

Dynamics of host plant use and species diversity in *Polygonia* butterflies (Nymphalidae)

E. WEINGARTNER, N. WAHLBERG & S. NYLIN

Department of Zoology, Stockholm University, Stockholm, Sweden

Keywords:

ecological speciation;
host shift;
polyphagy;
specialist.

Abstract

The ability of insects to utilize different host plants has been suggested to be a dynamic and transient phase. During or after this phase, species can shift to novel host plants or specialize on ancestral ones. Expanding the range of host plants might also be a factor leading to higher levels of net speciation rates. In this paper, we have studied the possible importance of host plant range for diversification in the genus *Polygonia* (Nymphalidae, Nymphalini). We have compared species richness between sistergroups in order to find out if there are any differences in number of species between clades including species that utilize only the ancestral host plants ('urticalean rosids') and their sisterclades with a broader (or in some cases potentially broader) host plant repertoire. Four comparisons could be made, and although these are not all phylogenetically or statistically independent, all showed clades including butterfly species using other or additional host plants than the urticalean rosids to be more species-rich than their sisterclade restricted to the ancestral host plants. These results are consistent with the theory that expansions in host plant range are involved in the process of diversification in butterflies and other phytophagous insects, in line with the general theory that plasticity may drive speciation.

Introduction

The importance of ecological shifts for speciation processes (Schluter, 1998, 2000, 2001) has been studied in various groups of organisms, such as cichlid fishes (for example Schlieven *et al.*, 1994), insects (Bush, 1969; Via, 1999; Brown *et al.*, 2000) and lizards (Losos, 1992). In insects, the ability *per se* to feed on plants has been demonstrated to be involved in diversification processes (Mitter *et al.*, 1988), probably as a result of the chemical diversity of plants as a resource. The dominant strategy among herbivorous insect species seems to be specialization on a set of closely related plants (Eastop, 1973; Ehrlich & Murphy, 1988; Ward & Spalding, 1993). However, Janz *et al.* (2001), when studying the butterfly tribe Nymphalini (Nymphalidae), found that generalists seemed to be more apical in the phylogeny than the specialists and they proposed that host plant range might

be a dynamic trait, with host plants being added as well as lost from the repertoire. This result was further supported by Nosil (2002) in a study where he compared the transition rates between generalization and specialization in 15 insect groups using previously published phylogenetic studies, and found only a slightly higher overall rate from generalization to specialization than *vice versa*, with trends varying strongly among taxa.

It has been proposed (Futuyma, 1989; Mitter & Farrell, 1991) that the diversity of plants, in particular their chemical diversity, could be a factor involved in the strong diversification of herbivorous insects, but if so, the mechanism is not yet understood. According to what could be called the 'explosive adaptive radiation theory', a 'key' character evolves in a lineage that enables it to explore new niches. The availability of new resources as well as new areas to colonize, with other selection pressures and release from competition, could promote speciation processes (see Futuyma, 1986). An example could be the chemical defenses of plants, which are thought to often be limiting for exploitation of the plants by insects (Ehrlich & Raven, 1964). As soon as an insect has been able to overcome that defense, an opportunity

Correspondence: Elisabet Weingartner, Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden.
Tel.: +46 8 164047; fax: +46 8 167715;
e-mail: elisabet.weingartner@zoologi.su.se

for diversification can occur (Ehrlich & Raven, 1964; Mitter *et al.*, 1988). Another hypothesis is what could be called the 'plasticity theory' where species carrying genotypes for plasticity have the ability to (in this case) broaden their resource use (West-Eberhard, 1989, 2003). Such plasticity can function as preadaptations to novel environments and allow organisms to respond differently depending on the environmental conditions. Diversification may be promoted by a process in which different phenotypic variants (in this case with different host plant ranges) become fixed in different subpopulations.

A possible contributing mechanism for the expansion of host plant range in butterflies, of interest for the 'plasticity theory' in particular, might be that some larvae have kept a chemical 'memory' for plants used earlier in the history of the lineage, as suggested by Janz *et al.* (2001) (see also Futuyma *et al.*, 1993, 1994, 1995 for an example concerning beetles). They are therefore pre-adapted to utilize several ancestral host plants not presently used by the female when ovipositing. During certain conditions, where the selective regime changes, this ability can, however, be used and as a result such species are able to rapidly expand their diet. Because of for example competition, predation or physiological trade-offs, some species will later respecialize, some might shift to novel host plants and some might keep the broadened repertoire. If this 'moment' of expanded host plant use, which might last for thousands or millions of years in some cases, can promote diversification (because of higher speciation rate, lower extinction rate or both), we should often see an asymmetric pattern in phylogenies. Clades that include species with a broadened host plant range should be more species-rich than sisterclades including only specialists. This is especially likely to be true if the species in the sisterclade use only ancestral hosts, i.e. hosts used by the taxa just outside of the comparison, because if they instead today specialize on one or more novel hosts this might in fact reflect a 'moment' of expanded host plant range, which has already passed.

Janz *et al.* (2001) found such an asymmetry when comparing the *Nymphalis* + *Polygonia* clade with its sisterclade *Aglais*. The latter genus consists of a maximum of five species (including *Aglais io*, formerly in *Inachis*) that specialize on the ancestral hosts Urticaceae and the related Cannabaceae whereas the *Nymphalis* + *Polygonia* clade includes at least 20 species using a wide range of host plants from different families. Broadening of the host plant repertoire was suggested to have happened in the common ancestor of *Nymphalis* and *Polygonia* although several of the species have since re-specialized on Urticaceae, Ulmaceae and/or Cannabaceae.

Our belief is that the broader host plant range might well have contributed to diversification in this group of butterflies. However, to test this proposition it is needed to study the process in more detail. For this, detailed phylogenies and host plant information is necessary,

which limits the possibilities for true statistical tests. However, it is possible to investigate whether the observed patterns in a phylogeny is consistent with the theory or not, and it can be tested through a series of such investigations in different taxa and at different taxonomical levels.

In the present study we focus on the evolution of host plant use within *Polygonia* and its possible role in diversification. The comma butterfly, *P. c-album*, has been the object of a whole line of studies regarding butterfly and host plant interactions, such as female oviposition preferences and larval performances and information processing in ovipositing behaviour e.g. (Nylin, 1988; Janz *et al.*, 1994; Nylin & Janz, 1996; Janz & Nylin, 1997; Janz *et al.*, 2001). The genus is of particular interest as it contains both generalist and specialist species (see Table 1). The host plant use in close relatives to *Polygonia* is also well known. The ancestral host plants in the tribe Nymphalini (Urticaceae, Ulmaceae and Cannabaceae; see Janz *et al.*, 2001) belong to the plant clade Rosid 1B, specifically the families in the former Urticales, which are now known as the 'urticalean rosids' (Chase *et al.*, 1993; Soltis *et al.*, 2000; Suitsma *et al.*, 2002).

Our hypothesis at this taxonomical level is that clades consisting only of species that are specialized on the ancestral host plants, the 'urticalean rosids', should be less species-rich than their sisterclades if those clades contain species with a broader, or at least potentially broader, host plant repertoire. Our rationale for this was that the former type of clades most likely re-specialized on 'urticalean rosids' soon after the broadening of the host plant range, or at least earlier than in their sisterclades. Hence, they have been specialists for most of their evolutionary history. Thirdly, if this is indeed the case, we address the question of whether the observed patterns support the 'explosive adaptive radiation theory' or the 'plasticity theory'.

Methods

The genus *Polygonia* belongs to the tribe Nymphalini, which has been investigated earlier in a phylogenetic context (Janz *et al.*, 2001; Nylin *et al.*, 2001; Wahlberg & Nylin, 2003). Nylin *et al.* (2001) published a study of the Nymphalini based on morphological, behaviour and ecological characters as well as nucleotide sequence data from the mitochondrial gene ND1 and the nuclear gene *wingless*. Wahlberg & Nylin (2003) reanalysed the previous data set and included new sequence data from the mitochondrial gene for *cytochrome oxidase subunit I* (COI) and the nuclear gene for *Elongation Factor 1 alpha* (EF-1 α). A phylogeny with focus explicitly on the genus *Polygonia* and also including the species *P. haroldi*, *P. oreas* and the subspecies *P. gracilis zephyrus* is in preparation (N. Wahlberg, E. Weingartner and S. Nylin) and this information has been utilized here (Fig. 1). As the

Table 1 Species in *Polygonia*, their host plants and geographical region.

Species	Area	Host plant	Host plant family	Host plant clade
<i>P. c-album</i>	Palearctic	<i>Urtica</i>	Urticaceae	Urticalean rosid
		<i>Ulmus</i>	Ulmaceae	Urticalean rosid
		<i>Humulus</i>	Cannabaceae	Urticalean rosid
		<i>Salix</i>	Salicaceae	Malpighiales
		<i>Ribes</i>	Grossulariaceae	Saxifragales
		<i>Betula</i>	Betulaceae	Fagales
		<i>Corylus</i>	Corylaceae	Fagales
		<i>Parietaria</i> *	Urticaceae	Urticalean rosid
		<i>Vaccinium</i> *	Ericaceae	Ericales
<i>P. c-aureum</i>	Palearctic	<i>Humulus</i>	Cannabaceae	Urticalean rosid
<i>P. comma</i>	Nearctic	<i>Urtica</i> *	Urticaceae	Urticalean rosid
		<i>Urtica</i>	Urticaceae	Urticalean rosid
<i>P. egea</i>	Palearctic	<i>Urtica</i>	Urticaceae	Urticalean rosid
		<i>Laportea</i>	Urticaceae	Urticalean rosid
		<i>Boehmeria</i>	Urticaceae	Urticalean rosid
		<i>Humulus</i>	Cannabaceae	Urticalean rosid
		<i>Parietaria</i>	Urticaceae	Urticalean rosid
<i>P. faunus</i>	Nearctic	<i>Urtica</i> *	Urticaceae	Urticalean rosid
		<i>Soleirolia</i> *	Urticaceae	Urticalean rosid
		<i>Alnus</i>	Betulaceae	Fagales
		<i>Betula</i>	Betulaceae	Fagales
		<i>Rhododendron</i>	Ericaceae	Ericales
		<i>Vaccinium</i>	Ericaceae	Ericales
		<i>Ribes</i>	Grossulariaceae	Saxifragales
		<i>Populus</i>	Salicaceae	Malpighiales
		<i>Salix</i>	Salicaceae	Malpighiales
<i>Urtica</i> *	Urticaceae	Urticalean rosid		
<i>P. g-argenteum</i>	Mexican endemic	?		
<i>P. giganteum</i>	Palearctic	?		
<i>P. gracilis</i>	Nearctic	<i>Ribes</i>	Grossulariaceae	Saxifragales
		<i>Salix</i>	Salicaceae	Malpighiales
		<i>Alnus</i> *	Betulaceae	Fagales
<i>P. haroldi</i>	Mexican endemic	<i>Ribes</i> ?	Grossulariaceae	Saxifragales
<i>P. interrogationis</i>	Nearctic	<i>Boehmeria</i>	Urticaceae	Urticalean rosid
		<i>Urtica</i>	Urticaceae	Urticalean rosid
		<i>Ulmus</i>	Ulmaceae	Urticalean rosid
		<i>Humulus</i>	Cannabaceae	Urticalean rosid
		<i>Celtis</i>	Celtidaceae	Urticalean rosid
<i>P. oreas</i>	Nearctic	<i>Ribes</i>	Grossulariaceae	Saxifragales
<i>P. progne</i>	Nearctic	<i>Betula</i>	Betulaceae	Fagales
		<i>Rhododendron</i>	Ericaceae	Ericales
		<i>Ribes</i>	Grossulariaceae	Saxifragales
<i>P. satyrus</i>	Nearctic	<i>Urtica</i>	Urticaceae	Urticalean rosid
		<i>Humulus</i>	Cannabaceae	Urticalean rosid
		<i>Salix</i> †	Salicaceae	Malpighiales
<i>P. g. zephyrus</i>	Nearctic	<i>Ulmus</i>	Ulmaceae	Urticalean rosid
		<i>Menziesia</i>	Ericaceae	Ericales
		<i>Rhododendron</i>	Ericaceae	Ericales
		<i>Ribes</i>	Grossulariaceae	Saxifragales

Refs: (Scott, 1986; Nylin, 1988; Tolman & Lewington, 1997; Layberry *et al.*, 1998; Krogen, 2000; Soltis *et al.*, 2000; Tuzov *et al.*, 2000; Guppy & Shepard, 2001; Sytsma *et al.*, 2002).

Species names in bold depict taxa here considered as specialists on urticalean rosid plants.

*Host plant has been accepted in laboratory studies.

†Known to be used by a population in Arizona.

position of *Kaniska* is still very unclear (in the analysis of morphological data, it is sister to *Polygonia* whereas analyses of the molecular sequences of COI, *wingless* and EF-1 α put it at a basal position in the *Nymphalis*

clade), we have in this study only considered *Polygonia sensu stricto*. In the phylogeny *P. gracilis* and *P. g. zephyrus* are treated as two separate taxa although they are most likely conspecific (Layberry *et al.*, 1998; Opler & Warren,

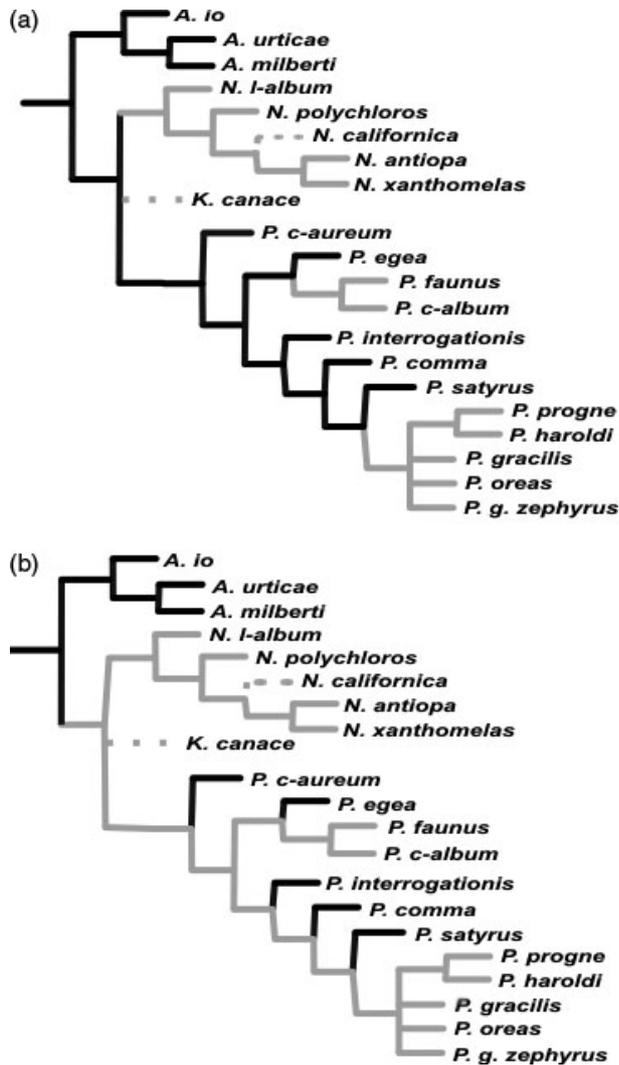


Fig. 2 Phylogeny of *Polytonia*, *Nymphalis* and *Aglais* (Wahlberg *et al.* in prep.) with host plant use. Regarding the position of *Nymphalis californica*, we have preferred the phylogeny of Wahlberg & Nylin (2003) as it also includes morphological, ecological, behaviour data as well as sequences of the mtDNA ND1. Because of the uncertain position of *Kaniska canace* that branch is unresolved. The use of urticalean rosids are marked in black lineages, species with wide host plant ranges are marked in grey and specialization on plant families outside the urticalean rosids are marked with dotted lineages. See also Discussion. (a) the most parsimonious scenario where host plants have been added to the repertoire or where species have shifted to novel host plants (b) scenario where the ancestor to *Nymphalis* + *Polytonia* broadened the host plant repertoire. Several re-specializations have then occurred back to the urticalean rosids.

clade including *P. haroldi*, *P. progne*, *P. gracilis*, *P. g. zephyrus* and *P. oreas*, feeding on Ulmaceae, Betulaceae, Salicaceae and the novel hosts Ericaceae and Grossulariaceae.

Discussion

Regarding predictions from host plant utilization, the clade under study is of course too small to even theoretically obtain either one large comparison, where clades differ significantly in species number, or a high number of smaller comparisons that could be subjected to e.g. a sign test. Still, our results from the four sistergroup comparisons within *Polytonia* do indicate that clades using a broader host plant range are more species-rich than their sistergroups specializing on the ancestral urticalean rosids as hosts. In no case, the opposite pattern was found.

The taxonomy in the Nymphalini clade is not yet fully unraveled. Closely related to *Polytonia* is the genus *Nymphalis* (*sensu stricto*), which contains species utilizing plants from several clades within eurosid I (Soltis *et al.*, 2000), such as Betulaceae, Salicaceae, the urticalean rosids, Rosaceae and Rhamnaceae. Several of the main host plant families are thus in common between the genera, indicating an ancestral ability to potentially feed on them. However, the sistergroup to *Nymphalis* + *Polytonia* is *Aglais* (in the wide sense, including *A. io*), known to be restricted to the urticalean rosids. Comparing species numbers in *Aglais* against *Nymphalis* + *Polytonia* gives us a further comparison in favour of the tested hypothesis, as noted earlier (Janz *et al.*, 2001; Table 2 comparison no. 5). Again, this comparison is not phylogenetically independent of any of the others, but highlights the consistency of the pattern that clades that specialize on the ancestral hosts have fewer species.

Thus, it seems that host plant utilization may well have been involved in the diversification processes in this group of butterflies. Studies on other taxa are under way to test the generality of this finding among butterflies and other phytophagous insects, but to obtain data for such broad studies they have to be made on a phylogenetic level that does not permit detailed investigation of the actual processes involved. The present data set presents an opportunity to attempt to resolve the question of whether the 'explosive adaptive radiation theory' or the 'plasticity theory' provides the most likely explanation for observed patterns.

Figure 2 summarizes the phylogenetic patterns that can be observed. In this figure, species specializing (or nearly so) on the ancestral hosts are marked in black. Note that several species of *Polytonia* belong to this category, so from simple parsimony it would seem that the ancestral specialization on urticalean rosids continued within *Polytonia* (the black 'backbone' of the phylogeny in Fig. 2a), with broadening of the host plant repertoire happening twice. The first expansion then happened in the ancestor of *P. faunus* and *P. c-album*, the other in the ancestor of *P. haroldi*, *P. progne*, *P. oreas*, *P. gracilis* and *P. g. zephyrus*, in the latter case evidently followed by a loss of the urticalean rosids as hosts (an exception is *P. g. zephyrus*, which

can use *Ulmus*). In the case of *P. oreas* and *P. gracilis*, we can only rely on literature reports that they feed on Grossulariaceae; their ability to feed on other plants has not, as far as we know, been tested. The host plant of *P. haroldi* is not known, but has been suggested to be Grossulariaceae as individuals have been found in *Ribes*-rich areas (Krogen, 2000). We consider these three species as potentially polyphagous on the host plants used by the genus.

However, another plausible explanation for the observed pattern, and the one we prefer, is that a broadening of the range actually happened already in the ancestor of *Polygonia* + *Nymphalis* (Fig. 2b), with one or more additional plant colonizations following within *Polygonia*. Although this is a slightly more complex interpretation, it is strongly supported if we also take into consideration the fact that most of the novel host plants in *Polygonia* do not seem to represent independent colonizations of new host plants. The families Salicaceae and Betulaceae are important hosts for both *Nymphalis* and *Polygonia*, and the families Grossulariaceae and Ericaceae are important parts of the repertoire for both of the major clades within *Polygonia* (*P. haroldi* + *P. progne* + *P. oreas* + *P. g. zephyrus* + *P. gracilis* and *P. c-album* + *P. faunus*), but rarely used by butterflies outside of the genus. Therefore, some of the apparent colonizations of these families are likely to be nonindependent to a degree, caused by some common ability to feed on them (Janz *et al.*, 2001). An expanded host plant range most likely thus is basal (grey 'backbone' of the phylogeny in Fig. 2b) with several respecializations back to the urticalean rosids causing the pattern superficially observed.

As mentioned in Methods, it is important to note that the two characters ('specialist on urticalean rosids' and 'using a broader host plant range') are not mutually exclusive and an analysis of the patterns should thus not be considered as a simple parsimony analysis, but needs to take into account the complete picture of host plant utilization. Thus, the interpretation that broadening of host plant range is ancestral to the *Nymphalis* + *Polygonia* clade, and specialization on urticalean rosids a secondary event within this clade, is further supported if we also take into consideration variation among such 'specialists'. Whereas almost all species of Nymphalini outside of *Nymphalis* + *Polygonia* predominantly use Urticaceae as hosts, most often *Urtica* itself, the five *Polygonia* 'specialists' on urticalean rosids (*P. c-aureum*, *P. egea*, *P. comma*, *P. interrogationis* and *P. satyrus*) have a different host plant range (Janz *et al.*, 2001). They utilize several host plant families from within the urticalean rosids (Table 1), generally with a preference for some genus other than *Urtica*.

For a host plant shift to take place, the female has to accept a new plant for ovipositing and the larvae must be able to digest the plant. It is known that females make mistakes and oviposit on plants not normally used, or

oviposit on plants that are even lethal to the larvae (Chew, 1977; Nylin *et al.*, 2000). Several studies also show that larvae can often use a wider range of hosts than that actually used by the female for ovipositing (Wiklund, 1975; Thomas *et al.*, 1987; Janz *et al.*, 2001). Thompson *et al.* (1997) suggest that plant polyploidy can be a route to reach a transient phase of expanded host plant use.

Shifts between the different urticalean rosids seems to have occurred commonly in Nymphalini (Janz *et al.*, 2001), which may not be very surprising as behavioural and physiological preadaptations may facilitate shifts between similar species (Thomas *et al.*, 1987). However, the clade consisting of *P. progne*, *P. haroldi*, *P. oreas*, *P. gracilis* and *P. g. zephyrus* may have lost these ancestral host plants entirely (Fig. 2), although they are used by all other *Polygonia* species [except *P. faunus*, but this species can utilize *Urtica dioica* in the laboratory (Janz *et al.*, 2001)]. In the experiment conducted by Janz *et al.* (2001), larvae of Nymphalini butterflies were tested for their ability to use the host plants used by other species in the tribe. *Polygonia g. zephyrus* was the only species tested of the genus that was not able to use *U. dioica*; however, *P. oreas*, *P. gracilis*, *P. haroldi* and *P. progne* were not tested.

To categorize a species as a specialist or generalist, which needs to be performed in order to test the 'plasticity theory' (West-Eberhard, 1989, 2003), is not entirely straightforward. Firstly, there may be variation within species where some populations use diverse plant species while others are specialists. *Polygonia satyrus* is evidently such a case where the population in Arizona has been reported to feed on *Salix*, which is not known to be used by other populations (Scott, 1986). In the most thoroughly investigated species, *P. c-album*, some populations (like the Swedish one) have a very wide host plant range whereas others (like the English) are much more restricted to *Urtica* (Nylin, 1988; Janz & Nylin, 1997). Secondly, there may be similarities between plant families in e.g. chemical compounds, because of convergence or (more commonly) because of evolutionary relatedness, making the plants more or less equal as host plants despite being placed in separate families. These practical problems can be handled by carefully specifying what is considered to be a specialist, but a third problem is more difficult in theory and practice, namely the evolutionary dynamics of host plant range (Janz *et al.*, 2001). The presence of such dynamics means that we can only see the present situation, and the evolutionary process has to be reconstructed. This is what we have tried to do above in interpreting the pattern in *Polygonia* as a widening of the host plant range followed by several specialization and respecialization events.

In this study, we compared monophyletic clades that only use urticalean rosids, with their sisterclades that use several host plants besides – or instead of – the urticalean

rosids. If, for simplicity, we define all urticalean rosids as essentially the 'same' host plant, the former type of clade includes only specialists whereas in the latter type of clades there may be generalist but also specialist species included. They are either specialists on the urticalean rosids or on novel host plants. The urticalean rosid specialists were then used by us for new comparisons. This is unfortunate in terms of strict hypothesis-testing, but is an unavoidable consequence of the evolutionary dynamics. We are looking at a moment in evolution where some species have broadened the host range whereas other species have already lost host plants. This means that the comparisons within *Polygonia* can be thought of as being between clades that have specialized on urticalean rosids for some time up to and including the present (even though they once had a wider range) and clades where some species currently use other hosts. We assume that even the specialists within the latter type of clades stem from lineages, which have been generalists for a larger proportion of their evolutionary time than those in the sister clade. This is because shifts to the families novel for *Polygonia* (Ericaceae and Grossulariaceae) most likely took time to achieve and took place during a generalist phase, whereas respecialization on the ancestral host may happen more easily and more quickly on an evolutionary timescale. Thus, generalist clades have more species than specialist clades, and our results are consistent with the 'plasticity theory'. They could perhaps also be seen as consistent with the 'explosive adaptive radiation theory', if it was the novelty of the families used by the polyphagous clades that was important for speciation, and not the wide host plant range. However, the fact that most of the 'novel' families actually are shared between species in different parts of the tree speaks for the importance of range rather than for novelty, and hence for the 'plasticity theory'.

Another point in favour of the 'plasticity theory' in this particular case may be the timescales involved. There is a fossil of an *Aglais* species (Kozlov *et al.*, 2002), dated to 11–16 Myr before present. Thus, the split between the *Aglais* and the *Nymphalis* + *Polygonia* clades happened at least 11 Ma, and so then did the initial broadening of the host plant range in the latter clade according to our interpretation. A difference in species richness of just a few species built up over such time scales does not imply an explosive adaptive radiation because of ecological release from competition immediately after a host shift, the process implied by e.g. Ehrlich & Raven (1964), but could be consistent with a higher net diversification rate during a relatively long-lasting polyphagous stage. To more firmly investigate this aspect, age estimates of branches based on molecular clocks will be needed.

There are of course other factors that could, perhaps in combination with host plant use, explain the differences in species numbers that we see. For example, *Polygonia* seems to have had higher net diversification rates in the Nearctic following two separate colonizations from the

Palaearctic (Wahlberg *et al.*, in prep.). However, we can only speculate as to whether this was because of higher speciation rates or lower extinction rates. The potential of a broad host plant range could have been advantageous when the ancestor colonized the Nearctic, and establishment of different locally adapted populations may have promoted speciation in a process where some taxa re-specialized on the urticalean rosids whereas other species specialized on other host plants or kept the broad host plant repertoire.

To conclude, the most important process for the higher net rate of diversification in *Polygonia* and *Nymphalis* than in the sister clade *Aglais* may well have been the ability of these butterflies to broaden their host plant range, with an associated ability to colonize new areas and persist in old areas under change, and perhaps also with differences in host plant use aiding in ecological speciation. This is consistent with the general theory of plasticity as a driver of biodiversity (West-Eberhard, 1989, 2003). However, it remains to be investigated if this is a generally valid explanation for diversification within other butterflies and phytophagous insects.

Acknowledgments

First of all we would like to thank all the people who provided us with specimens for the phylogenetic investigation, without which this study could not have been performed; Jim Beck, Anton Chichvarkhin, Slobodan Davkov, Runar Krogen, James Kruse, Andrew B. Martynenko, Georg Nygren, Jeff Oliver, Bob Parsons, Katy Prudic, Michel Tarrier, David Threatful and Mark Walker. We are especially grateful to Norbert Kondla, Michael Leski and Andrew Warren for providing us with specimens as well as with valuable information regarding the butterflies and to Niklas Janz and anonymous reviewers for useful comments on the manuscript.

References

- Brown, J.M., McPeck, M.A. & May, M.L. 2000. A phylogenetic perspective on habitat shifts and diversity in the North American *Enallagma* damselflies. *Syst. Biol.* **49**: 697–712.
- Bush, G.L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* **23**: 237–251.
- Chase, M.W., Soltis, D.E., Olmstead, R.G., Morgan, D., Les, D.H., Mishler, B.D., Duvall, M.R., Price, R.A., Hills, H.G., Qiu, Y.-L., Kron, K.A., Rettig, J.H., Conti, E., Palmer, J.D., Manhart, J.R., Sytsma, K.J., Michaels, H.J., Kress, W.J., Karol, K.G., Clark, W.D., Hedrén, M., Gaut, B.S., Jansen, R.K., Kim, K.-J., Wimpee, C.F., Smith, J.F., Furnier, G.R., Strauss, S.H., Xiang, Q.-Y., Plunkett, G.M., Soltis, P.S., Swensen, S.M., Williams, S.E., Gadek, P.A., Quinn, C.J., Eguiarte, L.E., Golenberg, E., Learn, G.H. Jr, Graham, S.W., Barrett, S.C.H., Dayanandan, S. & Albert, V.A. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcl*. *Ann. Mo. Bot. Gard.* **80**: 528–580.

- Chew, F.S. 1977. Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. *Evolution* **31**: 568–579.
- Churkin, S.V. 2003. Taxonomic notes on *Polygonia* Hubner, [1818] (Lepidoptera, Nymphalidae) with the description of a new subspecies. *Helios (Moscow)* **4**: 132–147.
- Eastop, V.F. 1973. Deductions from the present day host plants of aphids and related insects. In: *Insect/Plant Relationships* (H. F. v. Emden, ed.), pp. 157–178. Blackwell Scientific publications, London, UK.
- Ehrlich, P.R. & Murphy, D.D. 1988. Plant chemistry and host range in insect herbivores. *Ecology* **69**: 908–909.
- Ehrlich, P.R. & Raven, P.H. 1964. Butterflies and plants: a study in coevolution. *Evolution* **18**: 586–608.
- Futuyma, D.J. 1986. *Evolutionary Biology*. Sinauer Associates, Sunderland, Massachusetts.
- Futuyma, D.J. 1989. Macroevolutionary consequences of speciation: inferences from phytophagous insects. In: *Speciation and Its Consequences* (D. Otte & J. A. Endler, eds), pp. 557–578. Sinauer Associates, Sunderland, Massachusetts.
- Futuyma, D.J., Keese, M.C. & Scheffer, S.J. 1993. Genetic constraints and the phylogeny of insect–plant associations: responses of *Ophraella communa* (Coleoptera: Chrysomelidae) to host plants of its congeners. *Evolution* **47**: 888–905.
- Futuyma, D.J., Walsh, J.S. Jr., Morton, T., Funk, D.J. & Keese, M.C. 1994. Genetic variation in a phylogenetic context: responses of two specialized leaf beetles (Coleoptera: Chrysomelidae) to host plants of their congeners. *J. Evol. Biol.* **7**: 127–146.
- Futuyma, D.J., Keese, M.C. & Funk, D.J. 1995. Genetic constraints on macroevolution: the evolution of host affiliation in the leaf beetle genus *Ophraella*. *Evolution* **49**: 797–809.
- Guppy, C.S. & Shepard, J.H. 2001. *Butterflies of British Columbia*. UBC Press in collaboration with the Royal British Columbia Museum, Toronto, Canada.
- Janz, N. & Nylin, S. 1997. The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. *Proc. Roy. Soc. Lond. B Biol.* **264**: 701–707.
- Janz, N., Nylin, S. & Wedell, N. 1994. Host plant utilization in the comma butterfly: sources of variation and evolutionary implications. *Oecologia* **99**: 132–140.
- Janz, N., Nyblom, K. & Nylin, S. 2001. Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. *Evolution* **55**: 783–796.
- Kozlov, M.V., Ivanov, V.D. & Rasnitsyn, A.P. 2002. Order Lepidoptera Linné, 1758. The butterflies and moths (=Papilionida Laicharting, 1781). In: *History of Insects* (A. P. Rasnitsyn & D. L. J. Quicke, eds.), pp. 220–227. Kluwer Academic Publishers, Dordrecht, Germany.
- Krogen, R. 2000. Records of *Polygonia haroldi* (Dewitz, 1877) in Sonora, Mexico (Lepidoptera, Nymphalidae). *Atalanta* **31**: 67–70.
- Layberry, R.A., Hall, P.W. & Lafontaine, J.D. 1998. *The Butterflies of Canada*. University of Toronto Press, Toronto, Canada.
- Losos, J.B. 1992. The evolution of convergent structure in Caribbean *Anolis* communities. *Syst. Biol.* **41**: 403–420.
- Mitter, C. & Farrell, B. 1991. Macroevolutionary aspects of insect–plant relationships. In: *Insect-Plant Interactions* (E. Bernays, ed.), pp. 35–78. CRC Press, Boca Raton, Florida.
- Mitter, C., Farrel, B. & Wiegmann, B. 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *Am. Nat.* **132**: 107–128.
- Nosil, P. 2002. Transition rates between specialization and generalization in phytophagous insects. *Evolution* **56**: 1701–1706.
- Nylin, S. 1988. Host plant specialization and seasonality in a polyphagous butterfly, *Polygonia c-album* (Nymphalidae). *Oikos* **53**: 381–386.
- Nylin, S. & Janz, N. 1996. Host plant preferences in the comma butterfly (*Polygonia c-album*): do parents and offspring agree? *Ecoscience* **3**: 285–289.
- Nylin, S., Bergström, A. & Janz, N. 2000. Butterfly host plant choice in the face of possible confusion. *J. Insect Beh.* **13**: 469–482.
- Nylin, S., Nyblom, K., Ronquist, F., Janz, N., Belicek, J. & Källersjö, M. 2001. Phylogeny of *Polygonia*, *Nymphalis* and related butterflies (Lepidoptera: Nymphalidae): a total-evidence analysis. *Zool. J. Linn. Soc.* **132**: 441–468.
- Opler, P.A. & Warren, A.D. 2002. *Butterflies of North America. 2. Scientific Names List for Butterfly Species of North America, North of Mexico*. Gillette Museum Publications, Fort Collins, Colorado.
- Schliweng, U., Tautz, D. & Pääbo, S. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* **368**: 629–632.
- Schluter, D. 1998. Ecological causes of speciation. In: *Endless Forms Species and Speciation* (D. J. Howard & S. H. Berlocher, eds), pp. 114–129. Oxford University press, New York.
- Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, New York.
- Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.* **16**: 372–380.
- Scott, J.A. 1986. *The Butterflies of North America*. Stanford University Press, Stanford, California.
- Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M., Savolainen, V., Hahn, W.H., Hoot, S.B., Fay, M.F., Axtell, M., Swensen, S.M., Prince, L.M., Kress, W.J., Nixon, K.C. & Farris, J.S. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcl*, and *atpB* sequences. *Bot. J. Linn. Soc.* **133**: 381–461.
- Sytsma, K.J., Morawetz, J., Pires, J.C., Nepokroeff, M., Conti, E., Zjhra, M., Hall, J.C. & Chase, M.W. 2002. Urticalean rosids: circumscription, rosid ancestry, and phylogenetics based on *rbcl*, *trnL-F*, and *ndhF* sequences. *Am. J. Bot.* **89**: 1531–1546.
- Thomas, C.D., Ng, D., Singer, M.C., Mallet, J.B., Parmesan, C. & Billington, H.L. 1987. Incorporation of a European weed into the diet of a North American herbivore. *Evolution* **41**: 892–901.
- Thompson, J.N., Cunningham, B.M., Segreaves, K.A., Althoff, D.M. & Wagner, D. 1997. Plant polyploidy and insect/plant interactions. *Am. Nat.* **150**: 730–743.
- Tolman, T. & Lewington, R. 1997. *Butterflies of Britain and Europe*. HarperCollins Publishers, London, UK.
- Tuzov, V.K., Bogdanov, P.V., Churkin, S.V., Dantchenko, A.V., Devyatkin, A.L., Murzin, V.S., Samodurov, G.D. & Zhdanko, A.B. 2000. *Guide to the Butterflies of Russia and Adjacent Territories (Lepidoptera, Rhopalocera)*. Pensoft Publishers, Sofia, Bulgaria.
- Via, S. 1999. Reproductive isolation between sympatric races of pea aphids. I. Gene flow restriction and habitat choice. *Evolution* **53**: 1446–1457.
- Wahlberg, N. & Nylin, S. 2003. Morphology versus molecules: resolution of the positions of *Nymphalis*, *Polygonia*, and related genera (Lepidoptera: Nymphalidae). *Cladistics* **19**: 213–223.

- Ward, L.K. & Spalding, D.F. 1993. Phytophagous British insects and mites and their food-plant families: total numbers and polyphagy. *Biol. J. Linn. Soc.* **49**: 257–276.
- West-Eberhard, M.J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20**: 249–278.
- West-Eberhard, M.J. 2003. *Developmental Plasticity and Evolution*. Oxford University Press, New York.
- Wiklund, C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* **18**: 185–197.

Received 29 November 2004; revised 11 July 2005; accepted 25 July 2005