Evolutionary Assembly of Communities in Butterfly Mimicry Rings

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ABSTRACT: Species co-occurrence in ecological communities is thought to be influenced by multiple ecological and evolutionary processes, especially colonization and competition. However, effects of other interspecific interactions and evolutionary relationships are less explored. We examined evolutionary histories of community members and roles of mutualistic and parasitic interactions (Müllerian and Batesian mimicry, respectively) in the assembly of mimetic butterfly communities called mimicry rings in tropical forests of the Western Ghats, India. We found that Müllerian mimics were phylogenetically clustered, sharing aposematic signals due to common ancestry. On the other hand, Batesian mimics joined mimicry rings through convergent evolution and random phylogenetic assembly. Since the Western Ghats are a habitat island, we compared species diversity and composition in its mimicry rings with those of habitat mainland to test effects of biogeographic connectivity. The Western Ghats consisted of fewer mimicry rings and an overall smaller number of aposematic species and mimics compared to habitat mainland. The depauperate mimicry rings in the Western Ghats could have resulted from stochastic processes, reflecting their long temporal and spatial isolation and trickling colonization by the mimetic butterfly communities. These results highlight how evolutionary history, biogeographic isolation, and stochastic colonization influence the evolutionary assembly and diversity of ecological communities.

Keywords: phylogenetic community ecology, community dynamics, island biogeography, Batesian mimicry, Müllerian mimicry.

Introduction

Community assembly, whereby species from a regional pool come in contact and form local communities through ecological interactions, is influenced and maintained by multiple ecological and evolutionary processes. A plethora of theories have been proposed to understand community assembly either by focusing on geographic isolation and area or invoking niche-based processes (MacArthur and Wilson 1967; Diamond 1975; Leibold 1995; Chase and Myers 2011; Mittelbach and Schemske 2015). The size of an area, its geographical isolation, and colonization and extinction rates are widely believed to dictate community structure in an island biogeography framework (MacArthur and Wilson 1967; Kadmon and Allouche 2007; Harmon-Threatt and Ackerly 2013). Niche-based processes, influenced by biotic and abiotic factors such as species interactions, local environments, habitat filtering, and competitive exclusion, also shape community assembly (Diamond 1975; Leibold 1995; Chase and Myers 2011; Mittelbach and Schemske 2015). Further, neutral processes such as stochastic demographics and statistical probabilities of births and deaths of species could determine community diversity and structure in which species are assumed to have similar competitive and dispersal abilities (Hubbell 2001). In recent years, the influence of diversification rates and historical contingency on community assembly has also been highlighted in explaining community assembly (Webb 2000; Wiens 2011; Birand et al. 2012; Fukami 2015; Mittelbach and Schemske 2015; Pigot and Etienne 2015).

In the past two decades, phylogenetic community ecology has provided an integrated framework to study ecological and evolutionary processes and their roles in community assembly (Webb et al. 2002; Cavender-Bares et al. 2009; Fukami 2015; Mittelbach and Schemske 2015). It explicitly allows incorporation of species' evolutionary relationships (a proxy for species similarity based on the concept of phylogenetic conservatism) and then investigates the relative role of evolutionary and ecological processes on community structure (Webb 2000; Webb et al. 2002; Cavender-Bares et al. 2004, 2009; Wiens 2011). Among the various ecological interactions, habitat filtering and competition have been investigated extensively while assessing species coexistence in a phylogenetic community framework (Helmus et al. 2007; Cavender-Bares et al. 2009; Mayfield and Levine 2010; Pellissier et al. 2013). Coexistence of phenotypically similar species is believed to be possible because of habitat filtering. On

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the other hand, closely related co-occurring species may be phenotypically different as a result of species-specific adaptations and/or character displacement due to competition (Cavender-Bares et al. 2009). Competition could also drive extinction or local exclusion of species that may be phenotypically similar either due to phylogenetic conservatism or convergence. Recently developed methods aim at testing these possibilities and specifically deal with the role of competition and habitat filtering in an explicit phylogenetic framework (Webb 2000; Cavender-Bares et al. 2004; Helmus et al. 2007; Kraft et al. 2007; Mayfield and Levine 2010).

Unlike competition, influences of mutualistic and parasitic interactions in shaping diversity and composition of communities are relatively poorly understood (Stachowicz 2001; Bascompte and Jordano 2007). They have also not been widely investigated in a community phylogenetic framework. Here, we explore the role of both these interactions in structuring communities using mimetic butterflies in a phylogenetic community framework. Wing color pattern mimicry is widespread among butterflies, and a specific warning (aposematic) wing pattern is often shared between several sympatric species that form a community called a mimicry ring. These aposematic wing patterns are usually protected by chemical defenses that make at least a few prey species from mimicry rings unpalatable to predators, which learn to avoid aposematic prey based on initial experience (Skelhorn and Rowe 2006, 2010). Diverse mimicry rings with many aposematic species and numerous mimics show two types of species interaction: (*a*) Two or more chemically defended species, which drive mimicry rings, share an aposematic wing pattern that could reduce the net density-dependent predation involved in educating naïve predators, and thus they have a mutualistic relationship with each other (Müller 1879; Wickler 1968; Ruxton et al. 2004). We will refer to chemically defended prey as aposematic species when a mimicry ring contains a single aposematic species and refer to them as Müllerian comimics when a mimicry ring contains more than one aposematic species that mimic each other. (*b*) Species that are palatable but have mimetic wing patterns similar to that of the aposematic species may experience reduced predation and gain fitness advantage from this Batesian mimicry at the expense of the aposematic species/ Müllerian comimics. Thus, Batesian mimics have a parasitic relationship with the aposematic species (Bates 1862; Wallace 1889; Wickler 1968). Both positive (mutualistic) and negative (parasitic) interactions could simultaneously be present and influence community diversity and structure in mimicry rings. We will henceforth refer to aposematic species/Müllerian comimics as the Müllerian component, Batesian mimics as the Batesian component, and all the aposematic and Batesian mimetic species within a single mimetic community together as a mimicry ring.

Mimicry rings are well-defined species assemblages with specific spatially and temporally well-characterized interactions that qualify them to be true ecological communities: (*a*) Aposematic species/Müllerian comimics—and their aposematic wing patterns—are established in space and time once their local density crosses a threshold beyond which populations may be sustained after having educated naïve predators in the area (Ruxton et al. 2004). Because of the density-dependent advantage of Müllerian mimicry, a mimicry ring saturated with Müllerian mimics should be better protected than one with fewer Müllerian mimics and, therefore, be an evolutionarily stable community. Here, the stability is of the aposematic wing pattern, not necessarily of the constituent species that may change over space and time, although the core Müllerian mimics are likely to drive mimicry rings in the long term. (*b*) Distributional ranges and occurrence of Batesian mimics are constrained by ranges of aposematic species and by frequency-dependent selection imposed by predators, since Batesian mimics lose the advantage of mimicry in absence or low relative abundance of the aposematic species (Pfennig et al. 2001, 2007; Ries and Mullen 2008; Pfennig and Mullen 2010). Thus, mimicry rings saturated with Batesian mimics should be weakly protected and therefore be an evolutionarily unstable community. (*c*) Mimicry influences annual phenology, daily activity patterns, and behaviors of Batesian mimics in relation to the aposematic species that they mimic (Waldbauer et al. 1977; Huheey 1980; Brodie 1981; Waldbauer 1988), similar to classic communities involving plants and pollinators (Bartomeus et al. 2011), prey and predators (Preisser et al. 2005), and hosts and parasites/parasitoids (Seppälä et al. 2004). (*d*) Similar to other well-defined local communities, local mimicry rings are drawn from the regional pool of species and their evolutionary histories, influenced by ecological and genetic contingency and local interspecific interactions (Mallet and Gilbert 1995; Harper and Pfennig 2007; Elias et al. 2008; Marek and Bond 2009; Alexandrou et al. 2011; Chazot et al. 2014).

The role of Müllerian mimicry—that is, positive/mutualistic interactions—in shaping community structure and diversity has recently been studied in the Neotropical *Heliconius* and ithomiine butterfly communities (Elias et al. 2008; Chazot et al. 2014). It may also have influenced diversification in the Neotropical *Limenitis* butterflies (Mullen 2006) and North American velvet ants (Wilson et al. 2012). However, the role of Batesian mimicry—that is, parasitic/negative interactions—has not been adequately studied in a community context. The combined role of both these types of mimicry has also not been studied in the evolutionary assembly, diversity, and structure of mimicry rings. Here, we attempt to characterize evolutionary assembly of entire mimicry rings including Batesian and Müllerian components using a phylogenetic framework. To do this, we first reconstructed phylogenetic relationships between aposematic species and Batesian mim-
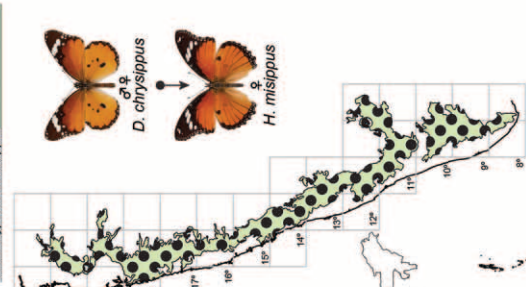
Eucharis mimicry ring

	J F M A M J J A S O N D
Model	Delias eucharis
Mimic	Pioneris sita

D. eucharis ♂♀ — P. sita ♂♀
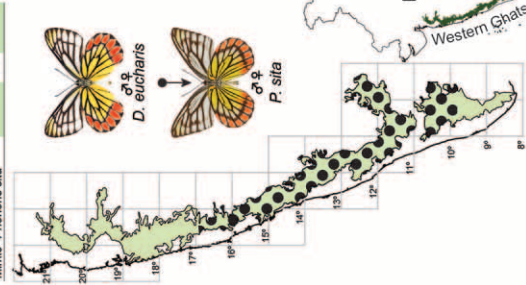
chrysippus mimicry ring

	J F M A M J J A S O N D
Model	Danaus chrysippus
Mimic	Hypolimnas misippus

D. chrysippus ♂♀ — H. misippus ♀

hector mimicry ring

	J F M A M J J A S O N D
Model	Pachliopta hector
Mimic	Papilio polytes

P. hector ♂♀ — P. polytes, f. romulus ♀
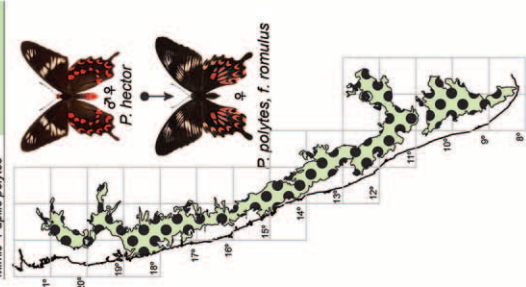
Euploea mimicry ring

	J F M A M J J A S O N D
Model	Euploea sylvester
Model	Euploea core
Model	Euploea klugii
Mimic	Papilio clytia
Mimic	Papilio dravidarum
Mimic	Hypolimnas bolina

E. klugii ♂♀ — E. core ♂♀
E. sylvester ♂♀ — P. clytia, f. clytia ♂♀ — P. dravidarum ♂♀
H. bolina ♀

Pachliopta mimicry ring

	J F M A M J J A S O N D
Model	Pachliopta pandiyana
Model	Pachliopta aristolochiae
Mimic	Papilio polytes

P. pandiyana ♂♀ — P. aristolochiae ♂♀ — P. polytes, f. stichius ♂♀

genutia mimicry ring

	J F M A M J J A S O N D
Model	Danaus genutia
Model	Cethosia mahratta
Mimic	Elymnias caudata
Mimic	Argynnis castetsi

C. mahratta ♂♀ — D. genutia ♂♀
A. castetsi ♂♀ — E. caudata ♀

Tirumala mimicry ring

	J F M A M J J A S O N D
Model	Tirumala septentrionis
Model	Tirumala limniace
Model	Parantica nilgiriensis
Model	Parantica aglea
Model	Idea malabarica
Mimic	Papilio clytia
Mimic	Pareronia hippia
Mimic	Pareronia ceylanica

I. malabarica ♂♀
T. limniace ♂♀ — P. aglea ♂♀ — P. clytia, f. dissimilis ♂♀
T. septentrionis ♂♀ — P. nilgiriensis ♂♀ — P. hippia ♀ — P. ceylanica ♀

India
Western Ghats

Legend:
↕ : Müllerian mimicry
↑↓ : Batesian mimicry
● : Aposematic species
↑ : Batesian mimics

E60

ics. We then explored patterns of relatedness and convergence in wing patterns with respect to Müllerian and Batesian mimicry (in this article, we will refer to advergence—a common term in mimicry literature to describe how a mimic arrives at the aposematic phenotype while the aposematic species remains largely unchanged—as convergence. This is strictly for convenience since most nonspecialists are only familiar with the term convergence and often tend not to distinguish between the two processes). Specifically, using community phylogenetic methods, we tested whether the evolution of wing patterns within each mimicry ring was due to phylogenetic relatedness or convergence. For these purposes, we studied butterfly mimicry rings in the Western Ghats of southern India, which is a globally recognized biodiversity hot spot (Myers et al. 2000) due to its high species diversity and endemism (Gunawardene et al. 2007). These mimicry rings are well characterized with respect to their wing color patterns (figs. 1, B1; Su et al. 2015; figs. B1, B2 are available online), with additional ecological information on the spatial and temporal overlap between their members (figs. 1, B1, B2) so that this may serve as a suitable study system. The choice of the Western Ghats butterfly mimicry rings also allowed us to study how island biogeographic considerations may constrain or otherwise influence diversity and composition of mimicry rings. This is because the evergreen forests of the Western Ghats are isolated by more than 1,500 km from those in the Himalayan and Indo-Burmese regions, which are sources of butterfly diversity for the sinks of the Western Ghats (Kunte 2013). Thus, the local butterfly mimicry rings in the Western Ghats are expected to be drawn from a larger, regional species pool in the Himalayan/Indo-Burmese region following biogeographic considerations such as isolation and colonization. Since the Western Ghats are physically part of the mainland, they may be considered a habitat island instead. We compared diversity and composition of mimicry rings in the Western Ghats with those in Hong Kong—a small oceanic island—and two habitat mainland areas, the Eastern Himalaya and the Malay Peninsula, to study mimicry rings in the mainland-island context.

Using the butterfly mimicry rings in the Western Ghats, we tested the following two hypotheses based on the classical mimicry theory (the mutually exclusive hypotheses 1a and 1b) and on the island biogeography theory (hypothesis 2):

1a. Both Müllerian and Batesian mimicry result from convergent evolution. The original formulation of the explanation for Müllerian mimicry was based on the observation that phylogenetically unrelated species—that is, polyphyletic groups—shared common aposematic patterns (Müller 1879). Recent studies on diversification of wing coloration and mimicry rings in *Heliconius* and ithomiine butterflies (cited above) indeed show that (i) members of different aposematic butterfly and moth clades may share an aposematic pattern (i.e., they are Müllerian comimics) and (ii) closely related aposematic species often belong to different mimicry rings. Batesian mimicry, by its very nature, is expected to be a product of convergent evolution (Bates 1862). Thus, both Müllerian and Batesian mimetic components would be products of convergence.

1b. Both Müllerian and Batesian mimicry evolve in closely related groups and are thereon phylogenetically constrained. Recent genomic and developmental genetic investigations suggest that convergent trait evolution with respect to wing patterns of butterflies may be due to conserved genetic and developmental programs (Gilbert 2003; Nadeau 2016). Therefore, if aposematism evolves in a particular clade, both Müllerian and Batesian mimicry may be more likely to evolve in sister groups because of parallelism from recent shared evolutionary genetic history. Further, if there is selection to maintain mimetic resemblance, the initial evolution of Müllerian or Batesian mimicry may constrain subsequent evolution of divergent wing patterns. Therefore, both Müllerian and Batesian mimetic components in mimicry rings may be phylogenetically clustered. Thus, hypotheses (1a) and (1b) are largely mutually exclusive alternatives based on taxonomic/phylogenetic observations (1a) and more recent understanding of the developmental genetic bases of wing pattern formation in butterflies (1b). The relative frequency of these two patterns in the evolution of mimicry rings is yet unknown.

2. Island biogeography: mimicry rings in habitat islands are species depauperate, in general, and specifically in their Batesian mimetic components. Islands host species assemblages that are drawn from larger mainland (regional) pools, presumably as a random process (MacArthur and Wilson 1967). The probability of Batesian mimics and aposematic species establishing in a specific spot at the same time—or

Figure 1: Mimicry rings in the Western Ghats, India, showing spatial and temporal overlap between Batesian mimics and aposematic species and their mimicry phenotypes. Each mimicry ring is named after the predominant species or genus of aposematic species. In the phenological tables, J–D represent months in a year; monthly occurrence of aposematic species and Batesian mimics are shown in green, and absence is shown in white; and in each mimicry ring, aposematic species are listed before Batesian mimics, separated by a black line. Most aposematic species and Batesian mimics overlap in time. The distributional maps on the outline of the Western Ghats show spatial overlap between aposematic species and Batesian mimics. Green areas represent distributions of aposematic species, where darker green areas show more restricted distributions of one or more aposematic species when multiple aposematic species exist in mimicry rings. Black spots on these maps show distributions of Batesian mimetic species, with yellow spots representing narrower distributions of some of the Batesian mimetic species (see fig. B2 for distributional ranges of individual species). Distributional ranges of Batesian mimics are embedded within the distributional ranges of aposematic species, signifying ecological dependence of Batesian mimics on the presence of aposematic species.

mimics following aposematic species into a habitat island—should be low. However, aposematic species may be able to establish in a habitat island at a much greater frequency than the mimics since aposematic species can colonize and establish independently, whereas mimics cannot. Thus, mimicry rings in habitat islands should generally be fewer in number and/or smaller in size, especially in their Batesian components.

Methods

Butterfly Mimicry Rings in the Western Ghats and Taxon Sampling

A total of 25 butterfly species form seven mimicry rings in the Western Ghats of southern India (figs. 1–3, B1, B2; Su et al. 2015). The Müllerian components in these mimicry rings include 15 species, and the Batesian components include 10 species, from three families: Papilionidae (6 species), Nymphalidae (15 species), and Pieridae (4 species). Here, we refer to these seven mimicry rings after the most common aposematic species in each mimicry ring, and when multiple common Müllerian comimics comprise mimicry rings, by the genus name of the predominant aposematic species. These mimicry rings and mimetic relationships are defined by the aposematic color patterns that are shared between the Batesian mimics and aposematic species (Su et al. 2015) as well as spatial and temporal overlap between species (figs. 1, B1, B2; data from Padhye et al. 2012; Kunte et al. 2016). Thus, these mimicry rings fit the classical concept of a community not only because (*a*) these species have formed local assemblages that share relevant functional phenotypes (aposematic coloration and associated behaviors) that help them coexist and function as a community but also because (*b*) their overlapping spatial and temporal occurrence is dependent on specific ecological (mutualistic and parasitic) interactions (note that distributional ranges of Batesian mimics are smaller and always embedded within the ranges of the aposematic species; figs. 1, B2). The Batesian mimic and aposematic species' relationship in many but not all of these species has been experimentally demonstrated using predators (Larsen 1992, 2007; Uesugi 1995, 1996) and extensively studied especially in the *chrysippus* (Edmunds 1966; Smith 1973, 1976; Gordon et al. 2010) and *Pachliopta* mimicry rings (Uesugi 1995, 1996; Kitamura and Imafuku 2010). In the remaining mimicry rings, aposematic species–Batesian mimic relationships are inferred from natural history information on larval host plant chemistry, phenotypes of caterpillars, and behavior and phenology of adults (Wynter-Blyth 1957; Kunte 2000; Kunte et al. 2016).

We sampled all these species and included them in the analysis presented below. We generated a complete molecular phylogeny of all the butterfly mimicry rings in the Western Ghats for subsequent analysis. We also used published sequences of a few species from sister genera and tribes for a better phylogenetic resolution. We downloaded these sequences along with those of the moth outgroups from GenBank (Heikkilä et al. 2012; table S1, available online). We collected most of the new material used in this study in the field following research and collecting permits from state forest departments. We preserved the specimens in ethanol, which are now deposited in the Research Collections of the National Centre for Biological Sciences (NCBS), Bangalore. We included in the phylogeny two species—*Troides minos* and *Acraea terpsicore*—that are known to be aposematic but subsequently excluded them from the analysis of mimetic communities since they are not part of mimicry rings but are single species with unique aposematic patterns. Mimicry types mapped in figure 3 were taken from Su et al. (2015), who present a detailed quantification of wing color discriminability among members of the Western Ghats butterfly mimicry rings.

Molecular Data Set and Phylogenetic Analyses. We generated DNA sequence data for 29 species, including the 25 mimicry ring members for three mitochondrial markers (*cytochrome c oxidase I, tRNA leucine,* and *cytochrome c oxidase II*) and two nuclear markers (*elongation factor I-alpha* and *wingless*) using standard polymerase chain reaction (PCR) primers and protocols that are commonly used to reconstruct butterfly phylogenies (Heikkilä et al. 2012). We sequenced both the DNA strands, cleaned sequences using Geneious 7.1.7, and aligned the sequences using MUSCLE with default settings (Edgar 2004). The final data set consisted of 3.5 kb combined sequence data each for 88 specimens (table S1). The newly generated sequences are available on GenBank (accession nos. KX467789 to KX467872). We used Bayesian and maximum likelihood methods to reconstruct phylogenetic trees. We used PartitionFinder to choose the best partition schemes for mitochondrial and nuclear markers along with corresponding models of sequence evolution using the greedy algorithm and models = MrBayes or raxml set of models and a Bayesian information criterion (BIC) to compare the best-fit models (Lanfear et al. 2012). We performed a partitioned Bayesian analysis using MrBayes 3.2 (Huelsenbeck and Ronquist 2001). PartitionFinder suggested a total of three partitions with the likelihood score of lnL −59,913.96 and BIC 124,976.40: (*a*) mitochondrial markers with GTR+I+G, (*b*) nuclear *EF I-alpha* with SYM+I+G, and (*c*) nuclear *wingless* with K80+I+G substitution models. Base frequencies, rates for the GTR, SYM, and K80 models, and the shape parameter of the gamma distribution were estimated from the data in MrBayes 3.2 separately for each partition. The program was run for 50 million generations wherein sampling was done for every 1,000 generations. We used split frequency below 0.01 to assess stationarity and to set the burn-in in MrBayes 3.2, and we then built a consensus tree using the remaining trees. We also evaluated stationarity using the program Tracer

v1.4.1. We performed maximum likelihood analysis using RAxML with three data partitions and the GTR+I model. This was done using a web server (http://embnet.vital-it.ch/raxml -bb/) with 1,000 bootstraps. In addition, we separately analyzed the nuclear data set using the Bayesian and maximum likelihood methods with the settings mentioned above. The resultant phylogenetic trees have been deposited in TreeBase.

Phylogenetic Community Ecology. We used the Bayesian molecular phylogeny of the butterfly mimicry rings of the Western Ghats to calculate mean pairwise distances (MPD) between all species within the Batesian and Müllerian components of each mimicry ring. In addition, we calculated the mean nearest taxon distance (MNTD)—the mean distance separating each species in the mimicry ring from its closest relative. We also calculated the net relatedness index (NRI) and the nearest taxon index (NTI; Webb 2002) for each mimicry ring to test the differences between phylogenetic distances in the observed communities and neutral communities generated with a randomization method. NRI uses MPD of an assemblage, and NTI is based on MNTD. If NRI and NTI values are positive, then communities are phylogenetically clustered, whereas negative values indicate that communities are phylogenetically overdispersed. We used taxa.labels as a null/neutral model, which randomizes tips of the phylogeny. We did not use other randomization methods for lack of species abundance or density data. We carried out 10,000 runs to create pseudoassemblages. We performed these phylogenetic community analyses using the R package picante (Ihaka and Gentleman 1996). Merits and usefulness of these distance matrices in community phylogenetics have been discussed elsewhere (Webb et al. 2002). Additionally, we quantified phylogenetic signal using Pagel's λ (Pagel 1999) across mimicry rings to test whether wing patterns were conserved or products of convergent evolution. For Pagel's λ method, we calculated the maximum likelihood estimate of Pagel's λ and for the model with λ = 0. We then compared these models based on the negative likelihood scores using likelihood ratio test and Akaike information criterion values. Pagel's λ analyses was performed in the R package geiger (Harmon et al. 2008).

Mimicry Ring Diversity and Composition in Habitat Islands and Mainlands. We compared mimicry ring diversity and composition across a habitat island (the Western Ghats) and an oceanic island (Hong Kong) with mimicry rings in two mainland areas (the Eastern Himalaya and the Malay Peninsula). We compiled the lists of Batesian mimics and aposematic species in individual butterfly mimicry rings in these four areas from their complete butterfly inventories and previous work on mimicry rings (Evans 1932; Wynter-Blyth 1957; Corbet et al. 1992; Bascombe et al. 1999; Su et al. 2015). Mimicry ring diversity in the Malay Peninsula

is likely to be an underestimate since the moth fauna of this area has not been adequately studied for mimetic relationships and has not been suitably illustrated. Many zygaenid, epicopeiid, and other aposematic moths are expected to be members of the Malayan butterfly mimicry rings, as they are in the Eastern Himalaya and other parts of the Indo-Australian Region. We used Kruskal-Wallis tests for comparing the size of mimicry rings and the proportion of aposematic species to mimics.

Results

Phylogenetic Community Analysis

Our Bayesian and maximum likelihood analyses recovered a well-supported butterfly phylogeny (fig. 2) that shows the overall distribution of aposematic species, Müllerian comimics, and Batesian mimics nested within and broadly corresponding with previously known taxonomic groupings under Papilionidae, Nymphalidae, and Pieridae (Heikkilä et al. 2012). Figure 2 also provides branch support for phylogenetic relationships of the aposematic species and Batesian mimics that are used in subsequent statistical analyses (table 1) and trait mapping (fig. 3). Mapping of the aposematic species and Batesian mimics on a pruned phylogeny of the mimicry rings of the Western Ghats showed that both aposematism and Batesian mimicry had evolved multiple times and independently of each other (figs. 2, 3). However, Müllerian components in each mimicry ring formed monophyletic groups (fig. 3), with these exceptions: (*a*) the *genutia* mimicry ring included two aposematic species—*Danaus genutia* and *Cethosia mahratta*—from distantly related clades, and (*b*) in the *Tirumala* mimicry ring, the monophyletic *Tirumala-Parantica* clade was joined by *Idea* from the sister clade (strength of the phylogenetic signal, Pagel's λ, for each mimicry ring is given in table 1). Thus, the Müllerian component of each mimicry ring resulted largely from diversification of aposematic clades with the aposematic signal shared due to common ancestry, not due to convergence among distantly related, dissimilar aposematic species as hypothesized in the original and classical framework of Müllerian mimicry (hypothesis [1a]). The phylogenetic clustering of Müllerian mimicry components (figs. 2, 3) was further supported by the phylogenetic community analysis ("Müllerian component" in table 1). The NRI and NTI values for Müllerian mimicry components were positive, and they were significantly different from zero, indicating that the Müllerian components were phylogenetically clustered, supporting hypothesis (1b).

On the other hand, Batesian mimics in the Western Ghats joined mimicry rings due to convergence, as expected under hypothesis (1a) ("Batesian component" in table 1). The NTI and NRI values of Batesian components of most of the
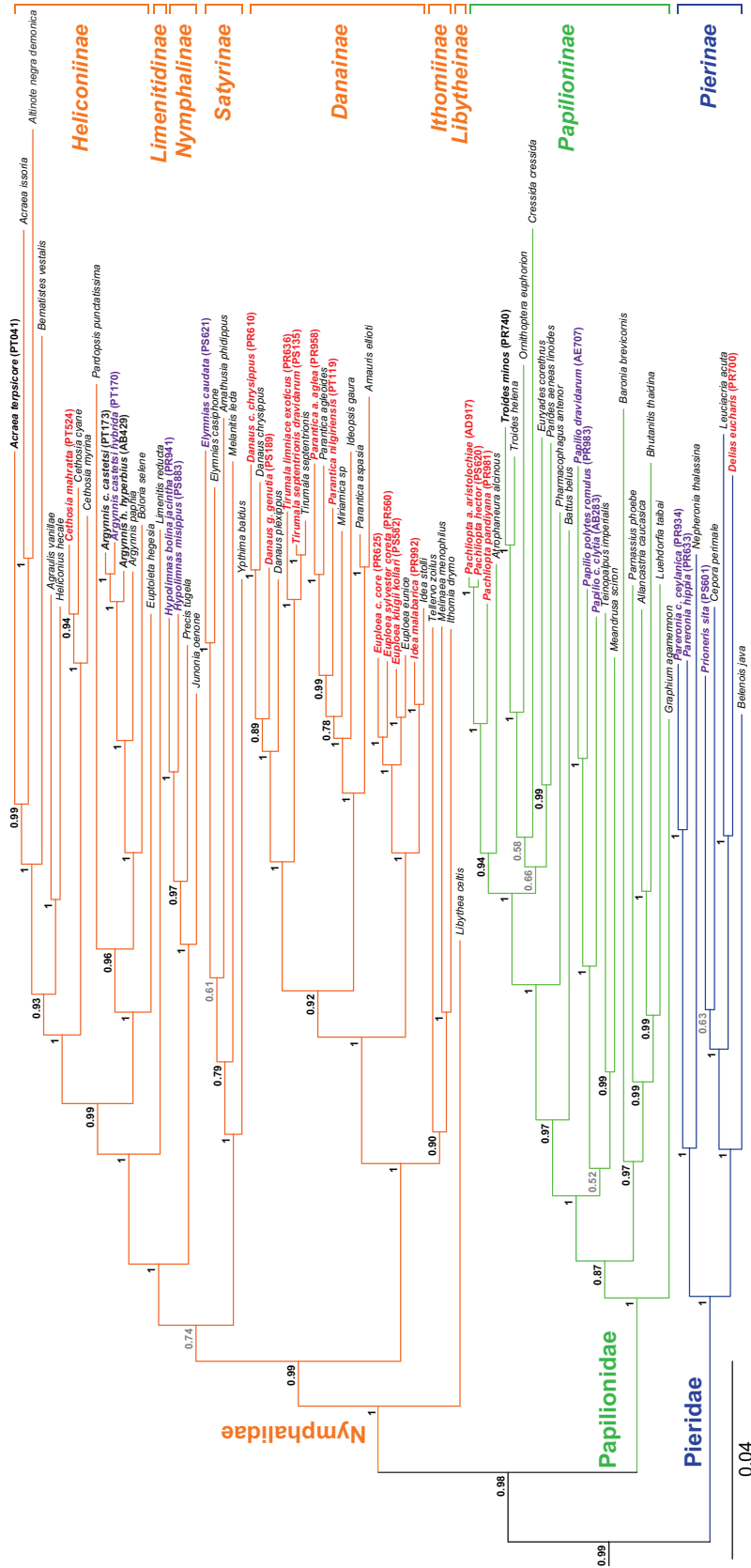
Figure 2: Bayesian phylogram showing phylogenetic relationships of aposematic and mimetic butterflies in the mimicry rings of the Western Ghats in relation to the overall phylogeny of butterflies. Posterior probability is shown at each node (nonsignificant values are indicated in gray). Names of species and voucher codes of specimens sequenced for this study are indicated in boldface. Aposematic species/Müllerian comimics and Batesian mimics are highlighted; their exact relationships are shown in figures 1 and 3.

Table 1: Mimicry ring assembly in the butterfly communities of the Western Ghats with respect to ecological interactions and trait evolution

Part, mimicry ring	N (species)	Net relatedness index			Nearest taxon index			Phylogenetic signal		
		MPD	NRI	P	MNTD	NTI	P	Pagel's λ_0/λ ($-\ln$L)	P	ΔAIC
Entire mimicry ring:										
eucharis	2	.19	1.37	.21	.19	1.36	.26	$-6.9/-4.7$	**.03**	**4.75**
Tirumala	8	.29	1.23	.21	.11	2.04	.09	$-15/-13.4$	**.03**	**4.4**
hector	2	.25	.77	.28	.25	.79	.29	$-6/-11.9$	1	-12
Euploea	6	.27	1.62	.21	.12	1.85	.09	$-14.05/-13.2$	.22	-1.5
Pachliopta	3	.18	2.38	.21	.12	2.07	.09	$-9.02/-13.5$	1	-8.67
chrysippus	2	.33	$-.15$	.38	.33	$-.19$	.42	$-6.7/-8.3$	1	-3
genutia	4	.32	.04	.38	.28	$-.51$	.67	$-10.7/-9.8$	.15	2.1
Batesian component:										
Tirumala	3	.26	.89	.39	.16	1.44	.33	$-9/-7.02$	**.02**	**3.96**
Euploea	3	.29	.32	.39	.22	.57	.37	$-9.15/-10.19$	1	-2.08
genutia	2	.33	$-.25$	.39	.33	$-.2$	.39	$-6.81/-5.95$	.19	1.7
Müllerian component:										
Tirumala	5	.16	4.53	**.003**	.07	2.7	**.005**	$-12.33/-10.3$	**.04**	**4.7**
Euploea	3	.04	4.88	**.003**	.03	3.13	**.002**	$-9.4/-5.7$	**.006**	**7.5**
Pachliopta	2	.04	4.97	**.003**	.02	3.36	**.002**	$-7/-10.6$	1	-7.2
genutia	2	.08	2.4	**.04**	.08	2.4	**.04**	$-6.8/-5.4$	**.002**	3.2

Note: All mimicry rings included Batesian components, but only those mimicry rings with more than one aposematic species included Müllerian components. Net relatedness index (NRI) and nearest taxon index (NTI) are two indexes that describe whether communities are phylogenetically clustered or overdispersed. Positive NRI and NTI values that are significantly different from zero indicate phylogenetically clustered communities, whereas negative values indicate overdispersion. Pagel's λ tests for phylogenetic signal in tree topology are as compared with a null tree, that is, a tree with transformed $\lambda = 0$. Statistically significant P values are indicated in boldface. MPD = mean pairwise distance; MNTD = mean nearest taxon distance.

mimicry rings were positive but not significantly different from zero, indicating that they were products of convergent evolution. However, Batesian mimics were assembled through a phylogenetically/taxonomically complex process of convergence; that is, some Batesian mimics were from sister groups of aposematic species, and some mimics were much more distantly related from different genera and families. That is, the extent of convergence was variable: while *Prioneris*, *Papilio polytes*, and *Argynnis* joined mimicry rings within their taxonomic tribes and subfamilies, *Pareronia*, *Papilio clytia*, *Papilio dravidarum*, *Elymnias*, and *Hypolimnas* joined mimicry rings across taxonomic subfamilies and families. Thus, convergence in the second set of Batesian mimics spanned across tens of millions of years of evolutionary divergence (time-calibrated molecular phylogenies showing times of divergence between most of the clades containing Batesian mimics and aposematic species in the Western Ghats mimicry rings may be found elsewhere; Wahlberg et al. 2009).

The mimicry rings on the whole (inclusive of Müllerian and Batesian components) were neither phylogenetically clustered nor overdispersed ("Entire mimicry ring" in table 1). This lack of pattern in phylogenetic clustering or overdispersion at the level of the entire mimicry rings could be a product of opposing patterns of phylogenetic clustering in Müllerian components (hypothesis [1b]) and convergence in Batesian components (hypothesis [1a]).

Island Biogeographic Effects on Mimicry Ring Diversity and Composition

Mainland areas, that is, the Eastern Himalaya and the Malay Peninsula, had greater mimetic diversity as reflected in the total number of mimicry rings, sizes of mimicry rings, and numbers of aposematic species and Batesian mimics compared to islands (tables 2, S1; fig. 4). This was true irrespective of whether the island was a habitat island (the Western Ghats) or an oceanic island (Hong Kong). Moreover, mainlands harbored significantly larger mimicry rings compared to islands (Kruskal-Wallis test, df = 1, P = .05; fig. 4; table 2). However, the ratio of aposematic species to Batesian mimics in individual mimicry rings was similar among mainlands and islands, that is, composition of mimicry rings with respect to relative sizes of Müllerian and Batesian components in individual mimicry rings did not differ between mainlands and islands (Kruskal-Wallis test, df = 1, P = .68; table 2; fig. 4). The island mimicry rings were depauperate not only because they had overall lower mimetic diversity (as above) but also because the five mimicry rings that were shared between mainlands and islands had fewer aposematic species and/or mimics in islands (fig. 5a–5e). The nature of reduction in the size of the shared mimicry rings was unpredictable: some mimicry rings lost more aposematic species, while others lost more Batesian mimics when they were established
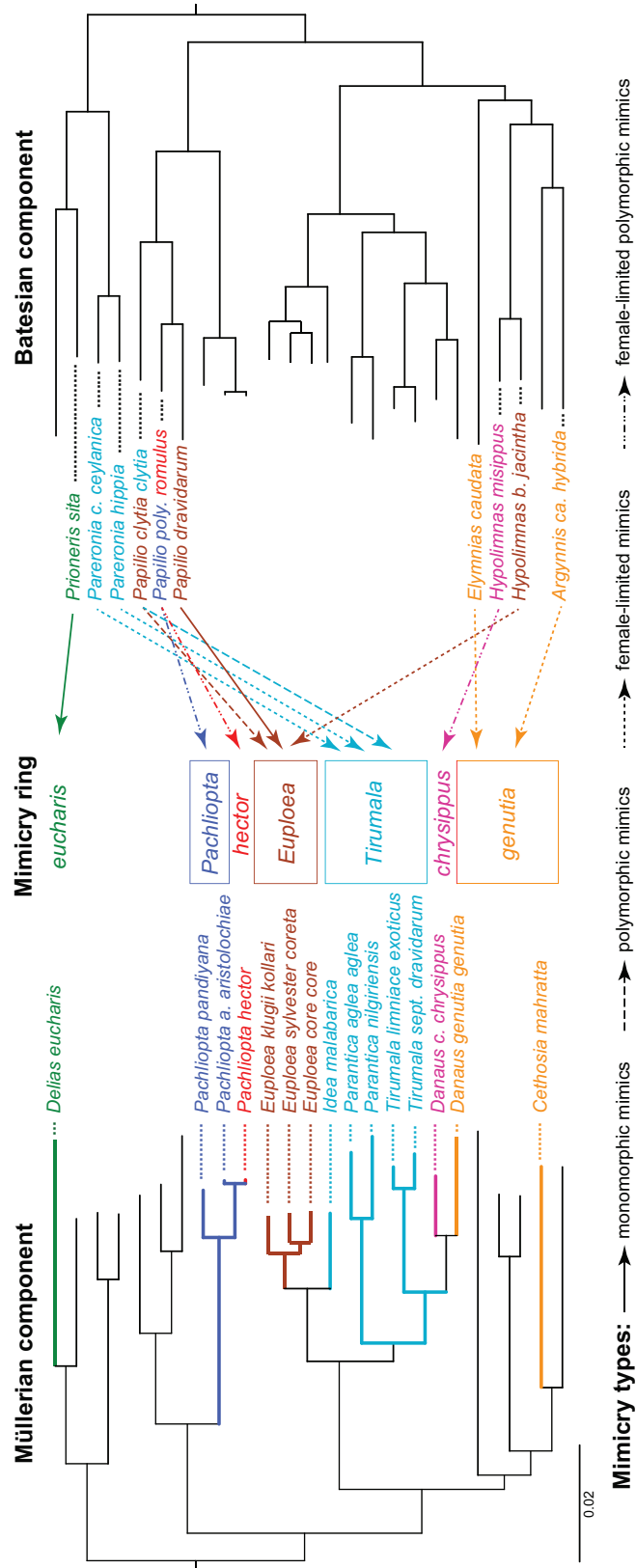
Figure 3: Evolutionary assembly of communities in butterfly mimicry rings of the Western Ghats. Mirror phylogenies—derived from figure 2—show relationships of aposematic species (*left*) and Batesian mimics (*right*), with their mimicry rings in the center. Monophyletic groups that form Müllerian components of mimicry rings are indicated in boldface on the left. Arrows from mimics point to the mimicry rings of which they are a member, coded by the mimicry type that they exhibit in terms of sex limitation and polymorphism.

Table 2: Mimetic diversity across the four regions considered and between the islands (Western Ghats and Hong Kong) and mainlands (Eastern Himalaya and Malay Peninsula)

	No. of mimicry rings	Total no. of species in all mimicry rings	No. of aposematic species	No. of Batesian mimics	Size of mimicry rings (range)	Proportion of aposematic species to Batesian mimics
Western Ghats	7	25	15	10	3.9 ± 2.34 (2–8)	1.9 ± .22
Hong Kong	8	24	16	8	3.1 ± 1.72 (2–7)	1.8 ± .81
Eastern Himalaya	13	74	40	34	6.2 ± 4.36 (2–16)	2.1 ± .67
Malay Peninsula	15	76	49	27	5.7 ± 4.79 (2–16)	2.0 ± 1.05
Islands	…	…	…	…	3.5 ± 1.99 (2–8)	1.8 ± .59
Mainlands	…	…	…	…	6 ± 4.52 (2–16)	2.0 ± .88

Note: Mean size of mimicry rings (mean ± SD species) for each region and for the mainland-island comparison was calculated from the total number of species per mimicry ring, including the Müllerian and Batesian components.

in islands (fig. 5*f*). Thus, the prediction of the island biogeography theory (rich mainlands, depauperate islands) was supported but not necessarily in having fewer Batesian mimics.

Discussion

The evolution and persistence of mimicry provides interesting insights into evolutionary dynamics and behavioral evolution (Fisher 1958; Sheppard 1975; Vane-Wright and Ackery 1984; Ruxton et al. 2004). Investigations into the inheritance and molecular aspects of mimicry have also illuminated genetic controls and developmental processes that shape iconic adaptations (Fisher 1958; Ford 1975; Sheppard 1975; Joron et al. 2011; Reed et al. 2011; Kunte et al. 2014; Le Poul et al. 2014; Wallbank et al. 2016). However, this multifaceted adaptation has been sparsely utilized in community ecological studies (Gilbert and Smiley 1978; Beccaloni 1997; DeVries et al. 1999; Elias et al. 2008, 2009; Hill 2010; Chazot et al. 2014). This is unfortunate because the well-defined interactions among members of mimetic communities (mutualistic among Müllerian comimics, parasitic from the Batesian mimics) and the nature of strong selection (natural selection by predation) provide some unusually clear predictions regarding evolutionary assembly of mimetic communities. These factors are not always clear in the evolutionary assembly of other kinds of communities. The role of mutualistic interactions and evolutionary contingency in shaping Müllerian components have recently been studied in South American butterfly mimicry rings (Elias et al. 2008, 2009; Chazot et al. 2014). These studies were among the first to use an evolutionary framework, phylogenetic community methods, and extensive field data to investigate community ecology of butterfly mimicry rings. However, they also exclusively focused on the Müllerian components of mimicry rings. Our study appears to be the first to encompass both Müllerian and Batesian components in using a phylogenetic community framework to test ideas regarding evolutionary assembly of mimicry rings. Further, incorporating concepts from island biogeography enabled us to understand how the diversity and composition of mimicry rings may be affected by isolation. Below we discuss in detail implications of our two sets of findings in the context of the evolution of mimicry and community dynamics on the whole.

Monophyletic Müllerian Mimics, Polyphyletic, and Divergent Batesian Mimics

Mimicry rings in South America (Beccaloni 1997) and the Malay Peninsula (table S1 from Corbet et al. 1992) often consist of aposematic butterflies and moths from vastly different clades separated by long evolutionary time (10–100 million years). This is clearly a case of convergence on shared aposematic patterns under selection for Müllerian mimicry that may reduce net predation pressure on aposematic species. In contrast, when butterfly mimicry rings in the Western Ghats contained multiple Müllerian mimics, they tended to be related species from monophyletic groups. Müllerian mimicry therefore appears to be a phylogenetically deterministic process in the butterfly mimicry rings of the Western Ghats. That is, Müllerian mimics emerge from speciation process within monophyletic clades of aposematic butterflies. It is conceivable that Müllerian mimicry in the Western Ghats mimicry rings has largely evolved from stabilizing selection on the locally well-established (protected) wing patterns of aposematic species, with this selection persisting through speciation events, which constrains wing patterns of aposematic sister species from diverging from each other. This type of Müllerian mimicry due to shared ancestry should indeed be expected. The fact that many biologists think of Müllerian mimicry as arising necessarily or at least largely from convergence may be a historical accident: Müller formulated his theory of mimicry to explain surprising convergence between phylogenetically divergent lineages, which must have made a stronger case for Müllerian mimicry. However, Müllerian mimicry by shared
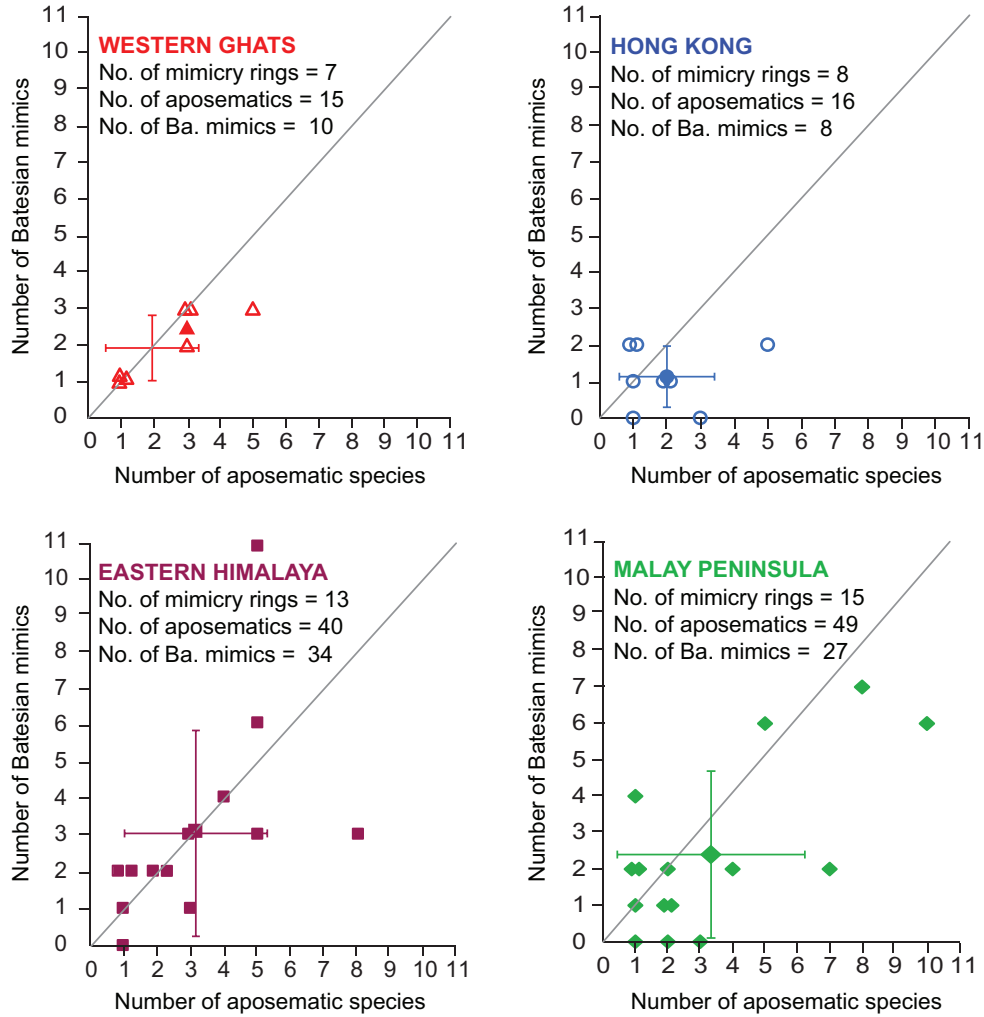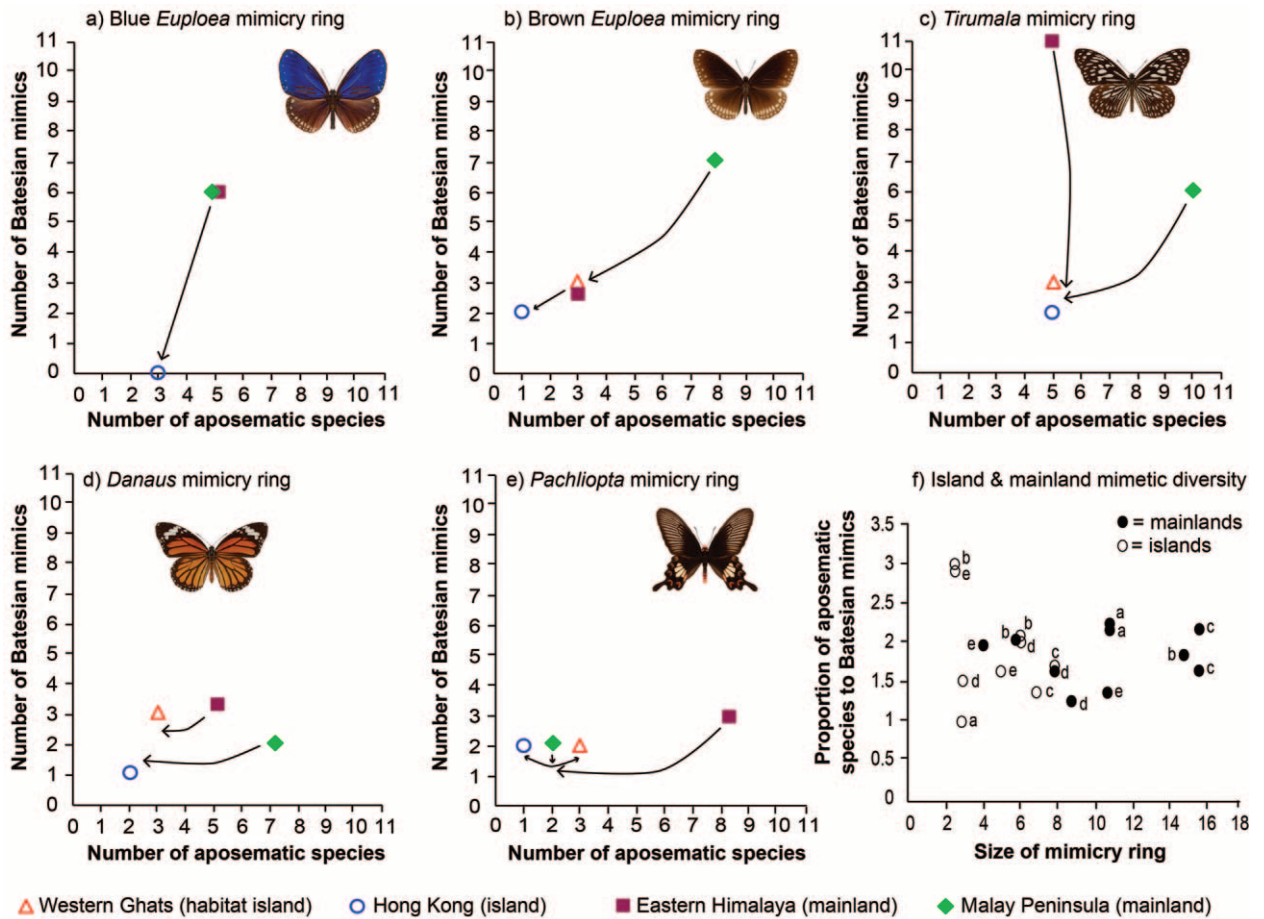
Figure 4: Species diversity and mimetic composition among butterfly mimicry rings in Asian habitat islands (the Western Ghats and Hong Kong; empty symbols) and mainlands (Eastern Himalaya and Malay Peninsula; filled symbols). Overlapping points have been slightly displaced for clarity. Means and standard deviations calculated from all sympatric mimicry rings are shown for each region.

ancestry, stabilizing selection, and/or phylogenetic inertia should not only be expected to be present but in fact to be common and widespread across phylogenetic lineages in all mimicry rings. Although the Western Ghats mimicry rings show support for this pattern, it should be noted that our inference is based on complete sampling of mimicry rings in the Western Ghats but not complete sampling of all the global species in each Müllerian mimetic clade. It is possible that some more cases of small-scale convergence may still be detected within the Müllerian components when all the sister species in these clades are analyzed. This may happen, for example, when some closely related species converge back to a particular mimicry ring after their immediate ancestors had diverged to join a different mimicry ring. Such fine phylogenetic patterns, however, would not affect our overall results

since such small-scale convergent Müllerian mimicry will still show a strong signature of being phylogenetically clustered in the community ecological sense.

Phylogenetically more diverse mimicry rings in South America could have resulted from two additional possibilities that have not been adequately studied or considered: (*a*) selection for Müllerian mimicry is relatively stronger in South America due to a much greater number of mimicry rings, diverse aposematic species, and/or more discriminating predators, all of which may lead to selection for convergence and greater similarity among Müllerian mimics; and (*b*) mimicry rings in South America have evolved under persistent selection pressure over much more prolonged periods of time in which such an extent of convergence was possible.

Figure 5: Comparison of species diversity and mimetic composition among mimicry rings that are shared between Asian habitat islands (empty symbols) and mainlands (filled symbols) reveals that the same mimicry rings in habitat islands are relatively depauperate.

There are interesting parallels and contrasts with other mimetic communities with respect to our findings. Müllerian mimicry rings of the Andean butterflies show strong effects of elevational filtering and weak but significant phylogenetic clustering, suggesting that these mimetic communities are likely to be shaped by mutualistic interactions (Elias et al. 2008; Chazot et al. 2014). On the other hand, color patterns among the Müllerian mimicry rings of South American catfishes are the products of convergent evolution from very distinct clades. Catfishes in each mimicry ring have distinct morphological traits related to resource acquisition; therefore, both Müllerian mimetic convergence and phylogenetic conservatism of resource-acquisition-related morphology appear to determine structure in this community (Alexandrou et al. 2011). Among North American ant assemblages, Müllerian mimicry evolved independently multiple times rather than being a result of common ancestry (Wilson et al. 2012). However, these studies usually did not explicitly test the relative incidence of Müllerian mim-

icry due to convergence versus due to diversification within monophyletic clades and phylogenetic niche conservatism with respect to aposematic phenotype. Moreover, there is an important difference between these previous studies and our study that limits direct comparison of patterns of community assembly: we have assessed mimicry ring assembly involving three diverse butterfly families and the entire mimetic community (Müllerian as well as Batesian components) in a given area, whereas previous studies had largely been restricted to mimicry rings that narrowly focused on Müllerian components from smaller subfamilies and genera. Community phylogenetic studies involving entire and large mimicry rings in Southeast Asia and South America will be helpful in making more meaningful comparisons in the future.

Batesian mimics are, of course, expected to be largely a result of convergent evolution stemming from the stochastic process of mutation and selection. This process leads to the resemblance of wing patterns between Batesian mimics and distantly related aposematic species. This expectation is

satisfactorily met in the mimicry rings of the Western Ghats, where Batesian mimics were invariably from different clades compared to the aposematic species. This pattern was not affected by the type of mimicry shown by different species: monomorphic, female-limited, and polymorphic mimics all showed a similar tendency to converge on aposematic species in all the mimicry rings (fig. 3). However, there was a somewhat unexpected pattern: sister species/groups in the Batesian components of the Western Ghats mimicry rings usually did not participate in the same mimicry ring. This leads to another interesting phylogenetic and evolutionary possibility. While coming from a highly divergent phylogenetic background, Batesian mimics display a surprising level of convergent evolution toward the wing patterns of aposematic species. However, following speciation events within their clades, sister or otherwise closely related Batesian mimics then undergo further divergent evolution to participate in very different mimicry rings that have little overlap in their wing color patterns. The closely related species *Hypolimnas bolina* and *Hypolimnas misippus* are excellent examples of this type of divergent evolution within Batesian mimetic clades, where *H. bolina* mimics largely brown/black aposematic *Euploea* species and *H. misippus* mimics largely tawny, black-and-white aposematic *Danaus* species (figs. 1, 3, B1). Evolution of highly divergent mimetic wing patterns within the Batesian mimetic *Papilio* butterflies is another fascinating example. Here, the complexity of divergence is compounded by female-limited mimetic polymorphism within *Papilio polytes* and in *Papilio clytia*, in which different forms within each sex mimic wing patterns of very different aposematic species (figs. 1, 3, B1). It is conceivable that such divergent wing pattern evolution in closely related Batesian mimetic species that participate in different mimicry rings is fueled by frequency-dependent selection on Batesian mimicry, which may reduce competition in Batesian mimicry space (Sheppard 1959; Barrett 1976; Mallet and Joron 1999; Kunte 2009). This highlights underappreciated differences in selection and the level of divergence expected between Müllerian and Batesian mimicry systems. In Müllerian mimicry, sister species should be expected to be under strong selection for phylogenetic niche conservatism in terms of mimetic traits because the advantage of Müllerian mimicry is density dependent (Müller 1879; Ruxton et al. 2004). That is, Müllerian mimics will be better protected as mimicry rings get saturated with more Müllerian mimics (in terms of both species and the number of individuals), perhaps reinforcing speciation without wing pattern divergence. In contrast, Batesian mimics lose the mimetic advantage beyond a certain threshold because the advantage of Batesian mimicry is frequency dependent. Beyond this threshold mimic frequency, Batesian mimetic clades may thrive only if their members further diverge from existing mimetic patterns into novel mimetic space—that is, in new mimicry rings—to avoid competition (Sheppard 1959, 1962;

Kunte 2009). Thus, selection for the evolution of divergent mimetic traits is expected to become more acute as Batesian mimics increase in frequency, mimicry rings get saturated with Batesian mimics, and mimetic clades diversify. The remarkably polymorphic *P. polytes* and *P. clytia* in the Western Ghats and *Papilio memnon* and *Papilio dardanus* in Southeast Asia and Africa may be representing this stage in cladistic proliferation and strong selection for continued Batesian mimetic divergence in mimicry rings.

The community phylogenetic analyses presented above show that both mutualistic (i.e., Müllerian) and parasitic (i.e., Batesian) interactions have shaped the evolutionary assembly of mimetic communities in the Western Ghats. However, the mutualistic interactions were largely facilitated by phylogenetic inertia, whereas the parasitic interactions were strictly facilitated by convergent evolution. This is in contrast to other highly mutualistic communities such as plants-pollinators and plants-frugivores, where the interacting classes of partners (plants and animals) are inherently different and phylogenetically very distantly related. This has prompted the extensive use of network analysis to study these communities. Recently, the strength of community phylogenetic framework has been emphasized to infer community structure in both these classes of mutualistic partners, which may exhibit phylogenetic inertia in one or both classes (Sargent and Ackerly 2008; Cavender-Bares et al. 2009). However, there are mixed signatures of phylogenetic inertia in such mutualistic interactions. In some plant-pollinator communities, plants were phylogenetically clustered, whereas pollinators were unrelated within their class of partners (Fontaine and Thébault 2015). In other communities, both plant and pollinator classes had low phylogenetic relatedness within their class of partners (Rafferty and Ives 2013). In light of these mixed phylogenetic signals in the classic mutualistic interactions between plants and animals, Müllerian mimicry may prove to be a special case. Here, community assembly may be significantly influenced by phylogenetic inertia—driven by positive density-dependent selection on Müllerian mimicry—in the context of mutualistic interactions.

Biogeographic Isolation, Trickling Colonization, and Depauperate Mimicry Rings in the Western Ghats

Although the Western Ghats are part of mainland India and Asia, they have been considered a habitat island for many groups of organisms that inhabit wet evergreen forests. This is because the dry plains and hills of central India have posed a dispersal barrier between the evergreen forests in the Himalaya and the Western Ghats (Karanth 2003). As a result, the Western Ghats have acted as a habitat island refuge and an important cradle of diversification for ancient lineages such as amphibians and centipedes

(Biju and Bossuyt 2003; Joshi and Karanth 2013). The butterfly fauna of the Western Ghats, on the other hand, is highly derived with no endemic radiations, most of its members having originated in clades that are very diverse in Indo-China, southeastern Asia, and the Palaearctic region (Kunte 2013). It is also relatively species poor, with a smaller percentage of endemics compared to, for example, amphibians and odonates (Gunawardene et al. 2007). The butterfly fauna of the Western Ghats has thus apparently been assembled through trickling colonization, followed by occasional speciation events especially in the evergreen forests (Kunte 2013). The same process may have led to the evolutionary assembly of butterfly mimicry rings in the Western Ghats and other habitat/oceanic islands such as Hong Kong. As expected from their long periods of isolation and other island biogeographic constraints on colonization, establishment, and diversification (MacArthur and Wilson 1967), we demonstrated that the Western Ghats support fewer mimicry rings and a smaller number of Batesian mimics and aposematic species. It is likely that the Western Ghats provided a much smaller window of time and lower ecological stability in terms of selection pressures and available gamma diversity (regional species pool) from which members of local mimicry rings could be drawn. This could explain the largely monophyletic origins of the Müllerian mimics in each mimicry ring. This could also explain why, when mimicry rings are shared between mainlands and islands, those in islands tend to have fewer aposematic species and/or mimics: the apparently random loss of aposematic species and mimics in the Western Ghats could be a result of island biogeographic stochasticity in colonization and establishment. Beyond these neutral or nearly neutral processes, it remains to be seen whether and to what extent this community assembly and diversity has been influenced by more specific selection pressures such as toxicity and chemical defenses of the aposematic species, density- and frequency-dependent selection on mimicry, and diversity and phenology of predators in the Western Ghats. Perhaps over a sufficiently long evolutionary time, the Western Ghats may accumulate a greater number of mimicry rings as well as polyphyletic mimicry rings that span deeper phylogenetic divergences, similar to the South American mimicry rings.

In this study, we focused exclusively on phylogenetic methods to probe evolutionary assembly of mimicry rings. However, community assembly and persistence are determined by multiple factors such as demographics of individual species, dispersal abilities, and strengths of selection on species-level interactions. Inclusion of several of these factors in a single study system may be much more promising, although this has not been attempted so far. Such a study may go a long way in utilizing the strength of mimicry rings as a model system in community ecological studies.

APPENDIX A

Supplementary Table

Table A1: Species included in the phylogenetic analysis along with their GenBank accession numbers

	COI-tRNAleu-II	*EF1*	*Wingless*
Outgroup:			
Tineidae:			
Scardia boletella	GU828467	. . .	. . .
Castniidae:			
Paysandisia archon	GU828412	. . .	. . .

	COI-tRNAleu-II	EF1	Wingless
Copromorphidae:			
Carposina smaragdias	GU929775	…	…
Cossidae:			
Cossus cossus	GU828403	…	…
Drepanidae:			
Thyatira batis	GU828380	…	…
Elachistidae:			
Depressaria depressana	EU141359	…	…
Geometridae:			
Geometra papilionaria	GU828457	…	…
Ingroup:			
Nymphalidae: Heliconiinae:			
Acraea terpsicore	KX467789	KX467818	KX467845
Acraea issoria	GQ376195	EU275636	EU275426
Altinote negra	EU275573	EU275708	EU275501
Bematistes vestalis	EU275570	EU275718	EU275511
Pardopsis punctatissima	EU275571	EU275719	EU275512
Argynnis c. castetsi	KX467816	KX467844	KX467871
Argynnis c. hybrida	KX467815	KX467843	KX467870
Argynnis h. hyperbius	KX467790	KX467819	KX467846
Argynnis paphia	AY090200	AY090166	AY090133
Boloria selene	HQ161222	HQ161294	HQ161167
Euptoieta hegesia	DQ922865	DQ922897	DQ922833
Cethosia mahratta	KX467817	…	KX467872
Cethosia cyane	DQ922870	DQ922902	DQ922838
Cethosia myrina	EU275514	EU275621	EU275410
Agraulis vanillae	AY748102	…	…
Heliconius hecale	AY090202	AY090168	AY090135
Nymphalidae: Danainae:			
Danaus c. chrysippus	KX467794	KX467822	KX467849
Danaus chrysippus	GU365907	AY296142	…
Danaus g. genutia	KX467807	KX467835	KX467862
Danaus plexippus	DQ018954	DQ018921	DQ018891
Euploea c. core	KX467795	KX467823	KX467850
Euploea klugii kollari	KX467808	KX467836	KX467863
Euploea sylvester coreta	KX467793	KX467821	KX467848
Euploea eunice	GU365910	GU365939	GU365958
Idea malabarica	KX467805	KX467833	KX467860
Idea stolli	GU365915	GU365944	GU365963
Parantica a. aglea	KX467802	KX467830	KX467857
Parantica nilgiriensis	KX467814	KX467842	KX467869
Parantica agleoides	GU356920	GU365929	AF246603
Parantica aspasia	GQ864799	GQ864893	GQ864487
Tirumala limniace exoticus	KX467797	KX467825	KX467852
Tirumala septentrionis dravidarum	KX467806	KX467834	KX467861
Tirumala septentrionis	GU365923	GU365937	GU365957
Amauris ellioti	AY218234	AY218523	AY218272
Ideopsis gaura	GU365916	GU365925	AF246592
Miriamica sp.	GU365919	GU365928	GU365950
Tellervo zoilus	GQ864812	GQ864906	GQ864499
Melinaea menophilus	DQ069240	DQ073032	AF014146
Ithomia drymo	DQ069238	DQ073030	DQ073014
Nymphalidae: Satyrinae:			
Elymnias caudata	KX467839	KX467866	KX467839

	COI-tRNAleu-II	EF1	Wingless
Elymnias casiphone	DQ338760	DQ338900	DQ338627
Melanitis leda	AY090207	AY090173	AY090140
Ypthima baldus	DQ338875	DQ339033	DQ338742
Amathusia phidippus	DQ018956	DQ018923	DQ018894
Nymphalidae: Nymphalinae:			
Hypolimnas bolina jacintha	KX467829	KX467856	KX467829
Hypolimnas misippus	KX467840	KX467867	KX467840
Precis tugela	AY788671	AY788809	AY788569
Junonia oenone	AY788646	AY788765	AY788525
Nymphalidae: Libytheinae:			
Libythea celtis	AY090198	AY090164	AY090131
Nymphalidae: Limenitidinae:			
Limenitis reducta	AY090217	AY090183	AY090150
Papilionidae: Papilioninae:			
Pachliopta a. aristolochiae	KX467791	KX467820	KX467847
Pachliopta hector	KX467810	KX467838	KX467865
Pachliopta pandiyana	KX467803	KX467831	KX467858
Troides minos	KX467799	KX467827	KX467854
Atrophaneura alcinous	AF170876	AF173416	. . .
Troides helena	AF170878	AF173418	. . .
Euryades corethrus	AY804356/AY804392	AY804428	. . .
Ornithoptera euphorion	AY919291	. . .	. . .
Parides aeneas	AY804357/AY804393	AY804429	. . .
Battus belus	AY804350/AY804386	AY804422	. . .
Cressida cressida	AY919289	GQ268399	. . .
Pharmacophagus antenor	AY919288	AY919293	GQ268410
Papilio dravidarum	KX467792	. . .	. . .
Papilio c. clytia	KX467789	KX467818	KX467845
Papilio polytes romulus	KX467804	KX467832	KX467859
Teinopalpus imperialis	GQ268351/GQ268358	GQ268393	. . .
Meandrusa sciron	GQ268352/GQ268359	GQ268394	GQ268400
Graphium agamemnon	AF170874	AF173414	. . .
Papilionidae: Baroninae:			
Baronia brevicornis	AF170866	AF173406	AY569044
Papilionidae: Parnassiinae:			
Parnassius phoebus	JN204959	JN204976	JN204917
Allancastria caucasica	DQ351042	DQ351122	DQ351149
Bhutanitis thaidiana	DQ351037	DQ351117	DQ351141
Luehdorfia taibai	DQ351034	DQ351114	. . .
Pieridae: Pierinae:			
Pareronia c. ceylanica	KX467800	KX467828	KX467855
Pareronia hippia	KX467796	KX467824	KX467851
Prioneris sita	KX467809	KX467837	KX467864
Cepora perimale	DQ082757	AY870524	DQ082804
Leuciacria acuta	DQ082762	AY870592	DQ082810
Nepheronia thalassina	HQ689641	. . .	. . .
Belenois java	AY954587	AY870593	AY954617
Delias eucharis	KX467798	KX467826	KX467853

Note: Species sequenced for this study are indicated in boldface.

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Left, Euploea sylvester is a common Batesian model in the Western Ghats. *Center, Danaus genutia* is a widespread aposematic species that acts as a Batesian model in the Western Ghats. *Right, Prioneris sita* is an uncommon Batesian mimic in the Western Ghats butterfly mimicry rings. Photo credit: Krushnamegh Kunte.