

Mutual coevolution in Müllerian mimicry?

Arguably, new data suggest yes

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My research on *Heliconius* butterflies has been motivated by one main question: did *H. erato* and *H. melpomene* influence each other's wing patterns? I personally find this an interesting question for two reasons. First, classical mimicry theory, following from Müller's model of 1879 (1) predicted mutual convergence (2) (3). It's therefore of great interest for the history of science to know whether this prediction was met in the real world. Second, the nature of coevolution between these species must surely be key to understanding the counterintuitive diversity of their mimic wing patterns.

Butterfly mimic has prompted a rich range of evolutionary theory, leading to calls for new data to contribute on the numerous theoretical debates (4). I'm, therefore, especially interested in applying new methods of analysis to see what the data say.

We've previously looked at the timing of divergences in the two species, taking into account their population sizes (5), and at reconstructing their biogeographic histories using phylogeographic models (6). Most recently, my co-authors and I have applied new methods of machine learning to directly analyse wing pattern convergence across the Natural History Museum collection of these species (7).

Comparative analyses

After statistically exploring wing pattern convergence across our entire dataset of ≈ 1200 butterflies and a reduced dataset with hybrids excluded (analyses which together make up the majority of our paper), we then dug down into details of 4 comparative analyses (which are the main subject of this blog post). These were pairwise comparisons (covering 12 subspecies in total) including matched mimic pairs of sister-groups (or close relatives). Comparative analyses like these give information on the likely direction of evolution from the ancestral type of phenotype to the descendent type of phenotype within each species (Aside 1).

Aside 1. Comparative analysis aims to help get past the problem that we don't usually know directly what ancestors looked like (in contrast to examples with an excellent fossil record, which isn't the case for butterflies, or where we can watch each evolutionary step like in experimental bacterial evolution or evolutionary simulations). However, one question inherent to comparative analysis is how to polarise the arrow of evolutionary change. Which of two living sister groups is most likely to be the most representative of

their ancestral phenotype? To answer this question we used independent information from their published genetic phylogenies, biogeographic distribution and discussions in the literature (and you can see a more detailed discussion of this in the paper itself). We also ran each comparative analysis backwards for comparison (with a reversed arrow of evolutionary change), as well as with hybrids included versus excluded.

Case study 1. Quantitative data on an old argument

*‘[Because *H. erato* is generally more abundant... there is no doubt that its presence has strongly influenced the evolution of the *H. melpomene* pattern. Thus, to be certain that coevolution has occurred, it must only be shown that *H. melpomene* has some reciprocal impact on the evolution of *H. erato*.]’* (8)

One of our comparative analyses (which is briefly discussed in our paper and presented in a supplementary figure) was selected because it relates to an interesting (and long-running) discussion in the *Heliconius* literature. In the 1983 edition of the book *Coevolution*, Professor Gilbert suggested that one way to see whether *H. melpomene* had ever influenced *H. erato* was to look for something broadly analogous to a knock-out experiment: where the geographic range of *H. erato* extends beyond a potential influence from *H. melpomene*, did *H. erato* evolve different wing patterns? Prof Gilbert hypothesised that it had in the case of *H. erato petiverana* from Mexico.

With our quantitative analyses of the wing patterns, we found that outside the local mimicry group with *H. melpomene*, *H. erato petiverana* has diverged onto a pattern with a narrower hindwing band than that of the nearby co-mimics. So, comparative analysis of wing patterns meets the hypothesis under a reciprocal influence on mimicry from *H. melpomene*.

However, in his recent blog post discussing our paper (9), Prof Mallet suggests that this one case could essentially be a coincidence that doesn't itself prove that *H. melpomene* was influencing *H. erato*. The very fact that *H. erato* and *H. melpomene* share most of their geographic ranges means we have few opportunities for such natural knock-out experiments.

So, is there an example of positive convergence that actually demonstrates mutual coevolutionary influence?

Case study 2. Novelty through reciprocal convergence

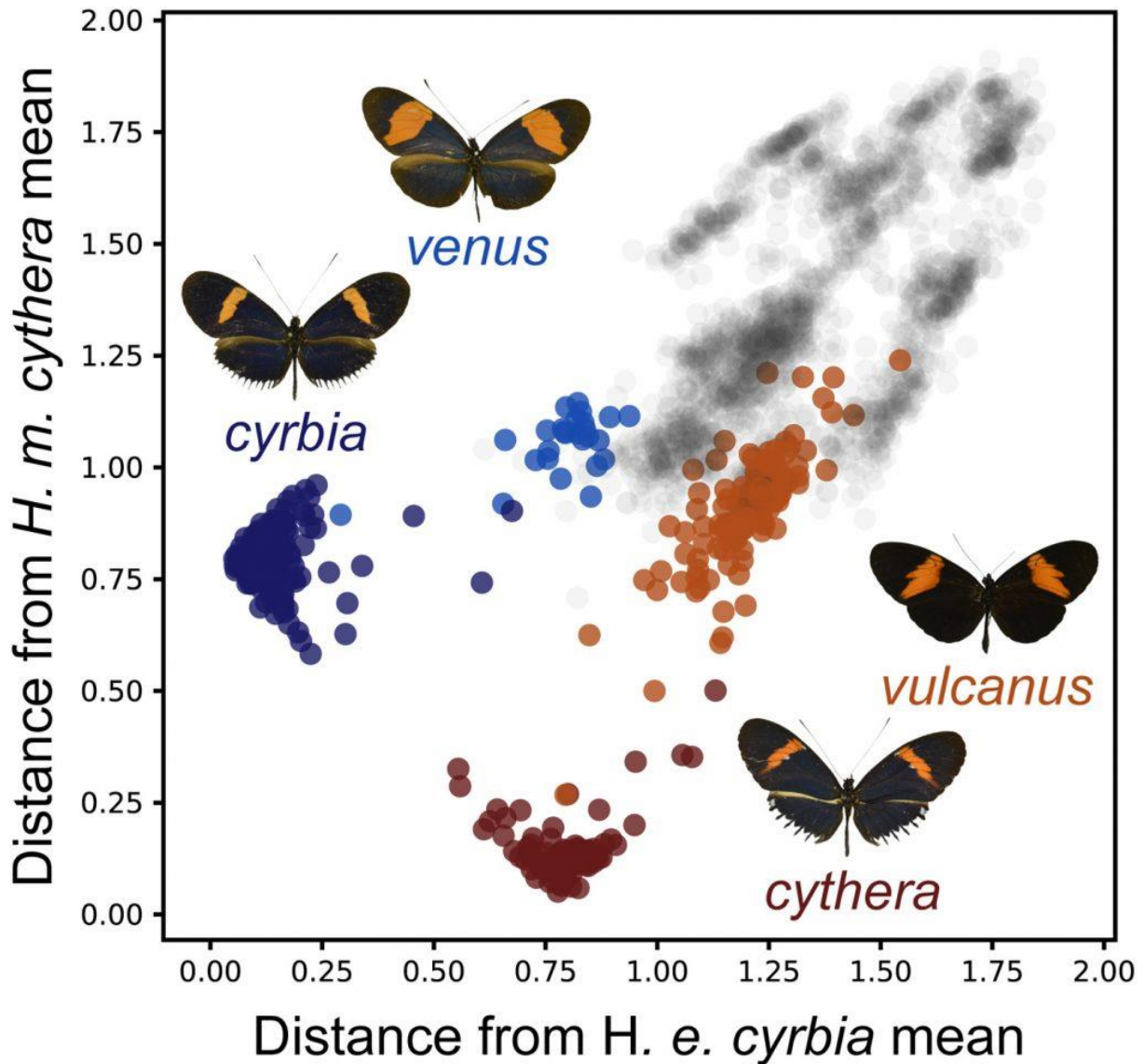


Figure. Comparative analysis of convergence between *H. erato cyrbia* and *H. melpomene cythera* relative to their sister groups *H. erato venus* and *H. melpomene vulcanus* (Figure 4 of (7))

While examples of convergence between *H. erato* and *H. melpomene* abound, it's often **tricky** to test precisely which way the influence ran between them. However, our quantitative analyses of the *H. erato*–*melpomene* mimicry system reveal an example which, we argue, statistically demonstrates reciprocal convergence *and* provides new information on evolutionary **novelty**. This is a comparative analysis of the blue co-mimics (*H. erato cyrbia* and its phenotypic sister group *H. erato venus*, plus their matched co-mimics *H. melpomene cythera* and *H. melpomene vulcanus*, Aside 2).

Aside 2. This comparative analysis was the also one where we had the most independent information to reconstruct the most likely polarity of evolutionary change. The co-mimics *H. erato cyrbia* and *H. melpomene cythera* have some features that are unusual or unique among the studied subspecies (like strong blue iridescence (10) and a white marginal fringe), suggesting that their wing patterns are relatively recently derived within the radiations, rather than being the ancestral phenotype. Biogeographic distributions and previous phylogeographic reconstructions also suggest that these subspecies are at the extreme of a mini-radiation West of the Andes (6), again suggesting that their patterns are comparatively recently evolved within each species.

When we compare the locations of these four subspecies in the phenotypic space generated by the machine learning algorithm (Figure), this demonstrates with statistical significance that *H. erato cyrbia* and *H. melpomene cythera* have each converged on the other, relative to the positions of their phenotypic sister groups. We calculate that, in this case, *H. melpomene* has converged 1.6 times further than *H. erato*.

So, *H. melpomene* has converged the most but *H. erato* has still converged quite markedly on *H. melpomene*. This is very much in line with the predictions of classical Müllerian mimicry theory: convergence is mutual (because everyone benefits) but there is somewhat more convergence by the species which generally shows smaller population sizes (and therefore gains the greatest fitness benefits from mutual mimicry) (1) (2).

Further to this, an examination of the butterflies which are most representative of these subspecies (closest to their subspecies centroid) illustrates that this mutual convergence involved a reciprocal transfer of pattern features between the lineages, which generated a brand new pattern. Now this concept (double switcheroo!) is potentially confusing (and, to our knowledge, newly identified), though we suggest it follows logically from classical mimicry theory (Aside 3).

Aside 3. Advergence (in the sense of one sided evolution) involves coevolutionary transfer of one or more previously existing pattern features from one evolutionary lineage to another (3). This case of convergence (which one could think of as reciprocal advergence in different pattern features) correspondingly involves the reciprocal coevolutionary transfer of pattern features between the two lineages.

To be specific, this comparative analysis suggests that *H. melpomene cythera* has taken on more blue colouration from *H. erato* but that *H. erato cyrbia* has taken on a narrower forewing band from *H. melpomene*. So, each species has adopted a feature that already existed locally in the other species, demonstrating reciprocal (and therefore, strict)

coevolution. And, the end result is a new pattern (bright blue with narrow forewing bands) which combines features from both lineages and didn't exist previously in either.

Incidentally, therefore, the point Prof Mallet raises in his post (9) about *H. erato cyrbia* being the most blue of these subspecies is perfectly compatible with our results and discussion. Otherwise interesting elements of their patterns, such as the novel hindwing fringe, present in both *H. erato cyrbia* and *H. melpomene cythera* are also not directly relevant here. This is precisely because these pattern elements don't exist in either of their sister groups (and therefore don't in themselves provide any information on the direction or reciprocity of advergence).

Perhaps I can further illustrate the main concept with a semi-representative toy example. I am half English (Hoyal) and half Scottish (Cuthill). So my sibling and I grew up with both the classic Scottish breakfast of porridge and typical English breakfasts like, um, toast. If my sibling and I rejected tradition to eat entirely different breakfasts of pop tarts and McMuffins, this would give maximum breakfast divergence, with two new-fangled breakfasts and increased breakfast diversity of four in total. If we both favoured the English side and adopted toast, we can compare this to one-sided advergence with no increase in overall breakfast diversity. However, if we both started eating porridge with toast croutons we would have created a whole new fusion food, showing both Scottish and English influences. Despite us converging on the same breakfast, diversity would also have increased to three different breakfasts! I admit that porridge with croutons doesn't sound very appetising but perhaps that's apt since *Heliconius* butterflies aren't supposed to taste nice either.

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