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Insect–plant interactions: the evolution of component communities

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SUMMARY

Because plant resistance to different herbivores seems generally not to be genetically highly correlated, selection by herbivores for plant resistance traits and for investment in such traits is likely to be strongly influenced by the species composition of a plant species' associated community of enemies. We summarize evidence that the host associations of specialized herbivorous insects are often phylogenetically very conservative, and include an analysis of host associations of eastern North American leaf beetles (Chrysomelidae). The great majority of these feed on the same plant families as their congeners in other biogeographic regions. The phylogenetic evidence for conservatism is complemented by a survey of several species of *Ophraella* (Chrysomelidae) for genetic variation in feeding responses to and survival on host plants of congeric species. In about half the cases, no genetic variation was discerned. Genetic variation was displayed most often in responses to plants closely related to the species' natural hosts. Biases in patterns of genetic variation may therefore underlie the phylogenetic conservatism of host use. Long-lasting associations of plants with specialized herbivores may provide opportunity for coevolution.

1. COMPONENT COMMUNITIES, PLANT LIFE HISTORIES AND INSECT DIETS

Root (1973) designated a plant species and the species associated with it, such as herbivores and their predators, a 'component community'. We will restrict our use of the term to the herbivorous arthropods. Such a component community varies with geography and ecological conditions, and overlaps with other plant species' component communities to the extent that the insects have broader or narrower host ranges.

In this paper, we sketch some of our attempts to understand the influences on the diversity and identity of the species of herbivorous insects in plants' component communities. We emphasize the evolution of insect host associations, but our questions bear on the evolution of plant life histories to the extent that the composition of a component community affects the evolution of a plant's defences, phenology and demographic characters. Herbivory has been postulated by many authors to have affected the evolution of flowering, fruiting and vegetative phenology, masting, age at first reproduction, and a host of morphological and chemical characters, and some (all too few) of these hypotheses have been supported by experimental evidence (Marquis 1992). Costs of resistance (preventing damage by insects) and of tolerance (compensating for tissue lost to herbivory) may affect allocation to growth and reproduction (Simms 1992). Several authors, for example, have postulated that allocation to defence is greatest in slowly growing plant species and those that grow in resource-poor environments (Janzen 1974; Coley *et al.* 1985).

The diversity and identity of a plant's herbivore fauna, rather than simply its biomass and the toll taken in reproductive output, will affect the evolution of defences to the degree that different defences are required to combat different enemies. A broadly effective defence will have correlated effects – perhaps measured by a positive genetic correlation in resistance – on different insects. Conversely, defences might have negatively correlated effects if a feature that deters one herbivore species is an attractant or feeding stimulant to another. Instances of both positive and negative correlations have been described, but most of the few reported genetic correlations in resistance to different herbivore species have not differed significantly from zero (Rausher 1992). This is puzzling, in view of the taxonomically broad deterrent and/or antibiotic effects of many secondary compounds in laboratory tests, but as genetic correlation studies generally use whole plants, the low genetic correlations in resistance may signal idiosyncratic species-specific responses of different insects to multiple plant characters (Futuyma & May 1992). Moreover, traits that confer generalized resistance might arise rarely but become fixed rapidly, eroding the variation necessary for intraspecific study. In any case, present evidence suggests that the efficacy of defensive characters depends on the identity of the herbivore species, so the composition of a component community should affect the course of plant evolution.

What determines the diversity and composition of a plant's fauna? The many factors include plant architecture, breadth of the species' geographic distribution and the duration of residence in a region (Strong *et al.* 1984). At least some introduce plant species are attacked by fewer insect species than in their region of origin (Roeske *et al.* 1976; Zwölfer 1988). Thus history plays a role; but how deep a history must be taken into account? Specifically, what role does phylogenetic history play, compared to rapid, recent adaptation, in determining a plant's insect fauna? This is the major focus of our efforts.

Systematic entomologists have long known that in many taxa, related insects tend to feed on related plants – they are phylogenetically conservative in diet. Ehrlich & Raven (1964) summarized many such examples in the larval diets of butterflies, and used these as a foundation for their speculative scenario of long-term coevolution. they postulated that (1) insects' diets are determined largely by deterrent, attractant and toxic plant secondary compounds; (2) selection by insects leads to the evolution of new plant defences; (3) occasional evolution of a truly novel or efficacious chemical defence may liberate a plant lineage from most of its herbivores and foster diversification of the lineage in a relatively enemy-free 'adaptive zone'; and (4) insect species associated with other plants eventually adapt to the radiating plant clade and themselves then diversify, occupying the diverse resources that these plants present. Without evaluating the validity or likelihood of all points in this scenario, we aim in our work (1) to develop quantitative assessments of the importance of phylogeny in insect host associations, that is a conspicuous feature of Ehrlich and Raven's model; and (2) to assess the possible role of genetic constraints as factors in the phylogenetic conservatism of diet. That is, has the history of host associations been guided not only by ecological sources of selection, but also by available genetic variation?

2. PHYLOGENETIC CONSERVATISM OF HOST-PLANT CHOICE

Phylogenetic conservatism in host use might be assessed in several ways. In the absence of absolute datings, which is typical for insect/host associations, the rate or frequency of change in host choice is most usefully compared with that of cladogenesis, by mapping host use on insect phylogenies inferred from other characters. This approach has been used to ask how frequently the divergence of sister species has been accompanied by a difference in host family, often used as a criterion of 'major' host shift (Strong *et al.* 1984), as the great majority of individual insect herbivore species are restricted to plants of a single family (Bernays & Chapman 1994). An initial survey of 25 insect groups ranging from subgeneric to subfamily rank (Mitter & Farrell 1991), chosen solely because a cladogram was available, suggested that on average, sister species retain the same host family about 80% of the time (range 33–100%). In nine of these clades, which contain from eight to 126 species, there is no variation at all in host family use. Conservatism at this level probably represents a preponderance of small changes in the evolution of traits controlling diet, rather than complete stasis, because related insect species very often use different confamilial host species or genera. For example, although all 13 species of *Ophraella* leaf beetles are restricted to Asteraceae, nearest relatives seldom feed on the same plant genus (Funk *et al.* 1995).

In a few instances, absolute ages can be plausibly assigned to such conserved host associations. Usually these estimates are indirect. Thus, fossils are lacking for the lepidopteran suborder Heterobathmiina, comprising about ten extant congeners in southern South America, all feeding on *Nothofagus* (Fagaceae; Humphries *et al.* 1986). From its cladistic position with respect to known fossils of other lineages, however, *Heterobathmia* can be inferred to date from the Lower Cretaceous or earlier (125 Mya; Labandeira *et al.* 1994), while *Nothofagus* is known from the Upper Cretaceous. Thus, this lineage of moths has perhaps been restricted to the same host genus for at least 70 million years. Fossils of endophagous herbivory in which both the host and the herbivore can be identified, particularly leaf mines, are beginning to provide more direct evidence for long duration of host association. Thus, Labandeira *et al.* (1994) describe fossil leaf mines from the mid-Cretaceous (97 Mya) which are attributable to the extant nepticulid moth genus *Ectodemia*. The hosts are undescribed relatives of modern Platanaceae, and the mine is described as 'remarkably similar' to that of an extant congener that feeds on *Platanus*.

Comparison of insect and host-plant phylogenies provides another kind of clue on evolutionary stability of host choice. In conjunction with other evidence (Mitter & Farrell 1991), significant match between such phylogenies can be taken to indicate that the insects have diversified in tandem with the host lineage, allowing the age of the insects' host preferences to be inferred from that of the hosts. Thus, the apparently closely parallel phylogenies of *Phyllobrotica* and related leaf beetles and their host-plants in the order Lamiales allows this association to be reasonably dated to the mid-Tertiary from the fossil record of lamialean pollen, although fossils for the beetles are lacking (Farrell & Mitter 1990). Close concordance of phylogenies on this scale appears to be rare (Mitter & Farrell 1991), but approximate match, over much longer time spans, may be more widespread. For example, among the basal (non-ditrysian) lineages of Lepidoptera, the sole conifer feeders, Agathiphagidae (two species) are sister group to nearly all the rest, including all groups feeding ancestrally and predominantly on angiosperms (Nielsen 1989). Similarly cladistically basal, species-poor groups feeding on 'gymnosperms' are characteristic of other holometabolous herbivore groups of similar or greater age, such as Hymenoptera (sawflies: Naumann 1991) and, among the beetles, Chrysomeloidea (leaf beetles and allies; e.g. Kuschel & May 1990) and Curculionoidea (weevils; Anderson 1993). These apparently relictual groups have probably been associated continuously with 'gymnosperms' since before the Cretaceous rise of the angiosperms, which are now host to most herbivore species in these orders (review in Powell *et al.* 1997).

Some of the strongest evidence on conservatism and duration of host-taxon choice comes from comparison

Table 1. *Incidence of shared host-plant families among genera of Chrysomelidae in New York State and three other biogeographic regions*

(Chrysomelid genera are classified by number of plant families (k) used as hosts by New York species. In (a), the expected number of NY genera that share at least one plant family with congeners in another region (e.g. Europe) was calculated as GP_k, where G is the number of beetle genera in NY, k is the number of plants families in the diet of a NY genus, P_k is the probability that congeners in Europe include in their diet at least one of k specified plant families, K is the number of families in the diet of a genus in Europe, p_K is the proportion of genera in Europe that feed on K families, N is the number of plant families eaten by European congeners of NY beetles, f is the fraction of NY host families that occur in the diet of all European congeners, and $P_k = k\Sigma_K p_K f/N$.)

(a) Observed and expected numbers of New York genera sharing at least one host family with congeners in other regions

No. host families in NY (k):	1	2	$\geqslant 3$
Europe			
No. sharing/no. shared genera	15/16	9/9	2/2
Expected no. sharing	0.88	1.00	0.94
Western North America			
No. sharing/no. shared genera	11/15	6/6	6/7
Expected no. sharing	0.47	0.38	0.82
Tropical America			
No. sharing/no. shared genera	13/14	6/6	3/5
Expected no. sharing	0.46	0.39	1.11

(b) Mean proportion of host families of New York chrysomelid genera shared with congeners in other regions. The number of shared chrysomelid genera is in parentheses

No. host families used in NY:	1	2	3	$\geqslant 3$
Proportion shared in				
Europe	0.94 (16)	0.55 (9)	—	0.63 (2)
Western North America	0.81 (15)	0.50 (6)	0.33 (2)	0.34 (5)
Tropical America	0.93 (13)	0.75 (6)	0.00 (1)	0.22 (4)

of relatives occurring in different biogeographic regions. (This approach was applied to plant demographic traits by Ricklefs & Latham 1992.) For example, Moran (1989) showed that the complex life cycle of melaphidine aphids alternates between mosses and sumacs (*Rhus*) in both eastern North America and eastern Asia, a geographic disjunction that may be more than 40 million years old. We have pursued this theme in a very preliminary analysis of the diet of leaf beetles (Chrysomelidae), focusing on the 90 genera we know (from literature and examination of the Cornell University insect collection) to occur in New York State (NY). Excluding genera with very polyphagous species or poorly documented diets (e.g. those in subfamily Donaciinae, which feed on aquatic plants, and Cryptocephalinae, which feed largely on decaying matter), we could identify 56 genera for which reasonably reliable host records could be found in the entomological literature for *both* at least one of the NY species and for *at least one* congeneric species in any of three other biogeographic regions: temperate Europe, western North America (wNA) (Rocky Mountains and west) and tropical America (Mexico and south). In the few cases in which NY beetles are classified as conspecific with congeners in other regions, we deleted host records of the species in those regions. Of the 56 genera, the NY representatives of 31 each feed on a single plant family, 14 are recorded from two families, and 11 from $\geqslant 3$ families. Europe harbours 27 of the NY genera, wNA 29 and tropical America 25. In aggregate, the hosts of these genera include 40 plant families in NY, 41 in Europe, 25 in wNA and 26 in tropical America, the latter two areas having been less studied.

There are several ways of characterizing the similarity of host associations across different regions. For instance, we asked, of the 27 NY genera shared with Europe, what fraction use at least one plant family that is also the host of European congeners. The answer is apparently 26/27: 15 of 16 genera recorded from one plant family in NY use the same family in Europe, and all of the 11 that use two or more families in NY feed on at least one of these families in Europe. We calculated the expected number of such matches from the probability of drawing at random the family (families) used by each genus in NY from the 41 plant families used in Europe by congeners of all NY beetles. The expected numbers of shared host associations, by this calculation, were far lower than the observed numbers (table 1a). The incidence of shared use of plant families between NY and either wNA or tropical America was equally high and equally non-random (table 1a). Table 1b includes the results of another approach to the data: calculating the mean proportion of host families used by a NY genus that are also hosts of congeners in each of the other regions. Especially for genera that in NY are restricted to one or two host families, these proportions are very high. We infer from this analysis that the chrysomelid fauna of NY – and of eastern North America, where many of the NY genera are broadly distributed – has been assembled, in part since the Pleistocene and undoubtedly in part before then, from lineages that invaded from other regions and which, almost to a beetle, retained their ancestral host-family associations. (The same conclusion applies to colonization in the reverse direction.) That is not to deny that the eastern North American species have adapted to different species or genera of plants – many have done so – but their adaptation has been taxonomically strongly circumscribed. A preliminary review of the chrysomelid fauna of the midwestern United States (specifically, that of Missouri; Riley & Enns 1979) pointed to a similar conclusion (Farrell & Mitter 1993).

3. GENETIC VARIATION IN RELATION TO HOST SHIFTS

The phylogenetic conservatism of diet in many phytophage clades suggests the hypothesis that the evolution of host associations is guided not only by ecological sources of selection (e.g. rarity of the normal host, competition, host-associated predation), but also by 'internal' constraints that could be manifested as genetic correlations or limitations on genetic variation. That is, some conceivable host shifts may be more likely than others, for genetic reasons. Futuyma *et al.* (1993, 1994, 1995) have explored this hypothesis by screening for heritable variation in responses of several host-specialized species of *Ophraella* leaf beetles (Chrysomelidae) to host plants of their congeners. *Ophraella* is a North American genus, in which each of the 13 known species feeds on one or more species within one of four tribes of Asteraceae.

The genetic work has been pursued in the context of a provisional history of host shifts in the genus, inferred from the most parsimonious distribution of host taxa on a phylogeny of *Ophraella* based on mitochondrial DNA sequences (figure 1). (This phylogeny is mostly congruent with an earlier estimate based on morphology and allozymes.) The *Ophraella* phylogeny is not highly congruent with that of the hosts, providing one of several lines of evidence for host-switching rather than cospeciation, but closely related species and populations frequently feed on plants in the same tribe, and in a few instances, cospeciation cannot be ruled out. The question was whether genetic variation might more frequently be detected in responses to either (a) plants closely related to a species' normal host, or (b) host plants of sister species, or otherwise closely related species, of beetles, representing host shifts realized during phylogeny. That is, might the presence vs. apparent lack of genetic variation predict the phylogenetic history of adaptation to new hosts? In brief, evidence for heritable variation was sought as variance among half-sib or (in some cases) full-sib families in feeding responses of neonate larvae and newly eclosed adults to a plant species, and in larval survival. Animals were confined singly with discs of leaf tissue of one plant species, without choice, and the area consumed after 24 hr was measured. Leaf tissue was replaced periodically in survival tests. Variation in each of four species of *Ophraella* was scored with respect to four to six plant species that are hosts of *Ophraella* species other than the one tested. Although all species provided evidence of genetic variation with respect to at least one test plant, we were unable to detect genetic variation in 14 of 16 tests of larval survival and in 18 of 39 tests of larval or adult consumption. In some but not all of the negative cases, virtually all individuals refused to feed and soon died. These results are strikingly at variance with most studies of *Drosophila* and other organisms, in which most characters display heritable variation. Although clearly we can never say that genetic variation in a character is absolutely lacking, the evident differences in magnitude of genetic variation in responses to different plants suggest greater potential for adaptation to some than to others.

In both of the two cases in which genetic variation in larval survival was detected, the test plant was in the same subtribe (Ambrosiinae) as the beetle's normal host. We used likelihood ratio tests for association

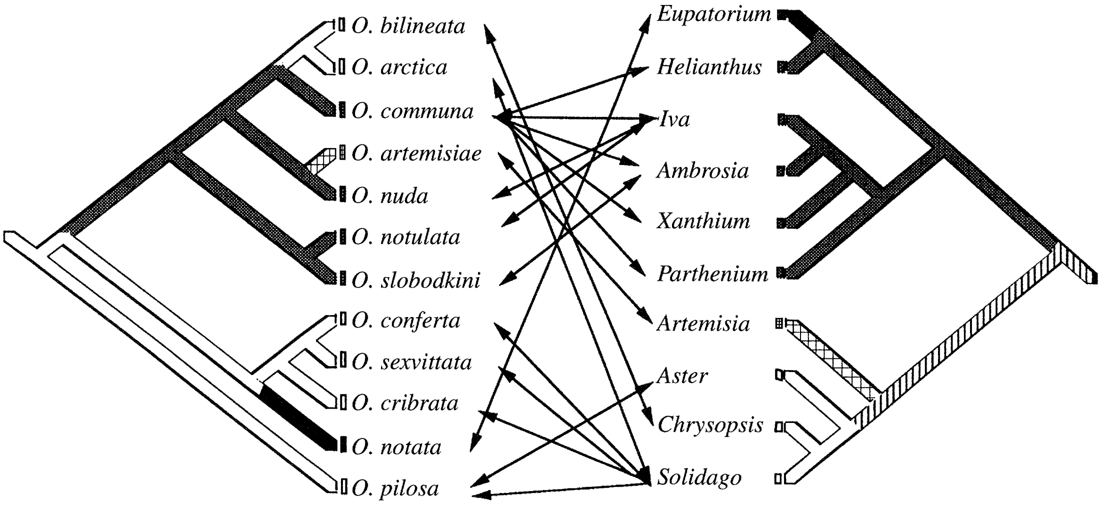

Figure 1. The estimated phylogenies of the leaf beetle genus *Ophraella* (left) and its host plants (right). Lines between the tips of the trees indicate host associations, and the shading of the *Ophraella* tree represents the most parsimonious history of evolutionary shifts between host tribes (open areas denote Astereae; cross-hatched areas denote Anthemidae; solid areas denote Eupatorieae; medium shaded areas denote Heliantheae), correspondingly shaded on the host-plant phylogeny (striped areas denote common ancestors). In a complete phylogeny of Asteraceae, many tribes and genera would be inserted among those shown. The *Ophraella* phylogeny is based on mitochondrial DNA sequences, and that of the plants chiefly on RFLP and sequence analysis of chloroplast DNA; see Funk *et al.* (1995) for methods and references.

Table 2. *Tests for association between detected* (+) *and undetectable* (–) *genetic variation in consumption, by larval or adult* Ophraella, *of hosts of their congeners, and each of several aspects of plant or* Ophraella *phylogeny*

(One-tailed exact probabilities obtained by likelihood-ratio tests (STATEXACT package)[a].)

	–	*N*	*p*
(*a*) Test plant in same or different tribe as host of beetle species scored			
Same	7	1	0.0373
Different	14	17	
(*b*) Test plant represents or not an immediate host shift on *Ophraella* phylogeny, with respect to beetle species scored			
Does	6	3	0.3116
Does not	15	15	
(*c*) Test plant is, or is not, host of an *Ophraella* species in the same major clade as the species scored[b]			
Is	12	4	0.0288
Is not	9	14	

[a] Modified from Futuyma *et al.* (1995).

[b] The major clades (see figure 1) are (1) *pilosa*; (2) *conferta-notata*; (3) *bilineata-slobodkini*.

between the presence vs. 'absence' of genetic variation in consumption, and several aspects of plant and insect phylogeny. Plants in the same tribe of Asteraceae as a species' normal host were significantly more likely to evoke genetically variable consumption than plants in different tribes (table 2*a*). No association was found between genetic variation and whether or not the test plant represented an immediate host shift in the *Ophraella* phylogeny. But genetic variation was more frequently manifested in consumption of hosts of closely related *Ophraella* species (those in the same major clade) than hosts of more distantly related species (table 2*c*). Because closely related *Ophraella* species generally have hosts in the same tribe of Asteraceae, we cannot tell whether genetic variation is more strongly correlated with plant relationships or beetle relationships. Perhaps, though, the distinction is unimportant; what is important is that the genetic data, *mirabile dictu*, are consistent with the major feature of phylogenetic history, namely that shifts among closely related plants are more frequent than among distantly related plants.

4. CONCLUSION

Taxonomic, phylogenetic and now genetic evidence are consistent in affirming that in many (but not all) groups of host-specialized insects, host shifts occur most frequently among closely related plants, perhaps due to biases in available genetic variation. Whether we should be surprised by these constraints and by the conservatism of insect diet, or should simply take them as one more instance of Darwinian gradualism, of *Natura non facit saltum*, perhaps depends on what constraints we imagine might inhere in such features as chemoreception, central processing of sensory input and detoxification of plant compounds. Since very little is known about these mechanisms, much less their capacity for variation, we can say little about what constraints to expect.

We do not wish to imply that phylogenetic history is all-important in explaining insect/plant associations. It does not account for the associations of highly polyphagous species or of the fairly numerous instances of closely related species with distantly related hosts. But it is nonetheless clear that evolutionary history, extending back many millions of years, leaves a significant imprint on the composition of the component communities that must exert selection on plant characteristics. These patterns speak of opportunity for prolonged, consistent selection imposed by long-term associations, perhaps resulting in coevolved adaptation; and, conversely, of possible shifts in or relaxation of selection on plants that have escaped their specialized herbivores by colonizing different regions. Evolutionary ecologists have only begun to address such questions.

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