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Maintaining mimicry diversity: optimal warning colour patterns differ among microhabitats in Amazonian clearwing butterflies

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Mimicry is one of the best-studied examples of adaptation, and recent studies have provided new insights into the role of mimicry in speciation and diversification. Classical Müllerian mimicry theory predicts convergence in warning signal among protected species, yet tropical butterflies are exuberantly diverse in warning colour patterns, even within communities. We tested the hypothesis that microhabitat partitioning in aposematic butterflies and insectivorous birds can lead to selection for different colour patterns in different microhabitats and thus help maintain mimicry diversity. We measured distribution across flight height and topography for 64 species of clearwing butterflies (Ithomiini) and their co-mimics, and 127 species of insectivorous birds, in an Amazon rainforest community. For the majority of bird species, estimated encounter rates were non-random for the two most abundant mimicry rings. Furthermore, most butterfly species in these two mimicry rings displayed the warning colour pattern predicted to be optimal for anti-predator defence in their preferred microhabitats. These conclusions were supported by a field trial using butterfly specimens, which showed significantly different predation rates on colour patterns in two microhabitats. We therefore provide the first direct evidence to support the hypothesis that different mimicry patterns can represent stable, community-level adaptations to differing biotic environments.

1. Introduction

One of the most intensively studied examples of adaptation is Müllerian mimicry, where groups of unpalatable species display a common warning colour pattern and thereby share the cost incurred through predator learning [1]. Butterflies provide many examples of mimicry 'rings' comprising multiple species with extremely similar patterns (e.g. [2]) that have evolved through convergence [3]. Furthermore, numerous field experiments have demonstrated very strong stabilizing selection, which explains this convergence as predicted by classical Müllerian mimicry theory [1,4]. However, surprisingly, mimicry patterns are also highly diverse [5], both across space and within communities, with more than 10 butterfly mimicry rings occurring at a single Amazonian locality [2]. Shifts between mimicry patterns have long been considered a likely cause of ecological speciation [6], as sexual selection on colour pattern and natural selection against hybrid individuals can rapidly result in reproductive isolation, even in the presence of gene flow [7–15].

Spatial variation in predator communities over distances of a few kilometres to hundreds of kilometres is a likely factor in maintaining intraspecific variation in warning colour patterns [16–21], with strong natural selection driving narrow geographical colour pattern clines [17,22,23]. Seasonal variation in predators also facilitates the maintenance of alternative defensive strategies [24]. However, the processes responsible for maintaining mimicry diversity within communities are less well understood. Two classes of hypotheses have been proposed. In the first, colour pattern diversity is viewed as an unstable phenomenon, resulting either from geographical overlap between largely allopatric mimicry patterns or from rapid evolution of new patterns that, once abundant, experience only weak selection for convergence [5]. Such communities represent a dynamic equilibrium, either because mimicry rings offering less protection are continuously ‘rescued’ by immigration [25,26] or because selection constantly drives convergence but is counter-balanced by rapid diversification.

By contrast, the second class of hypotheses views distinct mimicry rings as adaptations to varying abiotic or biotic environments, and thus as representing stable niches related to predator defence. Several studies have confirmed height stratification of mimicry rings in ithomiine [3,27,28] and nocturnally roosting *Heliconius* butterflies [29]. Mimicry rings may also be segregated with respect to forest disturbance [3,29–32] and topography [3]. Species that share host plants often mimic each other, probably because adults are constrained to fly in similar microhabitats by the distribution of their host plants [27,33].

There are several possible explanations for such microhabitat segregation in mimicry rings. Papageorgis [34] proposed that diverse warning colour patterns in Amazonian butterflies might be maintained by different patterns having a ‘dual-signal’ function of both camouflage and warning against different vegetation backgrounds related to flight height and ambient light. An alternative hypothesis is that different patterns represent adaptations not to physical variation among microhabitats, but to ecological variation in the predator community. If predators show microhabitat segregation similar to mimicry rings, then different predator species may be most familiar with different mimicry patterns, and selection for convergence across microhabitats will be low [5,27,29,30].

Gompert *et al.* [35] provided theoretical support for the hypothesis that microhabitat preferences in predators and prey can promote mimicry diversity. In that study, strong microhabitat segregation in predators drove microhabitat segregation among mimicry rings, and thereby fostered coexistence of several mimicry rings [35]. Furthermore, on a broader scale, it has been shown that habitat patches several kilometres apart can represent alternative mimicry optima, supporting polymorphisms within species [16,26,36]. However, the optimality of mimicry patterns in finer-scale microhabitats has never been tested. Here, we test this hypothesis for the first time by studying ithomiine butterflies (Nymphalidae: Ithomiini) and their avian predators in a diverse Amazonian rainforest community in eastern Ecuador. Ithomiines, known as ‘clearwing butterflies’ after the transparent wings of many species, inhabit Neotropical forests below 3000 m, with some 60 species in the most diverse communities of the western Amazon. All species are believed to be unpalatable [37] and participate in mimicry ‘rings’ with other ithomiines or putatively unpalatable butterflies, especially the Heliconiinae [38], in addition to presumed palatable Batesian mimics. Ithomiine butterflies dominate these mimicry rings in both species diversity and abundance [2]. Although there are almost no published observations of predation on ithomiines, the primary predators driving the evolution of mimicry are believed to be insectivorous birds. These are the only abundant predators with sufficiently developed colour vision to explain precise mimicry [13,39–42].

We adopted two approaches to test our hypothesis. First, in our study community, we measured the distribution of butterflies and birds with respect to two principal microhabitat axes, flight height and topography, which are known to influence ithomiine mimicry pattern abundance at the study site [3]. We then used these data to estimate the relative encounter rates between mimicry patterns and individual bird species, and therefore test whether butterfly species were, on average, most likely to encounter birds that were most familiar with their colour pattern. Second, we conducted an experimental field trial with dead butterfly specimens to directly measure predation rates on colour patterns in different microhabitats. We use the resulting data to address the question of whether microhabitat segregation in birds and butterflies can lead to the stable coexistence of multiple mimicry patterns.

2. Material and methods

(a) Study groups

Our study group included all ithomiines and co-mimetic butterflies (co-mimics). In the absence of data on butterfly palatability to a range of insectivorous birds, we assumed that all non-ithomiine co-mimics might potentially be Müllerian mimics. Eight mimicry rings involving ithomiines were recognized based on similarity in wing pattern characters and parallel geographical variation in wing pattern [2,3,33,43]. Although human and bird vision differ, we assume that shared wing pattern characters visible to us and used to classify mimicry must also be important cues for predators because these characters show convergent evolution. Moreover, experiments show that birds learn, after attacking unpalatable butterflies, to avoid palatable butterflies that humans classify as co-mimics [44,45], and models of animal vision suggest that birds are unlikely to be able to discriminate between butterflies that are regarded as mimetic by humans [46].

Several bird species present at the study site are known to be predators of butterflies, such as jacamars (Galbulidae) [47,48] (J.C.R.W. 1997–2016, personal observation) and some flycatchers [42,49,50], but these are species characteristic of forest edges, large light gaps or forest canopy. We know of no published evidence of insectivorous birds that are regular predators of butterflies in the understorey, yet some must be to drive the evolution of understorey mimicry rings. We therefore assumed that all potentially insectivorous birds could be important selective agents, and used Ridgely & Greenfield’s guide [51] to determine such insectivorous birds (see electronic supplementary material, S3). Manakins (Pipridae) are predominantly frugivorous but also eat insects and were thus included in our analyses.

(b) Study location

The study was conducted at the Napo Wildlife Center, Orellana, Ecuador, a topographically variable area with relatively undisturbed forest (see electronic supplementary material, S1). Data on the topographic distribution of butterflies were obtained by K.R.W., M.E. and C.D.J. sampling eight 30 m-diameter plots, located in pairs with one on a ridge and one in the adjacent valley, along the ‘Parrot Trail’ (240–300 m, 0°31′ S, 76°23′ W). Birds were sampled by J.C.R.W. in the same eight plots as butterflies and during additional timed transect walks along ridge and valley trails between and near the plots.

(c) Species abundance and distribution

Fieldwork was conducted from 16 October to 15 December 2005. We recorded butterfly distribution and abundance during 30 min sampling and observation periods in each plot, from 08.00 to 17.00. Ridge plots were surveyed for a total of 23 h among all plots, and the same for valley plots. Plots were patrolled continuously during the 30 min sampling period and attempts made to capture all mimetic butterflies using hand-nets, up to 9 m above the ground. Specimens were either killed and retained or marked and released, and we recorded the time of day, species or mimicry pattern (if unidentified), sex and initial flight height. Observers carried entomological nets with metal handles composed of up to 12 sections each 0.6 m in length, with these gradated handles facilitating flight height estimation.

Birds were recorded in the same plots from 04.20 to 18.00 h, concentrating in particular between 06.30–11.00 and 15.00–17.00 h when bird activity was greatest. A total of 44 h observation time was spent in ridge plots and the same time in valley plots. Birds were also recorded during timed walks along ridge and stream trails between Parrot Trail plots (15 h spent in ridge walks and the same in valley walks). Species were identified by sight and call using prior experience and Ridgely & Greenfield's guide [51]. For all individuals, we recorded time of day, species, and initial flight or perch height.

(d) Mimicry pattern encounter rates for bird species

To characterize butterfly and bird distribution, we assigned each butterfly and bird individual to one of eight microhabitats, representing combinations of two topography categories (ridge and valley) with four flight height categories (0–1 m, 1–2 m, 2–3 m, above 3 m). Flight height intervals were based on our observations of significant differences in mimicry rings between the ground and 3 m, and a sharp decline in observed numbers of butterfly individuals above 3 m. These data were used to estimate the relative frequency of encounters between each bird species and each of the eight mimicry patterns. For a given bird species (k) and mimicry pattern (i), we summed the product of bird abundance (I_{kj}) and butterfly abundance (B_{ij}) in each of the eight microhabitats (j) and divided by the sum of these products across all mimicry patterns, as an estimate of the relative encounter rate (M_{ik}) of that mimicry pattern in comparison with others.

Therefore, the relative mimicry pattern encounter rate for bird species k and mimicry pattern i is

$$M_{ik} = \frac{\sum_{j=1}^{8} I_{kj} \times B_{ij}}{\sum_{i=1}^{8} \sum_{j=1}^{8} I_{kj} \times B_{ij}}.$$

We then used a permutation approach to test for non-random encounter rates between different mimicry patterns and individual bird species, which might occur due to microhabitat segregation. We permuted mimicry pattern among butterfly individuals to generate 500 'null' communities, maintaining the same numbers of individuals in each mimicry ring and the same butterfly abundance distribution among microhabitats. For each null community, we calculated relative mimicry encounter rates (M_{ik}) as above, for the 25 most abundant bird species (greater than 10 individuals recorded) in the community. We then compared our empirical values of M_{ik} with those in the 500 null communities to address two questions:

> *H1. Within individual bird species, do the encounter rates of different mimicry patterns differ significantly from those expected if there were no microhabitat segregation of mimicry patterns?* We focused on the mimicry pattern encountered most frequently by each bird species since that is the pattern that species is most likely to avoid, and therefore the pattern that should be optimal for co-existing butterflies to display. For each bird species k and mimicry pattern i, the frequency of null communities with the highest M_{ik} equal or greater than the highest empirical M_{ik} represents the probability of such a high encounter rate being the result of chance (a one-tailed test).
>
> *H2. Within the entire bird community, do a significant number of bird species most frequently encounter a mimicry pattern other than the most abundant pattern?* The two most abundant mimicry patterns recorded were 'eurimedia' (37%) and 'hermias' (31%) (see Results; electronic supplementary material, S4), so to simplify analyses, we focused on encounter rates of these two patterns. Empirically, 19 out of 25 bird species had the highest empirical encounter rate for the less abundant pattern 'hermias' (see Results; electronic supplementary material, S5). The frequency of null communities with 19 or more bird species having $M_{\text{hermias}\ k}$ as the highest pattern encounter rate represents the probability of such a biased community being the result of chance (a one-tailed test).

(e) Birds encountered by butterfly species

We then examined whether butterfly species tend to most often encounter birds that are most familiar with their colour pattern, and hence that are most likely to avoid them. First, we calculated the weighted average rate of encounters ($\overline{M}_{ij}$) of each of the eight mimicry rings (i) within each of the eight microhabitats (j) across all bird individuals (all bird species, $k = 1$–129) observed in a given microhabitat (I_j).

The average relative encounter rate for mimicry pattern i of birds occurring in microhabitat j is

$$\bar{M}_{ij} = \frac{\sum_{k=1}^{129} M_{ik} \times I_{kj}}{\sum_{k=1}^{129} I_{kj}}.$$

Finally, for each butterfly species (h), we calculated weighted average mimicry encounter rates ($\overline{M}_{hi}$) of birds occurring in the microhabitats where that butterfly species was recorded, by weighting bird-mimicry encounter frequencies ($\overline{M}_{ij}$) with observed butterfly abundance (B_{hj}) in each microhabitat and summing across microhabitat.

The average relative encounter rate for mimicry pattern i of birds encountering butterfly species h is

$$\bar{M}_{hi} = \frac{\sum_{j=1}^{8} \bar{M}_{ij} \times B_{hj}}{\sum_{j=1}^{8} B_{hj}}.$$

These final data indicate the mimicry pattern that will be most familiar to birds encountering a given butterfly species, and the pattern with the highest ($\overline{M}_{hi}$) should be the optimal pattern for that butterfly species. As we found that the second most abundant pattern 'hermias' was predicted to be optimal for 15 of the 21 species with that colour pattern (see Results; electronic supplementary material, S6), we tested whether the association between predicted and actual optimal patterns was greater than expected by chance, by permuting predicted optimal patterns among all butterfly species 500 times.

(f) Differential predation

We tested whether predation rates differed between mimicry patterns and microhabitats using dead butterfly specimens. Because we found differences in the two predominant mimicry patterns ('eurimedia' and 'hermias') across topography (between ridges and valleys), we designed the experiment to test whether topography had an effect on predation rate of these two patterns. Ithomiines belonging to 'eurimedia' and 'hermias' mimicry rings were collected outside of predation study plots and at random with respect to species, killed and attached with cyanoacrylate glue to the tips of sticks that were driven into the ground (electronic supplementary material, S7A,B). The bottom of each stick was sprayed with locally obtained insect repellent up to 10 cm above the ground to deter terrestrial scavengers. Butterflies were placed alternately with wings open or closed (both natural postures for resting ithomiines), from 1 to 1.5 m above the ground. At each of 10 sites (five on a ridge and five in the adjacent valley, each separated by 100–200 m), we placed two pairs of 'eurimedia' and 'hermias' butterflies approximately 5 m apart, with each pair containing one 'eurimedia' and one 'hermias' individual approximately 1 m apart (electronic supplementary material, S7D), with individuals randomized with respect to species. Predation study sites were located outside of study plots but in similar microhabitats, where ithomiines were observed flying. A total of 10 butterfly individuals of each mimicry pattern were thus distributed across five ridge sites, and a further 10 individuals of each mimicry pattern were distributed across five adjacent stream sites. The study was conducted during the latter part of the same fieldwork period in which butterfly and bird surveys were conducted, and sites were checked twice daily, once at dawn and once at dusk. At each check, the number and pattern of predated individuals were recorded. Bird predation was inferred where wings were observed to be torn (e.g. electronic supplementary material, S7C) or entirely missing, with the body intact, or when the body was observed to be torn consistent with a bird (rather than arthropod) attack. No other scavengers were observed attacking the specimens. Damaged or missing specimens were replaced, and sites were moved approximately 20 m each day to reduce predator habituation. Specimens were checked 34 times in total.

We used a maximum-likelihood approach to test for differences in predation with respect to the two mimicry patterns and the two microhabitats, pooling data for all specimens within these four categories. Given the low numbers of predation events, we felt that it would be unreasonable to attempt to include additional parameters (such as study site and wing position) into modelling variation in predation rate. We calculated the values of the predation probabilities of the two patterns within one microhabitat, or of one pattern across two microhabitats, that maximized the log-likelihood functions for the observed predation results, and we computed the corresponding maximum log-likelihood value. Next, we calculated the maximum log-likelihood under the assumption that these predation probabilities were the same (the null hypothesis) and compared that with the maximum log-likelihood where predation probabilities were allowed to differ. A likelihood ratio test was used to test for the significance of the difference between the two log-likelihood scores, with d.f. = 1. See electronic supplementary material, S8 for further details.

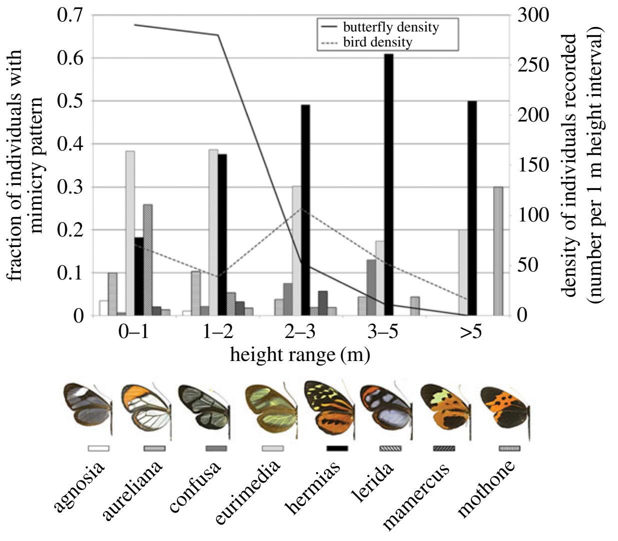

Figure 1. Relative butterfly mimicry pattern abundance (bars) and butterfly and bird density (numbers of individuals per 1 m height band) (lines) recorded at different heights above the ground.

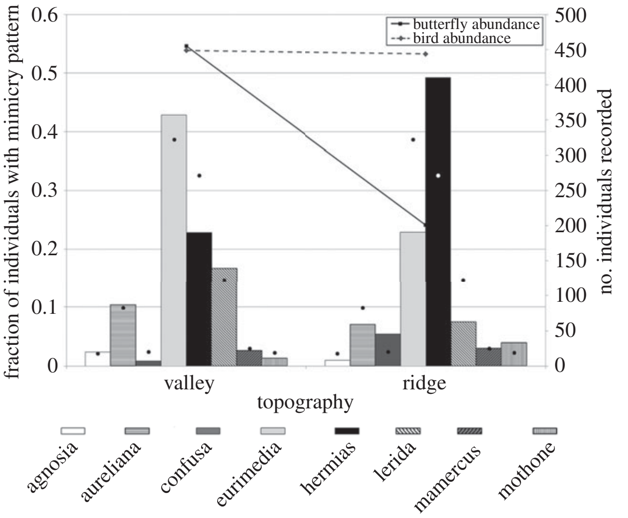

Figure 2. Relative butterfly mimicry pattern abundance (bars) and numbers of butterfly and bird individuals recorded (lines) in valley and ridge sites. Black and white dots represent relative abundances of mimicry patterns that would be expected if butterflies were distributed randomly with respect to topography.

3. Results

In our eight study plots (electronic supplementary material, S1), we recorded 656 individuals of 64 species of butterflies, distributed across eight mimicry rings (figure 1; electronic supplementary material, S2). Very similar relative abundances were recorded for the most common mimicry rings by different observers. Dominant groups were Ithomiini (49 species) and Heliconiinae (five species). A total of 127 species and 893 individuals of birds were recorded and identified as potential predators of Lepidoptera (see electronic supplementary material, S3). Dominant families included Tyrannidae, Thamnophilidae, Furnariidae, Thraupidae, Bucconidae and Picidae, representing 63% of all species.

Aposematic butterfly density declined sharply with height above 3 m, whereas bird density showed a peak at 2–3 m and a more gradual decline with height (figure 1). Overall, 'eurimedia' was the dominant mimicry pattern, comprising 241 (37%) of all individuals, followed by 'hermias' (203, 31%) and 'lerida' (91, 14%), but the fraction of the community occupied by these patterns varied across height. 'Lerida' and 'eurimedia' patterns were dominant from 0 to 1 m, 'eurimedia' and 'hermias' equally dominant from 1 to 2 m, and 'hermias' dominant in height categories above 2 m, reaching more than 60% of the community from 3 to 5 m (figure 1). With respect to topography, more than twice as many butterflies were recorded in valley sites compared with ridge sites, whereas bird abundance was similar across these two categories (figure 2). 'Eurimedia' was the dominant pattern (43% of individuals) in valley sites, followed by 'hermias' (23%), whereas 'hermias' was dominant (49%) in ridge sites, followed by 'eurimedia' (23%) (figure 2).

Based on the distribution of birds and butterflies (electronic supplementary material, S4) among the eight topography-flight height microhabitats, 19 of the 25 most abundant bird species were estimated to encounter the second most abundant mimicry pattern ('hermias') most frequently, and 16 of these

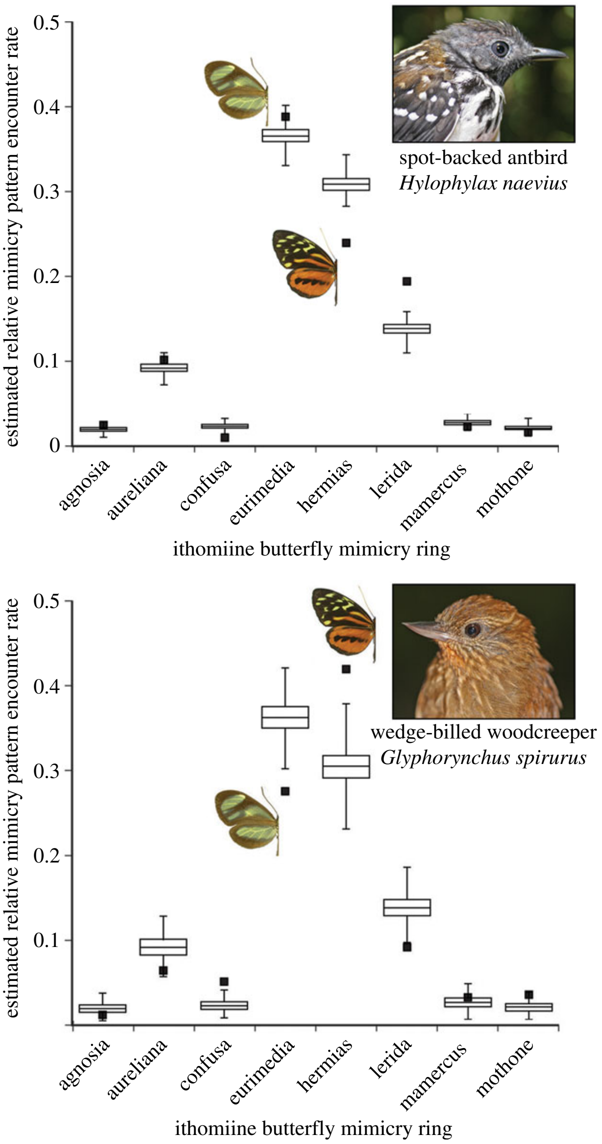

Figure 3. Estimated relative encounter rates of eight ithomiine butterfly mimicry rings by two potential bird predators during the study. Black squares show observed values and standard box-plots represent a distribution of values generated under a null model of no microhabitat segregation of mimicry rings (500 simulations). The low-flying spot-backed antbird was estimated to encounter more ‘eurimedia’ and fewer ‘hermias’ in the field than expected under the null model, while the opposite was true for wedge-billed woodcreeper, which showed a preference for midstorey and ridge-tops where the ‘hermias’ mimicry ring tended to fly. (Online version in colour.)

species encountered ‘hermias’ significantly more often than expected by chance (H1, $p < 0.05$) (electronic supplementary material, S5; e.g. figure 3). Out of the six bird species encountering ‘eurimedia’ most frequently, two encountered ‘eurimedia’ significantly more often than expected by chance (H1, $p < 0.05$) (electronic supplementary material, S5; e.g. figure 3). As a community, the number of bird species encountering ‘hermias’ most frequently was significantly higher than in null communities without microhabitat segregation of mimicry patterns (H2, $p = 0.04$ of finding this number, i.e. 19, or more in 500 permuted communities).

Estimates of the average mimicry encounter rates of predators co-occurring with each butterfly species resulted in 10 of 12 species in the most abundant mimicry ring (‘eurimedia’) being predicted to have the optimal colour pattern for predator avoidance (electronic supplementary material, S6). In other words, the average bird predator encountering these ‘eurimedia’ species is more likely to have previously encountered that colour pattern than any other. Of the 21 species within the second most abundant mimicry ring (‘hermias’), 15 were predicted to have the optimal colour pattern for predator defence ($p < 0.01$ of finding 15 or more ‘hermias’ with an optimal pattern when expected optimal patterns were permuted among all butterfly species 500 times). Within ‘hermias’, there was no correspondence between rarity and species identified as having suboptimal patterns; most notably, the optimal pattern for the most abundant ‘hermias’ species, *Hypothyris semifulva*, was predicted to be ‘eurimedia’, as this was a relatively low-flying valley species that overlapped most with other non-mimic ‘eurimedia’ species. Species in all other mimicry rings were predicted to have suboptimal patterns, as their optimal patterns were predicted to be either ‘eurimedia’ or ‘hermias’ (electronic supplementary material, S6).

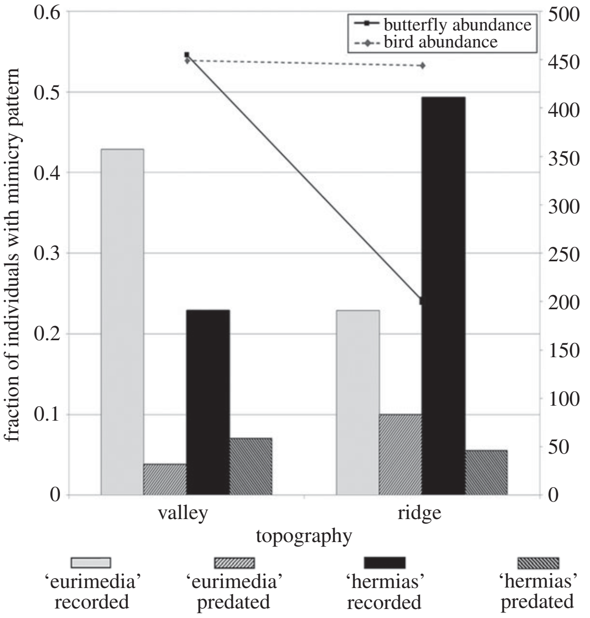

Figure 4. Results of experimental field predation study. Relative butterfly mimicry pattern abundance recorded in surveys (solid bars), fraction of butterflies attacked in field trials (hatched bars), and numbers of butterfly and bird individuals recorded in surveys (lines) in valley and ridge sites.

In the predation study, a total of 340 trials (checks for predation of specimens) were conducted for each combination of mimicry pattern and microhabitat. At ridge sites, 34 ‘eurimedia’ and 19 ‘hermias’ were predated, while at valley sites, 24 ‘hermias’ and 13 ‘eurimedia’ were predated (figure 4). In terms of predation on different mimicry patterns, ‘eurimedia’ was significantly more predated on ridges than ‘hermias’ ($P_H = 0.056$ and $P_E = 0.100$; $p = 0.03$), while ‘hermias’ was more predated at streams than ‘eurimedia’ ($P_H = 0.071$ and $P_E = 0.038$; $p = 0.06$). Across microhabitats, ‘eurimedia’ was significantly more predated on ridges than in valleys ($p = 0.001$), while predation rates on ‘hermias’, although higher at streams, did not differ significantly across microhabitats ($p = 0.4$). Because the morning and evening checks of specimens were conducted in the same site, prior to moving specimens to another site, some independence of data is potentially lost because a single bird is more likely to be responsible for predation events recorded at those two times. We therefore analysed the morning and evening data independently, as above. Most predation events were recorded at the morning check of sites (61 out of 90 predation events); 'eurimedia' was significantly more predated on ridges than 'hermias' ($P_{\mathrm{H}} = 0.029$ and $P_{\mathrm{E}} = 0.067$; $p = 0.020$), while 'hermias' was significantly more predated at streams than 'eurimedia' ($P_{\mathrm{H}} = 0.058$ and $P_{\mathrm{E}} = 0.023$; $p = 0.020$). Across microhabitats, 'eurimedia' was significantly more predated on ridges than in valleys ($p = 0.004$), while predation rates on 'hermias', although higher at streams, did not differ significantly across microhabitats ($p = 0.06$). All comparisons were non-significant for the smaller evening dataset.

4. Discussion

Our study provides the first empirical support for the hypothesis that microhabitat segregation in warningly coloured butterflies and avian insectivores can maintain a diversity of Müllerian mimetic warning colour patterns within communities [27,29,32,35]. This is the first time that both mimetic butterflies and their predators have been studied together at the microhabitat scale, and both our analytical approach and experimental results support the idea that different warning colour patterns can be optimal for anti-predator defence in different microhabitats. Our study thus extends research on how variation in predator communities helps maintain warning colour pattern polymorphisms within prey species at larger spatial scales [16–22,26], to show that predator community structure can also promote warning colour pattern diversity across species within a single prey community.

It is likely that height and topography, through their effects on microclimate variables such as temperature and humidity [52], affect two important aspects of ithomiine ecology: choice of host plant and male mate-locating sites. Ithomiine caterpillars feed almost exclusively on Solanaceae plants, and different clades of butterflies have specialized on particular plant clades [53]. Host plants are regarded as significant in determining ithomiine flight height [27] and spatial distribution [33], and we also documented marked preferences for ridge or valley sites among ithomiine host plants (K.R.W. & M.E. 2005, unpublished data) that may help explain specific preferences for topographic microhabitats. Furthermore, we also noted that males tended to maintain territories where they awaited females (termed 'perching' by Scott [54]) at similar heights and in similar topographic microhabitats to those where their mimicry rings typically fly.

Birds also showed distinct preferences for vertical foraging stratum and topography, consistent with previous studies (e.g. [55]). The similar height and topographic distributions of birds and mimicry patterns resulted in the encounter rates of different mimicry patterns being significantly different for individual bird species. The great majority of the most abundant insectivorous birds occurred in the midstorey and canopy, and thus were estimated to preferentially encounter the second most abundant but highest flying mimicry pattern ('hermias'). A smaller number of understorey birds were estimated to most frequently encounter the most common understorey mimicry ring ('eurimedia'). Topographic preferences among predators and prey strengthened these patterns, since high-flying species of both birds and butterflies also tended to occur more commonly on ridge-tops. As a consequence, both the most abundant ('eurimedia') and the second most abundant pattern ('hermias') were predicted to be optimal in different microhabitats for the majority of species in each mimicry ring.

If colour patterns serve as microhabitat-specific anti-predator defences, then the differing abundance in ridge and valley sites of the two most common patterns, 'hermias' and 'eurimedia', leads to clear predictions of relative predation rates in the field trials. In all comparisons (between mimicry patterns within a single microhabitat and between microhabitats within a single mimicry pattern), empirical predation rates were, as expected, inversely related to observed abundances of mimicry patterns. Most notably, at ridge sites, 'hermias' was approximately twice as abundant as 'eurimedia', and predation rates on 'eurimedia' were overall 1.8 times as high as for 'hermias'. The opposite was observed in valleys, where 'eurimedia' was approximately twice as abundant as 'hermias', and predation rates on 'hermias' were 1.9 times as high as for 'eurimedia'. These data thus support the conclusion that the 'eurimedia' pattern was optimal in valley sites and the 'hermias' pattern optimal on ridges, despite these microhabitats being only 100–300 m apart (see electronic supplementary material, S1).

The overall dominance of the two most abundant mimicry patterns and segregation by flight height that we observed were consistent with three other studies at Ecuadorian Amazonian sites spaced across a three-decade period [27,32,56]. These broad patterns of abundance and flight height partitioning thus seem to be a general feature of ithomiine communities in this region. However, even though microhabitat segregation can help maintain the coexistence of these two most common mimicry patterns, the remaining six patterns were never predicted to be optimal in our analysis of butterfly and bird microhabitat distributions. It is likely that at least some patterns, such as 'agnosia', might prove to be optimal in marginal microhabitats, such as forest edges and secondary growth, that were not well represented in our study. In addition, we did not consider temporal changes in bird and butterfly distribution. For example, the lowest-flying mimicry ring, 'lerida', was most active early in the morning, perhaps exposing it to a distinct suite of predators in comparison with later-flying mimicry rings. Furthermore, temporal partitioning of mimicry rings also occurs throughout the year [30], which may also be coincident with seasonal changes in the predatory bird fauna, perhaps selecting for different optimal defences at different times of year (e.g. [24]). Our first analysis also assumes equivalence among insectivorous birds and among mimicry patterns. Neither of these are likely to be true, and some bird species are likely to account for a disproportionate number of attacks. Nevertheless, our data suggest that the majority of bird species, regardless of abundance, are sufficiently restricted in microhabitat as to encounter particular mimicry patterns at non-random rates. Furthermore, we made the simplifying assumption that the most abundant patterns are the best protected, but differences in unpalatability, detectability and escaping ability are also likely to be significant [57]. Finally, because of predator generalization, some rare patterns (e.g. 'mamercus') may be avoided by predators that have been educated by encounters with similar but more abundant (e.g. 'hermias') mimicry rings.

Alternatively, suboptimal patterns may be maintained because there is little selection for a mimicry switch [5,32]. If community composition shifts over time, weak selective pressures for convergence may not persist long enough to effect change and similarly protected patterns may coexist indefinitely [58]. Similar shifts in community composition may occur over space; some of the rarer mimicry rings in our study community may be maintained by continuous migration from source regions where they are more abundant, such that patterns that are apparently suboptimal in one area are optimal in another [16,17,19,20,26,36,59].

Our study supports the idea that any ecological shift that results in a mimetic butterfly species being exposed to new suites of predators, such as a change in host plant or mate-locating strategy linked to different microhabitats, probably initiates selection for phenotypic change that could ultimately lead to speciation. Previous studies of Neotropical butterflies have shown that predation has morphological, physiological and behavioural consequences [38,60]. Here, we confirm that shifts in microhabitat are likely to also result in strong selection on warning colour patterns. Concerted changes in wing pattern and microhabitat have indeed apparently occurred multiple times in the ithomiine community that we studied [3], driving ecological convergence. Furthermore, shifts in mimetic wing pattern are associated with both pre-zygotic and post-zygotic reproductive isolation in mimetic butterflies [10,12,13,15]. Our results suggest that at least some coexisting mimetic patterns can also be considered ecological niches in their own right [61], rather than by-products of processes operating at larger spatial and temporal scales. Partitioning of species among these niches should help to maintain community species richness in some of the most biologically diverse ecosystems in the world.

Finally, our research contributes to knowledge of the complexity of ecological interactions linking plants, herbivores and predators, and adds to a growing body of literature showing that diversity in anti-predator defence can be maintained by differing abiotic and biotic microenvironments [62–69]. Although competition has usually been seen as the principal driving force for ecological divergence and adaptive radiation [70], predation is likely to be just as important, if not more so, in communities where competition is minimal [71–75].

Ethics. Research and collection permits were provided by the Ministerio del Ambiente, Ecuador, with the support and collaboration of the Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.

Data accessibility. Distribution databases for butterflies and birds recorded in this study are included as electronic supplementary material.

Authors' contributions. C.D.J., K.R.W. and J.C.R.W. conceived the study; all authors contributed to the design of the field experiments; K.R.W., M.E. and C.D.J. collected field data on butterflies and microhabitats; J.C.R.W. collected field data on birds; K.R.W. and M.E. carried out statistical analyses; K.R.W. wrote the first draft of the manuscript; and all authors contributed to significantly revising and improving the draft. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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References

1. Müller F. 1879 *Ituna* and *Thyridia*; a remarkable case of mimicry in butterflies. *Trans. Entomol. Soc. Lond.* **1879**, xx–xxix.
2. Beccaloni GW. 1997 Ecology, natural history and behavior of ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). *Trop. Lepid.* **8**, 103–124.
3. Elias M, Gompert Z, Jiggins C, Willmott KR. 2008 Mutualistic interactions drive ecological niche convergence in a diverse butterfly community. *PLoS Biol.* **6**, 2642–2649. (doi:10.1371/journal.pbio.0060300)
4. Sherratt TN. 2008 The evolution of Mullerian mimicry. *Naturwissenschaften* **95**, 681–695. (doi:10.1007/s00114-008-0403-y)
5. Joron M, Mallet J. 1998 Diversity in mimicry: paradox or paradigm? *Trends Ecol. Evol.* **13**, 461–466. (doi:10.1016/S0169-5347(98)01483-9)
6. Bates HW. 1862 Contributions to an insect fauna of the Amazon Valley: Lepidoptera: Heliconidae. *Trans. Linn. Soc. Lond.* **23**, 495–566. (doi:10.1111/j.1096-3642.1860.tb00146.x)
7. Jiggins CD, Estrada C, Rodrigues A. 2004 Mimicry and the evolution of premating isolation in *Heliconius melpomene* Linnaeus. *J. Evol. Biol.* **17**, 680–691. (doi:10.1111/j.1420-9101.2004.00675.x).
8. Kronforst MR, Young LG, Kapan DD, McNeely C, O'Neill RJ, Gilbert LE. 2006 Linkage of butterfly mate preference and wing color preference cue at the genomic location of *wingless*. *Proc. Natl Acad. Sci. USA* **103**, 6575–6580. (doi:10.1073/pnas.0509685103)
9. Mavarez J, Salazar CA, Bermingham E, Salcedo C, Jiggins CD, Linares M. 2006 Speciation by hybridization in *Heliconius* butterflies. *Nature* **441**, 868–871. (doi:10.1038/nature04738)
10. Chamberlain NL, Hill RI, Kapan DD, Gilbert LE, Kronforst MR. 2009 Polymorphic butterfly reveals the missing link in ecological speciation. *Science* **326**, 847–850. (doi:10.1126/science.1179141)
11. Muñoz AG, Salazar C, Castaño J, Jiggins CD, Linares M. 2010 Multiple sources of reproductive isolation in a bimodal butterfly hybrid zone. *J. Evol. Biol.* **23**, 1312–1320. (doi:10.1111/j.1420-9101.2010.02001.x)
12. Merrill RM, Gompert Z, Dembeck LM, Kronforst MR. 2011 Mate preference across the speciation continuum in a clade of mimetic butterflies. *Evolution* **65**, 1489–1500. (doi:10.1111/j.1558-5646.2010.01216.x)
13. Merrill RM, Wallbank RW, Bull V, Salazar PC, Mallet J, Stevens M, Jiggins CD. 2012 Disruptive ecological selection on a mating cue. *Proc. R. Soc. B* **279**, 4907–4913. (doi:10.1098/rspb.2012.1968)
14. Finkbeiner SD, Briscoe AD, Reed RD. 2014 Warning signals are seductive: relative contributions of color and pattern to predator avoidance and mate attraction in *Heliconius* butterflies. *Evolution* **68**, 3410–3420. (doi:10.1111/evo.12524)
15. Jiggins CD, Naisbit RE, L. CR, Mallet J. 2001 Reproductive isolation caused by color pattern mimicry. *Nature* **411**, 302–305. (doi:10.1038/35077075)
16. Kapan DD. 2001 Three-butterfly mimicry system provides a field test of Müllerian mimicry. *Nature* **409**, 338–340. (doi:10.1038/35053066)
17. Chouteau M, Angers B. 2011 The role of predators in maintaining the geographic organization of aposematic signals. *Am. Nat.* **178**, 810–817. (doi:10.1086/662667)
18. Valkonen JK, Nokelainen O, Niskanen M, Kilpimaa J, Björklund M, Mappes J. 2012 Variation in predator species abundance can cause variable selection pressure on warning signaling prey. *Ecol. Evol.* **2**, 1971–1976. (doi:10.1002/ece3.315)
19. Nokelainen O, Valkonen J, Lindsted C, Mappes J. 2014 Changes in predator community structure shifts the efficacy of two warning signals in Arctiid moths. *J. Anim. Ecol.* **83**, 598–605. (doi:10.1111/1365-2656.12169)

20. Willink B, García-Rodríguez A, Bolaños F, Pröhl H. 2014 The interplay between multiple predators and prey color divergence. *Biol. J. Linn. Soc.* **113**, 580–589. (doi:10.1111/bij.12355)
21. Hegna RH, Mappes J. 2014 Influences of geographic differentiation in the forewing warning signal of the wood tiger moth in Alaska. *Evol. Ecol.* **28**, 1003–1017. (doi:10.1007/s10682-014-9734-7)
22. Mallet J, Barton NH. 1989 Strong natural selection in a warning-color hybrid zone. *Evolution* **43**, 421–431. (doi:10.2307/2409217)
23. Sherratt TN. 2006 Spatial mosaic formation through frequency-dependent selection in Müllerian mimicry complexes. *J. Theor. Biol.* **240**, 165–174. (doi:10.1016/j.jtbi.2005.09.017)
24. Mappes J, Kokko H, Ojala K, Lindström L. 2014 Seasonal changes in predator community switch the direction of selection for prey defences. *Nat. Commun.* **5**, 1–7. (doi:10.1038/ncomms6016)
25. Joron M, Iwasa Y. 2005 The evolution of a Mullerian mimic in a spatially distributed community. *J. Theor. Biol.* **237**, 87–103. (doi:10.1016/j.jtbi.2005.04.005)
26. Joron M, Wynne IR, Lamas G, Mallet J. 1999 Variable selection and the coexistence of multiple mimetic forms of the butterfly *Heliconius numata*. *Evol. Ecol.* **13**, 721–754. (doi:10.1023/A:1010875213123)
27. Beccaloni GW. 1997 Vertical stratification of ithomiine butterfly (Nymphalidae: Ithomiinae) mimicry complexes: the relationship between adult flight height and larval host-plant height. *Biol. J. Linn. Soc.* **62**, 313–341. (doi:10.1006/bijl.1997.0165)
28. Medina MC, Robbins RK, Lamas G. 1996 Vertical stratification of flight by ithomiine butterflies (Lepidoptera: Nymphalidae) at Pakitza, Manu: national Park, Perú. In *Manu: the biodiversity of southeastern Peru* (eds DE Wilson, A Sandoval), pp. 211–216. Washington, DC: Smithsonian Institution.
29. Mallet J, Gilbert L. 1995 Why are there so many mimicry rings? Correlations between habitat, behavior and mimicry in *Heliconius* butterflies. *Biol. J. Linn. Soc.* **55**, 159–180. (doi:10.1111/j.1095-8312.1995.tb01057.x)
30. DeVries PJ, Lande R, Murray D. 1999 Associations of co-mimetic ithomiine butterflies on small spatial and temporal scales in a neotropical rainforest. *Biol. J. Linn. Soc.* **67**, 73–85. (doi:10.1006/bijl.1998.0288)
31. Estrada C, Jiggins CD. 2002 Patterns of pollen feeding and habitat preference among *Heliconius* species. *Ecol. Entomol.* **27**, 448–456. (doi:10.1046/j.1365-2311.2002.00434.x)
32. Hill RI. 2009 Habitat segregation among mimetic ithomiine butterflies (Nymphalidae). *Evol. Ecol.* **24**, 273–285. (doi:10.1007/s10682-009-9305-5)
33. Willmott KR, Mallet J. 2004 Correlations between adult mimicry and larval host plants in ithomiine butterflies. *Proc. R. Soc. Lond. B* **271**, S266–S269. (doi:10.1098/rsbl.2004.0184)
34. Papageorgis C. 1975 Mimicry in neotropical butterflies. *Am. Sci.* **63**, 522–532.
35. Gompert Z, Willmott KR, Elias M. 2011 Heterogeneity in predator micro-habitat use and the maintenance of Müllerian mimicry diversity. *J. Theor. Biol.* **281**, 39–46. (doi:10.1016/j.jtbi.2011.04.024)
36. Chouteau M, Arias M, Joron M. 2016 Warning signals are under positive frequency-dependent selection in nature. *Proc. Natl Acad. Sci. USA* **113**, 2164–2169. (doi:10.1073/pnas.1519216113)
37. Brown KS. 1984 Adult obtained pyrrolizidine alkaloids defend ithomiine butterflies against a spider predator. *Nature* **309**, 707–709. (doi:10.1038/309707a0)
38. Chai P, Syrgley RB. 1990 Predation and the flight, morphology, and temperature of Neotropical rain-forest butterflies. *Am. Nat.* **135**, 748–765. (doi:10.1086/285072)
39. Chai P. 1986 Field observations and feeding experiments on the responses of rufous-tailed jacamars (*Galbula ruficauda*) to free-flying butterflies in a tropical rain forest. *Biol. J. Linn. Soc.* **29**, 161–189. (doi:10.1111/j.1095-8312.1986.tb01772.x)
40. Finkbeiner SD, Briscoe AD, Reed R. 2012 The benefit of being a social butterfly: communal roosting deters predation. *Proc. R. Soc. B* **279**, 2769–2776. (doi:10.1098/rspb.2012.0203)
41. Langham GM. 2005 Rufous-tailed jacamars and aposematic butterflies: do older birds attack novel prey? *Behav. Ecol.* **17**, 285–290. (doi:10.1093/beheco/arj027)
42. Pinheiro CEG. 2011 On the evolution of warning coloration, Batesian and Müllerian mimicry in Neotropical butterflies: the role of jacamars (Galbulidae) and tyrant-flycatchers (Tyrannidae). *J. Avian Biol.* **42**, 277–281. (doi:10.1111/j.1600-048X.2011.05435.x)
43. Jiggins CD, Mallarino R, Willmott KR, Bermingham E. 2006 The phylogenetic pattern of speciation and wing pattern change in Neotropical *Ithomia* butterflies (Lepidoptera: Nymphalidae). *Evolution* **60**, 1454–1466. (doi:10.1111/j.0014-3820.2006.tb01224.x)
44. Brower JVZ. 1958 Experimental studies of mimicry in some North American butterflies. Part I. The Monarch, *Danaus plexippus*, and Viceroy, *Limenitis archippus archippus*. *Evolution* **12**, 32–47. (doi:10.2307/2405902)
45. Brower JVZ. 1958 Experimental studies of mimicry in some North American butterflies. Part II. *Battus philenor* and *Papilio troilus*, *P. polyxenes* and *P. glaucus*. *Evolution* **12**, 123–136. (doi:10.2307/2406023)
46. Llaurens V, Joron M, Thery M. 2014 Cryptic differences in colour among Müllerian mimics: how can the visual capacities of predators and prey shape the evolution of wing colours? *J. Evol. Biol.* **27**, 531–540. (doi:10.1111/jeb.12317)
47. Burton PJK. 1976 Feeding behavior in the paradise jacamar and the swallow-wing. *Living Bird* **15**, 223–238.
48. Chai P. 1996 Butterfly visual characteristics and ontogeny of responses to butterflies by a specialized tropical bird. *Biol. J. Linn. Soc.* **59**, 37–67. (doi:10.1006/bijl.1996.0053)
49. Pinheiro CEG. 1996 Palatability and escaping ability in neotropical butterflies: tests with wild kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biol. J. Linn. Soc.* **59**, 351–365. (doi:10.1006/bijl.1996.0069)
50. Pinheiro CEG. 2003 Does Müllerian mimicry work in nature? Experiments with butterflies and birds (Tyrannidae). *Biotropica* **35**, 356. (doi:10.1646/02128)
51. Ridgely RS, Greenfield PJ. 2001 *The birds of Ecuador, volume II: field guide*. London, UK: Christopher Helm.
52. Checa MF, Rodriguez J, Willmott KR, Liger B. 2014 Microclimate variability significantly affects the composition, abundance and phenology of butterfly communities in a highly threatened Neotropical dry forest. *Fla. Entomol.* **97**, 1–13. (doi:10.1653/024.097.0101)
53. Willmott KR, Freitas AVL. 2006 Higher-level phylogeny of the Ithomiinae (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonisation and diversification. *Cladistics* **22**, 297–368. (doi:10.1111/j.1096-0031.2006.00108.x)
54. Scott JA. 1976 Mate locating behavior of the western North American butterflies. *J. Res. Lepid.* **14**, 1–40. (doi:10.1016/B978-0-12-024914-5.50008-5)
55. Stotz DF, Fitzpatrick JW, Parker TA, Moskovits DK. 1996 *Neotropical birds: ecology and conservation*. Chicago, IL: Chicago University Press.
56. Drummond BA. 1976 Comparative ecology and mimetic relationships of ithomiine butterflies in Eastern Ecuador. PhD thesis, University of Florida, Gainesville, FL.
57. Mallet J. 2001 Causes and consequences of a lack of coevolution in Müllerian mimicry. *Evol. Ecol.* **13**, 777–806. (doi:10.1023/A:1011060330515)
58. Chouteau M, Angers B. 2012 Wright's shifting balance theory and the diversification of aposematic signals. *PLoS ONE* **7**, e34028. (doi:10.1371/journal.pone.0034028)
59. Brown KS, Benson WW. 1974 Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata* (Lepid. Nymph.). *Biotropica* **6**, 205–228. (doi:10.2307/2989666)
60. Srygley RB, Chai P. 1990 Predation and the elevation of thoracic temperature in brightly-colored, neotropical butterflies. *Am. Nat.* **135**, 766–787. (doi:10.1086/285073)
61. Chazot N, Willmott KR, Paola SE, Toporov A, Hill R, Jiggins C, Elias M. 2014 Mutualistic mimicry and filtering by altitude shape the structure of Andean butterfly communities. *Am. Nat.* **183**, 26–39. (doi:10.1086/674100)
62. Agrawal AA, Fishbein M. 2006 Plant defence syndromes. *Ecology* **87**(Suppl.), S132–S149. (doi:10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2)
63. Bursell J, Dyck J. 2003 Background matching and evolution of cryptic colors of selected passerines in deciduous woodlands. *Lundiana* **4**, 511–559.
64. Caro TM, Graham CM, Stoner CJ, Vargas JK. 2006 Adaptive significance of antipredator behavior in artiodactyls. *Anim. Behav.* **67**, 205–228. (doi:10.1016/j.anbehav.2002.12.007)

65. Cooper WE, Whiting MJ. 2007 Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. *Ethology* **113**, 661 – 672. (doi:10.1111/j.1439-0310.2007.01363.x)
66. Fine PVA, Miller ZJ, Mesones I, Irazuzta S, Appel HM, Stevens MHH, Sääksjärvi I, Schultz JC, Coley PC. 2006 The growth-defence trade-off and habitat specialization by plants in Amazonian forests. *Ecology* **87**(Suppl.), S150 – S162 (doi:10.1890/0012-9658(2006)87[150:TGTAHS]2.0.CO;2)
67. Mikolajewski DJ, De Block M, Rolff J, Johansson F, Beckerman AP, Stoks R. 2010 Predator-driven trait diversification in a dragonfly genus: covariation in behavioral and morphological antipredator defence. *Evolution* **64**, 3327 – 3335. (doi:10.1111/j.1558-5646.2010.01078.x)
68. Petrin Z, Schilling EG, Loftin CS, Johansson F. 2010 Predators shape distribution and promote diversification of morphological defences in *Leucorrhinia*, Odonata. *Evol. Ecol.* **24**, 1003 – 1016. (doi:10.1007/s10682-010-9361-x)
69. Walsh MR, Post DM. 2011 Interpopulation variation in a fish predator drives evolutionary divergence in prey in lakes. *Proc. R. Soc. B* **278**, 2628 – 2637. (doi:10.1098/rspb.2010.2634)
70. Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
71. Abrams PA. 2000 Character shifts of prey species that share predators. *Am. Nat.* **156**, S45 – S61. (doi:10.1086/303415)
72. Meyer JR, Kassen R. 2007 The effects of competition and predation on diversification in a model adaptive radiation. *Nature* **446**, 432 – 435. (doi:10.1038/nature05599)
73. Nosil P, Crespi BJ. 2006 Experimental evidence that predation promotes divergence in adaptive radiation. *Proc. Natl Acad. Sci. USA* **103**, 9090 – 9095. (doi:10.1073/pnas.0601575103)
74. Vamosi SM. 2005 On the role of enemies in divergence and diversification of prey: a review and synthesis. *Can. J. Zool.* **83**, 894 – 910. (doi:10.1139/z05-063)
75. Arbuckle K, Speed MP. 2015 Antipredator defenses predict diversification rates. *Proc. Natl Acad. Sci. USA* **112**, 13 598 – 13 602. (doi:10.1073/pnas.1509811112)