us that host races are a type of genotypic cluster species, but did not specify explicit biological criteria related to host use, sympatry, assortative mating or gene flow. (Biological criteria were, however, used in the definition of host races by Berlocher & Feder (2002)). Feder, like us, uses significant genetic distinctness as the key criterion for genotypic clusters, whether species or host races. However, Feder (1998, p. 139) used a likelihood method to classify sympatric populations as species only 'if a sample of individuals can be sorted into two genotypic clusters such that there is a less than 5% chance in misassigning a randomly chosen individual from one cluster into the opposing cluster.' A rate of misassignment of more than 5% would imply host races (or some other subspecific category). However, as Feder points out (p. 142), this makes the host race/species distinction highly dependent on the number of differentiated loci or genetic characters available for examination. An example of why this might cause difficulties is given by the moth *Zeiraphera diniana*, whose larch and pine host races differ at three identified allozyme loci: two autosomal and one sex-linked. Males in Lepidoptera, which are chromosomally homogametic ZZ, have two alleles at each sex-linked locus, and *Zeiraphera* males can be classified to the host race with less than 0.4% error (Emelianov *et al.* 2001). Females, being chromosomally heterogametic ZW, are hemizygous for the important sex-linked locus and therefore provide less information on which to base host race identification; they can be individually classified to host race using these the three allozyme loci only with a much higher error rate (4–10%; see Emelianov *et al.* 2002). Using the criterion of Feder (1998), males would be good species while females of the same biotypes might be host races! Nevertheless, our disagreement with Feder (1998) is minor as Feder clearly intended to define host races as genotypic clusters that lack strong reproductive isolation (e.g. Feder 1998, pp. 130, 142; Berlocher & Feder 2002, p. 776): in our view, measurement of actual gene flow or verification of actual hybrids (e.g. Feder *et al.* 2001) is the best way to do this, rather than using error rates in identification of the pure host races.

Therefore, host races in our definition and in those of Feder (1998) and Berlocher & Feder (2002) are differentiable from morphs within polymorphic populations, but they are an arbitrarily defined subset of genotypic cluster species. Distinguishing host races from species is only useful because most systematists would hesitate to name taxa that may have few fixed differences and that exchange genes at a rate greater than 1% per generation. Our definition of host races attempts to combine and clarify ideas used in previous definitions and to demonstrate an intermediate stage in the continuum from polymorphism to species useful in the study of speciation. We justify the category 'host race' because of its heuristic utility; we do not claim any fundamental and separate reality for the host race as a taxon.

3. CASE STUDIES: STEPS IN THE CONTINUUM

Host race status has been asserted for many insect biotypes. Here, we attempt to determine whether published examples are host races according to our criteria, categorizing them as: (i) single polymorphic populations, which generally lack good evidence for host fidelity or stable genetic variation between hosts in sympatry (§ 3a); (ii) probable host races, which have sympatric, host-associated populations that are genetically differentiated but lack crucial evidence about actual rates of hybridization or gene flow (§ 3b); (iii) confirmed host races with genetic differentiation and also evidence for significant levels of hybridization (§ 3c); and (iv) sibling species, which similarly show genetic differences in sympatry but generally have evidence showing that hybridization rates are very

Table 1. Case studies. (minus, evidence against; plus, evidence for; question mark, unknown or dubious; plus/minus, mixed evidence; n/a, not applicable.)

	Host race criteria									
case study	1*a*. different hosts	1*b*. exhibit host fidelity	2. coexist in sympatry	3*a*. genetically differentiated	3*b*. differentiation is spatially replicable	4*a*. mate assortatively	4*b*. hybridize and back-cross in the wild	5*a*. adapted to natal host	5*b*. hybrids less fit than parentals	host race status (alternative status)
(*a*) cases of intraspecific host associations not considered to be host races										
1. mountain pine beetle (*Dendroctonus ponderosae*) (Coleoptera: Scolytidae)	lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*)	?	+	?+	?	?−	?	−	+/−	no (?within generation selection)
2. fall webworm; red- vs. black-headed larval forms (*Hyphantria cunea*) (Lepidoptera: Arctiidae)	various broad-leaved trees	−	+	n/a	n/a	?	?	−	?	no (no differences within larval forms; forms are sibling species, but not host-associated)
3. small ermine moth (*Yponomeuta padellus*) (Lepidoptera: Yponomeutidae)	hawthorn (*Crataegus* spp.), blackthorn (*Prunus* spp.)	−	+	+/−	?	−	?	−	?	? no (polymorphism)
(*b*) cases considered probably host races										
4. soapberry bug (*Jadera haematoloma*) (Hemiptera: Rhopalidae)	soapberry (*Sapindus saponaria*, *Serjania brachycarpa*), balloon vine (*Cardiospermum* spp.), golden rain trees (*Kolreuteria* spp.)	+	?	+	?	?	?	+	?	? yes (but maybe not sympatric)
5. spiraea aphid (*Aphis citricola*) (Homoptera: Aphididae)	thunberg spiraea (*Spiraea thunbergii*), Satsuma (*Citrus unshiu*)	?	+	+	?+	+	?	+	?	? yes
6. aphids (*Cryptomyzus galeopsidis*) (Homoptera: Aphididae)	redcurrant (*Ribes rubrum*), blackcurrant (*Ribes nigrum*)	+	+	+	?	+/−	?+	+	?+	? yes
7. pea aphids (*Acyrthosiphon pisum* Harris) (Homoptera: Aphididae)	alfalfa (*Medicago sativa*), red clover (*Trifolium pratense*)	+	+	+	+	+	?	+	+	? yes
8. ladybird beetles (*Epilachana niponica, E. yasutomii*) (Coleoptera: Coccinellidae)	thistle (*Cirsium* sp.), blue cohash (*Caulophyllum robustum*)	+	+	?+	?	+	?+	+	−	? yes
9. sawflies (*Platycampus luridiventris*) (Hymenoptera: Tenthredinidae)	Alders (*Alnus glutinosa, Alnus incana*)	+	+	+	+	+	?	+	?	? yes
10. apple maggot and ‘flowering dogwood fly’ (*Rhagoletis pomonella*) (Diptera: Tephritidae)	hawthorn (*Crategus mollis*), flowering dogwood (*Cornus florida*)	+	+	+	+	+	+/−	?	+	? yes

11. goldenrod ball gallmaker (*Eurosta solidaginis*) (Diptera: Tephritidae)	goldenrod sp. (*Solidago altissima, S. gigantea*)	+	+	+	+	+	?+	+	+	? yes
(*c*) cases considered host races										
12. willow leaf-beetle (*Lochmaea capreae*)	birch (*Betula pubescens*), sallow (*Salix caprea*)	+	+	+	+	+	+	+/−	?−	yes
13. larch budmoth (*Zeiraphera diniana*) (Lepidoptera: Tortricidae)	larch (*Larix* spp.), pine (*Pinus cembra*)	+	+	+	+	+	+	+/−	?	yes
14. apple maggot (*Rhagoletis pomonella*) (Diptera: Tephritidae)	apple (*Malus pumila*), hawthorn (*Crategus mollis*)	+	+	+	+	+	+	+	?+	yes
(*d*) cases considered sibling species										
15. *Muellerianella* complex: (Homoptera: Delphacidae) (*M. brevipennis, M. fairmairei, M. extrusa*)	velvet grass (*Holcus lanatus*), soft grass (*H. mollis*), tufted hair grass (*Deschampsia cespitosa*), purple moor grass (*Molina caerulea*)	+	+	+	?	+	?−	+	+	no (sibling species)
16. brown planthopper (*Nilaparvata lugens*) (Homoptera : Delphacidae)	weed grass (*Leersia hexandra*), cultivated rice (*Oryza sativa*)	+	+	+	+	+	−	+	−	no (sibling species)
17. treehoppers (*Enchenopa binotata*) (Homoptera: Membracidae)	hoptree (*Ptelea trifoliata*), bittersweet (*Celastrus scandens*), black locust (*Robinia pseudacacia*), redbud (*Cercis canadensis*), black walnut (*Juglans nigra*), butternut (*Juglans cinerea*), *Viburnum* sp.	+	+	+	+	+	−	+	?	no (sibling species)
18. fall armyworm (*Spodoptera frugiperda*) (Lepidoptera: Noctuidae)	corn (*Zea mays*), rice (*Oryza sativa*)	+	+	+	+	+	?−	?	+/−	? no (sibling species)
19. hairstreak butterflies (*Mitoura nelsoni, M. miri, M. siva*) (Lepidoptera: Lycaenidae)	incense cedar (*Calocedrus decurrens*), cypress (*Cupressus macnabiana*), juniper (*Juniperus occidentalis*)	+	?−	+	?−	+/−	?	?	?	? no (sibling species)
20. apple maggot (*Rhagoletis pomonella*), blueberry maggot (*Rhagoletis mendax*) (Diptera: Tephritidae)	hawthorn (*Crategus mollis*), blueberry (*Vaccinium corymbosum*)	+	+	+	+	+	−	?	?	no (sibling species)
21. apple maggot (*Rhagoletis pomonella*), snowberry fly (*Rhagoletis zephyria*)	rosaceae (*Crataegus* & *Malus* spp.), snowberry (*Symphoricarpus*)	+	+	+	+	+	?−	?	?	no (sibling species)

low or absent (§ 3d). These classifications are a best estimate on the basis of current information and may need to be reviewed as further relevant work is carried out. Our results are summarized in table 1.

Some cases of well-studied biotypes, for instance in *Eurosta* or *Acyrthosiphon*, provide excellent exemplars of speciation via host shift, because clear fitness trade-offs have been measured (e.g. Craig *et al.* 2001; Via 2001). Yet these systems are classified here only as probable host races because rates of gene flow and hybridization have not yet been characterized fully. The list of cases discussed below is not exhaustive and is biased towards systems tested for several of our criteria. Host race or biotype status has been proposed in a scattered entomological literature for a large number of other taxa, especially within the Aphididae (reviewed in Thième 1987; Tauber & Tauber 1989; Guldemond & Mackenzie 1994); we here review a range of cases, but have not aimed for complete coverage.

(a) *Biotypes probably representing polymorphic populations*

(i) *Case 1: the mountain pine beetle* Dendroctonus ponderosae (*Coleoptera: Scolytidae*) *on lodgepole pine* (Pinus contorta) *and limber pine* (P. flexilis)

Weak allozyme differentiation between host-associated biotypes was initially reported (Sturgeon & Mitton 1986). However, genetic differences between hosts and between populations are of similar magnitude; i.e. the differences are not 'spatially replicable' under our criterion 3*b*. Later investigations showed no evidence for allozyme differentiation in the autumn (Langor & Spence 1991); allozyme differentiation at esterases was, however, evident after overwintering, suggesting that selection during the winter could be a cause (Langor & Spence 1991). Mixed beetle pairs consisting of males and females from different hosts were less likely to lay fertile eggs on lodgepole pine than pairs collected from the same species of pine; on limber pine only, progeny from mixed pairs had lower dry weight and fat content than those pairs of beetles collected from the same host species (Langor *et al.* 1990). However, the offspring of all cross types are fertile, differences in egg laying were not observed on limber pine, and neither development time nor mortality differed between any brood types on either host; limber pine was generally a better host for any pairs in which both sexes came from the same tree species (Langor *et al.* 1990). Field-collected adults from the two hosts differ in morphology (Sturgeon & Mitton 1986), but possible effects of within-generation selection or phenotypic plasticity on morphology have not yet been ruled out. Insects on lodgepole pine begin emerging approximately one week earlier than those on limber pine, but peak and late emergence on the two hosts overlaps for about two months of the year (Langor 1989). The observed differences may thus be due either to phenotypic plasticity and/or within-generation natural selection, rather than to stable genetic differences between host-associated populations. Stable genetic differences do not seem improbable, but their demonstration awaits further work. We therefore classify these forms tentatively as members of a single polymorphic population.

(ii) *Case 2: red- or black-headed biotypes of the fall webworm* Hyphantria cunea *(Lepidoptera: Arctiidae) on various hosts*

The fall webworm consists of polyphagous 'red-headed' and 'black-headed' larval forms with overlapping host use that have fixed allozyme differences and strongly assortative pheromone-mediated mating behaviour; these forms therefore seem likely to be sibling species, but neither is strongly host-associated (Jaenike & Selander 1980; McIntee & Nordin 1983; McLellan *et al.* 1991). Differentiation along host plant lines within colour pattern forms has not, to our knowledge, been intensively studied. However, no significant differentiation in allozyme frequency was found between populations of the red-headed form on black walnut and black cherry (Jaenike & Selander 1980), so that there is no evidence for host race status within either colour form.

(iii) *Case 3: the small ermine moth* Yponomeuta padellus (*Lepidoptera: Yponomeutidae*) *on hawthorn* (Crataegus *spp.*) *and* Prunus *spp.*

Sympatric, host-associated larval populations of the small ermine moth collected from several sites differed in allozyme frequency over a number of years (Menken 1981, 1982; Raijmann & Menken 2000), but good supporting evidence that this differentiation is maintained in the face of gene flow, and is not simply due to population substructuring or within-generation selection, does not appear to have been obtained (Brookes & Butlin 1994). While differences are often found between hosts, allele frequencies in many host/population combinations appear to be in a state of long-term flux (Raijmann & Menken 2000). There is no evidence of assortative mating from a field experiment (Brookes & Butlin 1994) and larvae from different hosts appear to differ little in their preference for or fitness on various hosts in the laboratory (Kooi *et al.* 1991), except that *Prunus spinosa* seems a better host for all individuals than *Crataegus* (Menken *et al.* 1992). Gene flow was measured only via an F_{ST} approach (Raijmann & Menken 1992), which is not suitable for the estimation of actual gene flow (*m*) or hybridization (see § 4b). Host choice and actual gene flow or hybridization rates have not, to our knowledge, been investigated. We therefore classify these biotypes provisionally as polymorphic populations.

(b) *Biotypes representing probable host races*

(i) *Case 4: the soapberry bug* Jadera haematoloma (*Hemiptera*: *Rhopalidae*) *on soapberry* (Sapindus saponaria), Serjania brachycarpa *and balloon vine* (Cardiospermum *spp.*) *versus golden rain trees* (Kolreuteria *spp.*)

The soapberry bugs in the southern USA show adaptation to particular host plants in the length of the proboscis or 'beak' used to reach the seeds in variably inflated fruits of their sapindaceous host plants. In Florida, populations infesting the balloon vine *Cardiospermum corindum* have recently colonized the introduced flat-seeded golden rain tree *Kolreuteria elegans* and historical collections show that there has been a concomitant reduction in soapberry bug beak length in Florida over the last 20–50 years. In the southcentral USA, a similar colonization by soapberry bugs of introduced round-podded golden rain trees

Kolreuteria paniculata and the balloon vine *Cardiospermum halicacacum* from a host that lacks inflated pods (*Sapindus saponaria*) has been associated with increases in soapberry bug beak length over a similar period (Carroll & Boyd 1992). Transfer experiments have shown that beak length differences between populations infesting different hosts are both genetically based and adaptive (Carroll *et al.* 1997, 1998). It is not yet clear that these differences can be maintained in sympatry (Carroll *et al.* 1997), although this does not seem improbable. Thus, while the soapberry bug provides excellent evidence for rapid host adaptation, it is still not clear whether these forms are ever sympatric or normally hybridize at appreciable levels. We therefore tentatively place this example in the category of probable host races, although they could merely be geographic morphs or races.

(ii) *Case 5: the spiraea aphid* Aphis citricola (*Homoptera*: *Aphididae*) *on satsuma* (Citrus unshiu) *and thunberg spiraea* (Spiraea thunbergii)

The average emergence dates of spiraea aphid populations on satsuma and thunberg spiraea differ by approximately one month in samples from a number of different localities, and are under genetic control (Komazaki 1986, 1990). The two forms occur sympatrically, and laboratory-bred hybrids survive well on thunberg spiraea in a fieldcage but not on citrus because the nymphs hatch before bud break (Komazaki 1986). The potential for hybridization between these forms in the field has not, to our knowledge, been investigated, although there is considerable (but incomplete) allochronic isolation of adults (Komazaki 1986, 1998). Overall, genetic differentiation and the probability of hybridization suggests probable host race status.

(iii) *Case 6: the aphid* Cryptomyzus galeopsidis (*Homoptera*: *Aphididae*) *on redcurrant* (Ribes rubrum) *and blackcurrant* (Ribes nigrum) *primary hosts*

Populations of the aphid *Cryptomyzus galeopsidis* on redcurrant and blackcurrant primary hosts (the hosts where sexual forms reproduce) differ genetically at allozymes, but will hybridize when housed together (Guldemond 1990*a*; Guldemond & Dixon 1994; Guldemond *et al.* 1994). However, the fitness of the single hybrid clone that was tested appeared reduced compared with its parents, as it produced fewer mature sexual females (Guldemond 1990*a*). There is some pre-mating isolation between blackcurrant males and redcurrant females in the presence of natural hosts because blackcurrant males show strong host preference, but hybridization in the opposite direction occurs freely in choice experiments (Guldemond *et al.* 1994). Males do not appear to differentiate between pheromones of redcurrant- and blackcurrant-associated females (Guldemond & Dixon 1994). Populations on both primary hosts share a secondary host (the host where asexual forms produced later in the season feed), the hemp nettle (*Galeopsis tetrahit*). Migratory forms of both biotypes tend to prefer their native host, although, in the case of the redcurrant biotype, this preference was not expressed by all tested clones (Guldemond 1990*b*). The existence of hybrid clones (although hybridization frequency was not estimated) led us to assign probable host race status to this case.

(iv) *Case 7: the pea aphid* Acyrthosiphon pisum (*Homoptera*: *Aphididae*) *on alfalfa* (Medicago sativa) *and red clover* (Trifolium pratense)

Populations of the pea aphid *Acyrthosiphon pisum* on alfalfa and red clover crops differ in allozyme allele frequencies and host choice (Via 1999) and exhibit a strong preference in the laboratory for their own host (Caillaud & Via 2000). The two forms hybridize in the laboratory and semi-diagnostic allele frequencies of foundresses in newly planted fields compared with those of aphids in the same fields later in the season suggested that *ca.* 11% of new migrants to clover fields are from alfalfa and 9% of migrants to alfalfa come from clover (Via 1999). The survival of aphids migrating to the alternative host is much lower than on the natal host (Via 1991*a*,*b*, 1999; Via *et al.* 2000) and the frequencies of alleles associated with the alternative host declined in new host plant fields during the season (Via 1999). Several generations of successful reproduction by the parthenogenetic migratory forms must take place before the sexual forms are produced (Caillaud & Via 2000; Via *et al.* 2000). These results make it unclear whether survival of clones on their non-hosts is sufficient to generate appreciable late-season hybridization. Quantitative traits affecting host choice and survival on each host map to the same few chromosomal regions, confirming genetic trade-offs in host adaptation (Hawthorne & Via 2001). Gene frequency differentiation between the host-associated forms on adjacent hosts is higher than that between distant populations on the same host, suggesting that gene flow is greater within than between host races (Via 1999). However, gene flow between host races in the wild has been estimated only via F_{ST} and a drift-gene flow equilibrium assumption, which is almost certainly not valid here (§ 4b above). Because the actual rate of hybridization is unknown (the genetic differentiation observed is consistent with a variety of rates, including a complete lack of hybridization (Via 1999)), this case is classified with probable rather than confirmed host races.

(v) *Case 8: ladybird beetles* Epilachna niponica (*Coleoptera*, *Coccinellidae*) *on thistle* (Cirsium *spp.*) *and* E. yasutomii *on blue cohash* (Caulophyllum robustum)

Ladybird beetles *Epilachna niponica* on thistle and *E. yasutomii* on blue cohash differ in size and shape (Katakura 1981) and average development time to adult (*E. niponica* take *ca.* 35 days but *E. yasutomii* need only *ca.* 30 days; Katakura & Hosogai (1994)). Mating tends to occur on the host (Katakura *et al.* 1989). Larvae of both 'species' have reduced survival on the alternative host (Katakura & Hosogai 1994) and, in the laboratory, adults prefer to feed on the host from which they were collected in the wild (Katakura & Hosogai 1994). Despite these differences, the two forms hybridize in the laboratory without sex-ratio distortion and hybrids survive as well on either host as the native parental type (Katakura & Hosogai 1994). In the absence of host plants, mating between the two forms is random (Katakura & Hosogai 1994). Hybrids are intermediate in size, develop more slowly than

E. yasutomii and sometimes more rapidly than *E. niponica* (Katakura & Hosogai 1994). Because *E. niponica* and *E. yasutomii* have long and overlapping mating seasons, allochronic isolation might not be extensive; females of both types mate multiply and there is no evidence of conspecific sperm precedence (Katakura & Hosogai 1994). The frequency of hybridization and backcrossing in the wild has not, to our knowledge, been investigated, but the other evidence points at genetic differentiation and probably at least host race status.

(vi) *Case 9: the sawfly* Platycampus luridiventris (*Hymenoptera*: *Tenthredinidae*) *on two species of alder* (Alnus glutinosa *and* A. incana)

Sympatric populations of this sawfly associated with the alder species *Alnus glutinosa* and *A. incana* differ in larval morphology and female oviposition preference (Heitland & Pschorn-Walcher 1992); these differences are well-marked and are probably genetic. Allozyme differences between the biotypes in sympatry are pronounced and much greater than those between geographically distant populations on the same host (Herbst & Heitland 1994). Larvae of both types develop faster on their natal host, although survival does not differ (Heitland & Pschorn-Walcher 1992). Emergence of adults from *A. incana* occurs on average about 10 days earlier than those from *A. glutinosa*, although emergence takes place over about a month so there is plenty of potential for hybridization. Actual rates of hybridization between *A. glutinosa* and *A. incana* populations have not, to our knowledge, been studied in either the field or laboratory. Following Herbst & Heitland (1994), we tentatively place this case in the probable host race category.

(vii) *Case 10:* Rhagoletis pomonella (*Diptera*: *Tephritidae*) *on hawthorn* (Crataegus mollis) *and the 'flowering dogwood fly' on flowering dogwood* (Cornus florida)

These two biotypes are often sympatric and exhibit only frequency differences at up to seven of 17 polymorphic allozyme loci (Berlocher 1999) and at mtDNA (Smith & Bush 1996). They are partially allochronic, have slightly reduced hybrid fitness and exhibit strong differences in host preference (Berlocher 1999). Only some components of gene flow have been directly measured and the results are inconclusive; Berlocher (1999) estimated that gene flow between the two in sympatry may be as much as 2%, assuming a selection/migration balance at allozyme loci. This estimate is strongly dependent on the model and values of divergent selection assumed; balancing selection for polymorphism in each form, for example, would invalidate Berlocher's method. Although these forms have recently been recommended for species status under a 'non-strict' version of the biological species concept (Berlocher 1999), we use the likelihood of gene flow to place them tentatively in the host race category. However, if gene flow were much lower than in Berlocher's estimates, they would become separate species under our criteria.

(viii) *Case 11: the goldenrod ball gallmaker* Eurosta solidaginis (*Diptera*: *Tephritidae*) *on two goldenrod species* (Solidago altissima *and* S. gigantea)

Populations of *Eurosta solidaginis* using the different goldenrod species *Solidago altissima* and *S. gigantea* are significantly genetically differentiated at allozymes (Waring *et al.* 1990), although few differences were found at mtDNA (Brown *et al.* 1996). Individuals have a higher survival on their natal than their alternative host (Craig *et al.* 1993, 1997). Mating is strongly assortative when host plants are present, but much less so when they are absent (Craig *et al.* 1993; Itami *et al.* 1998), which is due in a large part to heritable differences in host choice by the adults (Craig *et al.* 2001). Differences in emergence time also contribute to reproductive isolation (Craig *et al.* 1993; Horner *et al.* 1999). Estimates of gene flow between biotypes of *Eurosta* have not been obtained, although in some conditions, such as high spring temperature, which reduces allochronic isolation, hybridization appears particularly probable (Itami *et al.* 1998). Allozyme frequency divergence between host races varies geographically and is correlated with the abundance of the *S. gigantea* host; a likely explanation is that gene flow obliterates differences more effectively when one of the hosts is rare (Itami *et al.* 1998). The observation that about 3% of insects collected from the wild have intermediate oviposition preference, as seen in laboratory hybrids, also suggests gene flow and the high fitness of some hybrids and backcrosses on particular host plant genotypes would presumably allow backcrossing to occur (Itami *et al.* 1998; Craig *et al.* 2001), even though fitness is generally much lower in hybrids than in pure forms (Craig *et al.* 1997). In conclusion, it seems very likely that these forms are host races, but this is not yet certain due to lack of accurate estimates of gene flow.

(c) *Biotypes representing host races*

(i) *Case 12: the willow leaf-beetle* Lochmaea capreae (*Coleoptera*: *Chrysomelidae*) *on birch* (Betula pubescens) *and willow* (Salix caprea)

Populations of this beetle infest different hosts and host preference is inherited rather than simply conditioned by larval environment (Mikheev & Kreslavsky 1980). The ability to develop on birch is inherited as a dominant character in interracial matings (Kreslavsky *et al.* 1981), while ability to develop on willow and poplar seems to be present in birch populations. These host-associated genetic differences are widespread in western Russia, but break down near Lake Baikal and further east, where the host-associated traits become polymorphic (Kreslavsky & Mikheev 1993). Assortative mating is relatively weak when the beetles are confined together, but is greatly enhanced in the field by strong host choice. Rates of hybridization between host races in a sympatric site were estimated as 1–3% based on studies of assortative mating, host choice and the presence of putative hybrids (Kreslavsky *et al.* 1981). These studies of the birch and willow forms show widespread, genetically based host associations and strong assortative mating with gene flow between forms of 1% or greater in areas of sympatry. We therefore classify this as an example of host races, under our definition.

Recently, a new 'bog bilberry race' on bilberry and other hosts (Ericaceae) has been found; it is of uncertain biological status and is possibly a separate host-associated species (Mikheev 1998). Thus, in this group, there appears to be a series of host-associated forms ranging from polymorphisms to host races and species exchanging very few, if any, genes. (Note: publications are all in Russian; we used abstracts and secondary sources extensively

(Kondrashov & Mina 1986; Emelianov *et al.* 2002; I. Emelianov, personal communication).).

(ii) *Case 13: the larch budmoth* Zeiraphera diniana (*Lepidoptera*: *Tortricidae*) *on European larch* (Larix decidua) *and cembran pine* (Pinus cembra)

Populations of the larch budmoth *Zeiraphera diniana* coexist in mixed forests of larch and pine in the Alps. They have heritable differences in a number of traits, including colour of larvae, female pheromone blend, male pheromone response and host choice (Baltensweiler 1977, 1993; Day 1984; Priesner & Baltensweiler 1987*a*,*b*; Baltensweiler & Priesner 1988; Emelianov *et al.* 1995, 2001, 2002). Larch- and pine-associated moths also differ in allozyme frequency at three loci and this differentiation has been stable since at least 1994 (Emelianov *et al.* 1995, 2001). Gene flow has been directly estimated at *ca*. 2–4% per generation from the combined results of mate choice at close range in the laboratory (Drès 2000), field experiments on host choice (Emelianov *et al.* 2002) and pheromone-mediated cross-attraction (Emelianov *et al.* 2001). Insects showing the pheromone response patterns typical of hybrids have also been found in natural populations (Priesner & Baltensweiler 1987*a*). Sympatry, genetic differentiation and gene flow give evidence for host race status by our criteria.

(iii) *Case 14: the apple maggot* Rhagoletis pomonella (*Diptera*: *Tephritidae*) *on apple* (Malus pumila) *and hawthorn* (Crataegus *spp.*)

Apple- and hawthorn-infesting forms of *Rhagoletis pomonella* are perhaps the best-characterized pair of insect host races (Bush 1969; Bush & Smith 1998; Feder 1998). The two forms differ in time of emergence (Smith 1988) and host choice in the field (Feder *et al.* 1994). Differences in allele frequency at six allozyme loci have been maintained within a number of sites throughout 11 years of study (Feder 1998; see also Feder *et al.* 1990, 1993), although some allozymes showing differentiation are clinally distributed within host races (Feder *et al.* 1988; McPheron *et al.* 1988; Feder & Bush 1989*b*; Berlocher 1996). Field studies of several components of actual gene flow, including host preference and temporal co-occurrence of mature adults, suggest that the rate of exchange of migrants between the two populations in a zone of sympatry is *ca*. 6% per generation (Feder *et al.* 1994). Linkage disequilibrium between host-associated loci within each form also suggests that gene flow is occurring (Barton *et al.* 1988; Feder & Bush 1991), which has been estimated most recently at *ca*. 4.3% (Feder *et al.* 1998). However, other factors may be involved: in some locations, disequilibria existed at loci that had similar frequencies within both biotypes (Feder & Bush 1991). Apple and hawthorn flies are likely to mate randomly when they encounter one another on the same host plant (Feder *et al.* 1994) and there is no evidence of an intrinsic reduction in hybrid fitness (Reissig & Smith 1978). However, recently it has been shown that fitness trade-offs exist due to adaptation to different temperatures and fruit phenologies (Feder *et al.* 1997*a*,*b*; Feder & Filchak 1999; Filchak *et al.* 1999, 2000). Overall, the sympatry, host associations and evidence for significant levels of gene flow demonstrate this classic example to be a host race, by our criteria.

(d) ***Biotypes representing sibling species***

(i) *Case 15: the* Muellerianella *complex* (*Homoptera*: *Delphacidae*). Muellerianella brevipennis, M. fairmairei, *and* M. extrusa *on several grass species* (*see table 1*)

In laboratory experiments, all three species mate preferentially with conspecifics (Booij 1982*a*). Hybrid broods from all interspecific crosses are much smaller than non-hybrid broods; they are also female biased, and male hybrids are predominantly infertile (Booij 1982*a*), although backcross broods were bred from some hybrid females (Booij 1982*a*). Performance on one anothers' hosts is usually very poor (Booij 1982*b*). The calls by which *M. brevipennis*, *M. extrusa* and *M. fairmairei* males communicate with potential mates differ (Booij 1982*c*) and although the extent to which this affects their long range cross attraction has not been directly investigated, acoustic behaviour strongly influences mate choice in closely related taxa (Booij 1982*c*; and references therein). Despite this, there is evidence that, in some areas, the forms may come into contact with each other and hybridize. Pairs of species are sometimes found in close proximity (Booij 1982*b*) and putative *M. fairmairei* × *M. brevipennis* hybrid females have been collected from one such site (Booij 1982*a*). The balance of current evidence does, however, point towards a level of hybridization of less than 1% per generation and the reduced chance of backcrossing also supports their species status.

(ii) *Case 16: the brown planthopper* Nilaparvata lugens (*Homoptera*: *Delphacidae*) *on weed grass* (Leersia hexandra) *and cultivated rice* (Oryza sativa)

Brown planthoppers found on the weed grass *Leersia hexandra* and on cultivated rice *Oryza sativa* display heritable differentiation in a number of traits with respect to host choice, mate choice and survival. Crosses suggested that few genes are involved in each trait and that a recent shift to rice has occurred (Butlin 1996; Sezer & Butlin 1998*a*,*b*). Although viable and fertile F_1 hybrids can be produced, laboratory tests of mate choice suggest that the two populations do not hybridize in the wild; only a single putative hybrid was found in a crowded population cage containing males and females of both forms (Heinrichs & Medrano 1984; Claridge *et al.* 1985). When insects were played mating calls of members of their own population and of those found on the alternative host, both males and females responded only rarely, and with reduced vigour, to calls from members of the other population (Claridge *et al.* 1985). Because of the lack of evidence for gene flow between the two forms and its improbability in the wild, Claridge *et al.* (1985, 1997) argue that they are separate species rather than merely host races, a view with which we concur.

(iii) *Case 17: treehoppers of the* Enchenopa binotata (*Homoptera*: *Membracidae*) *complex on various hosts* (*see table 1*)

Members of this treehopper complex differ in nymphal colour pattern between hosts (Wood 1980) and have greater levels of allozyme frequency differentiation between than within hosts (Guttman *et al.* 1981). In spite of high levels of precopulatory activity between pairs from different hosts in laboratory cages (Wood & Guttman 1982), very low levels of hybridization occurred in the laboratory in the absence of host plants (Wood 1980). In the wild, there is considerable evidence for virtually complete allochronic isolation due to the timing of egg hatch with host bud burst (Wood & Guttman 1982). Females preferred to oviposit on their native hosts, and when forced to oviposit on incorrect hosts, egg hatch and survival of nymphs was poor (Wood 1980; Wood & Guttman 1983). Although the possibility that some of the forms may be host races has not been completely discounted, the biotypes so far discovered are most likely to hybridize at a rate of less than 1% per generation, and we therefore follow Wood & Guttmann (1982) in classifying these forms as separate host-associated species.

(iv) *Case 18: the fall armyworm* Spodoptera frugiperda (*Lepidoptera*: *Noctuidae*) *on corn* (Zea mays) *and rice* (Oryza sativa)

Rice- and corn-associated *Spodoptera frugiperda* can produce viable hybrids in the laboratory (Pashley & Martin 1987; Whitford *et al.* 1988), but there is evidence for hybrid sterility in at least one cross direction (Pashley & Martin 1987; Pashley *et al.* 1992). Both long-range cross attraction and hybridization at close range are highly, although incompletely assortative, the former due at least in part to the females' tendency to call at different times of the night. The two taxa have frequency differences at several allozyme loci (Pashley 1989*a*,*b*; Pashley *et al.* 1992) and fixed differences at a restriction fragment length polymorphism (Lu *et al.* 1992). Rates of hybridization in nature have not been directly estimated, but they are assumed low; we therefore classify this example as a case of separate species.

(v) *Case 19: the hairstreak butterflies* Mitoura nelsoni (*Lepidoptera*: *Lycaenidae*) *on incense cedar* (Calocedrus decurrens), M. muiri *on cypress* (Cupressus macnabiana) *and* M. siva *on juniper* (Juniperus occidentalis)

Three closely related hairstreak butterfly taxa with different conifer larval hosts have been studied in California. The taxa are normally separated on the basis of wing colour pattern differences and host association, but are virtually indistinguishable using allozyme frequency data. Divergences at mtDNA sequences are also small (0.2–1.1%) and haplotypes are shared among taxa. Nonetheless, populations of *Mitoura muiri* in the coast range are differentiated from other populations, so the authors argue that host use is driving divergence (Nice & Shapiro 2001). Although the authors suggest that these forms might be host races, under our definition the forms are not yet well enough studied to make a judgment. In particular, there seems to be no evidence either for sympatry or hybridization. We therefore provisionally place these forms as separate species on the basis of the colour pattern data, but another possibility is that they are little more than geographical races of a widespread species with a locally adaptive mosaic host associations, similar to that found in *Euphydryas editha* (Thomas & Singer 1998).

(vi) *Case 20: the apple maggot* Rhagoletis pomonella (*Diptera*: *Tephritidae*) *on hawthorn* (Crataegus *sp.*) *and the blueberry maggot* R. mendax *on blueberry* (Vaccinium corymbosum)

Populations of *R. pomonella* and *R. mendax* have unique allozymes at 11 loci (Feder & Bush 1989*a*; Feder *et al.* 1989; Berlocher 1995). A survey of hundreds of individuals of both types failed to reveal any putative hybrid genotypes, despite the co-occurrence of sexually mature adults on intertwined hawthorn and blueberry bushes (Feder & Bush 1989*a*; Feder *et al.* 1989). Thus, the rate of actual gene flow between the forms appears considerably less than 1% per generation and we classify this as an example of separate host-associated species.

(vii) *Case 21: the apple maggot* Rhagoletis pomonella (*Diptera*: *Tephritidae*) *on hawthorn and apple* (Crataegus & Malus *spp.*) *and the snowberry maggot* R. zephyria *on snowberry* (Symphoricarpos *spp.*)

Rhagoletis zephyria can be distinguished from *R. pomonella* on the basis of allozymes. Several putative F_1 hybrids could be identified in a sample of over 1000 individuals from an area of sympatry between the two species. However, 'hybrid' genotypes of this kind are also expected in small numbers on the basis of random assortment of alleles present in pure populations; thus, there is no good evidence for active hybridization. In any case, if it happens at all, hybridization is rare, possibly about 0.09% per generation (Feder *et al.* 2001). On this basis, the hybridization rate is considered too low (and it may be much lower) for host race status under our criteria; instead, *R. zephyria* is classified as a separate species.

4. EMPIRICAL EVIDENCE FOR SPECIATION VIA HOST SHIFT

(a) *How common are host races?*

In cases where host race designation is suspected, there is insufficient evidence to resolve the host race status of eight (case studies 4–11) of the 11 pairs of probable host races discussed above. Because of a continued shortage of detailed information (Tauber & Tauber 1989), it is therefore not possible to draw very definite conclusions about the frequency of host races in nature. The lack of data is most pronounced in relation to our criteria (4*a*) and (4*b*) dealing with assortative mating and gene flow between the forms, which we argue are critical for distinguishing them from species. Members of the most likely systems show differentiation along host plant lines, will interbreed in the laboratory and have levels of genetic differentiation compatible with continuing gene flow in nature. However, while several components of gene flow have often been studied, estimates of actual gene flow are rare.

Nonetheless, host races have been confirmed in three out of 21 studies, 14% of the sympatric, phytophagous insect biotype systems in which the possibility has been investigated reasonably thoroughly. This conservative estimate seems likely to rise, because current data suggest the presence of eight more (case studies 4–11); in all, over half of the investigated biotypes are at least probably host races, under our criteria. Of course, the studies carried out to date have concentrated on insects in which the presence of host races seems particularly likely; in most cases, there was prior evidence of host-associated differentiation between populations of a presumed sympatric species. However, a number of other recent studies suggest that cryptic, host-associated differentiation may be rather common in phytophagous insects. Taxonomic revisions of several groups, by taking account of new behavioural, allozyme, or DNA sequence characters, have detected sympatric, monophagous biotypes within presumed polyphagous species. Recent examples include bark beetles *Dendroctonus brevicornis* (Kelley *et al.* 1999) and fruitflies of the genus *Blepharoneura* (Condon & Steck 1997). Intensive studies of agricultural pests have also begun to uncover population substructuring along host plant lines (Bourguet *et al.* 2000; Shufran *et al.* 2000), the starting point for many of the more detailed studies described here. It is also true that host plant adaptation potentially leading to host race formation can proceed extremely rapidly. For example, the soapberry bug *Jadera haematoloma* (Carroll & Boyd 1992), the apple maggot *R. pomonella* (Bush & Smith 1998) and the checkerspot butterfly *E. editha* (Thomas & Singer 1998) have all produced host-adapted forms rapidly within the last century or so. If host race formation also rapidly leads to speciation (see below), it may be that host races appear rare mainly because they are quickly superseded by host-associated species, even though host races are a stage through which many speciating phytophagous lineages pass. Thus, although the number of phytophage host races discovered so far is small, the number of insect systems that may conceal them is potentially very large, and, if the pattern observed in the data presented here is representative of other systems, host races may indeed be a common phenomenon.

(b) *Diversity and phylogeny as evidence for sympatric speciation*

The enormous number of sympatric, closely related insect species specialized on different host plants (e.g. Farrell 1998), has led several biologists to argue that allopatric vicariance would be an almost impossible mechanism to explain diversity in this group (Bush 1975; Price 1980; Bush & Smith 1998). The existence of host races, particularly in a group containing sympatric host-specific species (for example, in *Rhagoletis*; Bush & Smith (1998)), is then argued to form strong evidence for speciation via host shift. Shifts onto flowering plants are associated with greater diversification in multiple beetle lineages (Farrell 1998). However, this argument is somewhat weakened by a simple exponential model of allopatric speciation. Imagine a single phytophagous insect species, the ancestor of all modern phytophagous insects; if it were to speciate due to isolation in only two geographical regions, and if the new sibling species then reinvaded one another's ranges after speciation had been achieved, only about 21 further cycles of isolation, bifurcation and sympatry would be required for its descendants to produce 2^{22} (4.2 million) phytophagous insect species. The world's continents undoubtedly supply many more than two isolated regions and it does not seem improbable that many more than 20 cycles of isolation were available over the last 60–100 million years when the majority of phytophagous insects feeding on flowering plants evolved. Those who support allopatric speciation do not deny that adaptive radiation onto novel host plants is important in speciation; only that it is not achieved in sympatry. It is therefore necessary to examine arguments that can distinguish allopatric from sympatric speciation more clearly.

Recently, phylogenetic analysis has been suggested as a powerful method to test theories of sympatric versus allopatric speciation (Bush & Smith 1998; Berlocher 1998, 2000; Barraclough & Vogler 2000; Via 2001). This method is clearly a valuable use for DNA and other genetic data: for instance, phylogenetic analysis suggests that the *pomonella* group of *Rhagoletis* speciated rapidly and sympatrically, while the congeneric *suavis* group, which do not typically undergo host shifts, have speciated more slowly and in allopatry (Bush & Smith 1998). However, the method should be used cautiously in cases where gene flow may continue after speciation, or where shared ancestral polymorphisms may be common. Genealogies of particular DNA sequences in closely related species will typically prove reticulate with respect to the species tree; in fact, the simple bifurcating phylogeny of species imagined and required in these tests of speciation may be merely an abstraction or consensus of actual genealogies, with little empirical content of its own (Wang *et al.* 1997; Kliman *et al.* 2000). For instance, DNA data indicating a monophyletic clade of species occurring in sympatry may be wrongly interpreted as indicating sympatric speciation. The apparent 'monophyly' could instead be due to introgression of alleles occurring after speciation. Specific theories and empirical data on sympatric divergence may thus provide a more critical means of distinguishing modes of speciation than these arguments based on overall diversity and phylogeny.

(c) *Sympatric speciation theory*

Earlier scepticism towards the possibility of sympatric speciation (e.g. Mayr 1963; see also Tauber & Tauber (1989) for a review) has recently been largely overcome (Bush 1994; Via 2001). A pioneer of sympatric speciation, Bush (1993, p. 239) argued that three main conditions likely in phytophagous insects were favourable for sympatric speciation: (i) that a shift to a new habitat occurs; (ii) that the habitat selection and habitat fidelity is under genetic control; and (iii) that mating takes place in the new habitat. Recent refinements to models of sympatric speciation, e.g. the assumption that diverging traits are polygenic (Doebeli 1996) rather than monogenic as in earlier versions of Bush's model (e.g. Bush & Howard 1986), suggest a more readily achievable set of conditions for its operation than previously believed (Tregenza & Butlin 1999). Dieckmann & Doebeli (1999) model a population dependent on a single resource of unimodal distribution such as seeds of differing sizes. Individuals can differ in three traits: (i) an ecological character that determines resource use, such as beak size; (ii) a marker character upon which mate choice is based, such as colour; and (iii) a mating character that determines whether mate choice is assortative, disassortative, or random with respect to the marker character. Each trait is controlled by a number of additive diallelic loci. The carrying capacity of the resource is highest when individuals have an intermediate phenotype, but those with extreme phenotypes suffer less from density- and frequency-dependent competition for the resource. Initially, the population evolves towards the intermediate phenotype. The resultant competition amongst conspecifics then causes disruptive selection favouring individuals with extreme phenotypes. However, because of recombination, divergence leading to a bimodal phenotypic distribution cannot occur if there is random mating. In the model, gene flow between forms with dissimilar phenotypes is reduced by a positive feedback loop initiated by an association (linkage disequilibrium) between particular ecological and mate choice 'marker' alleles. The initial linkage disequilibrium favours individuals with the tendency to mate assortatively, leading to increased disequilibrium in the next generation, which in turn increases selection for assortative mating, until reproductive isolation is achieved. The model can produce sympatric speciation even with recombination of 50% between loci. Kondrashov & Kondrashov (1999) demonstrated a similar result, although in their simulations a bimodal phenotype was produced initially by intense disruptive selection before any assortative mating evolves.

Both of these models could be criticized in that they pose unrealistic selective regimes. Speciation occurs in the Dieckmann & Doebeli (1999) model only because the population's phenotypic variance is constrained to be smaller than that of the resource distribution in the environment, so that the phenotypic mean can evolve, but not the variance; thus, a single population cannot exploit the resource spectrum fully. It seems likely that real populations would have some genetic variance to allow greater generalization: by using a broader resource spectrum, a generalist population might avoid speciation. In the Kondrashov & Kondrashov (1999) model, sympatric speciation occurs only once the phenotype has become bimodal under the force of selection alone, leading to strong pressures for reinforcement. Perhaps in most real cases, bimodal phenotypes will not evolve in totally homogeneous, sympatric environments, except in the case where a single gene of major effect (a 'supergene') or chromosomal rearrangement allows distinct phenotypes to persist without being destroyed by recombination. In known cases, such as in mimicry polymorphisms (Turner 1984), dominance and other modifying effects evolve to prevent the production of unfit intermediates, rather than reinforcement. One might therefore draw the conclusion from these theoretical models that, while possible, sympatric speciation requires unlikely conditions.

However, authors of these and other recent theoretical papers stress that difficulties in generating linkage disequilibrium between ecological adaptation and mate-choice loci are largely eliminated if divergence of an ecological trait causes assortative mating via pleiotropy (Maynard Smith 1966; Rice 1984; Rice & Hostert 1994; Dieckman & Doebeli 1999; Kondrashov & Kondrashov 1999; Schluter 2001; Via 2001; Kirkpatrick & Ravigné 2002). An initial reduction in gene flow caused by disruptive selection on one trait then aids divergence in other traits subject to less intense disruptive selection, which themselves pleiotropically reduce gene flow further, leading to a positive feedback loop that can result in speciation (Rice 1984; Rice & Hostert 1994; Hawthorne & Via 2001). After divergence in the initial traits, the process is similar in population genetic terms to the accumulation of pre- and post-mating isolation during allopatric or partially allopatric speciation (Rice & Hostert 1994).

(d) *Sympatric speciation via host shift as a two-stage process*

Host races provide a potential intermediate in the route between local polymorphisms and sympatric species. Using our criteria, of course, host races themselves are a kind of species, although many people would not regard them as full species because they undergo significant gene flow with other host races. The host race category breaks up the problem of speciation via host shift into two parts (see also Kondrashov & Mina 1986): problem 1, the evolution of host races within formerly panmictic populations; problem 2, evolution of fully reproductively isolated species from host races. In typical models, the entire process of speciation, from panmictic population to a completely isolated pair of species, has been considered together (e.g. Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999). Breaking up the process may have the advantage of focusing attention on the likelihood of each more limited stage; if it could be shown that each stage was probable, then any apparent improbability of the entire process would be refuted. The first problem amounts to the evolution of a bimodal genotypic (and phenotypic) distribution and corresponds most closely to classical models of sympatric speciation, but does not require a complete cessation of gene flow. The second part of the process consists of reducing gene flow between the genotypic clusters to a very low level and may occur by a continuation of the initial process, or via different processes, such as reinforcement.

(i) *Problem 1: evolution of host races via pleiotropy*

Because their life cycle and mating behaviour are often strongly affected by their host plant, specialist phytophagous insects are particularly probable candidates for restrictions to gene flow via pleiotropy (Bush 1969, 1975, 1994; Bush & Smith 1998; Via 2001). The most straightforward route by which a host shift can reduce gene flow is via a system of mating on the host, as in the *R. pomonella* group (Bush 1969; Feder *et al.* 1994) or many aphids (Guldemond & Mackenzie 1994; Caillaud & Via 2000). Evolution of novel host choice expressed in both sexes would then lead simply to the formation of assortatively mating host races. At first, the only genetic differences would be due to host choice, but given the assortative mating generated by host choice, further genetic differences improving adaptation to the host (for instance, matching the emergence time to the phenology of the host) would both be favoured by natural selection and could themselves reduce gene flow still further. However, assortative mating might also evolve via pleiotropy in less direct ways. For example, host-plant chemistry can affect cuticular hydrocarbons (Stennett & Etges 1997), which often play an important role in mate choice (Coyne *et al.* 1994; Ferveur 1997; Tregenza & Wedell 1997; Singer 1998). Host-plant phenology may also influence the developmental timing of insects directly, causing seasonal isolation (Wood & Guttman 1982; Smith 1988; Langor 1989). Even more generally, hosts are usually locally clumped in space as well as in time, so that host choice is liable to cause spatially or allochronically mediated assortative mating, even in species such as *Z. diniana* where mate attraction is via pheromones independent of the host (Emelianov *et al.* 2001).

The physiological changes necessary for a population to be founded on a new host may often be minimal. Phytophagous insect larvae from several genera can complete development in the laboratory on hosts not used in the wild (Smiley 1978). It is even possible that host-choice evolution might be driven by the effects on assortative mating, rather than the other way round: Colwell (1986) has made the suggestion that sexual selection drives specialist host plant associations in hummingbird flower mites. Recently described examples of excellent survival on non-native hosts include beetles *Oreina elongata* (Coleoptera: Chrysomelidae; Ballabeni & Rahier (2000)) and *Dendroctonus ponderosae* (Coleoptera: Scolytidae; Cerezke (1995)) and leafminers *Liriomyza helianthi* (Diptera: Agromyzidae; Gratton & Welter (1998)). Of course, the ability to survive on a novel host in protected conditions does not always translate into the ability to survive in the field, because ecological factors other than nutrition, e.g. levels of parasitism and predation, may be important. Nonetheless, in principle, all that may be required to initiate a successful host shift is a genetic change in host preference.

In conclusion, theory predicts that sympatric speciation (and also sympatric host race formation) is possible in the absence of pleiotropy. Nonetheless, pleiotropy between host choice and assortative mating provides a likely and straightforward route for evolution of the linkage disequilibria leading to separate genotypic clusters. Pleiotropy seems especially probable in phytophagous insects, because their hosts are spatially and temporally patchy. This argument for pleiotropy amounts to a suggestion that ecological adaptation often results in a degree of 'micro-allopatry' or 'parapatry' due to spatial separation of mates on different hosts. On the one hand, as explained above (criterion 2), where hosts co-occur, we regard them for the purposes of this article as 'sympatric', even though they may be clustered. On the other hand, this kind of host race formation is sympatric in the sense that natural selection, rather than an external geographical barrier, is the major factor triggering speciation of initially panmictic populations. The pleiotropy argument for the evolution of sympatric host races can therefore be viewed as a means of resolving the semantic argument between those who believe that all speciation requires allopatry and those who support the idea that natural selection may often cause speciation in sympatry. Pleiotropy (or any 'micro-allopatry, or 'parapatry' induced by the host association) makes divergence significantly more likely.

(ii) *Problem 2: species from host races via reinforcement*

Speciation may ultimately result from the evolution of host races by a continuation of the same positive feedback process: ecological improvements cause even more pleiotropic assortative mating, which allows further ecological improvements, and so on. Alternatively, adaptations may have other epistatic effects, on hybrid fitness for example, which will increase selection against immigrant genes.

However, once linkage disequilibria are sufficient to produce a bimodal genotypic distribution of host races, other routes to speciation may also become important (Kondrashov & Mina 1986). In particular, direct selection for assortative mating due to hybrid disadvantage (reinforcement) becomes a probable sympatric force in speciation (Noor 1999). Reinforcement has for a long time seemed unlikely, because it was hard to imagine how linkage disequilibria between different loci affecting hybrid unfitness and mate choice could build up (Felsenstein 1981); but if pleiotropy is a common route from ecological adaptation to initial assortative mating, as suggested here for the evolution of host races, the problem may be less severe than traditional panmictic genetic models would suggest. The existence of host races between which gene flow occurs provides empirical evidence that such linkage disequilibria can be stably maintained by selection, in spite of gene flow.

Another feature of many models of reinforcement has been to assume that populations meet at clinal hybrid zones, areas where '…an allele typical of one taxon monotonically replaces an allele typical of another taxon along linear transects …' (Cain *et al.* 1999, p. 1343). Because selection for assortative mating occurs only in the narrow band of contact, these models predict that the evolution of assortative mating would be hindered by gene flow from the rest of the population (Barton & Hewitt 1981; Sanderson 1989; Butlin 1989). The theoretical difficulty of building novel linkage disequilibria between genes for hybrid inviability and those for mate choice in narrow hybrid zones, and a paucity of clear experimental evidence, has resulted in scepticism towards reinforcement (see Noor (1999) for a critical review). By contrast, sympatry as we define it above (criterion 2) can include population structures more like a mosaic zone, i.e. '…characterized by abrupt reversals of gene frequencies at diagnostic loci along linear transects… caused by a patchy distribution of the differentiated taxa and their hybrids' (Cain *et al.* 1999, p. 1343). The results of a computer simulation conducted by Cain *et al.* (1999) support predictions (Harrison & Rand 1989; see also Guldemond & Dixon 1994; Howard 1986) that reinforcement is more likely in hybridizing taxa that overlap broadly than in those that form part of a clinal hybrid zone. Host races clustered on different host plants are likely to form a patchy, mosaic hybrid zone throughout their area of sympatry and reinforcement is therefore potentially much more important in these systems (Guldemond & Dixon 1994). There is little evidence for reinforcement in suspected host-race systems (but see Guldemond & Dixon 1994), but *Drosophila* data suggest that pre-mating isolation is much greater in closely related sympatric species pairs than in equally related allopatric species pairs (Coyne & Orr 1997), which supports the predictions of the reinforcement hypothesis.

(e) *Is the formation of host races likely to lead to sympatric speciation?*

Did host races in sympatry today diverge during a past period of allopatry? In the case of *R. pomonella* on apple and hawthorn, at least, they did not. Historical records show that the apple host was introduced within the range of hawthorn and it is extremely unlikely that the two were ever allopatric (Bush 1969, 1994; Bush *et al.* 1989), although they may of course have been partially separated by patchy host–plant distribution. Support for speciation via host shift also comes from comparisons with several other host-associated biotypes in *Rhagoletis*. *Rhagoletis pomonella* and *R. mendax*, the apple and blueberry flies, are good species in sympatry, as is the snowberry fly *R. zephyria*, while host races of *R. pomonella* exist on apple and hawthorn, and the 'flowering dogwood fly'/*R. pomonella* pair is somewhat intermediate. This series provides a continuity argument that the formation of sympatric host races in this genus is likely to lead to speciation (Payne & Berlocher 1995; Berlocher 1998, 1999; Bush & Smith 1998; Feder 1998, Feder *et al.* 1998; but see Barraclough & Vogler (2000) for a different view of similar data). As already mentioned, comparison between the *R. suavis* and *R. pomonella* species groups shows that sister species of the former are slowly evolving, have largely allopatric or parapatric distributions and are not associated with different hosts, whereas members of the latter group have speciated recently and are all sympatric and restricted to different hosts (Bush & Smith 1998). This comparison argues for an important role of host shift in the rapid sympatric formation of *Rhagoletis* species. Similar evidence for a continuum between polymorphisms, host races and host-associated species exists in the chrysomelid genus *Lochmaea* (Kreslavsky *et al.* 1981; Kreslavsky & Mikheev 1993; Mikheev 1998).

The main difficulty for the theory of sympatric speciation has always been to explain how selection can cause multilocus differentiation correlated with habitat use and mate choice in the presence of gene flow. By providing a continuum of examples in which host-associated differentiation is maintained in spite of actual (or probable) gene flow, the studies discussed here show empirically that host races, genetically differentiated populations exchanging genes in sympatry, can act as stable intermediates along the route to sympatric speciation. It does not even particularly matter for this argument whether these host races have themselves evolved in allopatry; sympatric host races are being used only to demonstrate that a sympatric route is available. Our examples show that this is probable, not only in the 'model system' of *Rhagoletis*, but also in many other less well-studied groups. We cannot, perhaps, completely rule out the idea that, at some greater or lesser level of gene flow than in the host races we have reviewed, there is a hitherto undetected hiatus for sympatric speciation. However, this would seem to be a somewhat untenable argument given the diversity of stable intermediates found so far.

5. APPLICATIONS OF AN UNDERSTANDING OF HOST RACES IN PEST CONTROL AND CONSERVATION

The existence and formation of host races can be an important consideration in applied biology. Plans to slow adaptation of pests to transgenic cultivars, for example, rely heavily on gene flow from populations in sympatric, transgene-free refuges to swamp resistance alleles selected by the transgenic host (Bourguet *et al.* 2000). Refuges normally consist of transgene-free plantings of the crop host, but wild host species could form part of the refuge of some generalist pests (Gould 1998). Quantification of gene flow between populations on cultivated and wild host species would then be very useful. For example, Bourguet *et al.* (2000) found that populations of the European corn borer *Ostrinia nubilialis* on cultivated maize *Zea mays* are genetically distinguishable from sympatric populations found on the wild host sagebrush (*Artemisia* sp.), possibly as a result of non-random mating. Gene flow might also be reduced between populations on transgenic and non-transgenic plantations of the same crop. Gould (1994) suggests that even highly resistant individuals can be expected to suffer reduced growth rates when feeding on transgenic crops and might experience phenology-mediated reproductive isolation from non-resistant populations on refuge crops.

Clarke & Walter (1995) argue that many biological control programmes believed to have employed multiple population 'strains' of the same biological control agent in fact used partially or completely reproductively isolated taxa. Thus, the relative merits of various control techniques, e.g. using multiple species versus single species of control agent, or introducing several versus single populations of a particular agent, have been obscured. Meanwhile, Frey & Frey (1995) demonstrated that pheromone traps used to monitor the pest *Quadraspidiotus perniciosus* also collect males of the sibling species *Q. zonatus*. Frey and Frey used traps containing artificial pheromones, which are known frequently to attract males of non-target species, but natural pheromone-mediated cross attraction has been observed between cryptic host races of the larch budmoth *Zeiraphera diniana* (Emelianov *et al.* 2001) and is probable between other host races that communicate via pheromones. Thus, monitoring of pests in general, as well as biological control programmes, need to consider the possibilities of biotypes or host races in organisms of applied interest.

Conversely, the recognition of host races as distinct evolutionary units adds to the debate concerning how populations are prioritized for conservation. Many conservation policies have focused on species in the traditional 'biological' sense: groups that do not hybridize (O'Brien & Mayr 1991; Brownlow 1996; Crandall *et al.* 2000). Host races, however, contribute to biological diversity despite appreciable gene flow and may be incipient or actual species under some definitions. In the view of Crandall *et al.* (2000), ecological differences should be considered on an equal par with 'genetic exchangeability' (i.e. gene flow) in conservation, and a number of other conservationists have argued that hybridizing or hybridized taxa can be important components of biodiversity worth conserving (e.g. Allendorf *et al.* 2001). In these taxa, reproductive competition via hybridization may become an important means of extinction (Rhymer & Simberloff 1996). Moreover, Duffy's suggestion that cryptic sibling species are individually likely to be more vulnerable to extinction through habitat destruction and disturbance than more strongly differentiated species (Duffy 1996) should apply especially strongly to specialized host races. For example, Berlocher (1999) argues that the 'flowering dogwood fly' (*Rhagoletis* cf. *pomonella*) is in danger of extinction because of a fungal disease affecting its host *Cornus florida* across the eastern USA.

6. CONCLUSIONS

Convincing evidence for actual or probable host races, as defined here, has been provided by a number of recent intensive studies, particularly of tephritid flies of the genus *Rhagoletis*. Host races form an intermediate stage between polymorphism and full species, and we argue that thinking of sympatric speciation via host shift in two stages (a transition from polymorphism to host race, followed by a transition from host race to reproductively isolated species) is a useful way of analysing the speciation process. The empirical studies reviewed here suggest that host races could be common and that this route to sympatric speciation is likely. Several factors make sympatric speciation via host shift seem much more likely than believed until recently. These are: (i) the likelihood of assortative mating via pleiotropy arising during the evolution of host choice and host adaptation, even in species which do not necessarily mate on their host; (ii) a theoretically plausible and empirically demonstrated ability of host races to maintain multiple genetic differences in linkage disequilibrium, in spite of appreciable gene flow; and (iii) the plausibility of further divergence, and especially reinforcement, in cases where linkage disequilibrium already exists between divergent traits and where populations are in close contact throughout large portions of their range.

However, there is probably not yet sufficient empirical evidence to draw conclusions about the actual frequency of sympatric speciation. Current examples of known and probable host races suggest a stable route for sympatric speciation via host shift, but a critic might argue that there is a hitherto undetected hiatus in levels of gene flow along this route. In the majority of studies of potential host races discussed here, firm conclusions about the level of gene flow have not been reached. There is therefore a need for further studies to understand gene flow between host races and other biotypes intermediate between panmictic populations and good species. Such studies are important not only for understanding speciation, but will also have many other applications in agriculture and conservation.

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REFERENCES

Allendorf, F. W., Leary, R. F., Spruell, P. & Wenburg, J. K. 2001 The problems with hybrids: setting conservation guidelines. *Trends Ecol. Evol.* **16**, 613–622.

Ballabeni, P. & Rahier, M. 2000 Performance of leaf beetle larvae on sympatric host and non-host plants. *Entomol. Exp. Appl.* **97**, 175–181.

Baltensweiler, W. 1977 Colour polymorphism and dynamics of larch budmoth populations (*Zeiraphera diniana* Gn., Lep. Tortricidae). *Mitteil. Schweiz. Entomol. Gesellsch.* **50**, 15–23.

Baltensweiler, W. 1993 A contribution to the explanation of the larch budmoth cycle, the polymorphic fitness hypothesis. *Oecologia* (*Berl.*) **93**, 251–255.

Baltensweiler, W. & Priesner, E. 1988 Studien zum Pheromon-Polymorphismus von *Zeiraphera diniana* Gn. (Lep., Tortricidae). 3. Anflugspezifität männlicher Falter zweier Wirtsrassen an synthetische Pheromonquellen. *J. Appl. Entomol.* **106**, 217–231.

Barraclough, T. G. & Vogler, A. P. 2000 Detecting the pattern of speciation from species-level phylogenies. *Am. Nat.* **155**, 419–434.

Barton, N. H. & Hewitt, G. M. 1981 Hybrid zones and speciation. In *Evolution and speciation* (ed. W. R. Atchley & D. S. Woodruff), pp. 109–145. (Essays in honour of M. J. D. White.). Cambridge University Press.

Barton, N. H., Jones, J. S. & Mallet, J. 1988 No barriers to speciation. *Nature* **336**, 13–14.

Bell, M. A. & Foster, S. A. (eds) 1994 *The evolutionary biology of the threespine stickleback*. Oxford University Press.

Berlocher, S. H. 1995 Population structure of *Rhagoletis mendax*, the blueberry maggot. *Heredity* **74**, 542–555.

Berlocher, S. H. 1996 Population structure of *Rhagoletis pomonella*, the apple maggot fly. *Heredity* **77**, 83–99.

Berlocher, S. H. 1998 Can sympatric speciation via host or habitat shift be proven from phylogenetic and biogeographic evidence? In *Endless forms. Species and speciation* (ed. D. J. Howard & S. H. Berlocher), pp. 99–113. New York: Oxford University Press.

Berlocher, S. H. 1999 Host race or species? Allozyme characterization of the 'flowering dogwood fly' a member of the *Rhagoletis pomonella* complex *Heredity* **83**, 652–662.

Berlocher, S. H. 2000 Radiation and divergence in the *Rhagoletis pomonella* species group: inferences from allozymes. *Evolution* **54**, 543–557.

Berlocher, S. H. & Feder, J. L. 2002 Sympatric speciation in phytophagous insects: moving beyond controversy? *Ann. Rev. Entomol.* **47**, 773–815.

Booij, C. J. H. 1982*a* Biosystematics of the *Muellerianella* complex (Homoptera, Delphacidae), hybridisation studies. *Genetica* **57**, 161–170.

Booij, C. J. H. 1982*b* Biosystematics of the *Muellerianella* complex (Homoptera, Delphacidae), host-plants, habitats and phenology. *Ecol. Entomol.* **7**, 9–18.

Booij, C. J. H. 1982*c* Biosystematics of the *Muellerianella* complex (Homoptera, Delphacidae), interspecific and geographic variation in acoustic behaviour. *Z. Tierpsychol.* **58**, 31–52.

Bourguet, D., Bethenod, M. T., Trouve, C. & Viard, F. 2000 Host-plant diversity of the European corn borer *Ostrinia nubilialis*: what value for sustainable transgenic insecticidal Bt maize? *Proc. R. Soc. Lond.* B **267**, 1177–1184. (DOI 10.1098/rspb.2000.1126.)

Brookes, M. I. & Butlin, R. K. 1994 Population structure in the small ermine moth *Yponomeuta padellus*: an estimate of male dispersal. *Ecol. Entomol.* **19**, 97–107.

Brown, J. M., Abrahamson, W. G. & Way, P. A. 1996 Mitochondrial DNA phylogeography of host races of the goldenrod ball gallmaker, *Eurosta solidaginis* (Diptera: Tephritidae). *Evolution* **50**, 777–786.

Brownlow, C. 1996 Molecular taxonomy and the conservation of the red wolf and other endangered carnivores. *Conserv. Biol.* **10**, 390–396.

Bucheli, E., Gautschi, B. & Shykoff, J. A. 2000 Host-specific differentiation in the anther smut fungus *Microbotryum violaceum* as revealed by microsatellites. *J. Evol. Biol.* **13**, 188–198.

Bush, G. L. 1969 Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* **23**, 237–251.

Bush, G. L. 1975 Modes of animal speciation. *Ann. Rev. Ecol. Syst.* **6**, 339–364.

Bush, G. L. 1992 Host race formation and sympatric speciation in *Rhagoletis* fruit flies (Diptera: Tephritidae). *Psyche* **99**, 335–357.

Bush, G. L. 1993 A reaffirmation of Santa Rosalia, or why are there so many kinds of *small* animals? In *Evolutionary patterns and processes* (ed. D. R. Lees & D. Edwards), pp. 229–249. London: Linnean Society of London, Academic Press.

Bush, G. L. 1994 Sympatric speciation in animals: new wine in old bottles. *Trends Ecol. Evol.* **9**, 285–288.

Bush, G. L. & Howard, D. J. 1986 Allopatric and non-allopatric speciation: assumptions and evidence. In *Evolutionary processes and theory* (ed. S. Karlin & E. Nevo), pp. 411–438. New York: Academic Press.

Bush, G. L. & Smith, J. J. 1998 The genetics and ecology of sympatric speciation: a case study. *Res. Popul. Ecol.* **40**, 175–187.

Bush, G. L., Feder, J. L., Berlocher, S. H., McPheron, B. A., Smith, D. C. & Chilcote, C. A. 1989 Sympatric origins of *Rhagoletis pomonella*. *Nature* **339**, 346.

Butlin, R. 1989 Reinforcement of premating isolation. In *Speciation and its consequences* (ed. D. Otte & J. A. Endler), pp. 158–179. Sunderland, MA: Sinauer Associates.

Butlin, R. K. 1990 Divergence of emergence time of host races due to differential gene flow. *Heredity* **65**, 47–50.

Butlin, R. K. 1996 Co-ordination of the sexual signalling system and the genetic basis of differentiation between populations of the brown planthopper, *Nilaparvata lugens*. *Heredity* **77**, 369–377.

Caillaud, M. C. & Via, S. 2000 Specialized feeding behavior influences both ecological specialization and assortative mating in sympatric host races of pea aphids. *Am. Nat.* **156**, 606–621.

Cain, M. L., Andreasen, V. & Howard, D. J. 1999 Reinforcing selection is effective under a relatively broad set of conditions in a mosaic hybrid zone. *Evolution* **53**, 1343–1353.

Carroll, S. P. & Boyd, C. 1992 Host race radiation in the soapberry bug: natural history with the history. *Evolution* **46**, 1052–1069.

Carroll, S. P., Dingle, H. & Klassen, S. P. 1997 Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. *Evolution* **51**, 1182–1188.

Carroll, S. P., Klassen, S. T. P. & Dingle, H. 1998 Rapidly evolving adaptations to host ecology and nutrition in the soapberry bug. *Evol. Ecol.* **12**, 955–968.

Cerezke, H. F. 1995 Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in three pine hosts. *Can. Entomol.* **127**, 955–965.

Claridge, M. F. 1988 Species concepts and speciation in parasites. In *Prospects in systematics* (ed. D. L. Hawksworth), pp. 92–111. Oxford: Systematics Association, Clarendon Press.

Claridge, M. F., den Hollander, J. & Morgan, J. C. 1985 The status of weed-associated populations of the brown planthopper, *Nilaparvata lugens* (Stål): host race or biological species? *Zool. J. Linn. Soc.* **84**, 77–90.

Claridge, M. F., Dawah, H. A. & Wilson, M. R. 1997 Species in insect herbivores and parasitoids: sibling species, host races and biotypes. In *Species: the units of biodiversity* (ed. M. F. Claridge, H. A. Dawah & M. R. Wilson), pp. 247–272. London: Chapman & Hall.

Clarke, A. R. & Walter, G. H. 1995 'Strains' and the classical biological control of insect pests. *Can. J. Zool.* **73**, 1777–1790.

Clay, K., Dement, D. & Rejmanek, M. 1985 Experimental evidence for host races in mistletoe (*Phoradendron tomentosum*). *Am. J. Bot.* **72**, 1225–1231.

Colwell, R. K. 1986 Population structure and sexual selection for host fidelity in the speciation of hummingbird flower mites. In *Evolutionary processes and theory* (ed. S. Karlin & E. Nevo), pp. 475–495. London: Academic Press.

Condon, M. A. & Steck, G. J. 1997 Evolution of host use in fruit flies of the genus *Blepharoneura* (Diptera: Tephritidae): cryptic species on sexually dimorphic host plants. *Biol. J. Linn. Soc.* **60**, 443–466.

Coyne, J. A. & Orr, H. A. 1997 'Patterns of speciation in *Drosophila*' revisited. *Evolution* **51**, 295–303.

Coyne, J. A., Crittenden, A. P. & Mah, K. 1994 Genetics of a pheromonal difference contributing to reproductive isolation in *Drosophila*. *Science* **265**, 1461–1464.

Cracraft, J. 1989 Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In *Speciation and its consequences* (ed. D. Otte & J. A. Endler), pp. 28–59. Sunderland, MA: Sinauer Associates.

Craig, T. P., Itami, J. K., Abrahamson, W. G. & Horner, J. D. 1993 Behavioral evidence for host race formation in *Eurosta solidaginis*. *Evolution* **47**, 1696–1710.

Craig, T. P., Horner, J. D. & Itami, J. K. 1997 Hybridization studies on the host races of *Eurosta solidaginis*: implications for sympatric speciation. *Evolution* **51**, 1552–1560.

Craig, T. P., Horner, J. D. & Itami, J. K. 2001 Genetics, experience, and host-plant preference in *Eurosta solidaginis*: implications for host shifts and speciation. *Evolution* **55**, 773–782.

Crandall, K. A., Bininda-Demonds, O. R. P., Mace, G. M. & Wayne, R. K. 2000 Considering evolutionary processes in conservation biology. *Trends Ecol. Evol.* **15**, 290–295.

Day, K. 1984 Phenology, polymorphism and insect-plant relationships of the larch budmoth, *Zeiraphera diniana* (Guenée) (Lepidoptera: Tortricidae), on alternative conifer hosts in Britain. *Bull. Entomol. Res.* **74**, 47–64.

Dieckmann, U. & Doebeli, M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354–357.

Diehl, S. R. & Bush, G. L. 1984 An evolutionary and applied perspective of insect biotypes. *Ann. Rev. Entomol.* **29**, 471–504.

Doebeli, M. 1996 A quantitative genetic competition model for sympatric speciation. *J. Evol. Biol.* **9**, 893–909.

Drès, M. A. 2000 Gene flow between host races of the larch budmoth *Zeiraphera diniana* (Lepidoptera: Tortricidae). PhD thesis, University of London.

Duffy, J. E. 1996 Species boundaries, specialization, and the radiation of a sponge-dwelling alpheid shrimp. *Biol. J. Linn. Soc.* **58**, 307–324.

Emelianov, I., Mallet, J. & Baltensweiler, W. 1995 Genetic differentiation in the larch budmoth *Zeiraphera diniana* (Lepidoptera: Tortricidae): polymorphism, host races or sibling species? *Heredity* **75**, 416–424.

Emelianov, I., Drès, M., Baltensweiler, W. & Mallet, J. 2001 Host-induced assortative mating in host races of the larch budmoth. *Evolution* **55**, 2002–2010.

Emelianov, I., Simpson, F., Narang, P. & Mallet, J. 2002 Host alighting choice as a cause of reproductive isolation between host races of the larch budmoth *Zeiraphera diniana*. *J. Evol. Biol.* (In the press.)

Farrell, B. D. 1998 'Inordinate fondness' explained: why are there so many beetles? *Science* **281**, 555–559.

Feder, J. L. 1998 The apple maggot fly, *Rhagoletis pomonella*: flies in the face of conventional wisdom. In *Endless forms. Species and speciation* (ed. D. J. Howard & S. H. Berlocher), pp. 130–144. New York: Oxford University Press.

Feder, J. L. & Bush, G. L. 1989*a* A field test of differential host-plant usage between two sibling species of *Rhagoletis pomonella* fruit flies (Diptera: Tephritidae) and its consequences for sympatric models of speciation. *Evolution* **43**, 1813–1819.

Feder, J. L. & Bush, G. L. 1989*b* Gene frequency clines for host races of *Rhagoletis pomonella* in the midwestern United States. *Heredity* **63**, 245–266.

Feder, J. L. & Bush, G. L. 1991 Genetic variation among apple and hawthorn host races of *Rhagoletis pomonella* across an ecological transition zone in the midwestern United States. *Entomol. Exp. Appl.* **59**, 249–265.

Feder, J. L. & Filchak, K. E. 1999 It's about time: the evidence for host plant-mediated selection in the apple maggot fly, *Rhagoletis pomonella*, and its implications for fitness trade-offs in phytophagous insects. *Entomol. Exp. Appl.* **91**, 211–225.

Feder, J. L., Chilcote, C. A. & Bush, G. L. 1988 Genetic differentiation between sympatric host races of the apple maggot fly *Rhagoletis pomonella*. *Nature* **336**, 61–64.

Feder, J. L., Chilcote, C. A. & Bush, G. L. 1989 Are the apple maggot, *Rhagoletis pomonella*, and blueberry maggot, *Rhagoletis mendax*, distinct species? *Entomol. Exp. Appl.* **51**, 113–123.

Feder, J. L., Chilcote, C. A. & Bush, G. L. 1990 Regional, local and microgeographic allele frequency variation between apple and hawthorn populations of *Rhagoletis pomonella* in western Michigan. *Evolution* **44**, 595–608.

Feder, J. L., Hunt, T. A. & Bush, G. L. 1993 The effects of climate, host phenology and host fidelity on the genetics of apple and hawthorn infesting populations of *Rhagoletis pomonella*. *Entomol. Exp. Appl.* **69**, 117–135.

Feder, J. L., Opp, S. B., Wlazlo, B., Reynolds, K., Go, W. & Spisak, S. 1994 Host fidelity is an effective premating barrier between sympatric races of the apple maggot fly. *Proc. Natl Acad. Sci. USA* **91**, 7990–7994.

Feder, J. L., Roethele, J. B., Wlazlo, B. & Berlocher, S. H. 1997*a* Selective maintenance of allozyme differences among sympatric host races of the apple maggot fly. *Proc. Natl Acad. Sci. USA* **94**, 11 417–11 421.

Feder, J. L., Stolz, U., Lewis, K. M., Perry, W., Roethele, J. B. & Rogers, A. 1997*b* The effects of winter length on the genetics of apple and hawthorn races of *Rhagoletis pomonella* (Diptera: Tephritidae). *Evolution* **51**, 1862–1876.

Feder, J. L., Berlocher, S. H. & Opp, S. B. 1998 Sympatric host-race formation and speciation in *Rhagoletis* (Diptera: Tephritidae): a tale of two species for Charles D. In *Genetic structure and local adaptation in natural insect populations* (ed. S. Mopper & S. Y. Strauss), pp. 408–441. New York: Chapman & Hall.

Feder, J. L., Williams, S. M., Berlocher, S. H., McPheron, B. A. & Bush, G. L. 2001 The population genetics of the apple maggot fly, *Rhagoletis pomonella* and the snowberry maggot, *R. zephyria*: implications for models of sympatric speciation. *Entomol. Exp. Appl.* **90**, 9–24.

Felsenstein, J. 1981 Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* **35**, 124–138.

Ferveur, J. F. 1997 The pheromonal role of cuticular hydrocarbons in *Drosophila melanogaster*. *BioEssays* **19**, 353–358.

Filchak, K. E., Feder, J. L., Roethele, J. B. & Stolz, U. 1999 A field test for host-plant dependent selection on larvae of the apple maggot fly, *Rhagoletis pomonella*. *Evolution* **53**, 187–200.

Filchak, K. E., Roethele, J. B. & Feder, J. L. 2000 Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* **407**, 739–742.

Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S. & Balcomb, K. C. 1998 Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can. J. Zool.* **76**, 1456–1471.

Frey, J. E. & Frey, B. 1995 Molecular identification of six species of scale insects (*Quadrispidiotus* sp.) by RAPD–PCR: assessing the field specificity of pheromone traps. *Mol. Ecol.* **4**, 777–780.

Futuyma, D. J. & Mayer, G. C. 1980 Non-allopatric speciation in animals. *Syst. Zool.* **29**, 254–271.

Gallun, R. L., Starks, K. J. & Guthrie, W. D. 1975 Plant resistance to insects attacking cereals. *Ann. Rev. Entomol.* **20**, 337–357.

Gibbs, H. L., Sorenson, M. D., Marchetti, K., de L. Brooke, M., Davies, N. B. & Nakamura, H. 2000 Genetic evidence for female host-specific races of the common cuckoo. *Nature* **407**, 183–186.

Glazner, T. G., Devlin, B. & Ellstrand, N. C. 1988 Biochemical and morphological evidence for host race evolution in desert mistletoe, *Phoradendron californicum* (Viscaceae). *Plant Syst. Evol.* **161**, 13–21.

Gould, F. 1991 The evolutionary potential of crop pests. *Am. Sci.* **79**, 496–507.

Gould, F. 1994 Potential problems with high-dose strategies for pesticidal engineered crops. *Biocontrol Sci. Tech.* **4**, 451–461.

Gould, F. 1998 Sustainability of transgenic insecticidal cultivars: integrating pest genetics and ecology. *Ann. Rev. Entomol.* **43**, 701–726.

Grant, P. R. & Grant, B. R. 1992 Hybridization of bird species. *Science* **256**, 193–197.

Gratton, C. & Welter, S. 1998 Oviposition preference and larval performance of *Liriomyza helianthi* (Diptera: Agromyzidae) on normal and novel host plants. *Environ. Entomol.* **27**, 926–935.

Guldemond, J. A. 1990*a* Evolutionary genetics of the aphid *Cryptomyzus*, with a preliminary analysis of the inheritance of host plant preference and host alternation. *Entomol. Exp. Appl.* **57**, 65–76.

Guldemond, J. A. 1990*b* Choice of host plant as a factor in reproductive isolation of the aphid genus *Cryptomyzus* (Hompoptera, Aphididae). *Ecol. Entomol.* **15**, 43–51.

Guldemond, J. A. & Dixon, A. F. G. 1994 Specificity and daily cycle of release of sex-pheromones in aphids: a case of reinforcement. *Biol. J. Linn. Soc.* **52**, 287–303.

Guldemond, J. A. & Mackenzie, A. 1994 Sympatric speciation in aphids. I. Host race formation by escape from gene flow. In *Individuals, populations and patterns in ecology* (ed. S. R. Leather, A. D. Watt, N. J. Mills & K. F. A. Walters), pp. 367–378. Andover, UK: Intercept.

Guldemond, J. A., Dixon, A. F. G. & Tigges, W. T. 1994 Mate recognition in *Cryptomyzus* aphids: copulation and insemination. *Entomol. Exp. Appl.* **73**, 67–75.

Guttman, S. I., Wood, T. K. & Karlin, A. A. 1981 Genetic differentiation among host plant lines in the sympatric *Echenopa binotata* Say complex (Homoptera: Membracidae). *Evolution* **35**, 205–217.

Harrison, R. G. & Rand, D. M. 1989 Mosaic hybrid zones and the nature of species boundaries. In *Speciation and its consequences* (ed. D. Otte & J. A. Endler), pp. 111–133. Sunderland, MA: Sinauer Associates.

Hawthorne, D. J. & Via, S. 2001 Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature* **412**, 904–907.

Heinrichs, E. & Medrano, F. 1984 *Leersia hexandra*, a weed host of the rice brown planthopper, *Nilaparvata lugens* (Stål). *Crop Prot.* **3**, 77–85.

Heitland, W. & Pschorn-Walcher, H. 1992 Biological differences between populations of *Platycampus luridiventris* feeding on different species of alder (Hymenoptera: Tenthredinidae). *Entomol. Genet.* **17**, 185–194.

Herbst, J. & Heitland, W. 1994 Genetic differentiation among populations of the sawfly species *Platycampus luridiventris*, associated with different alder species (Hymenoptera, Tenthredinidae). *Entomol. Genet.* **19**, 39–48.

Horner, J. D., Craig, T. P. & Itami, J. K. 1999 The influence of oviposition phenology on survival of the host races of *Eurosta solidaginis*. *Entomol. Exp. Appl.* **93**, 121–129.

Howard, D. J. 1986 A zone of overlap and hybridization between two ground cricket species. *Evolution* **40**, 34–43.

Itami, J., Craig, T. & Horner, J. 1998 Factors affecting gene flow between the host races of *Eurosta solidaginis*. In *Genetic structure and local adaptation in natural insect populations* (ed. S. Mopper & S. Strauss), pp. 375–404. New York: Chapman & Hall.

Jaenike, J. 1981 Criteria for ascertaining the existence of host races. *Am. Nat.* **117**, 830–834.

Jaenike, J. & Selander, R. K. 1980 On the question of host races in the fall webworm, *Hyphantria cunea*. *Entomol. Exp. Appl.* **27**, 31–37.

Jiggins, C. D. & Mallet, J. 2000 Bimodal hybrid zones and speciation. *Trends Ecol. Evol.* **15**, 250–255.

Jonsson, B. & Jonsson, N. 2001 Polymorphism and speciation in Arctic charr. *J. Fish Biol.* **58**, 605–638.

Katakura, H. 1981 Classification and evolution of the phytophagous ladybirds belonging to the *Henosepilachna vigintiomaculata* complex (Coleoptera, Coccinellidae). *J. Fac. Sci. Hokkaido Univ. VI Zool.* **22**, 301–378.

Katakura, H. & Hosogai, T. 1994 Performance of hybrid ladybird beetles (*Epilachna* spp.) on the host plants of parental species. *Entomol. Exp. Appl.* **71**, 81–84.

Katakura, H., Shioi, M. & Kira, Y. 1989 Reproductive isolation by host specificity in a pair of phytophagous ladybird beetles. *Evolution* **43**, 1045–1053.

Kelley, S. T., Mitton, J. B. & Paine, T. D. 1999 Strong differentiation in mitochondrial DNA of *Dendroctonus brevicornis* (Coleoptera: Scolytidae) on different species of ponderosa pine. *Ann. Entomol. Soc. Am.* **92**, 193–197.

Kirkpatrick, M. & Ravigné, V. 2002 Speciation by natural and sexual selection. *Am. Nat.* **159**, S22–S35.

Kliman, R. M., Andolfatto, P., Coyne, J. A., Depaulis, F., Kreitman, M., Berry, A. J., McCarter, J., Wakeley, J. & Hey, J. 2000 The population genetics of the origin and divergence of the *Drosophila simulans* complex species. *Genetics* **156**, 1913–1931.

Komazaki, S. 1986 The inheritance of egg hatch timing of the overwintering egg among populations of *Aphis citricola* Van der Groot (Homoptera: Aphididae) on the two winter hosts. *Kontyû* **54**, 48–53.

Komazaki, S. 1990 Variation in the hatch timing of the overwintering egg among populations of *Aphis spiraecola* Patch (Homoptera: Aphididae) collected from different host plants and localities in Japan. *Appl. Entomol. Zool.* **25**, 27–34.

Komazaki, S. 1998 Difference of egg diapause in two host races of the spiraea aphid, *Aphis spiraecola*. *Entomol. Exp. Appl.* **89**, 201–205.

Kondrashov, A. S. & Kondrashov, F. A. 1999 Interactions among quantitative traits in the course of sympatric speciation. *Nature* **400**, 351–354.

Kondrashov, A. S. & Mina, M. V. 1986 Sympatric speciation: when is it possible? *Biol. J. Linn. Soc.* **27**, 201–223.

Kooi, R. E., Vandewater, T. P. M. & Herrebout, W. M. 1991 Host plant selection and larval food acceptance by *Yponomeuta padellus*. *Proc. Koninklijke Nederlandse Akad. Wetenschap. C. Biol. Sci.* **94**, 221–232.

Kreslavsky, A. G. & Mikheev, A. V. 1993 Gene geography of racial differences in *Lochmaea capreae* L. (Coleoptera, Chrysomelidae) and the problem of sympatric speciation. *Zool. Zhurnal* **72**, 50–58.

Kreslavsky, A. G., Mikheev, A. V., Solomatin, V. M. & Gritzenko, V. V. 1981 Genetic exchange and isolating mechanisms in sympatric races of *Lochmaea capreae* (Coleoptera, Chrysomelidae). *Zool. Zhurnal* **60**, 62–68.

Langor, D. W. 1989 Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera, Scolytidae). *Can. Entomol.* **121**, 149–157.

Langor, D. W. & Spence, J. R. 1991 Host effects on allozyme and morphological variation of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera, Scolytidae). *Can. Entomol.* **123**, 395–410.

Langor, D. W., Spence, J. R. & Pohl, G. R. 1990 Host effects on fertility and reproductive success of *Dendroctonus ponderosae* Hopkins (Coleoptera, Scolytidae). *Evolution* **44**, 609–618.

Lu, G. & Bernatchez, L. 1999 Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. *Evolution* **53**, 1491–1505.

Lu, Y.-J., Adang, M. J., Isenhour, D. J. & Kochert, G. D. 1992 RFLP analysis of genetic variation in North American populations of the fall armyworm moth *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Mol. Ecol.* **1**, 199–208.

McIntee, E. E. & Nordin, G. L. 1983 Electrophoretic comparison of two types of fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera, Arctiidae), occurring in central Kentucky. *J. Kans. Entomol. Soc.* **56**, 190–198.

McKenzie, J. A. & Batterham, P. 1994 The genetical, molecular and phenotypic consequences of selection for insecticide resistance. *Trends Ecol. Evol.* **9**, 166–169.

McLellan, K. A. M., Nordin, G. L. & Haynes, K. F. 1991 Chemical communication and reproductive isolation in two types of the fall webworm (Lepidoptera, Arctiidae). *Ann. Entomol. Soc. Am.* **84**, 118–123.

Macnair, M. R. 1989 The potential for rapid speciation in plants. *Genome* **31**, 203–210.

Macnair, M. R. & Gardner, M. 1998 The evolution of edaphic endemics. In *Endless forms. Species and speciation* (ed. D. J. Howard & S. H. Berlocher), pp. 157–171. New York: Oxford University Press.

McPheron, B. A., Smith, D. C. & Berlocher, S. H. 1988 Genetic differences between host races of *Rhagoletis pomonella*. *Nature* **336**, 64–66.

Mallet, J. 1995 A species definition for the Modern Synthesis. *Trends Ecol. Evol.* **10**, 294–299.

Mallet, J. 2001*a* The speciation revolution. *J. Evol. Biol.* **14**, 887–888.

Mallet, J. 2001*b* Gene flow. In *Insect movement: mechanisms and consequences* (ed. I. P. Woiwood, D. R. Reynolds & C. D. Thomas), pp. 337–360. Wallingford, UK: CAB International (Proceedings of a Symposium at the Royal Entomological Society, London).

Mallet, J. 2001*c* Species, concepts of. In *Encyclopedia of biodiversity*, vol. 5 (ed. S. A. Levin), pp. 427–440. San Diego, CA: Academic Press.

Mallet, J., McMillan, W. O. & Jiggins, C. D. 1998 Estimating the mating behavior of a pair of hybridizing *Heliconius* species in the wild. *Evolution* **52**, 503–510.

Marchetti, K., Nakamura, H. & Gibbs, H. L. 1998 Host race formation in the common cuckoo. *Science* **282**, 471–472.

Maynard Smith, J. 1966 Sympatric speciation. *Am. Nat.* **100**, 637–650.

Mayr, E. 1942 *Systematics and origin of species*. New York: Columbia University Press.

Mayr, E. 1963 *Animal species and evolution*. Cambridge, MA: Harvard University Press.

Mayr, E. 1970 *Populations, species, and evolution*. Cambridge, MA: Harvard University Press.

Menken, S. B. J. 1981 Host races and sympatric speciation in small ermine moths, Yponomeutidae. *Entomol. Exp. Appl.* **30**, 280–292.

Menken, S. B. 1982 Biochemical genetics and systematics of small ermine moths (Lepidoptera, Yponomeutidae). *Z. Zool. Syst. Evolutions-Forschung* **20**, 131–143.

Menken, S. B. J., Herrebout, W. M. & Wiebes, J. T. 1992 Small ermine moths (*Yponomeuta*): their host relations and evolution. *Ann. Rev. Entomol.* **37**, 41–66.

Mikheev, A. V. 1998 A new form of *Lochmaea* (Coleoptera, Chrysomelidae) from bog bilberry, bilberry and wild rosemary. *Zool. Zhurnal* **77**, 431–437.

Mikheev, A. V. & Kreslavsky, A. G. 1980 Interrelations of the willow and birch races of *Lochmaea capreae* L. (Coleoptera, Chrysomelidae) with food plants. *Zool. Zhurnal* **59**, 705–714.

Mopper, S. & Strauss, S. (eds) 1998 *Genetic structure and local adaptation in natural insect populations*. New York: Chapman & Hall.

Nice, C. C. & Shapiro, A. M. 2001 Population genetic evidence of restricted gene flow between host races in the butterfly genus *Mitoura* (Lepidoptera: Lycaenidae). *Ann. Entomol. Soc. Am.* **94**, 257–267.

Nickrent, D. L. & Stell, A. L. 1990 Biochemical systematics of the *Arceuthobium campylopodum* complex (dwarf mistletoes, Viscaceae). 2. Electrophoretic evidence for differentiation in two host races of hemlock dwarf mistletoe (*Arceuthobium tsugense*). *Biochem. Syst. Ecol.* **18**, 267–280.

Noor, M. A. F. 1999 Reinforcement and other consequences of sympatry. *Heredity* **83**, 503–508.

O'Brien, S. J. & Mayr, E. 1991 Bureaucratic mischief: recognizing endangered species and subspecies. *Science* **251**, 1187–1188.

Pashley, D. P. 1989*a* Host-associated genetic differentiation in fall armyworm (Lepidoptera: Noctuidae): a sibling species complex? *Ann. Entomol. Soc. Am.* **79**, 898–904.

Pashley, D. P. 1989*b* Host-associated differentiation in armyworms (Lepidoptera: Noctuidae): an allozymic and mitochondrial DNA perspective. In *Systematics association*, special vol. 39 (ed. H. D. Loxdale & J. D. Hollander), pp. 103–114. Oxford: Clarendon Press.

Pashley, D. P. & Martin, J. A. 1987 Reproductive incompatibility between host strains of the fall armyworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* **80**, 731–733.

Pashley, D. P., Hammond, A. M. & Hardy, T. N. 1992 Reproductive isolating mechanisms in fall armyworm host strains (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* **85**, 400–405.

Paterson, H. E. H. 1985 The recognition concept of species. In *Species and speciation* (ed. E. S. Vrba), pp. 21–29. Pretoria: Transvaal Museum (Transvaal Museum Monograph, 4).

Payne, J. A. & Berlocher, S. H. 1995 Phenological and electrophoretic evidence for a new blueberry-infesting species in the *Rhagoletis pomonella* sibling species complex. *Entomol. Exp. Appl.* **75**, 183–187.

Porter, A. H. 1990 Testing nominal species boundaries using gene flow statistics: the taxonomy of two hybridizing admiral butterflies (*Limenitis*: Nymphalidae). *Syst. Zool.* **39**, 131–148.

Price, P. W. 1980 *Evolutionary biology of parasites*. Princeton University Press.

Priesner, E. & Baltensweiler, W. 1987*a* Studien zum pheromon-polymorphismus von *Zeiraphera diniana* gn. (Lep., Tortricidae). 1. Pheromon-reaktionstypen männlicher falter in europäischen wildpopulationen, 1978–1985. *J. Appl. Entomol.* **104**, 234–256.

Priesner, E. & Baltensweiler, W. 1987*b* Studien zum pheromon-polymorphismus von *Zeiraphera diniana* gn. (Lep., Tortricidae). 2. Pheromon-reaktionstypen männlicher falter bei F_1-hybriden dreier wirtsrassen. *J. Appl. Entomol.* **104**, 433–448.

Quicke, D. L. J., Donoghue, A. M. & Brace, R. C. 1983 Biochemical-genetic and ecological evidence that red/brown individuals of the anemone *Actinia equina* comprise two morphs in Britain. *Marine Biol.* 77, 29–37.

Raijmann, L. E. L. & Menken, S. B. J. 1992 Population genetical evidence for host-race formation in *Yponomeuta padellus*. In *Proc. 8th Int. Symp. on Insect-Plant Relationships* (ed. S. B. J. Menken, J. H. Visser & P. Harrewijn), pp. 209–211. Dordrecht: Kluwer Academic.

Raijmann, L. E. & Menken, S. B. J. 2000 Temporal variation in the genetic structure of host-associated populations of the small ermine moth *Yponomeuta padellus* (Lepidoptera: Yponomeutidae). *Biol. J. Linn. Soc.* **70**, 555–570.

Reissig, W. H. & Smith, D. C. 1978 Bionomics of *Rhagoletis pomonella* on *Crataegus*. *Ann. Entomol. Soc. Am.* **71**, 155–159.

Rhymer, J. M. & Simberloff, D. 1996 Extinction by hybridization and introgression. *Ann. Rev. Ecol. Syst.* **27**, 83–109.

Rice, W. R. 1984 Disruptive selection on habitat preference and the evolution of reproductive isolation: a simulation study. *Evolution* **38**, 1251–1260.

Rice, W. R. & Hostert, E. E. 1994 Laboratory experiments on speciation: what have we learned in forty years? *Evolution* **47**, 1637–1653.

Sanderson, N. 1989 Can gene flow prevent reinforcement? *Evolution* **43**, 1223–1235.

Schilthuizen, M. 2000 Dualism and conflicts in understanding speciation. *BioEssays* **22**, 1134–1141.

Schluter, D. 2001 Ecology and the origin of species. *Trends Ecol. Evol.* **16**, 372–380.

Schluter, D. & Nagel, L. M. 1995 Parallel speciation by natural selection. *Am. Nat.* **146**, 292–301.

Sezer, M. & Butlin, R. K. 1998*a* The genetic basis of host plant adaptation in the brown planthopper (*Nilaparvata lugens*). *Heredity* **80**, 499–508.

Sezer, M. & Butlin, R. K. 1998*b* The genetic basis of oviposition preference differences between sympatric host races of the brown planthopper (*Nilaparvata lugens*). *Proc. R. Soc. Lond.* B **265**, 2399–2405. (DOI 10.1098/rspb.1998.0590.)

Shufran, K. A., Burd, J. D., Anstead, J. A. & Lushai, G. 2000 Mitochondrial DNA sequence divergence among greenbug (Homoptera: Aphididae) biotypes: evidence for host-adapted races. *Insect Mol. Biol.* **9**, 179–184.

Singer, T. L. 1998 Roles of hydrocarbons in the recognition systems of insects. *Am. Zool.* **38**, 394–405.

Smiley, J. T. 1978 Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science* **201**, 745–747.

Smith, D. C. 1988 Heritable divergence of *Rhagoletis pomonella* host races by seasonal asynchrony. *Nature* **336**, 66–67.

Smith, J. J. & Bush, G. L. 1996 Phylogeny of the genus *Rhagoletis* (Diptera: Tephritidae) inferred from DNA sequences of mitochondrial cytochrome oxidase II. *Mol. Phylogenet. Evol.* **7**, 33–43.

Stennett, M. D. & Etges, W. J. 1997 Premating isolation is determined by larval rearing in cactophilic *Drosophila mojavensis*. III. Epicuticular hydrocarbon variation is determined by use of different host plants in *Drosophila mojavensis* and *Drosophila arizonae*. *J. Chem. Ecol.* **23**, 2803–2824.

Strong, D. R., Lawton, J. H. & Southwood, T. R. E. 1984 *Insects on plants*. Cambridge, MA: Harvard University Press.

Sturgeon, K. B. & Mitton, J. B. 1986 Allozyme and morphological differentiation of mountain pine beetles *Dendroctonus ponderosae* (Coleoptera, Scolytidae) associated with host tree. *Evolution* **40**, 290–302.

Tauber, C. A. & Tauber, M. J. 1989 Sympatric speciation in insects: perception and perspective. In *Speciation and its consequences* (ed. D. Otte & J. A. Endler), pp. 307–344. Sunderland, MA: Sinauer Associates.

Taylor, E. B. & McPhail, J. D. 1999 Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (*Gasterosteus*): insights from mitochondrial DNA. *Biol. J. Linn. Soc.* **66**, 271–291.

Templeton, A. R. 1989 The meaning of species and speciation: a genetic perspective. In *Speciation and its consequences* (ed. D. Otte & J. A. Endler), pp. 3–27. Sunderland, MA: Sinauer Associates.

Theron, A. & Combes, C. 1995 Asynchrony of infection timing, habitat preference, and sympatric speciation of schistosome parasites. *Evolution* **49**, 372–375.

Thième, T. 1987 Members of the complex of *Aphis fabae* Scop. and their host plants. In *Population structure, genetics and taxonomy of aphids and Thysanoptera* (ed. J. Holman), pp. 314–323. The Hague: SPB Academic Publishing (Proceedings of an International Symposium held at Smolenice, Czechoslovakia, 9–14 September 1985).

Thomas, C. D. & Singer, M. C. 1998 Scale-dependent evolution of specialization in a checkerspot butterfly: from individuals to metapopulations and ecotypes. In *Genetic structure and local adaptation in natural insect populations* (ed. S. Mopper & S. Strauss), pp. 343–374. New York: Chapman & Hall.

Thorpe, W. H. 1930 Biological races in insects and allied groups. *Biol. Rev.* **5**, 177–212.

Tregenza, T. & Butlin, R. K. 1999 Speciation without isolation. *Nature* **400**, 311–312.

Tregenza, T. & Wedell, N. 1997 Definitive evidence for cuticular pheromones in a cricket. *Anim. Behav.* **54**, 979–984.

Turelli, M., Barton, N. H. & Coyne, J. A. 2001 Theory and speciation. *Trends Ecol. Evol.* **16**, 330–343.

Turner, J. R. G. 1984 Mimicry: the palatability spectrum and its consequences. In *The biology of butterflies* (ed. R. I. Vane-Wright & P. R. Ackery), pp. 141–161. London: Academic Press (Symposia of the Royal Entomological Society of London, 11).

Van Valen, L. 1976 Ecological species, multispecies, and oaks. *Taxon* **25**, 233–239.

Via, S. 1991*a* The genetic structure of host plant adaptation in a spatial patchwork: demographic variability among reciprocally transplanted pea aphid clones. *Evolution* **45**, 827–852.

Via, S. 1991*b* Specialized host plant performance of pea aphid clones is not altered by experience. *Ecology* **72**, 1420–1427.

Via, S. 1999 Reproductive isolation between sympatric races of pea aphids. I. Gene flow restriction and habitat choice. *Evolution* **53**, 1446–1457.

Via, S. 2001 Sympatric speciation in animals: the ugly duckling grows up. *Trends Ecol. Evol.* **16**, 381–390.

Via, S., Bouck, A. C. & Skillman, S. 2000 Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in parental environments. *Evolution* **54**, 1626–1637.

Wang, R. L., Wakeley, J. & Hey, J. 1997 Gene flow and natural selection in the origin of *Drosophila pseudoobscura* and close relatives. *Genetics* **147**, 1091–1106.

Wang, J. Y., Chou, L. S. & White, B. N. 1999 Mitochondrial DNA analysis of sympatric morphotypes of bottlenose dolphins (genus: *Tursiops*) in Chinese waters. *Mol. Ecol.* **8**, 1603–1612.

Waring, G. L., Abrahamson, W. G. & Howard, D. J. 1990 Genetic differentiation among host-associated populations of the gallmaker *Eurosta solidaginis* (Diptera, Tephritidae). *Evolution* **44**, 1648–1655.

Whitford, F., Quisenberry, S. S., Riley, T. J. & Lee, J. W. 1988 Oviposition preference, mating compatibility, and development of two fall armyworm strains. *Florida Entomol.* **71**, 234–243.

Wood, T. K. 1980 Divergence in the *Enchenopa binotata* Say complex (Homoptera: Membracidae) effected by host plant adaptation. *Evolution* **34**, 147–160.

Wood, T. K. & Guttman, S. I. 1982 Ecological and behavioral basis for reproductive isolation in the sympatric *Enchenopa binotata* complex (Homoptera Membracidae). *Evolution* **36**, 233–242.

Wood, T. K. & Guttman, S. I. 1983 *Enchenopa binotata* complex: sympatric speciation? *Science* **220**, 310–312.

Zuber, D. & Widmer, A. 2000 Genetic evidence for host specificity in the hemi-parasitic *Viscum album* L. (Viscaceae). *Mol. Ecol.* **9**, 1069–1073.