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Butterfly host plant range: an example of plasticity as a promoter of speciation?

Sören Nylin · Niklas Janz

Abstract Mary Jane West-Eberhard has suggested that plasticity may be of primary importance in promoting evolutionary innovation and diversification. Here, we explore the possibility that the diversification of phytophagous insects may have occurred through such a process, using examples from nymphalid butterflies. We discuss the ways in which host plant range is connected to plasticity and present our interpretation of how West-Eberhard's scenario may result in speciation driven by plasticity in host utilization. We then review some of the evidence that diversity of plant utilization has driven the diversification of phytophagous insects and finally discuss whether this suggests a role for plasticity-driven speciation. We find a close conceptual connection between our theory that the diversification of phytophagous insects has been driven by oscillations in host range, and our personal interpretation of the most efficient way in which West-Eberhard's theory could account for plasticity-driven speciation. A major unresolved issue is the extent to which a wide host plant range is due to adaptive plasticity with dedicated modules of genetic machinery for utilizing different plants.

Keywords Butterflies · Insects · Polygonia · Host plants · Development ·
Phenotypic accommodation · Genetic accommodation · Niche · Resource use

Introduction

The idea that phenotypic plasticity can play a major role in evolution is not new (see Shapiro 1976; West-Eberhard 2003, 2005). However, it was pushed to the background of evolutionary biology from the 1960's onwards, in favour of theory and evidence concerned only with variation shown to have a direct genetic basis—rather than plastic variation under genetic control (Shapiro 1976). Interest in plastic phenotypic variation later increased again (see e.g. Stearns 1989; Gotthard and Nylin 1995; Schlichting and Pigliucci

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1998), and recently Mary Jane West-Eberhard has suggested that plasticity may even have a more primary role than genetic mutations in the origin of evolutionary novelties (West-Eberhard 2003) and may therefore also promote speciation (see also West-Eberhard 1989). These ideas remain controversial (de Jong and Crozier 2003; Braendle and Flatt 2006; Moczek 2007).

Here we will explore how a specific case, the evolution of host plant range in phytophagous insects, may relate to West-Eberhard's theory and examine the evidence that plasticity in host plant use may promote speciation. For this we will focus on our data from nymphalid butterflies.

Host plant plasticity as a driver of diversification?

Host plant range and plasticity

West-Eberhard (2003) defines phenotypic plasticity broadly as "the ability of an organism to react to an environmental input with a change in form, state, movement, or rate of activity". Host plant range can be connected to such plasticity in several ways (Nylin et al. 2005) and the case of alternative genotypes using one or several hosts was used to illustrate evolution of phenotypic plasticity in the influential quantitative genetics model by Via and Lande (1985). Most obviously, the host plant is one of the most important environmental aspects for the developing offspring, and if females put eggs on several types of hosts her offspring need to be able to cope with the varying situations. Hosts plants may differ chemically and require different detoxification schemes (Li et al. 2002). More subtle differences in nutrients, water content etc. are also present between host species, affecting larval life history traits and consequently fitness (larval performance; Thompson 1988). To use alternative hosts successfully offspring also need to be able to plastically adjust to this variation and preserve life cycle regulation (Wedell et al 1997; Tikkanen et al. 2000), a real challenge in for instance seasonal environments which put constraints on optimal development (Abrams et al. 1996). An ovipositing female accepting several alternative hosts can in addition be said to be more plastic per se than a more specialized female, because this is most likely a result of her responding to a wider range of environmental input.

There is still limited evidence for (in a strict sense) adaptive plastic responses to specific host plants from most insect–plant associations. Such evidence could consist e.g. of induced expression of different detoxification genes on different plants (Li et al. 2002). In a less strict sense, responses such as prolongation of development time on host plants where larval growth rate is low, to preserve adult size (Nylin 1988) could also be termed an adaptive response (Gotthard and Nylin 1995), although in this case it is much less clear whether a response to a specific plant is involved. In many other cases at least some of the alternative host plants included in the range of generalists will be clearly suboptimal as hosts, resulting in low fitness in every respect, and it is then possible or even likely that the insect lacks plastic responses that are specifically adapted to these plants. However, West-Eberhard's definition (above) does not require the plasticity to be strictly adaptive, and clearly different host plants nearly always affect the form or state of developing juveniles differently. Moreover, the pure ability for at least some individuals to survive to reproduction on poor alternative hosts could well be called adaptive plasticity, compared to genotypes with no fitness at all on anything but a narrow host plant range (Gotthard and Nylin 1995). It suggests the presence of genetic machinery able to cope with a wider range of environments, probably often involving physiological adjustments, i.e. plasticity.

West-Eberhard's theory

At the risk of misrepresenting West-Eberhard's ideas, which are much more thoroughly presented elsewhere (West-Eberhard 1989, 2003), we will very briefly outline the steps of evolutionary transitions using her terminology (in italics)—leading up to how plasticity might facilitate speciation (cf. Fig. 1).

According to this scenario, the first step of an evolutionary change would often be that the phenotype is modified in a new situation through existing plasticity, without genetic change, something she calls *phenotypic accommodation*. This step actually seems to be the most controversial aspect of her theory (de Jong and Crozier 2003; Braendle and Flatt 2006; Moczek 2007). Following West-Eberhard's definition, this should not really be the case when it comes to the concept as such, as it is just a statement of the fact that an organism will try do as well as possible in any situation; if the situation is novel any adjustments to cope with the situation has to be done through behaviour or within the limits of existing plasticity in morphology, physiology and life history. The controversial part rather seems to be West-Eberhard's more or less explicit suggestion that qualitatively different and ultimately adaptive evolutionary novelties might result from such plastic responses. For instance, she frequently returns to the example of a two-legged goat which compensated for congenital paralysis of its front legs by behavioural and morphological accommodation, and speculates that morphological innovations in bipedal primates and
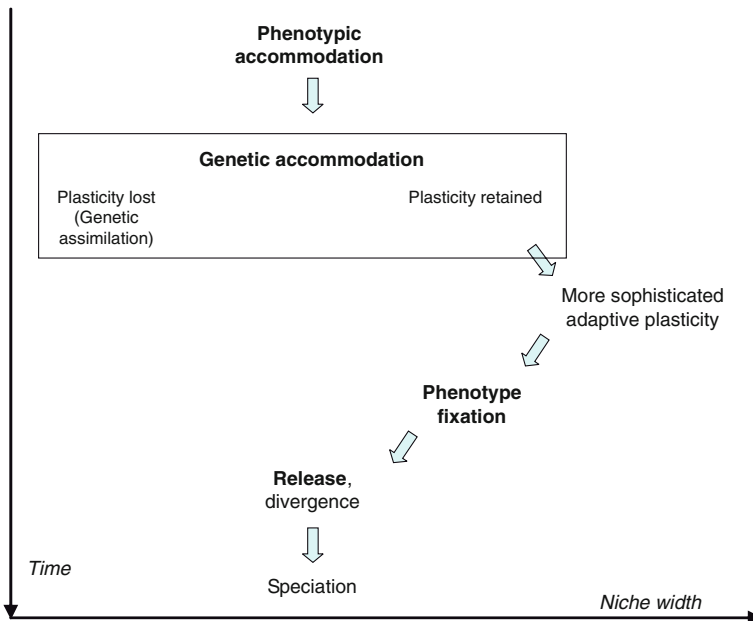

Fig. 1 Our interpretation of how evolutionary changes in ecological niche width relates to the different steps in the scheme for how plasticity could drive speciation, according to West-Eberhard (2003; her terminology in bold letters). Increasing plasticity and generalization (wider niche) to the right in the figure. Note that genetic assimilation can also occur in the "release" phase. There is also a more direct route (not shown) that can be imagined from immediate genetic assimilation to speciation, if the resulting fixation of the phenotype leads to reproductive isolation without a phase with increased niche width. The scope for this to happen should however be less than if a range of adaptive plastic phenotypes has first evolved

kangaroos could have been aided by similar plastic responses (West-Eberhard 2003, 2005). This far-fetched example has done nothing to promote general acceptance of her theory, and we suggest that a better example to illustrate phenotypic accommodation would be a butterfly larva trying to cope with a situation created by an oviposition mistake made by its mother, so that it finds itself on a novel plant for which it lacks specific adaptations.

If the new situation occurs often enough over several generations, and keeps inducing the modified phenotype, genetic changes which improve fitness can be selected for in a process of *genetic accommodation.* This process can be aided by e.g. maternal effects and by learning or induction of traits, because they mean that a plastic trait can be induced in many individuals with varying genetic backgrounds even within a single generation, so that an individual's genotype is not the only determinant of trait expression. Genetic accommodation includes both "traditional" genetic assimilation (where the induced phenotype becomes fixed, or at least more constitutively expressed) and selection for an improved conditional phenotype and improved trait regulation, with the plasticity retained (see Suzuki and Nijhout 2006 for an example). Thus, selection acts on the *developmental switches* that integrate environmental and genetic input to determine which pathway downstream development of phenotypic traits will follow, and it acts on the downstream pathways themselves, improving the resulting phenotypes. The presence of switch points (any conditional branching point in development) means that selection to a degree can act independently on the alternative phenotypes (or downstream trait *modules*); there is some *character release* from the genetic correlations among traits which otherwise prevents developmentally related phenotypes to evolve in different directions even when selection on them differs.

The release of one potential phenotype is higher when it is often the one which is actually induced (so that selection is most effective on this phenotype), and further accelerated if there is *phenotype fixation*, i.e. if only one phenotype is expressed (either due to genetic fixation or because of a consistent environment). Genetic phenotype fixation can occur without selection (i.e. without a stage of genetic accommodation), purely as a result of genetic drift or mutation, when one phenotype is not exposed to and hence not preserved by selection (see also Pfennig and Murphy 2002). It can also be the result of genetic assimilation. Whatever the cause, once one phenotype has been fixed there can be rapid evolution of local specialization and of evolutionary modifications leading to divergence between subpopulations. Such divergence precedes reproductive isolation and can facilitate isolation and speciation.

Applying the theory to host plant range

How could West-Eberhard's ideas apply to the case of insect host plant range? One problem when attempting to answer this question is that her theory is developed mostly in terms of alternative morphological phenotypes resulting from plastic developmental variation. The utilization of one or the other alternative host plant is in contrast a multivariate phenotype, as it potentially involves differences in host searching by females, host recognition by females and larvae, metabolization and detoxification by larvae, and differences in other traits that are co-adapted with host plant utilization. However, the complex nature of host plant utilization as a phenotypic trait also increases the scope for plasticity and developmental switches; rarely if ever will there be a single gene solely determining differences in host plant use.

Most phytophagous insects are relatively specialized (Thompson 1994), and host plant use is phylogenetically constrained so that related insects feed on related (and thus similar) plants, in for instance the butterflies (Ehrlich and Raven 1964; Janz and Nylin 1998). This implies that there is a need for host-specific genetic machinery for host recognition and metabolization, perhaps as a result of the great diversity of plants as food, chemically and otherwise (Ehrlich and Raven 1964).

However, females of phytophagous insects sometimes lay their eggs on plants that are not part of the normal range of hosts (Larsson and Ekbom 1995; Nylin et al. 2000) and in some taxa they even oviposit on almost any substrate and leave the newly hatched larvae to disperse for themselves, in which case many will not find a normal host (Tammaru et al. 1995). Most juvenile individuals ending up in such situations will not survive, but occasionally some will be able to metabolize the new plant, however poorly, as a side-effect of existing genetic machinery. Both finding and being able to use the new plant seems more probable if it is related to existing hosts, and indeed shifts between more closely related plants seem to happen more frequently, at several taxonomical levels (Janz and Nylin 1998). Following the same reasoning, it should be easier to re-colonize an ancestral host plant than to colonize an entirely novel host, because enough of the old machinery may persist for the plant to both be recognized as a potential host and to be metabolized to some degree.

There is evidence of such re-colonization (in West-Eberhard's terminology an example of *recurrence homoplasy*—i.e. when shared traits conflict with phylogeny but still are due to common ancestry) in butterflies of the subfamily Nymphalinae, where a limited number of plant taxa have been repeatedly colonized (Janz et al. 2001; Nylin and Wahlberg in press). From the tribe Nymphalini (cf. Fig. 2) there is also direct evidence from larval establishment trials that larvae can retain some capacity to feed on ancestral hosts for very long time spans (Janz et al. 2001). In this tribe the ancestral host clade is the "urticalean
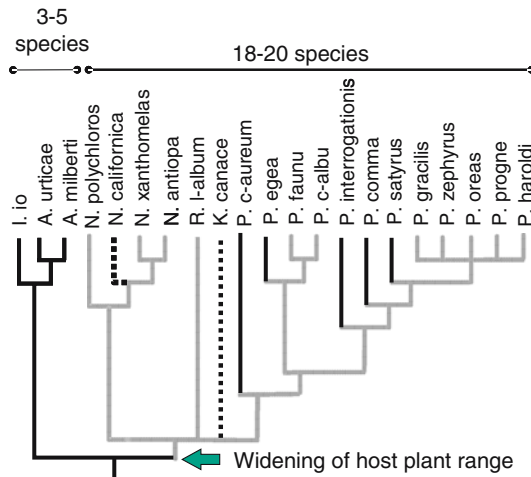

Fig. 2 Phylogeny of a section of the butterfly tribe Nymphalini with reconstructed host plant utilization and species numbers (based on Janz et al. 2001; Weingartner et al. 2006). Lineages depicted in black are specialized on urticalean rosid plant families as larval hosts. Lineages in grey use different combinations of a limited number of taxa: urticalean rosids and the families Salicaceae, Betulaceae, Grossulariaceae (*Ribes*) and Rosaceae. *Dashed lineages* are specialized on novel host families which no other species in the subfamily Nymphalinae utilize: Rhamnaceae in the case of *Nymphalis californica* and Smilacaceae and other monocotyledons in the case of *Kaniska canace*

rosids" (Urticaceae, Ulmaceae etc.) but the host plant range increased at some point, probably first in the ancestor of *Nymphalis* + *Polygonia* + *Kaniska* to include at least Salicaceae and Betulaceae, and then again higher up in the tree to include e.g. the genus *Ribes* in several species of *Polygonia*.

While some species—like the comma butterfly *P. c-album*—remain polyphagous, many species have since re-specialized on urticalean rosids or other plants, sometimes on entirely novel plant clades (Fig. 2). We have suggested that this implies that polyphagous species are more likely to colonize such novel plants (Janz et al. 2001), which is compatible with West-Eberhard's notion that plasticity can facilitate evolutionary innovation. The ability to feed on an entirely novel plant can only occur through phenotypic accommodation, where the organism does its best to preserve function and form in a novel environment. This has to be done via homeostatic regulation and compensatory behaviour (e.g. larvae searching out the best plant tissue to feed on), within the limits of plasticity adapted to the ancestral host plant range, and it follows that an organism with a wider range should be more likely to survive a novel situation. More polyphagous species are also more likely to oviposit on low-fitness novel hosts in the first place (Janz and Nylin 1997), something which as noted above could be described as them being more plastic in their response to environmental input.

If inclusion of the new plant in the normal range of hosts is important enough for fitness, genetic accommodation will follow (or perhaps in extreme cases even rapid genetic assimilation with loss of earlier hosts—left path in Fig. 1). This could happen for instance if the normal host plants have become scarce, due to an environmental change, or after colonization of a new geographical area by the insect. There will then be selection for improved host finding, recognition and metabolization of the new plant, as well as selection on traits that need to be co-adapted to host use, e.g. life history traits and diapause regulation (Janz et al. 1994; Wedell et al. 1997). The evolutionary response to such selection is constrained by genetic correlations among responses to different plants, or in other words by the fact that the machinery and co-adapted traits still have to work for ancestral plants (cf. the model of Via and Lande 1985, where genetic correlations among environments is what constrains the evolution of plasticity). However, some degree of character independence (release) may be possible due to developmental switch points. If both old and new hosts remain important for the population, selection can over time act on the switches themselves to permit more sophisticated adaptations to different host plants, with dedicated modules for their utilization.

A possible outcome, sooner or later in this process, is phenotype fixation, if the new host becomes so important that the insect locally only uses this plant. This fully releases adaptation to the new plant from genetic constraints (and adaptations to alternative hosts are no longer shielded from drift or mutation), and more radical modifications are then possible accompanied by increased specialization on the new plant. Because the host plant is such an integral part of the life cycle of a polyphagous insect, several kinds of traits can be expected to diverge, including those affecting reproductive isolation (habitat choice and mating). Thus, such trait divergence in subpopulations feeding on alternative hosts could facilitate speciation in sympatry or allopatry (see also below, Janz and Nylin 2007 and e.g. Dres and Mallet 2002; Nosil 2007). Note that a specialized species which has followed this route would differ from one which has gone through a process of genetic assimilation with loss of plasticity (without an intervening evolutionary phase with adaptation to new hosts), in that it may retain modules that have evolved for the use of other plants. It may thus have a hidden potential to feed on them again in the future (this is why we have not placed this evolutionary stage in the leftmost column of Fig. 1). This may relate to phenomena such as re-colonizations of ancestral plants (above) and perhaps to the fact that species often retain

relatively wide total host plant ranges despite local specialization (Fox and Morrow 1981; Bergström et al. 2004).

The evidence that diversity of plant use drives insect diversification

Is there any evidence of this process, or something similar to it, having contributed to the tremendous diversification of phytophagous insects? First, clades of phytophagous insects are more rich in species than their sister clades (Mitter et al. 1988). Moreover, the rate of diversification seems to be connected to the diversity of plant use. For instance, Farrell (1998) showed that among phytophagous beetles, clades feeding on the very diverse angiosperms are more diverse than sister taxa feeding on less diverse basal plant taxa. Gómez-Zurita et al. (2007) have recently suggested that chrysomelid beetles are much younger than their host plants and did not co-diversify with them, but if so this does not change the fact that the angiosperm-feeding beetles seem to have radiated in part because of the diversity of their hosts and the wide range of niches that they represent.

From nymphalid butterflies similar evidence is found at several taxonomical levels. In the family as a whole, butterfly clades that include a larger number of plant clades in the total range of reliably reported hosts have more species than sister clades using a more narrow range (Janz et al. 2006). In the subfamily Nymphalinae, the urticalean rosids is the ancestral host clade, and species diversity is higher in parts of the subfamily which have colonized the novel orders Lamiales and Asterales (Nylin and Wahlberg in press). Interestingly, although these colonization events are very ancient, it is still evident that they were facilitated by plasticity. For instance, Asterales was colonized 35–40 Mya from an ancestor feeding on Lamiales, but Lamiales and Asterales are still used side by side in many genera of the tribe Melitaeini (Nylin and Wahlberg in press). In another part of the subfamily, the tribe Nymphalini mentioned above, diversity is higher in clades that use a wider or different range of hosts than only the ancestral urticalean rosids (Fig. 2; Janz et al. 2001), and this is true also within the genus *Polygonia* (Fig. 2; Weingartner et al. 2006).

The connection between diversity of host use and insect diversity thus seems relatively clear, but the connection to plasticity perhaps less so. In some of the examples mentioned most or all of the insects involved are in fact specialists, although they belong to clades where different species feed on different hosts. However, it is notoriously difficult to do phylogenetic reconstructions of niche width because such ecological traits often change too quickly relative to speciation rates (Stireman 2005), and insect host plant range is often evolutionary labile in this manner (Nosil 2002). Specifically, given an overall trend towards specialization (likely to commonly be the case in phytophagous insects, since most are specialists), even if there are episodes of reversals of this trend most recent species will be specialists. The traces of polyphagy in the past can then be seen only as a clade of specialists feeding on a more diverse array of plants. We have argued previously that such clades with a disparate host use should in fact be seen as evidence of a wider host range in the past, relative to sister taxa where all species feed on a single plant clade (Janz et al. 2006). It is evidence of host shifts having taken place at some point in time, and shifts are only possible via a state where the insect have some ability to use both the old and the new host, and probably a wider range as well, i.e. a more plastic state.

Although specialization on different hosts is what ultimately might facilitate speciation, the fuel for this process must come from evolutionarily transient stages where the insect is at least potentially able to feed on a wider range of hosts; that is, if diversity of plant use drives the diversification of phytophagous insects this must happen through oscillations in

host range (Janz and Nylin 2007). This process could occur in sympatry via host plant races, or via a stage in allopatry where specialization on different plants is favoured in different parts of the range due to e.g. variation in plant distributions or latitudinal climatic variation (Nygren et al. 2006; Janz and Nylin 2007). The latter alternative could be facilitated by the fact that a wider host plant range should often lead to larger geographic distributions, over more diverse environments (Janz and Nylin 2007: see also Yeh and Price 2004 regarding plasticity and colonization ability in general).

When we now scrutinize West-Eberhard's scenario for plasticity driving speciation (West-Eberhard 1989, 2003), and how it might apply to insect host plant range, it turns out that our oscillation theory is fully compatible with her scenario and that this example has the potential to demonstrate its applicability and importance. Regarding insect/host plant-relationships and speciation, research has focused on the evolutionary phase where specialists evolve from generalists, e.g. by formation of host plant races which might eventually become separate species (and West-Eberhard also focuses primarily on this phase in her theories on how plasticity might drive speciation). However, a generalist phytophagous insect first need to evolve the ability to feed successfully on a range of plants, i.e. they must stem from relatively more specialized species which were at first only able to include the novel hosts as a by-product of traits permitting use of the existing hosts. This is the gist of our oscillation hypothesis (Janz and Nylin 2007), and we here suggest the possibility that it could be expanded to a general ecological theory of how plasticity-driven speciation is related to niche width:

This is because in our opinion the clearest hypothetical route from phenotypic accommodation to speciation (right path in Fig. 1) should go from a relatively specialized state to a more generalist state and then back to a more specialized state. In the first stage, individuals are specialized in the sense that they lack specific adaptation to the novel environment, and only have some potential to use it with the help of phenotypic accommodation. Genetic accommodation to the new range of environments then follows, including evolution of more sophisticated plasticity with dedicated developmental modules—adaptations to a generalist lifestyle. However, as only phenotype fixation of one or the other of this suite of traits permits full character release and rapid divergence, re-specialization is necessary to promote speciation. In other words, oscillations in niche width could be the most efficient way for plasticity to promote diversification in an ecological context.

An unresolved issue

There is one aspect of the scenario presented above that needs clarification. To what extent does the genetic machinery for recognizing and metabolizing plants consist of specific developmental modules, linked by developmental switches? There is some evidence that machinery associated with feeding on ancestral hosts can persist over long time spans, permitting re-colonization (Janz et al. 2001; Nylin and Wahlberg in press), but is this machinery a preserved dedicated module or is the ability to feed on the ancestral plant just a side-effect of the same ability to feed on old and new plants that permitted a shift in the first place? If evidence is found showing that genes that are specifically adapted for feeding on ancestral plants in fact do persist, do internal switches also persist, so that the insect to some degree can respond adaptively to both old and new plants?

And this is just an example of a more fundamental question: to what degree does any example of a wide host range represent adaptive developmental plasticity? True, West-Eberhard's definition of developmental plasticity and her process of phenotypic

accommodation do not call for plasticity to be strictly adaptive (and as noted above, there is a weaker sense in which the ability to feed on a wider range of plants can be termed adaptive per se). The result of genetic accommodation to a new host plant would by definition be adaptive in a strict sense, as it is a result of selection for using the plant. However, it can only happen to the degree that this module can develop independently because of the presence of at least a crude developmental switch (the simplest of which would be a direct, initially non-adaptive, plastic effect of host plants on development).

Furthermore, it would seem that the later stages in her scenario—full character release and rapid modification of the new phenotype—can only be powerful processes if more sophisticated switches and thus more independent dedicated developmental modules have evolved, prior to phenotype fixation. The best evidence for the presence of such switches and modules would be demonstrations of clearly adaptive plasticity, with specific responses to different host plants. This would show that such species are in fact *polyspecialists*, adapted to several niches, rather than true generalists adapted to a wide niche (West-Eberhard 2003). Future research will have to show to what extent there is such evidence from insect–plant systems, or whether a wide host plant range more often is permitted by "general-purpose genotypes" (Shapiro 1984), capable of taking on distantly related plants using the same basic genetic machinery. Although the latter possibility would not rule out a role for West-Eberhard's ideas in insect–plant studies, it would weaken the case for explaining the tremendous diversification of phytophagous insects.

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