

On oscillations and flutterings—A reply to Hamm and Fordyce

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The diversification of plant-feeding insects is seen as a spectacular example of evolutionary radiation. Hence, developing hypotheses to explain this diversification, and methods to test them, is an important undertaking. Some years ago, we presented the oscillation hypothesis as a general process that could drive diversification of this and similar interactions, through repeated expansions and contractions of host ranges. Hamm and Fordyce recently presented a study with the outspoken intention of testing this hypothesis where they concluded that the oscillation hypothesis was not supported. We point out several problems with their study, owing both to a misrepresentation of our hypothesis and to the methods. We provide a clarifying description of the oscillation hypothesis, and detail some predictions that follow from it. A reanalysis of the data demonstrated a troubling sensitivity of the “SSE” class of models to small changes in model specification, and we caution against using them for tests of trait-based diversification. Future tests of the hypothesis also need to better acknowledge the processes behind the host range oscillations. We suspect that doing so will resolve some of the apparent conflicts between our hypothesis and the view presented by Hamm and Fordyce.

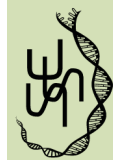
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In a recent article in *Evolution*, Hamm and Fordyce (2015) published an analysis of “Patterns of host plant utilization and diversification in the brush-footed butterflies,” which was presented as a test of our “oscillation hypothesis” (OH) (Janz et al. 2006; Janz and Nylin 2008; Nylin and Janz 2009). This study joins another recent article (Hardy and Otto 2014) in claiming that macroevolutionary patterns among Nymphalid butterflies are not compatible with the OH. While we were pleased to note their shared interest in macroevolutionary dynamics, we are concerned by their portrayal of the OH as well as the applicability and interpretation of their analyses. It should be noted that our comment deals only with the aspects of these articles that pertain to our hypothesis.

We focus on three of our primary concerns. The first is that one of the main predictions in the Hamm and Fordyce article attributed to our OH is, in fact, not a prediction of the OH. The second is that some of the models used were questionable choices for testing the hypothesis. The third concern is that the results

of Hamm and Fordyce were ambiguous, and were actually often not in disagreement with the OH. Yet this ambiguity and potential agreement with the OH was not reflected in the authors’ conclusions.

We suspect that some of the issues we have with the portrayal of the OH by Hamm and Fordyce (and Hardy and Otto) are caused by misunderstandings of our hypothesis, but some issues are probably caused by diverging views of how host shifts happen and how changes in host use may influence patterns of speciation. We will therefore begin with a short description of the OH to make it clear how we envision the process and where we think it differs from the alternatives expressed in these two articles. Next, we offer a reanalysis of the Hamm and Fordyce dataset to demonstrate the troubling sensitivity of the models used to small changes in input variables and initial parameters. Finally, we argue that the conclusions regarding the OH made by Hamm and Fordyce, as well as by Hardy and Otto, are not substantiated.



The Oscillation Hypothesis

Our first clarification is that the OH consists of two parts. The first is largely microevolutionary, and deals with how novel host plants are incorporated during host expansions and how as a consequence insect lineages can diversify in resource use. The second part is largely macroevolutionary, and predicts that these episodes of wider host use should lead to elevated diversification rates. These parts contribute different pieces to the puzzle that is the oscillation hypothesis. To some extent they are independent, in that evidence for one is not necessarily evidence for the other, but they are connected. The particulars of the microevolutionary part affects the specific patterns expected at the macroevolutionary level.

An essential tenet of the first part is that host shifts represent the endpoints of a process that involves at least two components: a host expansion followed by a loss of the ancestral host (specialization). This is, in a very condensed form, an example of a host range oscillation. The period of multiple host use may be brief, but can also extend over considerable lengths of time, and involve many host species. The main objective of this part of the hypothesis is to explain how novel plants are incorporated, but also how this affects the overall patterns of host plant colonization in a clade.

An early inspiration for the hypothesis came from the surprisingly high amount of host plant colonizations seen in the tribe Nymphalini (Janz et al. 2001), something that seemed to contradict observations of high host plant conservatism in butterflies (Ehrlich and Raven 1964; Janz and Nylin 1998). This observation has later been generalized as the “parasite paradox” (Agosta et al. 2010): groups of highly specialized parasites appear to shift hosts more readily than expected, given their conservative and specialized host associations.

An important key in the resolution of this paradox is that there are two types of oscillations, and the difference between them is important (Fig. 1). The first kind involves colonizations of truly novel hosts that are not represented in the evolutionary past of the lineage in question. These should be rare events. The other kind represents recolonizations of ancestral hosts that have been lost and should be much more common (c.f. Ouvrard et al. 2015).

Any successful colonization requires some preexisting ability to use the host. This may also appear paradoxical, but since selection can only act on expressed traits, the colonizing insect must show some positive realized fitness on the novel host already at the first encounter. This is known as ecological fitting (Janzen 1985; Agosta 2006), and is a necessary first step that sets the stage for further evolutionary modification of the trait. In the terminology of West-Eberhard, phenotypic plasticity in the insect can allow for phenotypic accommodation to a novel plant, later followed by genetic accommodation (West-Eberhard 2003; Nylin and Janz 2009).

In the case of recolonizations, it is easy to see how there can be a significant overlap between the abilities required to feed on current hosts and those required to recolonize ancestral hosts that may have been lost through specialization. Indeed, it appears that the ability to use “lost” hosts may remain for a considerable time, making recolonizations common (Futuyma et al. 1995; Janz et al. 2001; Nylin et al. 2015). The result is a dynamic and complex pattern of host use, where species vary both in host range and actual hosts used, but appear to draw their hosts from a common pool of plants (Fig. 1). These changes in host use can be very rapid, as they are effectively changes in actual host use within a relatively stable potential host range. Colonization of such ancestral “lost” hosts is a form of recurrence homoplasy (West-Eberhard 2003; Nylin and Janz 2009), and we believe that it is crucial to understanding host range dynamics.

Preexisting abilities can also be coopted to handle truly novel hosts through ecological fitting (Agosta and Klemens 2008; Agosta et al. 2010). Indeed, there is a sense in which “diversity begets diversity” also for host use (Janz et al. 2006); the potential overlap in the abilities required to handle existing and novel hosts should be higher in generalist species, due to their higher degree of plasticity in host preference and metabolism (García-Robledo and Horvitz 2011). The circumstances that may trigger such expansions are likely to be connected to climatic or other large-scale changes causing biotic turnover in ecological communities (Winkler et al. 2009; Jahner et al. 2011; Nyman et al. 2012; Hoberg and Brooks 2015).

Another important consequence is that it is important to maintain the identity of the hosts used when testing the OH. This is the first point that Hamm and Fordyce failed to take into account. Implicit in their reasoning is a view where species can shift associations freely and instantaneously, unconstrained by history and plant phylogeny. This assumption is even made explicit in the other recent study claiming to find phylogenetic evidence against the OH (Hardy and Otto 2014), which used a similar methodology as Hamm and Fordyce.

Hardy and Otto (2014) rejected the OH and instead suggested an alternative scenario (the “musical chairs hypothesis”) that implied instant shifts in host use among specialized species. To the extent that we can detect an alternative hypothesis in the Hamm and Fordyce article, it appears to be based on similar thinking. It is worth noting however that Hardy and Otto had to incorporate a host use “lability” parameter in order to support their alternative hypothesis. Interestingly though, since the only states in the model were “specialist” and “generalist,” the term represented lability in host range. In other words: host range oscillations. To the extent that their methodology is reliable (see below), their proposed solution relies on a “lability” term that is left unexplained. We believe that the first part of the OH outlined above provides an

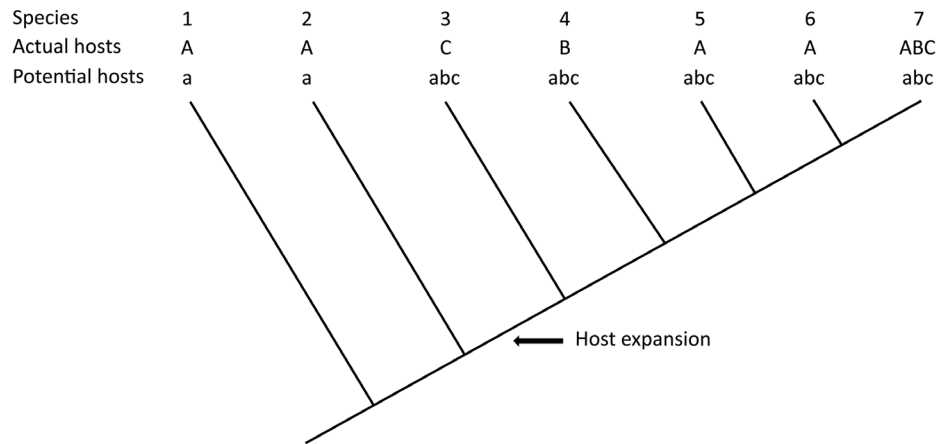


Figure 1. A schematic representation of oscillations in actual and potential host range. The ancestral state (species 1–2) is specialization on host A. The arrow indicates an event where the host range was expanded to also include the novel hosts B and C. Species 3–6 later specialized on one of A–C as actual hosts, but retained some capacity to potentially use all of the hosts (a–c). Thus, species 7 could later again expand its actual host range to include A–C. Note that there are more species in the clade consisting of species 3–7, with more diverse host use than in the sister clade (species 2), but that actual polyphagy (species 7) is recent and has not promoted diversification.

explanation for why some lineages have a “labile” host use and others do not (Fig. 1).

The second part of our hypothesis predicts that clades that have undergone the oscillations outlined above should be more species-rich compared to clades that have remained specialized on the same host (Janz et al. 2006). The argument behind this is that host expansions are necessary to provide the “fuel” for host-driven diversification, whatever the mechanism behind the actual speciation events. One possibility is that large geographic distributions tend to be associated with expanded host ranges (Päivinen et al. 2005; Jahner et al. 2011; Slove and Janz 2011; Slatyer et al. 2013), and that species with larger distributions will tend to become fragmented with time due to both neutral and adaptive processes (DeChaine and Martin 2004; Thompson 2005). Another possibility is sympatric speciation via “host races” specializing on different parts of the extended host repertoire. We do not expect the differences in speciation rates to be necessarily dramatic, but that they can nevertheless result in considerable amounts of diversification over time. It is worth pointing out that even if host plants can play a direct role in speciation (through for example host races), at least in the case of butterflies we expect the majority of these speciation events to be allopatric (Janz and Nylin 2008). In these cases, host associations only play a passive role in speciation, by increasing the likelihood of placing populations in vicariance. Most of the subsequent specialization would then occur in allopatry (c.f. Rich et al. 2008). Importantly, both types of host-driven speciation involve an element of specialization, either as a direct cause of speciation (as with host races) or as a passive consequence of speciation (as in allopatric speciation). Hence, in both cases, the process would soon run out of fuel unless it is

somehow being “refueled” with new host associations. We argue that the oscillations described above can provide that fuel.

We should thus expect a connection between host breadth and speciation, but this is not to say that generalist lineages should diversify at higher rates than specialist lineages. This may sound like a contradiction, but if polyphagy is evolutionarily ephemeral, any direct link between the two will be lost in time (Fig. 1). It is the repeated oscillations that we believe should lead to higher diversification rates, not the generalist state. Or, to put it another way, we do expect lineages with a wider range of potential hosts (as indicated by a more diverse host use in the clade) to diversify at a higher rate, but such lineages will often be made up of species with narrow ranges of actual hosts.

Testing the Right Hypothesis

In summary, host range oscillations should lead to diversification of host use, as well as increased “lability” in host range, and such repeated oscillations should increase the average rate of speciation. We want to emphasize though that we do not believe that such oscillations are the sole source of insect diversification. Precisely for this reason, we included a reciprocal sister group comparison in our first test of the hypothesis, as a means to test for causality behind the contrasts in species richness (Janz et al. 2006). We found that groups with higher host diversity were consistently more species-rich than their sister groups. On the other hand, the reciprocal test showed that groups with high species richness did not necessarily have higher host diversity than their sister clades. In other words, while higher host diversity was almost always followed by higher species-richness, some

groups diversified for other reasons. Importantly though, in these cases the higher species richness should not be, and were not, accompanied by higher host diversity.

Hence, when Hamm and Fordyce in the first test in their article concluded that major differences in diversification rates among nymphalid butterflies were not correlated with wide host ranges, it was not the OH but our alternative hypothesis they tested. Their results were not surprising; we came to the same conclusion, albeit using a different methodology, nearly a decade ago (Janz et al. 2006).

Before going into details about the methodology, we would like to end this part by listing several explicit predictions that follow from the OH, many of which should be testable (or have been tested) using phylogenetic methods (see references for more elaboration):

1. Clades that undergo oscillations should have higher diversification rates, so that clades with more diverse host use should tend to have more species than their sister clades. However, since species may diversify for many reasons, species rich clades should not necessarily be expected to have a more diverse host use (Janz et al. 2006).
2. While clades with diverse host use could be comprised of species specialized on different plants, such clades should also contain more generalist species (Nylin and Wahlberg 2008).
3. Following a host expansion, different descendant clades may follow different paths with regard to host use, but we should expect plants used in related clades to occasionally turn up as hosts within the more dominating plant theme, that is the broader collection of hosts used by this lineage of herbivores (Nylin and Wahlberg 2008).
4. Host shifts should predominantly involve ancestrally used host plants, forming part of a “potential” repertoire, that is we expect much recurrence homoplasy (Janz et al. 2001; Nylin and Janz 2009; Nylin et al. 2015).
5. Phylogenetic signal should be stronger for “potential” hosts than for actually used hosts (c.f. Janz et al. 2001; Nylin et al. 2015).
6. Truly novel host colonizations should be more common in generalists (Janz et al. 2001).
7. Generalists should have larger geographic ranges, which would increase the likelihood of allopatric speciation (Slove and Janz 2011).

Choosing the Right Model

The second troubling aspect of the Hamm and Fordyce article from our perspective is that some of the methods were not particularly well suited to test the OH. Moreover, the results were ambiguous; some outcomes were not in agreement with the OH,

but many were. For reasons that are not clear to us, the authors chose to emphasize the deviating results. Here, we focus on one case that is particularly illustrative, for several reasons. Much of this critique also applies to the analyses by Hardy and Otto (2014).

Hamm and Fordyce estimated diversification rates in relation to host plant breadth across the phylogeny, using the models BiSSE (with host range coded as a binary character) and MuSSE (with host range coded as a multistate character), as implemented in the R package “diversitree” (FitzJohn 2012). As should be clear from the preceding section, an obvious shortcoming of these analyses is that they do not take into account which plants make up the host range. As described above, the history of host use is an important predictor for future host colonizations in the OH (Janz et al. 2001; Nylin et al. 2015). Moreover, there was no measure of host plant relatedness, only a uniform scale of number of plant families used. Again, this could also have important consequences for the outcome.

Nevertheless, even setting these caveats aside, the analyses gave very different results depending on how host range was coded. When using a binary coding, and restricting the “specialist” state to genera using only one family, the model yielded a result where specialists had higher rates of diversification than generalists. This result could be construed as going against the OH (with the important caveats given above regarding other sources of diversification, as well as actual vs. potential hosts). However, with all other methods of coding, the results were in agreement even with a simplified interpretation of the OH that states that generalists should have higher diversification rates than specialists. The authors argued that more inclusive definitions of specialists (such as being restricted to two plant families or one order) are not “biologically informative,” a statement that we find quite remarkable, and rather unsubstantiated. What is interesting is that different ways of coding host range yielded such different results, and it would have been interesting to see a more thorough discussion of this. On the face of it, it does seem a little counterintuitive that speciation events are shifted towards the generalist category when this category is made less inclusive. This in itself should be a reason for some concern.

Interestingly, the MuSSE results indicated that both mono- and polyphagous states had higher diversification rates than intermediate states. This also appears somewhat puzzling, but may perhaps be explained by the large subfamily of Satyrinae—many of which are specialized on grasses—which presumably accounts for much of the diversification on specialist branches. The diversification of Satyrinae on the geographically widespread grasses is an interesting special case, which we discussed in our original publication and that has also seen more extensive treatment since then (Peña and Wahlberg 2008; Peña et al. 2010).

As tests of the OH, another significant limitation of the BiSSE and MuSSE models is that they only allow for anagenetic

changes in host range. That is, specialization and colonization cannot happen during speciation events, something that is highly problematic when the hypothesis under test predicts a relationship between speciation and changes in host range. In this respect, the Hardy and Otto analysis did somewhat better, as they also used the BiSSE-ness alternative, which does allow for cladogenetic change in host use.

A Reanalysis

To further explore the usefulness of the “SSE” modeling approach, we have reanalyzed the dataset (available at <http://doi.org/10.5061/dryad.p5v8g>) using the similar model ClaSSE (Cladogenetic State change Speciation and Extinction), also available in the *diversitree* package. Like BiSSE-ness, ClaSSE can explicitly model both anagenetic and cladogenetic state changes (Goldberg and Igić 2012), making it a somewhat more realistic choice over BiSSE and MuSSE. See Supplementary Material 1 for a description of the method and a more detailed account of the results.

First, according to the estimated posterior probability distribution of each parameter, our results correspond qualitatively with the results from Hamm and Fordyce, for the parameters that represent anagenetic change (transition rates). Note, however, that the inclusion of cladogenetic state change alters the results related to speciation rates (Fig. S1). Even when the “specialist” state was restricted to genera using only one family, diversification rates were higher for generalists whether it was linked to state change or not. The highest rate was the speciation of generalists without state change, followed by the speciation of generalist lineages into specialist daughter species. Speciation rates of parent specialist lineages with and without state change were similar and at least 10 times smaller than that of generalist lineages.

In order to understand why our results differed from those of Hamm and Fordyce, we evaluated the sensitivity of the analysis to the initial parameters of the maximum likelihood estimation. Surprisingly, small changes in such parameters yielded very different results (Fig. S2), showing that the “SSE” modeling approach lacks robustness.

Evidently, relatively small changes to the model were enough to produce results that are in accordance with the expectations from a simplified version of the OH, even if there was still a high sensitivity to character coding and model specification. Moreover, the ClaSSE model shares many of the other issues with regard to testing the OH, in that it ignores all of the qualifications given above. Finally, and perhaps even more disturbing, others have cautioned against current implementations of these methods for investigating trait-dependent diversification at all, as they tend to produce spurious associations between character state and speciation rate (Type I error) due to phylogenetic pseudoreplication

and other unknown model inadequacies (Maddison and FitzJohn 2015; Rabosky and Goldberg 2015).

Conclusions

The main conclusion from our reanalysis of Hamm and Fordyce’s data is that the “SSE” models are so sensitive to small changes in input variables and model specification that they can potentially give any result you want. In the light of this, and the other problems mentioned above, we would caution against using the “SSE” models to test the OH specifically and for testing trait-based diversification in general.

We do welcome the interest in the oscillation hypothesis, and look forward to a continued discussion of it in the future, for example on how to work out accurate and fair tests of it. To do this, we consider it crucial to acknowledge the processes that we mean are causing the host range oscillations, and to preserve the identity of the plants in the insects’ host ranges. This may also serve to resolve some of the apparent conflicts between our hypothesis and the alternatives recently presented by Hamm and Fordyce and Hardy and Otto. For example, the evolutionary “tinkering” among descendant species, where they mix and match between plants contained within an ancestral oscillation, may provide an explanation for the host use “lability” suggested by Hardy and Otto (2014).

Oh, and the word “oscillation” should not be taken too literally. We do not mean to imply that host expansions happen with regular frequency and amplitude. Perhaps “fluttering,” as suggested by Hamm and Fordyce, would be a more accurate description. But then again, would not “the fluttering hypothesis” sound kind of silly?

DATA ARCHIVING

The doi for our data is 10.5061/dryad.p5v8g.

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Supporting Information

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Table S1. Model fitting results in a maximum likelihood framework.

Figure S1. Posterior probability densities of estimates of speciation (λ), extinction (μ) and transitions (q) rates from MCMC analyses when specialists were defined as feeding on one plant family (A), two or fewer plant families (B), three or fewer plant families (C), and four or fewer plant families (D).

Figure S2. Posterior probability densities of parameters estimates from MCMC analyses when specialists were defined as feeding on one plant family, for different combinations of starting parameters.