The Oscillation Hypothesis of Host-Plant Range and Speciation

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From a humble beginning in the early Cretaceous, angiosperm plants have quickly conquered the earth so that they now make up one of the most ubiquitous and species-rich groups (Crane et al. 1995; Wikström et al. 2001; Stuessy 2004; Friis et al. 2005). Likewise, the pioneer insects that once colonized this novel resource have multiplied to such an extent that they have become an ecologically dominating group in all terrestrial ecosystems (Mitter et al. 1988; Farrell 1998). Together, the seed plants and the insects that feed on them make up a good half of all described species, and their diversification is among the most remarkable in the history of life, both in terms of magnitude and relative speed. Consequently, if we want to understand the processes that generate biodiversity on earth, this is a good place to start.

Even though it is clear that both seed plants and plant-feeding insects have undergone rapid diversification to a much larger extent than their respective sister groups, we have a surprisingly poor understanding of why this has happened. The analogous diversification of these groups has led to the idea that they must have diversified together, reciprocally influencing each other's cladogenesis (Ehrlich and Raven 1964). However, apparent disparity in the relative timing of the diversification of the two groups has led many to suggest that they may have undergone rapid speciation for reasons that are not necessarily connected (Jermy 1984; Janz and Nylin 1998). Furthermore, while explanations for how insects could have influenced the diversification of flowering plants have typically focused on pollination (Pellmyr 1992; Waser 1998; Dodd et al. 1999; Grimaldi 1999), explanations for the potential impact of plants on the diversification of insects have often revolved around herbivory (Mitter et al. 1988; Farrell 1998; Kelley et al. 2000).

Here, we will primarily deal with the latter question: how the utilization of flowering plants as food resources could have promoted speciation rates in insects. Seed plants are different from many other food resources. As already mentioned, the resource itself has quickly diversified, and a typical consequence of this seems to the development of high resource specialization among the insects that feed on them. Relative host specialists dominate most groups of plant-feeding insects, and there are indications that many polyphagous species often show considerable geographic specialization (Thompson 2005). Flowering plants may be an abundant resource, but different plant species offer very different chemical challenges, and it appears difficult to be able to cope with more than a few plant species at a time. These difficulties can be both metabolic (Via 1991; Joshi and Thompson 1995; Mackenzie 1996; Agrawal 2000) and neurological (Bernays and Wcislo 1994; Janz and Nylin 1997; Bernays 2001).

This widespread specialization is a natural candidate in the search for mechanisms behind the high speciation rates among these insects and has often figured in such discussions (Jaenike 1990; Futuyma 1991; Thompson 1994; Kelley et al. 2000; Hawthorne and Via 2001). However, understanding the reasons for host specialization is just the beginning. The proposed role of specialization is that it can aid population fragmentation, either by the formation of host races (Bush 1975; Feder et al. 1988; Carroll and Boyd 1992; Hawthorne and Via 2001) or by an increased likelihood of geographic fragmentation (Peterson and Denno 1998; Kelley et al. 2000). Under both these scenarios, specialization acts as a pruning process; it increases the likelihood of population subdivision and speciation by removing plants from the repertoire. Thus, by itself, this process would very soon run out of fuel.

The next challenge then, is to understand what processes generate novel variation in host use, the processes that have driven the spread of plant-feeding insects across the phylogeny of flowering plants. Even though there is a considerable conservatism in host-plant use among groups of related

herbivorous insects, plant-feeding insects have, to various extents, conquered all major groups of flowering plants. How and why does the *interaction* diversify? What are the relative roles of host-range expansions and host shifts?

This is an important part of our hypothesis for how plant diversity generates diversity in the insects that feed on them, but a final, and fundamental, part remains: does this diversification of the interaction indeed lead to elevated speciation rates? It is the purpose of this chapter to suggest a comprehensive explanation for the generation of variation in host use, the subsequent pruning of this variation, and how it can influence the diversification rates of plant-feeding insects.

The Oscillation Hypothesis

We will first briefly outline our general hypothesis for how diversity of phytophagous insects may be promoted by oscillations in host-plant range, before going into the process in more detail in later sections. The hypothesis is related to both the biogeographical concept of "taxon pulses" first described by Erwin (1981) and the smaller-scale oscillations described by M. C. Singer (this volume) as "peristaltic evolution."

Most phytophagous insects are specialists on a group of plants, at the species level or at a higher taxonomical level (Fig. 15.1 box a). As noted above, such specialization has a limited potential to create diversity, unless the process of specialization is at least occasionally reversed.

For an increase in host-plant range (Fig. 15.1 box b), not only the plant preferences of females need to change, but also the ability of juveniles to feed on more than one plant taxon, unless the expansion involves only very similar plants or plants to which the insect is for some other reason preadapted (see "Colonizations and Host-Range Expansions"). Once a wider host-plant range has evolved, it may lead to speciation through the formation of more specialized host-plant races, in sympatry or parapatry (Fig. 15.1, the direct route from box b to box e). A more general process may perhaps occur via a geographical range expansion (Fig. 15.1, box c), facilitated by the ability to feed on more than one plant group. The evidence for a link between host-plant range and geographical range is reviewed in "Diet Breadth and Geographical Range," below. The initial colonizers during such a range expansion may well be members of populations or species that are prone to dispersal and show high levels of gene flow, preventing local adaptation. However, a strong dispersive tendency should often be a short-lived evolutionary stage. As was noted by Futuyma (1998, pp. 575–576) "natural selection against alleles that promote dispersal is almost inevitable." This is because alleles for dispersal tend to remove themselves automatically from local populations, because dispersion is risky and mortality during this phase high, and because alleles for staying put keep organisms in a habitat where they have a chance to become locally adapted.
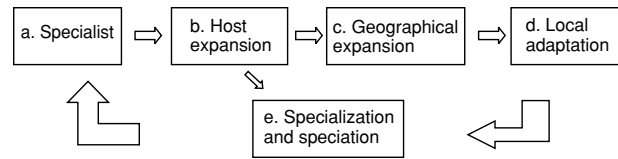

FIGURE 15.1. A scheme for oscillations in host-plant range promoting higher rates of speciation.

Local adaptation is bound to follow as soon as gene flow is no longer ubiquitous (Fig. 15.1, box d). Life histories and other seasonal adaptations will evolve to fit local conditions, and so will host-plant utilization. Local host-plant specialization should often reoccur (Fig. 15.1, box e; see "Specialization and Fragmentation") because females are expected to evolve to prefer the plants that maximize their fitness, given the local patterns of seasonality, the local abundances of potential host plants, the life-history consequences of feeding on one plant or the other, *and* the fitness consequences of these particular life histories under the local patterns of seasonality and climate. Speciation may be facilitated by the resulting geographic variation in host-plant preferences and life histories (to some extent this will be a coadapted package), through processes of ecological speciation (see "Speciation").

For an understanding of the processes governing host-plant range (Fig. 15.1, boxes a, b, and e) it is necessary to study the preferences of females (including the genetics and mechanistic aspects, e.g., oviposition stimulants), as well as the performance of offspring when reared on different host plants, in other words, the adaptive and nonadaptive plasticity of offspring—especially in fitness-related life-history traits. To address the process generating biodiversity (Fig. 15.1, boxes c through e) we need to make comparisons between populations and species, including phylogenetic studies.

It should be noted that in this chapter we use the concept of plasticity in a way similar to West-Eberhard (2003), that is, to refer to a potential to follow different developmental pathways. This concept of developmental plasticity is related to both phenotypic and evolutionary plasticity, because it may be expressed in either way. In the context of host plants, a potential in an insect lineage to develop on more than one host can be expressed either as oligo- or polyphagy, or as frequent evolutionary shifts between hosts in the potential range, or both.

Colonizations and Host-Range Expansions

As plant-feeding appears to have repeatedly led to increased species richness among insects (Mitter et al. 1988; Farrell 1998), a logical conclusion would be that there is something about plants as a resource that increases the likelihood of speciation (or decreases the likelihood of extinction). So, what is it that is so special about plants?

As mentioned in the introduction, the most striking aspect of the seed plants is that they are themselves such a highly diverse group. They are diverse in terms of species numbers but also in terms of internal chemistry and external physical structures. The seed plants have conquered all major habitats of the world and are, indeed, defining features of many of them, such as the rain forests, the grassland prairies or steppes, and so on. It would seem then that an important key to understanding the diversification of plant-feeding insects lies in understanding the diversification of host-plant use among these insects. What has caused them to spread across the seed plants to such an extent? Taking the butterflies as an example, Janz and Nylin (1998) showed that the ancestor of the butterflies probably colonized a relatively derived plant within the clade that now contains Fabaceae, Rosaceae, and the "urticalean rosids" (Urticaceae and relatives). If this is true, the present patterns of host-plant use must have been caused by colonizations from these ancestral plants onto an already diverse group; there is no indication that the process of plant diversification has in itself promoted the spread of butterflies onto them.

Many studies have pointed out the conservative aspect of host-plant use among plant-feeding insects, where related insects tend to feed on related plants (e.g., Ehrlich and Raven 1964; Futuyma and Mitter 1996; Janz and Nylin 1998; Thompson 2005). Yet, in spite of this, these insects have managed to colonize a substantial portion of the seed plants in a relatively short time. A closer look at what was going on among the butterflies within the tribe Nymphalini revealed an almost chaotic picture, with a large number of shifts between distantly related plants (Janz et al. 2001). Furthermore, there are examples of truly rapid changes in host use, with host shifts occurring in observable time as responses to, for example, changes in human land use (Strong 1974; Strong et al. 1977; Tabashnik 1983; Singer et al. 1993). Apparently, the available data point in different directions; host-plant use cannot possibly be conservative and opportunistic at the same time. Or can it?

Futuyma and colleagues found that host shifts within the beetle genus *Ophraella* tended to involve the plants that were already used by other congeneric species (Futuyma et al. 1993, 1994, 1995). Hence, even if host shifts could potentially be numerous, they were not randomly distributed across plant taxa but appeared to be constrained to plants that were used by related species. A similar pattern was later seen in the butterfly tribe Nymphalini (Janz et al. 2001), as well as in a number of other groups (Nosil 2002). Within the Nymphalini, a dozen plant families were reconstructed to have been independently colonized 29 to 37 times within a phylogeny of less than 30 terminal species, some families as many as 5 to 9 times. This is a truly remarkable number, considering the size of the butterfly clade under investigation, and certainly not something that could be characterized as a conservative host use. This led to the conclusion that many of these colonizations were in

fact not independent; the defining trait that allowed the colonization, the "preadaptation," was probably more ancestral than the actual colonization events themselves. This ancestral event could have been an actual colonization of the plant that was followed by a secondary loss from the repertoire, but where much of the essential "machinery" needed to utilize the plant was retained. But it could also be a more literal preadaptation, where an evolved trait (like a new enzyme) makes the colonization of a given plant possible. A series of larval establishment tests on a wide range of plants (known hosts of the group as well as a sample of non-host-plant groups) also showed that the larvae were often capable of feeding and surviving on a wider range of plants than were actually used as hosts by a species. Moreover, the additional plants were invariably plants that had, according to the phylogenetic reconstruction, been used as a host by an ancestral butterfly. Hence, the study contrasted the actual host range, the range of plants that are actually oviposited on and used as hosts at a given time, with the potential host range, meaning the total number of plants that an insect is capable of using (or where there exists genetic variation for feeding within the population). This distinction between actual and potential host ranges should be kept in mind when reading this chapter, as it will be fundamental to understanding our further reasoning.

Apparently, host use can be very dynamic and even opportunistic, but only within a restricted set of plants that appear to be shared among a group of insects. How, then, do genuinely novel associations evolve? Janz et al. (2001) found that most of the changes in host use seemed to be concentrated in periods of expanded host ranges. There was a strong tendency for colonizations to lead to periods of multiple host use (host-range expansions), rather than to immediate host shifts. "Immediate" in this context means before the next speciation event, so even the few examples of so-called immediate host shifts might have involved extended periods of multiple host use. During these periods, further colonizations were more common than during periods of specialized host use. Furthermore, the few examples of radical host shifts in the tribe, to plants outside the typical set of plants used by the group, seemed to be happening during these polyphagous phases. This pattern has recently been confirmed and further elaborated by Weingartner et al. (2006). In that study, the colonization of novel hosts did not appear to be caused by chemical breakthroughs in the sense of Ehrlich and Raven (1964), but rather by a slower accumulation of hosts during times of increased plasticity in resource use (cf. West-Eberhard 2003). In both studies on the Nymphalini butterflies, there were also clear indications that the plastic phases of expanded host ranges were evolutionarily transient; there were clear tendencies to respecialize on either the ancestral host or one of the newly incorporated hosts (Janz et al. 2001; Weingartner et al. 2006).

Reconstructing ancestral host range is difficult for several reasons (cf. Stireman 2005) and will require very detailed data on host use and well-resolved complete phylogenies to
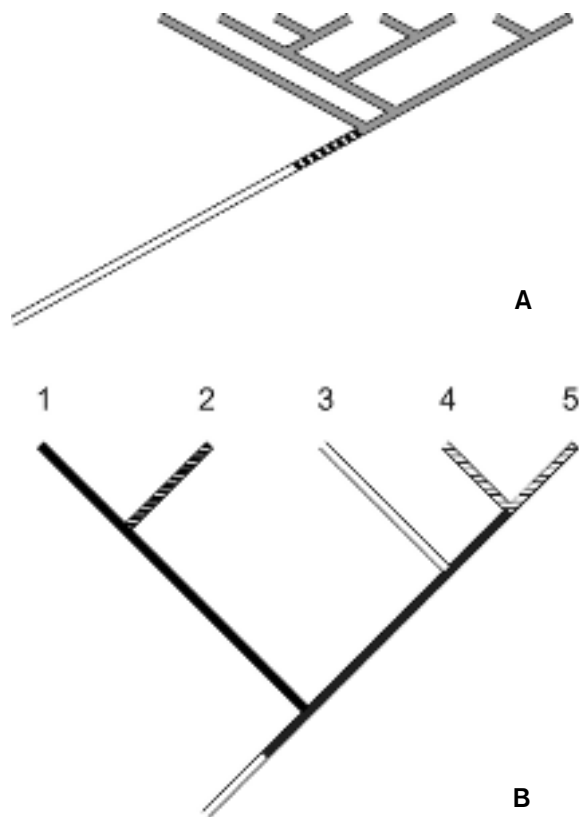
FIGURE 15.2. Schematic representations of the "explosive radiation scenario" (A) and "plasticity scenario" (B). Under the former we expect a short stage of shifting from the ancestral host (white) to the novel (gray) over a stage where perhaps only one of these two hosts were used (striped). Under the latter we expect a long-lasting stage (black) of at least potential ability to feed on several plant taxa, with respecializations on the ancestral host (white) as well as on different novel hosts (all striped) in some species.

have any chance of success. Moreover, a lesson from the Nymphalini studies is that even so, ancestral host ranges will tend to be underestimated because of the nature of host-range evolution (Janz et al. 2001; Weingartner et al. 2006). In many cases, the phylogenetic traces of a host-range expansion will be lost with time; a period of expanded host range followed by specialization on one of the novel hosts will in retrospect appear as a clean host shift, once all traces of the additional hosts are lost (cf. species 2, 4, and 5 in (Fig. 15.2B). Indeed, a respecialization on the ancestral host will often be impossible to detect at all once enough time has passed, and it will thus look as if nothing has happened at all (cf. species 3 in Fig. 15.2B). In these cases, establishment tests might provide additional clues to the reconstruction of ancestral host ranges (Janz et al. 2001); or, if this is not possible, the combined host ranges of a clade appears to be a relatively accurate estimation of past host-range expansions, even if it is not possible to tell whether there has been one or several expansions (Janz et al. 2001, 2006).

To sum up, it appears that host-plant colonizations typically lead to host-range expansions rather than to immediate host shifts, and that such periods of expanded host ranges facilitate further colonization events, including the inclusion of truly novel hosts into the repertoire. As a consequence, host expansions are probably an important part of the process that has allowed plant-feeding insects to spread across the seed plants.

Diet Breadth and Geographical Range

If host expansions are to contribute to increased diversification rates among plant-feeding insects, they must somehow increase the likelihood of a species to subdivide into distinct subpopulations. At a first glance, this might not seem very likely. After all, multiple-host use implies increased behavioral and physiological plasticity, which should buffer against environmental heterogeneity and thus, rather, act to counterbalance local adaptations and population fragmentation. What host expansions can accomplish, however, is to help set the stage for other factors, which do lead to population fragmentation, to start acting.

Many factors may influence the geographic distribution of a species, but the distribution of its available resources sets the ultimate boundaries for where the insect can live and reproduce. For a plant-feeding insect, the occurrence of acceptable larval host plants will determine its possible limits of distribution. As two plant species will not be likely to have the exact same distribution, a wider host range should allow a plant-feeding insect to spread over a wider geographic area. There is some evidence for this, especially from the British Isles, where patterns of butterfly distribution are particularly well documented (Quinn et al. 1998; Dennis et al. 2000). Regional studies from Germany (Brändle et al. 2002), Japan (Kitahara and Fujii 1994), Finland (Päivinen et al. 2005), and the United States (Nitao et al. 1991) also confirm this picture. All these studies were limited in geographical and/or taxonomical scope, but until a more comprehensive study of a more global scope is conducted, the weight of evidence is definitely in favor of a general positive correlation between the diet breadths of insect species and the size of their geographical ranges.

There are at least two mechanisms by which such a correlation could arise. First, an alternative host with a geographical distribution that is partly overlapping with the ancestral host may be colonized. This would allow the insect to expand its geographical range into the areas where the novel host grows, but where the ancestral host does not. In this scenario, the novel host is colonized within the original area of distribution, and the geographical range expansion is a secondary process. The colonization of the novel host has simply opened up a larger area of suitable habitat.

Alternatively, a novel host could be colonized as a consequence of active dispersal into areas where the ancestral host does not exist. This, however, would require a preexisting capacity to both recognize the novel plant as a host (so

that the female will accept it for oviposition), as well as a corresponding preexisting capacity of the larvae to grow and survive on the plant. It may not seem like a very plausible scenario, but there are some features of the interaction that may make it more likely. As described in the previous section, most colonizations and host shifts seem to involve plants that either are used by close relatives or have been used as hosts in the past. Such plants may share important characteristics with the presently used host, which makes them more likely to be recognized as hosts and to support at least some larval survival. Alternatively, the insect may be literally preadapted to the plant, because it has already been used historically, which means that many of the adaptations needed to cope with the plant are already present. Similarly, the many examples of parallel colonizations of the same plant group documented in the butterfly tribe Nymphalini (Janz et al. 2001; Weingartner et al. 2006) can be explained by a shared plesiomorphic trait that facilitates the colonization of a particular plant.

This process, where a geographical range expansion leads to a colonization or host shift with negligible initial evolutionary change, has been called "ecological fitting'' (Janzen 1985). When a species arrives at a new location, its survival there will be determined by its fit into the local ecosystem. If it cannot find suitable resources or habitat to exploit, it will simply not survive to be a part of the local community.

Ecological fitting has recently received renewed attention in biogeography, where it has become clear that species interactions within a community are often not evolved in place but have instead evolved elsewhere and exist in the present context due to secondary dispersal and ecological fitting (Wilkinson 2004; Brooks and Ferrao 2005). The vegetation of Ascension Island serves as a good example of the process of ecological fitting. When Darwin passed by the island on the Beagle on his way back to England, he described the island as a barren rock, "entirely destitute of trees" (Darwin 1839). Today its slopes are covered by a cloud forest, a complex, species-rich ecosystem that has formed in less than 200 years (Wilkinson 2004). In this case, plant dispersal to this remote island has to a large extent been carried out by humans, which has certainly increased the speed of the process dramatically and thus given the processes of local adaptation and coevolution less of a chance. Nevertheless, it shows that a complex community *can* form almost entirely through a series of ecological fittings (Wilkinson 2004). It is clear that species with wider environmental tolerance will be more likely to succeed in fitting into a novel community. Hence, the capacity to (potentially) utilize a wider range of hosts should facilitate successful geographical range expansions.

We do not mean to say that coevolution and local adaptation are not important processes in the shaping of species interactions, but these processes can start acting only *after* the interaction has come into existence in the first place, through biotic expansion and ecological fitting. A good example of this can be seen in the recent host shift of some populations of the prodoxid moth *Greya politellla* in the mountains of Idaho. Throughout most of its geographical range, it feeds on plants of the genus *Lithophragma* (Saxifragaceae). In central Idaho, some populations have shifted to the related plant *Heuchera grossularifolia*, a biogeographically complex set of diploid and autopolyploid populations (Segraves et al. 1999). Although the moths attack plants of both ploidies, they preferentially attack tetraploids over diploids (Thompson et al. 1997). When presenting diploid and tetraploid *Heuchera* plants along with the native *Lithophragma* plants to a population that has had no known prior contact with the novel host species, these moths laid almost all eggs in their native host (Janz and Thompson 2002). Clearly, the moths were not well adapted to the novel host. Even so, they did lay some eggs in the novel host, which showed that the potential for a host colonization was there, should the local plant community change, or should they disperse to a nearby locality where only the novel host was present. In this example, the initial colonization of the novel plant is made possible through ecological fitting, while the subsequent increase in preference and survival, as well as the higher preference for tetraploid variants, must have evolved locally, after the colonization.

Specialization and Fragmentation

The general tendency among plant-feeding insects to evolve toward increased specialization in the host-plant utilization is well documented (Thompson 1994). As mentioned in the introduction, this pervasive trend toward increased specialization has been suggested to play an important role in the ongoing diversification of plant-feeding insects (Bush 1975; Feder et al. 1988; Carroll and Boyd 1992; Peterson and Denno 1998; Kelley et al. 2000; Hawthorne and Via 2001; Morse and Farrell 2005).

The main question we face for the general hypothesis outlined in this chapter is whether such specialization can decrease gene flow among populations of geographically widespread species, by selecting for different patterns of host use in different parts of an insect's geographical range.

Local populations often differ in the degree of specialization of their species interactions, and indeed with what species they interact, leading to geographic selection mosaics across the distributions of interacting species (Thompson 1994, 2005). The importance of such selection mosaics in this context is that they provide the opportunity for evolution to follow diverging paths in different parts of a species' geographical range. There can be several reasons for such divergent selection. Even on small geographical scales, habitat fragmentation may be enough to cause differences in local availability of potential hosts (Singer et al. 1989; Kuussaari et al. 2000); and, depending on connectivity between habitat patches, such differences may lead relatively quickly to genetic differences in host preference and performance (Singer et al. 1993; Singer and Thomas 1996). In other cases, the mere presence or absence of additional

species, such as competitors, predators, and parasites, can cause differences in local selection pressures. Such is the case in the interaction between the *Greya* moths mentioned in the previous section and their saxifragaceous hosts, where the local presence or absence of additional pollinators determines whether the interaction is mutualistic or parasitic, and hence the direction of selection on both the insect and the plant (Thompson et al. 2004).

Obviously, the larger the geographical range, the larger the chance that a species will experience different conditions in different parts of its range. Members of a widespread species may find themselves in diverse climatic conditions, each requiring specific local adaptations. In the temperate zones, conditions and requirements change dramatically with latitude, and it is not surprising that patterns of host use and specialization do too (Scriber 1973). Each potential plant will have its specific life-history consequences (and these too may change with latitude), and what is favorable in a strictly univoltine northern population may not be favored in a multivoltine southern population.

A good example of this is the host use within the butterfly species complex *Papilio glaucus/canadensis* in the eastern United States. Host preference and detoxification abilities differ between populations, with a sharp cline in a hybrid zone in the North American Great Lakes region (Scriber 1988, 1994; Scriber et al. 1991, this volume). This highly polyphagous butterfly feeds on several trees, and while some hosts are shared across most of its geographical range, the southern *P. glaucus* variant mainly uses *Magnolia* and *Liriodendron*, while the northern *P. canadensis* variant mainly feeds on *Populus*. The two variants are now considered true species (Hagen et al. 1991), and there are good indications that divergent host utilization played a part in the speciation process (Scriber 1994).

Even where relative host-plant ranking is the same across a latitudinal cline, degree of specialization on the preferred host can change due to differences in voltinism (Nylin 1988; Scriber and Lederhouse 1992). While northern univoltine populations of the Eurasian butterfly *Polygonia c-album* regularly use hosts from seven families in five orders, bi- or multivoltine southern populations feed almost exclusively on the preferred host *Urtica dioica*, which can support the higher growth rates needed to fit several generations into the favorable season (Nylin 1988; Janz et al. 1994; Janz and Nylin 1997). These differences in specificity are genetically determined, and like in the *Papilio* example above, the differences in host preference are largely sex-linked (Janz 1998, 2003; Nylin et al. 2005). Sex-linked genes are disproportionately represented among the reported genetic differences between closely related species in the Lepidoptera (Sperling 1994; Prowell 1998), suggesting a role in speciation. *Polygonia c-album* is a widespread, polyphagous species in which current gene flow probably prevents further fragmentation. However, there is a potential for further divergence and speciation should these populations become more isolated in the future.

All in all, there is good evidence that local populations of widespread species will often evolve toward specialization on a subset of the original host range. Moreover, different requirements throughout the distributional range will often lead to variable outcomes, so that populations are likely to specialize on different plants.

Speciation

At this stage we need to ask ourselves how host plants might be directly or indirectly connected to speciation events in phytophagous insects. The different modes of speciation are traditionally classified according to geography, from sympatric speciation (where the new species form without physical or geographic isolation, within a single ancestral population) to allopatric speciation (where the incipient species are first completely isolated from each other). Many other modes have been suggested as part of this general scheme; the most important of these (for our purposes) is the intermediate mode: parapatric speciation (where the incipient species occur in different parts of the ancestral range and are thus partially genetically isolated by distance).

Recently, it has been suggested that it may be more useful to classify speciation models according to the mechanisms responsible for the evolution of reproductive isolation (Schluter 2000, 2001; Via 2001). In such schemes, the major distinction is according to whether reproductive isolation evolves primarily because of chance events (such as genetic drift) or because of selection. A further distinction can be made according to whether barriers to gene flow evolve as a result of ecologically based selection differing between environments ("ecological speciation" [Schluter 2000, 2001; Rundle and Nosil 2005]) or other forms of selection (such as sexual selection) where reproductive isolation is not primarily due to ecological differences between environments. It is in the category of ecological speciation that host plants are likely to have their most direct effects, and this category cuts across all of the geographical categories. The role of host plants in speciation has been reviewed by Berlocher and Feder (2002), Drès and Mallet (2002), and Funk et al. (2002) (and see also several other chapters in this volume). However, these treatments typically focus on the role of host-plant specialization in speciation, rather than on host-plant range, so we will briefly outline how we believe a wide range of potential hosts may promote speciation under different modes of speciation.

SYMPATRIC SPECIATION

This mode of speciation has always been controversial, but there has recently been a strong reappraisal of the importance of sympatric speciation in nature (Via 2001). It is interesting to note, however, that in the latest major synthesis of the field, Coyne and Orr (2004) conclude that sympatric speciation is theoretically possible, but that necessary conditions are more stringent than for allopatric speciation, which, in their opinion, should thus remain the null model for speciation.

They also critically review the evidence from nature and find only a few cases where sympatric speciation seems "plausible." All of them involve differences in resource use, suggesting that ecologically based divergent selection may well be important for this mode of speciation. None of the suggested cases of sympatric speciation involving "host races" survive their scrutiny, usually because an allopatric phase during the formation of the host races cannot be ruled out. In line with the recent trend toward classification according to isolating mechanism rather than geography, we can still conclude that the cases reviewed by Berlocher and Feder (2002[AuQ2]) and Drès and Mallet (2002) (such as the famous *Rhagoletis* system) represent evidence that differences in host-plant utilization between incipient species can contribute strongly toward their isolation in sympatry and *perhaps* can result in speciation, even without an allopatric phase.

What is usually not recognized enough, however, is the simple fact that host-plant races cannot form at all if the ancestral species is strictly specialized on a single host plant. In the *Rhagoletis* system (see Berlocher and Feder 2002 for references), the ancestral race of *R. pomonella* evidently fed on hawthorn, and a new race formed on introduced apple. But where did the ability to feed on apples come from? Clearly, it must have been part of a potential range of hosts even before apples were introduced. There must have been at least some ability to recognize and feed on this host, an ability that could later be fine tuned in a process of "genetic accommodation" (sensu West-Eberhard 2003). The probability of such an evolutionary event should increase with a wider host-plant range. Furthermore, assortative mating is necessary for reproductive isolation to evolve in sympatry. In the case of host-plant-driven speciation this could be due to mate choice being influenced by plant-derived substances, a tendency to mate on or near the host plant, differences in plant phenology isolating the populations in time, or differences in plant habitat isolating them in space. All of these possibilities would seem more likely the more different the plants are, and with a wider ancestral host-plant range the differences are likely to be larger.

In our own study organisms, the butterflies, host-plant-driven sympatric speciation (or speciation involving a sympatric phase where the reproductive isolation is strengthened by selection) seems less likely than in some other phytophagous insects. Butterflies are typically very mobile as adults, making strong isolation due to differences in plant habitat requirements unlikely (but not impossible, since even a mobile insect can choose to stay in one habitat if this is favored by selection). They do not typically mate on the host plant, and indeed the adult phase is often only very weakly linked to the larval host plant. Adults do not feed on the host plant used by larvae, in contrast to many phytophagous beetles. We do not rule out the possibility of sympatric speciation, however, especially in sedentary butterflies such as some blues (Lycaenidae), or in cases where plant-derived pheromones are of strong importance for mating. Plant-derived toxic substances could also play a role via aposematic coloration, mimicry, and sexual selection (Willmott and Mallet 2004).

PARAPATRIC SPECIATION

Populations that are isolated by distance may diverge because of environmental differences and divergent selection, even if they exchange genes, and reproductive isolation can evolve as a by-product of the differentiation (Coyne and Orr 2004). It is clearly conceivable that differences in host-plant utilization could contribute to such speciation events, because different host plants may be optimal to use in different parts of the geographical range (see "Specialization and Fragmentation"), and genes for using a particular host (including both preference traits and performance traits) could be part of a whole coadapted set of genes that also includes life-history and diapause characteristics. In the *Rhagoletis* case, for instance, the host-plant races differ in their acceptance of fruits for oviposition (but not in survival, so both hosts are "potential" hosts in our terminology) and also in having pupal diapause regimes that adapt them to the fruiting times of their respective hosts.

Host-plant-driven parapatric speciation should leave a signal in the form of sister species with abutting distributions, differing in host-plant use. As resolved phylogenies become available for butterflies and other phytophagous insects, it will be of interest to search for such evidence. The challenge, as usual for speciation studies, will be to determine whether such pairs of sister species really formed in parapatry or allopatry, but this distinction is of less importance for our purposes. It should also be added that a wider host-plant range could affect rates of parapatric speciation in a more general way: a wider host range may increase the geographical range of the species (see "Diet Breadth and Geographical Range") and hence set the scene for any environmental factor that varies over this range to contribute to divergence between subpopulations and eventually speciation.

TWO-STAGE MODELS

It may well be that the geographical extremes of sympatric and allopatric speciation are rare in their "ideal" form; perhaps real speciation events typically occur between these extremes (Rundle and Nosil 2005). One such intermediate form would be when differentiation starts in allopatry, but reproductive isolation is completed during a stage of secondary contact between the populations. In the allopatric stage there can be divergent selection between the different environments. In the later sympatric or parapatric stage the resulting ecological differences between the incipient species may be of great importance in preventing too-high levels of gene flow, and selection may also act to increase the differences further. This could occur, for instance, because of selection to reduce competition between the two forms, or through selection against the production of unfit

hybrids, perhaps even leading to incipient species preferring to mate with their own kind (reinforcement).

It can easily be seen how differences in host-plant utilization that have evolved in allopatry may be involved in such a process. For instance, Forister (2005) has shown how correlations between preference and performance on particular host plants that have evolved in allopatry are broken by hybridization in the lycaenid butterfly *Mitoura* species complex, which may reduce gene flow between host races. Under this two-stage scenario, a wider host-plant range in the ancestral population should increase the probability that differences in host-plant use will evolve during the allopatric stage, forming the raw material for later completion of the ecological speciation.

ALLOPATRIC SPECIATION

The general importance of this mode of speciation is not denied even by the most ardent champions of sympatric speciation. Allopatric speciation is a likely mode for two reasons: first, the populations involved are physically/geographically isolated from each other to begin with and are thus free to evolve in different directions without gene flow; second, this means that *both* divergent selection and chance processes can contribute to the differentiation and eventual reproductive isolation. Thus, allopatric speciation is possible even when the habitats are identical.

We would like to stress that host-plant-driven speciation is not ruled out even if speciation is always strictly allopatric. The simplest scenario would be when a wider host-plant range increases the geographical range of a species, creating opportunities for later geographical isolation, and for a speciation process that does not further involve the host plants (this would not qualify as ecological speciation in the strict sense). Colonization of a single novel host, which is found in many habitats, such as the colonization of grasses by satyrine butterflies, could promote allopatric speciation in a similar way. It is worth pointing out that such a colonization event always involves *at least* a short stage of using both the old and the new plant, and probably typically involves a more polyphagous stage (see "Colonizations and Host-Range Expansions" and " Synthesis: Speciation Rates"). It is also clearly possible that differential use of host plants in the incipient species could contribute further toward their eventual reproductive isolation. The host plant is a key part of the life of any phytophagous insect, and isolation could evolve as a by-product of divergent selection that involves the host plants in one way or the other, causing hybrids to be unfit for extrinsic reasons (sensu Coyne and Orr 2004; hybrids viable but lack a suitable niche) or intrinsic reasons (hybrids inviable or sterile, e.g., due to epistatic interactions among parental genes).

Synthesis: Speciation Rates

How can host-plant range affect speciation rates? First of all, a distinction has to be made between rates of speciation per se and net speciation rates—the sum of both extinctions and speciation events. The latter measure is the one that is (more or less explicitly) applied when species numbers are simply compared between two sister clades, the standard method to assess the effect of some extrinsic or intrinsic factor on speciation rates. Effects of such factors on extinction risk may thus confound the comparisons, a problem that can only be avoided with methods that explicitly model the probabilities of both speciation and extinction through evolutionary time (Barraclough and Nee 2001). Large, reasonably complete phylogenies and data on branch lengths are necessary for such studies.

Although this has not yet been studied phylogenetically, we find it likely that host-plant range affects not only speciation probability but also extinction risk. Ecological data showing that populations of specialist butterflies have declined over the last decades, at the same time as populations of more polyphagous species have been able to increase and expand their ranges (see "Diet Breadth and Geographical Range") are suggestive in this respect, although not proof of actual species extinctions. If present, this effect of a wider host-plant range on extinction risk would affect the number of species in a clade positively, namely, in the same direction as the effect that we predict on speciation probabilities. Here, we focus the discussion on the latter aspect, but the available data is on species numbers (net speciation rates), and it should be kept in mind that differences in extinction risk may also have contributed to the observed patterns.

As noted above, there is evidence that phytophagous insect taxa are more species rich than their nonphytophagous sister taxa (Mitter et al. 1988), so that the plant-feeding habit evidently somehow promotes higher net speciation rates. This could be due to the fact that feeding at a lower trophic level increases the amount of available resources, or it could be due to the greater diversity of the plant resources as compared to, for example, animal tissues as food (Mitter et al. 1988). The first explanation cannot easily be ruled out as a contributing factor, but it is possible to investigate whether plant diversity has had an effect on insect diversity—over and above any effects of resource abundance—by studying the effects of host-plant range and host-plant shifts on speciation rates within a phytophagous insect taxon. Importantly, Farrell (1998) showed that angiosperm-feeding beetle clades have more species than their sister clades, evidence that angiosperm diversity is part of the explanation for beetle diversity.

At least implicitly, this is the reasoning behind many insect-plant studies, since Ehrlich and Raven's inspiring paper on butterfly-plant interactions (1964). These authors reasoned that plant taxa differ strongly in their (particularly chemical) properties, as a result of selection to defend themselves against herbivory. A plant species that invents a new defence may be free of herbivory and as a result be able to speciate at a higher rate, creating a whole clade of chemically similar species. Because of the chemical diversity among such clades, it is a challenge for an insect to colonize

a new host-plant taxon, but if it manages to do so it may be able to speciate at a higher rate in this new adaptive zone. The pattern that we observe today, where related butterflies feed on related plants, could have created by this rather diffuse form of coevolution (Ehrlich and Raven 1964) or simply through a combination of host-plant conservatism and some insect speciation occurring between relatively rare host-plant shifts, without evoking coevolution (Janz and Nylin 1998). In any case, it would seem that such phylogenetic patterns, where host-plant records have a tendency to follow insect taxonomical groupings, suggest that there is some sort of link between plant variation and insect diversity.

However, it is not clear what the link is (Weingartner et al. 2006). Is it that phytophagous insects tend to quickly radiate into many species when they shift from an old to a new plant taxon? Let's call this scenario (which is consistent with Ehrlich and Raven's [1964], with or without coevolution) the "explosive adaptive radiation scenario." Versions of this scenario are generally invoked to explain the diversity of angiosperm-feeding insects, and often in case studies of host-plant shifts (e.g., Farrell 1998; Cook et al. 2002; Marvaldi et al. 2002). Or is it, rather, that what matters for high net speciation rates in an insect taxon is that it has a wide range of potential hosts (i.e., with several taxonomically distant plant taxa), whether or not they are actually used as hosts at a given evolutionary moment? Let's call this the "plasticity scenario," because a wide potential range means that some "machinery" for plant recognition and metabolization must be present (albeit perhaps often in an imperfect form) even for plants not currently utilized. Such species must be both more evolutionarily plastic and more phenotypically plastic than extreme specialists. The connection is obvious to West-Eberhard's idea that developmental plasticity may promote diversification, by providing more types of "building blocks" for selection to act upon (West-Eberhard 1989, 2003).

In a series of butterfly studies at different taxonomical levels, we are investigating the relative importance of these—not mutually exclusive—scenarios. They may be difficult to separate in practice using phylogenetic techniques, but we have proposed a few possible criteria (Weingartner et al. 2006; Nylin and Wahlberg, in press). First, the explosive radiation process would seem more likely if the plant and insect clades involved are of similar age. Explicit reasons are seldom given for why insects should speciate when colonizing a novel host taxon. It is often said that the new host is a new adaptive zone, but this only means that different ecological niches on this host will be more similar to each other than to niches on other hosts (cf. Futuyma 1998). This could even lower the rate of speciation, if the ancestral host or range of hosts was ecologically more diverse than the new zone. We see three possibilities for the observed patterns of radiation on novel host taxa. The colonization may have occurred early in the evolution of a radiating plant taxon and the insects then rode on this

wave of plant divergence and diverged along with the formation of new niches (as suggested for beetles colonizing angiosperms at an early stage of angiosperm radiation [Farrell 1998]). Such a radiation would also be explosive to the extent that the plant radiation was rapid. There may instead (or also) be "empty niches" in the new zone because it is largely free from competition from other phytophagous animals (this was the process envisaged by Ehrlich and Raven [1964]). This possibility is also more likely if the clades are of similar age, because if an insect colonizes a plant clade that has been in existence for a long time, there is no strong reason to expect it to be free of competitors. A plant clade that diverged recently could, in contrast, have been successful in its radiation because of a new defence that excludes herbivores (Ehrlich and Raven 1964; Farrell et al. 1991).

For the plasticity scenario, age of the plant clades is not as strong an issue, and a third possibility to explain radiation after colonizations is actually that a host-plant shift only looks like a shift from one zone (plant A) to another (plant B) on a phylogeny, because we are studying it long after it happened. The insect may have colonized an ancient and already well-diversified plant taxon, and done so during a stage when it was using both plant A and B and several others as well (a polyphagous species would seem more likely to encounter, accept, and survive on a novel host). The general drive toward specialization after stages of more generalist feeding (Janz et al. 2001; Nosil 2002) will tend to obscure such patterns. Perhaps it has also sometimes obscured the fact that much of the insect diversification occurred in a stage when species in the clade had a wide range of potential hosts, as a result of having a wide zone rather than a novel and/or empty one?

A second criterion could thus be the timing of diversification. Both scenarios postulate an increased net diversification rate in the insect clade following colonization, but the pattern of diversification over time can be expected to differ. An explosive radiation process of ecological release from competition should lead to a fast diversification over a short time span immediately following the colonization. The plasticity scenario, rather, predicts a higher than earlier, but not necessarily much higher, rate of diversification, sustained over a relatively long time span. Thirdly, the pattern of host-plant usage over time is expected to differ between the scenarios (Fig. 15.2). Under the explosive radiation scenario we expect to see a shift from one plant clade to the other, with only a short period of using both hosts, because fitness is expected to be much higher on the new host if it is free of competition or superior in another way that supposedly explains the radiation. Such shifts are likely to look instantaneous when traced onto a phylogeny long after the event. Under the plasticity scenario we may instead see phylogenetic traces of a relatively long-lasting potentially polyphagous stage. This could be in the form of polyphagous species even today using both the ancestral and the novel plants, higher taxa where some species use the novel plant clade and others use the ancestral hosts
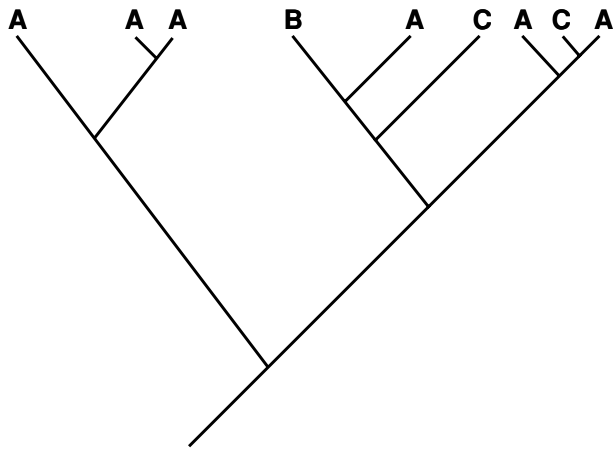
FIGURE 15.3. A hypothetical insect phylogeny with the host plants of the species in the recent environment represented by letters above terminal branches. Although all of the species are specialists, the total range of hosts used in the right-hand clade is wider. This pattern indicates that there must have been several shifts between plants A, B, and C, and that most likely the species at the internal nodes of the phylogeny, the ancestors of recent species, were at least potentially able to feed on more than one of these plants.

(suggesting recolonization), and species that have colonized yet other plant clades, such events presumably being facilitated by the wide potential range of hosts. Finally, testing juveniles for the ability to survive on nonhosts is a fourth key piece of evidence for distinguishing between scenarios (Janz et al. 2001).

To begin with, it should be determined whether diversity of plant utilization is really strongly linked to insect diversity within clades of phytophagous insects. If this is so, a clade where the total range of plants used (all of the involved species could actually be specialists today; cf. (Fig. 15.3) is wider than in the sister clade should on average contain more species. A similar logic was applied in Farrell's beetle study (1998) mentioned above, contrasting ancestral feeding habits (cycads and conifers) with derived feeding on the more diverse angiosperms. In such a study on nymphalid butterflies (Janz et al. 2006), we made use of recent advances in the knowledge of phylogeny of the family Nymphalidae to create sister-group comparisons where the clades differed in diversity of host-plant use, taking into account both number of plant families used and the number of different orders to which they belong.

We found 22 sister-group comparisons differing in diversity of host-plant use, and in 18 of these the number of species was larger in the clade with the most diverse host-plant use, a significant correlation in accordance with our prediction. Host plants can hardly be the only factor that drives speciation rates, and this is demonstrated by the fact that if sister groups were instead chosen in the reciprocal manner, according to whether they differed in the number of species, the correlation was weaker; 16 out of 24 contrasts

had a more diverse host use in the more species-rich clade (not significant in a sign test). Importantly, this also shows that the causality behind our observed pattern is unlikely to have been the opposite one, that is, species-rich clades do not automatically have a more diverse host-plant use.

The reported pattern could conceivably have also resulted at least in part from colonizations of novel hosts followed by radiation, although we find it likely that diverse host-plant use in a clade generally represents a wide potential range in the clade, in line with the plasticity scenario (Fig. 15.3). Furthermore, the explosive radiation scenario should often produce the opposite pattern, where the happy colonizers have radiated dramatically on a single novel host clade, and a smaller group of species in the sister group is doing more poorly on a more diverse set of ancestral hosts.

In any case, there is a need for more detailed studies. In one such (Nylin and Wahlberg, in press), host-plant shifts in the subfamily Nymphalinae were studied, using a recent phylogeny (Wahlberg et al. 2005). Traditionally, there are three tribes in the subfamily: Nymphalini, Kallimini, and Melitaeini. Nymphalini was found to be the sister group to Kallimini plus Melitaeini, but Kallimini was found to be a paraphyletic "grade," with some genera being closer to Melitaeini than others. The "urticalean rosid" clade (Urticaceae and relatives) is the ancestral host taxon for Nymphalini (Janz et al. 2001), and it was found to also be the likely ancestral host clade for Nymphalinae as a whole. A major host-plant shift to the order Lamiales is superficially evident at the base of Kallimini plus Melitaeini, and a second major colonization of a novel order—Asterales— occurred early in the evolution of Melitaeini. This would at first glance seem consistent with the explosive radiation scenario and the general scheme of Ehrlich and Raven (1964). However, a closer investigation reveals that in the basal parts of the Kallimini grade there are species feeding on both urticalean rosids and Lamiales, genera where different species specialize on one or the other of these orders, and several other respecializations on urticalean rosids after the "shift" to Lamiales. In fact, even though this is a very ancient event (probably about 60 million years ago [Wahlberg, 2006]) we can still see traces of what looks like a long-lasting stage of a wider potential host range. Most likely this range once included other plants besides urticalean rosids and Lamiales, but no traces now remain of these more minor hosts.

A long-lasting stage with a wider host-plant range is even more evident in the case of the more recent colonization of Asterales, which is used alongside Lamiales in many genera and even some species throughout the Melitaeini. Work on dating these phylogenies (Wahlberg, 2006) gives further insights. We find both cases of colonizations of (at the time) young plant clades, and other cases where it is clear that the plant clades involved are much older than the butterfly clades (Nylin and Wahlberg, in press).

Finally, returning to the case of Nymphalini (Janz et al. 2001; sections above), but focusing more closely on species

numbers (Weingartner et al. 2006), we find that although only a limited number of contrasts can be made (and some of them are not phylogenetically independent of each other), all of them support our predictions and the general pattern of host use is consistent with the plasticity scenario. The genus *Aglais*, whose larvae feed on the ancestral urticalean rosids, has fewer species than the sister clade *Nymphalis* plus *Polygonia,* whose members use a much wider range of host plants. Based on the fact that the same set of host plants have been repeatedly recolonized in the latter clade, and the fact that juveniles show some capacity to feed on many nonhosts within this set but not on other plants (Janz et al. 2001), we believe that the "backbone" of this clade has a wide potential host-plant range. Within *Polygonia*, there seems to have been several independent respecializations on one or the other family of urticalean rosids, and interestingly this seems to halt the higher speciation rates. In all such instances, there are more species in the sister group, which includes species that use the novel host families.

Conclusion

Host-plant range is dynamic over evolutionary time (Janz et al. 2001; Nosil 2002). We suggest that it is precisely because host specialization is *not* a "dead end" that the guild of plant-feeding insects has been able to become so rich in species. Many previously investigated insect-plant systems could benefit from looking at them again with fresh eyes, not only at the important and very interesting phase where specialization on different plants does its work and may promote speciation, but also at the earlier phase where new host plants were added to the potential range, creating the fuel for host-plant-driven speciation.

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