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Diversification at the Insect-Plant Interface

Insights from phylogenetics

Brian D. Farrell, Charles Mitter, and Douglas J. Futuyma

and plants and their insect enemies together constitute more than half of all known terrestrial species and are food for most of the rest. Their interaction is probably responsible, directly and indirectly, for much of terrestrial diversity (Ehrlich and Raven 1964). Yet we are only beginning to understand how the diversity of insect-plant assemblages is determined.

The phytophagous insects associated with a particular plant taxon form an ecological unit convenient for study, because an herbivore species typically attacks only a few related plants. Considerable study (reviewed in Strong et al. 1984) has yielded little evidence that diversity in such assemblages is limited by interspecific interactions such as competition (but see Jaenike 1990, Zwickler 1988), once accorded a dominant role in community structure (MacArthur 1972). Reflecting a broader shift from equilibrium to contingent explanations in ecology (Ricklefs and Schluter in press), there is a growing consensus that phytophage community diversity reflects primarily a balance among independent rates of successful colonization of new hosts, speciation on those hosts, and extinction. These rates in turn will depend, in ways yet unclear, on the geographic and phylogenetic history of the community and its constituent species.

The outstanding example of a historical model of insect-plant communities is Ehrlich and Raven’s (1964) hypothesis of coevolution, which has profoundly stimulated research on insect-plant interactions. These authors postulated an endless evolutionary arms race whose elements are origin of a new chemical defense in some plant lineage, which by reducing herbivore attack allows those plants to increase in abundance and eventually in diversity; and subsequent evolution of insect counteradaptations to these defenses, permitting insect radiation in the adaptive zone represented by the newly diversified plant group. Current differences in diversity and ecological dominance among insect and plant groups are taken to represent different stages in the historical sequence of “escape and radiation” (Thompson 1989). This concatenation of individual fitness, abundance, and macroevolutionary success, although a cardinal theme of the modern evolutionary synthesis (Simpson 1953), is by no means well established, having faced vigorous recent opposition (e.g., Gould 1985).

Although Ehrlich and Raven’s argument rested largely on taxonomic patterns of plant secondary chemistry and insect host-plant use, most subsequent work on coevolution has concerned its possible ecological and genetic mechanisms (Thompson 1989). Full understanding of the evolution of insect-plant communities, including definitive tests of the escape-and-radiation model, require complementary study of their long-term history. Reflecting the current resurgence of the comparative approach in biology generally, spurred in turn by advances in phylogeny reconstruction and molecular systematics, there is now a growing literature on the phylogenetics of insect-plant associations. In this article, we review several broad issues emerging from these studies concerning the imprint of evolutionary history on insect-plant communities:

- What aspects of insect host use are evolutionarily conservative? If the evolution of new preferences occurs readily, the local distribution of insects over plant species should adjust quickly to local host abundance or quality; if there are strong genetic barriers to such evolution, local associations should reflect instead their long-term histories.
• How old are the associations between particular extant insect and plant lineages, and to what extent have such lineages diversified in tandem? Long-continued associations provide the greatest opportunity for reciprocal evolutionary influence.

• Is there evidence for the escape-and-radiation steps of Ehrlich and Raven's scenario? That is, do phylogenetic comparisons of extant species reveal escalating sequences of plant defenses and insect counter-adaptations? Do lineages bearing these innovations show accelerated diversification?

• To what extent do the macro-evolutionary phenomena outlined above determine the current diversity and structure of insect-plant associations?

Phylogenetic constraints on host use

The evolutionary lability of trophic habits, which will determine the degree to which community structure can be understood as simply the outcome of natural selection, is a recurring issue in ecology. Genetic variation for host-use traits is common in phytophagous insects, and these herbivores rapidly colonize at least some introduced plant species (Strong et al. 1984). Although not all such colonizations entail genetic change, rapid colonization suggests that host use might evolve readily. However, genetic theory and experimental evidence are equally consistent with the existence of strong barriers to such evolution, which may require simultaneous change in several genetically independent traits (Futuyma and Moreno 1988, Gould 1991, Jaenike 1990).

Phylogenetic evidence can help resolve the issue of evolutionary constraint on host choice (Mitter and Farrell 1991). The history of host use in an insect clade can be estimated using a cladogram (i.e., a phylogenetic tree)—a branching diagram depicting the sequence of divergence of extant species from a common ancestor (e.g., Figures 6, 7, and 8)—derived from other (e.g., morphological or molecular) evidence. The preferences of the common ancestors implied by the phylogeny are taken to be those that would account for the habits of the extant species with the fewest evolutionary changes. If such histories show that change in preference is rare, or is restricted to hosts that are in some way most similar, it would be reasonable to infer that genetic barriers to adoption of new hosts have constrained the evolution of diet.

So far, few cladograms for phytophagous insects have been produced (approximately two dozen), but they provide initial quantitative support for the conventional wisdom among entomologists (but see Jermy 1984) that related insect species use related plants; change in host-plant family typically accompanies less than 17% of speciation events (Figure 1; Mitter and Farrell in 1991). This stricture is probably a response to similarity in plant chemistry, but exactly how and why plant chemistry plays such a central role in insect diet evolution is still much debated (Bernays and Graham 1988, Jaenike 1990, Moran 1988).

One test, as yet little exploited, for the genetic constraint suggested by such phylogenetic patterns considers the pattern of genetic variation for potential use of hosts that an insect species does not currently attack. To the extent that genetic constraints have guided the evolution of host affiliation, host shifts that have occurred in evolution should be reflected in genetic variation within insect species that exemplify the feeding habits immediately before those shifts, whereas genetic variation in these same species should be less abundant for hosts to which shifts have not subsequently occurred.

For example, phylogenetic analysis of the Asteraceae-feeding leaf beetle genus Ophraella (Futuyma and McCaffery 1990) reveals a cluster of three closely related species: two feed on ragweed (Ambrosia) and the third feeds on marsh elder (Iva). The association with Iva has apparently been derived from the Ambrosia feeding habit. Futuyma and collaborators1 predicted and confirmed that both of the species that retain the ancestral association with Ambrosia display a genetically based propensity to feed on Iva when deprived of Ambrosia. One of these species has also been screened (via analysis of differences among families) for genetic variation in feeding response to goldenrod (Solidago) and boneset (Eupatorium), plants that only distantly related species of Ophraella consume.

The phylogeny estimate indicates that Eupatorium has apparently never been host to the Ambrosia-feeding lineage, and Solidago has apparently been a host of the lineage only in the distant past, if at all. The Ambrosia-feeding species will not feed, and cannot survive, on Solidago, and it shows no evidence of genetic variation for the ability to do so—a result that conforms to the genetic constraint hypothesis. Nevertheless, this species does display genetic variation in feeding response to Eupatorium, in apparent contradiction of the genetic constraint hypothesis, although there is as yet no evidence that it can survive on this plant.2

Although comparable studies are virtually nonexistent, this initial evidence is largely consistent with the genetic constraints hypothesis. Complementary evidence might also come from surveys of the apparent evolutionary sources of herbivore colonists currently adapted to particular plants.

Conservatism in the assembly of plant faunas

Phylogenetic conservatism of host-plant choice could limit the diversity of herbivores on particular plant species by restricting invasion of such

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1D. J. Futuyma, M. Keese, and S. Scheffer, 1992, unpublished manuscript.
2See footnote 1.
host-based insect communities to a small subset of preadapted species. Explicit phylogenetic studies are lacking, but the operation of such evolutionary filters is suggested by broad taxonomic patterns in some plant faunas. For example, insects that attack the taxonomic subgroup within the carrot family (Umbelliferae) that bears angular furanocoumarins, highly unusual secondary compounds, have apparently evolved only in insect groups previously adapted to the more widespread, probably more primitive, linear furanocoumarins (Berenbaum 1983).

A broadly similar pattern emerges for the clade comprised of the plant families Asclepiadaceae and Apocynaceae, which share a defense syndrome of latex canals containing toxic secondary compounds. The herbivores of these plants are mostly aposematic (i.e., apparently advertise, via bright coloration, their toxicity or distastefulness to predators), often sequester plant toxins for defense against predators, and are both specialized and conservative in feeding habits. Their nearest relatives nearly always feed either on other plant groups with latex canals or on one of just ten families in the same subclass, Asteridae (Figure 2). This example also suggests colonization by a restricted set of preadapted lineages.3


Age and persistence of insect-plant associations

If insect host use were sufficiently conservative, associations of particular insect and plant taxa might persist over extensive periods of geological time. The contemporary distribution of insects over plant species might then reflect in part the relative ages of those species. Moreover, long-continued associations, in which the interacting lineages diversify together, should provide the greatest opportunity for coevolution sensu Ehrlich and Raven. Conversely, if the particular associations have evolved much more recently, it is unlikely that any subsequent coevolution has transpired (e.g., Miller page 50 this issue).

At the scale of geological epochs, there is some evidence that the fossil ages of major insect herbivore clades correspond to those of their predominate host groups (Zwölfer 1978); moreover, the basal diversification within such insect groups are often roughly concordant with host phylogeny. For example, the Mesozoic fossils of cerambycid and scolytid beetles represent primitive groups today (and, presumably, then) mostly associated with conifers, whereas advanced, more recent members of these families mostly attack the correspondingly younger flowering plants (Linsley 1961, Wood 1982). The older beetle groups thus appear to have retained host preferences established before the younger plant groups were available.

Recent research is revealing similar patterns at finer scales, undermining the conventional wisdom that the insect fossil record is hopelessly incomplete. For example, the host taxa used by extant genera of chrysomeloid and curculionoid beetles known also from Paleocene-Eocene fossils are significantly older than those used by beetle genera for which the oldest fossils date only to the Oligocene or Miocene (Figures 3 and 4; Farrell and Mitter in press). Thus, the primitive chrysomelid genus Donacia is reported from the same Paleocene shales as its present-day host Nymphaea (Crowson 1981), a relatively primitive angiosperm, whereas chrysomelid genera currently affiliated with composites and Convolvulaceae (e.g., Cassida and relatives) appear only in fossils of Oligocene and Miocene age (Farrell and Mitter in press). The older of these associations are, thus, likely to have persisted for 55–65 million years (see also Hickey and Hodges 1973, Opler 1973). Many coincident, apparently relictual geographic distributions of associated insects and plants further suggest long-continued interactions (Eastop 1973, Farrell and Mitter in press, Humphries et al. 1986, Linsley 1963, Moran 1989).

Parallel diversification

Many insect-plant associations, it appears, have persisted for much of the Tertiary or longer. Currently associated insect and plant lineages may, therefore, have diversified to some degree in concert, raising the possibility that their radiation reflects their interaction. One expectation under such parallel diversification is that the phylogenetic order of divergence among specific herbivores should correspond to that among their host taxa. Depending on the details of the evolutionary process (Mitter et al. 1991), such concordance might range from exact match (under truly simultaneous speciation) to broad, imperfect correlation (e.g., under episodic plant escape and radiation, and subsequent insect recolonization).

There have been few explicit studies of parallel insect-plant phylogeny; closer collaboration between insect and plant systematists is needed. Among 14 assemblages for which at
least partial phylogenies are available (Mitter and Farrell 1991), more than half showed at least some suggestion of phylogeny concordance (Figure 5), but obvious, extensive matching was seen only in two ecologically similar beetle genera (Figure 6) whose particularly intimate dependence on their hosts may be especially conducive to parallel diversification (Farrell 1991, Farrell and Mitter 1990, in press).

With few exceptions, the individual species or subspecies of Phyllobrotica (Chrysomelidae) and of Tetraopes (Cerambycidae) attack single, differing species of congeneric herbaceous plants (Scutellaria [Lamiaceae] and Asclepias [Asclepiadaceae], respectively), whereas their nearest relatives attack tropical woody relatives of the same plant groups. The adults both mate and feed on the flowers and uppermost leaves of the host, and the larvae attack the roots. This combination of feeding habits is probably exceptionally damaging (Brown 1990), raising the likelihood of an evolutionary response by the host plants. Long-term fidelity to the host group may be further promoted by dependence of the apparently aposromatic adult beetles on host toxins, such as iridoid or cardiac glycosides, for defense against their predators.

Less-intimate dependence on the host may partly explain why species of the external-feeding, cryptic leaf beetle genus Ophraella show little phylogenetic concordance with their hosts, single or multiple genera of Asteraceae in several tribes that diversified before Ophraella did (Futuyma and McCafferty 1990). Thus, these beetles have shifted, during or after speciation, among preexisting plants, and the evidence strongly suggests that host shifts occurred primarily among chemically similar plants. Ophraella may exemplify a predominant pattern among phytophagous insects in that only a restricted range of related hosts is attacked (Figure 1), but insect cladogenesis has neither accompanied nor closely followed plant cladogenesis.

The statistically significant match between phylogeny estimates for Tetraopes and Phyllobrotica and their respective hosts (e.g., Figure 6) strongly suggests diversification in concert, but it could conceivably have arisen instead by herbivore host-shift and speciation that tracked chemical or other traits correlated with plant phylogeny. For Phyllobrotica and Tetraopes, this alternative seems unlikely because host fossils and beetle geographic distributions suggest that the beetle and host-plant clades are equivalent in age. Fossil, geographic, and molecular datings are expected to be important in sorting out the complex mixtures of conserved and recent associations, which are probably common in groups of less extreme host specificity (e.g., Zwölfer 1988).

Evolution and arms races

Phylogenetic evidence thus far reinforces the view that insect-plant antagonisms are rarely so exclusive and persistent as to promote coevolution between particular pairs of species (see also Miller page 50 this issue),

Figure 3. (a) Dorsal aspect of fossil of Neotropical palm-feeding leaf beetle genus Delocrania, from 25–35 million-year-old Dominican amber. Specimen is nearly indistinguishable from extant species in Central America. Delocrania is currently extinct in the Caribbean. (b) Dorsal aspect of an extant species of Delocrania, collected from the Peruvian rainforest canopy by T. Erwin and B. Farrell. Specimens courtesy of the Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC.

Figure 4. Paleontological ages of some extant beetle-host plant affilliations (Farrell and Mitter in press). Phytophagous beetle genera currently affiliated with older (mid-Tertiary) plant groups appear significantly earlier in the fossil record than beetles currently affiliated with younger (Mesozoic) groups (Chi-square = 36.7; p < 0.001; d.f. = 4).
Several systems are currently under study. For example, Berenbaum (1983) has postulated for Umbelliferae and other plant groups an evolutionary sequence of increasingly toxic and complex coumarin compounds, each reducing attack by enemies adapted to the antecedent defense. *Asclepias* milkweeds show an apparent phylogenetic progression toward more toxic and complex cardenolides, which, moreover, become increasingly concentrated in the latex, where their effects against herbivores should be maximal (Nelson et al. 1981). Initial studies suggest that the highly diverse, more advanced, toxic milkweeds are free from the arcticid moths and chrysomelid beetles that attack chemically and phylogenetically more primitive congeners. A subset of *Tetrastes* beetles, which are one of the few herbivores of these advanced milkweeds, might represent a recent breakthrough in an arms race (Farrell 1991, Farrell and Mitter in press).

**Coevolution and adaptive radiation**

A second fundamental assertion of Ehrlich and Raven's coevolution model is that improved defenses and counteradaptations have led to increased diversification of the lineages in which they arose. Phylogenetic analysis is beginning to provide more rigorous tests (e.g., via replicated sister group comparisons; Mitter et al. 1988) of such adaptive radiation hypotheses than do the conventional ascription of evolutionary success to whatever features happen to distinguish large groups (Farrell et al. 1991, Mitter et al. 1988). Thus, the species diversity of a lineage in which a new adaptation has arisen is contrasted though pairwise, reciprocal adaption is known in a few instances (e.g., between particular species of heliconine butterflies and host *Passiflora* [Gilbert 1990]) and may emerge in other intimate associations, such as that of *Phyllobrotica* and *Scutellaria*. On the other hand, many sets of related phytophage species (genera or higher taxa) typically show conserved associations with broader host taxa (e.g., plant genera or families). Thus, contemporary insect-plant interactions could well reflect the diffuse coevolution implicit in Ehrlich and Raven's (1964) essay (i.e., the evolutionary responses of an insect or plant group to a broad spectrum of resource or enemy species).

Phylogenies could provide support for the diffuse coevolution hypothesis by revealing evolutionary trends of increasingly effective adaptation for attack and defense (though Vermeij [1987] cautions that the earlier stages of escalation may often be lost to extinction, preventing their study). For such progressions, there is little definitive evidence, which is likely to require a conjunction of phylogenetic and experimental approaches.

![Phylogenetic diagram](image)

Figure 6. Phylogeny estimate of *Phyllobrotica* leaf beetles compared with host Lamiales phylogeny synthesized from the published literature (Farrell and Mitter 1990). Beetle taxa are placed opposite their hosts (*Phyllobrotica quadrimaculata* and *Phyllobrotica decorata* both attack *Scutellaria galericulata*, in the Palearctic and Nearctic, respectively), except for *Phyllobrotica phystostegiae* and its host *Physostegia*, which are marked by asterisks. Cladogram correspondence is significant or nearly so under several randomization models. The exceptional association of *Phyllobrotica phystostegiae* with the perennial mint *Physostegia* probably represents recent colonization from an annual, xeric-adapted ancestral host in the same habitat.

Figure 5. Frequency distribution of correspondence (x-axis) between the phylogenies of 14 independent insect groups and the phylogenies of their respective host-plant groups. The phylogeny correspondence is Colles' consensus index (see Farrell and Mitter 1990) and ranges from 0 (no correspondence) to 1 (complete correspondence). The phylogenies of most groups show some correspondence to host relationships, as they might if insects generally either diversify in concert with their host plants or track host qualities correlated with plant phylogeny. Additional evidence (e.g., from fossil, biogeographic, or molecular datings) is necessary to discriminate among these or other possible causes of this pattern. (Graph based on unpublished data from Mitter and Farrell 1991.)
most cogently to that of its sister group (Figure 7), which by definition has had equal time for speciation and extinction and which should differ in the fewest other characteristics (relative to other more distantly related groups). Replication of such sister-group comparisons is possible when the same trait has arisen (through convergence) multiple times independently, allowing statistical control for the characters that might be confounded with the trait of interest in any one comparison.

The sister-group approach has been applied to the evolution of plant secretory canals bearing latex or resin (Farrell et al. 1991), a syndrome that has evolved many times independently and for which there is strong evidence of an antiharbivore function (Dussourd and Eiser 1987). Lineages characterized by such canals are consistently more species-rich than their non–canal-bearing sister groups, strongly suggesting that defense escalation can promote plant radiation (Farrell et al. 1991). Other convergent, apparently defense-related, plant traits await similar analysis.

Recent inventories of tropical forests, in which canal bearers are a prominent element, suggest that species bearing these defenses have consistently elevated population sizes (Boam 1986, France et al. 1976), possibly in part because they are avoided by leaf-cutting ants (Stradling 1978). This observation supports the still-controversial notion that population size is both evolutionarily persistent (reviewed in Rickles 1989) and linked, albeit by still-undescribed mechanisms, to the adaptive superiority and evolutionary success of lineages (Lidgard and Johnson 1989).

The results from sister-group analysis also support another of Ehrlich and Raven’s broad postulates, that insect diversification has been greatly accelerated by association with higher plants, which has evolved (from earlier predaceous or saprophagous habits) in at least 50 independent insect lineages whose collective species diversity accounts for more than half of all insects (Mitter et al. 1988). Whether the escape-and-radiation model (as opposed to the larger resource base afforded to phytophages, compared with predators) accounts for the spectacular success of phytophages is unknown: there are as yet no phylogenetic studies of the many possible examples of radiation after colonization of newly diversified plant groups (e.g., Berenbaum 1983). One alternative explanation, that rapid speciation is characteristic of parasitic organisms in a broader sense (Price 1980), seems unlikely: the many insect clades parasitizing animals, rather than plants, show no evidence of elevated diversification rates, compared with sister groups having other feeding habits.

Global patterns in diversity

Insect-plant coevolution, like other macroevolutionary interactions, is likely to have a strong geographic component (Darlington 1957, Vermeij 1987). Plants and insects can escape their predators or competitors either by evolving an adaptation or by invading a biota that initially lacks countermeasures to the adaptations (i.e., plant defenses or insect host uses traits) they already have. For example, although some introduced plants accumulate herbivores rapidly (Strong et al. 1984), others remain relatively herbivore-free for periods ranging from decades to millions of years. For instance, Eucalyptus was brought from Australia, where it has many insect enemies, to North America early in this century, but it still has few enemies in North America. The thistle tribe Cardueae, host to a diverse, specialized fauna in its Palearctic center of origin, has few insect enemies in the New World, despite the proliferation of more than 100 endemic Cardueae species since its invasion in the Miocene (Zwölfer 1988). Whether such geographic escape repeatedly promotes plant diversification (and subsequent radiation of colonizing herbivores) has yet to be tested.

Elements of the escape-and-radiation model may help to explain the striking latitudinal gradients of plant and insect species diversity. The current extensive regions of temperate climate date only to the global cooling and drying trend beginning in the early Tertiary (Wolfe 1978). Because plant families nearly all date back to before the Tertiary, most temperate plant groups are derived from ancestors that lived in tropical environments. Harsh climate has surely limited invasion of or survival in Tertiary temperate regions to those plant groups able to evolve appropriate adaptations. For example, the herbaceous habit of the northern temperate representatives of many primitively woody, tropical lineages allows overwintering underground (i.e., escape) during the most severe season (Wing and Tiffney 1987).

Figure 7. Hypothetical example of one comparison of the relative diversity between sister groups. Clade A, marked by an advance in defense (2), is more diverse than its sister group, clade B, which retains the primitive defense (1). By definition, sister groups (A and B) are the same age (Hennig 1966); thus, this difference in diversity would reflect different rates of diversification.


example, has evolved only in insect groups whose tropical representatives show some form of seasonal quiescence (Tauber et al. 1986). Herbivores, whose host use seems so often evolutionarily conservative, face the additional obstacle of finding suitable hosts in the depauperate temperate flora. They might therefore be expected to show even more pronounced latitudinal diversity gradients than insects of more generalized trophic habits.

The strikingly different latitudinal-diversity gradients in two dominant beetle families, one herbivorous and one predaceous, provide some initial support for these conjectures (Farrell and Erwin 1988, Farrell and Mitter in press). In forest canopy samples at Tambopata, an ecologically diverse site in the Peruvian Amazon, species of rove beetles, the largest group of predators, are distributed evenly across habitats of different floristic composition, with species diversity and abundance predictable from the total canopy foliage volume (Farrell and Erwin 1988). In contrast, most species of leaf beetles, the dominant phytophagous group, are restricted to a single canopy type with diversity and abundance little related to foliar volume, as might be expected of specialized herbivores.

The leaf beetles, which are far more diverse at a single Peruvian locality (i.e., 750 species) than in a much larger temperate area that was thoroughly sampled for both beetle families (Indiana has 286 species of leaf beetles), appear to present a much steeper latitudinal-diversity gradient (Chi-square = 75.8; p < 0.001; d.f. = 1) than the rove beetles (302 and 287 species, respectively, in Peru and Indiana). The hypothesis that steeper latitudinal diversity gradients in leaf beetles reflect evolutionary conservatism of these host specializations is supported by the fossil record. Leaf and rove beetles both appear to have arisen in the Jurassic (Crowson 1981). However, the major diversification of leaf beetles, in contrast to rove beetles, apparently occurred much later, coincident with the generic-level diversification of their mostly tropical host groups, which have only infrequently entered temperate floras.

Among the leaf beetles and other tropical herbivore groups that do reach the temperate zone, radiation may be promoted by special adaptation to the temperate flora, for example, by shift onto dominant temperate plant groups (Farrell and Mitter in press, Mitter and Farrell in press). This hypothesis awaits rigorous test, but there are many suggestive examples. For instance, the temperate fauna of noctuid moths is dominated by a huge, evolutionarily advanced cutworm clade, typically ground-dwelling and polyphagous on herbaceous plants, whereas relatively primitive noctuids are primarily arboreal feeders, mostly host specific, and most diverse in tropical forests (Holoway 1989).

In recent decades, historical explanations for latitudinal diversity gradients have been overshadowed by equilibrial theories based on inherent differences between temperate and tropical environments (e.g., Janzen 1967, Pianka 1978, Stevens 1989). Resolution of this debate has been hampered by the lack of control for the greatly differing ages of temperate and tropical climatic conditions. One solution is to restrict diversity com-

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**Figure** 8. Hypothetical example of a primitively tropical clade (i.e., its earliest evolution occurred in South America and Central America [SA and CA, respectively]) with recently evolved temperate representatives (which occur only in North America [NA]). The tropical element has more species only because it is older; the rate of diversification is higher in the temperate zone.
comparision to sister groups, of equal age by definition (Figures 7 and 8). Only a few temperate/tropical sister-group comparisons can as yet be identified for herbivorous insects, but in these comparisons there is no suggestion of a trend toward faster diversification in the tropics (Farrell and Mitter in press). This result is at least consistent with the view of diversity gradients as reflecting the tropical origins of most higher taxa (Stebbins 1974).

A sobering implication of the historical view, long appreciated by agricultural and forest entomologists (e.g., Burke et al. 1986, Krysan and Miller 1986, Wood 1982), is that much of the structure and diversity of temperate-plant communities will be intelligible only as relics of (or release from the constraint of) ancient but fast-disappearing tropical associations. In almost every respect, tropical biotas are insufficiently known, but ignorance of tropical insect-plant interactions is truly profound. Only a very small fraction of tropical insect species has been described, and for a majority of those that have been described, no ecological information—not even a single host record—exists. Most of the questions we have raised cannot be satisfactorily studied using only temperate zone species, because essential information on their close tropical relatives is lacking. Many of the major questions about organismal diversity and evolution, of which the questions about insect-plant relationships are a small sample, will require both conservation of tropical ecosystems and concerted systematic and ecological study of their denizens.

Conclusions

There is substantial evidence that much of the evolution of currently affiliated insect and plant lineages has occurred over similar geological time intervals, although cases of strictly parallel diversification are rare. There is also increasing evidence that insects are often conservative with respect to the evolution of new host affiliations; hence, the structure and diversity of insect-plant communities seem strongly influenced by a long history. There is some evidence that successive escalations in plant defense have been matched by insect counteradaptation and that these counteradaptations, in turn, have stimulated the diversification of insects and plants. Thus, the available evidence on the evolution of insect-plant communities, although still sparse, is largely consistent with the conclusions reached by Ehrlich and Raven (1964).

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