Ehrlich and Raven Revisited: Mechanisms Underlying Codiversification of Plants and Enemies

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Abstract

After almost 50 years of scrutiny, the ideas that Ehrlich and Raven presented in their classical paper on the coevolution between butterflies and plants are still very much alive. Much of this interest has involved the potential for codiversification, both in how the interaction itself diversifies and how the interaction affects modes and rates of speciation. Despite high levels of conservatism and specialization, diversification of the interaction appears to be mainly a consequence of host shifts, but this somewhat paradoxical conclusion can be understood by an appreciation of the ecological as well as genetic mechanisms behind host shifts. There are several ways that the interaction can influence speciation, with or without host-plant-based divergent selection on reproductive barriers. One current debate is over the relative importance of radiations following shifts to new adaptive zones and elevated rates of speciation in groups with plastic and diverse host use.

INTRODUCTION

It is now nearly 50 years since Ehrlich and Raven published their paper called "Butterflies and Plants: A Study in Coevolution" (Ehrlich & Raven 1964). Rarely has a single paper ignited such a scientific wildfire as this one: As of April 2011 the Thomson Reuters® Web of Science database listed 1,242 citations, and the paper still gets a healthy 60–80 new citations each year. But the influence of this paper goes far beyond numbers such as these; the paper inspired the creation of new fields of research. Of course, the idea that insects and plants evolved together was not entirely new (see, for example, Dethier 1941, Mode 1958, Gilbert 1979), but Ehrlich and Raven managed to put the idea into a general framework that was both comprehensive and provocative. When reading the paper today, one may be surprised by its relative shortage of data, but nevertheless, it contained ideas that many of us have spent our careers testing and developing.

The main observation was not only that there was a broad taxonomic correspondence between groups of butterflies and the plants they fed on, but also that above this observation there was a connection to plant secondary chemistry that sometimes transcended taxonomic relatedness. They suggested that these patterns were the results of an ongoing coevolutionary arms race in which an enhanced plant chemical defense selects for an improved ability of the butterflies to deal with it and where this, in turn, selects for novel defensive compounds in the plants (Ehrlich & Raven 1964). These processes should then result in a series of taxonomic radiations in butterflies and associated plants following the evolution of novel defense or resistance traits. Thus the theory contained a mixture of micro- and macroevolutionary processes, undoubtedly one reason for its general appeal but possibly also a cause of some confusion.

Although Ehrlich and Raven did meet with some criticism (e.g., Jermy 1984, Strong 1988), the concept of coevolution was, in general, enthusiastically adopted. Too enthusiastically, some would say. Arguably, one of the reasons for the concept's appeal was the vagueness of its definition—leaving ample room for the reader's own interpretation—but with time this vagueness started to be seen as a problem. A term that can mean anything will eventually end up meaning nothing, and two attempts to salvage the term from being hollowed out came from Janzen (1980) and Brooks (1979).

When Janzen attempted to sharpen the definition of the coevolutionary process (Janzen 1980), he made two important points. First, he emphasized the specificity of the interaction by distinguishing between strict and diffuse coevolution, where the former referred to specific interactions between two populations and the latter referred to interacting species assemblages without necessitating strict reciprocity on the population or species level. The need to demonstrate this reciprocity was the other important point. One cannot claim coevolution unless one has demonstrated reciprocal adaptive change in both interacting entities and that this change is caused by selection exerted by the other interactor, something that turned out to be exceedingly difficult to demonstrate, at least with strict coevolution (see Thompson 1994). Another unfortunate consequence was that diffuse coevolution somehow often came to be seen as a second-class version of strict or "true" coevolution, even though such diffuse coevolution probably has played a major role in the evolution of coevolving species assemblages such as plants and pollinators or plants and herbivores (Strauss et al. 2005, Haloin & Strauss 2008).

Brooks (1979), by contrast, noted that the term had been used for two very different phenomena that he called "coaccommodation" (or coadaptation) and "cospeciation." He then discussed the various scenarios that could give rise to cospeciation. Interestingly, Brooks stated that there was no necessary connection between the two phenomena; coadaptation can occur without cospeciation, and vice versa. Some years later, Mitter & Brooks (1983) reviewed several types of macroevolutionary outcomes of species associations and proposed phylogenetic methods to separate "association by descent" (cospeciation) from patterns caused by colonization. They explicitly noted that the "escape-and-radiate" scenario originally outlined by Ehrlich and Raven should not be expected to involve cospeciation, but rather asynchronous radiations of the associated lineages that are initiated by evolutionary breakthroughs in the ongoing arms race. Nevertheless, in spite of actually stating that most of the available data at the time suggested that the history of butterfly-plant associations had been more influenced by colonization and host shifts than by association by descent (Mitter & Brooks 1983), the idea that coevolution should be manifested in parallel cladogenesis through cospeciation became widespread (e.g., Miller 1987, Page 1993).

Hence, although the distinctions and sharpening of terms that both Janzen (1980) and Mitter & Brooks (1983) attempted were in many ways well grounded, the responses to these articles were not always constructive. The "take-home" message that many took from these papers was that coevolution had to involve intricate series of matching coevolved traits among unique sets of interacting populations on the population level and strictly matching phylogenies (cospeciation) on the species level. This raised the perceived bar so high that virtually no example succeeded to clear it.

However, the study of coevolution took a new turn in 1994 with the publication of Thompson's book *The Coevolutionary Process* (Thompson 1994). Thompson claimed that previous attempts to understand coevolution had been constrained by either a too narrow or too wide perspective on the interacting entities. Much of the coevolutionary dynamics occurred at a level between locally interacting populations and cladogenesis. Interacting populations do not exist in an ecological vacuum; they are connected to other populations to various degrees in a network that Thompson called the geographic mosaic. This mosaic may vary in both time and space and can hide a substantial degree of "cryptic" variation. What may appear to be a diffuse interaction could in reality hide a number of local populations that vary both in the identity and range of species used (Thompson 2005). At any given time, some populations within this mosaic may be involved in a close interaction with reciprocal adaptations and counter-adaptations (coevolutionary hot spots) while others may not (coevolutionary cold spots) (Thompson 1999, Gomulkiewicz et al. 2000).

The fitness effects of the same species interaction may also vary both spatially and temporally for both interacting species, depending on, e.g., the presence of other interactors (Thompson & Cunningham 2002, Thompson & Fernandez 2006). Most importantly, the outcome of the interaction is a result of processes that act not only locally within populations (selection, drift, local extinction), but also geographically between populations (dispersal, migration), so that traits that originated in a coevolutionary hot spot may spread to populations with different selection regimes through trait remixing (Thompson 1997, 2005).

With this view, there is no reason to expect that a given pair of interacting populations should always be engaged in "strict" coevolution, even if there is a fair amount of reciprocal adaptation going on between the species in question. On the contrary, the theory predicts a great deal of variation in the strength (and even direction) of reciprocal selection (Thompson 1994, 2005). Moreover, it may not always be predictable which traits will spread across the geographic mosaic to eventually become fixed at the species level and which will be lost as a result of local extinctions.

A BROAD COEVOLUTIONARY FRAMEWORK

Much due to the efforts of Thompson and his colleagues, coevolution once again became a fertile field of research from the late 1990s onward. But one consequence of the geographic mosaic theory that some still may find troubling is that the macroevolutionary patterns expected to arise from the coevolutionary process are not very clear—or rather, not necessarily predictable. The connection between the coevolutionary process and patterns of speciation is still not well understood (Thompson 2009, Yoder & Nuismer 2010), and even if the details are worked out, it may be overly optimistic to expect the coevolutionary process to result in a distinctly recognizable pattern of speciation. Thompson (1994) pointed out that the coevolutionary mosaic, just like the original scenario of coevolution posited by Ehrlich and Raven, should not be expected to result in parallel cladogenesis. Cospeciation may be one possible outcome of the coevolutionary process (e.g., Farrell & Mitter 1990) but certainly not something to be expected a priori.

The problem is twofold: There can be coevolution without cospeciation, but also cospeciation without coevolution. Interacting species can cospeciate simply by experiencing the same vicariance events (Brooks 1979; Brooks & McLennan 1991, 2002). A further complication is that matching phylogenies can arise from processes other than cospeciation. Reciprocal asynchronous radiations (Ehrlich & Raven 1964); sequential evolution (Jermy 1984), where herbivores track plant speciation; or resource tracking (e.g., Brooks & McLennan 2002), where herbivores track specific resources in the plants, all can potentially lead to parallel phylogenies, although speciation in the interacting clades is separated in time.

Incorporating clade age into the analysis has revealed that diversification of herbivores often occurs significantly later than that of their host plants, and in at least some cases, the associated clades have shown high levels of congruence in spite of their apparent difference in age (Percy et al. 2004, Smith et al. 2008). Using a simulation approach De Vienne et al. (2007) demonstrated how host shifts to closely related hosts can result in high levels of congruence without cospeciation. The process involved in these examples could be either reciprocal (but asynchronous) radiation events or some variant of sequential evolution or resource tracking. Thus, the situation is far from straightforward, with different processes capable of giving rise to similar macroevolutionary patterns and the same microevolutionary process capable of giving rise to different macroevolutionary patterns. The issue of linking patterns of host use to patterns of speciation is complex and the subject of considerable controversy [see Ronquist & Sanmartín (2011) also in this volume].

Terminology in the field reflects this confusion. Different authors often use the terms quite differently, and it is my understanding that much of the heated debates in the field of coevolution can be traced to misunderstandings surrounding terminology. However, one must also appreciate that there is a real difficulty here. Coevolution is a multifaceted phenomenon, and there are opposing objectives when trying to encompass as much of that variation while proposing more stringent definitions.

It is understandable that this situation has resulted in calls for more exact definitions, and considering that the previous efforts were not very successful, it may feel tempting to make another attempt and to perhaps try to make the term even more stringent and precise. However, although there may be a need for separate terms to describe and define the many ways in which species can affect each other's evolution, there is also a need for a more general term that embraces all this variation. After all, one reason why authors keep straying away from the stricter definitions may be that there is indeed a demand for a broader term. Hence, I argue for a broader usage of coevolution, where it is seen more as a framework than a definition.

An inherent problem with all stringent definitions of coevolution is that the term can only be applied a posteriori, after intense study of an interaction—that is, if it meets the criteria. Even then, it will often be open for debate whether the interpretation is correct, i.e., if the interaction is an example of "true" coevolution. I believe there is a case to be made for having an inclusive term for all the diverse instances in which we want to refer to interacting species that are coevolving as in "evolving together." This would help to shift the focus from the potentially pointless discussion of whether a specific pattern qualifies as "real" coevolution to the much more interesting question of what particular (coevolutionary) processes have shaped the interaction under study and of their possible macroevolutionary effects.

Several authors have already made suggestions along these lines (Futuyma & Slatkin 1983, Brooks & McLennan 2002, Agosta et al. 2010), and I believe that this view of coevolution is also inherent in the geographic mosaic theory (Thompson 2005), where one of the main points is that the nature of the interaction can vary substantially on both temporal and spatial scales. This is how I use the term in this review—as a framework to study evolutionary species interactions where the specific tempo and mode of the association are what we are trying to unravel. Is the interaction reciprocal or unidirectional? How is it varying in time and space? Are the interacting entities parts of diffuse species assemblages? Is the interaction influencing patterns of speciation and extinction? Such patterns can also be reciprocal (e.g., cospeciation) or unidirectional (e.g., resource tracking), or they could be alternating between unidirectional patterns in both directions (reciprocal radiations).

COEVOLUTIONARY DIVERSIFICATION 1: NICHE DIVERSIFICATION

Plants—in particular, angiosperm plants—and the groups of insect enemies that feed on them are strikingly species-rich groups, and from a geological perspective, this species richness has a relatively recent history. However, equally striking is the diversity of the interaction; there is hardly a single plant species that is not used as food by at least one insect species. Hence, plant-feeding insects have not only spread across the whole span of the angiosperm phylogeny, including the shallowest tips of the tree, but they also invented an impressive number of feeding modes along the way (Lawton 1983).

Such niche diversification could have been achieved in two ways: Insects have become distributed across the plant phylogeny either as a result of cospeciation or by means of colonization and host shifting. Although not mutually exclusive, these processes represent fundamentally different routes to achieve widespread taxonomical distribution.

The Parasite Paradox

Two long-standing general observations about insect-plant associations are that they tend to be both taxonomically conservative and highly specialized (Ehrlich & Raven 1964, Futuyma & Mitter 1996, Janz & Nylin 1998, Kergoat et al. 2007, Winkler & Mitter 2008). Taxonomic conservatism should be expected only to the extent that plant phylogeny reflects some relevant (typically chemical) similarity among plants. Though probably a good default assumption, this is not necessarily the case (Becerra 1997, Wahlberg 2001). From the point of view of insects, other plant characteristics may sometimes affect relevant aspects of plant chemistry to an equal extent, such as plant growth form (Feeny 1976, Janz & Nylin 1998, Heidel-Fischer et al. 2009). Moreover, in groups that shift feeding habits, e.g., from external to internal feeding, this habit may be more conservative than plant phylogeny (Nyman et al. 2006).

Nevertheless, both the high taxonomic conservatism and high degree of specialization certainly appear to hold as broad generalizations, and at a first glance, this may seem to suggest that shifts between hosts should be rare and that, consequently, niche diversification of plant-feeding insects should mainly be driven by cospeciation. This would imply that novel host associations mainly arise as insects speciate as a consequence of host speciation, where the two descendant insect species become specialized on each of the two newly formed host species. Considering this, the rarity of cospeciation in insect-plant associations appears striking (e.g., Roy 2001, Lopez-Vaamonde et al. 2003, Braby & Trueman 2006). How, then, can a conservative and highly specialized interaction give rise to the rate of host shifts that is required to explain the impressive niche diversification of plant-feeding insects?

This is the "parasite paradox" (Agosta et al. 2010): Parasites (broadly speaking, including many plant-feeding insects) appear to shift hosts much more often than they "should," considering their highly specialized and conservative feeding habits. The problem with host shifts is even larger if one considers what is involved in moving from one host to another. As the famous quote goes, "the host plant is not just something fed on, it is something lived on" (Kennedy 1953), and to successfully shift from feeding on plant A to plant B will require correlated changes in whole suites of characters that are involved in recognition, handling, metabolization, detoxification, etc. To resolve the paradox, one needs to dissect the anatomy of a host shift and appreciate that it is a multipart process with both ecological and evolutionary components.

First, the large-scale conservatism seen in many groups of plant-feeding insects hides a great deal of short-term evolutionary dynamics—the conservatism does not seem to be as evident on a finer phylogenetic resolution (Dobler et al. 1996, Janz et al. 2001). Phylogenetic studies of a finer scale have also revealed that transition rates between generalization and specialization can vary substantially between groups. Whereas some studies have shown trends for increased specialization (Moran 1988, Kelley & Farrell 1998), others have shown the opposite pattern (e.g., Scheffer & Wiegmann 2000, Janz et al. 2001), suggesting that any trend in one or the other direction depends mostly on the evolutionary phase this group is in during the slice of time under study (Janz et al. 2001, Nosil & Mooers 2005).

There are also many examples of rapid changes in host use, sometimes on human-observable time scales. An early example was provided by Tabashnik (1983), who showed that some populations of the butterfly *Colias philodice eriphyle* had shifted from their native fabaceous hosts to cultivated alfalfa in Colorado. The shift by some populations of the tephritid fruit fly *Rhagoletis pomonella* from hawthorn to cultivated apples is another well-known example (Bush 1994). Indeed, the problems with invasive species stand as living examples of the pervasiveness of rapid host shifts. A successful invasion of insects into a novel community often involves a shift to a locally available plant, and invasions of foreign plant species are often also followed by rapid colonization by local insects (Keeler & Chew 2008, Agosta et al. 2010, Harvey et al. 2010).

The First Step

What makes a host shift possible? Some interesting clues can be found by examining cases where recent host shifts have been studied in detail. Two well-documented cases of rapid evolution of insect host use come from Lepidoptera in the western United States. The prodoxid moth *Greya politella* is a pollinating seed parasite that throughout most of its geographic range is closely associated with *Lithophragma parviflorum*. In spite of its close affiliation with its host, several populations in the northern Rocky Mountains have independently colonized another saxifragous plant, the local endemic *Heuchera grossulariifolia* (Segraves et al. 1999, Thompson et al. 2004). *H. grossulariifolia* occurs in both diploid and tetraploid variants and moths that have access to both variants have been shown to preferentially attack tetraploids (Thompson et al. 1997). A study using moths from a population that remained on the ancestral host revealed that these moths were very reluctant to oviposit in the novel plant, and that when they did, they did not differentiate between plants of different ploidy levels (Janz & Thompson 2002). This shows that moth populations living on the novel host have developed specific adaptations to it, but also that moths remaining on the ancestral host already had some capacity to recognize and utilize this novel plant. Hence, some ability to use *H. grossulariifolia* appears to have existed in *G. politella* prior to the shift.

Perhaps even more striking are the examples of rapid human-induced changes in host use that have been documented by Singer and colleagues in the butterfly *Euphydryas editha*, which occurs across much of the western United States and feeds on several plants in Scrophulariaceae and related families. During the last decades, Singer and colleagues have documented several cases of rapidly changing host associations, involving in turn the colonization of the introduced exotic plant *Plantago lanceolata* (Thomas et al. 1987), a host shift instigated by a change in phenology due to logging (Singer et al. 1993), and a broadening of the host range following recolonization of a patch that had previously gone extinct (Singer et al. 2008). Again, although the novel situations resulted in evolutionary changes in host use, the authors conclude that at least in one of the cases, and most likely in all three, the capability to utilize the novel host must have existed in the colonizing population prior to the shift in host use (Singer et al. 2008).

In all these examples, the sometimes rather substantial evolutionary changes that resulted in a host shift began with a shift in expression of a pre-existing trait that was triggered by some change in the conditions of the insect. When Janzen (1985) first called attention to this phenomenon, he called it "ecological fitting," a term that has recently gained popularity as a tool to understand the crucial first step in the process leading to evolutionary changes in host use (see Agosta 2006, Agosta et al. 2010).

When a species is exposed to novel conditions, resulting from migration or changes in the local environment, the most common outcome may well be that it will not be able to persist—the novel conditions will simply be too different, too hostile. However, in some cases, the species will—more or less by accident—"fit" into the novel situation, in the sense that some individuals will show some realized fitness. Natural selection can work only on traits that are expressed, and the novel conditions will make new parts of the organisms' reaction norms visible to selection. Hence, the ecological fit is a requirement for future modifications by natural selection that may perfect the adaptation to the novel conditions. Agosta & Klemens (2008) used the term "sloppy fitness space" to describe the phenomenon that organisms typically possess some degree of potential fitness outside the range of conditions under which they evolved. This potential is crucial for two reasons: Organisms can fit into novel conditions, and they can subsequently adapt to these conditions (Agosta & Klemens 2008, Agosta et al. 2010).

Novel Associations

The concept of sloppy fitness space links ecological fitting to the more general explanation for evolutionary novelty outlined by West-Eberhard (2003), who used the term "phenotypic accommodation" to describe when the phenotype is modified in a new situation through existing plasticity without genetic change (see also West-Eberhard 2005, Crispo 2007, Nylin & Janz 2009). Again, this first step may be followed by genetic modifications through natural selection ("genetic accommodation"), but it is the environmentally induced altered expression patterns that set the stage for such evolutionary change.

These phenotypic responses to a novel environment are not arbitrary (West-Eberhard 2005) but are the result of ancestral developmental responses; they reflect past functionality. For this reason, we should expect host shifts more often than not to involve plants that have been used in the insect's evolutionary past, which indeed seems to be the case (Futuyma et al. 1995, Janz et al. 2001, Scriber et al. 2008). Such evolutionary recurrence can also explain why the dynamics of host-plant use can appear opportunistic at smaller scales, yet conservative at larger scales; if insects predominantly shift back and forth within a limited set of plants from their evolutionary past, many of these shifts will not be detected in higher-level phylogenetic reconstructions. This will make the problem of accurately reconstructing traits that change frequently (cf. Schluter et al. 1997) even larger, because history tends to erase its own tracks. As a consequence, if such recurrent evolution is common, there is a substantial risk that rates of host shifts in plant-feeding insects are grossly underestimated.

However, it is important to understand that, even though the developmental responses may be ancestral, the conditions under which they are expressed can be novel and, hence, lead to novel outcomes (West-Eberhard 2003). Thus, shifts to novel plants may occur if there is enough overlap between the developmental pathways required to utilize the plant in question and some ancestral functionality. It follows that more plasticity will allow a wider range of such overlaps. Thus, polyphagy should increase not only the likelihood of shifts to closely related or ancestral plants, but also the probability of having more "radical" host shifts to entirely novel plants (Janz et al. 2001, Nylin & Janz 2009, Agosta et al. 2010). Consequently, the diversification of host use through colonization of novel host plants appears to be closely linked to the evolution of host-plant range.

Host-Range Evolution

Studies on host-range evolution have primarily focused on understanding the widespread specialization. However, the ubiquitousness of specialization may be somewhat deceptive. The examples of rapid and opportunistic host colonization given above indicate that host-range expansions may have been more common than phylogenetic reconstructions would suggest. Just as ancestral host shifts may be difficult to reconstruct phylogenetically if evolutionary recurrence is common, so will ancestral host-range expansions be erased from history if these are transient phases and re-specialization on ancestral hosts is common (Janz et al. 2001, Weingartner et al. 2006).

As host-range evolution appears to play an important role in the diversification of insect host use, it is increasingly frustrating that both the mechanistic basis and the macroevolutionary patterns of host-range evolution continue to be so elusive (cf. Nosil & Mooers 2005, Stireman 2005, Nyman 2010). Part of the problem lies in the definition of the trait. What may look like a wide host range to a human observer may, in fact, be "more of the same" from the point of view of the insect, where the traits that make plants acceptable as resources are shared among multiple hosts (Brooks & McLennan 2002, Agosta et al. 2010). There are also reasons to suspect that insects can achieve wide host ranges in fundamentally different ways: either through the accumulation of separate sets of specialized metabolic pathways (polyspecialists) or through the evolution of generalized enzyme systems (true generalists) (Nylin & Janz 2009). The macroevolutionary consequences of these alternative routes of host-range expansion will be quite different.

Our understanding of host-range evolution is further hampered by the fact that its mechanistic basis is still poorly understood. The identification of the NSP (nitrile-specifying protein) glucosinolate detoxification gene as a key innovation involved in the host-plant shift to Brassicales by butterflies in the Pierinae (Wheat et al. 2007) was an excellent example of how genetic mechanisms can be linked to macroevolutionary patterns. Wheat et al. (2007) showed that NSP activity matched the occurrence of glucosinolate in their hosts, that this detoxification mechanism likely evolved shortly after the diversification of the Brassicales, and that the colonization of this plant group has led to adaptive radiation in the Brassicales-feeding Pierinae.

The detoxification of furanocoumarins in the plant families Apiaceae and Rutaceae has also been suggested as a key innovation that has allowed butterflies in the genus *Papilio* to utilize and diversify on these plants (Berenbaum 1983, Berenbaum et al. 1996). Furanocoumarins are narrowly distributed among plant groups, and few insects have been able to colonize these plants. Here, the key innovation is less distinct but appears to have involved changes in the cytochrome P450 family of detoxification enzymes (Berenbaum et al. 1996, Berenbaum 2002, Mao et al. 2007).

Using a somewhat different approach, Heidel-Fischer et al. (2009) used molecular methods to test predictions from macroevolutionary patterns of conservatism in host use. Rather than looking for specific key innovations, they looked for similarities and differences in gene expression among larvae feeding on plants with different levels of similarity. As mentioned above, chemical similarity between plants is often assumed to be correlated with phylogeny, although deviations from this rule certainly exist. One possible systematic source of such a deviation is the "plant apparency" theory first suggested by Feeny (1976), which states that trees, which are apparent plants that cannot easily avoid being found by herbivores, need a chemical defense that is not so easy to overcome. Therefore, they will tend to converge on a set of constitutive chemical defenses such as tannins, terpenes, and flavonoids that have a quantitative, dosage-dependent effect. Such a defense may be efficient but is more expensive to produce than an inducible toxin-based defense, which is typically found in herbs. Using a setup with three natural hosts of the polyphagous butterfly *Polygonia c-album*, Heidel-Fischer et al. (2009) showed higher similarity in gene expression among plants that shared either a common ancestry (urticalean rosids) or growth form (trees) than that found among plants that differed in both these aspects.

Much more needs to be done along these lines, and this research area will likely provide the most important new insights and breakthroughs within the field of evolutionary insect-plant interactions in the years to come. The development of increasingly sophisticated and affordable molecular methods is now opening possibilities that until very recently were considered impossible and will, I hope, result in a burst of evolutionarily and phylogenetically informed mechanistic studies of host-plant utilization.

To sum up this section, there is a paradox created by the observation of long-term conservatism in insect-plant interactions and widespread specialization, on the one hand, and the accumulating examples of relatively rapid host shifts, on the other. This paradox can be partly resolved by a reappraisal of the processes involved in a host shift. First, many seemingly novel associations are not truly novel, but instead represent evolutionary reversals to ancestral associations. Second, novel species associations can arise if there is enough overlap between existing functionality and the requirements to utilize the plant in question. As a consequence, there should be a correlation between plasticity (e.g., polyphagy) and colonization of novel plants.

COEVOLUTIONARY DIVERSIFICATION 2: TAXONOMIC DIVERSIFICATION

Diversification in Plants and Phytophagous Insects

Flowering plants in the mid-Cretaceous provided a large and diversifying resource that was colonized by several lineages of insects, and this new way of life evidently resulted in increased net speciation rates among these groups (Mitter et al. 1988), to the extent that herbivorous insects today make up roughly one-fourth of all described species on Earth (Strong et al. 1984). The joint success of these groups is intriguing, and it is a reasonable assumption that the causes for the success can, at least to some extent, be found in the nature of the interaction. There is evidence for broad climatic correlations of some of the major diversification events in both plants and insect herbivores (Labandeira 2006, Peña & Wahlberg 2008), but correlations do not say much about whether the actual drivers of diversification were abiotic or biotic in nature.

The idea that the interaction has been driving the diversification of these groups has been inherent in most work on the codiversification of herbivorous insects and plants ever since Ehrlich & Raven (1964) put forth their theory of reciprocal radiation. However, in spite of almost five decades of research, we still know disturbingly little about what the details of these processes might be. Because herbivory has arisen repeatedly, it has been possible to show that there is an overall increase in net diversification rates among herbivorous insects, by comparing them to their nonherbivorous sister groups (Mitter et al. 1988). The reciprocal effect—that herbivory is driving plant diversification—is more difficult to test, as there are no control groups of plants without herbivory. It is interesting to note that given the original treatment by Ehrlich and Raven of this issue, plant speciation should not be directly linked to herbivory, but to the absence of herbivory; radiation of plants was expected to follow the evolution of novel chemical defenses that would free them from herbivore attack. Hence, there is an important asymmetry in the way that plants and insects were thought to affect each other's speciation rates. Although plants may be directly involved in speciation of the insects that feed on them, insects play a very indirect role in the actual speciation events of plants under this scenario.

Even if the effect of herbivory may be difficult to test, whether specific defense compounds or structures have led to increased diversification rates in the plant lineages that contain them can be tested. Farrell et al. (1991) made use of the fact that a secretory canal with resin or latex is a well-defined structure that has evolved repeatedly in several groups of plants. Hence, they could use a methodology similar to that used by Mitter et al. (1988) to demonstrate that this purportedly defensive trait has indeed resulted in higher diversification rates among plants. Later studies have shown that the pattern is likely to be more complex than this. One of the best-studied examples of latex-defended plants is the genus *Asclepias*. Agrawal et al. (2009) presented evidence for adaptive radiation in the genus. Surprisingly, however, this radiation was associated with a decline in defensive investments, and one of the traits showing such a declining pattern was latex secretion. Evolution of defense traits in the genus *Asclepias* appears not to be simply a matter of a key modification followed by radiation, but rather of a complex pattern of several defensive strategies that are mixed and matched throughout evolution to evade the current community of herbivores (Agrawal et al. 2008).

Returning to the possible effect of herbivory on the diversification of the herbivorous insects, we find that feeding on (angiosperm) plants promotes diversification, but it is not entirely clear how exactly this occurs. As food resources, flowering plants stand out as chemically and structurally diverse, which has been the main focus of interest in most diversification scenarios following Ehrlich and Raven. However, plants are also an abundant resource, which could conceivably also promote diversification as an effect of the trophic cascade (e.g., Hawkins et al. 2003). Moreover, resource abundance and wide geographic distribution can introduce other types of extrinsic variation that are mediated by the plant resource, such as variations in habitat, climate, and other local conditions. For example, it has been suggested that the impressive diversification of grass-feeding butterflies in the tribe Satyrini has largely been an effect of the spread of grasses into all imaginable habitats of the world in the Oligocene (Peña & Wahlberg 2008, Peña et al. 2010).

The Role of the Interaction

Plant-feeding insects have for a long time been favorite examples of sympatric speciation, but it has always remained a controversial topic (Bush 1969, Berlocher & Feder 2002, Futuyma 2008). However, in the past decade, we have seen a shift in focus from a geographically based classification of speciation modes to one based on the mechanisms that are responsible for the reproductive barriers between incipient species. Ecological speciation—where reproductive isolation is mainly the result of divergent selection through ecological interactions—has received a tremendous amount of interest in recent years (Rundle & Nosil 2005, Funk & Nosil 2008, Schluter 2009, Matsubayashi et al. 2010). Divergent selection can be involved both in the initial divergence among populations (Hawthorne & Via 2001, Emelianov et al. 2003) and in completing the speciation process through reinforcement (Servedio & Noor 2003).

Under ecological speciation, at least part of the process leading to speciation can take place in allopatry (Rundle & Nosil 2005), thus blurring the line between the traditional geographic modes of speciation. For example, divergent selection between populations feeding on allopatrically separated plants may lead to accumulation of different adaptations that prevent hybridization upon secondary contact (Funk 1998, Linnen & Farrell 2010).

If the habit of feeding on plants has been driving the diversification of plant-feeding insects, the great interest in and attractiveness of ecological speciation is understandable. However, despite the many examples of host-plant-driven ecological speciation (Matsubayashi et al. 2010), there is some disagreement over its prevalence. Even though several studies have highlighted the connection between changes in host use and speciation rates (Scheffer & Wiegmann 2000, Janz et al. 2006, Nyman et al. 2006, McLeish et al. 2007), an increase in rate of speciation does not necessarily imply that ecological speciation is driving it.

Drawing on a broad database of approximately 200 phytophagous insect clades, Winkler & Mitter (2008) estimated that 50% of the speciation events involved shifts to a different host-plant species and, hence, were candidates for ecological speciation. More recently, Nyman et al. (2010) arrived at a similar figure (54%) in a study of higher-nematine sawflies. However, when attempting to correct for time since divergence, they saw that the probability of sister species having different niches was strongly affected by the time since their most recent common ancestor. After applying this correction, they instead estimated that only 22% of the sister-species pairs would have had nonoverlapping niches at the time of divergence. Whether these figures are high or low depends on how prevalent one thinks that ecological speciation has been in the first place. Though these studies show that host-driven ecological speciation could have played an important role in the diversification of plant-feeding insects, they also show that a majority of the speciation events may have other explanations.

Nyman (2010) has suggested that the likelihood that a colonization of a novel host will lead to speciation depends on its similarity to the ancestral host(s). If it is too similar, colonization is likely but will not lead to disruptive selection; if it is too different, it will not be colonized at all. Hence, host-plant-mediated disruptive selection should be most likely at intermediate similarities between hosts. The problem is that “similarity” is not easily defined and will vary substantially between groups (Nyman 2010). A proper understanding of this “subjectivity of similarity” will require a much better appreciation of the resource base of an insect (also in terms of cues for host location and identification). Again, phylogenetic relationships among plants may provide a good shorthand for degree of similarity, but in reality, insects do not base their diet on phylogenetic distances between plants. Indeed, different insects feeding on the same plant groups may perceive their degree of similarity quite differently (Brooks & McLennan 2002, Nyman 2010).

But host-plant use can play an important role in the speciation process without being directly involved in either the formation or completion of the reproductive barrier. One such indirect effect is related to the observation that insects with wide host ranges tend to have larger geographical distributions (Päivinen et al. 2005, Slove & Janz 2011). The causal link between these traits could go both ways. On the one hand, as the combined distribution of multiple host plants will typically be larger than the distribution of either of the plants alone, incorporation of novel hosts into the repertoire should tend to increase the potential geographic distribution of the insect (Janz & Nylin 2008). On the other hand, a more widespread distribution increases the likelihood of coming into contact with novel plants, some of which may function as alternative hosts. These alternatives are, in fact, not mutually exclusive, as the second alternative requires a pre-existing capability to recognize and use the alternative hosts upon encounter (see above) (Agosta & Klemens 2008, Agosta et al. 2010). Yet another way of increasing the potential geographic distribution is to colonize a plant group that is geographically widespread, such as the grasses (Peña & Wahlberg 2008).

Large geographic distributions can increase the likelihood of population fragmentation and speciation in several ways. For example, conditions will be likely to vary in different parts of the distribution, which can lead to allopatric divergent selection that may or may not be host plant based (cf. Thompson 2005). Wiens (2004) has also argued that niche conservatism can lead to fragmentation of large distributions when environmental conditions change, leading to vicariance among the remaining populations occupying the ancestral ecological niche. Phylogenetic and biogeographic studies of psyllid radiations on the Canary Islands revealed that these were dependent on the diversity and availability on the islands of the necessary food resources; host-plant availability facilitated the spread of the insects across the islands (with or without associated host shifts), but actual speciation was mostly allopatric and had little to do with host use (Percy 2003). Hence, one consequence of a diverse host use can be that it increases the likelihood of creating vicariant distributions among populations, thus promoting diversification without being involved in divergent selection on the reproductive barrier.

Escape and Radiate, and Its Alternatives

Following the hypothesis of reciprocal radiation by Ehrlich & Raven (1964), much effort has been devoted to the search for key innovations that could either exclude herbivores from a group of plants or allow some insects to attack a previously well-defended group of plants. According to this escape-and-radiate scenario, these innovations would open up new adaptive zones that, in turn, could lead to bursts of diversification. Some such examples have been discussed, such as the novel abilities that allowed butterflies in Pierinae and *Papilio* to colonize and radiate on Brassicales (Wheat et al. 2007), Apiaceae, and Rutaceae (Berenbaum et al. 1996). A different approach was taken by Fordyce (2010), who investigated a sample of butterfly phylogenies and found that clades where a historical major host shift had occurred often showed increased diversification rates directly after the shift. Clades with no such shift typically showed less variation in diversification rates through time. Using a similar approach for estimating lineage accumulation through time, Strutzenberger & Fiedler (2011) suggested that the Neotropical geometrid moth genus *Eois* underwent a more rapid early diversification during the Miocene, followed by a declining diversification rate toward present times. This correlates broadly with the diversification of the main host plants in the genus *Piper*, but also with increased Andean uplift and climatic changes.

The idea that key innovations can lead to evolutionary radiation has thus received empirical support, but it is questionable if the mass of diversification in plants and their insect herbivores can be attributed to such key innovations. It is also possible that species interactions can affect speciation rates in less dramatic ways, leading to a less spectacular elevation of diversification rates that still may, in time, result in substantial differences in species numbers among clades (Janz & Nylin 2008, Rabosky 2009, Scriber 2010). This plasticity scenario (Nylin & Wahlberg 2008) can be exemplified with the oscillation hypothesis (Janz et al. 2006, Janz & Nylin 2008), where repeated fluctuations in host-plant range among clades of oligophagous insects can result in elevated net speciation rates. According to this hypothesis, the diversifying process is driven by the subdivision of widespread populations with wide host ranges into several populations with more restricted geographic distribution (and potentially also host ranges). This may be followed, once again, by a host-range expansion that, in turn, will allow the insect to increase its geographic distribution, and the process can repeat itself. In this scenario, it is not the major chemical breakthroughs that boost diversification; instead, the repeated oscillations in host range constitute a "diversification engine" that raises net speciation rates. The oscillations are maintained through the ability to retain essential parts of the genetic machinery to utilize ancestral hosts (see previous section). This allows for evolutionary recurrence so that insects can "mix and match" among a set of potential host plants and, thus, expand and contract the actual host range as the conditions change through time.

The oscillation hypothesis was originally formulated in a nonreciprocal manner, i.e., as affecting only insects (Janz et al. 2006, Janz & Nylin 2008). However, evolutionary recurrence of plant defenses is also possible (e.g., Donoghue 2005), and this could affect plant diversification in an analogous way. Any given defensive strategy will decrease in efficiency as specialized insects accumulate with time. In such a situation, the ability to mix and match between a pool of defensive options would probably be beneficial (cf. Agrawal 2007, Agrawal et al. 2008, Kursar et al. 2009) and may lead to an effect on plant diversification along the lines of the oscillation hypothesis. Indeed, most examples of adaptive radiation linked to herbivore defenses have not demonstrated radiation following a single key innovation, but rather a continuous process of escalation and diversification of multiple herbivore defense strategies through time (Agrawal et al. 2009, Becerra et al. 2009, Kursar et al. 2009). Interestingly, this would also explain the somewhat surprising finding of Agrawal et al. (2009) that radiation in *Asclepias* was associated with a decline in defensive investment in some defensive traits.

As with other cases where conflicting scenarios have been proposed to explain the same phenomenon, the issue is not to decide which is right and which is wrong but to try to understand their relative contributions to the phenomenon and to disentangle their effects. This is an interesting question that may turn out to be quite difficult, not the least because the two alternatives are overlapping to some extent. The probability of a major host shift seems to be positively influenced by polyphagy (see previous section), and as ancestral polyphagy is difficult to recover, it is quite possible that many examples of major host shifts did occur during periods of host-range expansion that have now been lost in history. Nevertheless, there are some distinct differences in the patterns that would be expected under the two scenarios (cf. Nylin & Wahlberg 2008).

The escape-and-radiate scenario predicts a burst of diversification following an evolutionary breakthrough. This could be the evolution of a novel defensive chemical on the plant side or a novel capacity to deal with a hitherto well-defended plant group on the insect side. This would open up a novel evolutionary opportunity, and the theory predicts that the plants or insects should undergo rapid speciation to fill up the new adaptive zones, followed by a return to a more “normal” rate of speciation (e.g., Fordyce 2010, Strutzenberger & Fiedler 2011). In contrast, the plasticity scenario predicts a slower but more persistent elevation of speciation rates associated with groups of insects that retain the necessary plasticity to expand their host ranges when the conditions favor this (Janz et al. 2006).

Nevertheless, in reality, there are some problems with differentiating between the scenarios. For example, defining a “key innovation” worthy of leading to an evolutionary radiation is problematic without resorting to circular reasoning (key innovations are often identified by such effects). In the case of plant-feeding insects, one possibility is to look for “major” historical shifts in host use and test if these have led to higher diversification rates than the sister clades (e.g., Fordyce 2010). There are problems, though, with defining what constitutes a “major” host shift within any particular clade (Nyman 2010) as well as with the fact that not all major host shifts should have equal effects on diversification under the escape-and-radiate scenario (Lopez-Vaamonde et al. 2003). To some extent, the scenario relies on processes that will almost by necessity be idiosyncratic for each case; each key innovation is unique, and generalizations between them may be troublesome. For example, some “major” host shifts may involve plant groups that do not contain evolutionarily novel defenses—some may simply be less defended—and some plant groups may be too small to sustain the expected evolutionary radiations, even if they are well defended. This makes taxon sampling challenging.

The plasticity scenario should, in principle, be more general in scope; it will work as an engine of speciation whenever certain general premises are fulfilled. It is not tied to any particular key event and is not necessarily restricted to plant-herbivore systems (cf. Hoberg & Brooks 2008, Larkin et al. 2008, Kruger et al. 2009). A disadvantage is that it is still vaguely formulated. At this point, it is unclear what level of variation is required for the process to work, and this, in turn, is likely to vary between clades (cf. Nyman 2010). The opportunity to test the theory also relies on the existence of within-group variation in host-plant-related plasticity, which is not necessarily the case. Furthermore, the retained plasticity in resource use could also affect the other side of the diversification coin, by lowering extinction rates within a clade. These effects may be difficult to disentangle, especially for deep nodes in a phylogeny.

A test of the relative significance of the two scenarios should be carried out on clades of relatively recent age, partly owing to the difficulty of reconstructing deep nodes (especially with traits that change frequently) and partly owing to the fact that the different effects of the two scenarios should be most easy to tease apart at the finer resolution that such comparisons would allow. Even if major host shifts are typically associated with periods of host-range expansion, relatively recent such events could make up good test cases, because predictions clearly differ between scenarios. The escape-and-radiate scenario predicts that the lineage following the major host shift shows higher species richness, whereas the plasticity scenario predicts the opposite, at least if the shift is a true shift and not just a further host-range expansion.

Clearly, despite its long history, the codiversification between insect herbivores and their host plants has much left in need of unraveling. It is an exceedingly diverse interaction where the mode of interaction varies substantially across species, and even within species. As such, making broad generalizations becomes difficult, and it has proven challenging to differentiate between general and idiosyncratic causes for the patterns observed. Nevertheless, we have seen some important recent advances, in methodology as well as in theory. Much of the progress made during the past decades has come from the continuing development and application of phylogenetic methods, which is somewhat ironic considering that Ehrlich & Raven (1964) explicitly claimed that we would never be able to infer the history of these interactions. In retrospect, the rise of phylogenetics may have been one of the most important breakthroughs following the publication of "Butterflies and Plants."

In addition, because of the enormous variation in this interaction, thoroughly worked-out case studies from different systems are extremely valuable. As with much of biology, it is no bold guess that a common denominator for many of the future advancements in this field will be associated with the fast-paced development of new molecular tools and methods that may unravel the links between functional genomics and macroevolution. But tools and methodology alone will not answer any questions, and it will be a continuing challenge for all evolutionary biologists to find ways of putting them to good use.

FUTURE ISSUES

1. The use of molecular genomics to unravel the mechanisms behind plant defenses, insect host shifts, specialization, and speciation has the potential to lift the veil from some of the elusive connections between micro- and macroevolution, such as how traits among the interacting species influence each other's rate of speciation.
2. The effects of key innovations leading to bursts of diversification need to be disentangled from the more even-paced effect of elevated net speciation rates in lineages with retained plasticity in host use or herbivore defense.
3. Increasingly sophisticated use of time-calibrated phylogenies needs to be made to investigate the actual timing and rate of diversification and to link such events more conclusively to other factors that may have been of importance, be they biotic or abiotic.

4. More examples that document the ecological and genetic issues involved in the modification of species interactions, such as the colonization of novel hosts or the modulation of plant resistance traits, are needed.
5. Further insights from phylogenetic reconstructions and historical explanations are needed in fields where they so far have had relatively little penetration, such as in community and population ecology.

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