EIGHTEEN

The Phylogenetic Dimension of Insect-Plant Interactions: A Review of Recent Evidence

ISAAC S. WINKLER AND CHARLES MITTER

The dramatic expansion of research on insect-plant interactions prompted by Ehrlich and Raven's (1964) essay on coevolution focused at first mainly on the proximate mechanisms of those interactions, especially the role of plant secondary chemistry, and their ecological consequences. Subsequently, in parallel with the resurgence of phylogenetics beginning in the 1970s and 1980s, there arose increasing interest in the long-term evolutionary process envisioned by Ehrlich and Raven (e.g., Benson et al. 1975; Zwölfer 1978; Berenbaum 1983; Mitter and Brooks 1983; Miller 1987). Since the early 1990s, spurred in part by the increasing accessibility of molecular systematics, there has been a happy profusion of phylogenetic studies of interacting insect and plant lineages. The results so far have reinforced skepticism about the ubiquity of the particular macroevolutionary scenario envisioned by Ehrlich and Raven, now commonly termed "escape and radiation" coevolution (Thompson 1988). However, this model continues to inspire and organize research on the evolution of insect-plant assemblages because it embodies several themes of neo-Darwinism, each of interest in its own right, which have been taken up anew in the modern reembrace of evolutionary history. In this chapter we attempt to catalog some of the postulates about phylogenetic history derivable from Ehrlich and Raven's essay and evaluate their utility for explaining the structure of contemporary insect-plant interactions.

The escape and radiation model (reviewed in Berenbaum 1983) tacitly assumes, first, that the traits governing species' interactions, such as insect host-plant preference, are phylogenetically conserved due to constraints such as limited availability of genetic variation. Such constraints create time lags between successive insect and plant counteradaptations, allowing the lineage bearing the most recent innovation to increase its rate of diversification. Second, a related general implication is that, because of genetic or other constraints on evolutionary response to new biotic surroundings, the structure of present-day insect-plant interactions (e.g., who eats whom) will be governed more by long-term evolutionary history than by recent local adaptation. This postulate parallels a broader recent shift in thinking about community assembly, from a focus on equilibrium processes to a greater appreciation of the role of historical contingency (Webb et al. 2002; Cattin et al. 2004; DiMichele et al. 2004). Third, the radiation component of escape and radiation perfectly encapsulates the "new synthesis" view, lately enjoying a revival (Schluter 2000), that diversification is driven primarily by ecological interactions. Insect-plant interactions have figured prominently in the modern reexamination of all three of these broad postulates.

This chapter surveys the recent evidence on the phylogeny of insect-plant interactions, focusing chiefly on among-species differences in larval host-plant use by herbivorous insect lineages (largely neglecting pollinators, which are treated by Adler in this volume), and organized around the themes sketched above. We draw mostly on literature of the past dozen years, that is, subsequent to early attempts at a similar survey (e.g., Mitter and Farrell 1991; Farrell and Mitter 1993). Given the great diversity of phytophage life histories and feeding modes, full characterization of host-use evolution will require, in addition to hypothesis tests in particular groups, the estimation of relative frequencies of alternative evolutionary patterns across a broad sampling of lineages. Our emphasis here is on the latter approach. A complete catalog is no longer feasible, but we have made a concerted and continuing effort to compile as many phylogenetic studies of phytophagous insect groups as possible. These are entered into a database that at this writing contained over 1000 entries, many of which were obtained from the Zoological Record database. Our analyses and conclusions are based chiefly on approximately 200 of these reports that contain both a phylogenetic tree and information on

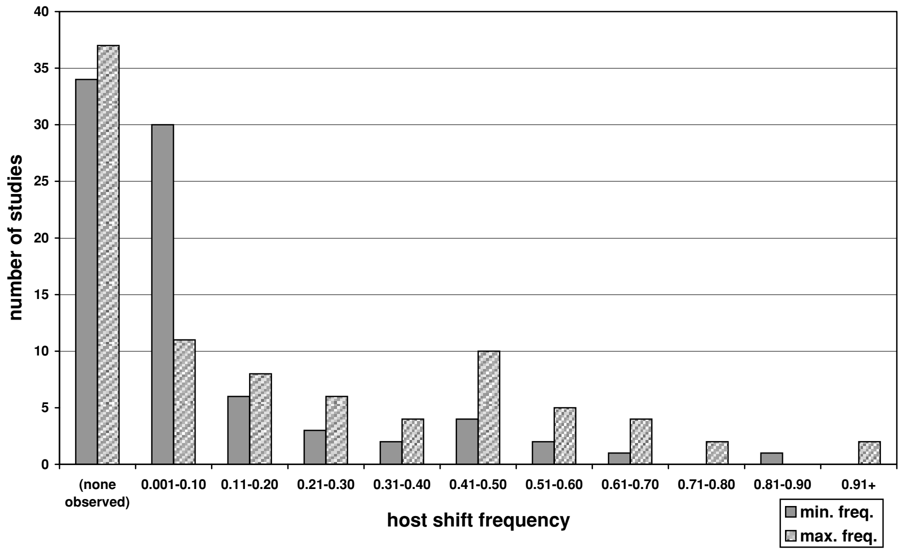

FIGURE 18.1. Frequency of host shifts per speciation event for 93 phytophagous insect phylogenies, calculated by dividing number of host-family shifts observed on phylogeny by number of included in-group species (solid bars, maximum host-shift frequency), and by total number of described species in the ingroup clade (hatched bars, minimum host-shift frequency). For references and taxa included, see Online Supplementary Table S2

host-plant use. Many of the phylogenies are based on DNA sequences, while for others the chief evidence is morphology. This database, intended as a community resource to promote further synthesis, is available at www.chemlife.umd.edu/entm/mitterlab, as are the data compilations and other supplementary materials mentioned in the text. Our nomenclature follows APGII (2003) for angiosperm families and higher groups, and Smith et al. (2006) for ferns.

Conservatism of Host-Plant Use

Full understanding of the influence of evolutionary history on insect-plant associations will require a broad accounting of the degree to which the different dimensions of the feeding niches of phytophagous insects are phylogenetically conserved. Much evidence on some aspects of this question has accumulated in the past decade.

Conservation of Host-Taxon Associations

The strongest generalization that can be made about the evolution of host-plant use is that related insect species most often use related hosts. This long-standing conclusion is now supported by numerous studies in which the history of host-taxon use has been reconstructed, most often under the parsimony criterion, on an insect phylogeny inferred from other characters. An early compilation (Mitter and Farrell 1991) of the few phylogenetic studies then available (~25) suggested that on average, less than 20% of speciation events were accompanied by a shift to a different plant family; strictly speaking, the compilation was of the fraction of branches subtended by the same node on the phylogeny that have diverged in host-family use, as inferred under the parsimony criterion. We have now repeated that calculation using essentially all applicable phylogenies we could find, totaling 93 (27 Coleoptera, 28 Hemiptera, 19 Lepidoptera, 12 Diptera, 5 Hymenoptera, and 1 each of Thysanoptera and Acari [honorary insects for the purposes of this chapter]). Some of the uncertainty in host-shift estimates comes from incomplete sampling of species. In the earlier compilation, host-shift frequency was calculated as the total number of host-family shifts inferred under the parsimony criterion, divided by one less than the number of sampled species with known hosts. This should be an unbiased estimate of the actual frequency of host shifts, if the included species are a random subset of the clade sampled. However, sampling in phylogenetic studies is often deliberately overdispersed across subclades (e.g., genera within a tribe), which should tend to inflate the average evolutionary distance among sampled species and hence the apparent frequency of host shifts. To evaluate the importance of this effect, we also calculated a corrected frequency estimate, dividing the number of shifts detected on the phylogeny by the total number of species with known hosts, including ones not included in the phylogenetic study. We will refer to these two estimates, in the order here described, as maximum versus minimum. In further contrast to the earlier tabulation, this one excluded the relatively few polyphagous species (defined here as those using more than two plant families); several phylogenies including a high proportion of polyphagous species were excluded, as well. A detailed tabulation of the phylogenies is given in the Online Supplementary Table S2, while the results are summarized in (Fig. 18.1).

The histogram of Fig. 18.1 shows a result very similar to that of the earlier tabulation, underscoring the prevalence of host conservatism. The distributions of host-family shift frequencies, strongly right-skewed, have medians of 0.08 (maximum frequency) and 0.03 (minimum frequency). Statistical tests of the hypothesis of nonrandom phylogenetic conservatism in host-genus or host-family use have now become routine within studies of the kind tabulated here. These most often use the so-called PTP test (permutation tail probability [Faith and Cranston 1991]), in which the null distribution is generated by random redistribution of the observed host-family associations across the insect phylogeny. Significant "phylogenetic signal" has been detected in nearly every instance (e.g., Table 18.2). In addition, several authors have used randomization tests on frequencies of shift among different host families or groups thereof to show that these preferentially involve related high-rank host taxa (Janz and Nylin 1998; Ronquist and Liljeblad 2001); conservatism at the level of major angiosperm clades (APGII 2003) is probably common as well.

It is widely accepted that conserved host-taxon associations primarily reflect conserved recognition of and other adaptations to plant secondary chemistry, but this assumption has been difficult to test because of the generally close correlation of chemistry with plant taxonomy. Several cases of mismatch between host-chemical and taxonomic similarity have now been examined phylogenetically and shown closer correspondence of insect phylogeny to chemistry than plant relatedness (Becerra 1997; Wahlberg 2001; Kergoat et al. 2005). Recent studies include reexamination of classic examples (Dethier 1941; Feeny 1991) of repeated shifts by lepidopterans between unrelated host families bearing similar secondary compounds (e.g., Lauraceae, Rutaceae, and/or Apiaceae [Berenbaum and Passoa 1999; Zakharov et al. 2004; Berenbaum, this volume]). This subject is by no means exhausted, as many more such syndromes surely await documentation. It should be noted, however, that herbivore groups feeding on plants without distinctive chemical defenses or on undefended plant parts can also show similarly specialized, conserved host associations (e.g., leafhoppers [Nickel 2003]).

Variation in Rates of Major Host Shift

Although conservatism is pervasive, phylogenetic studies continue to document great variation among phytophage lineages in the frequency of "major" host shifts (e.g., to different plant families). Establishing patterns to this variation will be a key step toward understanding the constraints on diet evolution. Many predictors for differential host-shift rates have been advanced (reviewed in Mitter and Farrell 1991), some invoking properties of plant taxa and/or communities, others invoking traits of the phytophages. Attempts to test these, however, remain few, and the subject seems ripe for further synthesis. In one of the few explicit analyses, Janz and Nylin (1998) present evidence that among butterflies, shifts among major angiosperm clades are less frequent in herb feeders than tree feeders. Nyman et al. (2006) found that internally feeding nematine sawfly clades have colonized significantly fewer plant families than their externally feeding sister groups. Radiations on oceanic islands have been suggested to undergo exaggerated divergence in niches, including host-plant use, compared to continental relatives (e.g., Schluter 1988). In the only test for phytophages, the eight genera of delphacid planthoppers endemic to various Pacific islands were found to have a significantly higher mean rate of host-family shift (two times higher), and frequency of polyphagy, than the 52 continental genera (Wilson et al. 1994); systematic work in progress will permit reanalysis with better control for phylogeny. Possible explanations for elevated host-shift rates on islands include limited availability of preferred hosts of colonizers, lesser chemical distinctiveness among host species due to relaxed herbivore pressure, and absence of continental competitors and/or insect natural enemies (reviewed in Wilson et al. 1994). Further comparisons to insular radiations may help to identify causes of the prevailing host specificity and conservatism of mainland phytophages.

Compilations of host-shift rates as in Online Supplementary Table S2 should permit further tests of hypotheses about differential host conservatism. Following Fagan et al. (2002), we used phylogenies from the literature to concatenate all the groups in the table into a single metaphylogeny (presented in Online Supplementary Fig. S3). One can then map onto the phylogeny the inferred host-shift frequencies plus the distribution of traits postulated to affect them (e.g., internal versus external feeding). The metatree can then be divided into a maximal number of independent regions (contrasts), each consisting of a set of contiguous branches and containing an inferred evolutionary change in the putative predictor trait. For each contrast, a single response measure is calculated (e.g., the difference in mean host-shift frequency between groups having the opposing states of the predictor variable). Paired comparisons are then used to test for a consistent effect of the predictor variable on host-shift frequency. In a first analysis, strong support was found for elevated mean frequency of host-family shifts inferred from just the oligophagous species (i.e., polyphages not scored) in lineages that include one or more polyphagous species, as opposed to lineages lacking polyphages (12/12 contrasts differing in the same direction; $P < 0.0001$, sign test). This finding supports the conjecture (e.g., Janz and Nylin, this volume) that rapid shift among host taxa and polyphagy of individual species are related phenomena.

It has often been suggested (e.g., Farrell and Mitter 1990) that dependence on host-derived toxins for larval and/or adult phytophage defense should reduce the likelihood of major host shifts. This postulate has had no formal comparative test. However, recent phylogenetic evidence suggests that use of such defenses itself is in general not so conservative, or so intimately tied to larval diet, as might be supposed (Dobler et al. 1996; Dobler 2001), probably because herbivores often have multiple defenses. Thus, in the chrysomelid beetle subtribe Chrysomelina (Termonia et al. 2001; Kuhn et al. 2004) the ancestral larval defense is entirely autogenous, but there have been two independent origins, within Salicaceae-feeding lineages, of dependence on host-derived salicin. Within one of these groups there has been subsequent addition of a second type of defense, based on a combination of autogenous and host-derived pathways, followed by multiple host shifts to another family (Betulaceae) from which salicin is not available. Availability of more than one defense-metabolism pathway may likewise have facilitated repeated host-family shifts in other groups, such as the tropical chrysomeline genus *Platyphora* (Termonia et al. 2002). Moths of the typically aposematic family Arctiidae are one of several groups that have converged on defensive use of plant-derived pyrrholizidine alkaloids (PAs), while producing endogenous other toxins as well. A recent phylogeny for arctiids implies a single origin of larval feeding on PA-containing plants and sequestration of PAs that are retained into the adult stage (Weller et al. 1999). In a species-rich subclade of the ancestrally PA-plant-feeding lineage, there have been repeated shifts to non-PA larval hosts, implying lack of constraint by chemical dependence. Adult defense, however, shows strong apparent phylogenetic inertia, as adults in this subclade have evolved to actively collect and use PAs. A similar "constraint" explanation was proposed for the propensity of adults in one African and one New World galerucine chrysomelid subtribe to feed on, and use in courtship and defense, toxic cucurbitacins from Cucurbitaceae, which are at present fed on by larvae in just a single genus in each subtribe. Recent phylogenetic evidence (Gillespie et al. 2003, 2004), however, strongly supports independent New World and Old World origins for both larval and adult use of cucurbits, and points, albeit less strongly, to adult use arising first.

Other Conserved Aspects of Host Use

Most discussion of the impact of host-plant use on insect diversification has focused on host-taxon differences, but other conserved dimensions of the feeding niche have also been recognized (e.g., Powell 1980; Powell et al. 1998), including host growth form and habitat, plant part exploited, mode of insect feeding, and phenology of oviposition and feeding. Most herbivorous insects are specialized to particular host tissues, such as leaves, flowers, fruits, seeds, stems, or roots, in addition to particular host taxa. On any one plant part, moreover, insects are typically specialized for one of a great variety of feeding modes. For example, a partial list of feeding behaviors exhibited by insects that eat leaves includes galling, mining, leaf rolling or tying, and external folivory. The relative rates of evolution of the various niche dimensions are fundamental to assessing their roles in phytophage diversification.

Several authors have begun to quantify these rates and their variation. Cook et al. (2002) used a maximum likelihood approach to show that a genus of cynipid gall wasps shifts among host-plant organs more often than among sections of their host genus, oaks. Farrell and Sequeira (2004) used similar methods to demonstrate, conversely, that in chrysomeloid beetles, shift among major host clades outpaces shift among host tissues. Other reports reinforce this latter trend at the host species level (Condon and Steck 1997; Favret and Voegtlin 2004). However, studies of gallers are mostly consistent in finding rapid shift among host tissues (e.g., Yang and Mitter 1994; Plantard et al. 1997; Nyman et al. 2000; Dorchin et al. 2004); shifts in gall location, shape, and timing, often on the same host species, may be important facilitators of galler speciation. Host growth form (i.e., trees versus herbs) often shows very strong phylogenetic conservatism relative to host clade (Ronquist and Liljeblad 2001; Bucheli et al. 2002; Lopez-Vaamonde et al. 2003), but not always (Janz and Nylin 1998; Schick et al. 2003). Timing of oviposition or development with respect to host phenology is another dimension of host use that may frequently contribute to speciation, either on the same host or on a novel host (e.g., Wood 1993; Pratt 1994; Whitcomb et al. 1994; Harry et al. 1998; Filchak et. al. 2000; Weiblen and Bush 2002; Sachet et al. 2006).

A special form of oft-conserved host use, occurring in some groups of aphids and gall wasps (Cynipidae), is obligate alternation between different host taxa in successive generations. Host alternation may have originated multiple times in aphids (Moran 1988, 1992; von Dohlen and Moran 2000; von Dohlen et al. 2006), though this inference rests mostly on differences in the mode of host alternation and other life-history features, as the phylogenetic evidence cannot adequately distinguish between gains and losses of host alternation per se. Regardless, this kind of complex host association has clearly evolved only a few times, while the loss of one or the other host has occurred repeatedly within ancestrally host-alternating lineages (Moran 1992; see also Cook et al. 2002). The degree to which host alternation (as opposed to simply shifting to a different host) reflects constraint versus adaptation has been debated (Moran 1988, 1990, 1992; Mackenzie and Dixon 1990).

Parallelism, Reversal, and Genetic Constraints on Host Shift

Although conservatism of host-use traits can suggest the influence of phylogenetic "constraint" or "inertia" (Blomberg and Garland 2002), this interpretation is not automatic, as stabilizing selection is a plausible alternative (Hansen and Orzack 2005). The constraint interpretation would receive powerful support if one could demonstrate limitations on within-population genetic variation, for traits determining host use, that corresponded to the actual history of shifts undergone by the larger clade to which the test populations belonged. In a series of studies deserving wide emulation, Futuyma and colleagues (reviewed in Futuyma et al. 1995; see also Gassman et al. 2006) reconstructed the history of host use in oligophagous *Ophraella* leaf beetles, then screened four species for genetic variation in larval and adult ability to feed and survive on the hosts (various genera of Asteraceae, in several tribes) fed on by their congeners. In only 23 of 55 tests (species by host) was there any detectable genetic variation for ability to use the alternative host. Such variation as did appear was mainly for use of hosts of closely related beetle species; these plants were themselves closely related to the normal host. Thus, lack of available variation for use of alternative hosts is probably much of the explanation for the conserved association of this genus with Asteraceae. Other lines

TABLE 18.1

Summary of Host and Distribution Overlap versus Nonoverlap for 145 Sister-Species Pairs from 45 Phytophagous Insect Phylogenies

	Total Species Pairs	*Host Species Overlap*	*Host Species Overlap*	*Host Species Disjunct*	*Host Species Disjunct*	*Total Hosts Disjunct*	*Total Distributions Disjunct*
		Distributions Overlap	Distributions Disjunct	Distributions Overlap	Distributions Disjunct		
All pairs	145	27	48	26	44	48%	63%
Continental pairs only	101	22	27	22	30	52%	56%
Island pairs only	44	5	21	4	14	41%	80%

NOTE: Host species overlap, members of pair sharing at least one host species; host species disjunct, sharing no host species; distributions overlap, with >10% areal overlap in geographic distribution; distributions disjunct, with <10% overlap in geographic distribution. Details including sources in Online Supplementary Table S4.

of evidence, less direct, point to an analogous conclusion for other clades and traits. Many authors have noted (e.g., Janz and Nylin 1998; Hsiao and Windsor 1999; Janz et al. 2001; Swigoňová and Kjer 2004; Zakharov et al. 2004) that host-family use is often highly homoplasious (i.e., showing multiple independent origins of the same habit), sometimes with repeated colonizations of a single plant family inferred to be an ancestral host. Janz et al. (2001) tested the long-standing hypothesis that such a propensity reflects retained ability to use former hosts, finding that Nymphalini butterfly larvae of most species were willing to feed on the ancestral host *(Urtica),* regardless of what host they normally fed on. Some specific kinds of phylogenetic pattern also strongly suggest genetic constraint. Thus, in several unrelated groups of galling insects, it has been found that features such as gall structure or gall position on the plant follow an ordered multistep progression on the phylogeny, for example from simple to successively more complex (Nyman et al. 2000; Ronquist and Liljeblad 2001). If the evolution of such traits were not limited by genetic variation, it is hard to see why it should nonetheless follow the presumptive path of "genetic least resistance" (Schluter 2000). The nature and extent of genetic constraints, critical to a full understanding of host-use evolution, is an underexplored subject on which modern genetic/genomic approaches hold promise for rapid progress (e.g., Berenbaum and Feeny, this volume).

Conservatism, Host Shifts, and Speciation

Given the pervasive conservatism of higher-host-taxon use, one might wonder whether diet conservatism on a finer scale has been underestimated, and shifts to different host species consequently assigned too large a role in phytophagous insect speciation. One requisite for answering this question is a broad estimate of the proportion of speciation events that are accompanied by a change in host species. To our knowledge, no such survey has been published. We provide an estimate based on 145 presumptive sister species pairs found within 45 phylogenies of phytophagous insect genera or species groups in our database for which information about hosts and geographic distribution was available. Taxa other than confirmed species (e.g., host races or unconfirmed sibling species) were excluded. Each species pair was scored as sharing a host-plant species or not; pairs were also scored as having hosts from the same genus, family, or higher angiosperm clade (defined in APGII 2003). To contrast the frequency of host differences to that of differences in distribution, each sister pair was also scored as having distributions overlapping by 10% or more (subjectively estimated) versus <10%. No characterization of the accuracy of these phylogenies was attempted. A possible source of bias is that island radiations, which show a somewhat greater frequency of allopatry between sister species than continental forms and (surprisingly) a somewhat lower mean proportion of host differences, comprise over 25% of our data set. Therefore, we also present results with and without island lineages. Our tabulation and its sources are given in Online Supplementary Table S4, and the results are summarized in (Table 18.1).

Overall, about 48% of the divergence events we tabulated are associated with an apparent change in host species. This is our best estimate of the fraction of speciation events that could have been driven by host shifts (though of course we have no way of knowing whether the host differences actually accompanied speciation, rather than arising prior to or after speciation). Our results are consistent with a major role for host shifts in phytophage speciation, but not a ubiquitous one; we estimate that about half of all speciation events are unaccompanied by a host shift. Of course, many of the latter could have involved change in tissue fed upon or other aspects of host use.

Greater circumspection is required in interpreting our compilation of differences in distribution, which potentially bear on the controversial question of sympatric speciation

(Lynch 1989). The utility of phylogenetic evidence on this issue has been doubted, even dismissed, because species' distributions can shift rapidly (Barraclough and Vogler 2000; Losos and Glor 2003; Fitzpatrick and Turelli 2006). Thus, the proportion of sister species that are sympatric might reflect dispersal ability rather than frequency of sympatric speciation (Chesser and Zink 1994; Losos and Glor 2003). Indeed, allopatric speciation has recently been suggested to play a prominent role even in the *Rhagoletis pomonella* group, the poster child for sympatric speciation (Barraclough and Vogler 2000). Nonetheless, we follow Berlocher (1998) in holding the comparative approach worthy of further exploration. Berlocher suggested that there should be a higher frequency of sympatry between sister species in host shifting than in non-host-shifting taxa, if host differences are commonly important in allowing species to originate, or at least remain distinct, in sympatry. In our compilation, however, extant sister species using different host species were sympatric only slightly (and not significantly) more often than those not differing in host, 37% ($N = 70$) versus 36% ($N = 75$). This result seems to cast doubt on the ubiquity of divergence by sympatric host shift, but that interpretation may be too conservative. For example, among-group variation in dispersal ability, which we did not correct for, might obscure the "signal" for host-associated sympatric divergence in our tabulation. Moreover, the probability of sympatric divergence may depend strongly on how different the hosts are. Thus, sister species that differ in host genus used show a markedly higher frequency of sympatry (50%) than pairs whose hosts are congeneric if they differ at all (33%), though this difference was not statistically significant ($P = 0.189$, χ^2 test). This observation is at least consistent both with a role for "major" host differences in promoting sympatric divergence, and with the postulate that shifts to distantly related hosts are more likely in sympatry, which allows for prolonged prior adaptation (Percy 2003). We should note, finally, that the study of phytophagous insect speciation and host-shift mechanisms is being revolutionized by, among other advances, the advent of fine-scale, intraspecific molecular phylogenetics including phylogeography sensu Avise (2000). These applications of phylogenies are treated elsewhere in this volume.

Phylogenesis of Host Range

Special attention has focused on the evolution of diet breadth, namely, the diversity of host plants fed on by a single herbivore species. Restriction to a small subset of the available plants is a dominant feature of phytophagous insect ecology. In addition to demanding an explanation in its own right (Bernays and Chapman 1994), it has made herbivorous insects a leading exemplar for investigating the ecological and evolutionary consequences of specialization (Schluter 2000; Funk et al. 2002). Phylogenies can potentially serve three roles in the study of host range. First, they delimit independent contrasts for identifying traits or geographic and other circumstances whose occurrence is correlated with evolutionary changes in host range, facilitating both comparative and experimental studies of the adaptive significance and consequences of those changes. Second, the rate and direction of changes in host range inferred on a phylogeny can point to genetic/phylogenetic constraints or lack thereof on host-range evolution. Third, phylogenies can in principle detect differential effects of broad versus narrow host range on diversification rates. Analyses of the second and third kinds could potentially support nonadaptive, macroevolutionary explanations for the predominance of host specificity, such as more frequent speciation in specialists than in generalists, in contrast to hypotheses invoking a prevailing individual advantage (Futuyma and Moreno 1988).

The study of host-range evolution is still something of a conceptual and methodological tangle. A fundamental question is how to define host range. Although broad, somewhat arbitrary categories of relative specialization may often suffice to reveal evolutionary patterns (e.g., Janz et al. 2001), objective, quantitative measures may yield greater statistical power and allow more meaningful comparisons across studies (Symons and Beccaloni 1999). However it is defined, host range is surely a composite feature likely to reflect different combinations of (typically unknown) adult and immature traits in different groups. It is probably subject to a heterogeneous mix of influences that vary in relative strength with the scale of comparison. Small-scale changes in host range might reflect behavioral plasticity or local adaptation in response to differences in host abundance or quality, or host-associated assemblages of competitors, predators, or parasitoids (e.g., Singer et al. 2004; Bernays and Singer 2005). Such changes could also represent short-lived intermediate steps in the evolution of new specialist species (e.g., Hsiao and Pasteels 1999; Janz et al. 2001, 2006). In contrast, changes evident mainly on longer time scales, and spanning a greater range of diet breadths, could reflect less frequent but more pervasive evolutionary shifts involving multiple component adaptations. At any scale of examination, broader host range could result from different causes in different lineages.

Given the heterogeneity of potential causes, evolutionary patterns of host range are likely to differ widely among groups. Phylogenetic evidence has begun to accumulate, but we are far from having an adequate characterization of that variation, let alone an explanation. The most useful studies will be those in which (1) unambiguous distinctions are evident in host range, reflecting intrinsic differences among species (not higher taxa as in Berenbaum and Passoa [1999], contra Nosil [2002] and Nosil and Mooers [2005]), and (2) taxon sampling is dense enough to permit detection of evolutionary trends if these exist. Only a handful of the studies in our database appear to meet these criteria. We summarize the nine that we judged to come closest in (Table 18.2). No criticism is implied of any work not included in this somewhat subjective selection, particularly

TABLE 18.2

Synopsis of Nine Recent Studies Bearing on Phylogenetic Patterns of Host Range

Insect Taxon	*Taxon Sample*	*No. Specialists vs. no. Generalists*	*Criterion for Specialist vs. Generalist*	*Forms of Directionality Reported*	*Significant Host-Taxon Conservation?*	*Significant Host-Range Conservation?*	*Source*
Coleoptera: Chrysomelidae: *Oreina*	12/24 spp., spanning all ecological variation in genus	6 vs. 6	1 vs. > 1 host tribe	None	Host family and tribe conserved, $P = 0.01$ PTP	No: $P = 0.47$, PTP	Dobler et al. 1996
Coleoptera: Curculionidae: Scolytinae: *Dendroctonus*	18/19 spp. (position of remaining species taken from literature)	6 vs. 13	Using <½ vs. >½ of available host species	Specialists limited to tips of phylogeny	Host genus conserved, $P = 0.01$, PTP (authors)	No: $P = 1.00$, PTP (authors)	Kelley and Farrell 1998
Coleoptera: Bruchidae: *Stator*	21/22 spp. with known hosts	4 vs. 16	1 vs. > 1 host tribe	Generalists derived	Use of 1 of 4 host genera conserved, $P = 0.03$, PTP (authors)	No: $P = 1.00$, multiple tests (authors)	Morse and Farrell 2005
Lepidoptera: Nymphalidae: Melitaeini	10/10 gen., 65/250 spp.; sparse sampling in one large Neotropical clade	51 vs.14	1 vs. >1 host family	Host-family gains > losses	Host-family use conserved, $P = 0.003$ (author)	No for gen. vs. spec. ($P = 0.34$ PTP; yes ($P = 0.02$) for number of host families (1–6)	Wahlberg 2001

Lepidoptera: Nymphalidae: Nymphalini	27/70 spp.; most taxa in some nearctic lineages	17 vs. 10	1 vs. >1 host order	Specialist ancestor; host gains > losses	Host-family use conserved, $P = 0.01$, PTP (authors)	Marginal: $P = 0.06$, PTP	Janz et al. 2001
Lepidoptera: Nymphalidae: *Polygonia*	14/16 spp.	7 vs. 5	1 vs. >1 host order	Specialist ancestor; host gains > losses	Host-order use conserved, $P = 0.001$, PTP	No for gen. vs. spec. and number of host orders (1–5; $P > 0.30$, PTP)	Weingartner et al. 2006
Lepidoptera: Saturniidae: *Hemileuca*	22 populations in 17 spp./28 spp. total; excluded taxa may be synonyms	15 vs. 7	Using primarily 1 vs. >1 host family	None	Host-family use conserved, $P = 0.02$, PTP	No: $P = 1.00$, PTP (authors)	Rubinoff and Sperling 2002
Diptera: Tephritidae: *Tomoplagia*	19/59 spp.; sampling limited to part of Brazil	11 vs. 8, or 14 vs. 5, or 15 vs. 4	1 vs. >1 host genus, or subtribe, or tribe	Depends on criterion	No: $P > 0.18$ (PTP) for host subtribe use	No: $P > 0.50$, PTP, all criteria	Yotoko et al. 2005
Phasmida: Timematidae: *Timema*	14 spp. (17 taxa)/21 spp. (remainder described subsequently)	11 vs. 6	1 (95% of records) vs. >1 host genus	Generalist ancestor	Host genus conserved, $P < 0.04$ (authors)	No: $P = 0.59$, PTP	Crespi and Sandoval 2000

NOTE: See “Table References” for source information. Gen., generalist; PTP, permutation tail probability test; spec., specialist; spp., species.

since the tracing of diet breadth has only rarely been an explicit goal.

The strongest generalization evident so far is that host range is quite evolutionarily labile, much more so than use of particular host taxa. As a gauge of that lability, we tabulated the results of PTP tests (Faith and Cranston 1991) on degree of host specificity treated as a binary character with changes in the two directions equally weighted (one versus more than one host family, or other criteria specified by the authors or otherwise appropriate to the study group; about half these analyses were performed by the authors). In seven of nine cases, this test cannot reject a random distribution of host range on the phylogeny, whereas in each case but one, use of individual host taxa is significantly conserved. As several authors have noted, host range is clearly not subject to strong forms of phylogenetic constraint or "inertia" (Blomberg and Garland 2002), such as absolute irreversibility (Nosil and Mooers 2005; Yotoko et al. 2005). In fact, the paucity of obvious phylogenetic signal may complicate further characterization of host-range evolution by limiting the utility of some standard strategies of phylogenetic character analysis. Thus, when a two-state likelihood model is applied to estimate the relative rates of transition to and from specialization, the rates can most often be closely predicted from just the proportions of specialists and generalists among the terminal taxa (Nosil 2002; Nosil and Mooers 2005). This outcome, intuitively expected if the states are distributed randomly on the tree, might be taken to suggest that phylogenies have little to contribute to the understanding of host-range evolution. And indeed, it is possible that much of the variation in host range analyzed so far is in fact phylogenetically "random" in the sense of reflecting idiosyncratic local fluctuation, for example in the availability of, and/or selective advantage of using, particular hosts. This may be especially true when all the species within the study group are specialists in the broad sense of feeding on plants in, for instance, the same family.

As several authors have noted, however, it is plausible that larger-scale phylogenetic regularities remain to be discovered through the elaboration of more detailed, process-oriented models of host-range evolution (Stireman 2005). Multiple approaches can be distinguished. Thus, host range might be thought of as a trait phylogenetically ephemeral in itself, but with probabilities of change predictable from the states of other, more conserved features, inviting use of the "comparative method." For example, distribution of the use of two versus more than two tribes of legumes appears by itself to be random on a phylogeny of the seed beetle genus *Stator*. Closer inspection, however, shows that independent origins of broader host range are significantly concentrated in lineages that oviposit on predispersal seeds, rather than on intact seed pods or dispersed seeds (Morse and Farrell 2005).

An alternative approach focuses on the genetic and ecological mechanisms by which host range changes. Thus, Crespi and Sandoval (2000; see also Nosil et al. 2003) conclude that host specialization in *Timema* walking sticks comes about when host-associated color polymorphism in polyphagous ancestors is converted into species differences under disruptive selection by predators. Phylogenetic evidence by itself is consistent with but does not strongly establish ancestral polyphagy. However, that interpretation is supported by abundant experimental and other evidence. Similar logic is reflected in the elaboration of a novel hypothesis about butterfly host range (e.g., Janz et al. 2001; Weingartner et al. 2006; Janz and Nylin, this volume). A phylogeny for the nymphalid tribe Nymphalini suggests ancestral restriction to Urticales followed by repeated host-range expansions as well as contractions, with multiple ostensibly independent colonizations of a set of disparate plant families. Complementary experiments show that larvae of many species are able to feed on hosts not presently used by that species, but characteristic of their inferred ancestors and/or extant relatives. Retained latent feeding abilities may help to explain rapid expansions (and hence observed lability) of host range. Polyphagy may also facilitate radical host shifts (and/or further broadening of host range), given that less specialized species seem to generally make more oviposition mistakes (Janz et al. 2001), and has been suggested to thereby promote diversification (Janz et al. 2006; Weingartner et al. 2006; Janz and Nylin, this volume). This postulate stands in direct contrast to the prediction that specialization promotes faster speciation, for which evidence is currently lacking (see below).

Several of the foregoing hypotheses may apply to a broad phylogenetic pattern of host range in the noctuid moth subfamily Heliothinae (Mitter et al. 1993; Cho 1997; Fang et al. 1997; S. Cho, A. Mitchell, C. Mitter, J. Reiger, M. Matthews, submitted). A paraphyletic basal assemblage, species-rich and almost entirely oligophagous or monophagous (80% on Asteraceae), contrasts sharply with an advanced "*Heliothis* clade" containing a much higher proportion of polyphages. Host range is correlated with phylogeny, albeit weakly, but the most dramatic difference is in its much higher rate of change in the *Heliothis* clade. That lineage appears to have a set of conserved life-history features (higher fecundity, body size, and other traits) that are relatively permissive of changes in host range, while the low fecundity, small size, low vagility, and other traits of the more basal species may strongly disfavor host-range expansion. Phylogenetically controlled analyses of the life-history correlates of diet breadth are still too few, but the number is growing (e.g., Beccaloni and Symons 2000) and further synthesis seems imminent (Jervis et al. 2005).

With so many promising recent leads at hand, we can look forward to rapid progress in understanding of the phylogenetic patterns of host-range evolution.

Signatures of Long-Term History in Extant Insect-Plant Interactions

Strong conservatism of host taxon or other aspects of host-plant use raises the possibility that the current distribution of insects across plant species reflects some form of long-term synchrony in the diversification of those associates. One extreme form of synchronous evolution would be strict parallel phylogenesis or cospeciation, in which descendant lineages of the insect ancestor maintain continuous and exclusive association with the descendants of the ancestral plant species; the expected signature is a characteristic form of correspondence between the phylogenetic relationships, and the absolute ages, of the extant associates. Extensive methodological and empirical work on this general issue over the past 15 years, in many groups of organisms, has established that strict or nearly strict parallel phylogenesis is almost entirely limited to parasites and other symbionts that are directly transmitted between host parent and offspring individuals (e.g., Page 2003). However, variants of this scenario more likely for free-living phytophages have also been envisioned, involving intermittent and/or less specific association of insect species with particular host-plant taxa, and producing corresponding forms of incomplete phylogeny matching. Under escape and radiation coevolution, for example, the closest match is expected not between phylogenies per se, but between phylogenetic sequences of escalating plant defenses and insect counteradaptations (Mitter and Brooks 1983). The marks of other forms of shared evolutionary history might lie primarily elsewhere. For example, it has been proposed that differences in the predominant host associations of major phytophagous insect clades reflect differences in which plant groups dominated the global flora in the different eras in which those phytophages arose (Zwölfer 1978). The critical evidence on such postulates will often be absolute datings. For the full range of questions considered in this section, a combined approach from phylogenetics and paleontology is proving especially powerful (reviewed in Labandeira 2002; see also Grimaldi and Engel 2005). There is currently a surge of interest in molecular dating studies, driven in part by the increasing sophistication of methods for combining evidence from fossils and molecular divergence (reviewed in Magallón 2004; Welch and Bromham 2005), though the reliability of such datings is still poorly understood.

In this section we attempt to sketch out and evaluate the evidence for several forms of historical imprint on insect-plant associations. Such inquiry matters for two reasons. First, traces of shared long-term history imply that there has been at least the opportunity for prolonged reciprocal evolutionary influence—coevolution in a broad sense—and may even provide evidence on the nature and extent of that coevolution. Second, from the ecological point of view, unique marks of history imply that the assembly of extant insect-plant communities cannot be fully explained by just the current properties of local or regional species pools or even the evolutionary propensities of these; one may need also to invoke the contingent historical sequence in which particular insect and plant lineages appeared on earth (Farrell and Mitter 1993).

Early in the current era of phylogenetic studies, there was much interest in the possibility of parallel phylogenesis between insect and host-plant clades. There is now enough evidence to state with confidence that correspondence of phytophagous insect and host phylogeny is rare on the taxonomic scale at which it has most often been examined, namely within and among related insect genera. Even groups involved in obligate pollination mutualisms show much less correspondence with host phylogeny than previously assumed (Pellmyr 2003; Kawakita et al. 2004; Machado et al. 2005). An early compilation (Mitter and Farrell 1991) examined 14 studies, in only one of which was there unambiguous support for parallel phylogenesis. Here we tabulate a subset of 18 of the many relevant studies appearing since then, limited to papers in which the authors themselves drew conclusions about parallel cladogenesis (Table 18.3). In the great majority of these, there is little evidence, from either cladogram concordance or datings, for parallel diversification. Our sample undoubtedly underestimates the true prevalence of such negative evidence, as we did not include the many papers in which parallel cladogenesis is implicitly ruled out at the start. One exception to the rule is particularly instructive: a group of psyllids showed significant phylogeny concordance with its legume hosts, but molecular clock and fossil datings indicate that host diversification was likely complete before the group was colonized by these phytophages (Percy et al. 2004). Presumably, host shifts in these herbivores have been governed by plant traits correlated with plant phylogeny; it is less clear why colonization should start at the base of the host phylogeny. In light of this finding, it seems especially important that newly discovered instances of possible cladogram match, for example, as reported for a group of gracillariid moths that obligately pollinate their hosts (Kawakita et al. 2004), be investigated for equivalence of ages.

The few plausible cases for both cladogram match and equivalence of ages include two genera of herb-feeding beetles (leaf beetles on skullcap mints [Farrell and Mitter 1990]; longhorn beetles on milkweeds [Farrell and Mitter 1998; Farrell 2001]). The vast assemblage of figs and their mutualist wasp pollinators, the subject of many recent phylogenetic studies (Silvieus et al., this volume), shows clear elements of parallel diversification, although it now appears that host specificity and parallel speciation are much less strict than was formerly thought (Machado et al. 2005).

Datings based on fossils, molecular clocks, and biogeography also continue to identify other patterns suggesting long-continued, not necessarily coevolutionary interactions (e.g., von Dohlen et al. 2002). One of the most elaborate apparent historical interaction signatures involves *Blepharida* alticine leaf beetles and related genera. Beetle phylogeny shows only tenuous concordance with that of the chief hosts, *Bursera* and relatives (Burseraceae/Anacardiaceae), but much stronger match to a phenogram of leaf extract gas chromatography profiles (compounds not specified) (Becerra 1997). Shared geographic disjunction between the New World and African tropics implies comparable overall

TABLE 18.3

Synopsis of 18 Recent Studies Testing for Parallel Insect-Plant Phylogenesis at Lower Taxonomic Levels

Insect Order and Family	*Insect Clade*	*Host Clade(s)*	*Overall Phylogeny Correspondence Plausible?*	*Equivalent Ages Plausible?*	*Sources*
Coleoptera: Cerambycidae	*Tetraopes*	*Asclepias* (Apocynaceae)	Yes, significant cladogram similarity	Yes	Farrell 2001, Farrell and Mitter 1998
Coleoptera: Chrysomelidae	*Ophraella*	Asteraceae	No, cladograms do not match	No, beetles younger than hosts	Funk et al. 1995
Coleoptera: Chrysomelidae	*Blepharida*	Burseraceae	Maybe, depends on analysis	Yes	Bercerra 1997, 2003
Coleoptera: Curculionidae	*Anthonomus grandis* grp.	*Hampea* (Malvaceae)	No, cladograms do not match	Not tested	Jones 2001
Hymenoptera: Tenthredinidae	*Euurina* (Nematinae)	*Salix* (Salicaceae)	No, cladograms do not match	Not tested	Nyman et al. 2000, Roininen et al. 2005
Hymenoptera: Cynipidae	Major lineages of cynipids	Asteraceae, Lamiaceae, Fagaceae, Rosaceae, Papaveraceae	No, cladograms not significantly similar	Maybe (based on fossils, biogeography)	Ronquist and Liljeblad 2001
Hymenoptera: Agaonidae	Agaoninae	*Ficus* (Moraceae)	Yes,[a] but correspondence not universal	Yes	Machado et al. 2005
Hymenoptera: Agaonidae	*Apocryptophagus* (nonpollinators)	*Ficus* (Moraceae)	No, cladograms not significantly similar	Not tested	Weiblen and Bush 2002
Diptera: Tephritidae	*Urophora*	Cardueae (Asteraceae)	No, cladograms not significantly similar	No, flies younger than hosts	Brändle et al. 2005
Lepidoptera: Gracillariidae	*Epicephala*	*Glochidion* (Phyllanthaceae)	Maybe, depends on type of analysis	Not tested	Kawakita et al. 2004
Lepidoptera: Gracillariidae	*Phyllonorycter*	>30 families of angiosperms	No, cladograms not significantly similar	No (individual moth/host radiations tested)	Lopez-Vaamonde et al. 2003, 2006

Lepidoptera: Geometridae	Lithinini	Ferns, multiple families	No, multiple shifts to distantly related hosts	No, moths younger than hosts	Weintraub et al. 1995
Hemiptera: Aphididae	*Uroleucon*	Asteraceae	No, multiple shifts to distantly related hosts	No, aphids much younger than hosts	Moran et al. 1999
Hemiptera: Psyllidae	Arytaininae	Fabaceae: Genisteae of Macaronesia	Yes, significant cladogram similarity	No, psyllids much younger than hosts	Percy et al. 2004
Hemiptera: Psyllidae	*Calophya, Tainarys*	*Schinus* (Anacardiaceae)	Maybe, depends on group and analysis	Not tested	Burckhardt and Basset 2000
Hemiptera: Delphacidae	Tribes of delphacids	Various monocots	Little evidence for cladogram match	Maybe (ages uncertain)	Wilson et al. 1994
Hemiptera: Delphacidae	*Nesosydne*	Hawaiian silverswords (Asteraceae: Heliantheae, 3 genera)	Maybe, depends on analysis (sampling incomplete)	Yes	Roderick 1997
Acari: Eriophyidae	*Cecidophyopsis*	*Ribes* (Grossulariaceae)	No, cladograms do not match	No, mites younger than hosts	Fenton et al. 2000

NOTE: See "Table References" for source information.

[a] Machado et al. (2005) found fig and pollinator wasp phylogeny congruence to be nonsignificant and point out the paucity of evidence for cladogram matching of figs and their pollinating wasps at lower levels, as well. However, it is evident that substantial overall codivergence has occurred (Rønsted et al. 2005), and widespread (but not universal) congruence at lower levels still seems plausible (see also Weiblen and Bush 2002; Silvieus et al., this volume, and references therein).

ages (112 million years; but see Davis et al. 2002) for the interacting clades, and molecular clocks point to similar, younger ages for two associated beetle and plant subsets marked by corresponding innovations in resin canal defense and counterdefense (Becerra 2003). This case, an exemplar of the broad syndrome of parallel origins of resin/latex canal defenses and counteradaptations thereto (Farrell et al. 1991), is perhaps the most detailed to date for long-term insect-plant "arms race" sequences as envisioned by Ehrlich and Raven (1964; but see Berenbaum 2001), though evidence for the accelerated diversification expected with each innovation is lacking.

We digress here to note that such putative escalations of plant defense are underinvestigated and possibly rare. Aside from resin/latex canals, the two most strongly stated hypotheses involve evolutionary trends toward chemical complexity in coumarins and other secondary compounds in Apiaceae (reviewed in Berenbaum 2001) and in cardenolides of milkweeds (*Asclepias*; reviewed in Farrell and Mitter 1998). Although the modern revolution in plant phylogeny has underscored the conservatism of some major secondary chemistry types (e.g., Rodman et al. 1998), phylogenetic studies directed explicitly at the evolution of plant defense are still few (but see Armbruster 1997; Wink 2003; Rudgers et al. 2004). Agrawal and Fishbein (2006) mapped an array of putative defense traits that included total cardenolides (though not the hypothesized arms race aspects thereof) onto a molecular phylogeny for 24 *Asclepias* species. Rather than reflecting plant phylogeny, these traits appear to define three distinct, convergently evolved defense syndromes, each possibly optimal in the right circumstances. This implicit optimality/equilibrium view of plant defense is very different from the historically contingent view inherent in the arms race hypothesis. Under the latter, we expect some lineages to have acquired novel defenses that confer, at least temporarily, a ubiquitous fitness advantage over relatives lacking those innovations. The relative applicability of these two views of defense evolution across the diversity of plants and their defensive traits has yet to be determined.

Reinforcing the view that ancient host associations may have left widespread, if not numerically dominant, traces on contemporary assemblages is the increasing evidence for broad-scale correspondence between the ages of currently associated insect and plant groups, over time spans encompassing major evolutionary changes in the global flora. The case for this long-standing postulate (see Zwölfer 1978) is best developed for the beetle clade Phytophaga (Chrysomeloidea + Curculionoidea, ~135,000 species), whose hosts span the chief lineages of seed plants (Farrell 1998; Marvaldi et al. 2002; Farrell and Sequeira 2004). Recent phylogeny estimates show most of the basal phytophagous lineages in both superfamilies to feed exclusively on conifers or cycads, the most basal seed plants. The five gymnosperm-associated clades, totaling about 220 species, have apparently Gondwanan-relict distributions, and several are known as Jurassic fossils from the same deposits as are members of their present-day host groups. Within both superfamilies, moreover, there are early splits between monocot and (eu)dicot feeders, possibly established during the early divergence between these two main lineages of angiosperms (Farrell 1998). A similar pattern is evident, in abbreviated form, in the Lepidoptera, first known from the early Jurassic (Grimaldi and Engel 2005). Larvae of the most basal lineage (Micropterigidae) inhabit riparian moss and liverwort beds, apparently feeding on these and/or other plant materials. Their habits match those of the inferred common ancestor of Lepidoptera and their sister group Trichoptera (Kristensen 1997). Recent morphological and molecular phylogenies (Kristensen 1984; Wiegmann et al. 2000, 2002) firmly establish that the most basal lineage of the remaining Lepidoptera, which are otherwise mostly restricted to advanced angiosperms, consists of two Australasian species that feed inside cones of the conifer *Araucaria*. This association, which parallels basal gymnosperm feeding (specifically within reproductive structures) in Phytophaga (Farrell 1998), is quite plausibly viewed as predating the availability (or at least the dominance) of angiosperm hosts. It is, however, the only obvious such relictual habit in Lepidoptera. While other primitive lineages also have apparent Gondwanan-relict distributions, suggesting mid-Mesozoic ages, they feed on advanced (mainly eurosid) dicots, and their phylogenetic relationships correspond not at all to those of their chief host-plant taxa (Powell et al. 1998). Host use appears to evolve considerably faster in Lepidoptera than in Phytophaga, thus traces of earlier feeding habits are probably more quickly obliterated.

Ancient host associations in other phytophagous lineages that date to the early Mesozoic and before, less well characterized, await clarification by modern studies. Recent progress on phylogeny of sawflies (basal hymenopterans) (e.g., Schulmeister 2003), modern families of which date to the early Jurassic or even Triassic, should permit elucidation of the degree to which the multiple conifer feeding lineages, totaling several hundred species, represent ancestral habits. We can hope for similar enlightenment about the Aphidomorpha (aphids and relatives), probably Triassic in age, in which the phylogenetic positions of the few extant gymnosperm-associated lineages are still obscure (Heie 1996; Normark 2000; von Dohlen and Moran 2000; Ortiz-Rivas et al. 2004). Moreover, documentation of such deep-level relictual host associations may prompt reexamination of some younger groups for which synchronous diversification with hosts seems at first glance implausible. Thus, analysis of the more than 1000 species of cynipid gall wasps detected no significant overall phylogeny match with their host-plant families, mostly woody rosids and herbaceous asterids (Ronquist and Liljeblad 2001). However, recently discovered taxa have raised the possibility that the ancestral gall wasps, like one basal extant lineage, fed on Papaveraceae, a member of the most basal eudicot lineage, Ranunculales (but see Nylander 2004; Nylander et al. 2004). Fossils date the gall wasps to at least the late Cretaceous, thus it is possible that this habit has been retained since before the rise to prominence of the host groups commonly used today (Ronquist and Liljeblad 2001). A similar history is possible for some genera of leaf-mining agromyzid flies (Spencer 1990).

Aphids, agromyzids, and other groups may participate in another broad historical pattern that is receiving increased attention. Insect groups whose chief diversity is associated with modern (especially poaceous or euasterid) herbaceous plants in temperate regions might well have diversified in parallel with the great Tertiary expansion of open habitats and herbaceous vegetation, driven by global cooling, drying, and latitudinal climate stratification trends (Behrensmeyer et al. 1992; Graham 1999). This postulate, in need of rigorous test, shares some elements with escape-and-radiation coevolution, including the ascription of diversification to ecological opportunity, and the distribution of insect lineages across plants to long-term historical trends. The hypothesis predicts that phylogenies of these herbivores should exhibit trends toward use of successively younger host groups (and/or perhaps from trees to herbs), and subclade ages should roughly match those of their hosts and/or biomes (Dietrich 1999; von Dohlen and Moran 2000; von Dohlen et al. 2006). One among many candidate lineages is the so-called trifine Noctuidae (Noctuidae sensu stricto; more than 11,000 species). Trifines have a markedly higher ratio of temperate-to-tropical species than any other large family of Macrolepidoptera and, unlike those families, are mostly herb feeders instead of tree feeders. Recent phylogenies confirm that the trifine groups most closely adapted to open, boreal habitats, which are often ground-dwelling "cutworms" as larvae, are among the most derived (Holloway and Nielsen 1998; Mitchell et al. 2006).

Diversification of Phytophagous Insects

The extraordinary species richness of plant-feeding insects is a salient feature of terrestrial biodiversity (Strong et al. 1984). It is therefore not surprising that insect-plant interactions have been a prominent model in the modern revival of interest in diversification (Wood 1993; Schluter 2000; Coyne and Orr 2004). Full understanding of the diversification of phytophagous insects will require both detailed analysis of speciation (and extinction) mechanisms, and comparative study of broad diversification patterns. These enterprises are of course intertwined, and phylogeny is relevant to both. Our review, however, will focus mainly on the comparative aspect.

A fundamental question to be asked is whether the apparent exceptional diversity of phytophagous insects is actually the result of consistent clade selection (Williams 1992), rather than a coincidental impression created by a few groups whose hyperdiversity could reflect some other cause. Sister-group comparisons between independently originating phytophagous insect clades and their nonphytophagous sister groups, which control for clade age and other traits possibly influencing diversification rate, show that phytophages have consistently elevated diversities (Mitter et al. 1988). This conclusion is at least consistent with the results of an analysis screening for significant variation in diversification rate across the insect orders (Mayhew 2002). It should be noted that the finding rests at present on only a small fraction of the potential evidence, as the phylogenetic positions of most originations of insect phytophagy are only now beginning to be resolved. Thus, further test of this hypothesis is desirable.

Why should phytophagous insects have elevated diversification rates? Several broad hypotheses have been advanced. One possibility is adaptive radiation (Simpson 1953), redefined loosely by Schluter (2000) as "evolution of ecological diversity in a rapidly multiplying lineage" (p. 1). Vascular plants might constitute an "adaptive zone" providing an extraordinary diversity of underutilized, distinct resources on which insect specialization is possible. A contributing factor might be that more niches supporting a sustainable population size are available at the primary consumer level than to higher levels or to decomposers, no matter how those niches are filled. Diversification could be accelerated still further if plant diversity continually increases due to coevolution sensu Ehrlich and Raven (1964). In a contrasting, though complementary, hypothesis (Price 1980), phytophage diversity reflects instead a broad propensity of the "parasitic lifestyle" for rapid diversification, due in part to the ease with which populations of small, specialized consumers can be fragmented by the patchy distribution of hosts.

Some progress has been made toward sorting out these alternatives. The finding that insect groups parasitic on animals are, if anything, less diverse than their nonparasitic sister groups (Wiegmann et al. 1993) casts strong doubt on the primacy of the parasitic lifestyle hypothesis. The leading hypothesis, adaptive radiation, makes two chief predictions. One of these, the subject of a vigorous area of research (Via 2001; Berlocher and Feder 2002; Rundle and Nosil 2005; other chapters this volume), is that shifts to new plant resources should be a major contributor to the origin of new species. Earlier, we estimated that about 50% of speciation events in phytophagous insects involve shifts to a different host-plant species. This is an underestimate of the importance of plant resource diversity to speciation, because niche shifts within the same host-plant species (e.g., to different host organs or tissues) and changes in host range (with retention of at least one previous host) are not included. Comparative data, then, are at least consistent with a major role for host-related divergence in phytophage diversification. It should be noted that ecological differences between sister species can arise by multiple mechanisms before, during, or after speciation (Futuyma 1989; Schluter 2000). Even if host-related differences were incidental to speciation, however, a broad form of the adaptive zone or radiation hypothesis could be said to hold, if those differences produced higher net diversification rate by forestalling extinction due to competition for resources or enemy-free space. As the foregoing suggests, hypotheses attributing diversification to ecological differentiation have rarely been explicit about which of the many possible mechanisms are involved (reviewed in Allmon 1992). Ongoing ecological study of the importance of competition and natural enemies to phytophage fitness and host use (e.g., Denno et al. 1995; Murphy 2004) should help to distinguish among plausible candidate mechanisms.

A second prediction of the adaptive radiation hypothesis is that the diversification rate of a phytophagous lineage should be correlated with the number of plant resource niches available to it. The strongest evidence on this question so far comes from studies of the beetle clade Phytophaga. In each of 10 contrasts identified so far (Farrell 1998; Farrell et al. 2001), beetle groups feeding on conifers or other gymnosperms were less diverse than their angiosperm-feeding sister groups. To these can be added the contrast in Lepidoptera between the basal conifer-feeding lineage Agathiphagidae (two species) and its almost entirely angiosperm-feeding sister group Heterobathmiidae + Glossata (~160,000 spp.; Wiegmann et al. 2000). Although exceptions will undoubtedly be found (e.g., probably lachnine aphids [Normark 2000]; xyelid sawflies [Blank 2002]), elevated diversity of angiosperm feeders seems likely to remain one of the strongest diversification effects known (Coyne and Orr 2004) as the numerous additional contrasts are examined. Ascription of this trend to the much greater taxonomic and chemical diversity of flowering plants, rather than some unique historical circumstance or the global biomass difference between angiosperms and gymnosperms, gains credibility from the great variation in ages and geographic distributions among the contrasted lineage pairs, and the fact that some represent secondary return to gymnosperms (Farrell et al. 2001). It will now be of great interest to determine whether association of enhanced insect diversification with more diverse host groups holds on smaller plant-taxonomic scales as well.

Ehrlich and Raven (1964) speculated that diversification of the angiosperms was promoted by their novel and diverse secondary chemistry, which improved protection from herbivores. Correspondingly greater diversity in angiosperm-feeding insects than in related relict gymnosperm feeders is at least consistent with their hypothesis. Broad-scale escape and radiation coevolution is also lent credence by recent evidence that adaptations to and interaction with insects (and other organisms) have marked influence on plant diversification rates. Plant clades bearing latex or resin canals, one of the most elaborate plant defense syndromes known, were shown to be consistently more diverse than sister groups lacking such canals (Farrell et al. 1991). More recently, several types of innovations in reproductive structures, affecting pollinator fidelity or fruit dispersal, have also been shown to be associated with more rapid plant diversification (Sargent 2004; Bolmgren and Erikkson 2005; reviewed in Coyne and Orr 2004). Thus, mounting evidence supports a central tenet of the new synthesis, implicit in escape and radiation coevolution, namely that adaptations to biotic interactions have major influence on diversification.

While substantial progress has been made in establishing phytophage diversification patterns at the broadest scale, countless questions remain, particularly at shorter evolutionary time scales. There is almost no unambiguous evidence on whether repeated counteradaptations to plant defenses have accelerated insect diversification, as predicted under escape-and-radiation coevolution (but see Farrell et al. [2001] regarding mutualism with ambrosia fungi in bark beetles; parallel examples of fungal mutualism in cecidomyiid gall midges discussed by Bisset and Borkent [1988] and Gagné [1989] await further phylogenetic study). Numerous other causes have been postulated for differential diversification of phytophages, including, among others, species richness, secondary chemical diversity, growth form, and geographic distribution of the host group (e.g., Price 1980; Strong et al. 1984; Lewinsohn et al. 2005); mode of feeding, including plant tissue attacked, internal versus external feeding, and gall-making (and advanced forms thereof) (Ronquist and Liljeblad 2001); trenching and other forms of herbivore "offense" (Karban and Agrawal 2002); degree of food plant specialization; host-shift frequency; and various traits (often host-use-related) rendering phytophages less susceptible to natural enemies (Singer and Stireman 2005). Indeed, just about any trait that might be conserved on phylogenies becomes a plausible candidate. Ideally, one would like to determine the relative importance of and interactions among these factors, and compare them to other types of influence on diversification. In the Lepidoptera, for example, the most pervasive differential influence on diversification may prove to be the repeated evolution of ultrasound detectors allowing adults to avoid bat predation (e.g., Yack and Fullard 2000), rather than any "bottom-up" factor having to do with host plants.

Progress on testing such hypotheses has been quite limited so far, probably for several reasons. First, although phylogenies are accumulating rapidly, the detailed phylogenetic resolution needed to detect correlates of diversification rates is still lacking within most families of phytophagous insects; in some cases, even species diversities are not yet well characterized. Second, we are only beginning to understand the phylogenetic distributions of most candidate traits. Many of these appear to be much more evolutionarily labile than the relatively conserved features reviewed earlier. Rapid trait evolution can frustrate estimation of ancestral states, particularly when life-history information is incomplete, making reliable sister-group comparisons hard to identify. For example, our scan of published studies uncovered essentially no unambiguous contrasts between lineages with broader versus narrower species host ranges, though sister clades often differed in average host range. Moreover, the groups characterized by labile traits, when identifiable, will often be so recent that dissecting deterministic from stochastic influences on diversification would require a large number of comparisons. Sister-group comparisons remain the most robust and straightforward method for detecting traits correlated with diversification rate (Vamosi and Vamosi 2005). But, unless traits that vary mostly at lower taxonomic levels are to be dismissed as unlikely to influence diversification rates, additional approaches will be needed (Ree 2005).

Fortunately, there is now a diverse, rapidly growing literature on diversification rate analysis, a full survey of which is beyond the scope of this chapter. Any of several approaches might prove useful for testing the association of relatively labile traits with diversification rates, depending on the nature of the data. If the chief difficulty is that inferred trait origins do not clearly define sister-group comparisons, one might identify comparisons a priori, then score sister groups simultaneously for diversity and some appropriate measure of frequency of the predictor trait. To select potentially informative comparisons, one might employ one of the various model-based methods proposed for identifying significant shifts in rates of diversification (Sanderson and Donoghue 1994; Magallón and Sanderson 2001; Moore et al. 2004); possible drawbacks include the need for well-resolved phylogenies and high variance of trait frequency estimates in extremely asymmetrical comparisons. For quantitative predictor variables (e.g., average host range) a variant of the independent contrasts method is available (Isaac et al. 2003). When lack of deeper-level phylogeny resolution limits identification of sister groups, one might make independent comparisons among groups of different ages, using estimates of absolute or relative diversification rates (Purvis 1996; Bokma 2003; application in Nyman et al. 2006). For relatively recent radiations, average time between speciation events may be a more sensitive estimator of diversification rate than species numbers per se (Ree 2005). Clock-based temporal analyses of diversification can in principle also detect changes in diversification rate over time (e.g., Nee et al. 1992, 1996; Paradis 1997), allowing test of such refinements of the adaptive zone hypothesis as the postulated slowing of diversification as niches are filled (Simpson 1953; Schluter 2000). Recently, this and other approaches have been used to identify periods of accelerated insect diversification and correlate these with potential causes such as radiation of particular plant clades, or particular biogeographic events (e.g., McKenna and Farrell 2006; Moreau et al. 2006; but see Brady et al. 2006).

While phytophage diversification rate variation at lower levels is a daunting problem, even the analysis of relatively conserved traits remains underdeveloped. To underscore this point, we end with a summary of progress on one much-discussed issue that bears on the puzzle of phytophagous insect diversity, namely, the macroevolutionary consequences of internal versus external feeding. Both habits are widespread, although their frequencies differ markedly across insect phylogeny. Most hemimetabolous insect herbivores, in orders such as Orthoptera, Phasmida, Hemiptera, and Thysanoptera, are free-living external feeders, though some (e.g., thrips) may hide in flowers or other plant structures; the chief exceptions are gall-formers, which have evolved repeatedly in the piercing/sucking lineages. In contrast, larvae of a large fraction of phytophagous Holometabola, including the basal members of nearly all the major lineages, actively bore or mine inside living plants. External phytophagy has arisen infrequently in most holometabolous orders, or not at all (e.g., higher Diptera), while return to endophagy has occurred somewhat more often. Overall, the opposing traits seem sufficiently conserved, yet also sufficiently labile, to permit replicated sister-group comparisons.

Opposing predictions have been made about diversification under these contrasting feeding modes, drawing on broader theories about ecological specialization (reviewed in Wiegmann et al. 1993; Yang and Mitter 1994). Although analyses controlled for phylogeny are needed (Nyman et al. 2006), internal feeders appear to be more host specific than external feeders (e.g., Gaston et al. 1992). Greater specialization, as argued earlier, could promote speciation by increasing the strength of population subdivision and diversifying selection (e.g., Miller and Crespi 2003). Internal feeding could also be viewed as an adaptive zone providing escape from pathogens and some parasites, and desiccation or other physical stresses (Connor and Taverner 1997). Conversely (Powell et al. 1998; Nyman et al. 2006), one could predict that external feeding, by providing release from constraints on body size, voltinism, and leaf excision, might typically increase individual and (thereby) clade fitness. Moreover, by lowering the barriers to colonization of alternative hosts and habitats, exophagy might open more opportunities for speciation.

Sister-group contrasts between internal and external feeders are potentially numerous. For example, there is strong evidence for several to many independent transitions between internal and external larval feeding within Lepidoptera (Powell et al. 1998), Coleoptera-Phytophaga (Marvaldi et al. 2002; Farrell and Sequiera 2004), and basal Hymenoptera (sawflies), and between galling and free-living habits within Aphidoidea (von Dohlen and Moran 2000), Coccoidea (Cook and Gullan 2004), Psylloidea (Burckhardt 2005), and Thysanoptera (Morris et al. 1999). Surprisingly, however, from our literature survey we are able to extract at most eight unambiguous comparisons (Table 18.4). The only phylogenetic analysis study directed specifically at this question is that of Nyman et al. (2006); others are clearly needed.

Disregarding the one tie, five of the seven sister-group comparisons we identified show the external-feeding lineage to be more diverse than its internal-feeding closest relatives. Nyman et al. (2006), in a nonoverlapping set of comparisons within the sawfly subfamily Nematinae (Tenthredinidae), found external feeders to be more diverse in 10 of 13 sister-group contrasts. Taken together, these compilations yield a result just significant by a two-tailed sign test (external feeders more diverse in 15 of 20 pairs,

TABLE 18.4

Sister Group Diversity Comparisons Between Endo- and Exophytophage Lineages

Higher Taxon	*Internally Feeding Clade*	*Diversity*	*Externally Feeding Clade*	*Diversity*	*Sources*
Coleoptera: Chrysomelidae	Bruchinae + Sagriinae	3,300	Chrysomelinae + Criocerinae + others, minus secondary internal feeders	10,000	Farrell and Sequeira 2004
Hymenoptera	Cephidae + Siricidae + Anaxyelidae + Xiphydriidae, with parasitic subclade Vespina excluded	280	Pamphilidae + Megalodontesidae	350	Brown 1989, Heitland 2002, Schulmeister 2003
Hymenoptera	Blasticotomidae	9	Remaining Tenthredinoidea	7,000+	Nyman et al. 2006, Schulmeister 2003
Hymenoptera: Xyelidae	Xyelinae	71	Macroxyelinae	11	Blank 2002, Schulmeister 2003
Lepidoptera	Cossoidea	1,873	Zygaenoidea	2,115	Powell et al. 1998
Lepidoptera	Obtectomera minus Macrolepidoptera (part or all)	<22,0000	Macrolepidoptera	87,000	Powell et al. 1998
Lepidoptera: Heliodinidae	*Lamprolophus* + 9 genera	56	*Epicroesa* + *Philocoristis*	6	Hsu and Powell 2004
Thysanoptera: Phlaeothripidae	*Kladothrips*	22	*Rhopalothripoides* (+ 5 possibly related genera)	22	Crespi et al. 2004, Morris et al. 2002

NOTE: Compilation excludes nematine tenthredinid sawflies, studied by Nyman et al. (2006). See “Table References” for source information.

$P = 0.042$), corroborating the trend in an earlier, more limited compilation by Connor and Taverner (1997).

Although progress is evident, continued study of this question is desirable. The statistical significance of the observed trend is still marginal; several of the comparisons in Table 18.4 are based on provisional phylogenies, and in several the diversity differences are small; it will also be of much interest to separately test the effects of different categories of internal feeding (e.g., gallers versus miners), and of gains versus losses of external feeding. At the least, however, the current evidence appears to firmly reject the hypothesis of consistently faster diversification by internal feeders. The result parallels previous rejection of the hypothesis of higher diversification in animal-parasitic than free-living insects due to their exceptionally specialized lifestyles (Wiegmann et al. 1993). Together, these observations suggest that, even if phytophages are more ecologically specialized in some sense that other insects, specialization per se is an unlikely explanation for their exceptional diversity. Rather, the evidence increasingly points to the importance of the sheer diversity of niches available to insects feeding on plants, particularly flowering plants.

Synopsis and Conclusions

In this chapter we have attempted to compile and synthesize the recent literature (mainly since 1993) treating aspects of the phylogenesis of associated insects and plants. We have focused on phylogenies at the among-species level and higher, mostly for insects, and on their bearing on three general questions posed implicitly by Ehrlich and Raven’s hypothesis of coevolution. These are (1) the degree to which the various traits governing use of host plants are conserved during phylogenesis; (2) the degree to which contemporary associations show evidence, from phylogenies and other sources, of long-continued interactions between particular insect and plant lineages; and (3), the degree to which evolution in traits affecting their interactions affects the diversification rates of interacting insect and plant lineages. Our main conclusions are as follows:

1. Ubiquitous conservation of plant higher taxon use during insect phylogenesis is confirmed and quantified in a compilation of 93 phylogenies of mostly

oligophagous insect groups. The median frequency of shift to a different plant family is estimated to be about 0.03 to 0.08 per speciation event. Important initial insights have been gained on the reasons for this conservatism.

2. There are many hypotheses to explain among-clade variation in the frequency of among-plant-family shift, but few quantitative tests. The strongest evidence to date is for more frequent host shifting in tree feeders than in herb feeders among butterflies, and among oligophages within lineages that contain one or more polyphagous species than in lineages that do not (across 95 insect phylogenies). Recent case studies suggest that reliance on plant-derived compounds for insect defense poses less of a barrier to larval host shift than was formerly thought.
3. In contrast to the prevailing broad-scale host conservatism, shifts to a different host species have accompanied about 50% of 145 phytophage speciation events tabulated, consistent with a substantial but not universal role for host shifts in phytophage speciation. There is a suggestive but not statistically significant tendency for greater host differentiation between sympatric than allopatric species pairs.
4. The as yet limited evidence on phylogenetic patterns of host-plant range provides no support for directionality or other strong constraints but suggests an important distinction between ephemeral, phylogenetically random fluctuation, and larger-scale trends interpretable using experimental approaches combined with phylogenetic "comparative methods."
5. It is now clear that with very few exceptions, the host-use variation within and among phytophagous insect genera, in contrast to that in some vertically transmitted parasites and symbionts, reflects colonization of already-diversified hosts rather than any form of strict parallel phylogenesis. At the same time, however, evidence is increasing that associations established in the distant past, especially the Mesozoic, have left widespread if not numerically dominant marks on contemporary insect-plant assemblages; the full range of such historical "signatures" is only beginning to be explored.
6. Because phylogenetic studies directed specifically at plant defense evolution are still few, we do not yet know whether that evolution is characterized more by sequential coevolutionary "escalations," or by stably coexisting syndromes reflecting optimal adaptations for differing environments.
7. Replicated sister-group comparisons have established elevated diversification rates for phytophagous over nonphytophagous insects and for angiosperm over nonangiosperm feeders among phytophages, both at least consistent with diffuse insect-plant coevolution sensu Ehrlich and Raven (1964). Recent studies on plant diversification rates demonstrate a role for interaction with insects and other animals, likewise consonant with that theory, though most examples do not involve defense. Evidence on most phytophage diversification hypotheses (including "offense" innovations), however, has been slow to accumulate, and diversification studies at finer taxonomic scales, mostly lacking, may face methodological obstacles. A progress report on sister-group comparisons of internal versus external feeders effectively negates the hypothesis of faster radiation by endophages, thought to be more specialized, and strongly suggests the opposite trend.

Given the range of questions mapped out, the tools available, and the cornucopia of phylogenetic studies now ongoing in nearly all major herbivorous insect groups and their host plants, we can look forward to spectacular near-future advances in understanding of the evolution of insect-plant interactions, with increasing integration between phylogenetic and other perspectives.

Author's Note: For online supplementary tables and figures, go to www.chemlife.umd.edu/entm/mitterlab. These include the following:

- Item S1: Database of insect/plan phylogeny studies. FileMaker, Access formats.
- Item S2: Table compiling host-shift frequencies on phylogenies. Excel format.
- Item S3: Figure showing metaphylogeny of taxa included in table S2 for comparative analysis of host-shift frequency versus host range. PDF format.
- Item S4: Table compiling host and distribution differences for speciation events. Excel format.

Acknowledgments

We are grateful to Anurag Agrawal, Brian Farrell, Kathleen Pryer, Stephan Blank, and their coauthors for sharing unpublished material, to the editor and reviewers for helpful comments on the manuscript, and to the National Science Foundation and U.S. Department of Agriculture for financial support.

Table References

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

Becerra, J.X. 2003. Synchronous coadaptation in an ancient case of herbivory. Proc. Natl. Acad. Sci. USA 100: 12804–12807.

Blank, S.M. 2002. Biosystematics of the extant Xyelidae with particular emphasis on the Old World taxa (Insecta: Hymenoptera). Dissertation, Freie Universität Berlin.

Brändle, M., S. Knoll, S. Eber, J. Stadler, and R. Brandl. 2005. Flies on thistles: support for synchronous speciation? Biol. J. Linn. Soc. 84: 775–783.

Brown, W.L. 1989. Hymenoptera, pp. 652–680. In S.P. Parker (ed.), Synopsis and classification of living organisms. McGraw Hill, New York.

Burckhardt, D., and Y. Basset. 2000. The jumping plant-lice (Hemiptera, Psylloidea) associated with *Schinus* (Anacardiaceae): systematics, biogeography and host plant relationships. J. Nat. Hist. 34: 57–155.

Crespi, B.J., and C.P. Sandoval. 2000. Phylogenetic evidence for the evolution of ecological specialization in *Timema* walking-sticks. J. Evol. Biol. 13: 249–262.

Crespi, B.J., D.C. Morris, and L.A. Mound. 2004. Evolution of ecological and behavioral diversity: Australian *Acacia* thrips as model organisms. CSIRO, Canberra, Australia.

Dobler, S., P. Mardulyn, J.M. Pasteels, and M. Rowell-Rahier. 1996. Host-plant switches and the evolution of chemical defense and life history in the leaf beetle genus *Oreina*. Evolution 50: 2373–2386.

Farrell, B.D. 2001. Evolutionary assembly of the milkweed fauna: cytochrome oxidase I and the age of *Tetraopes* beetles. Mol. Phylogenet. Evol. 18: 467–478.

Farrell, B.D., and C. Mitter. 1998. The timing of insect/plant diversification: might *Tetraopes* (Coleoptera: Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved? Biol. J. Linn. Soc. 63: 553–577.

Farrell, B.D., and A.S. Sequeira. 2004. Evolutionary rates in the adaptive radiation of beetles on plants. Evolution 58: 1984–2001.

Fenton, B., A.N.E. Birch, G. Malloch, P.G. Lanham, and R.M. Brennan. 2000. Gall mite molecular phylogeny and its relationship to the evolution of plant host specificity. Exp. Appl. Acarol. 24: 831–861.

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

Heitland, W. 2002. U. Ord. Symphyta. Pflanzenwespen, sawflies. www.faunistik.net/DETINVERT/HYMENOPTERA/symphyta.html.

Hsu, Y.-F., and J.A. Powell. 2004. Phylogenetic relationships within Heliodinidae and systematics of moths formerly assigned to *Heliodines* Stanton. University of California Publications in Entomology, Vol. 24.

Janz, N., K. Nyblom, and S. Nylin. 2001. Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. Evolution 55: 783–796.

Jones, R.W. 2001. Evolution of the host plant associations of the *Anthonomus grandis* species group (Coleoptera: Curculionidae): phylogenetic tests of various hypotheses. Ann. Entomol. Soc. Am. 94: 51–58.

Kawakita, A., A. Takimura, T. Terachi, T. Sota, and M. Kato. 2004. Cospeciation analysis of an obligate pollination mutualism: have *Glochidion* trees (Euphorbiaceae) and pollinating *Epicephala* moths (Gracillariidae) diversified in parallel? Evolution 58: 2201–2214.

Kelley, S.T., and B.D. Farrell. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). Evolution 52: 1731–1743.

Lopez-Vaamonde, C., H.C.J. Godfray, and J.M. Cook. 2003. Evolutionary dynamics of host-plant use in a genus of leaf-mining moths. Evolution 57: 1804–1821.

Lopez-Vaamonde, C., N. Wikström, C. Labandeira, H.C.J. Godfray, S.J. Goodman, and J.M. Cook. 2006. Fossil-calibrated molecular phylogenies reveal that leaf-mining moths radiated millions of years after their host plants. J. Evol. Biol. 19: 1314–1326.

Machado, C.A., N. Robbins, M.T.P. Gilbert, and E.A. Herre. 2005. Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. Proc. Natl. Acad. Sci. USA 102: 6558–6565.

Moran, N.A., M.E. Kaplan, M.J. Gelsey, T.G. Murphy, and E.A. Scholes. 1999. Phylogenetics and evolution of the aphid genus *Uroleucon* based on mitochondrial and nuclear DNA sequences. Syst. Entomol. 24: 85–93.

Morris, D.C., M.P. Schwarz, S.J.B. Cooper, and L.A. Mound. 2002. Phylogenetics of Australian *Acacia* thrips: the evolution of behaviour and ecology. Mol. Phylogenet. Evol. 25: 278–292.

Morse, G.E., and B.D. Farrell. 2005. Ecological and evolutionary diversification of the seed beetle genus *Stator* (Coleoptera: Chrysomelidae: Bruchinae). Evolution 59: 1315–1333.

Nyman, T., A. Widmer, and H. Roininen. 2000. Evolution of gall morphology and host-plant relationships in willow-feeding sawflies (Hymenoptera: Tenthredinidae). Evolution 54: 526–533.

Nyman, T., B.D. Farrell, A.G. Zinovjev, and V. Vikberg. 2006. Larval habits, host-plant associations, and speciation in nematine sawflies (Hymenoptera: Tenthredinidae). Evolution 60: 1622–1637.

Percy, D.M., R.D.M. Page, and Q.C.B. Cronk. 2004. Plant-insect interactions: double-dating associated insect and plant lineages reveals asynchronous radiations. Syst. Biol. 53: 120–127.

Powell, J.A., C.M. Mitter, and B. Farrell. 1998. Evolution of larval feeding habits in Lepidoptera, pp. 403–422. In N.P. Kristensen (ed.), Handbook of zoology, Lepidoptera. Vol. 1: Systematics and evolution. W. de Gruyter, Berlin.

Roderick, G.K. 1997. Herbivorous insects and the Hawaiian silversword alliance: co-evolution or co-speciation? Pacific Sci. 51: 440–449.

Roininen, H., T. Nyman, and A. Zinovjev. 2005. Biology, ecology, and evolution of gall-inducing sawflies (Hymenoptera: Tenthredinidae and Xyelidae), pp. 467–494. In A. Raman, C.W. Schaefer, and T.M. Withers (eds.), Biology, ecology, and evolution of gall-inducing arthropods. Science Publishers, Enfield, NH.

Ronquist, F., and J. Liljeblad. 2001. Evolution of the gall wasp-host plant association. Evolution 55: 2503–2522.

Rønsted, N., G.D. Weiblen, J.M. Cook, N. Salamin, C.A. Machado, and V. Savolainen. 2005. 60 million years of co-divergence in the fig-wasp symbiosis. Proc. R. Soc. Lond. B 272: 2593–2599.

Rubinoff, D., and F.A.H. Sperling. 2002. Evolution of ecological traits and wing morphology in *Hemileuca* (Saturniidae) based on a two-gene phylogeny. Mol. Phylogenet. Evol. 25: 70–86.

Schulmeister, S. 2003. Simultaneous analysis of basal Hymenoptera (Insecta): introducing robust-choice sensitivity analysis. Biol. J. Linn Soc. 79: 245–275.

Wahlberg, N. 2001. The phylogenetics and biochemistry of host-plant specialization in melitaeine butterflies (Lepidoptera: Nymphalidae). Evolution 55: 522–537.

Weiblen, G.D., and G.L. Bush. 2002. Speciation in fig pollinators and parasites. Mol. Ecol. 11: 1573–1578.

Weingartner, E., N. Wahlberg, and S. Nylin. 2006. Dynamics of host plant use and species diversity: a phylogenetic investigation in *Polygonia* butterflies (Nymphalidae). J. Evol. Biol. 19: 483–491.

Weintraub, J.D., J.H. Lawton, and M.J. Scoble. 1995. Lithinine moths on ferns: a phylogenetic study of insect-plant interactions. Biol. J. Linn. Soc. 55: 239–250.

Wilson, S., C. Mitter, R.F. Denno, and M.R. Wilson. 1994. Evolutionary patterns of host plant use by delphacid planthoppers and their relatives, pp. 7–113. In R. F. Denno and J. Prefect (eds.), The ecology and management of planthoppers. Chapman and Hall, New York.

Yotoko, K.S.C., P.I. Prado, C.A.M. Russo, and V.N. Solferini. 2005. Testing the trend towards specialization in herbivore-host plant associations using a molecular phylogeny of *Tomoplagia* (Diptera: Tephritidae). Mol. Phylogenet. Evol. 35: 701–711.

References Cited

Agrawal, A.A., and M. Fishbein. 2006. Plant defense syndromes. Ecology 87: S132–S149.

APGII. 2003. An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Allmon, W.D. 1992. A causal analysis of stages in allopatric speciation, pp. 219–257. In D. Futuyma and J. Antonovics (eds.), Oxford surveys in evolutionary biology, vol. 8. Oxford University Press, Oxford.

Armbruster, W.S. 1997. Exaptations link the evolution of plant-herbivore and plant-pollinator interactions: a phylogenetic inquiry. Ecology 78: 1661–1674.

Avise, J.C. 2000. Phylogeography: the history and formation of species. Harvard University Press, Cambridge, MA.

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

Beccaloni, G.W., and F.B. Symons. 2000. Variation of butterfly diet breadth in relation to host-plant predictability: results from two faunas. Oikos 90: 50–66.

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

Becerra, J.X. 2003. Synchronous coadaptation in an ancient case of herbivory. Proc. Natl. Acad. Sci. USA 100: 12804–12807.

Behrensmeyer, A.K., J.D. Damuth, W.A. DiMichele, R. Potts, H.D. Sues, and S.L. Wing (eds.). 1992. Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago.

Benson, W.W., K.S. Brown, and L.E. Gilbert. 1975. Coevolution of plants and herbivores: passion flower butterflies. Evolution 29: 659–680.

Berenbaum, M.R. 1983. Coumarins and caterpillars: a case for coevolution. Evolution 37: 163-179.

Berenbaum, M.R. 2001. Chemical mediation of coevolution: phylogenetic evidence for Apiaceae and associates. Ann. Missouri Bot. Gard. 88: 45–59.

Berenbaum, M.R., and S. Passoa. 1999. Generic phylogeny of North American Depressariinae (Lepidoptera: Elachistidae) and hypotheses about coevolution. Ann. Entomol. Soc. Am. 92: 971–986.

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

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

Bernays, E.A., and R.F. Chapman. 1994. Host-plant selection by phytophagous insects. Chapman and Hill, New York.

Bernays, E.A., and M.S. Singer. 2005. Insect defences: taste alteration and endoparasites. Nature 436: 476.

Bisset, J., and A. Borkent. 1988. Ambrosia galls: the significance of fungal nutrition in the evolution of the Cecidomyiidae (Diptera), pp. 203–225. In K.A. Pirozynski and D.L. Hawksworth (eds.), Coevolution of fungi with plants and animals. Academic Press, London.

Blank, S.M. 2002. Biosystematics of the extant Xyelidae with particular emphasis on the Old World taxa (Insecta: Hymenoptera). Dissertation, Freie Universität Berlin.

Blomberg, S.P., and T. Garland. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. J. Evol. Biol. 15: 899–910.

Bokma, F. 2003. Testing for equal rates of cladogenesis in diverse taxa. Evolution 57: 2469–2474.

Bolmgren, K., and O. Eriksson. 2005. Fleshy fruits: origins, niche shifts, and diversification. Oikos 109: 255–272.

Brady, S. G., T. R. Schultz, B. L. Fisher, and P. S. Ward. 2006. Evaluating alternative hypothesis for the early evolution and diversification of ants. Proc. Nat'l. Acad. Sci. U.S.A. 103: 18172–18177.

Bucheli, S., J.F. Landry, and J. Wenzel. 2002. Larval case architecture and implications of host-plant associations for North American *Coleophora* (Lepidoptera; Coleophoridae). Cladistics 18: 71–93.

Burckhardt, D. 2005. Biology, ecology, and evolution of gall-inducing psyllids (Hemiptera: Psylloidea), pp. 144–157. In A. Raman, C. W. Schaefer, and T.M. Withers (eds.), Biology, ecology, and evolution of gall-inducing arthropods. Science Publishers, Enfield, NH.

Cattin, M.F., L.F. Bersier, C. Banašek-Richter, R. Baltensperger, and J. P. Gabriel. 2004. Phylogenetic constraints and adaptation explain food-web structure. Nature 427: 835–839.

Chesser, P.T., and R.M. Zink. 1994. Modes of speciation in birds: a test of Lynch's method. Evolution 48: 490–497.

Cho, S. 1997. Molecular phylogenetics of the Heliothinae (Lepidoptera: Noctuidae) based on the nuclear genes for elongation factor-1α and dopa decarboxylase. Ph.D. dissertation, University of Maryland, College Park.

Condon, M.A., and G.J. Steck. 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.

Connor, E.F., and M.P. Taverner. 1997. The evolution and adaptive significance of the leaf-mining habit. Oikos 79: 6–25.

Cook, L.G., and P.J. Gullan. 2004. The gall-inducing habit has evolved multiple times among the eriococcid scale insects (Sternorrhyncha: Coccoidea: Eriococcidae). Biol. J. Linn. Soc. 83: 441–452.

Cook, J.M., A. Rokas, M. Pagel, and G.N. Stone. 2002. Evolutionary shifts between host oak sections and host-plant organs in *Andricus* gallwasps. Evolution 56: 1821–1830.

Coyne, J.A., and H.A. Orr. 2004. Speciation. Sinauer, Sunderland, MA.

Crespi, B.J., and C.P. Sandoval. 2000. Phylogenetic evidence for the evolution of ecological specialization in *Timema* walking-sticks. J. Evol. Biol. 13: 249–262.

Davis, C.C., C.D. Bell, S. Mathews, and M.J. Donoghue. 2002. Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. Proc. Natl. Acad. Sci. USA 99: 6833–6837.

Denno, R.F., M.S. McClure, and J.R. Ott. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. Annu. Rev. Entomol. 40: 297–331.

Dethier, V. 1941. Chemical factors determining the choice of food plants by *Papilio* larvae. Am. Nat. 75: 61–73.

Dietrich, C.H. 1999. The role of grasslands in the diversification of leafhoppers (Homoptera: Cicadellidae): a phylogenetic perspective, pp. 44–49. In C. Warwick (ed.), Proceedings of the 15th North American Prairie Conference. Natural Areas Association, Bend, OR.

DiMichele, W.A., A.K. Behrensmeyer, T.D. Olszewski, C.C. Labandeira, J.M. Pandolfi, S.L. Wing, and R. Bobe. 2004. Long-term stasis in ecological assemblages: evidence from the fossil record. Annu. Rev. Ecol. Syst. 35: 285–322.

Dobler, S. 2001. Evolutionary aspects of defense by recycled plant compounds in herbivorous insects. Basic Appl. Ecol. 2: 15–26.

Dobler, S., P. Mardulyn, J.M. Pasteels, and M. Rowell-Rahier. 1996. Host-plant switches and the evolution of chemical defense and life history in the leaf beetle genus *Oreina*. Evolution 50: 2373–2386.

Dorchin, N., A. Freidberg, and O. Mokady. 2004. Phylogeny of the Baldratiina (Diptera: Cecidomyiidae) inferred from morphological, ecological and molecular data sources, and evolutionary patterns in plant-galler relationships. Mol. Phylogenet. Evol. 30: 503–515.

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

Fagan, W.F., E. Siemann, C. Mitter, R.F. Denno, A.F. Huberty, H.A. Woods, and J.J. Elser. 2002. Nitrogen in insects: implications for trophic complexity and species diversification. Am. Nat. 160: 784–802.

Faith, D.P., and P.S. Cranston. 1991. Could a cladogram this short have arisen by chance alone? On permutation tests for cladistic structure. Cladistics 7: 1–28.

Fang, Q.Q., S. Cho, J.C. Regier, C. Mitter, M. Matthews, R.W. Poole, T.P. Friedlander, and S.W. Zhao. 1997. A new nuclear gene for insect phylogenetics: dopa decarboxylase is informative of relationships within Heliothinae (Lepidoptera: Noctuidae). Syst. Biol. 46: 269–283.

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

Farrell, B.D. 2001. Evolutionary assembly of the milkweed fauna: cytochrome oxidase I and the age of *Tetraopes* beetles. Mol. Phylogenet. Evol. 18: 467–478.

Farrell, B., and C. Mitter. 1990. Phylogenesis of insect-plant interactions: have *Phyllobrotica* leaf beetles and Lamiales diversified in parallel? Evolution 44: 1389–1403

Farrell, B.D., and C. Mitter. 1993. Phylogenetic determinants of insect/plant community diversity, pp. 253–266. In R. E. Ricklefs and D. Schluter (eds.), Species diversity: historical and geographical perspectives. University of Chicago Press, Chicago.

Farrell, B.D., and C. Mitter. 1998. The timing of insect/plant diversification: might *Tetraopes* (Coleoptera : Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved? Biol. J. Linn. Soc. 63: 553–577.

Farrell, B.D., and A.S. Sequeira. 2004. Evolutionary rates in the adaptive radiation of beetles on plants. Evolution 58: 1984–2001.

Farrell, B.D., D. Dussourd, and C. Mitter. 1991. Escalation of plant defense: Do latex/resin canals spur plant diversification? Am. Nat. 138: 881–900

Farrell B.D., A.S. Sequeira, B.C. O'Meara, B.B. Normark, J.H. Chung, and B. H. Jordal. 2001. The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). Evolution 55: 2011–2027.

Favret, C., and D.J. Voegtlin. 2004. Speciation by host-switching in pinyon *Cinara* (Insecta: Hemiptera: Aphididae). Mol. Phylogenet. Evol. 32: 139–151.

Feeny, P. 1991. Chemical constraints on the evolution of swallowtail butterflies, pp. 315–339. In P.W. Price, T.M. Lewinsohn, G.W. Fernandes, and W.W. Benson (eds.), Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons, New York.

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

Fitzpatrick, B.M., and M. Turelli. 2006. The geography of mammalian speciation: mixed signals from phylogenies and range maps. Evolution 66: 601–615.

Funk, D.J., K.E. Filchack, and J. L. Feder. 2002. Herbivorous insects: model systems for the comparative study of speciation ecology. Genetica 116: 251–267.

Futuyma, D.J. 1989. Macroevolutionary consequences of speciation, pp. 557–578. In D. Otte and J. A. Endler (eds.), Speciation and its consequences. Sinauer, Sunderland, MA.

Futuyma, D.J., and G. Moreno. 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Syst. 12: 207–233.

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

Gagné, R.J. 1989. The plant-feeding gall midges of North America. Cornell University Press, Ithaca, NY.

Gassman, A.J., A. Levy, T. Tran, and D.J. Futuyma. 2006. Adaptations of an insect to a novel host plant: a phylogenetic approach. Funct. Ecol. 20: 478–485.

Gaston, K.J., D. Reavey, and G.R. Valladares. 1992. Intimacy and fidelity: internal and external feeding by the British microlepidoptera. Ecol. Entomol. 17: 86–88.

Gillespie, J.J., K.M. Kjer, C.N. Duckett, and D.W. Tallamy. 2003. Convergent evolution of cucurbitacin feeding in spatially isolated rootworm taxa (Coleoptera: Chrysomelidae; Galerucinae, Luperini). Mol. Phylogenet. Evol. 29: 161–175.

Gillespie, J.J., K.M. Kjer, E.G. Riley, and D.W. Tallamy. 2004. The evolution of cucurbitacin pharmacophagy in rootworms: insight from Luperini paraphyly, pp. 37–57. In P. Jolivet, J. A. Santiago-Blay, and M. Schmitt (eds.), New developments in the biology of Chrysomelidae. SPB Academic Publishing, The Hague, The Netherlands.

Graham, A. 1999. Late cretaceous and cenozoic history of North American vegetation north of Mexico. Oxford University Press, Oxford.

Grimaldi, D., and M.S. Engel. 2005. Evolution of the insects. Cambridge University Press, Cambridge, MA.

Hansen, T.F., and S.H. Orzack. 2005. Assessing current adaptation and phylogenetic inertia as explanations of trait evolution: the need for controlled comparisons. Evolution 59: 2063–2072.

Harry, M., M. Solignac, and D. Lachaise. 1998. Molecular evidence for parallel evolution of adaptive syndromes in fig-breeding *Lissocephala* (Drosophilidae). Mol. Phylogenet. Evol. 9: 542–551.

Heie, O.E. 1996. The evolutionary history of aphids and a hypothesis on the coevolution of aphids and plants. Boll. Zool. Agr. Bachic. 28: 149–155.

Holloway, J.D., and E.S. Nielsen. 1998. Biogeography of the Lepidoptera, pp. 423–461. In N. P. Kristensen (ed.), Handbook of zoology, Lepidoptera. vol. 1: Systematics and evolution. W. de Gruyter, Berlin.

Hsiao, T.H., and J.M. Pasteels. 1999. Evolution of host-plant affiliation and chemical defense in *Chrysolina-Oreina* leaf beetles as revealed by mtDNA phylogenies, pp. 321–342. In M. L. Cox (ed.), Advances in Chrysomelidae biology. Backhuys, Leiden, The Netherlands.

Hsiao, T.H., and D.M. Windsor. 1999. Historical and biological relationships among Hispinae inferred from 12S mtDNA sequence data, pp. 39–50. In M.L. Cox (ed.), Advances in Chrysomelidae biology. Backhuys, Leiden, The Netherlands.

Isaac, N. J. B., P. M. Agapow, P. H. Harvey, and A. Purvis. 2003. Phylogenetically nested comparisons for testing correlates of species richness: a simulation study of continuous variables. Evolution 57: 18–26.

Janz, N., and S. Nylin. 1998. Butterflies and plants: a phylogenetic study. Evolution 52: 486–502.

Janz, N., K. Nyblom, and S. Nylin. 2001. Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. Evolution 55: 783–796.

Janz, N., S. Nylin, and N. Wahlberg. 2006. Diversity begets diversity: host expansions and the diversification of plant-feeding insects. BMC Evol. Biol. 6: 4.

Jervis, M. A., C. L. Boggs, and P. N. Ferns. 2005. Egg maturation strategy and its associated trade-offs: a synthesis focusing on Lepidoptera. Ecol. Entomol. 30: 359–375.

Joy, J. B., and B. J. Crespi. 2007. Adaptive radiation of gall-inducing insects within a single host-plant species. Evolution 61: 784–795.

Karban, R., and A. A. Agrawal. 2002. Herbivore offense. Annu. Rev. Ecol. Syst. 33: 641–664.

Kawakita, A, and M. Kato. 2006. Assessment of the diversity and species specificity of the mutualistic association between *Epicephala* moths and *Glochidion* trees. Mol. Ecol. 15: 2567–2581.

Kawakita, A., A. Takimura, T. Terachi, T. Sota, and M. Kato. 2004. Cospeciation analysis of an obligate pollination mutualism: have *Glochidion* trees (Euphorbiaceae) and pollinating *Epicephala* moths (Gracillariidae) diversified in parallel? Evolution 58: 2201–2214.

Kergoat, G. J., A. Delobel, G. Fédière, B. Le Rü, and J.-F. Silvain. 2005. Both host-plant phylogeny and chemistry have shaped the African seed-beetle radiation. Mol. Phylogenet. Evol. 35: 602–611.

Kristensen, N. P. 1984. Studies on the morphology and systematics of primitive Lepidoptera (Insecta). Steenstrupia 10: 141–191.

Kristensen, N. P. 1997. Early evolution of the Lepidoptera + Trichoptera lineage: phylogeny and the ecological scenario. Mem. Mus. Natl. Hist. Nat. 173: 253–271.

Kuhn, J., E. M. Pettersson, B. K. Feld, A. Burse, A. Termonia, J. M. Pasteels, and W. Boland. 2004. Selective transport systems mediate sequestration of plant glucosides in leaf beetles: a molecular basis for adaptation and evolution. Proc. Natl. Acad. Sci. USA 101: 13808–13813.

Labandeira, C. C., 2002. The history of associations between plants and animals, pp. 26–74. In C. Herrera and O. Pellmyr (eds.), Plant-animal interactions: an evolutionary approach. Blackwell Science, Oxford.

Lewinsohn, T. M., V. Novotny, and Y. Basset. 2005. Insects on plants: diversity of herbivore assemblages revisited. Annu. Rev. Ecol. Evol. Syst. 36: 597–620.

Lopez-Vaamonde, C., H. C. J. Godfray, and J. M. Cook. 2003. Evolutionary dynamics of host-plant use in a genus of leaf-mining moths. Evolution 57: 1804–1821.

Losos, J. B., and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. Trends Ecol. Evol. 18: 220–227.

Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation, pp. 527–553. In D. Otte and J. A. Endler (eds.), Speciation and its consequences. Sinauer, Sunderland, MA.

Machado, C. A., N. Robbins, M. T. P. Gilbert, and E. A. Herre. 2005. Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. Proc. Natl. Acad. Sci. USA 102: 6558–6565.

Mackenzie, A., and A. F. G. Dixon. 1990. Host alternation in aphids: constraint versus optimization. Am. Nat. 136: 132–134.

Magallón, S. 2004. Dating lineages: molecular and paleontological approaches to the temporal framework of clades. Int. J. Plant. Sci. 165: S7-S21.

Magallón, S., and M. J. Sanderson. 2001. Absolute diversification rates in angiosperm clades. Evolution 55: 1762–1780.

Marvaldi, A. E., A. S. Sequeira, C. W. O'Brien, and B. D. Farrell. 2002. Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): do niche shifts accompany diversification? Syst. Biol. 51: 761–785.

Mayhew, P. J. 2002. Shifts in hexapod diversification and what Haldane could have said. Proc. R. Soc. Lond. B 269: 969–974.

McKenna D. D., and B. D. Farrell. 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. Proc. Natl. Acad. Sci. USA 103: 10947–10951.

Miller, D. G., and B. Crespi. 2003. The evolution of inquilinism, host-plant use and mitochondrial substitution rates in *Tamalia* gall aphids. J . Evol. Biol. 16: 731–743.

Miller, J. S. 1987. Host-plant relationships in the Papilionidae (Lepidoptera): parallel cladogenesis or colonization? Cladistics 3: 105–120.

Mitchell, A., C. Mitter, and J. C. Regier. 2006. Systematics and evolution of the cutworm moths (Lepidoptera: Noctuidae): evidence from two protein-coding nuclear genes. Syst. Entomol. 31: 21–46.

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

Mitter, C., and B. Farrell. 1991. Macroevolutionary aspects of insect-plant relationships, pp. 35–78. In E. A. Bernays (ed.), Insect/plant interactions, vol. 3. CRC Press, Boca Raton, FL.

Mitter, C., B. Farrell, and B. Wiegmann.1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? Am. Nat. 132: 107–128.

Mitter, C., R. W. Poole, and M. Matthews. 1993. Biosystematics of the Heliothinae (Lepidoptera: Noctuidae). Annu. Rev. Entomol. 38: 207–225.

Moore, B. R., K. M. A. Chan, and M. J. Donoghue. 2004. Detecting diversification rate variation in supertrees, pp. 487–533. In O. R. P. Bininda-Emonds (ed.), Phylogenetic supertrees: combining information to reveal the tree of life. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Moran, N. A. 1988. The evolution of host plant alternation in aphids: evidence for specialization as a dead end. Am. Nat. 132: 681–706.

Moran, N. A. 1990. Aphid life cycls: two evolutionary steps. Am. Nat. 136: 135–138.

Moran, N. A. 1992. The evolution of aphid life cycles. Annu. Rev. Entomol. 37: 321–348.

Moreau, C. S., C. D. Bell, R. Vila, S. B. Archibald, and N. E. Pierce. 2006. Phylogeny of the ants: diversification in the age of angiosperms. Science 312: 101–104.

Morris, D. C., L. A. Mound, M. P. Schwarz, and B. J. Crespi. 1999. Morphological phylogenetics of Australian gall-inducing thrips and their allies: the evolution of host-plant affiliations, domicile use and social behaviour. Syst. Entomol. 24: 289–299.

Morse, G. E., and B. D. Farrell. 2005. Ecological and evolutionary diversification of the seed beetle genus *Stator* (Coleoptera: Chrysomelidae: Bruchinae). Evolution 59: 1315–1333.

Murphy, S. M. 2004. Enemy-free space maintains swallowtail butterfly host shift. Proc. Natl. Acad. Sci. USA 101: 18048–18052.

Nee, S., A. O. Mooers, and P. H. Harvey, 1992. Tempo and mode of evolution revealed from molecular phylogenies. Proc. Natl. Acad. Sci. USA 89: 8322–8326.

Nee, S., T. G. Barraclough, and P. H. Harvey. 1996. Temporal changes in biodiversity: detecting patterns and identifying causes, pp. 230–252. In K. J. Gaston (ed.), Biodiversity: a biology of numbers and difference. Blackwell Scientific, Oxford.

Nickel, H. 2003. The leafhoppers and planthoppers of Germany (Hemiptera, Auchenorrhyncha): patterns and strategies in a highly diverse group of phytophagous insects. Pensoft Series Faunistica No. 28. Pensoft Publishers, Sofia, Bulgaria.

Normark, B. B. 2000. Molecular systematics and evolution of the aphid family Lachnidae. Mol. Phylogenet. Evol. 14: 131–140.

Nosil, P. 2002. Transition rates between specialization and generalization in phytophagous insects. Evolution 56: 1701–1706.

Nosil, P., and A. O. Mooers. 2005. Testing hypotheses about ecological specialization using phylogenetic trees. Evolution 59: 2256–2263.

Nosil, P., B. J. Crespi, and C. P. Sandoval. 2003. Reproductive isolation driven by the combined effects of ecological adaptation and reinforcement. Proc. R. Soc. Lond. B 270: 1911–1918.

Nylander, J. A. A. 2004. Bayesian phylogenetics and the evolution of gall wasps. Ph.D. dissertation, University of Uppsala, Uppsala, Sweden.

Nylander, J., F. Ronquist, J. P. Huelsenbeck, and J. L. Nieves-Aldrey. 2004. Bayesian phylogenetic analysis of combined data. Syst. Biol. 53: 47–67.

Nyman, T., A. Widmer, and H. Roinnen. 2000. Evolution of gall morphology and host-plant relationships in willow-feeding sawflies (Hymenoptera: Tenthredinidae). Evolution 54: 526–533.

Nyman, T., B. D. Farrell, A. G. Zinovjev, and V. Vikberg. 2006. Larval habits, host-plant associations, and speciation in nematine sawflies (Hymenoptera: Tenthredinidae). Evolution 60: 1622–1637.

Ortiz-Rivas, B., A. Moya, and D. Martínez-Torres. 2004. Molecular systematics of aphids (Homoptera: Aphididae): new insights from the long-wavelength opsin gene. Mol. Phylogenet. Evol. 30: 24–37.

Page, R. D. M. (ed.). 2003. Tangled trees: phylogeny, cospeciation and coevolution. University of Chicago Press, Chicago.

Paradis, E. 1997. Assessing temporal variations in diversification rates from phylogenies: estimation and hypothesis testing. Proc. R. Soc. Lond. B 264: 1141–1147.

Pellmyr, O. 2003. Yuccas, yucca moths and coevolution: a review. Ann. Missouri Bot. Gard. 90: 35–55.

Percy, D. M. 2003. Radiation, diversity, and host-plant interactions among island and continental legume-feeding psyllids. Evolution 57: 2540–2556.

Percy, D. M., R. D. M. Page, Q. C. B. Cronk. 2004. Plant-insect interactions: double-dating associated insect and plant lineages reveals asynchronous radiations. Syst. Biol. 53: 120–127.

Plantard, O., J. D. Shorthouse, and J. Y. Rasplus. 1997. Molecular phylogeny of the genus *Diplolepis* (Hymenoptera: Cynipidae), pp. 247–260. In G. Csoka, W. J. Mattson, G. N. Stone, and P. W. Price (eds.), Biology of gall inducing arthropods. Gen. Tech. Rep. NC-199. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN.

Powell, J. A. 1980. Evolution of larval food preferences in microlepidoptera. Annu. Rev. Entomol. 25: 133–159.

Powell, J. A., C. Mitter, and B. Farrell. 1998. Evolution of larval feeding habits in Lepidoptera, pp. 403–422. In N. P. Kristensen (ed.), Handbook of zoology, Lepidoptera. Vol. 1: Systematics and evolution. W. de Gruyter, Berlin.

Pratt, G. F. 1994. Evolution of *Euphilotes* (Lepidoptera: Lycaenidae) by seasonal and host shifts. Biol. J. Linn. Soc. 51: 387–416.

Price, P. W. 1980. Evolutionary biology of parasites. Monographs in population biology, vol. 15. Princeton University Press, Princeton, NJ.

Purvis, A. 1996. Using interspecies phylogenies to test macroevolutionary hypotheses, pp. 153–168. In P. H. Harvey, A. J. L. Brown, J. M. Smith, and S. Nee (eds.), New uses for new phylogenies. Oxford University Press, Oxford.

Ree, R. H. 2005. Detecting the historical signature of key innovations using stochastic models of character evolution and cladogenesis. Evolution 59: 257–265.

Rodman, J. E., P. S. Soltis, D. E. Soltis, K. J. Sytsma, and K. G. Karol. 1998. Parallel evolution of glucosinolate biosynthesis inferred from congruent nuclear and plastid gene phylogenies. Am. J. Bot. 85: 997–1006.

Ronquist, F., and J. Liljeblad. 2001. Evolution of the gall wasp-host plant association. Evolution 55: 2503–2522.

Rudgers, J. A., S. Y. Strauss, and J. F. Wendel. 2004. Trade-offs among anti-herbivore resistance traits: insights from Gossypieae (Malvaceae). Am. J. Bot. 91: 871–880.

Rundle, H. D., and P. Nosil. 2005. Ecological speciation. Ecol. Lett. 8: 336–352.

Sachet, J. M., A. Roques, and L. Després. 2006. Linking patterns and processes of species diversification in the cone flies *Strobilomyia* (Diptera: Anthomyiidae). Mol. Phylogenet. Evol. 41: 606–621.

Sanderson, M. J., and M. J. Donoghue. 1994. Shifts in diversification rate with the origin of angiosperms. Science 264: 1590–1593.

Sargent, R. D. 2004. Floral symmetry affects speciation rates in angiosperms. Proc. R. Soc. Lond. B 271: 603–608.

Schick, K., Z. W. Liu, and P. Goldstein. 2003. Phylogeny, historical biogeography, and macroevolution of host use among *Diastrophus* gall wasps (Hymenoptera: Cynipidae). Proc. Entomol. Soc. Wash. 105: 715–732.

Schluter, D. 1987. Character displacement and the adaptive divergence of finches on islands and continents. Am. Nat. 131: 799–824.

Schluter, D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. Am. Nat. 131: 799–824.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.

Schulmeister, S. 2003. Simultaneous analysis of basal Hymenoptera (Insecta): introducing robust-choice sensitivity analysis. Biol. J. Linn. Soc. 79: 245–275.

Simpson, G. G. 1953. The major features of evolution. Columbia University Press, New York.

Singer, M. S., and J. O. Stireman. 2005. The tri-trophic niche concept and adaptive radiation of phytophagous insects. Ecol. Lett. 8: 1247–1255.

Singer, M. S., Y. Carriere, C. Theuring, and T. Hartmann. 2004. Disentangling food quality from resistance against parasitoids: diet choice by a generalist caterpillar. Am. Nat. 164: 423–429.

Smith, A. R., K. M. Pryer, E. Schuettpelz, P. Korall, H. Schneider, and P. G. Wolf. 2006. A classification for extant ferns. Taxon 55: 705–731.

Spencer, K. A. 1990. Host specialization in the world Agromyzidae (Diptera). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Stireman, J. O. 2005. The evolution of generalization? Parasitoid flies and the perils of inferring host range evolution from phylogenies. J. Evol. Biol. 18: 325–336.

Strong, D. R., J. H. Lawton, and R. Southwood. 1984. Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge, MA.

Swigoňová, Z., and K. M. Kjer. 2004. Phylogeny and host-plant association in the leaf beetle genus *Trirhabda* LeConte (Coleoptera: Chrysomelidae). Mol. Phylogenet. Evol. 32: 358–374.

Symons, F. B., and G. W. Beccaloni. 1999. Phylogenetic indices for measuring the diet breadths of phytophagous insects. Oecologia 1119: 427–434.

Termonia, A., T. H. Hsiao, J. M. Pasteels, and M. C. Milinkovitch. 2001. Feeding specialization and host-derived chemical defense in chrysomeline leaf beetles did not lead to an evolutionary dead end. Proc. Natl. Acad. Sci. USA 98: 3909–3914.

Termonia, A., J. M. Pasteels, D. M. Windsor, and M. C. Milinkovitch. 2002. Dual chemical sequestration: a key mechanism in transitions among ecological specialization. Proc. R. Soc. Lond. B 269: 1–6.

Thompson, J. N. 1988. Coevolution and alternative hypotheses on insect plant interactions. Ecology 69: 893–895.

Vamosi, S. M., and J. C. Vamosi. 2005. Endless tests: guidelines for analyzing non-nested sister-group comparisons. Evol. Ecol. Res. 7: 567–579.

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

von Dohlen, C. D., and N. A. Moran. 2000. Molecular data support a rapid radiation of aphids in the Cretaceous and multiple origins of host alternation. Biol. J. Linn. Soc. 71: 689–717.

von Dohlen, C. D., U. Kurosu, and S. Aoki. 2002. Phylogenetics and evolution of the eastern Asian–eastern North American disjunct aphid tribe, Hormaphidini (Hemiptera: Aphididae). Mol. Phylogenet. Evol. 23: 257–267.

von Dohlen, C. D., C. A. Rowe, and O. E. Heie. 2006. A test of morphological hypotheses for tribal and subtribal relationships of Aphidinae (Insecta: Hemiptera: Aphididae) using DNA sequences. Mol. Phylogenet. Evol. 38: 316–329.

Wahlberg, N. 2001. The phylogenetics and biochemistry of host-plant specialization in Melitaeine butterflies (Lepidoptera: Nymphalidae). Evolution 55: 522–537.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Syst. 33: 475–505.

Weiblen, G. D., and G. L. Bush. 2002. Speciation in fig pollinators and parasites. Mol. Ecol. 11: 1573–1578.

Weingartner, E., N. Wahlberg, and S. Nylin. 2006. Dynamics of host plant use and species diversity in *Polygonia* butterflies (Nymphalidae). J. Evol. Biol. 19: 483–491.

Welch, J. J., and L. Bromham. 2005. Molecular dating when rates vary. Trends Ecol. Evol. 20: 320–327.

Weller, S. J., N. L. Jacobson, and W. E. Connor. 1999. The evolution of chemical defenses and mating systems in tiger moths (Lepidoptera: Arctiidae). Biol. J. Linn. Soc. 68: 557–578.

Whitcomb, R. F., A. L. Hicks, H. D. Blocker, and D. E. Lynn. 1994. Biogeography of leafhopper specialists of the shortgrass prairie: evidence for the roles of phenology and phylogeny in determination of biological diversity. Am. Entomol. 40: 19–35.

Wiegmann, B. M., C. Mitter, and B. Farrell. 1993. Diversification of carnivorous parasitic insects: extraordinary radiation or specialized dead end? Am. Nat. 142: 737–754.

Wiegmann, B. M., C. Mitter, J. C. Regier, T. P. Friedlander, D. M. Wagner, and E. S. Nielsen. 2000. Nuclear genes resolve Mesozoic-aged divergences in the insect order Lepidoptera. Mol. Phylogenet. Evol. 15: 242–259.

Wiegmann, B. M., J. C. Regier, and C. Mitter. 2002. Combined molecular and morphological evidence on the phylogeny of the earliest lepidopteran lineages. Zool. Scripta 31: 67–81.

Williams, G. C. 1992. Natural selection: domains, levels, and challenges. Oxford University Press, New York.

Wilson, S., C. Mitter, R. F. Denno, and M. R. Wilson. 1994. Evolutionary patterns of host plant use by delphacid planthoppers and their relatives, pp. 7–113. In R. F. Denno and J. Prefect (eds.), The ecology and management of planthoppers. Chapman and Hall, New York.

Wink, M. 2003. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. Phytochemistry 64: 3–19.

Wood, T. K. 1993. Speciation of the *Enchenopa binotata* complex (Insecta: Homoptera: Membracidae), pp. 300–317. In D. R. Lees and D. Edwards (eds.), Evolutionary patterns and processes. Academic Press, London.

Yack, J. E., and J. H. Fullard. 2000. Ultrasonic hearing in nocturnal butterflies. Nature 403: 265–266.

Yang, M. M., and C. Mitter. 1994. Biosystematics of hackberry psyllids (Homoptera: Psylloidea): a preliminary report, pp. 172–184. In P. W. Price, W. Mattson, and Y. Baranchikov (eds.), The ecology and evolution of gall-forming insects. Gen. Tech. Rep. NC-174. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN.

Yotoko, K. S. C., P. I. Prado, C. A. M. Russo, and V. N. Solferini. 2005. Testing the trend towards specialization in herbivore-host plant associations using a molecular phylogeny of *Tomoplagia* (Diptera: Tephritidae). Mol. Phylogenet. Evol. 35: 701–711.

Zakharov, E. V., M. S. Caterino, and F. A. H. Sperling. 2004. Molecular phylogeny, historical biogeography, and divergence time estimates for swallowtail butterflies of the genus *Papilio* (Lepidoptera: Papilionidae). Syst. Biol. 53: 193–215.

Zwölfer, H. 1978. Mechanismen und ergebnisse der co-evolution von phytophagen und entomophagen insekten und höheren pflanzen. Sonderbd. Naturwiss. Ver. Hamburg 2: 7–50.