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# Heterogeneity in predator micro-habitat use and the maintenance of Müllerian mimetic diversity

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## ABSTRACT

Müllerian mimicry, where groups of chemically defended species display a common warning color pattern and thereby share the cost of educating predators, is one of the most striking examples of ecological adaptation. Classic models of Müllerian mimicry predict that all unpalatable species of a similar size and form within a community should converge on a single mimetic pattern, but instead communities of unpalatable species often display a remarkable diversity of mimetic patterns (e.g. neotropical ithomiine butterflies). It has been suggested that this apparent paradox may be explained if different suites of predators and species belonging to different mimicry groups utilize different micro-habitats within the community. We developed a stochastic individual-based model for a community of unpalatable mimetic prey species and their predators to evaluate this hypothesis and to examine the effect of predator heterogeneity on prey micro-habitat use. We found that community-level mimetic diversity was higher in simulations with heterogeneous predator micro-habitat use than in simulations with homogeneous predator micro-habitat use. Regardless of the form of predation, mimicry pattern-based assortative mating caused community-level mimetic diversity to persist. Heterogeneity in predator micro-habitat use led to an increased association between mimicry pattern and prey micro-habitat use relative to homogeneous predator micro-habitat use. This increased association was driven, at least in part, by evolutionary convergence of prey micro-habitat use when predators displayed heterogeneous micro-habitat use. These findings provide a theoretical explanation for an important question in evolutionary biology: how is community-level Müllerian mimetic diversity maintained in the face of selection against rare phenotypes?

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## 1. Introduction

Müllerian mimicry is recognized as an exquisite example of ecological adaptation involving the convergent evolution of phenotypic signals among unpalatable species to share the cost of educating predators (Müller, 1879; Mallet and Joron, 1999). This evolutionary phenomenon was originally described by Müller (1879) to explain convergent warning colored wing patterns in neotropical butterflies. Specifically, Müller formulated a mathematical model involving two equally unpalatable co-occurring species with population sizes  $a_1$  and  $a_2$ . If the species are dissimilar  $n_k$  individuals of each species are consumed before they are recognized as distasteful. However, if these species are indistinguishable

the number consumed will be  $n_{k1} = a_1 n_k / (a_1 + a_2)$  and  $n_{k2} = a_2 n_k / (a_1 + a_2)$  for species 1 and 2, respectively.  $n_{k1}$  and  $n_{k2}$  will always be less than  $n_k$ , indicating that this mimetic relationship should be beneficial for members of both species (albeit more beneficial for members of the rarer species; Mallet and Joron, 1999). Whereas Müllerian mimicry has been most intensively studied in butterflies (e.g. Joron and Mallet, 1998; Mallet and Joron, 1999; Sherratt, 2008), it has also been documented in various other taxa including bumble bees (Plowright and Owen, 1980; Williams, 2007), hemipterans (Zrzavy and Nedved, 1999), dendrobatid frogs (Symula et al., 2001), temperate millipedes (Marek and Bond, 2009), and freshwater catfish (Alexandrou et al., 2011).

The classic model of Müllerian mimicry outlined above is expected to give rise to number-dependent selection against rare phenotypes (Joron and Mallet, 1998; Mallet and Joron, 1999), because individuals with rare phenotypes are not easily recognized by predators as unpalatable, and therefore, are more likely

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to be consumed (Mallet and Barton, 1989; Kapan, 2001). As a result, it has often been assumed that all members of an unpalatable species and all unpalatable species of similar size and form within a community should converge on a single mimetic form (Müller, 1879), and such assumptions have been supported by theoretical studies (e.g. the single patch model from Joron and Iwasa, 2005). However, polymorphisms within species or within communities of Müllerian mimics are rampant in nature. For example, the neotropical butterflies *Heliconius erato* and *Heliconius melpomene* are Müllerian co-mimics that exhibit remarkable intra-specific mimetic diversity. Each of these species has radiated into over 30 geographically distributed color pattern races, while converging on the same color pattern within any one locality (Brower, 1996; Jiggins and McMillan, 1997; Flanagan et al., 2004). More rarely, some species, such as the Amazonian butterfly *Heliconius numata*, have multiple mimicry forms within a locality. *H. numata* mimics various species of *Melinaea* butterflies with up to 11 of its 38 known mimetic color pattern forms occurring in a single population (Brown and Benson, 1974; Joron et al., 1999). Finally, local inter-specific mimetic variation within communities is ubiquitous. For example, unpalatable Neotropical ithomiine butterflies (Nymphalidae: Ithomiini) participate in numerous mimicry groups (rings) with up to eight distinct mimicry rings co-occurring in a given community (Beccaloni, 1997a; Joron and Mallet, 1998; DeVries et al., 1999; Willmott and Mallet, 2004; Elias et al., 2008).

Several hypotheses have been advanced to explain the apparent paradox of mimetic diversity among Müllerian mimics. Mallet and Joron (1999) suggested that selection against rare phenotypes may be relatively weak in many instances if predator behavior gives rise to number-dependent selection. For example, selection against rare phenotypes is expected to be minimal if  $n_k/N$  is much less than  $\frac{1}{100}$ , where  $N$  is the number of rare phenotype individuals. Genetic constraints may also limit mimetic convergence, particularly among species, which would lead to increased mimetic diversity. Spatial and temporal variation in the abundance of mimetic models have been suggested to contribute to diversity in mimetic forms of Müllerian mimics at various spatial scales (Mallet and Joron, 1999; Joron and Iwasa, 2005; Sherratt, 2006). Sherratt (2006) found that stochastic effects, coupled with limited migration among localities and strong frequency-dependent selection driven by predators, can lead to the maintenance of multiple stable mimetic forms separated by narrow hybrid zones (similar to patterns seen in nature in *H. erato* and *H. melpomene*). However, such coarse-scale spatial heterogeneity cannot explain local mimetic diversity. Joron and Iwasa (2005) similarly demonstrated that different mimetic forms can be maintained by spatial heterogeneity in the abundance of their mimetic model, particularly when the mimic is only mildly unpalatable, and that spatial heterogeneity combined with intermediate migration rates could account for local intra-specific diversity of mimetic forms, such as that observed in *H. numata*. In this model, the form that is less adapted to the local mimetic environment suffers heavier predation, but is constantly rescued by immigration from neighboring patches, thereby enabling stable, but dynamic polymorphism. This model assumes a fixed heterogeneous distribution of mimetic models, but does not explain how such a distribution initially evolves and is maintained. Thus, this model does not address rampant mimetic diversity at the community-level, as occurs among forest mimetic communities numerically dominated by ithomiine butterflies (Beccaloni, 1997a; Joron et al., 1999).

Concordant differences in micro-habitat use by suites of predators and prey, however, may function in a similar manner to the situation modeled by Sherratt (2006), but involving ecological instead of spatial segregation, and could explain

community-level Müllerian mimetic diversity (Mallet and Gilbert, 1995; Beccaloni, 1997a,b; DeVries et al., 1999; Elias et al., 2008). If both predators and mimetic prey differ in their micro-habitat use, selection for convergence of mimetic form among species experiencing different predators should be weak or non-existent. In such instances selection may instead favor increased similarity in micro-habitat use among co-mimics, thereby increasing the efficacy of their mimetic signal in educating predators (Elias et al., 2008, but see Alexandrou et al., 2011). Increased similarity in micro-habitat use among co-mimics could be achieved by convergent evolution of micro-habitat use (or selection against divergence), or by habitat filtering, whereby the probability of establishment in the community is higher for species with co-mimics occupying the same micro-habitat already established in the community. This hypothesis may explain, for example, the persistence of multiple mimicry rings within ithomiine butterfly communities. Differences in micro-habitat use have been detected among members of different ithomiine mimicry rings (Beccaloni, 1997b; DeVries et al., 1999; Elias et al., 2008; Hill, 2010), linked to host-plant distribution (Willmott and Mallet, 2004). Moreover, evidence suggests that avian insectivores partition micro-habitats in a similar manner to mimetic butterflies (Willmott et al. unpublished results). Here, we develop a stochastic individual-based model to test the hypothesis that predator heterogeneity in micro-habitat use can facilitate the maintenance of mimetic diversity at the community-level. Additionally, we investigate whether heterogeneity in predator micro-habitat use drives concordant heterogeneity in micro-habitat use among prey mimicry groups, and whether this is achieved in part by convergent evolution of prey micro-habitat use.

## 2. The model

We developed a stochastic, individual-based model for a community of unpalatable mimetic prey species and their predators to address the aforementioned questions. The model allows prey species' mimicry type and micro-habitat use to evolve. We assume a constant predator community. The number of prey species is also constant, and each prey species is composed of a set number of individuals (i.e., the prey population size is constant). Prey individuals exist in a niche space characterized by two orthogonal niche variables, which are bounded by 0 and 1. Each individual is assigned a niche value for each niche variable; the combination of values characterizes the individual's micro-habitat use (i.e., use of niche space).

We assume that mimicry pattern for the prey individuals is determined by a single genetic locus with a set number of alleles equal to the number of mimicry types modeled (e.g. Joron et al., 2006). If an individual is homozygous for a specific mimicry allele it has that allele's mimicry type. We have two alternative models of dominance for heterozygous individuals: the *equal dominance model* and the *dominance hierarchy model*. In the *equal dominance model* each mimicry allele type is dominant to and recessive to an equal number of alternative mimicry allele types. Thus, under this model none of the mimicry alleles has an inherent evolutionary advantage from an increased phenotypic frequency due to dominance. The *dominance hierarchy model* assumes that one mimicry allele type is dominant to all others, a second allele is dominant to all others except the first allele, a third allele is dominant to all others except the first two alleles, and so on until one reaches the last allele which is recessive to all alleles. We include the *dominance hierarchy model* because of its similarity to the genetic architecture of mimetic wing patterns documented in *H. numata* (Brown and Benson, 1974; Joron et al., 2006). We do not include incomplete dominance (i.e., intermediate patterns for heterozygotes) in our model. This is not because we believe incomplete

**Table 1**  
Model parameters and standard model conditions.

Parameter	Value	Description
$N_s$	10	Number of prey species
$\mu_n$	5000	Mean number of individual per species
$\sigma_n^2$	$2.5 \times 10^5$	Variance in the number of individuals per species
$n_k$	300	Number of individuals eaten per predator $\times$ mimicry group
$\nu$	0.0025	Variance between parent and offspring niche
$m$	0.0001	Mimicry mutation rate
$t$	1	Relative probability of among to within mimicry group mating

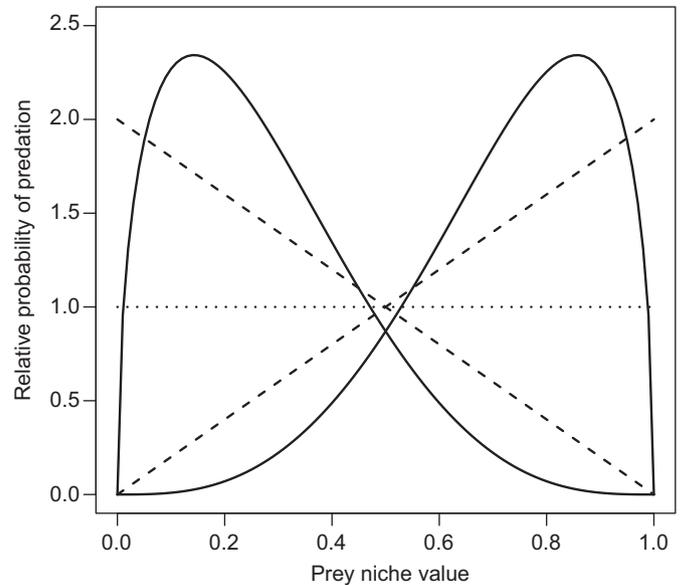
dominance is rare or unimportant, but because doing so within our current modeling framework would require specific and difficult to justify assumptions regarding how predators perceive heterozygous individuals or would result in all heterozygotes being consumed because of their initial rarity, and thus would not allow mimicry type to evolve within a species (or mimetic diversity to be lost).

We initialize the model with a set number of species ( $N_s = 10$ ) each initially fixed for one of five mimicry alleles. We set the population size of each species and the ecological niche of each individual by sampling random variables (Table 1). After initialization, the model cycles through rounds of predation and reproduction for a set number of iterations, which we equate with prey generations. Each model iteration begins with predation. We assume four distinct predator species, each of which consumes  $n_k$  individuals of each prey mimicry type (unless fewer than  $n_k$  individuals of a mimicry type exist, in which case all individuals of that mimicry type are consumed). Each predator species samples prey individuals following a predation function that is dependent on the prey's niche scores. We use a beta probability density function to describe predation, with parameters chosen to adjust the heterogeneity of predator micro-habitat use (Fig. 1).

Reproduction occurs for each model iteration following predation. The reproduction model we use assumes non-overlapping prey generations with a constant prey population size for each species (i.e., reproduction continues until a set population size has been achieved). We model reproduction by randomly drawing two individuals at a time from each species, which serve as parents for an individual in the next generation. This procedure implies the simplifying assumption that all individuals are hermaphroditic. We determine the micro-habitat of the offspring by sampling each niche variable from a normal distribution with a mean equal to the mean of the parents' niche variables and a specified variance ( $\nu$ ). The offspring inherits one of each of its parents' mimicry alleles (chosen at random and with equal probability) and the pair of alleles sampled determines that individual's mimicry type in accordance with the specified genetic dominance model. We allow mutations to an alternative mimicry allele with probability  $m$ . The alternative allele is then chosen from the set of mimicry alleles for the initial community (i.e., we do not allow completely novel mimicry alleles to enter the community). This sampling procedure is iterated until all individuals of the next generation have been generated (parents of offspring for the next generation are sampled with replacement).

### 2.1. Model simulations and analyses

We simulated prey species evolution according to the model described in Section 2 to explore the effect of heterogeneous predator micro-habitat use on mimetic diversity and prey micro-habitat use. We conducted an initial set of model simulations



**Fig. 1.** Plot of the relative probability of predation of individuals based on their niche value for a single niche variable. The relative probability (i.e., relative to other individuals of the same mimicry type) of a predator sampling a prey individual with niche scores  $x_1$  and  $x_2$  is  $P(\text{predation}|x_1, x_2) \propto x_1^{\alpha_1-1}(1-x_1)^{\beta_1-1} / B(\alpha_1, \beta_1) \times x_2^{\alpha_2-1}(1-x_2)^{\beta_2-1} / B(\alpha_2, \beta_2)$ , where  $\alpha_1$  and  $\beta_1$  are the parameters of the beta predation function for niche variable 1,  $\alpha_2$  and  $\beta_2$  are the parameters of the beta predation function for niche variable 2, and  $B$  is the beta function ( $B(\alpha, \beta) = \Gamma(\alpha)\Gamma(\beta)/\Gamma(\alpha+\beta)$ ). The dotted line corresponds to  $\alpha = 1, \beta = 1$ , the dashed lines correspond to  $\alpha = 1, \beta = 2$  and  $\alpha = 2, \beta = 1$ , and the solid lines correspond to  $\alpha = 1.5, \beta = 4$  and  $\alpha = 4, \beta = 1.5$ .

with specified, standard model parameter values for several demographic and genetic parameters (Table 1), but different forms of predator heterogeneity. We used three different sets of parameters for the predation functions to generate three predation models: *homogeneous predator micro-habitat use*, *moderately heterogeneous predator micro-habitat use*, and *strongly heterogeneous predator micro-habitat use* (Table 2 and Fig. 1). The specified parameter values for these functions were chosen so that the sum of predation probabilities across all predator species was nearly uniform across niche space despite variation in the degree of heterogeneity for individual predator species. We also included simulations with no predation. Simulations were conducted using the *equal dominance model* and the *dominance hierarchy model* for the genetic architecture of mimicry pattern. We conducted additional sets of simulations with different model parameter values to assess the generality of our results (see Appendix A for details). We conducted 100 replicate simulations for each set of model parameters.

To test the hypothesis that heterogeneity among predators in micro-habitat use promotes an increased maintenance of mimetic diversity at the community-level, we contrasted the effective number of mimicry groups at the completion of each replicate simulation under the standard model conditions with *homogeneous predator micro-habitat use*, *moderately heterogeneous predator micro-habitat use*, and *strongly heterogeneous predator micro-habitat use*. We calculated the effective number of mimicry groups for each community as  $\exp(-\sum_i p_i \ln p_i)$ , where  $p_i$  is the relative frequency of prey individuals with the  $i$ th mimicry pattern. We refer to this measure as mimetic diversity. This function is the exponential of the Shannon diversity index (a measure of entropy) and follows the formulation for effective diversity given by Jost (2006). The effective number of mimicry types is always less than or equal to the number of observed mimicry types. Specifically, a community with  $D$  effective mimicry types (i.e., a mimetic diversity of  $D$ ) is as diverse (i.e., has the

**Table 2**  
Parameter values for predation functions. Abbreviations for predator micro-habitat use models are defined in Fig. 3 and parameters for predation functions ( $\alpha$  and  $\beta$ ) are described in Fig. 1.

Model	Predator 1	Predator 2	Predator 3	Predator 4
HOMP	$\alpha_1 = \beta_1 = \alpha_2 = \beta_2 = 1$	$\alpha_1 = \beta_1 = \alpha_2 = \beta_2 = 1$	$\alpha_1 = \beta_1 = \alpha_2 = \beta_2 = 1$	$\alpha_1 = \beta_1 = \alpha_2 = \beta_2 = 1$
MHTP	$\alpha_1 = \alpha_2 = 1$ $\beta_1 = \beta_2 = 2$	$\alpha_1 = \alpha_2 = 2$ $\beta_1 = \beta_2 = 1$	$\alpha_1 = \beta_2 = 1$ $\alpha_2 = \beta_1 = 2$	$\alpha_1 = \beta_2 = 2$ $\alpha_2 = \beta_1 = 1$
SHTP	$\alpha_1 = \alpha_2 = 1.5$ $\beta_1 = \beta_2 = 4$	$\alpha_1 = \alpha_2 = 4$ $\beta_1 = \beta_2 = 1.5$	$\alpha_1 = \beta_2 = 1.5$ $\alpha_2 = \beta_1 = 4$	$\alpha_1 = \beta_2 = 4$ $\alpha_2 = \beta_1 = 1.5$

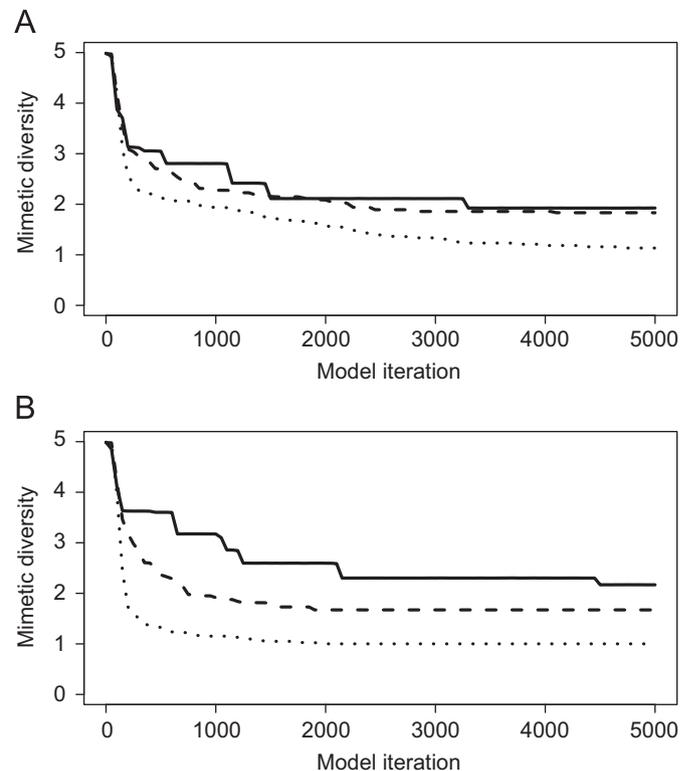
same entropy) as a community with exactly  $D$  mimicry groups all occurring with equal frequencies. We calculated effective mimetic diversity rather than the absolute number of mimicry groups, as the latter was quite sensitive to the mimicry mutation rate, as mutation often maintained mimicry groups with very few individuals (i.e., fewer than five).

We contrasted the strength of statistical association between mimicry group and prey micro-habitat use among simulations conducted with the standard model conditions and each form of predator micro-habitat use to test the hypothesis that increased heterogeneity in predator micro-habitat use can cause an increased association between mimicry group and prey micro-habitat use. We measured the association between mimicry group and the two niche scores of each individual by calculating Pillai's trace statistic in a multivariate analysis of variance framework. Pillai's trace is analogous to the coefficient of determination (i.e.,  $r^2$ ).

If the strength of association between mimicry type and prey micro-habitat use is due, at least in part, to niche convergence among co-mimics, we would predict increased evolution of prey micro-habitat use (i.e., increased change in prey micro-habitat use over time) with heterogeneity in predator micro-habitat use. To evaluate this hypothesis, we quantified prey micro-habitat use evolution by calculating the mean Euclidean distance (over the 10 prey species) between the initial and final mean bivariate niche values of each prey species. We contrasted the degree of niche evolution among simulations conducted with different forms of predator micro-habitat use.

### 3. Results

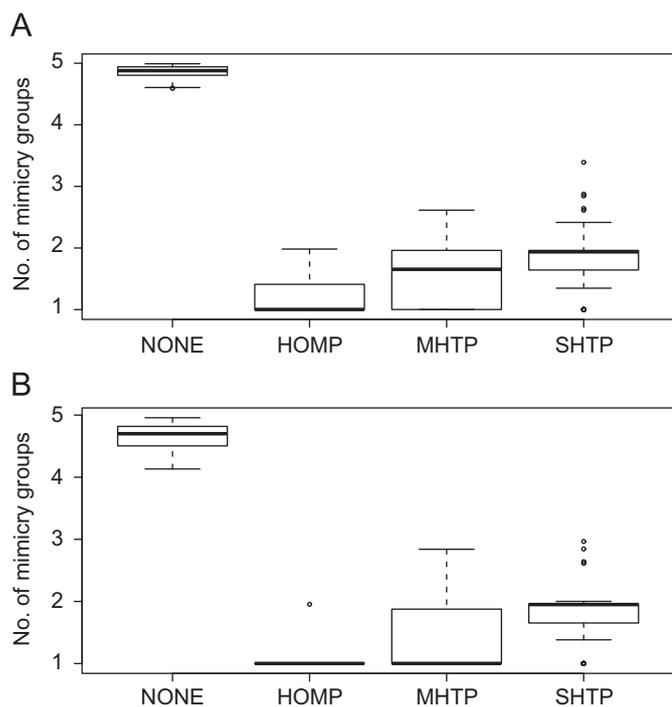
In the absence of predation all five mimicry groups persisted, and the effective number of mimicry groups (i.e., mimetic diversity) was always quite high (*equal dominance model*: mean=4.86, sd=0.098; *dominance hierarchy model*: mean=4.65, sd=0.096). Predation caused a reduction in mimetic diversity through time, which generally leveled off prior to the end of each simulation (Fig. 2). The form of predator micro-habitat use generally affected the extent that mimetic diversity was maintained (Fig. 3). Specifically, mimetic diversity was highest with *strongly heterogeneous predator micro-habitat use* (*equal dominance model*: mean=1.82, sd=0.370; *dominance hierarchy model*: mean=1.79, sd=0.369), intermediate with *moderately heterogeneous predator micro-habitat use* (*equal dominance model*: mean=1.55, sd=0.444; *dominance hierarchy model*: mean=1.39, sd=0.457), and lowest with *homogeneous predator micro-habitat use* (*equal dominance model*: mean=1.22, sd=0.308; *dominance hierarchy model*: mean=1.01, sd=0.095). Levels of community-level mimetic diversity were similar to the standard model for simulations with reduced predation pressure ( $n_k=150$ ). For example, with the *equal dominance model* and  $n_k=150$ , mean mimetic diversity ranged from 1.95 (*strongly heterogeneous*



**Fig. 2.** Mean mimetic diversity as a function of model iteration using the *equal dominance model* (A) and the *dominance hierarchy model*. (B) Results are shown for *homogeneous predator micro-habitat use* (dotted line), *moderately heterogeneous predator micro-habitat use* (dashed line), and *strongly heterogeneous predator micro-habitat use* (solid line).

*predator micro-habitat use*) to 1.28 (*homogeneous predator micro-habitat use*). Results with the *dominance hierarchy model* were similar, but are not shown. Mimetic diversity was higher in general with a reduced mimicry mutation rate ( $m=0.00001$ ), but was still highest with *strongly heterogeneous predator micro-habitat use* (mean=2.59, sd=0.623), and the lowest with *homogeneous predator micro-habitat use* (mean=1.95, sd=0.405). A lower parameter value for offspring niche variation yielded similar results to the standard model (results not shown). When we introduced weak assortative mating based on mimicry pattern type all simulated communities maintained all five mimicry groups regardless of the predation function, with mean values for mimetic diversity of 4.99 (sd=0.009; *strongly heterogeneous predator micro-habitat use*), 4.99 (sd=0.007; *moderately heterogeneous predator micro-habitat use*), and 4.99 (sd=0.009; *homogeneous predator micro-habitat use*).

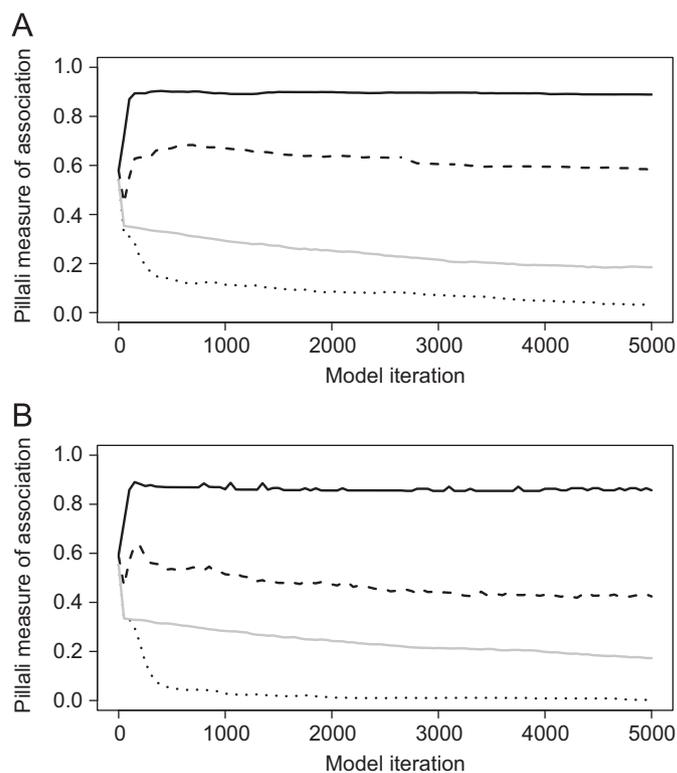
With the standard model parameters there was a clear increase in the strength of association between mimicry type and prey micro-habitat use (i.e., bivariate niche) with time when



**Fig. 3.** Boxplots show the effective number of mimicry groups for 100 replicate simulations with no predation (NONE), homogeneous predator micro-habitat use (HOMP), moderately heterogeneous predator micro-habitat use (MHTP), and strongly heterogeneous predator micro-habitat use (SHTP) using the equal dominance model (A) and the dominance hierarchy model (B). The effective number of mimicry groups differed significantly among simulations with different forms of predation (ANOVA: equal dominance model,  $F=64.73$ ,  $P<0.00001$ ; dominance hierarchy model,  $F=128.58$ ,  $P<0.00001$ ).

strongly heterogeneous predator micro-habitat use was simulated, whereas this association decreased with time when we modeled homogeneous predator micro-habitat use (Fig. 4). The strength of this association after 5000 model iterations differed among simulations conducted with different forms of predator micro-habitat under both the equal dominance model and dominance hierarchy model (Fig. 5 and Table 3). The strength of association between mimicry type and prey micro-habitat use for model simulations with a reduced strength of predation or lower mimicry mutation rate and simulations conducted with the standard model parameters were similar. A reduction in offspring niche variance decreased the association between mimicry type and prey micro-habitat use for all forms of predator micro-habitat use (Table 3).

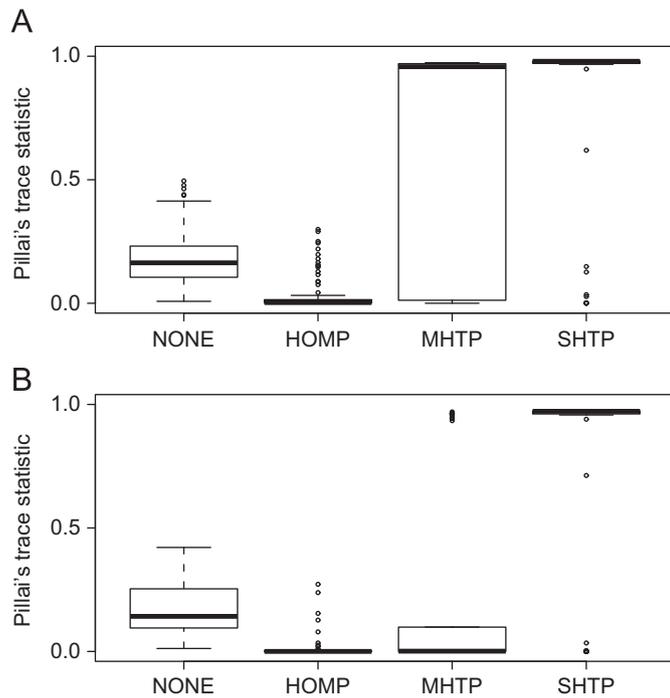
The rate and extent of prey micro-habitat use evolution increased when predator micro-habitat use was more heterogeneous. Specifically, with the equal dominance model for mimicry pattern genetic architecture, Euclidean distance measures of prey micro-habitat use evolution were 0.171 (sd=0.022; no predation), 0.176 (sd=0.022; homogeneous predator micro-habitat use), 0.426 (sd=0.027; moderately heterogeneous predator micro-habitat use), 0.478 (sd=0.027; strongly heterogeneous predator micro-habitat use; Fig. 6A). Similarly, with the dominance hierarchy model for mimicry genetic architecture, Euclidean distance measures of prey micro-habitat use evolution in the communities were 0.166 (sd=0.021; no predation), 0.168 (sd=0.022; homogeneous predator micro-habitat use), 0.425 (sd=0.026; moderately heterogeneous predator micro-habitat use), 0.477 (sd=0.027; strongly heterogeneous predator micro-habitat use; Fig. 6B). These results were not affected substantially by predation rate, mimicry mutation rate, offspring niche variation, or the presence of weak assortative mating (results not shown).



**Fig. 4.** Pillai's trace statistics of association between mimicry type and prey niche as a function of model iteration using the equal dominance model (A) and the dominance hierarchy model (B). Results are shown for homogeneous predator micro-habitat use (dotted line), moderately heterogeneous predator micro-habitat use (dashed line), strongly heterogeneous predator micro-habitat use (solid line), and no predation (solid gray line).

#### 4. Discussion

Our simulation results support the hypothesis that heterogeneity in micro-habitat use by predators leads to concordant heterogeneity in micro-habitat use by unpalatable, aposematic prey species and promotes the maintenance of warning color pattern diversity in communities of Müllerian mimics. Specifically, we detected approximately a 50% increase in the maintenance of mimetic diversity after 5000 generations for strongly heterogeneous predator micro-habitat use relative to homogeneous predator micro-habitat use. This result was robust to moderate variation in the genetic architecture of mimicry pattern, the strength of predation ( $n_R$ ), the mutation rate of the mimicry locus ( $m$ ), and offspring niche variance ( $v$ ). Nonetheless, even with heterogeneous predator micro-habitat use, community-level mimetic diversity generally declined over the course of the simulation. This loss of mimetic diversity can be attributed to predation, as simulations without predation always retained all five mimicry groups and had high measures of mimetic diversity (always  $>4$ ). Interestingly, moderate mimicry pattern-based assortative mating ( $t=0.8$ ; within species) also led to the maintenance of all five mimicry groups and high mimetic diversity ( $>4$ ). This suggests that the reduction in fitness experienced by rare mimetic forms within a species due to assortative mating limits the ability of new mimicry forms to spread and can maintain diversity of mimetic form at the community-level. This is potentially important as mimicry pattern-based assortative mating, even within populations, has been documented in mimetic *Heliconius* butterflies (Chamberlain et al., 2009). Although community-level mimetic diversity was lower with a homogeneous distribution of predators than with a heterogeneous



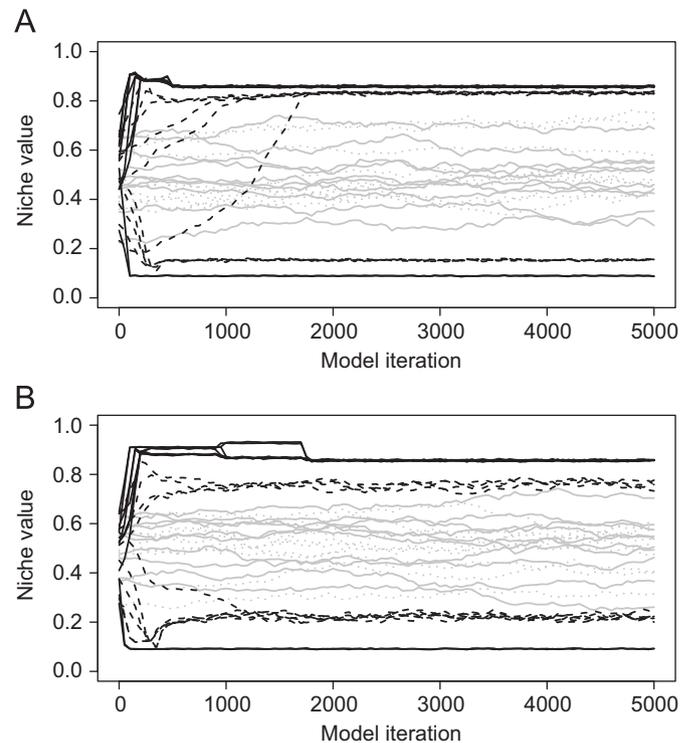
**Fig. 5.** Boxplots show Pillai's trace statistics of association for 100 replicate simulations with no predation (NONE), *homogeneous predator micro-habitat use* (HOMP), *moderately heterogeneous predator micro-habitat use* (MHTP), and *strongly heterogeneous predator micro-habitat use* (SHTP) using the *equal dominance model* (A) and the *dominance hierarchy model* (B). This measure of association differed significantly among simulations with different forms of predation (ANOVA: *equal dominance model*,  $F=189.86$ ,  $P < 0.00001$ ; *dominance hierarchy model*,  $F=163.33$ ,  $P < 0.00001$ ).

**Table 3**

Mean (standard deviation) of Pillai's trace statistic under different models. Abbreviations are as described in Fig. 3 except ED (*equal dominance model*) and DH (*dominance hierarchy model*).

Model	NONE	HOMP	MHTP	SHTP
Standard ED	0.18 (0.11)	0.03 (0.07)	0.58 (0.47)	0.89 (0.27)
Standard DH	0.17 (0.10)	0.00 (0.01)	0.42 (0.48)	0.86 (0.32)
$n_k=150$ ED	–	0.04 (0.08)	0.52 (0.45)	0.88 (0.27)
$n_k=150$ DH	–	0.01 (0.04)	0.24 (0.41)	0.83 (0.34)
$m=0.00001$ ED	0.37 (0.15)	0.10 (0.11)	0.83 (0.29)	0.86 (0.27)
$v=0.000625$ ED	0.20 (0.11)	0.03 (0.08)	0.19 (0.33)	0.76 (0.41)
$t=0.8$ ED	0.31 (0.17)	0.35 (0.18)	0.89 (0.22)	0.90 (0.20)

distribution of predators, the former did lead to instances where more than one mimicry group was maintained. These results suggest that heterogeneous predator distributions facilitate, but are not required, for community-level mimetic diversity. Thus, as suggested by Mallet and Joron (1999), under specific demographic and evolutionary circumstances, selection is simply not strong enough to preclude mimetic diversity, at least over short time-scales. These findings highlight an important point regarding the loss of mimetic diversity in our simulations. For our models, mimetic diversity loss is driven by mimicry evolution within species. This requires mutations that introduce alternative mimicry alleles into a prey species, the allele to be dominant to other alleles in the population or genetic drift to bring the allele to a high enough frequency for its phenotype to be expressed (as a homozygote), and a higher fitness than the mimicry type expressed by most members of that prey species. Any conditions that restrict the prevalence of these conditions should facilitate the maintenance of mimetic diversity under our model. These conditions might differ if



**Fig. 6.** Mean niche 1 value for each prey species as a function of model iteration using the *equal dominance model* (A) and the *dominance hierarchy model*. Results are shown for *homogeneous predator micro-habitat use* (dotted gray line), *moderately heterogeneous predator micro-habitat use* (dashed line), *strongly heterogeneous predator micro-habitat use* (solid line), and no predation (solid gray line). We detected a significant effect of predator heterogeneity on the extent of niche evolution in the prey community (ANOVA: *equal dominance model*,  $F=1689.22$ ,  $P < 0.00001$ ; *dominance hierarchy model* (B),  $F=1589.81$ ,  $P < 0.00001$ ).

our model included extinction and colonization of the community by prey species. In this case, the dynamics of mimicry maintenance would be effected more by the intrinsic rate of growth of the prey species and the initial population sizes of the colonizing species.

Our results show that heterogeneity in predator micro-habitat use increases the association between mimicry pattern and micro-habitat use in prey species. This increased association was due, at least in part, to niche convergence among co-mimics, as rates of niche evolution were higher when predators were distributed heterogeneously among micro-habitats. If this increased association had been due to constraints on niche divergence among co-mimics, or solely to evolution of mimicry pattern, we would have expected reduced niche evolution (for constraints on niche divergence) or similar rates of niche evolution (for only mimicry evolution) for heterogeneous predator micro-habitat use relative to homogeneous micro-habitat use. Concordant heterogeneity in the micro-habitat use of predator and prey species has been detected in neotropical communities of avian predators and unpalatable ithomiine butterflies (Willmott et al. unpublished results), with the latter possessing substantial local inter-specific diversity of mimetic forms (Beccaloni, 1997a; DeVries et al., 1999; Elias et al., 2008; Hill, 2010). Our theoretical results provide a potential explanation for these empirical data, namely that an initial heterogeneous predator distribution has driven this heterogeneous distribution of unpalatable prey with different mimetic patterns by acting as a selective force favoring niche convergence among co-mimics. Finally, our current model does not allow us to test whether habitat filtering can also lead to concordant heterogeneity of predators and mimetic prey species. However, using an

alternative model formulation we found support for this possibility (Gompert et al., unpublished results). Competition for resources can drive niche divergence among co-mimics if the negative effects of competition outweigh the benefit of more efficient predator signaling achieved by niche convergence (Alexandrou et al., 2011). Resource competition was not included in our model. However, convergence in micro-habitat does not necessarily lead to a net cost in mutualistic species (Gross, 2008), and empirical results indicate that convergence can occur despite competition (Elias et al., 2008). Thus, including competition would not necessarily alter the general patterns presented in this paper.

Theoretical research has explored the population dynamics of mutualistic interactions, such as those which occur among co-mimics, and competitive interactions (Gross, 2008; Kumazawa et al., 2009). These theoretical studies show that community-level species diversity and equilibrium population size are increased by mutualistic interactions. Our results indicate that the effect of mutualistic interactions on evolutionary dynamics can be quite different, as mutualism causes selection for niche convergence and convergence of mimetic form for species occupying the same niche. These evolutionary dynamics reduce diversity, at least in the absence of competitive interactions, which were not included in our model. Theoretical studies have also been conducted to explain intra-specific variation in mimicry forms over geographic distances (e.g. Joron and Iwasa, 2005; Sherratt, 2006). However, our simulations represent the first quantitative theoretical study with the primary aim of understanding mimetic diversity among species within a community, a ubiquitous situation. Whereas there are some similarities between our model and these earlier models, we believe that our model addresses fundamentally different questions than these models and offers several novel and important insights. Specifically, by allowing prey species' niches to evolve and not assuming a fixed mimetic environment we were able to investigate the complex relationship between the distribution of predators, mimicry pattern, and ecological niche, and thereby demonstrate that heterogeneous predator distributions drove heterogeneous micro-habitat use by unpalatable prey species, which in turn maintained increased local mimetic diversity.

Our findings have interesting implications for studies of speciation in mimetic taxa, and for community ecology in general. The effect of heterogeneous micro-habitat use by predators on prey micro-habitat use suggests an additional means by which mimicry may drive ecological speciation; mimetic shifts within species are suspected to be involved in speciation due to both increased predation on inter-form hybrids and the potential for assortative mating based on mimicry pattern (Mallet and Barton, 1989; Jiggins et al., 2001; Jiggins, 2008). If, (1) an unpalatable species co-occurs with different suites of predators and co-mimics in different communities, and (2) these predators and co-mimics in different communities occupy different micro-habitat space, then different populations of the focal unpalatable species may diverge in their micro-habitat use as a consequence of niche convergence or local habitat filtering. The resulting among-population divergence in micro-habitat use could isolate these populations both pre- (decreased probability of individuals using different micro-habitats coming into contact) and post-zygotically (hybrids may be less fit in either or both micro-habitat). From a community ecology perspective, our finding of increased maintenance of diversity of mimicry patterns for Müllerian mimics with heterogeneous predation should be applicable to most situations where the effectiveness of a signal or defense is linked to micro-habitat. Potential examples include floral displays used by plants to attract pollinators (Moeller, 2004), flash-signals used by carnivorous *Photuris* fireflies to

attract and devour *Photinus* fireflies (Lloyd, 1965; Lewis and Cratsley, 2008), the displays of carnivorous pitcher plants (Joel, 1988; Moran, 1996), and cryptic coloration in general (Main, 1987; Sandoval, 1994; Sandoval and Crespi, 2008). In these and other related situations one would predict correlations between signal or defense and micro-habitat use.

The simulation results we obtained are clearly dependent on the model assumptions we made (as are the results of all models). For example, we assumed a constant population size for each prey species, which was large enough to preclude the possibility of extinction. Incorporating extinction of prey species or colonization of the community by new prey species could alter the dynamics. We also assumed that predator species consumed  $n_k$  individuals of each mimicry type regardless of the prevalence of the mimicry type (if there were fewer than  $n_k$  individuals they were all consumed). An alternative modeling assumption would be to allow very rare mimicry types to suffer reduced predation (as they would be difficult to find), which might facilitate the persistence of rare mimetic forms. The choice of specific values for model parameters affected our results as well. For example, we specified values for the number of species, mimicry mutation rates, the strength of predation, etc. Although we explored various parameter values for several of the parameters, which had little effect on our model results, alternative parameter values could alter our findings. Unfortunately, too few accurate estimates of these parameters from natural communities exist to know for certain how appropriate the values we chose were.

In conclusion, the simulation results provide support for a potential solution to the apparent paradox of community-level diversity of mimetic forms in groups of Müllerian mimics despite general expectations that selection should purge such diversity. Specifically, we showed that heterogeneity in micro-habitat use by suites of predators promotes the persistence of multiple mimicry rings. The maintenance of diversity occurs because predator heterogeneity causes similar micro-habitat partitioning by unpalatable prey species, which experience selection primarily by their suite of predators. The results suggest that the association between mimicry type and prey micro-habitat use observed in the model simulations was due in part to niche convergence among co-mimics. Interestingly, we also found that moderate mimicry pattern-based assortative mating can also greatly facilitate mimetic diversity, which has not to the best of our knowledge been previously suggested.

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## Appendix A. Description of simulation conditions

We performed additional sets of simulations to assess the effect of different model parameter choices on the model results. For each set of new simulations the standard parameter values given in Table 1 were used except where specifically noted. These additional sets of simulations were conducted with each of the following modifications: reduced predation ( $n_k=150$ ), a decreased mimicry mutation rate ( $m=0.00001$ ), and decreased variance for sampling offspring niche variables ( $v=0.000625$ ).

Finally, we performed simulations that included moderate assortative mating based on mimicry pattern within each species reflecting behavior observed in some *Heliconius* species (Jiggins et al., 2001; Chamberlain et al., 2009). This was done by introducing the parameter  $t$ , which gives the relative probability of between mimicry group mating to within mimicry group matings (note, the standard model conditions are achieved with  $t=1$ ). Simulations were conducted with  $t=0.8$ . Models with each of these sets of parameter values were simulated under all three sets of predation parameters, and either both genetic architecture models (for reduced predation) or only the *equal dominance model*. For each set of simulations we monitored prey niche values and mimicry types through time. Source code for these models was written in C using the GNU Scientific Library (Galassi et al., 2009) and is available from Z.G. by request.

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