

Mimicry in *Heliconius* and Ithomiini butterflies: The profound consequences of an adaptation

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Abstract. Prey populations have evolved multiple strategies to escape predation. Camouflage is a strategy resting on avoiding detection by potential predators, whereas aposematism relies on advertising chemical defences with conspicuous warning signals. While camouflaged phenotypes are subject to negative frequency-dependent selection, aposematic preys are under positive frequency-dependence, where the efficiency of a signal increases with its own local abundance. Because of his “strength-in-number” effect, multiple chemically-defended species exposed to the same suite of predators gain a selective advantage from converging on the same warning signals. Convergence in warning signals is called Müllerian mimicry. Here, we review the results of recent genetic and ecological research on two well-studied groups of neotropical Müllerian mimetic butterflies, the genus *Heliconius* and the tribe Ithomiini, which advertise their unpalatability through conspicuous wing colour patterns. Mimicry represents a major adaptation in these groups, where the effects of selection extend well beyond mere phenotypic resemblance. Selection acts on other traits used as mating cues, on the genetic architecture of colour pattern and even on the ecological niche of species. The origin of mimicry itself and the coexistence of multiple mimicry patterns are well understood, but the ultimate drivers of mimicry diversity remain unclear.

1. Antipredator strategies

Natural selection acts on traits that improve the lifetime reproduction of individuals, which includes survival. For many organisms surviving means avoiding being eaten. Different species, especially among insects, have evolved strategies that enable them to avoid attacks [1]. Survival strategies are very diverse. Many are deceptive, such as camouflage, scaring predators off or deflecting them from their target. Perhaps less well known, another strategy, aposematism, rests instead on advertising noxious defences (or other ways of being unprofitable) by the means of warning signals.

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1.1 Deceptive strategies

Many prey rely on camouflage to survive, and are indistinguishable from the background of their environment. For instance, the sole fish has a colour pattern matching the sand floor of the ocean, which renders the fish difficult to detect [2]. Similarly, the wings of the peppered moth *Biston betularia* display a black-peppered pattern that matches light-coloured bark and associated lichen, on which the moth rests during the day [3]. A more subtle type of camouflage involves mimicking objects of no nutritious value for predators. Stick insects resemble twigs or leaves of their hostplant, which protect them from insectivorous vertebrates [4]. Early instar caterpillars of many species of swallowtail butterflies mimic bird droppings [5] and are ignored by predators. Some species, such as moths or butterflies display big eye spots that are believed to scare potential predators off [6]. Another strategy consists in diverting attacks from the vital part of the prey. Many butterfly and moth species exhibit tails or eyespots that attract predators' attacks [7]. One of the most spectacular cases is provided by the long and twisted tails of *Actias* moths (the only 3-D structure known in Lepidoptera wings), believed to lure bat predators away from the moth's body due to air flow and ultrasounds [8]. All of those strategies provide an immediate benefit to the prey by increasing its probability of avoiding predator detection or surviving attacks. Therefore, they are thought to increase fitness to all their carriers, and evolve readily. One characteristic of deceptive strategies is that their efficiency decreases with the increasing prevalence of the strategy, since predators can learn to detect common camouflage types, or may evolve counter-strategies to the most common lures. Recent studies have indeed shown a powerful component of negative frequency-dependence, which increases the survival of rare variants and therefore promotes diversity.

1.2 Warning signals and mimicry

In stark contrast to deceptive strategies, many prey have chemical compounds or other noxious substances and weapons, and overtly advertise such defences to potential predators during much of their times of activity. This strategy is called aposematism. Advertisement often takes the form of conspicuous warning signals that are learned, recognised and subsequently avoided by predators. For instance, the venomous coral snake exhibits black, brown and yellow rings. Similarly, many poisonous frogs, stinging wasps, or unpalatable butterflies such as the orange Monarch display vivid and contrasted colours. Such signals are avoided by most predators once they have tried and experienced their toxins. Predators are initially naïve and they have to attack and often taste the prey to realise that it is toxic or venomous. The benefits to the prey reside in the probability that a given predator has already experienced this prey type and will refrain from attacking it. Therefore, survival benefits depend upon the frequency of the prey type in the habitat. This is a form of frequency-dependence which favours the commonest forms. Of course, the benefit to adopting a warning colour that is common in the locality also applies beyond species boundaries. In other words, individuals from any prey species can benefit from mimicking a locally common defended prey. In effect, when individuals of two warning species are exposed to the same suite of individual predators, they benefit from sharing the same signal because this reduces in both species the per-capita cost of predator education [9]. Indeed, coexisting and sometimes distantly related aposematic species have evolved convergent warning signals, a phenomenon termed Müllerian mimicry, after the German biologist Fritz Müller, who formalized it first [9]. For example, Dendrobatid frog species in the Amazonian forest have evolved convergent skin colour patterns [10], while some neotropical aposematic butterflies and moths share conspicuous wing colour patterns (Fig. 1). Species that share warning signals are called co-mimics, and form mimicry "rings" that may comprise over 15 species locally (e.g., [11]). Edible prey may also benefit from displaying the same warning signals as defended preys. This deceptive form of mimicry is called Batesian mimicry, after the British naturalist Henry Bates, who reported striking similarity between harmless and toxic Amazonian butterflies [12].

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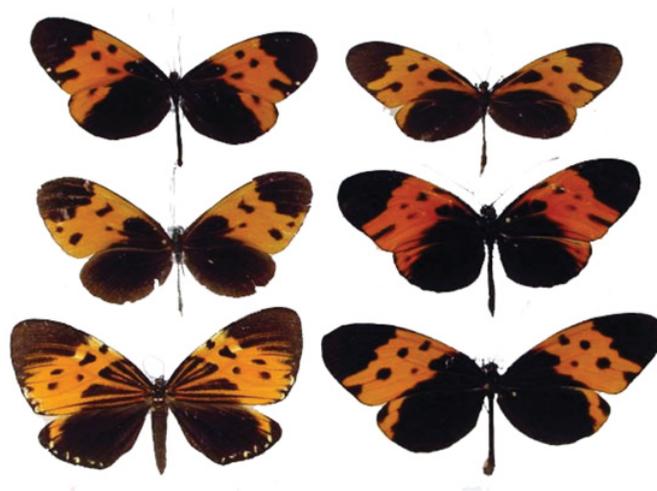


Figure 1. A common mimicry ring in the Andean foothills. Left column, from top to bottom: *Hypothyris mansuetus* (Nymphalidae: Ithomiini), *Hyposcada anchiala* (Nymphalidae: Ithomiini), *Chetone* sp. (Erebidae: Arctiinae). Right column, from top to bottom: *Mechanitis messenoides* (Nymphalidae: Ithomiini), *Heliconius numata* (Nymphalidae: Heliconiini), *Melinaea mothone* (Nymphalidae: Ithomiini).

Mimicry, and particularly Müllerian mimicry, has attracted the attention of evolutionary biologists because it is one of the few examples of adaptation where the fitness optimum is easily known and shared among many species. For this reason, mimicry has been the focus of numerous theoretical, genetic, and ecological studies, and has emerged as one of the best understood models of adaptation. Here, we review the most striking findings of Müllerian mimicry studies and we discuss the origin, evolution and unexpected consequences of one of the most spectacular adaptations.

2. Müllerian mimicry in butterflies: The neotropical genus *Heliconius* and tribe Ithomiini

Müllerian mimicry (hereafter, mimicry unless stated otherwise) has evolved in a wide panel of species [13]. The best documented cases, which are also the organisms that led to the description of mimicry [9, 12], are butterflies and moths. Two groups of neotropical butterflies have attracted considerable attention, because of their sizes and their ecological importance: the genus *Heliconius* and the tribe Ithomiini.

The neotropical genus *Heliconius* (Nymphalidae: Heliconiinae) comprises 46 described species that are all aposematic and engaged in Müllerian mimicry. *Heliconius* have conspicuous brightly coloured wing patterns, which make them easily detectable. They contain cyanogenic glycosides synthesized by larvae and adults from amino acids [14], or acquired by larvae from their hostplants, vines of the genus *Passiflora* [15].

The neotropical tribe Ithomiini (Nymphalidae: Danainae) comprises ca. 380 species and 50 genera. All species are aposematic and mimetic, although under certain light conditions some species may also be cryptic. Many ithomiine species have partly or entirely transparent wings, due to modified scale shape or orientation [16]. Yet, even transparent species exhibit conspicuous, recognizable patterns (Fig. 2). Male ithomiines are thought to acquire their chemical defences, pyrrolizidine alkaloids, at the adult stage, from decaying flowers or stems of Apocynaceae, Boraginaceae and Asteraceae [17]. Pyrrolizidine



Figure 2. The transparent ithomiine species *Greta enigma* in the Andes of Ecuador.

alkaloids are then transferred to females during copulation, as a nuptial gift. Ithomiines numerically dominate forest butterfly communities, and probably drive mimicry in multiple other Lepidoptera, including *Heliconius* species (Fig. 1) [18].

3. The paradox of Müllerian mimicry diversity

Selection on convergent wing colour pattern among mimetic butterflies is obviously strong, as illustrated by the striking similarity among distantly related species (Fig. 1). Such convergent selection is expected to reduce diversity of warning signals. Yet, diversity in warning signals is pervasive, at several geographical scales. Multiple mimicry patterns are observed among geographical regions, within community, and even within species within community. Is the diversity observed transient, or is it stable? If so, what maintains it?

3.1 Mimicry diversity among regions

Convergence in warning signal is driven by local predation pressure. Therefore, prey exposed to different communities of predators, such as communities of different regions, are not under selection for convergence in warning signals [19]. Drift or selective processes other than mimicry, such as detectability in different light environments, can therefore lead to the evolution of divergent warning signals among different regions. In practice, geographical diversity of mimicry patterns is the rule. The species pair *Heliconius erato* and *H. melpomene* provide a compelling example of such diversity. These two species, which diverged about 15 million years ago, mimic each other throughout their ranges. They harbour over 20 distinct mimicry patterns distributed as a spatial mosaic (Fig. 3). A spatially explicit theoretical model with segregated predators confirmed that under certain predation conditions (stochasticity in the presence of predators) spatial mosaics of mimicry patterns can emerge and stabilize [20]. In such mosaics, large patches contain a single mimicry pattern and are separated by narrow transition zones where several patterns co-occur. This demonstrate that warning signals and mimicry

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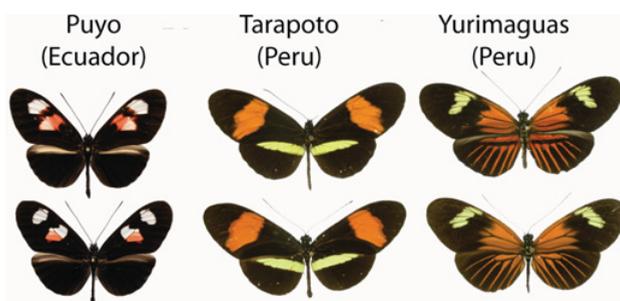


Figure 3. Co-mimetic subspecies of *Heliconius melpomene* (top) and *H. erato* (bottom) in three different regions of their common range.

are to a large extent conventional signals, established through the reinforcement, by local predators, of a local signal which happens to take over thanks to an initial numerical advantage. Once established and predominant in the local community, locally common patterns are very stable and cannot be displaced by rare, new mutants, unless, again, changes in the pressure exerted by predators allow drift to operate. However, the abrupt boundaries between one mimicry type and another can move in space according to numerical difference or processes such as genetic dominance [21, 22].

3.2 Mimicry diversity within community

While the geographical diversity of mimicry can be maintained by a simple spatial segregation of predator communities, mimicry diversity *locally* is more intriguing because prey are exposed to the same community of predators. Mimicry selection under positive frequency dependence favours convergence and should erode phenotypic diversity locally [9]. Yet, mimetic communities are extremely diverse. For instance, ithomiine butterflies from a single site form up to 18 distinct coexisting mimicry rings [23], a diversity which is not readily explained by current theories. One explanation could lie in the fact that local sites are a mosaic of microhabitats, such as canopy, understory, open forest, small ridges and valleys. If predators are segregated across microhabitat, butterflies in different microhabitats are exposed to different suite of predators, and there is little selective pressure for convergence on the same warning signals (Fig. 4). This situation is reminiscent of geographic segregation, at a smaller scale. However, at such a small scale, predator microhabitat niches may still overlap substantially. Theoretical models show that despite overlap in predator microhabitat niches, mimicry diversity can be maintained locally, across microhabitats [26]. Indeed, in real communities of ithomiine butterflies mimicry rings are significantly segregated along multiple microhabitat niche dimensions [11, 24, 25]. In addition, in these communities insectivorous birds, believed to be the principal predators, are similarly partitioned along the same microhabitat niche dimensions [27].

3.3 Mimicry diversity within species within community

In some cases, mimicry polymorphism can be observed within populations, where different individuals of the same species exhibit distinct warning patterns in the same locality. For instance, males and females may belong to distinct mimicry rings, as seen in certain sexually dimorphic ithomiine species [28], perhaps because sexes have very distinct ecologies. Local mimicry polymorphism is sometimes found among Batesian mimics [29]. In this case, however, diversity is readily explained by the parasitic nature of Batesian mimicry on the efficiency of the signals, promoting a diversity of mimicry strategies within the same population. By contrast, Müllerian polymorphism is extremely rare, and not readily explained.



Figure 4. Microhabitat niche partitioning among butterflies and their avian predators. Butterfly species that fly in the understory do not encounter the same predators as those that fly in the canopy. There is therefore little selective advantage for sharing the same warning patterns across microhabitats.

The butterfly *Heliconius numata* is an excellent example of polymorphic Müllerian mimetic butterfly [30]. Distinct morphs coexist, which join distinct mimicry rings dominated by large tiger-patterned ithomiine species (*Melinaea*, *Athyrtis*, *Mechanitis*, *Hypothyros* etc., Figs. 1 and 5). In this case, again, the micro-segregation of model species and their patchy distribution may translate into widely varying selection pressures between neighbouring sites, and result in a stable polymorphism in *H. numata* mainly driven by a migration-selection balance. A theoretical model showed that mimicry polymorphism could be stable under a certain range of toxicity and migration parameters, and could reach high levels of diversity if the heterogeneity of selection for alternative morphs in adjacent localities was associated with substantial mixing due to dispersal [31].

4. Evolutionary, genomic and ecological implications of Müllerian mimicry

Müllerian mimicry represents a major adaptation, whose consequences extend well beyond mere phenotypic resemblance. Mimicry affects intra- and interspecific communication, which is largely based on colour cues in butterflies. The evolution of mimicry is conditional on coexistence, and on the genomic and developmental capabilities of achieving the targeted colour pattern. Therefore, mimicry not only entails selection on colour patterns but also on other features, such as other traits used as mating cues, the genetic architecture of colour pattern elements and the ecological niche of species.

4.1 Mimicry and reproductive interference

One obvious issue linked to mimicry is reproductive interference: if species look so similar, how can individual distinguish mates of their own species? Reproductive interference has been reported among co-mimetic species [32, 33]. Mimicry might therefore drive the evolution of additional mating cues, such as sexual pheromones or other visual differences cryptic to would-be predators, which provides

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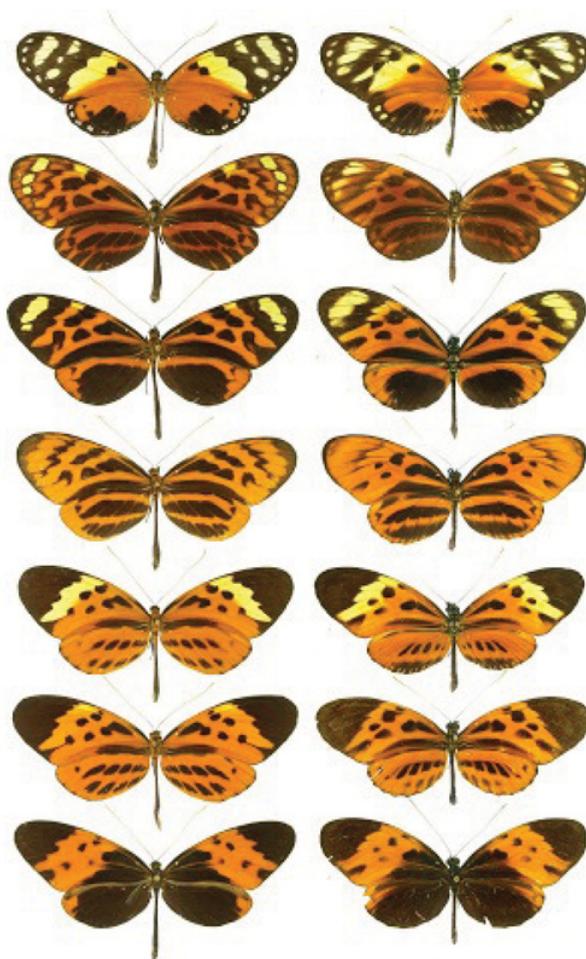


Figure 5. Seven morphs of *Heliconius numata* (right; from top to bottom: *silvana*, *elegans*, *aurora*, *arcuella*, *tarapotensis*, *timaeus*, *bicoloratus*), which mimic almost perfectly distinct *Melinaea* species (left; from top to bottom: *M. ludovica*, *M. satevis cydon*, *M. marsaeus rileyi*, *M. marsaeus phasiana*, *M. menophilus sspnov*, *M. menophilus hicetas*, *M. mothone*).

a reliable way to identify mates of the right species [32]. This may explain the recent findings that co-mimics in certain mimicry rings display subtle colour differences which are more striking under their own visual system than under the predators' vision [34, 35]. Such cryptic differences may therefore represent a private communication channel allowing co-mimics to discriminate among each other without interfering with the efficiency of the signalling to predators.

4.2 Mimicry as a driver of speciation

Much empirical evidence now supports the notion that mimicry can contribute to pre- and post-zygotic reproductive isolation. In species which join different mimicry rings in different regions, such as the geographic races of *H. erato*, *H. melpomene* and many other mimetic butterflies, inter-racial hybrids often have recombinant, non-mimetic wing patterns (Fig. 6). Given that non-mimetic prey suffer higher predation than mimetic ones [36], interracial hybrids are expected to suffer higher mortality due to

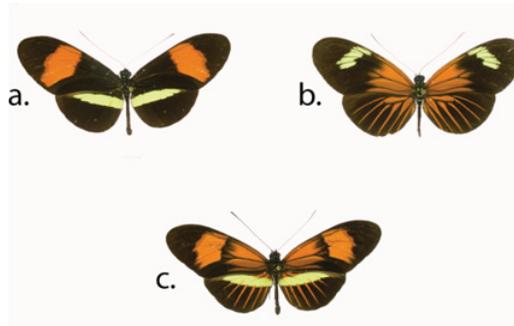


Figure 6. *Heliconius erato favorinus* (a.), *H. erato emma* (b.) and an interracial hybrid showing an intermediate, non mimetic wing colour pattern.

predation. Low-fitness hybrids therefore limit gene flow between populations with different mimicry patterns (post-zygotic isolation).

Mimicry is also involved in pre-mating reproductive isolation. *Heliconius* butterflies show assortative mating for wing colour pattern [37, 38], so shifts in mimicry pattern can be associated with shifts in mate preference. Linkage mapping studies even showed that preference loci map very close to loci underlying colour pattern variation [39, 40], enhancing the potential for colour pattern differences to act as a driver of speciation. Mimicry pattern is therefore sometimes taken as a good example of a “magic trait” driving speciation, since divergent natural selection can directly lead to assortative mating on the divergent trait.

Furthermore, because mimicry rings are segregated by microhabitat [11] and also altitude [23], shifts in mimicry pattern may be directly associated with shifts in microhabitat or altitude (hereafter, habitat), which may favour other ecological shifts such as habitat or larval hostplant shifts [28]. Divergent habitats or hostplants may cause reproductive isolation via spatial segregation (and therefore, assortative mating for habitat) and possibly hybrid maladaptation to habitat or hostplant. All these factors may act jointly and accelerate speciation. Although the role of mimicry in reproductive isolation was only tested empirically in a handful of species, phylogenetic signatures of association between mimicry pattern shifts and speciation events confirm a role of mimicry in diversification [41, 42].

Another, unexpected way mimicry can cause speciation is through hybridization between species belonging to very distinct mimicry rings. The novel wing colour patterns of hybrids may itself favour reproductive isolation from parental species. This is suspected to be the case for the species *H. heurippa* [43]. This species, with a narrow distribution range in Colombia, has a unique colour pattern combining a forewing red band similar to sympatric *H. melpomene* and a forewing white band like parapatric *H. cydno*. This pattern can be stabilised in the lab with a few generations of crosses between these species, and the red-patterning locus in natural *H. heurippa* shows signatures of introgression from a *H. melpomene* origin, into a genetic background closer to *H. cydno*. *Heliconius heurippa* is partly reproductively isolated from its putative parental species [44] and represents a separate genetic clusters from both putative parental species [45]. Theoretical work showed that the novel wing pattern formed by the combination of both parental origins may be sufficient to trigger reproductive isolation [46].

Those results demonstrate the strength of disruptive and frequency-dependent selection on visual signals due to mimicry, and its far-reaching consequences on other suites of traits and the entire genomes through reproductive isolation. This may explain how mimicry can facilitate speciation and diversification under many different evolutionary and ecological scenarios.

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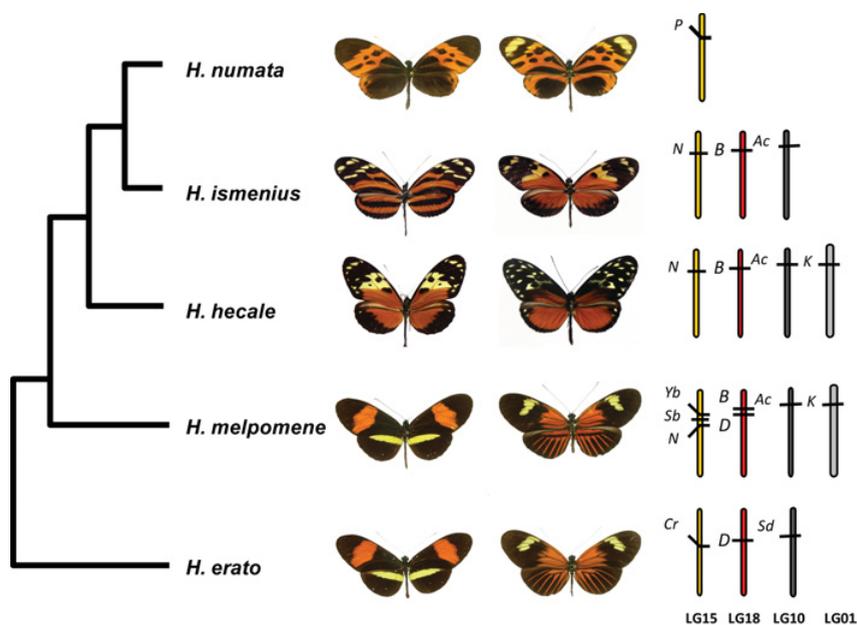


Figure 7. The “wing patterning toolkit” of *Heliconius* butterflies. Homologous regions in four linkage groups (LG) control most of wing pattern convergence and divergence across multiple species [47, 48].

4.3 How to become a good mimic?

Co-mimetic species, by definition, have similar wing colour patterns. How is phenotypic similarity achieved? *Heliconius* butterflies have been the focus of multiple studies unravelling the genomic bases of mimicry variation. Gene reuse (parallel evolution) and adaptive introgression appear as major routes to convergent and divergent mimicry patterns.

4.3.1 Gene reuse: The mimicry toolkit in *Heliconius*

Comparative analyses of genomic architectures controlling mimicry patterns in *Heliconius* reveal that homologous chromosomal regions control much of mimicry variations in most species (Fig. 7) [47–50]. A restricted set of genomic regions sitting mainly on 4 chromosomes is consistently involved in convergent and divergent variation in most species of the genus. This “wing patterning toolkit” of genes is therefore used at the genus level, and responds in a seemingly unconstrained way to selection for wing patterning variation in many different contexts.

The identity of the genes is now better known, as positional genetics and population genomic signals point to narrow intervals and allow identifying the genes targeted by selection. The major loci identified today are the transcription factor *optix* associated with variation in red elements [51, 52] as well as the melanism of proximal parts of the wing [47], the morphogen of the *Wnt* family, *WntA*, associated with melanisation of fore and hind wing median areas [47, 53, 54], and a novel cell-cycle regulator named *poik* and associated mainly with patterning of the proximal areas of wings [50]. Although the use of this toolkit across all lineages indicates that it is presumably ancestral to the genus, mimicry itself is not necessarily explained by common ancestry. For instance, *H. melpomene* and *H. erato* mimic each other

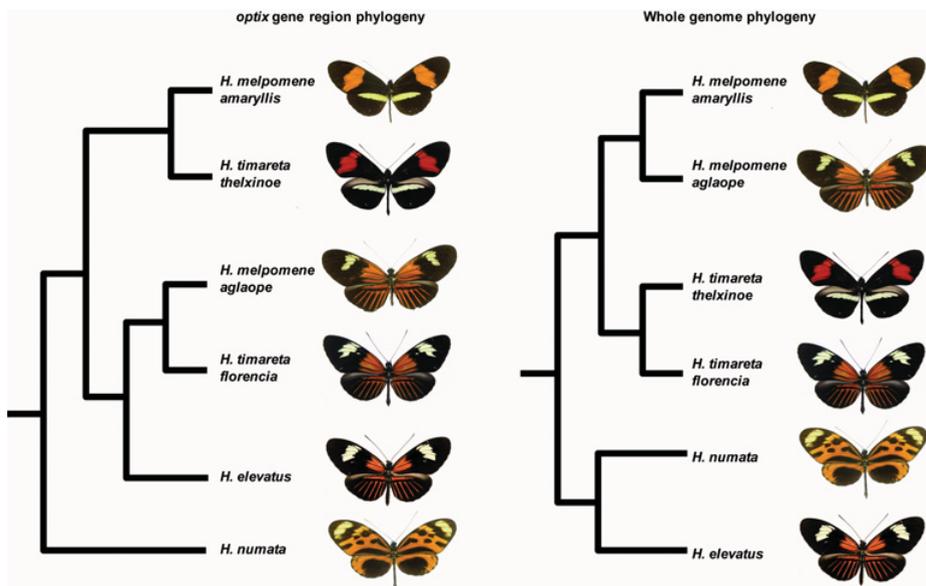


Figure 8. Phylogenetic relationships between DNA sequences from different *Heliconius* taxa within the region containing *optix* (left), compared to the phylogeny of the species based on multiple genes (right) [57]. Around *optix*, taxa cluster according to their colour pattern, not according to the species they belong to.

through allelic variation of the same set of genes, especially *optix*, but the alleles themselves are very different in both lineages [55, 56]. Therefore, although the genetic architecture is conserved, mimicry between lineages has occurred truly through convergent evolution.

4.3.2 Adaptive introgression

The expression of similar phenotypes does not always require genetic changes occurring in both lineages independently. Indeed, how could mimicry with another species be achieved more quickly and accurately than by acquiring the actual variants of the other species? This is possible when species are sufficiently closely related to occasionally hybridize and exchange beneficial alleles. This is thought to have occurred in the co-mimetic species *H. melpomene*, *H. timareta* and *H. elevatus* [57]. Genomic resequencing of wing pattern genes and surrounding regions in multiple species was used to investigate how phylogenetic trees varied in their topology along the chromosome. This showed that while most regions of the genome showed a classic tree topology where individuals clustered by species [58], irrespective of their wing patterns, the region containing *optix* showed a robust clustering by wing pattern phenotype, irrespective of species [57]. For instance, the co-mimetic races of *H. melpomene* and *H. timareta* clustered together, not with their con-specifics (Fig. 8). Similarly, sequences from the distantly related *H. elevatus* clustered with co-mimetic *H. melpomene*, not with its close relatives. Contrary to the true convergence found between distantly-related species such as *H. erato* and *H. melpomene*, here the wing-patterning alleles of closely related, mimetic species were showing a unique origin. This strongly suggested recent transfer of colour pattern alleles across species boundaries, although the direction of gene flow is unknown. Species may therefore capture adaptive variants from local races of other species. This process, called adaptive introgression, allows transferring “ready-made”, differentiated haplotypes, presumably containing multiple adaptive mutations, directly from one species to another and achieve immediate mimicry. This process may be more important in nature than previously realised [59].

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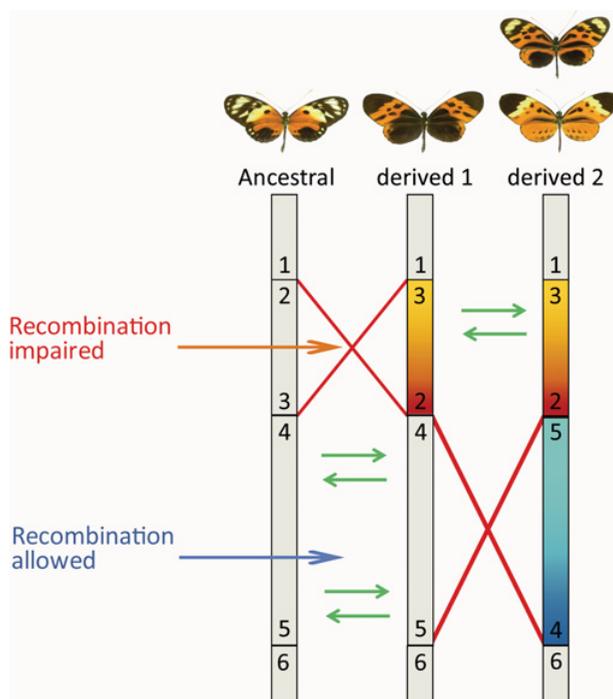


Figure 9. The genomic architecture of the supergene *P* in *Heliconius numata*. Haplotypes in the middle and on the right derive from ancestral haplotypes (shown on the left) via one or several inversions of chromosomal segments [60]. Derived haplotypes are dominant over ancestral ones.

4.4 The fantastic story of *Heliconius numata*: A highly evolved genomic architecture of mimicry

As a polymorphic Müllerian mimic, with different mimetic morphs coexisting in sympatry, *H. numata* poses a genetic challenge. If genes flow freely among morphs, how can this species display multiple complex mimetic phenotypes in a panmictic population without the formation of individuals with recombinant or heterozygous genotypes, as seen for instance in hybrid zones of other *Heliconius* species (Fig. 6)? Non-mimetic morphs tend to suffer high predation rates making the evolution of local polymorphism unlikely. A dissection of the genomic architecture of loci controlling colour pattern variation in *H. numata* revealed a special genomic architecture which appears to limit the formation of non-mimetic morphs [48, 60, 61] in response to selection against such morphs. First, unlike other *Heliconius* species, the entire variation of wing pattern of *H. numata* is controlled by a single genomic region, the supergene *P*, which is positionally homologous to the cluster of tightly-linked genes Yb-S-Sb from *H. melpomene* [48] (Fig. 7). Chromosomal inversion polymorphism is found at this locus, which was shown to reduce the rate of recombination between alternative genomic arrangements [60]. Different inversion types are associated with different categories of morphs, and represent tight “coadapted” blocks of non-recombining genes, maintaining in linkage disequilibrium combinations of characters producing good mimicry [60] (Fig. 9).

In addition, strong dominance regulates the phenotypes of heterozygotes between supergene alleles. Sympatric (but not parapatric) pairs of alleles exhibit hierarchical dominance relationships [61] (Fig. 10) and the mechanisms of dominance has most likely evolved under selection for improved mimicry in heterozygotes. The genetic architecture of polymorphism in *H. numata* appears to have responded to strong selection against non-mimetic phenotypes in an ecological context where polymorphism

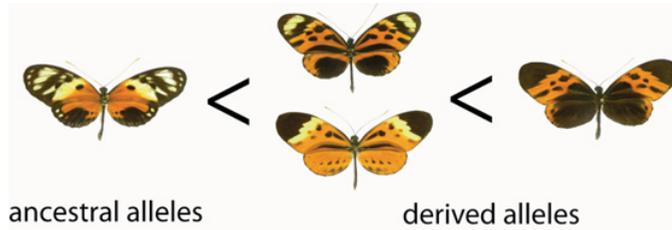


Figure 10. Dominance hierarchy among morphs and alleles in *Heliconius numata*. Sympatric morphs show a full pattern of dominance, while parapatric morphs show mosaic dominance.

and allelic diversity was maintained at high levels. Supergene architectures involving chromosomal rearrangements are known from several other types of systems where polymorphisms are maintained through powerful natural or sexual selection [62]. Those results demonstrate that strong selection maintaining mimicry variation can have an important influence on genome evolution.

4.5 Mimicry and the evolution of the ecological niche

4.5.1 Adaptive microhabitat niche partitioning

It is now well established that mimicry rings are often segregated by microhabitats, such as those dominated by Ithomiini butterflies in the neotropics [11, 24, 25]. For instance, species with so-called tiger patterns (combining areas of black, orange and yellow) tend to fly relatively high above ground, whereas species with transparent wings fly in the understory and low above ground. We can interpret this association either as an adaptive convergence in colour pattern among species sharing the same microhabitat, and/or an adaptive convergence in microhabitat preferences among species mimicking each other. Although theoretical models show that adaptive microhabitat convergence is possible [26], the fact that co-mimetic species share both their colour pattern and microhabitat niche does not necessarily indicate convergence. Because all species share a common ancestor, co-mimetic species could derive from a recent common ancestor, from which they would have inherited both their colour pattern and microhabitat niche. In that case microhabitat partitioning reflects shared ancestry, not adaptive convergence. However, in real communities microhabitat niches of co-mimetic ithomiine species are more similar than would be predicted by their phylogenetic relationships [11]. Microhabitat niche partitioning among mimicry rings is therefore not (fully) explained by common ancestry of the species composing them. This shows that selection for mimicry driven by predators can be powerful enough to influence the ecological preferences of species coexisting within a community.

4.5.2 Adaptive altitudinal niche partitioning

At a larger spatial scale, mimicry rings are also segregated ecologically, particularly along altitudinal gradients [23]. Similarly to microhabitat partitioning among mimicry rings, altitudinal segregation could be driven by selection, or merely the product of common ancestry. Microhabitat preferences are probably fairly labile, because shifts can happen locally due to substantial overlap in abiotic and biotic environment across microhabitats. By contrast, shifts in altitudinal niche entail dramatic changes, such as temperatures, precipitations, UV intake and hostplants. Adaptive altitudinal partitioning therefore appears less likely than adaptive microhabitat partitioning. Still, altitudinal niches of co-mimetic ithomiine species along the slopes of the Andes are more similar than would be predicted by their phylogenetic relationships [23]. This suggests that selection incurred by predation is strong enough to

adaptively shape altitudinal structure among mimetic butterflies despite the magnitude of the ecological differences involved.

5. Conclusion

5.1 A compelling illustration of the power of selection

Müllerian mimicry is a textbook example of adaptation. Convergence in warning signal is obvious even to the general public or school children. Fitness optima can easily be characterized, which facilitates theoretical studies of speciation. Several decades of study on Müllerian mimetic butterflies, particularly on the genus *Heliconius* and the tribe Ithomiini, revealed that the scope of predation-driven selection is incredibly large. Selection not only drives striking resemblance among the warning signals of different species, it also finely tunes their underlying genetic architecture and even impacts the evolution of multi-dimensional ecological niche.

However, in spite of the strong influence of selection in many aspects of mimicry, non-selective processes, such as migration and drift, may also play a surprisingly important role. Migration between localities dominated by different mimicry communities can contribute to unorthodox local polymorphism in *H. numata*, while drift may be one of the main requirements for the initial increase in frequency of novel warning signals, following which those signals can be maintained in communities.

5.2 Müllerian mimetic communities as highly coevolved assemblages

Müllerian mimetic communities are the result of a long history of coevolution, as testified by the adaptive niche evolution in Ithomiini or the evolution of sequential dominance only among co-existing morphs in *H. numata*. Highly coevolved systems may appear very stable (e.g., [63]), yet the tight links between species make them dependant on one another. Dramatic environmental changes such as those driven by humans in the post industrial area may disassemble communities and produce novel species assemblages [64, 65]. Community disassembly may be particularly harmful to Müllerian mimetic species, where the survival of rarer species depends heavily on the presence of abundant co-mimics [23].

5.3 Origin of mimicry: Ultimate and proximal causes

Müllerian mimicry originated independently in multiple lineages and is extremely common in all diverse insect communities across the world. Mimicry evolves secondarily, in response to two previous adaptations: (1) the evolution of defences against predators followed by (2) the evolution of warning signals. The ultimate cause of mimicry evolution is selection driven by predation pressure: species exposed to the same predators benefit from sharing warning signals. However, while the adaptive value of mimicry is well understood, researchers are just starting to unravel the proximal mechanisms by which mimicry evolves. Gene reuse (parallel evolution), adaptive introgression, and perhaps true convergent evolution (novel genes and developmental pathways) are candidate mechanisms, but their relative importance is still unknown. In any case, mimicry is a clear example of adaptation where selection can be easily characterised and quantified. As such, mimicry is a fantastic model for studying selection operating at multiple and integrated levels.

5.4 Origin of mimicry diversity?

While the ultimate causes of mimicry are well identified, the origin of mimicry diversity is still under debate. Models and empirical studies allow us to understand why mimicry diversity is stable, but how new mimetic forms evolve in the first place is still unclear. Mimicry could work perfectly without

any diversity. Yet all mimetic clades show a remarkable diversity of mimicry patterns. Why do novel warning signals appear so readily? Several hypotheses might explain the recurrent evolution of novel signals. In *Heliconius* butterflies, for instance, the same toolkit of genes is used in distinct species, controlling a very wide diversity of distinct mimicry types [47]. It is unknown whether the genes switching between mimicry types are special in their ontogeny or developmental position, but the diversity of phenotypes shown suggests a great lability of the genotype to phenotype link. Perhaps this lability owes to specificities in the structure of the regulation of those genes (complex cis-regulatory regions) which might minimize their pleiotropic effects and facilitate their recruitment by selection at multiple, specific times and tissues during development. The same loci can be reused to produce similar or different patterns, in different genetic backgrounds, which may facilitate again their capture by introgression. Perhaps selection for evolving mimicry in the first place imposes a strong sieve on the genetic architecture, and favours mimicry achieved by mutations of large effect, producing a sharp phenotypic change and achieving a sufficient resemblance to an incipient co-mimic to be picked by selection. Perhaps for those reasons, *Heliconius* butterflies, and possibly other mimetic lineages, may quickly respond to selection and readily evolve adaptive warning patterns, thereby explaining the rampant generation of novel variants. Most of those novel variants may be eliminated by selection. However, some manage to persist. Novel signals may escape extinction by locally or temporally relaxed selection by predators, or even just by chance [19, 66]. Theoretical and empirical studies are needed to better understand the initial drivers of mimicry diversity.

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