

## Research



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# Multiple models generate a geographical mosaic of resemblance in a Batesian mimicry complex

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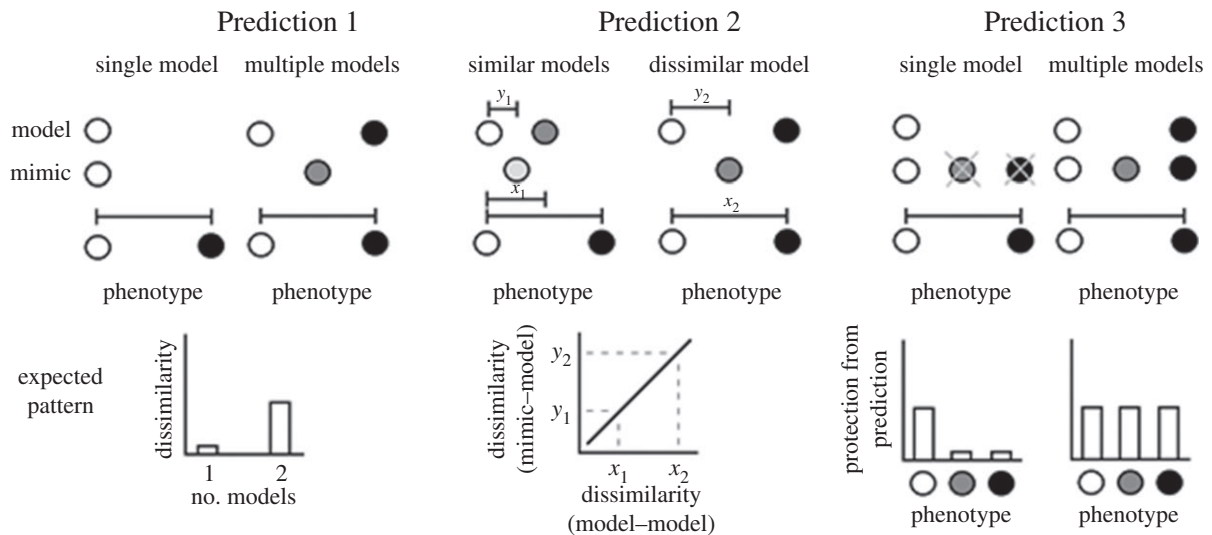
Batesian mimics—benign species that receive protection from predation by resembling a dangerous species—often occur with multiple model species. Here, we examine whether geographical variation in the number of local models generates geographical variation in mimic–model resemblance. In areas with multiple models, selection might be relaxed or even favour imprecise mimicry relative to areas with only one model. We test the prediction that model–mimic match should vary with the number of other model species in a broadly distributed snake mimicry complex where a mimic and a model co-occur both with and without other model species. We found that the mimic resembled its model more closely when they were exclusively sympatric than when they were sympatric with other model species. Moreover, in regions with multiple models, mimic–model resemblance was positively correlated with the resemblance between the model and other model species. However, contrary to predictions, free-ranging natural predators did not attack artificial replicas of imprecise mimics more often when only a single model was present. Taken together, our results suggest that multiple models might generate a geographical mosaic in the degree of phenotype matching between Batesian mimics and their models.

## 1. Introduction

Coevolution, the reciprocal adaptation resulting from ecological interactions, is an important driver of phenotypic evolution between interacting species [1,2]. Several studies have demonstrated that the form of ecological interactions between species can vary across a landscape (reviewed in [2]). This geographical variation underlies the geographical mosaic theory of coevolution [3,4].

The hypothesis of the geographical mosaic of coevolution has three parts [4]. First, the form of selection—its strength, direction and mode—varies across a landscape (i.e. selection mosaics are predicted). Second, coevolution is active in some locations (predicting hotspots, where species traits are tightly coevolved) but not in others (predicting coldspots, where traits match poorly). Third, gene flow between populations causes trait remixing that can generate mismatches in the traits of interacting species. This tripartite hypothesis characterizes a variety of ecological interactions, including prey–predator interactions [5,6], plant–pollinator interactions [7,8] and host–parasite interactions [9,10].

An ideal context in which to study geographical mosaics of coevolution is Batesian mimicry, which occurs when a harmless species (the mimic) evolves to resemble a defended species that predators avoid (the model) [11,12]. The evolution of Batesian mimicry might readily spawn geographical mosaics for the simple reason that mimics often co-occur with different model species



**Figure 1.** Predictions of the 'multiple models hypothesis' addressed in this study. (a) The resemblance between the mimic and the model should depend on the number of model species. Generally, the mimic should resemble its model (white circle) more precisely in regions where they co-occur exclusively (in the absence of other models) relative to regions where they co-occur with multiple models (white circle and black circle). (b) The resemblance between the mimic and the model should depend on the resemblance between local models. Among regions with multiple models, the mimic should generally resemble its model less precisely when local models resemble each other less (white circle and black circle =  $x_2$ ) relative to when local models resemble each other more (white circle and grey circle =  $x_1$ ). (c) The number of local models should affect the relative degree of protection received by precise and imprecise mimics. Imprecise mimics should not receive protection from predation in regions with a single model relative to precise mimics. However, imprecise mimics should be at least equally protected from predation as precise mimics in regions with multiple models. (Online version in colour.)

across their range [13–16]. Thus, a geographical mosaic in coevolution between a mimic and its various model(s) might arise because of geographical variation in the number of models present. For example, in regions where the mimic and its model are exclusively sympatric, predators should only experience selection to avoid the single local model. In such situations, only those mimics that most closely resemble the local model should receive protection from predation. Likewise, models might experience stronger selection to distinguish themselves from mimics in regions where they are the only target for mimics. Such regions where only a single model is present might therefore represent coevolutionary hotspots.

By contrast, if multiple models occur in sympatry, predators might avoid multiple models. Thus, in areas where more than one model is present, mimics that bear a vague resemblance to multiple models might receive as much protection from predation as precise mimics of a single model [17,18]. Consequently, the model should experience relaxed selection to distinguish themselves from mimics. Such regions where multiple models are present might therefore represent coevolutionary coldspots.

Previous studies of Batesian mimicry have proposed a potential mechanism that might explain this geographical mosaic: the 'multiple models hypothesis' of imprecise mimicry [17,18]. The multiple models hypothesis proposes that mimics might experience a selective trade-off to resemble multiple models and, as a consequence, possess features of several models to receive protection from predation [17,18]. Imprecise mimicry of multiple models is considered most likely to evolve in regions where models bear a resemblance to one another [18].

We sought to evaluate whether the multiple models hypothesis could explain a geographical mosaic in the degree of phenotype matching between a Batesian mimic and its model. To do so, we focused on the resemblance

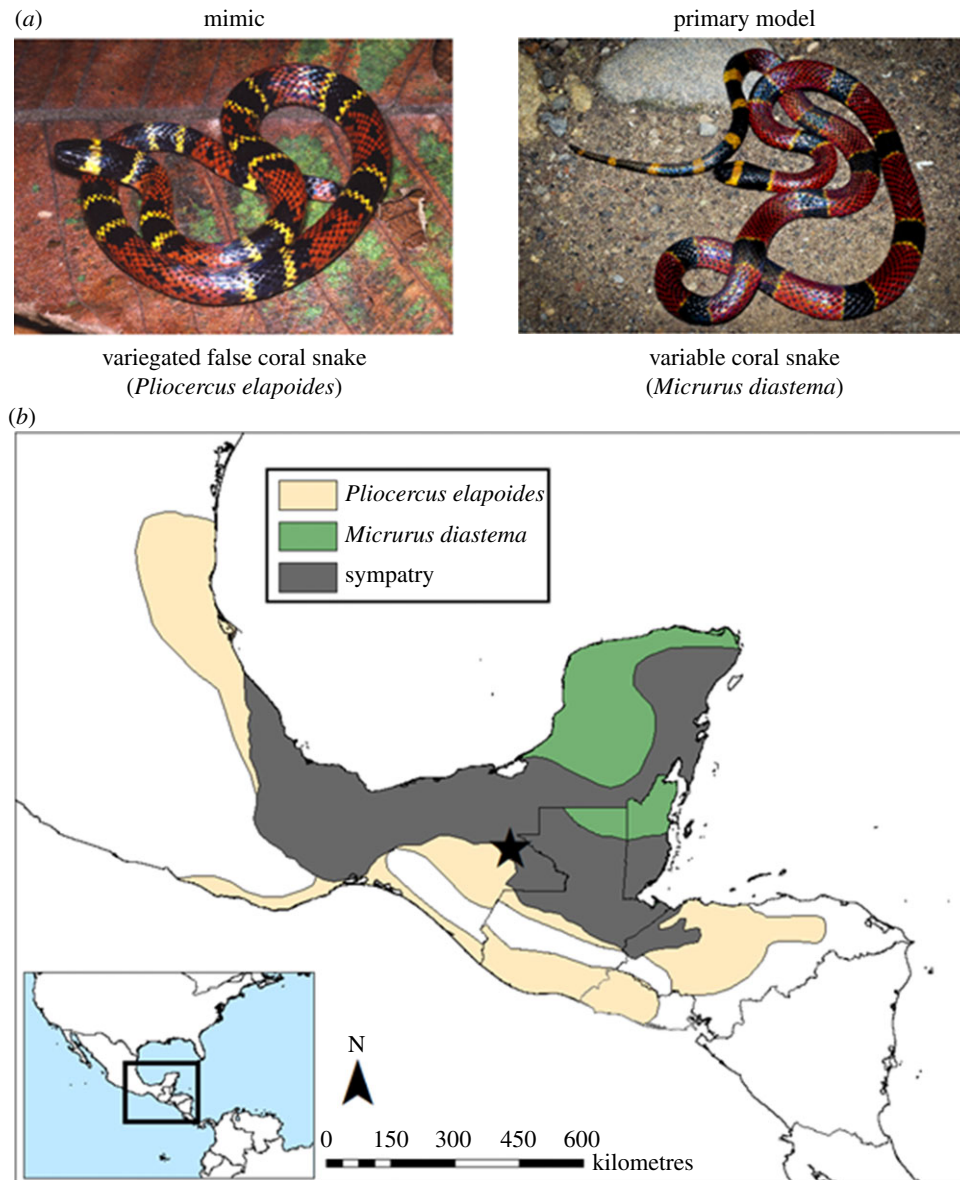
between a Batesian mimic and its 'primary' coral snake model that co-occurs with it throughout its range. Designating a primary model established a baseline to evaluate mimetic precision. Specifically, we conducted morphometric analyses to determine (1) whether mimics that co-occur with multiple, similar models match the primary model in phenotype less than mimics that are exclusively sympatric with it (figure 1a), and (2) whether, in regions with multiple sympatric models, mimics match the primary model less in phenotype when the resemblance between all sympatric models is poor as compared to when sympatric models resemble each other more closely (figure 1b). We then conducted field experiments to determine whether selection for mimicry differs between putative hotspots and coldspots. Specifically, the hypothesis predicted that selection would favour well-matched (precise) mimics in regions with a single model, but that selection would be relaxed on mismatched (imprecise) mimics in regions with multiple models (figure 1c).

## 2. Material and methods

### (a) Study system

More than 70 species of highly venomous, aposematically coloured coral snakes (*Leptomicrurus*, *Micruroides* and *Micrurus*) occur in the New World [19]. They serve as models for numerous species of mildly venomous and nonvenomous colubrid snakes [16,20]. Most mimics in the Neotropics co-occur with multiple coral snake models [16]. Here, we focus on one such coral snake mimicry complex: that involving the mildly venomous variegated false coral snake (*Pliocercus elapoides*) and its primary model, the variable coral snake (*Micrurus diastema*) (figure 2a).

Two features render this coral snake mimicry complex ideal for assessing whether the multiple models hypothesis can lead to a geographical mosaic in mimicry. First, although *M. diastema* probably serves as the model for *P. elapoides* throughout most of



**Figure 2.** (a) The variegated false coral snake (*Pliocercus elapoides*) mimics the venomous variable coral snake (*Micrurus diastema*). (b) The distribution of *P. elapoides* (the mimic) and *M. diastema* (*P. elapoides*'s most widely sympatric model). Star shows location where field experiments were conducted. (Online version in colour.)

its range, *P. elapoides* also co-occurs with several phenotypically distinct coral snake species over small portions of its range (figure 2b) [19,21]. Second, *P. elapoides* and *M. diastema* are both highly geographically variable in colour pattern [22,23]. Indeed, *P. elapoides* has long been recognized for its ability to resemble different sympatric coral snakes [24,25]. Thus, genetic constraints are unlikely to limit the ability of *P. elapoides* to match different models.

We considered *M. diastema* to be the primary model of *P. elapoides* in our study for several reasons. First, *P. elapoides* shares the highest degree of range overlap with *M. diastema* relative to other models [19,21]. Second, *M. diastema* is generally considered to be one of the most common coral snake species throughout southern Mexico [26,27]. Third, the mimic has been documented to exhibit parallel geographical variation in colour pattern with *M. diastema* but not with any other coral snake species [28].

### (b) Assessing phenotypic resemblance between mimics and models

To begin, we asked whether the resemblance between *P. elapoides* (the mimic) and *M. diastema* decreases as the number of local

models increases (Prediction 1; figure 1a), and as the phenotypic variation among these local models increases (Prediction 2; figure 1b). To evaluate these first two predictions, we conducted morphometric analyses of *P. elapoides* and several of its sympatric coral snake species.

Using museum specimens, we first photographed the dorsal surface of specimens with a digital camera (Canon Powershot SX130 IS; Canon Zooms Lens, 6.0–60.0 mm, 1:2.8–4.3). The width of each ring was measured from digital images using IMAGEJ v. 1.46 [29]. We collected data on phenotypic traits that had previously been shown to be targets of predator-mediated selection for coral snake mimics from other temperate and tropical regions: proportion of body covered by red bands, yellow bands, black bands, primary black bands and accessory black bands; number of red bands, yellow bands, black bands, primary black bands and accessory black bands [30–34]. All measurements were taken on the mid-dorsum of each snake, from snout to cloaca (see [35] for a detailed description on how measurements were taken). *Pliocercus elapoides* and *M. diastema* exhibit parallel geographical variation in band number and the relative lengths of their bands throughout their ranges [28], further suggesting that these traits are targets of predator-mediated selection. Although potentially important for predator



recognition, data on colours and spectral properties, such as reflectance, were not collected from museum specimens due to the fading of colours in fluid-preserved specimens.

We sampled 118 *P. elapoides* specimens and 313 coral snake specimens (4 *M. browni*, 259 *M. diastema*, 21 *M. elegans*, 7 *M. ephippifer*, 16 *M. hippocrepis*, 4 *M. latifasciatus*, 1 *M. limbatus* and 1 *M. nigrocinctus*) that occur within the range of both *P. elapoides* and *M. diastema*. We then used common principal component (PC) scores to quantify the degree to which *P. elapoides* and coral snake models resemble each other in phenotype. Specifically, a 'dissimilarity score' (D) was computed by taking the absolute value of the difference between PC scores between species (see [36] for a detailed description of the dissimilarity score). We used PC scores for the first 2 PC axes in all analyses, which explained 72% of the variance in phenotype (electronic supplementary material, table S1).

We then determined the identity and the number of model species that have been documented to co-occur within a 25 km radius of each *P. elapoides* specimen. To do so, we used range maps from Campbell & Lamar [19], as well as point occurrence data obtained from various museums (www.vertnet.org). Collection biases certainly underlie these data; however, less biased approaches of characterizing model co-occurrence (e.g. environmental niche models) could not be applied in our analyses given the restricted sampling of model species. We then compared the above PC scores of each *P. elapoides* specimen to the mean PC scores of each model species that was sampled within a 25 km radius. This radius allowed us to obtain sufficient sample sizes while also being on a scale relevant to avian and mammalian predators; qualitatively similar results are obtained when a 10 km and 50 km radius is used (electronic supplementary material, figure S1).

To test whether the resemblance between *P. elapoides* and *M. diastema* decreases as the number of local model species increases (Prediction 1), we compared the mean D of *P. elapoides* to its local *M. diastema* when *P. elapoides* is exclusively sympatric with *M. diastema* versus when *P. elapoides* is sympatric with *M. diastema* as well as with other model species using a linear discriminant analysis. The presence or absence of 'other' models was the response variable, and mean D in PC1 and PC2 were the predictor variables.

To test whether the resemblance between *P. elapoides* and *M. diastema* decreases as the phenotypic variation among local models increases (Prediction 2), we regressed the D of each *P. elapoides* specimen to its local *M. diastema* against the average D between local model species in regions where *P. elapoides* is sympatric with two models (*M. diastema* along with one other model species). Analyses for this section were done in JMP v. 14.0.0 (SAS Institute Inc., Cary, North Carolina, USA).

### (c) Assessing selection on intermediate mimics

Finally, we experimentally evaluated whether predator-mediated selection for imprecise, intermediate mimics is relaxed in the presence of multiple model species (Prediction 3). To do so, we conducted field experiments using artificial snake replicas. This technique has frequently been used to study coral snakes and their mimics in a variety of temperate [32–34,37–41] and tropical habitats [30,31,42–44]. Moreover, camera traps placed at these field sites have demonstrated the efficacy of this method [45]. Artificial snake replicas were designed and constructed following protocols described in [39]. Replicas made out of Sculpey III modelling clay were created based on morphometric analyses of traits (listed in 'Assessing phenotypic resemblance between mimics and models') measured from museum specimens of *M. diastema* and *M. elegans* from Mexico where the two species are sympatric. Four types of patterns were constructed: (1) a *M. diastema* mimic; (2) a *M. elegans* mimic (the most phenotypically distant model sympatric with *M. diastema*; electronic supplementary material, figure S2); (3) an intermediate between *M. diastema*

and *M. elegans* (electronic supplementary material, figure S3), which was created by using the average value of the *M. diastema* and *M. elegans* phenotype for each trait measured; and (4) a patternless brown control, resembling several locally abundant, nonvenomous snakes (e.g. *Adelphicos quadrivirgatus*, *Coniophanes bipunctatus*, *Geophis carinosus*, *Stenorrhina degenhardtii*, *Tantilla schistosa* and *Tantillita lintoni*). We do not know how similar the reflectance of the red and yellow clay is to the actual colours on live snakes. However, colours used to make replicas matched those used in previous studies that have employed this technique to study predation on coral snake colour patterns in the Neotropics (e.g. [30,31]).

Experiments were conducted along an elevational gradient in two natural protected areas in the northwestern portion of the Lacandon ecoregion in Chiapas, south Mexico: Metzabok Reserve (17.112° N, 91.625° W) and Nahá Reserve (16.975° N, 91.58° W) (figure 2). Although both protected areas are located only about 15 km apart, the elevation of Metzabok ranges from 520 m to 750 m, while the elevation of Nahá is higher, ranging from 800 m to 1150 m [46]. Whereas *M. diastema* can be found from sea level up to around 1500 m throughout its range in Mexico, *M. elegans* is only found at elevations greater than 800 m [27]. Indeed, *M. diastema* can be found at both Metzabok and Nahá; however, *M. elegans* has only been documented at Nahá [47]. Thus, one site (Metzabok) harboured a single model, whereas the other site (Nahá) harboured two models. Experiments were conducted at Nahá during June–July 2017 and Metzabok during July–August 2018 during the middle of the rainy season (June–September) when the surface activity of most tropical snake species is highest [48–50].

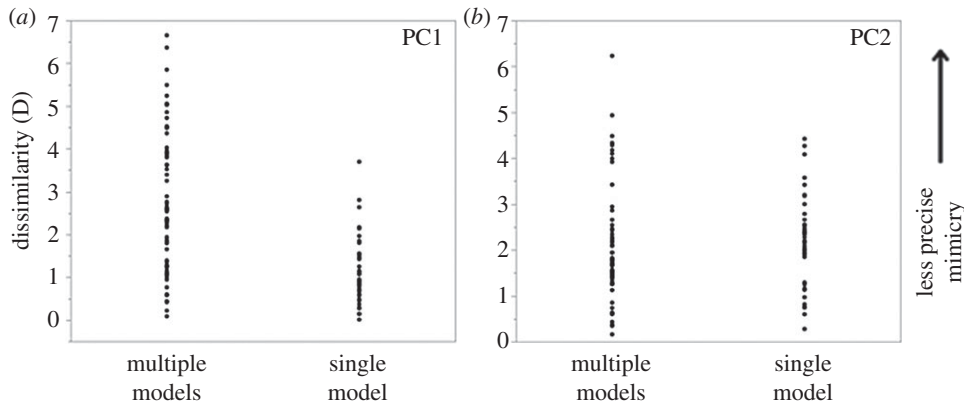
In the field, we placed replicas of each phenotype along infrequently used forest trails. Replicas were placed on leaf litter at 8–10 m intervals along the trails, 1–4 m off the edge and on alternating sides of the trails. The order of the four phenotypes was randomized once and that random order was repeated throughout the experiments. Replicas were arranged into transects that consisted of 10 replicas of each phenotype. We placed a total of 35 transects at Nahá (819–1111 m) and 21 transects at Metzabok (537–720 m) through premontane moist forest habitat. To expose the replicas to as much of the local predator community as possible, each transect was separated by at least 250 m. Replicas were checked for predation attempts at 6 days and 12 days after they were placed. On day 6, attacked and destroyed replicas were collected and replaced with new replicas to maintain an equal ratio of phenotypes until replicas were retrieved on day 12. Each replica was scored as having been attacked if it bore a mark diagnostic of a predatory attack (e.g. U- or V-shaped beak marks, carnivore bite marks; *sensu* [39]). Marks from rodents or insects were ignored, as these would not represent real threats to these snakes.

To test whether phenotypes vary in the protection that they receive from predation, we used generalized linear mixed models to model the probability of a replica being attacked (binary response) as a function of phenotype, with a logit link function and transect included as a random effect. We used the lme4 package in R v. 3.4.4 [51]. Sample sizes were too small to analyse mammalian and avian attacks separately. We also regressed the proportion of intermediate phenotypes attacked by predators in each transect against transect elevation. The significance of predictors was assessed using the likelihood ratio test (LRT).

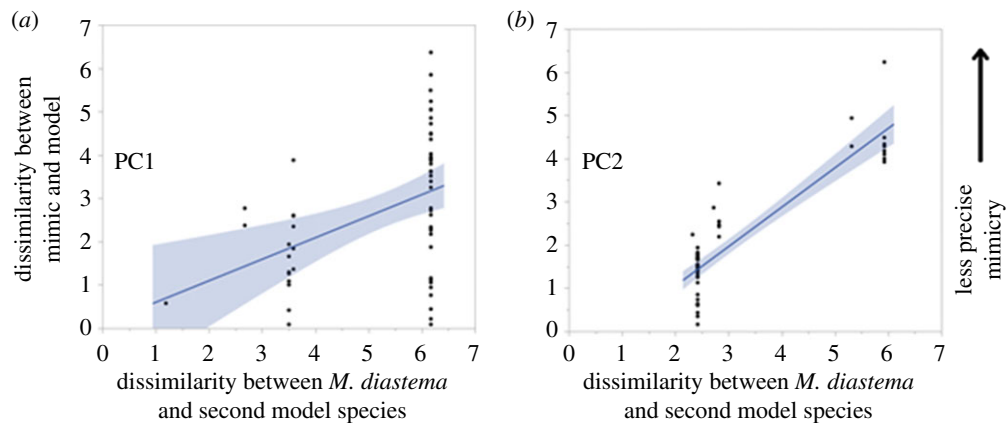
## 3. Results

### (a) Assessing phenotypic resemblance between mimic and models

The first two axes produced by the principal component analysis of colour pattern traits represented 72% of the total



**Figure 3.** Dissimilarity ( $D$ ) in PC1 (a) and PC2 (b) between the coral snake mimic, *Pliocercus elapoides*, and its model the variable coral snake, *Micrurus diastema*, depending on whether the mimic co-occurs with a single model (only *M. diastema*) or multiple models (*M. diastema* plus additional coral snake species). Each point represents the  $D$  for an individual mimic specimen.



**Figure 4.** Dissimilarity ( $D$ ) in PC1 (a) and PC2 (b) between the coral snake mimic, *Pliocercus elapoides*, and its model the variable coral snake, *Micrurus diastema*, as a function of the mean  $D$  in PC1 and PC2 between local *M. diastema* and local individuals of a second model species, respectively, in regions where *P. elapoides* co-occurs with one model in addition to *M. diastema*. Each point represents an individual mimic specimen. (Online version in colour.)

variation in phenotype among mimic and model species (electronic supplementary material, table S1). The first PC axis reveals a contrast between the relative proportions of dorsum red and black; the second correlates most strongly with the numbers of primary and accessory bands.

Our analyses of phenotypic resemblance between mimics and models were consistent with the predictions of the multiple models hypothesis (figure 1a). Specifically, consistent with Prediction 1, a discriminant analysis based on the first two PC axes misclassified significantly more mimics that co-occurred with *M. diastema* and other model species than mimics that only co-occurred with *M. diastema* (36.5% versus 11.6%; Fisher's exact test,  $p < 0.0001$ ), suggesting that mimics more precisely resemble *M. diastema* when *M. diastema* is the only local model (figure 3). Consistent with Prediction 2 (figure 1b), in regions with two models, mimetic precision to *M. diastema* decreased as the variation (i.e. distance) between *M. diastema* and the other local model increased ( $F_{2,54} = 64.08$ ,  $p < 0.0001$ ; figure 4).

### (b) Assessing selection on intermediate mimics

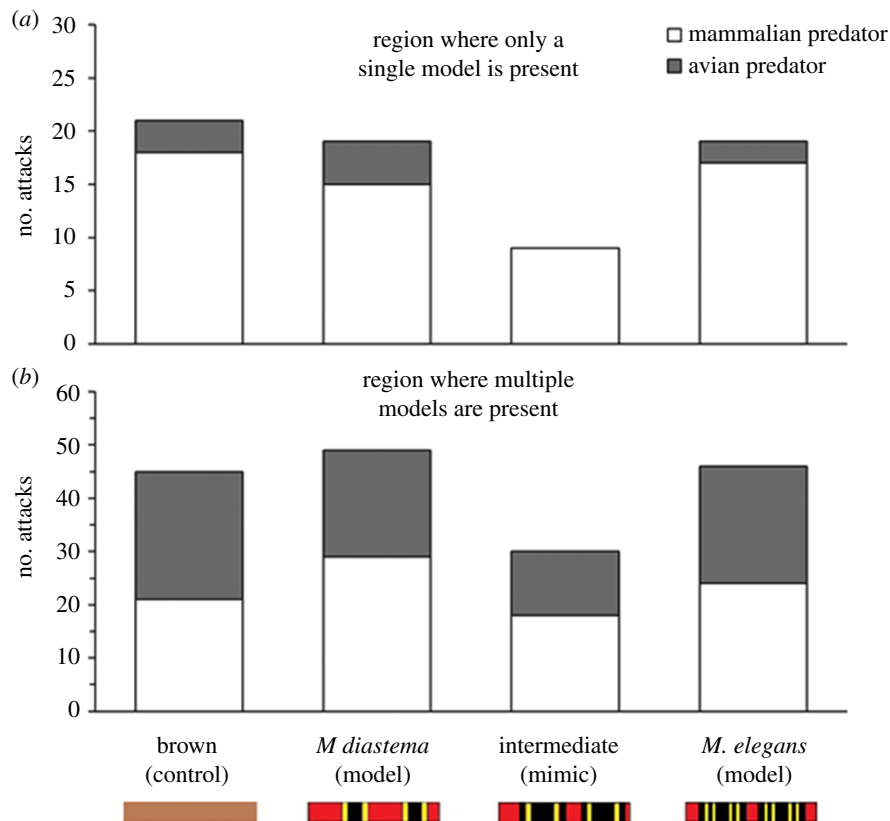
At Nahá, 176 attacks—78 avian attacks, 92 mammalian attacks and 6 attacks that could not be assigned to a predator type—were recorded on 1400 total models (350 of each phenotype), among the 35 transects (figure 5). We recorded 45 attacks on the brown control, 52 attacks on *M. diastema*, 32

attacks on the intermediate and 47 attacks on *M. elegans*. At Metzabok, 68 attacks—9 avian attacks and 59 mammalian attacks—were recorded on 840 total models (210 of each phenotype), among the 21 transects (figure 5). We recorded 21 attacks on the brown control, 19 attacks on *M. diastema*, nine attacks on the intermediate and 19 attacks on *M. elegans* (figure 5).

Contrary to Prediction 3 (figure 1c), all four phenotypes were equally likely to be attacked both at Metzabok, within the range of *M. diastema* only, and at Nahá, within the range of both *M. diastema* and *M. elegans* (Metzabok: LRT:  $\chi^2_3 = 6.67$ ,  $p = 0.083$ ; Nahá: LRT:  $\chi^2_3 = 4.99$ ,  $p = 0.172$ ; figure 5). There was no effect of transect elevation on the proportion of intermediate phenotypes attacked by predators (Spearman  $\rho = 0.1575$ ,  $p = 0.2747$ ; electronic supplementary material, figure S4).

## 4. Discussion

We evaluated whether the multiple models hypothesis could provide a mechanism explaining a geographical mosaic in imprecise mimicry. Our data are consistent with the first two predictions of this hypothesis (figure 1a,b). The mimic *P. elapoides* resembles its most broadly sympatric model more where they are exclusively sympatric than when mimics are sympatric with multiple models (figure 3) and



**Figure 5.** Results of field experiments. Number of attacks on each replica type at (a) Metzabok (537–720 m), which only occurs within the elevational range of *P. elapoides* and *M. diastema*, and (b) Nahá (819–1111 m), which occurs within the elevational ranges of *P. elapoides*, *M. diastema* and *M. elegans*. (Online version in colour.)

the resemblance of the mimic to this model in all trait dimensions decreases as the phenotypic distance between local models increases (figure 4). However, the results of our field experiment using artificial snake replicas did not reveal the predicted reduction in attacks on imperfect mimics when there were multiple models (figure 1c). Specifically, the predation on different mimics did not vary significantly between a putative hotspot (Metzabok) and coldspot (Nahá) (figure 5; electronic supplementary material, figure S4). However, the design of our experiment has low power to detect small differences in attack rates between phenotypes. Therefore, as with all studies of predation using replicas in the field, it is possible to have a high degree of confidence in significant differences, but more difficult to make inferences from a lack of differences. Notwithstanding the results of our field experiment, our data, taken together, suggest that a geographical mosaic in the number of models has indeed led to geographical variation in mimetic precision.

It might be asserted that such geographical variation in mimetic precision arises, not owing to geographical variation in the presence of the number of models, but owing to geographical variation in some other (unmeasured) aspect in their environment. While we cannot completely rule out this possibility, it seems improbable considering what is known about these snake species. First, *P. elapoides* occupies similar microhabitats as their models. Yet, *P. elapoides* shows parallel variation in morphology with *M. diastema*, whereas *M. elegans* is relatively invariable throughout its range [19,22,52]. In addition, it might be asserted that the geographical variation in resemblance that we have documented reflects phenotypic plasticity. However, phenotypic plasticity in coloration is not known from any coral snake

or coral snake mimic species and seems unlikely given that their coloration does not involve potentially environmentally dependent pigments, such as carotenoids [53,54].

We found no evidence that any of the phenotypes varied in protection from predation (figure 5; electronic supplementary material, figure S4). One possible explanation for this pattern is that the traits that varied between our models (proportions of colours and number of rings) are not the primary targets of selection by predators in this system. Although these traits have been suggested to be targets of predator-mediated selection in other regions in the New World [31,34], we do not know whether predators from our field sites use these traits to distinguish among potential prey. It is possible that traits that we did not (and could not) measure from museum specimens (such as the brightness, reflectance and adjacency of the coloration) are key for predators in this system. Nevertheless, the fact that *P. elapoides* and *M. diastema* vary extensively in parallel in band number and band width throughout their ranges suggests that these traits bear some selective value [28].

Whether *P. elapoides* and *M. diastema* coevolve remains unclear. Although we have shown that the mimic (*P. elapoides*) appears to evolve in response to its primary model (*M. diastema*), it is still uncertain whether the model evolves in response to its mimic. On the one hand, *M. diastema* is extensively variable throughout its range, suggesting that it has experienced selection to evolve away from mimics [23]. On the other hand, there is little evidence that a model in another coral snake mimicry complex with a particularly high mimetic load experiences selection to evolve away from mimics [55]. Thus, additional work is needed to evaluate whether adaptation between mimics and models is reciprocal in this mimicry complex.

Several factors we did not consider in this study might explain why *P. elapoides* varies geographically in mimicry. First, predator-mediated selection for mimicry might be weak or, more likely, fluctuate over time. Fluctuating selection is not unusual—in many mimicry complexes, the form and strength of selection can vary over time due to frequency dependence on mimic and model patterns [55–57]. Such selection can often lead to the evolution of diversity in Batesian mimicry [58]. Several potential avian predators are known to make regular migrations between low and high elevations in the Neotropics, and thus probably experience regions with single and multiple models [59]. In addition, variation in the abundance of naive predators throughout the year might lead to variation in selection for mimicry [55]. Indeed, *P. elapoides* can be quite variable in regions with multiple models: although mimics are often intermediate, some individuals precisely resemble only one model (electronic supplementary material, figure S5). The relative abundance of each model at our study site is not clear, as there have been no systematic efforts to sample coral snakes.

Alternatively, because *P. elapoides* occurs in sympatry with multiple models over a small proportion of its geographical range—and most commonly at intermediate elevations—mimics might vary in phenotype in such regions due to ‘trait remixing’ (i.e. gene flow, drift, local extinction and recolonization) among lower and higher elevations (cf. [60]). This hypothesis leads to the prediction that the symmetry of range overlap among different coral snake models might affect the relative amount of variation in mimic phenotypes among mimic species co-occurring with multiple models. For example, populations of mimics such as *P. elapoides*, that overlap highly asymmetrically with several models (i.e. mimics co-occur with one model over a large area and with other models in comparatively smaller pockets), might generally be more variable than comparable populations in mimic species that overlap several models more symmetrically.

Another non-mutually exclusive possibility is that *P. elapoides* might be so variable because the costs of mistakenly attacking coral snakes are so high [61]. The high costs of attacking coral snakes might relax selection for precise mimicry, thereby generating a flat selective surface where all intermediate phenotypes receive equal protection [32,37]. This hypothesis is consistent with previous work that has shown that tropical predators innately avoid coral snake patterns [62,63], that several coral snake mimics bear vague resemblances to coral snakes in the tropics [61], that the richness of coral snake mimics greatly exceeds the richness of coral snakes across much of the New World [16], and that the rate of evolutionary transitions from mimetic to cryptic coloration is nearly as high as the rate at which mimetic

coloration evolves from cryptic coloration among Neotropical coral snake mimics [16]. The results of our morphometric analyses and field experiments are also consistent with this hypothesis.

Our findings are consistent with previous empirical and theoretical work showing that multiple models can alter the precision of mimicry [13,18]. For example, Edmunds [13] found that ant-mimicking spiders with small ranges and single models were more precise mimics than wide-ranging species that overlapped several model species. In addition, Sherratt [18] showed that an intermediate mimicry can be favoured in the presence of multiple discriminable models as long as mimics co-occur with several models in either space or time. Other studies that have examined the role of multiple models in the evolution of mimicry to date have failed to obtain evidence that multiple models can have such an effect on mimics. For example, Darst & Cummings [14] found that a poison frog mimic that co-occurs with two poison frog models only resembled a single model well. Similarly, Penney *et al.* [64] and Taylor *et al.* [65] failed to find any evidence that hoverfly mimics were intermediate in phenotype between different model wasp and bee species.

In sum, variation in the number of models across the range of a mimic appear to generate a geographical mosaic in the degree of mimic–model resemblance. More empirical case studies are needed to assess the generality of mimicry in producing this coevolutionary pattern.

**Data accessibility.** Data have been deposited with Dryad Digital Repository: <https://doi.org/10.5061/dryad.r7360c7> [66].

**Authors' contributions.** C.K.A. conceived of the study, conducted morphological analyses and field predation experiments, performed statistical analyses and wrote the first draft of the manuscript. H.A.P.-M. carried out field predation experiments. D.W.K. performed statistical analyses. H.A.P.-M., D.W.K. and D.W.P. edited and approved the final draft of the manuscript.

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