Some current approaches to the evolution of plant–herbivore interactions

DOUGLAS J. FUTUYMA
Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA (Email: futuyma@life.bio.sunysb.edu)

Abstract

'Coevolution' between plants and herbivorous arthropods has several meanings: cospeciation, reciprocal adaptation, and a history of 'escape-and-radiation'. Few well documented examples of each are known. Most evolutionary research on insect-plant interactions concerns the adaptations of insects to plants or of plants to insects, but little of it expressly addresses reciprocal adaptation. Modern phylogenetic research confirms that host associations in many clades of specialized insects are evolutionarily conservative. An example from leaf beetles (*Ophraella*) is presented, in which the historical conservatism of host shifts is mirrored by patterns of paucity of genetic variation in the ability to use novel hosts. In several species of *Ophraella*, genetic variation was more often discerned in responses to plants closely related to the insect's normal host plant than to more distantly related plants. Thus availability of genetic variation might bias the evolution of host shifts, and account for the phylogenetic pattern. The difficult problem of showing that chemical and other resistance features of plants evolved for their defensive function is slowly yielding to investigation. One difficulty is that most insect herbivores are thought to be usually too rare to impose appreciable selection. Insects collectively could exert quite strong selection on resistance characters if these characters have genetically correlated effects across many species of herbivores (i.e., if selection were 'diffuse'). Surprisingly, the little available evidence does not suggest that pervasive genetic correlations are common. I conclude that more, and more multidisciplinary, research is needed to understand the evolution of plant resistance and defense.

Keywords: Chrysomelidae, coevolution, herbivory, insect–plant interactions, *Ophraella*, plant defenses.
Received 1 April 1999; revision received 30 August 1999; accepted 20 November 1999

Introduction

Almost all species of plants are consumed by herbivorous animals, among which insects are especially conspicuous in most terrestrial communities. Indeed, vascular plants and herbivorous insects together account for more than half of the described species of organisms. Their interactions have spawned immense amounts both of basic and of applied research by entomologists, botanists, ecologists and evolutionary biologists (although these distinctions are often arbitrary and many researchers have worked within several of these areas). To evolutionary biologists, one of the special points of interest is the possibility that plants and their herbivores engage in coevolution. In this paper, I will ask what this term may mean, describe several contemporary approaches to studying the evolution of plant–herbivore interactions and ask whether such studies actually address the issue of coevolution.

A very broad, almost colloquial sense in which the word 'coevolution' and related terms are used refers simply to adaptation of one species to properties of another species with which it has long had an opportunity to interact (in contrast to its response to species with which it has historically not had such opportunity). That species of *Paropsis* and other chrysomelid beetles feed on *Eucalyptus* in Australia, whereas no American species of insects feed on *Eucalyptus* introduced in California, is sometimes said to show that Australian insects have 'coevolved' with *Eucalyptus*, whereas American insects have not. Such a statement does not necessarily imply that *Eucalyptus* has evolved in response to attack by the beetles that feed on it.

A more complex characterization of 'coevolution' was introduced by Ehrlich & Raven (1964) in a paper that, more than any other, is cited as providing a theoretical framework for understanding and studying 'coevolution' of plants and herbivorous insects. Ehrlich & Raven based their ideas on the observations that (i) larvae of most species of butterflies (as is true of many other herbivorous insects) have specialized host–plant associations; (ii) related butterfly species often feed on related plants (e.g. most members of a tribe or other higher taxon of butterflies may feed on the same plant family); (iii) selection of host plants is based largely on taxon-specific plant compounds, including especially so-called 'secondary compounds'; and (iv) many of the secondary compounds that related plants hold in common have toxic or deterrent effects on nonadapted insects.

From these observations, Ehrlich & Raven proposed a scenario that they called 'coevolution', as follows.

1. Mutations that provide a plant with a new defensive chemical are fixed in the species by the natural selection that various species of herbivorous insects collectively impose.
2. As a result of the new defense, many species of insects that formerly fed on the plant no longer do so – the plant species 'escapes' from herbivory.
3. Because of its relative freedom from herbivory, the well-defended plant species becomes the ancestor of an adaptive radiation of descendant species, a clade or higher taxon, the members of which share the chemical defense that originated in their common ancestor.
4. In the course of time various species of herbivorous insects, from diverse groups not necessarily closely related to those that had formerly fed on the ancestral plant, become adapted to one or more members of the plant clade, which provide underutilized resources, or 'empty niches.' The insects' adaptation consists partly of tolerating the plants' characteristic chemical defense, or even using it as a stimulant to feeding or egg-laying.
5. Each such insect species gives rise to a clade of descendants that feed on different species in the plant clade. Thus related species of insects feed on related species of plants, although the diversification of the plants largely preceded the diversification of the insects that came to be associated with them.
6. In time, the entire process may be repeated, as some of the plant species evolve new defenses.

Ehrlich & Raven's coevolutionary hypothesis differs from hypotheses attributed to them by some later authors. As Ehrlich & Raven emphasized, their hypothesis was intended to explain diversity, by ascribing insect diversity to filling the niches that the diversification of plants provided, and ascribing plant diversity to the origins of new chemical defenses that temporarily freed the plants from most of their enemies. Ehrlich & Raven thus shared the common presumption that a trait that is advantageous for an individual organism should also promote 'evolutionary success' in the form of increased cladogenesis and species diversity. This, however, requires a logical leap that may not be justified. The mechanism connecting the two is seldom specified, although it might be postulated that the adaptation enhances the survival of populations that become different species (Allmon 1992). Nevertheless, it would seem that a trait which enhances individual fitness could also result in one or a few highly abundant species (such as the dominant conifers in taiga communities) as in a variety of related, individually less abundant species.

Another important point to recognize in the hypothesis of Ehrlich & Raven is that the evolution of individual species of plants and insects is largely *decoupled*: a plant evolves a defense that rids it of insects that fail to adapt to the plant's changed chemical constitution (i.e. they do not coevolve), and insects adapt to chemical properties that had evolved in a plant, or its ancestor, long before. Moreover, the adaptive radiation of a group of insects largely post-dates the adaptive radiation of the plants they adapt to: Ehrlich & Raven did not suggest that insects cospeciate with their host plants. Thus, although Ehrlich & Raven noted that almost all pierine butterflies feed on Capparales, they did not suggest that the phylogeny of the host plants should match that of their pierine associates.

By the late 1970s, the term 'coevolution' was being used in so many different ways that several authors argued that its meanings had to be clarified and restricted. Janzen (1980) and Futuyma & Slatkin (1983) proposed that the word should be restricted to mean *reciprocal adaptation* of two or more interacting species: an evolutionary change in one species, accompanied or followed by an evolutionary change in the other(s), due to natural selection imposed on both by the interaction between them. Generally, such changes transpire within species, but in some cases changes in features that affect the interaction may cause speciation, possibly even cospeciation (joint speciation of interacting lineages, as may occur in *Ficus* (figs) and its pollinating wasps (Herre *et al*. 1996)). Thompson (1989) provided a classification of the several meanings of 'coevolution', in which he referred to Ehrlich & Raven's scenario as 'escape-and-radiate coevolution', and distinguished it from both cospeciation and reciprocal adaptation.

Despite ubiquitous references to coevolution in the literature of plant–herbivore interactions, much of the research in this field of evolutionary ecology concerns the adaptation of herbivores to plants or of plants to herbivores, rather than coupled, reciprocal adaptation of each

to each. A large volume of reports seek to explain why many phytophagous insects are specialized (Futuyma & Moreno 1988; Jaenike 1990; Thompson 1994) and at least as large a number of reports have attempted to explain differences among plant taxa in the variety, kind and amount of chemical and physical defenses (e.g. Coley *et al.* 1985; Fritz & Simms 1992; Zangerl & Bazzaz 1992). These questions have been addressed largely by population biologists but the historical aspect of plant–herbivore associations, which loomed large in Ehrlich & Raven's paper, has recently drawn the attention of investigators using the methods of systematics. These are the contexts in which much contemporary research is carried out, as the following examples illustrate. These examples reflect my own current concerns, not the state of the subject as a whole.

Age and patterns of associations

Our understanding of the long-term history and pattern of relationships among plants and herbivores is based mostly on systematics of contemporary species, supplemented by meager information from the fossil record (Labandeira 1998a,b). Ehrlich & Raven (1964) described a pattern that was already well known to entomologists, namely that related species of butterflies commonly are specialized to feed, as larvae, on related plants. For example, most members of the subfamily Pierinae (whites) feed on Brassicaceae and related families, all Heliconiini feed on Passifloraceae and species of *Speyeria* (fritillaries) all eat *Viola*. In such instances the most parsimonious evolutionary inference is that the members of an insect taxon stem from a common ancestor that fed on that same kind of plant, so that the host association of these insects has been quite conservative. For example, we have no reason to suppose that any heliconiine butterflies have ever fed on any plants except Passifloraceae, ever since the common ancestor of the extant species.

Ehrlich & Raven (1964), writing before the development of modern phylogenetic methods, despaired of making any inferences about the history of insects' feeding habits, because these do not ordinarily fossilize. However, modern phylogenetic analyses, especially using molecular data, provide some important inferences. First, the phylogenies generally confirm many aspects of traditional classifications (e.g. Farrell 1998). Hence, many traditional statements about the host associations of major taxa of insects are valid descriptions of evolutionary lineages. Second, some of the associations of insect lineages with plant lineages are astonishingly old. For example, some phylogenetically basal lineages both of curculionoid beetles and of chrysomeloid beetles are associated with conifers and/or cycads; moreover, these insect lineages are known as fossils from Jurassic strata and are distributed today across the southern continents, suggesting descent from ancestors distributed across Gondwanaland (Farrell 1998). Farrell (1998) proposes that these lineages have been attached to conifers and cycads since the early Mesozoic, before angiosperms diversified – they have been feeding on the same lineages of plants while dinosaurs diversified, while the world was darkened by an extraterrestrial impact and while Poaceae and Asteraceae and most other angiosperm families were being born. From time-calibrated levels of DNA sequence difference (i.e. from applying approximate molecular clocks) we can estimate the age of some insect groups. The extant species of Heliconiini, for example, stem from a common ancestor that lived about 35 million years ago, during the late Eocene or early Oligocene period (Brower 1994).

The phylogenetic conservatism of the diets of many insects has an important implication for community ecologists, namely that the species diversity of a community, and its food-web structure, cannot be fully understood unless long-term evolutionary history is taken into account (Farrell & Mitter 1993; Futuyma & Mitter 1996). For example, 16 genera of specialized chrysomelid beetles, each of which feeds on only a single plant family in New York State, also occur in Europe. Fifteen of the 16 genera feed on the same plant family in Europe as they do in New York. Likewise, 13 of 14 genera of chrysomelids that are shared between New York and tropical America, and which feed on only a single plant family in New York, feed on the same family in tropical America (Futuyma & Mitter 1996). It therefore appears that the chrysomelid fauna of eastern North America has been assembled from lineages that invaded from other regions and which typically retain their ancestral host–family association, rather than adapting to new plant families in their new home. Evidently the community structure in New York would be quite different if some of these plant families did not occur there, or if the dispersal of the plants had not been accompanied by dispersal of their dependent insect groups.

A second inference from phylogenetic studies bears on one of the several possible meanings of the word 'coevolution.' That is the possibility of cospeciation, which, if repeated throughout a long history of association, would give rise to more or less congruent phylogenies of plants and their associated insects (Mitter & Brooks 1983; Mitter *et al.* 1991). Such cospeciation might be induced by the interaction; indeed, this may have occured in *Ficus*, which has apparently cospeciated with agaonine wasps that act not only as seed predators but also as species-specific pollinators (Herre *et al.* 1996). This is a special case, though, and cospeciation, if it occurs, must more often be a simple consequence of the evolution of reproductive isolation

between geographically isolated populations both of a plant and of its associated insect. That is probably the cause of the congruence that Farrell & Mitter (1990) found between the phylogenies of *Phyllobrotica* leaf beetles and their hosts, which are mostly mints in the genus *Scutellaria*. However, this is quite an unusual pattern. Most groups of insects do not cospeciate with their host plants. For example, *Ophraella* is a North American genus of leaf beetles (Chrysomelidae) that includes 14 described species, all of which are host-specific feeders on plants in four of the tribes of Asteraceae. A well-resolved phylogeny based on mitochondrial sequence data is mostly consistent with data from morphology and allozymes (Funk *et al.* 1995). The estimated phylogenies of *Ophraella* species and their host plants (Fig. 1) are largely incongruent. Moreover, other tribes of Asteraceae (not shown) should be intercalated among those in the diagram. The DNA sequence differences among species of *Ophraella* imply divergence since the Upper Miocene, whereas several of the plant tribes and even genera are known from the Lower Miocene (Futuyma & McCafferty 1990; Funk *et al.* 1995).

It is clear that many newly formed beetle species have shifted from ancestral hosts to other plant lineages, instead of diverging in concert with plant lineages. However, most such shifts are to plants in the same tribe, i.e. relatively closely related to the host used by the insect's ancestor. Presumably this is because related plants are similar in many properties, such as their sec-

ondary compounds, many of which are known to provide resistance to nonadapted insects because they act as toxins, as deterrents to feeding or egg-laying, or both. Becerra (1997) inferred the phylogeny both of Mexican species of *Blepharida*, a large genus of flea beetles, and of their host plants (in the genus *Bursera*), and also analyzed the similarity of the *Bursera* species with respect to resinous terpenes. She reported that chemical similarity among *Bursera* species differs from the estimated phylogenetic relationships to some extent and that host shifts of the beetles corresponded more with chemical similarity than with host phylogeny.

Genetic constraints on the evolution of new associations

The conservative diet in many insect groups suggests the hypothesis that insects may be genetically constrained, so that it is more likely that they shift to certain potential novel host plants than to others. Because evolution of a character requires that it be genetically variable within a species, genetic constraint on evolution of a character might consist in absence or paucity of genetic variation. However, studies of genetic variation in natural populations for more than four decades have led population geneticists generally to conclude that most characteristics are genetically variable, and that lack of genetic variation seldom limits response to selection (Lewontin 1974; Barker & Thomas 1987). Nonetheless, in several papers
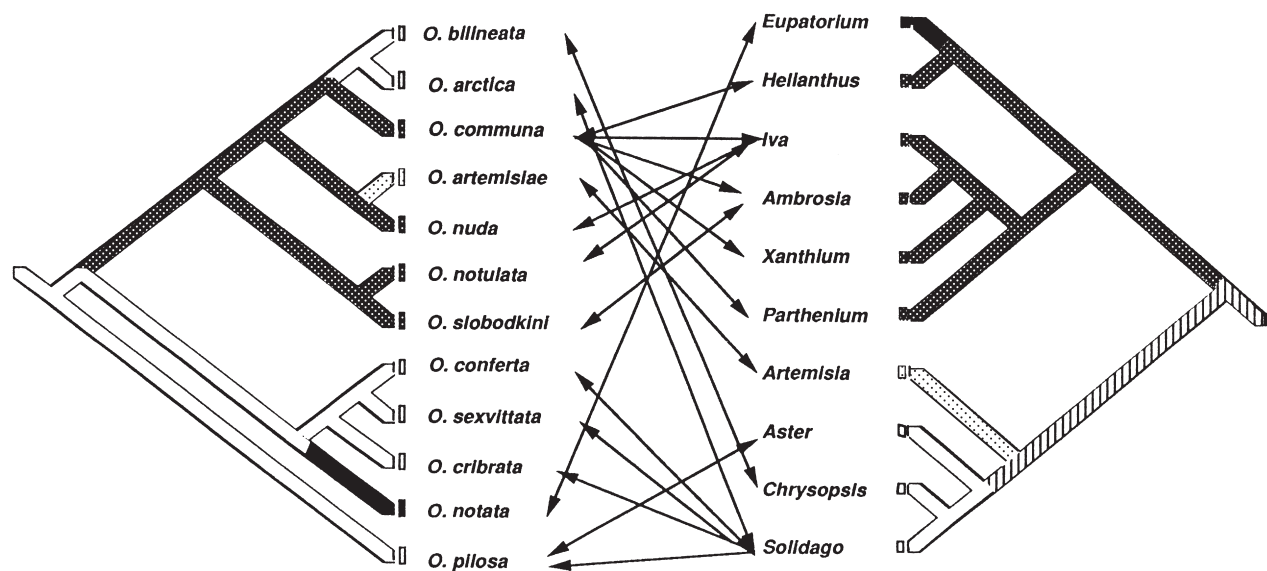
Fig. 1 Phylogeny of species of *Ophraella* (left) and their host plants (right). Arrows join *Ophraella* species to their hosts. Shadings distinguish tribes of Asteraceae. The most parsimonious history of associations with tribes of Asteraceae is indicated on the phylogeny of *Ophraella*. Genera and tribes of Asteraceae that are not used as hosts are not indicated in the plant phylogeny, even though many would be intercalated among those shown. (After Funk *et al.* 1995.) Host tribe: ☐, Asteraceae; ▨, Antemideae; ■, Eupatorieae; ▨, Heliantheae.

my colleagues and I have attempted to test the hypothesis that an insect species may have the genetic variation for characters required to shift to some plant species, but that it lacks the genetic variation needed to shift to other plants (Futuyma *et al*. 1993b, 1994, 1995). Moreover, we wished to know whether the pattern of genetic variation, or lack thereof, might explain an actual history of host shifts. That is, was the actual history any more likely, for genetic reasons, than other plausible histories that we might imagine?

The genetic study was carried out with four species of *Ophraella*. For each species, we estimated the heritable genetic variation in phenotypic characters that would be necessary for adaptation to a new host. One is feeding response. Like most host-specific insects, *Ophraella* species react to many nonhost plants by refusing to eat, even if they die. Thus we scored larvae and adults by measuring their consumption of discs of leaf tissue from plant species that are hosts of species of *Ophraella* other than the one being tested. We also determined the survival of larvae placed on such foliage, which was renewed as long as the larvae survived. For most combinations of beetle species and plant species, we used a half-sibling breeding design in which many male beetles were each mated to two females, and several offspring from each female were individually scored for feeding response to and survival on each plant species. In a few cases it was necessary to use offspring from wild-caught females, so information on paternity was lacking. Genetic variation was indicated by significant variance in a character among families from different sires or dams. Even if maternal effects exist (Futuyma *et al*. 1993a), the assumption that among-dam variance represents genetic variation is conservative, given that most population geneticists would assume that all the traits studied would be genetically variable.

Each species of beetle manifested genetic variation in response to some plants (Futuyma *et al*. 1995). But overall, we failed to find genetic variation for larval survival in 14 out of 16 combinations, and for feeding response we failed to find genetic variation in 18 of 39 cases. To appreciate the significance of this result, one must recall that for more than 50 years population geneticists have been reporting genetic variation in almost all traits studied in natural populations of plants and animals. Hence, most population geneticists are inclined to believe that absence or paucity of genetic variation seldom limits the response of a characteristic to natural selection. But in the case of *Ophraella*, the evidence strongly suggests that because of differences in availability of genetic variation, some directions of adaptation might be more likely than others. The only two cases in which we found evidence of genetic variation in larval survival entailed two species that normally feed on *Ambrosia* and *Iva*, closely related genera in the Ambrosiinae. Each species displayed genetic variation

in survival on the other species' host plant. Using a log-likelihood test on the 39 assays of feeding behavior, we found that beetle species were significantly ($P = 0.037$) more likely to display genetic variation in feeding responses to plants that are in the same tribe as their normal host, than they are to plants in different tribes. Thus the genetic data suggest that insects are more likely to adapt to plants closely related to their normal host than they are to distantly related plants – which conforms with the phylogenetic pattern in this genus (and in many other groups of herbivorous insects). These results, incidentally, have a bearing on such issues as the likelihood that insects introduced to a new region, either intentionally or accidentally, might adapt to economically important plants and become pests.

To summarize, most groups of host-specialized insects have diversified not by cospeciation with their host plants but by giving rise to species that shift to related plant lineages. These host shifts are often quite slight, in terms of plant taxonomy, so that many host associations are rather conservative over the course of many millions of years. This pattern suggests that limitations on genetic variation may constrain insects to adapting to closely related, chemically similar plants, and I have presented some evidence consistent with this hypothesis.

Plant resistance and diffuse coevolution

The evolutionary responses of plants to attack by herbivores pose a variety of questions that are in some ways more challenging than those surrounding the adaptations of herbivores to plants. I have done far less work in this area than many other people, so I will restrict myself mostly to the question, 'Do herbivore species have correlated responses to plant chemicals, so that they could, in aggregate, impose substantial selection for chemical defenses?'

I will use the word 'resistance' to refer to a characteristic of a plant that demonstrably reduces the damage inflicted by herbivores. I will use 'defense' to mean a resistance feature that has evolved *because* it reduces damage by herbivores. A 'defense' is therefore an adaptation to herbivory, whereas a resistance character need not be. Sclerophyllous leaves or thick cuticles might evolve to reduce water loss but incidentally provide resistance against some herbivores; they then would not be considered defenses.

Research on chemical resistance has been greatly influenced by three seminal papers. Dethier (1954) suggested that chemical compounds shared by different plants have facilitated insect host shifts from one plant family to another. Fraenkel (1959) proposed that defense against herbivory was the *raison d'être* of secondary plant compounds, such as alkaloids, cardenolides, terpenes and

glucosinolates. Ehrlich & Raven (1964) extended these propositions into the more elaborate scenario of 'escape-and-radiate coevolution' described earlier.

Not all of the elements of this scenario have been well documented, by any means, but a few points seem to have been well established. First, species in a higher taxon of plants typically share related compounds, such as glucosinolates in Capparales, iridoid glycosides in Scrophulariaceae and furanocoumarins in Apioideae. Second, each plant species typically has an amazingly diverse array of different compounds, including variations on a biosynthetic theme (such as several glucosinolates or terpenes) and different families of compounds (e.g. sesquiterpene lactones, phenolics, alkaloids and acetylenes all co-occur in *Ambrosia*). Third, many of these compounds are demonstrably toxic or in other ways physiologically harmful to insects, especially species that do not specialize on the plant, and many of them are repellants or deterrents of feeding or egg-laying. However, some compounds that provide resistance against nonadapted insects are used as feeding or oviposition stimulants by insects that specialize on the source plant (Rosenthal & Berenbaum 1992).

That these compounds provide resistance does not necessarily mean that they evolved for this function, and some authors have denied that they have (e.g. Jermy 1984). However, it is clear that herbivores in general, including herbivorous insects taken as a whole, often have pronounced deleterious effects on the plants' growth, survival and reproductive success and therefore have the potential for imposing natural selection for defensive characters (Crawley 1983; Marquis 1992). However, one must grant that many of the species of herbivorous insects that attack a plant species are individually so rare that it seems unlikely that they could, on their own, impose strong enough selection for a resistance character to outweigh whatever the energetic or other costs the character might have.

From the perspective of macroevolution, there has been one test of Ehrlich & Raven's hypothesis that the evolution of major new chemical defenses has promoted plant diversification. Farrell *et al.* (1991) contrasted the species diversity of pairs of sister clades. In each pair, one clade possesses a derived feature, namely canals that deliver latex or resin to sites of injury. Resin and latex have been shown experimentally to deter feeding by many insects. Farrell *et al.* found that in 14 of 16 sister-group pairs, the clade with canals has more species. Thus the hypothesis of Ehrlich & Raven has been supported in this one instance. It will be interesting to see whether the hypothesis will be supported with respect to other resistance characters, as more such comparisons are made.

It is not easy to show that a particular resistance character, such as a given chemical, is a defense, i.e. that it

evolved because of this function. Consider one of the few cases in which we *are* quite sure that a character evolved as a defense (Williams & Gilbert 1981). Larvae of heliconiine butterflies feed on tender young tissues of Passifloraceae. Because these are in short supply, larvae compete for food, and female butterflies avoid laying eggs in the vicinity of other eggs. Several species of *Passiflora* have modifications of the stipules or leaves that closely resemble *Heliconius* eggs and deter oviposition to some extent. We can be confident that the modified stipules are adaptations for defense because they appear specifically designed to resist particular, identifiable herbivores. However, the problem with most plant secondary chemicals, and with some morphological resistance characters such as trichomes, is that they do not show such evidence of design for *particular* enemies, so it is hard to deny the hypothesis that they evolved for other functions, such as waste storage, and that their effects on insects are incidental side-effects.

Hence the major approach to demonstrating the defensive function of resistance, or of particular characters that confer resistance, is to determine whether natural selection by herbivores acts on the character within populations. Following Lande & Arnold (1983), many workers attempt to demonstrate selection by estimating one or more fitness components and finding a relationship between fitness and a phenotypically variable character such as a morphological or chemical feature, or merely 'resistance' itself, measured as the complement of damage by herbivores. If the pattern of selection so found differs, depending on whether herbivores are present or absent, then selection may be attributed to herbivory. One may often at least conclude that the character is *maintained* because of its defensive function, even if its origin is uncertain.

The distinction is often made between pairwise (or specific) and diffuse coevolution. In pairwise coevolution, each of two interacting species – a plant and an insect – evolves in response to selection imposed by the other, independently of any other species. Diffuse (or guild, or multispecies) coevolution has been defined by Hougen-Eitzman & Rausher (1994) to mean coevolution in which the selective impact of each herbivore species on a plant is not independent of other herbivore species. This may be the case if the effects of different herbivores interact, as when damage by an early season insect affects the impact that a later-feeding insect species has on the plant (e.g. Juenger & Bergelson 1998). More interesting in the present context is that the plant's resistance to one herbivore may be genetically correlated with resistance to another. For example, genotypes that are more resistant to one enemy may be more susceptible to another. Thus there may exist a negative genetic correlation, representing a trade-off that may constrain the evolution of greater resistance.

Alternatively, a resistance trait may have similar effects on two or more herbivore species, so that resistances to both have a positive genetic correlation. In that case, the several herbivores collectively might exert correlated selection for greater resistance, even if each herbivore species is individually too rare to exert significant selection.

My own concern with this topic stems from a study by Hare & Futuyma (1978) on *Xanthium strumarium* (Asteraceae: Heliantheae), which has spiny fruits that are attacked by two seed predators, a tephritid fly and a tortricid moth. Both within and among local populations of the plant, these two insects had negatively correlated distributions, which led us to examine the correlations between attack and several morphological and chemical characters of the fruits. Except for burr size, which affected both insects similarly, the characters that were correlated with resistance to the two insects were generally different. There appeared not to be a trade-off in resistance. Nor was there any suggestion that the two insects would both select for any one character of the spines or for any one chemical. Thus, whatever coevolution might occur would presumably be 'pairwise.'

Some laboratory studies suggest that many plant compounds have broad-spectrum toxic or repellant effects on many insects (e.g. Miller & Feeny 1983). But the few studies of genetic correlations in resistance seem at odds with this conclusion. Rausher (1996) lists 11 studies in which the resistance of different genotypes of a plant species to two or more species of herbivorous insects or fungal pathogens had been measured in the natural environment. In the largest study, Maddox & Root (1990) scored the occurence of 17 species of insects on clones of *Solidago altissima* and calculated 136 genetic correlations between the abundance of pairs of species across different clones. They found a few clusters of insect species that tended to co-occur on the same plant genotypes, but the members of these clusters did not share any obvious taxonomic or functional commonality. In these several studies taken together only 20% of the 161 genetic correlations in resistance to various pairs of insect species were significant and positive, implying that the two insects might select for the same resistance character (or for pleiotropically related characters). In none of these studies was any specific resistance character measured.

My interpretation of these results is that positive genetic correlations are surprisingly uncommon. If, indeed, resistance to each insect is generally uncorrelated with resistance to most others, then selection is generally pairwise rather than diffuse; each insect species, in general, reacts idiosyncratically to different plant features, and few species collectively impose selection on any one character of the plant; at least, no one character contributes most of the variation in herbivore load. There is, indeed, evidence that different monoterpenes in thyme (*Thymus*) deter different species of herbivores and display different patterns of allelopathy and inhibition of pathogens (Linhart & Thompson 1999). Therefore one might suppose that the diverse, idiosyncratic responses of different insects have been the selective agents responsible for the great diversity of chemicals within a plant. However, that would appear unlikely if these insects are individually too rare to have major impacts on fitness.

If we are to gain confidence that resistance characters of plants are adaptations to reduce herbivory, it seems necessary to obtain considerably more evidence that individual species of insects impose appreciable selection for individual resistance factors, or else to demonstrate that correlated selection by multiple rare herbivores does so. To show this may require a more comprehensive approach than most researchers in this field have been able to mount, one that combines chemical, mechanistic analyses with field ecology and quantitative genetics. An ideal research program (Table 1) might identify one or

Table 1 Components of an idealized research program on selection for resistance traits and their representation in some published studies

Component of study	Berenbaum *et al.*[2]	Simms & Rausher[2]	Pilson[2]	Mauricio & Rausher[2]	Núñez-Farfán & Dirzo[2]
Identified traits	+			+	
Heritability	+	+	+	+	(+) [1]
r_G between traits	+			+	
Resistance measured	+	+	+	+	+
Two or more herbivores		+	+		+
Herbivores identified	+	+	+		+
Herbivore interaction measured			+		
Estimate fitness components	+	+	+	+	+
Relate fitness to resistances	+	+	+	+	+

[1]No statistically significant heritability of traits found. [2]Berenbaum *et al*. 1986, Simms & Rausher 1993, Pilson 1996, Mauricio & Rausher 1997, Núñez-Farfán & Dirzo 1994.

more putative resistance traits and would document their heritability and the genetic correlations among them: it would measure the resistance conferred by variable trait levels to two or more species of herbivores known to attack the plant, as well as these species' joint effect; it would estimate the genetic correlations between resistances to the several herbivores; and it would calculate the functional relationship between these resistances and plant fitness. In short, it would determine whether plant resistance characters are subject to correlated selection by diverse natural enemies, are subject to trade-offs due to opposing selection engendered by different herbivores, or are each subject to selection by one or a few herbivore species or by none. The published studies of natural selection by herbivores on plant resistance (Berenbaum *et al.* 1986; Simms & Rausher 1993; Núñez-Farfán & Dirzo 1994; Pilson 1996; Mauricio & Rausher 1997) are steps in this direction, but none meets all of these ideal criteria.

Conclusions

Remarkably few studies have actually addressed the question of whether, and in what sense, plants and herbivores coevolve. Phylogenetic studies have begun to cast light on the incidence of cospeciation and on the 'escape-and-radiate' hypothesis of Ehrlich & Raven (1964). Possibly the most promising way of obtaining evidence on coevolutionary processes will be to analyze geographic variation in interactions (Thompson 1999), but only a few such analyses have been carried out for plant–herbivore interactions (e.g. Berenbaum & Zangerl 1998). However, most studies of plants and their herbivores do not concern coevolution directly, although they have concerned questions that are ultimately relevant to coevolutionary hypotheses. Thus, to judge the potential for coevolution, and whether it may be specific or diffuse, requires that we demonstrate selection by herbivores on plant characteristics, that we understand the extent and causes of host specificity in herbivore diets and that we learn about historical patterns of interactions among species. These questions in themselves, moreover, are rich and important fields for study and raise problems in evolution and ecology at least as fundamental as coevolution. How can we determine the *raison d'être* of a trait such as a plant compound? Do characters that enhance individual fitness promote diversification of species and, if so, how? Do genetic constraints have important effects on rates and directions of evolution? How do genetic correlations affect the evolution of a species' interactions with other species? On such issues, plants and their herbivores furnish abundant opportunities for research that has only just begun.

References

Allmon W. D. (1992) A causal analysis of stages in allopatric speciation. *Oxford Surveys in Evolutionary Biology* **8**: 219–257.

Barker J. S. F. & Thomas R. H. (1987) A quantitative genetic perspective on adaptive evolution. In: *Genetic Constraints on Adaptive Evolution* (ed. V. Loeschcke) pp. 3–23. Springer, Berlin.

Becerra J. X. (1997) Insects on plants: macroevolutionary chemical trends in host use. *Science* **276**: 253–256.

Berenbaum M. R. & Zangerl A. R. (1998) Chemical phenotype matching between a plant and its insect herbivore. *Proceedings of the National Academy of Sciences USA* **95**: 13 743–13 748.

Berenbaum M. R., Zangerl A. R. & Nitao J. K. (1986) Constraints on chemical coevolution: wild parsnips and the parsnip webworm. *Evolution* **40**: 1215–1228.

Brower A. V. Z. (1994) Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato*, inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences USA* **91**: 6491–6495.

Coley P. D., Bryant J. P. & Chapin F. S. III (1985) Resource availability and plant antiherbivore defense. *Science* **230**: 895–899.

Crawley M. J. (1983) *Herbivory: the Dynamics of Animal–Plant Interactions*. University of California Press, Berkeley.

Dethier V. G. (1954) Evolution of feeding preferences in phytophagous insects. *Evolution* **8**: 32–54.

Ehrlich P. R. & Raven P. H. (1964) Butterflies and plants: a study in coevolution. *Evolution* **18**: 586–608.

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

Farrell B., Dussourd D. & Mitter C. (1991) Escalation of plant defenses: do latex and resin canals spur plant diversification? *American Naturalist* **138**: 881–900.

Farrell B. D. & Mitter C. (1990) Phylogeny of host-affiliation: have *Phyllobrotica* (Coleoptera: Chrysomelidae) and the Lamiales diversified in parallel? *Evolution* **44**: 1389–1403.

Farrell B. D. & Mitter C. (1993) Phylogenetic determinants of insect/plant community diversity. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R. E. Ricklefs & D. Schluter) pp. 253–266. University of Chicago Press, Chicago.

Fraenkel G. S. (1959) The *raison d'être* of secondary plant substances. *Science* **129**: 1466–1470.

Fritz R. S. & Simms E. L., eds. (1992) *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago.

Funk D. J., Futuyma D. J., Ortí G. & Meyer A. (1995) A history of host associations and evolutionary diversification for *Ophraella* (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. *Evolution* **49**: 1008–1017.

Futuyma D. J., Herrmann C., Milstein S. & Keese M. C. (1993a) Apparent transgenerational effects of host plant in the leaf beetle *Ophraella notulata* (Coleoptera: Chrysomelidae). *Oecologia* **96**: 365–72.

Futuyma D. J., Keese M. C. & Funk D. J. (1995) Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. *Evolution* **49**: 797–809.

Futuyma D. J., Keese M. C. & Scheffer S. J. (1993b) Genetic constraints and the phylogeny of insect–plant associations: responses of *Ophraella communa* (Coleoptera: Chrysomelidae) to host plants of its congeners. *Evolution* **47**: 888–905.

Futuyma D. J. & McCafferty S. S. (1990) Phylogeny and the evolution of host plant associations in the leaf beetle genus *Ophraella* (Coleoptera: Chrysomelidae). *Evolution* **44**: 1885–1913.

Futuyma D. J. & Mitter C. (1996) Insect–plant interactions: the evolution of component communities. *Philosophical Transactions of the Royal Society of London B* **351**: 1361–1366.

Futuyma D. J. & Moreno G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics* **19**: 207–233.

Futuyma D. J. & Slatkin M. (1983) Introduction. *Coevolution* (eds D. J. Futuyma & M. Slatkin) pp. 1–13. Sinauer Associates, Sunderland, MA, USA.

Futuyma D. J., Walsh J., Morton T., Funk D. J. & Keese M. C. (1994) Genetic variation in a phylogenetic context: responses of two specialized leaf beetles (Coleoptera: Chrysomelidae) to host plants of their congeners. *Journal of Evolutionary Biology* **7**: 127–146.

Hare J. D. & Futuyma D. J. (1978) Different effects of variation in *Xanthium strumarium* L. (Compositae) on two insect seed predators. *Oecologia* **37**: 109–120.

Herre E. A., Machado C. A., Bermingham E., Nason J. D., Windsor D. M., McCafferty S. S., van Houten W. & Bachmann K. (1996) Molecular phylogenies of figs and their pollinator wasps. *Journal of Biogeography* **23**: 521–530.

Hougen-Eitzman D. & Rausher M. D. (1994)) Interactions between herbivorous insects and plant-insect coevolution. *American Naturalist* **143**: 677–697.

Jaenike J. (1990) Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics* **21**: 243–274.

Janzen D. H. (1980) When is it coevolution? *Evolution* **34**: 611–612.

Jermy T. (1984) Evolution of insect-host plant relationships. *American Naturalist* **124**: 609–630.

Juenger T. & Bergelson J. (1998) Pairwise versus diffuse natural selection and the multiple herbivores of the scarlet gilia, *Ipomopsis aggregata*. *Evolution* **52**: 1583–1592.

Labandeira C. C. (1998a) Early history of arthropod and vascular plant associations. *Annual Review of Earth and Planetary Sciences* **26**: 329–377.

Labandeira C. C. (1998b) Plant–insect associations from the fossil record. *Geotimes* **43**: 18–24.

Lande R. & Arnold S. J. (1983) The measurement of selection on correlated characters. *Evolution* **37**: 1210–1226.

Lewontin R. C. (1974) *The Genetic Basis of Evolutionary Change*. Columbia University Press, New York.

Linhart Y. B. & Thompson J. D. (1999) Thyme is of the essence: biochemical polymorphism and multiple deterrence. *Evolutionary Ecology Research* **1**: 151–171.

Maddox G. D. & Root R. B. (1990) Structure of the encounter between goldenrod (*Solidago altissima*) and its diverse insect fauna. *Ecology* **71**: 2115–2124.

Marquis R. J. (1992) Selective impact of herbivores. In: *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics* (eds R. S. Fritz & E. L. Simms) pp. 301–325. University of Chicago Press, Chicago.

Mauricio R. & Rausher M. D. (1997) Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. *Evolution* **51**: 1435–1444.

Miller J. S. & Feeny P. (1983) Effects of benzylisoquinoline alkaloids on the larvae of polyphagous Lepidoptera. *Oecologia* **58**: 332–339.

Mitter C. & Brooks D. R. (1983) Phylogenetic aspects of coevolution. In: *Coevolution* (eds D. J. Futuyma & M. Slatkin) pp. 65–98. Sinauer, Sunderland, MA, USA.

Mitter C., Farrell B. D. & Futuyma D. J. (1991) Phylogenetic studies of insect–plant interactions: insights into the genesis of diversity. *Trends in Ecology and Evolution* **6**: 290–293.

Núñez-Farfán J. & Dirzo R. (1994) Evolutionary ecology of *Datura stramonium* L. in central Mexico: natural selection for resistance to herbivorous insects. *Evolution* **48**: 423–436.

Pilson D. (1996) Two herbivores and constraints on selection for resistance in *Brassica rapa*. *Evolution* **50**: 1492–1500.

Rausher M. D. (1996) Genetic analysis of coevolution between plants and their natural enemies. *Trends in Genetics* **12**: 212–217.

Rosenthal G. A. & Berenbaum M. R., eds. (1992). *Herbivores: Their Interactions with Secondary Plant Metabolites*, Vol. II, *Ecological and Evolutionary Processes*. Academic Press, San Diego.

Simms E. L. & Rausher M. D. (1993) Patterns of selection on phytophage resistance in *Ipomoea purpurea*. *Evolution* **47**: 970–976.

Thompson J. N. (1989) Concepts of coevolution. *Trends in Ecology and Evolution* **4**: 179–183.

Thompson J. N. (1994) *The Coevolutionary Process*. University of Chicago Press, Chicago.

Thompson J. N. (1999) Specific hypotheses on the geographic mosaic of coevolution. *American Naturalist* **153**: (Supplement): S1–S14.

Williams K. S. & Gilbert L. E. (1981) Insects as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. *Science* **212**: 467–469.

Zangerl A. R. & Bazzaz F. A. (1992) Theory and pattern in plant defense allocation. In: *Plant Resistance to Herbivores and Pathogens*: *Ecology, Evolution, and Genetics* (eds R. S. Fritz & E. L. Simms) pp. 363–391. University of Chicago Press, Chicago.