Mimicry and speciation (in *Heliconius*) in the light of ecology and evolution

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Title page: Picture of *Heliconius erato* taken in a butterfly zoo in the Netherlands

Abstract

The genus Heliconius shows remarkable divergence in wing colors and patterns. Due to Müllerian mimicry several mimicry rings receive protection from predation. It is thought that mimicry evolved between species due to mistakes made by the predator, leading to different selection on different warning color patterns within a species, shifting both species to a common warning color pattern.

Mimicry and speciation are two words that go hand in hand. Because of the strong selection on uncommon warning color forms by predators, hybridization is limited. Together with assortative mating and habitat adaptations, genetic differences can be maintained and more differences can accumulate leading to speciation. It is unknown how strongly these effects contribute to speciation and to learn more about mimicry and speciation scientist could starting working and manipulating this factors in theoretical computer models. Also more knowledge should be collected on the species that predate on Heliconius because they play an important role and very little is known about them.

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Introduction

Mimicry dates back a few years after the publication of Darwin's '*On the origin of species'*. Mimicry is mentioned the first time in a publication by Bates, after Bates corresponded with Darwin about the findings Bates made in the Brazilian Amazon during his 11 years journey. On this journey, Bates saw that certain groups of butterflies share characteristics in appearance and he argued that palatable species might mimic unpalatable species to receive protection from predators (Forbes, 2009).

Mimicry is still a hot topic on which much research has been done the last decades. This research covers different topics such as ecology, evolution and genetics. The last years, scientists are focusing on different main questions to get a better understanding of mimicry. First of all, research is focusing on the genetic and developmental background to understand how easily mimicry might evolve. Second, scientists want to know what kind of role the predator plays in the evolution of mimicry, because these predators generate the selective pressure in these mimicry systems. Third, how is it possible that different color warning patterns (polymorphism) continues to exist in mimicry systems? One would expect that all individuals that mimic an unpalatable species want to share a signal, because this is favorable, due to the shared costs that originate from teaching the predator that these individuals are unpalatable; therefore polymorphism will not maintain. Fourth, why does much imprecise mimicry exists? The individuals that mimic the unpalatable species best would receive most protection. This means that one would expect natural selection to optimize this mimicry. Fifth, how does mimicry enhance speciation and diversification? Because of the strong selection in mimicry systems, mimicry has been thought of a factor contributing to speciation (Pfenning, 2012).

In this thesis I will focus on the research done on the mimicry systems in the Nymphalidae's genus *Heliconius* and give a overview of the knowledge received from last centuries research on these systems, focusing on the ecological and evolutionary aspects answering the questions how mimicry has evolved in this genus and how mimicry can influence speciation. Before I do so, I will explain shortly the basics of mimicry and how the mimicry systems in *Heliconius* exactly work.

Batesian and Müllerian mimicry

In a mimicry system there are 3 roles for the species involved. First of all there is the role of the 'model'. The species being the model is always unpalatable and can display this to its predator by different signals such as a bad smell or bright colors on its body. The second role is the role of the 'dupe' which, as said, receives the displayed or emitted signals from the 'model'. This 'dupe', often the predator, learns thanks to its own experience, that the signals that are emitted by the 'model' are linked to bad taste or maybe even to illness after eating this 'model' and will therefore start avoiding this species. Then there is the last role, the 'mimic'. This is the species that displays the same signals as the 'model' does, but is always more palatable than the 'model' they mimic. The 'dupe' is deceived by the 'mimic', because it thinks that it encountered an unpalatable species and will therefore avoid it. Thanks to this fake display, the 'mimic' will receive protection and be less consumed by its predator (Pasteur 1982, and Rettenmeyer, 1970).

These days many different mimicry systems are recognized. Most common however is the 'protective' or 'defensive' mimicry. We use this definition for the cases in which a 'mimic' species receives protection from its predator (the 'dupe') by resembling a unpalatable third species (the 'model'). In general we can distinguish two different kinds of defensive mimicry; Batesian mimicry and Müllerian mimicry. The first one is the named after H. W. Bates and involves all systems in which a palatable species mimics an unpalatable species to gain protection from their common predator. In Müllarian mimicry multiple unpalatable species will show the same or closely similar warning signals. The benefit of this is, that the species will share the costs that mimicry still carries, because new born predators or predators with a weak mind will every now and then predate on the unpalatable species. By sharing the same warning signal, the number of individuals eaten per species will decline. Such a group of species sharing an identical signal is called a mimicry ring (Sherratt, 2008, Rettenmeyer, 1970 and Pfenning, 2012).

Shortly said: in Batesian mimicry the role of the model and the mimic is filled by two different species, whereas in Müllerian mimicry a species fills both roles.

Heliconius

The genus *Heliconius* shows a remarkable divergence and speciation. All members of these genus are unpalatable and have strong color signals and patterns that make this clear to the predators, which are mostly specialized avian predators. The best known predator of the Heliconius is the Rufous-tailed jacamars (*Galbula ruficauda*), which predates as a specialist on butterflies in the tropics and is found in areas where *Heliconius* butterflies occur as well (Langham, 2004). The genus is abundantly distributed from the tropical and subtropical regions of the New World, from South America to the southern parts of the United States. In any place one can often find several mimicry rings which change every 100 to 200 miles. In these mimicry rings several species of the genus *Heliconius* together with sometimes other less closely related species, mimic each other and display a common warning color pattern.

For example the two co-mimetic species *Heliconius erato* and *H. melpomene* are two sister species that have evolved different subspecies throughout the geographical range in which they occur. In any location the two species look identical, but throughout their geographical range their patterns change in concert, see figure 1 (Heliconius.org, 2014).
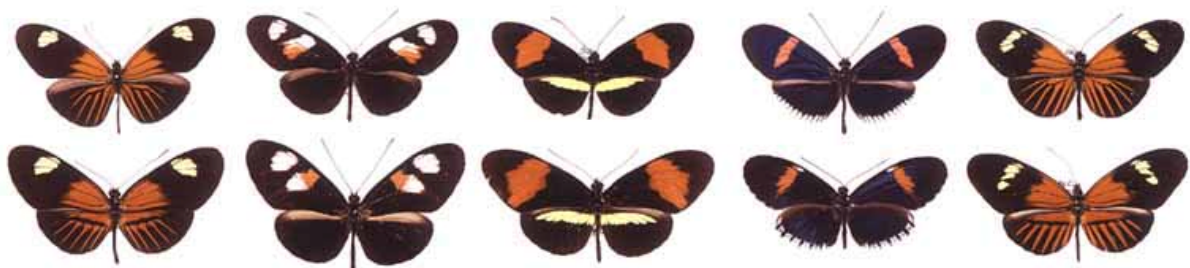

Figure 1. An example of the different forms that do exist in a single Heliconious species across a geographic range; Heliconius erato (top row) and H. melpomene (bottom row). Localities left to right: Zamora, Ecuador; Puyo, Ecuador; Tarapoto, Peru; Guayaquil, Ecuador; Yurimaguas, Peru. (From: http://www.heliconius.org/)

Studying the *Heliconius* gives biologists a great opportunity to look at speciation currently happening. The great geographical differences, great abundance and the ease in which these species can be bred in captivity allow researchers to take a closer look on how speciation occurs, revealing ecological as well as genetic processes.

Evolution of mimicry in *Heliconius*

Before we consider at the question in which ways mimicry might enhance speciation we want to know how Müllerian mimicry might have evolved. To explain the hypotheses explaining this we have a look at the following figures presented by Sheppard et al in 1985.

Figure 2 shows on the x-axis the phenotypic diversity in warning color pattern of species A. The y-axis shows the abundance of the different phenotypes, marked in the graph as a grey area, as well as the fitness (in this case protection) of the individual with a specific warning color pattern. Predators make mistakes and there will be inexperienced ones, not capable yet of determining which warning color pattern is linked to an unpalatable species of butterfly. This can lead to a certain level of protection for individuals that signal their unpalatability with a warning color pattern outside the range of patterns currently found in the species. This protection will decrease the further the pattern is away from the mode, resulting in directional selection towards the mode.
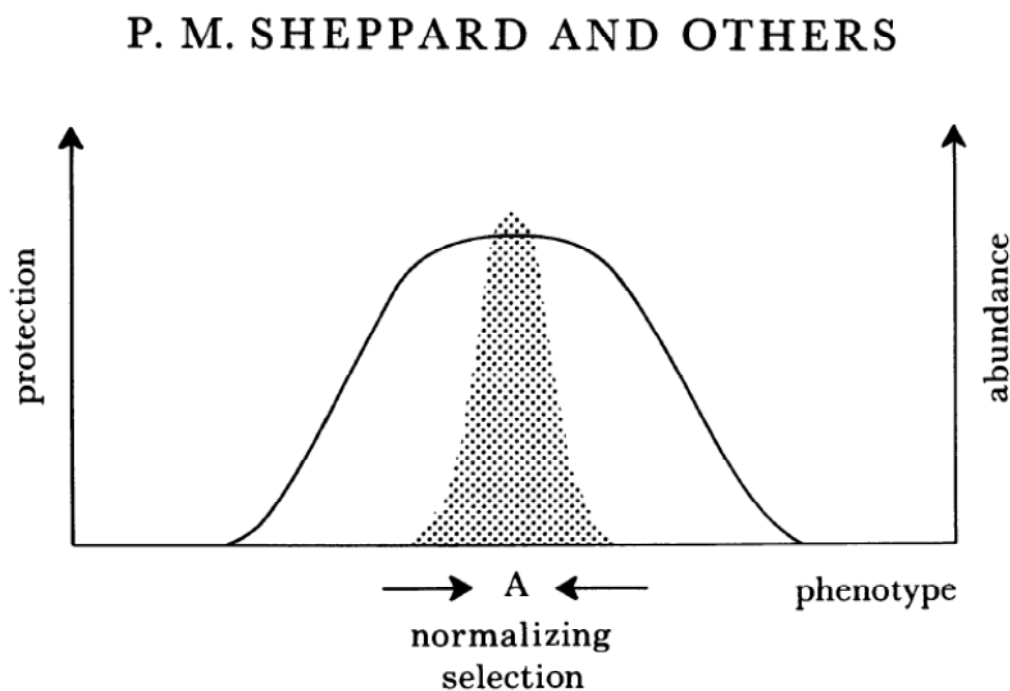

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Figure 2. Normalizing selection on the warning color pattern within species A. Abundance of the variation of warning color patterns plotted as shaded grey. Protection plotted with a line (from Sheppard et al., 1985).

If we take a look at figure 3 we see that another species, species B, has been added. This species behaves on his own exactly the same as species A; undergoing directional selection towards the most favorable warning color pattern. However, if we combine both species something interesting can be noticed that might explain the emergence of Müllerian mimicry among different species. If we have a individual of species B that has a pattern that does not fit the mean warning color pattern of species B; it has the same possibility as in previous example with species A of being mistaken for a mode of species B and escape predation. But what happens if we combine species A and species B and both phenotype distributions overlap? Individuals from the left tail of species B's graph might every now and then be mistaken for a mode of species B, but can also be mistaken for a mode of species A, because of the shared phenotype distribution. This slightly shared distribution might be due to phylogenetic history of both species or one or more major mutations altering the warning color pattern of one species. Due to the extra protection received by occasionally being mistaken for a individual of species A, the left tail of the distribution graph of species B will have a slighter higher fitness compared to the right tail of the graph. This will result in a directional selection towards the mode of species A. Of course the same story also applies to individuals in the right tail of the graph of species A, receiving extra protection and having a slightly higher fitness than the left tail, because it is occasionally being mistaken for a mode of species B. Eventually the two species will be shifted towards a common warning color pattern halfway between both species, resulting in Müllerian mimicry. In nature circumstances will not be as symmetrical as stated in this example. Differences in unpalatibility, flying season, visibility and so on will result in different selection pressures on both species. Because of these differences the new warning color pattern will be shifted from the exact middle towards one of the two species involved (Sheppard *et al*, 1985).
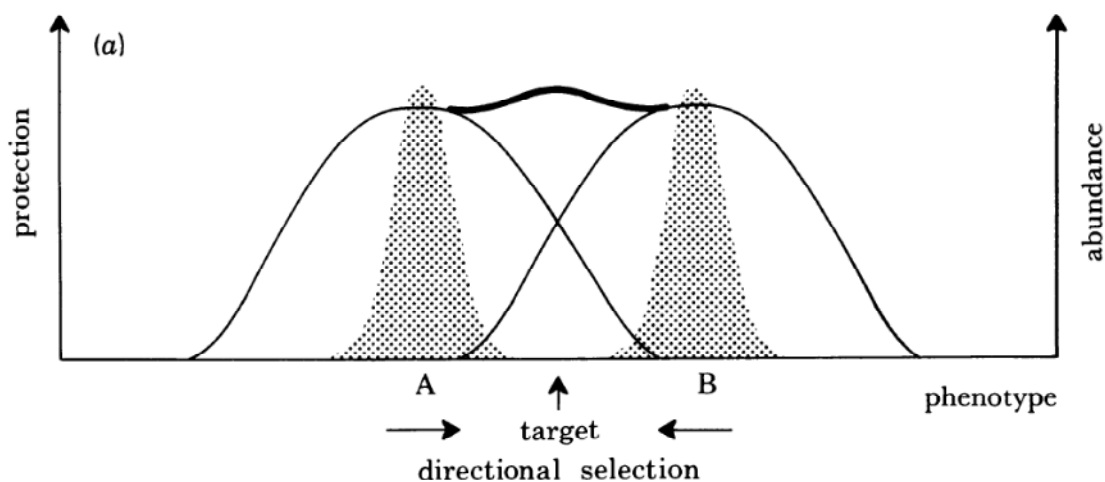

Figure 3. Directional selection on the warning color pattern within species A and B. Abundance of the variation of warning color patterns plotted as shaded grey. Protection plotted with a line (from Sheppard et al., 1985).

Speciation in *Heliconius*

There are several ways in which speciation can occur and the great diversity in the *Heliconius* butterflies has given scientists a great opportunity to look at processes leading to speciation in the *Heliconius* genus. Three species of *Heliconius*; namely *Heliconius erato*, *H. melpomene* and *H. himera* have been of interest to scientists for a long time. *Heliconius erato* and *H. melpomene* co-exist and mimic each other. In *H. erato*, about 30 parapatric races are described that inhabit areas spanning from a few to thousand square kilometers. In these different areas the races of *H. erato* correspond to the races of *H. melpomene*, having the same warning color patterns (figure 1).

However; in narrow contact zones the different races of one *Heliconious* species mate randomly and it has been found that there is little genetic difference between the species (outside the genetic differences leading to different warning color patterns) and speciation has not occurred. The third species *Heliconius himera* is a species that occurs instead of *H. erato* in certain areas and it is thought to be a example of an intermediate step in speciation. Genetic and morphological analysis confirm that *H. erato* and *H. himera* are very closely related. In the contact zones between *H. erato* and *H. himera*, random mating does not occur and parental types are more abundant than hybrids, in contrast with the interracial contact zones of *H. erato*, in which random mating does occur. Also, the interracial contact zones of *H. erato* are much wider than the contact zone between *H. himera* and *H. erato*. This smaller contact zone is a result of a lower hybridization between the two species showing that there is reproductive isolation. The isolation arises due to different mate preferences between the species based on the different warning color patterns. This shows us together with the genetics analyzed that indeed there is speciation going on in this example (McMillan & Jiggins, 1997).

Another example is formed by the three butterfly species *Heliconius cydno*, *H. melpomene* and *H. heurippa*. *H.cydno* and *H. melpomene* are two species that share overlapping habitats and are closely related. Both species belong to different mimicry rings. *H. cydno* has a black, with white and yellow warning signal and *H. melpomene* has a red with yellow and orange one. Also between these two species; hybridizing occurs at low frequencies. *H. heurippa* has a warning pattern intermediate between *H. cydno* and *H. melpomene*. *H. heurippa* replaces *H. melpomene* in certain areas as shown in figure 4. Cross-breeding experiments have shown that the warning color and pattern of *H. heurippa* can be generated by crossing *H. melpomene* and *H. cydno*. The pattern of *H. heurippa* was also found in different places where wild hybrids of these two species occur, making the origin of *H. heurippa* due to hybridization highly probable (Mavárez *et al*, 2006).
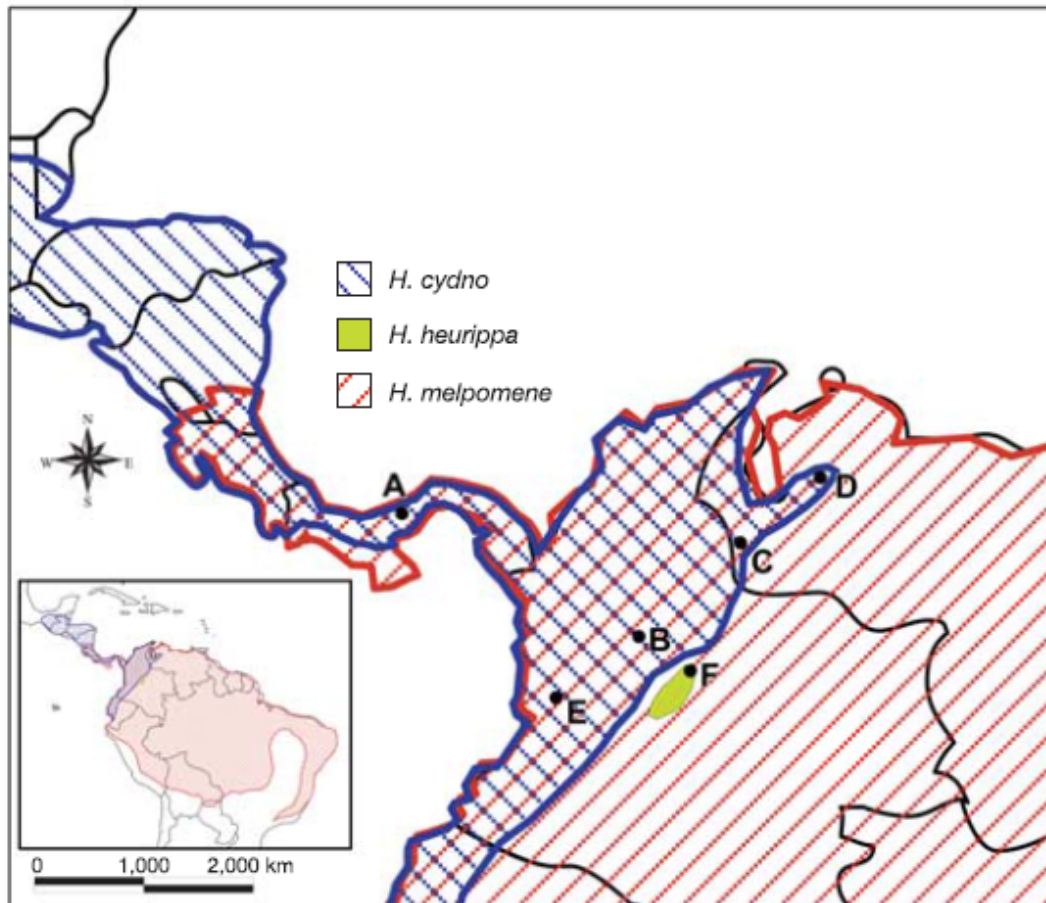
Figure 4. Geographical distributions of Heliconius cydno, H. heurippa and H. melpomene (Mavárez et al., 2006).

Polymorphism

As explained above there are some examples of *Heliconius* species that show evidence of recent divergence from other *Heliconius* species. This divergence appears to be much more recent than other genera of the tribe *Heliconiini* (Jiggins *et al*, 1996). It is hard to believe that there is such a large diversity in warning color pattern in and between species of *Heliconius*, because one would expect under the strong selection pressure rising from Müllerian mimicry systems exactly the opposite. In a Müllerian mimicry system; maximum protection is reached when all members share and display the same warning signal and individuals having another warning color pattern are not recognized as unpalatable and therefore are selected against; making polymorphism unlikely (Joron, 2005).It had been hypothesized that this diversity was able to develop in the Pleistocene glacial advances, forcing the *Heliconius* into divided subpopulations. Random extinctions of warning models in these subpopulations gave previously established warning patterns a selective advantage, leading to different mimetic warning patterns seen today over the geographical range. This theory sounds good, but it does not explain the rise of new warning patterns, because it cannot counteract against the purifying frequency dependent selection. It has also been shown that the radiation of warning patterns in *Heliconius* took place before the most recent glacial advance.

These days a new theory is accepted which explains the diversity by simple genetic drift. Genetic drift can only generate differences in the genetics of populations that is strong enough to counteract against the purifying frequency dependent selection by predation if there is population subdivision. Genetic analysis on populations of different *Heliconius* species shows that there is population subdivision over limited spatial scales which shows that the emergence of new patterns can arise through genetic drift (Kronforst & Gilbert, 2008). This theory is also supported by the fact that *Heliconius himera* and *H. heurippa*, two species that are not a member of any mimetic ring and each have their own warning color pattern, are very abundant in the areas they occur. New warning color patterns will only provide enough protection against predation if the frequency of this pattern (whether this pattern is part of a mimicry ring or not) is high enough. Due to the great abundance of *Heliconius himera* and *H. heurippa*, it is possible for these species to maintain an evolutionary stable pattern. This supports the hypotheses that mimicry is not necessary for new patterns to arise (as said before; one expects less polymorphism in Müllerian mimicry systems) and that this can be accomplished by genetic drift (Jiggins, 2008).

But genetic drift is not the only factor needed to obtain and maintain a new warning color pattern eventually leading to speciation. Other selective factors are as well important; for example assortative mating, ecological adaption and hybrid inviability. All these factors do however have a double role; on the one hand they constrain the initial rise of new warning patterns and on the other hand they maintain isolation between two recently split populations of *Heliconius* on their way to complete speciation (Mallet & Barton, 1989).

Selection on color patterns

As stated above, new warning color patterns will only establish in a population if the number of individuals having these new color patterns is sufficient to counteract against the purifying selection by predation. The selection pressure behind this mechanism is frequency dependent, meaning that this new color form will eventually receive enough protection if it manages due to genetic drift to reach an abundance high enough to teach the predators that this warning color pattern is also linked to a unpalatable species (Kronforst & Gilbert, 2008).

This same frequency dependent selection can also maintain isolation between two species because of the strong selection against rare hybrids that might appear in contact zones between two closely related species that are still able to crossbreed (Mallet, 1990) (see examples explained before). Because of the low abundance of the hybrids, the predator will not be familiar with this warning color and does not link this to unpalatability and will be predating on the warning color patterns that it did not learn to avoid more often compared to the more common ones. This frequency dependent selection on rare forms will result in disruptive selection, meaning that the differences in warning color patterns between the two species will remain and even strengthened, giving again genetic differences between the two species the opportunity to accumulate and eventually give speciation the chance to occur. This might sound in contradiction with figure 3, but here we are talking about a total different time scale on which such events happen, because the hybrids are immediately selected against by the predators.

Partner choice

Speciation will be boosted by ecological adaptations, which are adaptations like a warning color pattern that is under selection, that directly cause assortative mating. Assortative mating means that hybrids are rare (compared to the expected amount according to the laws of genetics) in contact zones of two closely related species and that the hybrids that do exist have non-mimetic intermediate warning color patterns, and frequency-dependent selection results in a strong selection against these hybrids (post mating isolation). Another factor influencing this lack of hybrids in the contact zones has been shown in several studies; mate recognition based on warning color pattern between some *Heliconius* species that have dramatically different color and warning patterns; mate recognition is based on color pattern instead of any chemical components (pre mating isolation) (Munoz *et al*, 2010 and Jiggins, 2008). This leads to less hybridization in the wild than expected (Jiggins *et al*, 2001). Due to this pre and post mating isolation other genetic differences between the two *Heliconius* species can accumulate and speciation can occur.

But how does assortative mating boost speciation? Assortative mating is a direct consequence of ecological adaptations of the *Heliconius*, in this case the warning color pattern. Such traits that are under divergent selection and also contribute to partner choice (non-random mating) are referred to as 'magic traits'. These magic traits make it possible to overcome a problem often found in theoretical studies done on speciation based on gene flow. It is theoretical difficult to have speciation if gene associations acquired by selection are removed by recombination. In this case pre mating isolation will not occur easily and speciation is unlikely to happen. In a magic trait, the genetic differences built up by divergent selection are maintained because the adult will choose to mate with an individual with the same characters in this trait, that is under divergent selection.

Hence; the genetic differences and associations in this species (between the two different forms) can accumulate easily and give a opportunity to eventually split into two species (Jiggins, 2008, Jiggins *et al*, 2001 and Servedio *et al*, 2011).

Ecology

In the example where *Heliconius himera* replaced *H. erato* in certain areas, there are also other ecological factors that might contribute to the completion of speciation. It is very obvious that there is a shift in habitat choice between these two species and that they live in two different niches. *H. himera* occurs in dry forests whereas *H. erato* occurs in tropical wet forest. This might influence speciation as well as partly explain the low densities of hybrids found between these two species, because both species inhabit different niches and are therefore less likely to encounter one another, creating pre-mating isolation (Jiggins *et al*, 1996).

Another problem that different ecological preferences of different species might explain, is the question why so much polymorphism still exists in the *Heliconius* while one would expect evolution of one main warning color pattern in Müllerian mimicry systems. Species living together in the same micro-habitat can maintain a similar warning color pattern, which results in different mimicry rings existing in one area, as can be found in the *Heliconius* genus. This can be explained by three rules which should be true for species living together in a mimicry ring.

First of all a mimic should be visible to the predator that also predates on the mimics model, so both species should live in a similar habitat together with their predator. Second, if a mimic adapts to an habitat already used by a model, the mimic should converge to the same color warning pattern. Third, if the warning color patterns have some effect on the habitat most favorable for this species, mimics sharing the same warning color pattern should live in the same habitat. It might for example be possible that a specific warning color pattern functions best around a specific community of plants, therefore species sharing the same warning color pattern will occur in the same place. Hence; different mimicry rings should be separated by different habitat use, which makes it possible for multiple mimicry rings to exists in one area (Mallet & Gilbert, 1995).

This means that if a population of a certain species will evolve to live in an, other micro-habitat (which is possible because there are different warning color patterns forms occurring in one species), this might be a positive factor contributing to speciation. Due to the divergence in micro-habitat choice the individuals of these two population are less likely to interact and encounter each other, giving genetic differences the chance to accumulate and speciation can be completed.

Predators

It is clear that predators play a very important role in both the evolution of mimicry systems as well as in speciation. Predators are the driving force creating the selection pressures. However not much is known about predator behavior and how they learn to remember their prey. It might even be the case that they do not learn to remember their prey at all but will just start feeding on a palatable species after accumulating too many toxins in their body. It however has been shown in two studies that Rufous-tailed jacamars (Galbula ruficauda), a bird that predates on butterflies in the tropics and is often found in the area's where *Heliconius* is found as well. By presenting butterflies of three different forms to the predators, that were caged, the level of predation on each form was measured and let to the conclusion that the predator predates less on the form that was local in the area where this predator was caught (Langham, 2004). A year later the same was done, but this time the butterflies warning color patterns were altered with ink, creating novel warning color patterns. Again the predators did predate more on this novel form, just as expected (Langham, 2006).

Imperfect mimicry

One expects mimicry to be perfected by natural selection because the best protection is gained if the mimic resembles the model perfectly. However, one finds much imperfect mimicry in nature; mimics that do not resemble their model as closely as we would expect. There are different hypotheses that can explain these findings, for example that we humans might interpret the signals of mimics in a different way compared with the predators; resulting in a finding of more mimicry systems than there actually are, because predators won't see these imperfect mimics as a mimicking species. It might also be possible that mimicry which in our eyes is imperfect, is not imperfect at all and the predator cannot discriminate between the different imperfect forms and the model.

Another hypotheses is called the 'character displacement hypotheses and explains the finding of imperfect mimicry through reproductive competition. Individuals of different species that mimic each other perfectly might have trouble finding the right partner to ensure offspring. This has been proven in a study on *Heliconius erato* and *H. melpomene*. These species spend quite some time in approaching and courting with females that share the same warning color pattern (Estrada & Jiggins, 2008). This suggests that the slight differences that exist (as shown in figure 1) between co-mimics can be explained by the fact that species cannot afford themselves to resemble each other too precisely, because this would lead into mate recognition problems (Kikuchi & Pfennig, 2013).

Discussion and conclusion

It is sometimes hard to distinguish the factors contributing to the evolution of mimicry, the rise of new warning color patterns and the rise of new species. These factors are generally the same. To make it easier to understand one must keep in mind that these processes might be occurring at the same time and that thanks to the rise of new warning color patterns new mimicry links can arise leading eventually to speciation.

Predators play a major role in the evolution of mimicry and speciation; because they create the necessary selection forces, however very little is known about how these predators behave in the wild and more research should be done on this important aspect. Scientist should first focus on which predators feed on these butterflies and how they interact with the mimicry system.

We have looked at different factors influencing speciation in *Heliconius* mimicry systems. We should however keep in mind that most of this factors have been tested in only a few cases between *Heliconius* species and that it is not known whether these systems apply for all *Heliconius*. Still we are fairly safe to say that there are several cases in which can be confirmed that assortative mating; ecological selection and strong disruptive selection are factors proven to have influenced recent and ongoing speciation in the genus *Heliconius*.
We can also conclude that the strongest factors influencing speciation in *Heliconius* are the selection against new warning color patterns (hybrids) by predation and assortative mating, which, as said, has been proven to be a 'magic trait' boosting speciation. To which degree all these factors influence speciation is hard to say and not much is known about this, so further research to answer this question is necessary (Jiggins *et al,* 1996).

To answer the more complicated questions on how predators behave within mimicry systems and to which degree the different factors mentioned influence speciation research should focus on the more theoretical part, building a computer model in which the several factors can be manipulated to see how speciation will respond to such a change.

The interesting theme about imperfect mimicry is also a subject in which more answers might be obtained if we put hypotheses explaining the phenomenon to the test in the genus *Heliconius*, because most of the hypotheses have been tested in Batesian mimicry, but have not received much attention in Müllerian mimicry (Kikuchi & Pfennig, 2013). What we also should notice is that there might be a problem explaining the divergence in *Heliconius*; could it maybe be that the hypotheses explaining imperfect mimicry due to problems with mate recognition is true and that this also contributed to the rapid divergence of the warning color pattern.

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