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Received: 5 September 2022 | Revised: 16 January 2023 | Accepted: 13 February 2023

DOI: 10.1111/ele.14198

LETTER

ECOLOGY LETTERS WILEY

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Funding information
Agence Nationale de la Recherche, Grant/Award Number: CLEARWING (ANR-16-CE02-0012); ATIP; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: CNPq 304291/2020-0; Darwin Initiative; FLMHN Museum Associates; French Ministry of Research (MENSR), Grant/Award Number: PhD Grant in Doctoral School 227; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2012/50260-6, 2013/50297-0 and 2021/03868-8; Human Frontier Science Program, Grant/Award Number: RGP0014/2016; INABIO & Ecuadorian Ministerio del Ambiente; Leverhulme Trust; National Geographic Society, Grant/Award Number: 5751-96; NSF, Grant/Award Number: 0103746, 0639977, 0639861, 0847582 and 1256742; RedeLep-SISBIOTA-Brasil, Grant/Award Number: CNPq 563332/2010-7

Editor: José María Gomez

Abstract

Understanding the mechanisms underlying species distributions and coexistence is both a priority and a challenge for biodiversity hotspots such as the Neotropics. Here, we highlight that Müllerian mimicry, where defended prey species display similar warning signals, is key to the maintenance of biodiversity in the c. 400 species of the Neotropical butterfly tribe Ithomiini (Nymphalidae: Danainae). We show that mimicry drives large-scale spatial association among phenotypically similar species, providing new empirical evidence for the validity of Müller's model at a macroecological scale. Additionally, we show that mimetic interactions drive the evolutionary convergence of species climatic niche, thereby strengthening the co-occurrence of co-mimetic species. This study provides new insights into the importance of mutualistic interactions in shaping both niche evolution and species assemblages at large spatial scales. Critically, in the context of climate change, our results highlight the vulnerability to extinction cascades of such adaptively assembled communities tied by positive interactions.

KEYWORDS
biodiversity hotspot, climatic niche, community composition, evolutionary convergence, extinction cascade, Müllerian mimicry, mutualistic interactions, Neotropical butterflies, spatial co-occurrence, species assemblages

INTRODUCTION

Traditionally, community and evolutionary ecology have focused on the interplay between antagonistic interactions (i.e. competition, predation) and common ancestry, and how this interplay drives both the assembly of communities and species niche evolution (Brown & Maurer, 1989; Kraft et al., 2007; Pianka, 1981; Webb

et al., 2002). However, more recently, many studies have extended this vision by documenting the importance of positive interactions in determining species coexistence and the stability of communities (Alexandrou et al., 2011; Elias et al., 2009; Hale et al., 2020; Mougi & Kondoh, 2012; Okuyama & Holland, 2008; Thébault & Fontaine, 2010), the co-evolution of functional traits (Guimarães et al., 2011, 2017; Newman et al., 2014; Nuismer et al., 2013; O'Brien et al., 2021), the support of ecosystem functions such as pollination or seed dispersal (Millennium Ecosystem Assessment, 2005) and the origins and maintenance of biodiversity (Bascompte & Jordano, 2007; Bastolla et al., 2009; Gross, 2008; Pascual-García & Bastolla, 2017).

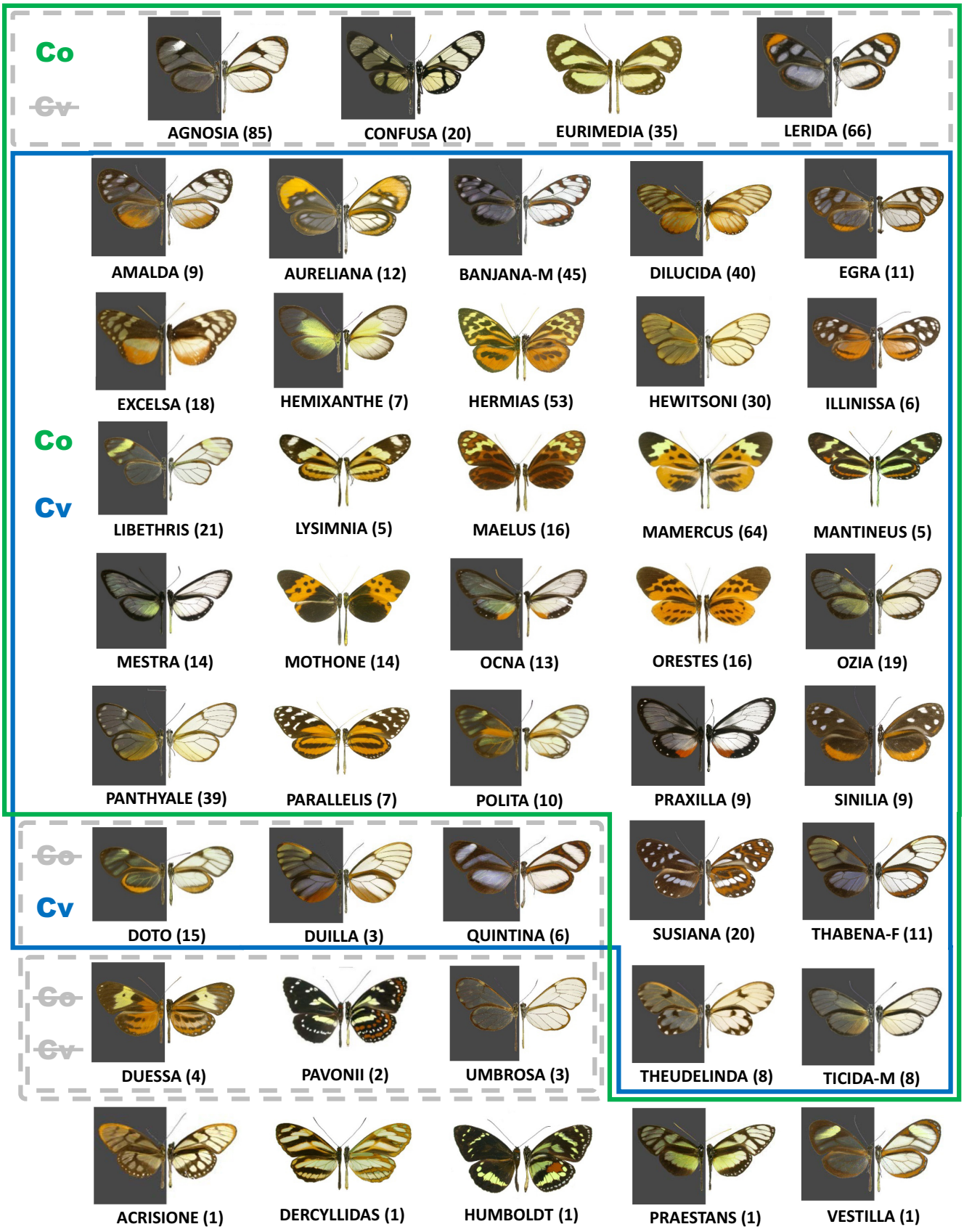
Positive and negative interactions are expected to have opposite consequences on the evolution of species traits and on the assembly of communities. Competitive interactions may drive character displacement (e.g. divergence in traits involved in resource use) and local competitive exclusion, leading to a decrease in ecological niche similarity among species within communities (Brown & Wilson, 1956; Dayan & Simberloff, 2005; Webb et al., 2002). By contrast, positive interactions are predicted to drive the convergence of traits that enhance the local co-occurrence of interacting species, leading to an increase in ecological niche similarity within communities (Aubier & Elias, 2020; Bruno et al., 2003; Elias et al., 2009; Nuismer et al., 2013; Thompson, 2005). However, the consequences of this interplay on community composition at large spatial scales and on the evolution of species climatic niche, which drive species distributions at such scales, remain poorly explored, outside of plant facilitation (Brooker et al., 2008; Valiente-Banuet & Verdú, 2007).

Species within ecological guilds are linked by the use of a common resource (e.g. trophic resources or micro-habitat space), thereby interacting negatively through exploitative competition. Yet, many species also engage in positive interactions (Crowley & Cox, 2011). For instance, birds commonly form multispecies flocks, which increases foraging efficiency (Wiley, 1971) and reduces predation risk (Beauchamp, 2004). Mixed-species groups of mammals often cooperate through beneficial joint hunting or shared vigilance (Stensland et al., 2003). Beyond ubiquitous facilitative interactions (Brooker et al., 2008), co-occurring plants can also benefit from jointly attracting shared pollinators (Moeller, 2004), driving convergence in flowering phenology (Sakai, 2002) as well as in their chemical and visual floral traits acting as cues for pollinators (Kantsa et al., 2017; Thomson & Wilson, 2008). Because intraguild systems may be simultaneously subject to the effects of both mutualistic interactions and competition, they appear particularly suited to investigate the outcome of positive and negative interactions in shaping community composition and species niche evolution.

Müllerian mimicry is an emblematic case of intraguild mutualism, where non-profitable prey species have evolved similar warning colour patterns (i.e. aposematic patterns) under positive frequency-dependent selection imposed by predators, which learn more efficiently to recognize and avoid patterns that are more common (Müller, 1879; Sherratt, 2008). Resulting sets of co-mimetic species, which share the same warning pattern, are called mimicry rings (Joron & Mallet, 1998; Mallet & Gilbert, 1995; Papageorgis, 1975; Weismann, 1904). As such, identifying sets of species locally engaged in mutualistic interactions (i.e. co-mimics) is relatively straightforward. Those species may often compete for resources (e.g. micro-habitat space or trophic resources), despite interacting mutualistically by sharing the cost of educating their naïve predators. Thus, Müllerian mimicry offers an excellent case study to explore the interplay between positive and negative interactions on natural communities. While Müllerian mimicry (hereafter, mimicry) has been observed independently in numerous taxa around the world, such as Hymenoptera (Williams, 2007; Wilson et al., 2015), Coleoptera (Motyka et al., 2021; Muñoz-Ramírez et al., 2016), frogs (Symula et al., 2001), fishes (Alexandrou et al., 2011), snakes (Sanders et al., 2006) and even birds (Dumbacher & Fleischer, 2001), it was historically described and formalized in the nineteenth century by Fritz Müller based on observations of Neotropical ithomiine and danaine butterflies (Müller, 1879).

The butterflies of the Neotropical tribe Ithomiini Godman & Salvin, 1879 (Nymphalidae: Danainae), commonly called clearwing butterflies because of the transparent wing areas seen in most species (McClure et al., 2019; Papageorgis, 1975; Figure 1), represent the most diverse radiation of mimetic butterflies, with 396 species documented to date. All species are engaged in Müllerian mimicry (Beccaloni, 1997a; Brown Jr. & Benson, 1974; Chazot et al., 2019), but at the same time may compete for various kinds of resources. Ithomiine larvae

FIGURE 1 Mimicry ring classification for Ithomiini butterflies. Wing patterns are classified into 44 groups defined as mimicry rings. Dorsal view is shown on the left side against a dark background to highlight transparency when present. Ventral view is shown on the right side. The number of species in each mimicry ring is provided in parenthesis aside the name of each ring. 'Co' symbolizes the presence (in green) or absence (strikethrough in grey) of a significant pattern of species spatial congruence within each mimicry ring. The green solid line frames all mimicry rings with significant species spatial congruence. 'Cv' symbolizes the presence (in blue) or absence (strikethrough in grey) of a lower variance in species climatic niche within each mimicry ring than expected from the phylogeny. When significant, this suggests an adaptive convergence of species climatic niche within the mimicry ring. The blue solid line frames all mimicry rings with significant signal for climatic niche convergence. The grey dashed lines frame all mimicry rings without significant signal for either spatial congruence or niche convergence, or both (double frame). Mimicry rings for which the tests could not be performed because they encompass only one ithomiine species each are displayed on the last line, without associated 'Co' and 'Cv' symbols associated. Photo credits: K. Willmott. Adapted from Doré et al. (2022).



are almost all confined to the plant family Solanaceae, in some cases sharing the same host plant species, which are often understory herbs or vines with limited foliage (Beccaloni et al., 2008; Drummond III & Brown Jr, 1987; Willmott & Mallet, 2004). Furthermore, adult males of most species may compete for access to composite flowers

(Asteraceae) and wilted borages (Boraginaceae) which provide them with the pyrrolizidine alkaloids needed for chemical protection against predators (Brown Jr, 1984; Trigo & Brown Jr, 1990), as well as sex pheromone precursors (Schulz et al., 2004).

Previous works on Ithomiini provided the first evidence that mutualistic interactions can partially outweigh competition and drive ecological convergence along multiple ecological axes that enhance local co-occurrence, such as microhabitat (DeVries et al., 1999; Elias et al., 2008; Gompert et al., 2011; Hill, 2010; Willmott et al., 2017), flight height (Beccaloni, 1997b; Elias et al., 2008) and hostplant preferences (Willmott & Mallet, 2004), and at broader scales across altitudinal gradients (Chazot et al., 2014). However, the extent to which ecological niche convergence driven by positive interactions applies at larger spatial scales remains largely unknown. Notably, the effects of mimicry on the evolution of species climatic niches, which contribute to determining global geographic distribution patterns, is of particular interest in the context of current and future climate changes.

This study aims to examine the impact of intraguild mutualistic interactions on community composition and climatic niche evolution of interacting species at a macroecological scale, using the butterfly tribe Ithomiini as a study system. Specifically, we investigated three questions:

(i) Does mimicry structure Ithomiini community composition by promoting the spatial congruence of phenotypically similar species at the scale of their geographic range?
(ii) Is the climatic niche of species more similar within than between mimicry rings, enhancing the spatial congruence of phenotypically similar species?
(iii) If so, does such similarity of climatic niche among phenotypically similar species arise from shared ancestry or from evolutionary convergence across distinct lineages?

MATERIALS AND METHODS

Data sources

Study system: The tribe Ithomiini

Ithomiini (Nymphalidae: Danainae) represents the most diverse radiation of mimetic butterflies, with 1542 subspecies distributed among 396 species, 42 genera and 10 subtribes (Chazot et al., 2019; see phylogeny in Figure S1). All species are engaged in Müllerian mimetic interactions. Ithomiini often numerically dominate butterfly communities in Neotropical forests from Mexico to northern Argentina (Chazot et al., 2019) and act as mimetic models for other Lepidoptera species (Beccaloni, 1997b; Brown Jr, 1988; Brown Jr. & Benson, 1974; Joron & Mallet, 1998). The classification of wing patterns defined on the basis of pattern similarity follows the most recent update (Doré et al., 2022), and comprises 44 mimicry rings (Figure 1; https://doi.org/10.5281/zenodo.5497876). This phenotypic-based classification outlines 'putative' mimicry rings (e.g. Sanders et al., 2006; Symula et al., 2001) in the sense that it delineates groups of biological entities with patterns assumed to be perceived as similar by predators (e.g. Hoyal Cuthill et al., 2019; Symula et al., 2001; Wilson et al., 2015).

Most Ithomiini species contain several subspecies, which often belong to distinct mimicry rings (Figure S12). In order to study the interplay between Müllerian mimicry and the distribution and climatic niche of ithomiine butterflies, we defined Operational Mimicry Units (OMUs; Doré et al., 2022) as the set of conspecific individuals that share the same mimicry pattern (Figure S2). As such, a mimicry ring typically comprises multiple OMUs representing different species. The 783 currently known OMUs in the Ithomiini tribe were the ecological units used for our analyses (Doré et al., 2022). For the sake of simplicity, we use 'co-mimetic species' and 'phenotypically similar species' in the text to refer to the OMUs sharing the same mimicry pattern.

Estimating community composition

In order to investigate the effect of mimicry on the composition of Ithomiini communities, we retrieved maps of the estimated distribution of all 783 OMUs obtained from species distribution models based on a data set of ca. 29,000 georeferenced occurrences (Doré et al., 2022; https://doi.org/10.5281/zenodo.4696055; https://doi.org/10.5281/zenodo.4673446). These models predicted the distribution of ithomiine butterflies based on the relationship between occurrences and associated climatic variables, forest cover and elevation. They provided scores interpreted as the likelihood of presence of each OMU within each community represented as a quarter-degree grid cell of ca. 30 km × 30 km. This approach allowed us to build a complete list of likelihood of presences of species and associated putative mimicry rings for each of the 21,415 communities (i.e. quarter-degree grid cells) considered within the entire Ithomiini range. We used those scores as predictions of OMUs assemblages in each community. A map of Ithomiini species richness based on those distribution is provided in Figure S3.

Describing the climatic niche of species

For each OMU, we extracted the set of climatic conditions found at its associated georeferenced records

in the occurrence database. We defined the climatic niche of each OMU as the centroid of these occurrence points within the climatic space expressed in four dimensions: mean annual temperature, mean annual specific humidity, temperature seasonality and specific humidity seasonality (Vega et al., 2017; MERRAclim v.2.0, https://doi.org/10.5061/dryad.s2v81, accessed on 04/02/2020). As such, each OMU was associated with a set of climatic data describing its mean climate, or its bioclimatic optimum (e.g. Barnagaud et al., 2012; Hof et al., 2010), strictly reflecting the centroid of its realized niche (Hutchinson, 1957; Soberón & Nakamura, 2009). Despite being a subset of the fundamental niche, measurements of the position of the realized niche in the environmental space based on occurrences can provide relevant insights on the evolution of the species fundamental niche (Gouveia et al., 2014), and are commonly used to investigate climatic niche evolution (Broennimann et al., 2012; e.g., Kozak & Wiens, 2010; Castro-Insua et al., 2018; Rolland et al., 2018).

Data analyses

R scripts to carry out all analyses are available on GitHub at https://github.com/MaelDore/ithomiini_convergence.

Community structure analyses

To examine whether phenotypically similar species co-occur more often than expected at random in communities, we employed a modified version of a community differentiation index: the I_{ST} (Hardy & Senterre, 2007). I_{ST} is analogous to the F_{ST} index used in population genetics. It quantifies differences in species composition across communities by partitioning additively the diversity between its alpha (within communities) and beta (between communities) components. In our framework, we apply I_{ST} to mimicry rings instead of species, using the number of species in each ring as the measure of abundance. As such, I_{ST} represents the mimicry turnover among our predicted communities, and a high

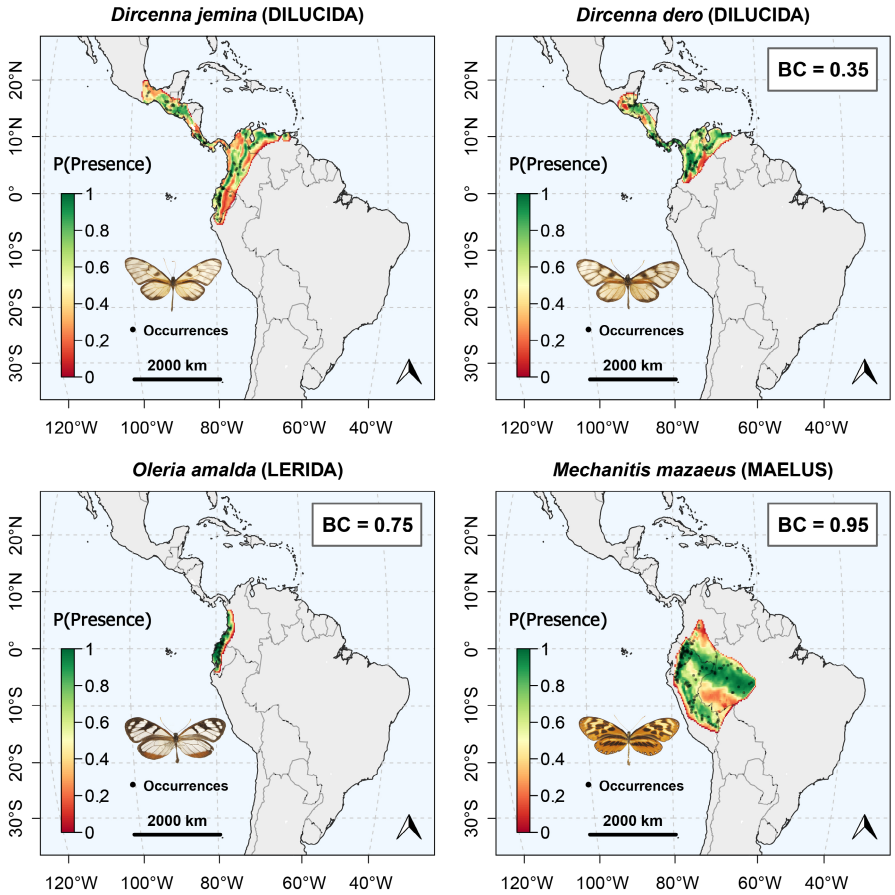


FIGURE 2 Illustration of spatial dissimilarity in distribution range between pairs of species. Spatial dissimilarity is quantified with Bray–Curtis distances (BC) based on the comparison of species likelihood of presence across each grid cell. *Dircenna jemina* within mimicry ring DILUCIDA is used as the reference (upper left). The three other species show an increasing BC distance (decreasing spatial congruence) with the reference. A co-mimetic species, *Dircenna dero* within mimicry ring DILUCIDA (upper right), shows the highest spatial congruence (BC = 0.35). Non-co-mimetic *Oleria amalda* within mimicry ring LERIDA (bottom left) and *Mechanitis mazaeus* within mimicry ring MAELUS (bottom right) display lower spatial congruence with the reference (BC = 0.75 and 0.95 respectively). Maps adapted from Doré et al. (2022). Photo credits: Nicolas Chazot, 2015.

I_{ST} reflects the spatial clustering of co-mimetic species within communities. This index conveniently allows us to quantify mimicry turnover at both global level and between pairs of communities. As such, we tested whether observed I_{ST} was significantly higher than expectations if mimicry patterns were distributed randomly among OMUs (as in Chazot et al., 2014).

We also developed a complementary approach to investigate if the dissimilarity between spatial distributions of species was lower for phenotypically similar species. We computed pairwise Bray–Curtis distances (Bray & Curtis, 1957) across the predicted distributions, obtained from species distribution models, of all pairs of OMUs with the R package *vegan* 2.5-4 (Oksanen et al., 2019; see SI Appendix 6). A high Bray–Curtis value corresponds to a large dissimilarity in species spatial distributions, while a low value relates to an important spatial overlap (Figure 2). We evaluated the significance of the mean value obtained for pairs of phenotypically similar species (i.e. putative co-mimics) by random permutation of mimicry patterns among the OMUs. We carried out this analysis for 39 putative mimicry rings for which the analysis could be performed since they hosted more than one species/OMU (Figure 1: mimicry rings showing significant spatial congruence are associated with a 'Co' symbol in green). In this framework, a significant spatial congruence between similar-looking OMUs provides evidence that this hypothesized 'putative' mimicry ring based on wing pattern similarity likely correspond to an 'effective' mimicry ring reflecting current positive ecological interactions in local communities supported by mimicry (Alexandrou et al., 2011; Sanders et al., 2006; Wilson et al., 2022).

Climatic niche similarity

Spatial congruence between phenotypically similar species may only be partially due to non-climatic dispersal limits (Soberon & Peterson, 2005), but a similar climatic niche would indicate a potential for future increase in the spatial congruence of such species associated with enhanced mutualistic interactions in the context of Müllerian mimicry. Thus, to examine whether mimetic interactions have led to the similarity of realized climatic niches between phenotypically similar species, thereby reinforcing their pattern of spatial congruence, we explored the relationship between mimetic turnover (i.e. pairwise I_{ST}) and climatic distances (i.e. Euclidian distances in a standardized multivariate climatic space formed by our four bioclimatic variables) between pairs of communities. First, we represented mimicry turnover and climatic diversity across all communities by projecting community pairwise distances (i.e. pairwise I_{ST} and Euclidean climatic distances) into three-dimensional RGB colour spaces employing Nonmetric Multidimensional Scaling (NMDS; Figure 3). Second, we tested whether such mimicry turnover between communities correlated with their climatic distances, hinting at an association between mimicry rings and specific climatic niches. We randomly subsampled 1000 communities in order to limit spatial autocorrelation and limit computation time. We applied partial Mantel tests and multiple regressions on distance matrices (MRM; Legendre et al., 1994) between pairwise I_{ST} and climatic distances taking into account a possible confounding effect of geographic distances (as in Chazot et al., 2014; Figure 4a–c). A significant positive correlation/effect means that communities undergoing similar climatic conditions display similar mimicry patterns, and vice versa. We performed these analyses a hundred times to ensure random subsampling of communities had no effect on the results (Tables S2 and S3).

To further investigate the similarity of realized climatic niches of species within each putative mimicry ring, we performed a perMANOVA on species climatic niche optimum observed from occurrences (i.e. mean bioclimatic conditions at centroids), with the climatic space reduced to two dimensions after applying a phylogenetic PCA (pPCA; Revell, 2009) on the four initial climatic variables (Figure 4d). This analysis aimed to detect whether co-mimetic OMUs shared their climatic niche optimum more than expected at random. Small mimicry rings with less than 10 OMUs were discarded because of their small sample size, which limits statistical power. As a result, 23 mimicry rings out of 44 (52.3%) were retained for the analysis, encompassing 619 OMUs among the 719 represented on the phylogeny (86.1%; see Figure S4). We also conducted post hoc pairwise comparisons between pairs of mimicry rings. Finally, complementarily to these analyses of niche dissimilarity based on distances between niche centroids, we explored differences in climatic niche overlap between co-mimetic OMUs (Figure S9, Table S4).

Climatic niche evolution

Spatial congruence and niche similarity within mimicry rings can be caused not only by adaptive convergence (selection favours increased overlap in range, and therefore increased similarity in climatic niche, more than predicted by phylogenetic relatedness), but also phylogenetic inertia (species inherit colour pattern and climatic niche associated with spatial range from their common ancestors). Thus, we further took into account the phylogeny in subsequent phylogenetic comparative analyses. First, we tested for the presence of phylogenetic signal in the evolution of both climatic niche and mimetic patterns (Losos, 2008; see Figure S10, Table S5) on a phylogeny of the Ithomiini tribe (Chazot et al., 2019; Figure S1) that includes 339 species (85.6%) out of the 396 found in the clade. Then, we simulated the stochastic evolution of species mean bioclimatic conditions observed

from occurrences (i.e. climatic niches optimum) under the best fitting neutral macroevolutionary model: a Brownian Motion with an additional Pagel's λ parameter ($\lambda = 0.408$) to account for the intensity of the phylogenetic signal (see Table S6, Figure S11).

Next, we performed a phylogenetic MANOVA to test whether any pattern observed with the perMANOVA was due to shared ancestry or whether it was caused by evolutionary convergence of the niche associated with mimicry. This test compares Wilk's λ statistics of MANOVAs, which quantify the proportion of variance in the climatic niche optimum that is not explained by mimicry rings, obtained from the observed climatic niche optimum extracted from occurrences, with the null distribution of this statistic obtained from simulated climatic niche optimum under the chosen neutral model of macroevolution. The p-value for this test corresponded to the probability of obtaining by chance a lower Wilk's λ statistic than the simulated values in the null distribution. As for the perMANOVA, small mimicry rings with less than 10 OMUs were discarded from the analysis because of their small sample size, which limits statistical power (see Figure S4).

Complementarily, we compared the observed pairwise mean climatic distance (i.e. Euclidean distances between niche centroids) between the niche optimum of co-mimetic OMUs standardized by the overall mean pairwise climatic distance across the entire tribe with the null distribution of that same statistic in our simulations. A lower value than the simulated values in the null distribution would indicate that co-mimetic OMUs display more similar climatic niche optimum than expected under the sole effect of the phylogenetic signal. We conducted this test for all co-mimics, and per putative mimicry ring (see Table S7).

RESULTS

Müllerian mimicry shapes community composition

We tested whether species sharing similar wing patterns (i.e. putative co-mimetic species) present significantly congruent distribution patterns at large spatial scales in two ways. First, we found a significantly high global mimicry turnover, as assessed by I_{ST} based on number of species in mimicry rings (Hardy & Senterre, 2007), compared to values obtained from random permutations of mimetic patterns among OMUs (Figure S5.A; I_{ST} obs = 0.164, mean I_{ST} null = 0.090, CI 95% = 0.103 and $p \leq 0.001$). This result is consistent with a global spatial clustering of phenotypically similar species within communities.

Second, we investigated whether phenotypically similar species tend to have similar spatial distributions, by examining whether the dissimilarity between the spatial distributions of OMUs was lower for co-mimetic OMUs as in Figure 2. Overall, we found that phenotypically similar species exhibited significantly lower mean Bray–Curtis distances (i.e. spatial dissimilarity) than expected at random (Figure S5.B; Mean BC obs = 0.896 across all pairs of co-mimics, mean BC null = 0.950, CI 5% = 0.946 and $p \leq 0.001$). Likewise, when the analysis was repeated for each putative mimicry ring comprising at least two species, 33 mimicry rings out of the 39 for which the analysis could be performed showed a significant pattern of spatial clustering (Figure 1: mimicry rings associated with 'Co' symbol in green). The remaining six non-significant mimicry rings all had low species richness (i.e. $N < 10$, except for DOTO) which constrains the statistical power of the permutation tests. As such, the pattern of large-scale spatial congruence of phenotypically similar species appeared largely ubiquitous in all regions of the Neotropics, and most putative mimicry rings qualify as effective mimicry rings depicting current mutualistic interactions (Table S1).

Mimicry patterns correlate with species climatic niche

Mimicry turnover correlates with climatic distances across communities

To investigate whether species belonging to the same mimicry ring tend to have similar realized climatic niche, thereby enhancing their potential for spatial congruence, we examined whether communities experiencing similar climatic conditions tend to harbour a similar predicted composition in mimicry patterns. The maps of mimicry turnover (Figure 3a) and climate diversity (Figure 3b) tend to show qualitatively similar patterns, with broad regional distinctions between the Atlantic Forest, the Pampas, the Cerrado and Caatinga, the Amazon Basin, the Andes and Central America. Yet, the Andes appear as an important geographic barrier to dispersal, drawing sharp contrasts in term of mimicry composition between the two sides of Cordilleras (Figure 3a), while climate appears relatively similar between sides (Figure 3b). Furthermore, we tested whether mimicry turnover between predicted communities correlated with the climatic distances between these communities (see Tables S2 and S3). In all tests, pairwise I_{ST} (i.e. mimicry turnover between communities) was correlated with the pairwise climatic distance between communities (Figure 4a: MRM: $\beta_{obs} = 0.367$, Q95% = 0.023 and p-value ≤0.001). Although pairwise I_{ST} was also correlated with geographic distance between communities (Figure 4b: MRM: $\beta_{obs} = 0.598$, Q95% = 0.024 and p-value ≤0.001), the correlation between pairwise I_{ST} and pairwise climatic distance between communities persisted even when accounting for spatial distance (Figure 4c, Figure S6.A: MRM: $\beta_{obs} = 0.216$, Q95% = 0.027 and

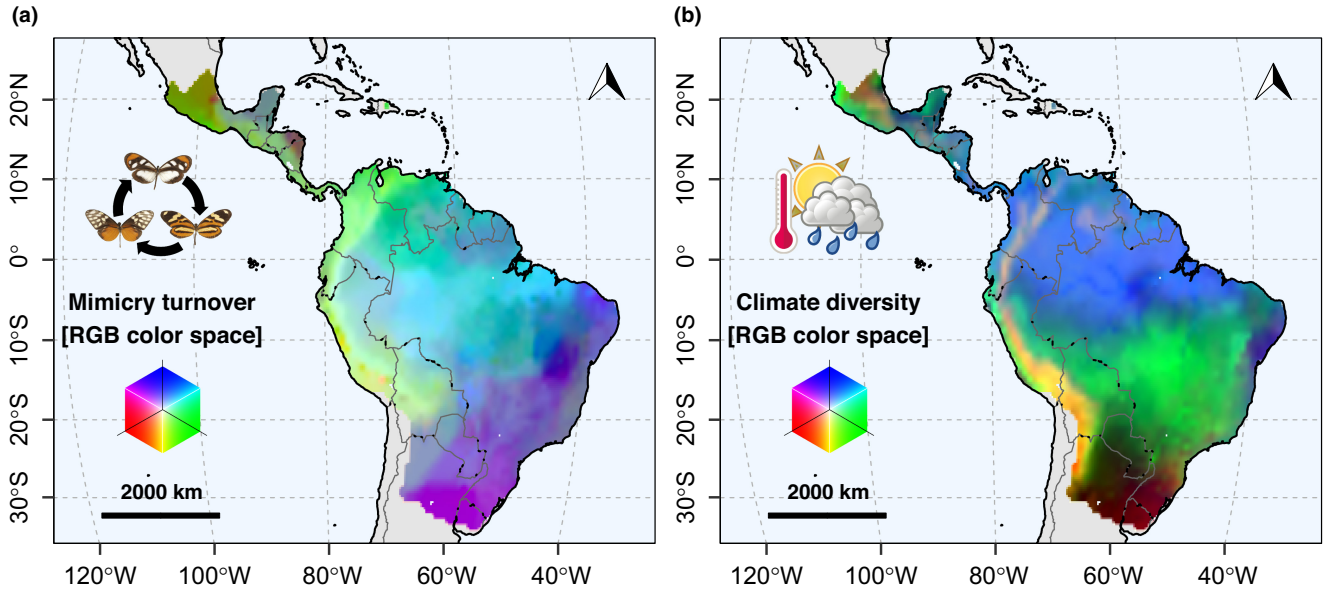


FIGURE 3 Mimicry turnover (a) and climate diversity (b) across communities. Colours represent coordinates in the RGB colour space. They relate to dissimilarity in the predicted mimicry composition (a) or climatic conditions (b) across all communities obtained from NMDS applied on pairwise mimicry turnover (a) and Euclidean climatic distances (b). Colours are not comparable between maps, but they reflect patterns of dissimilarity.

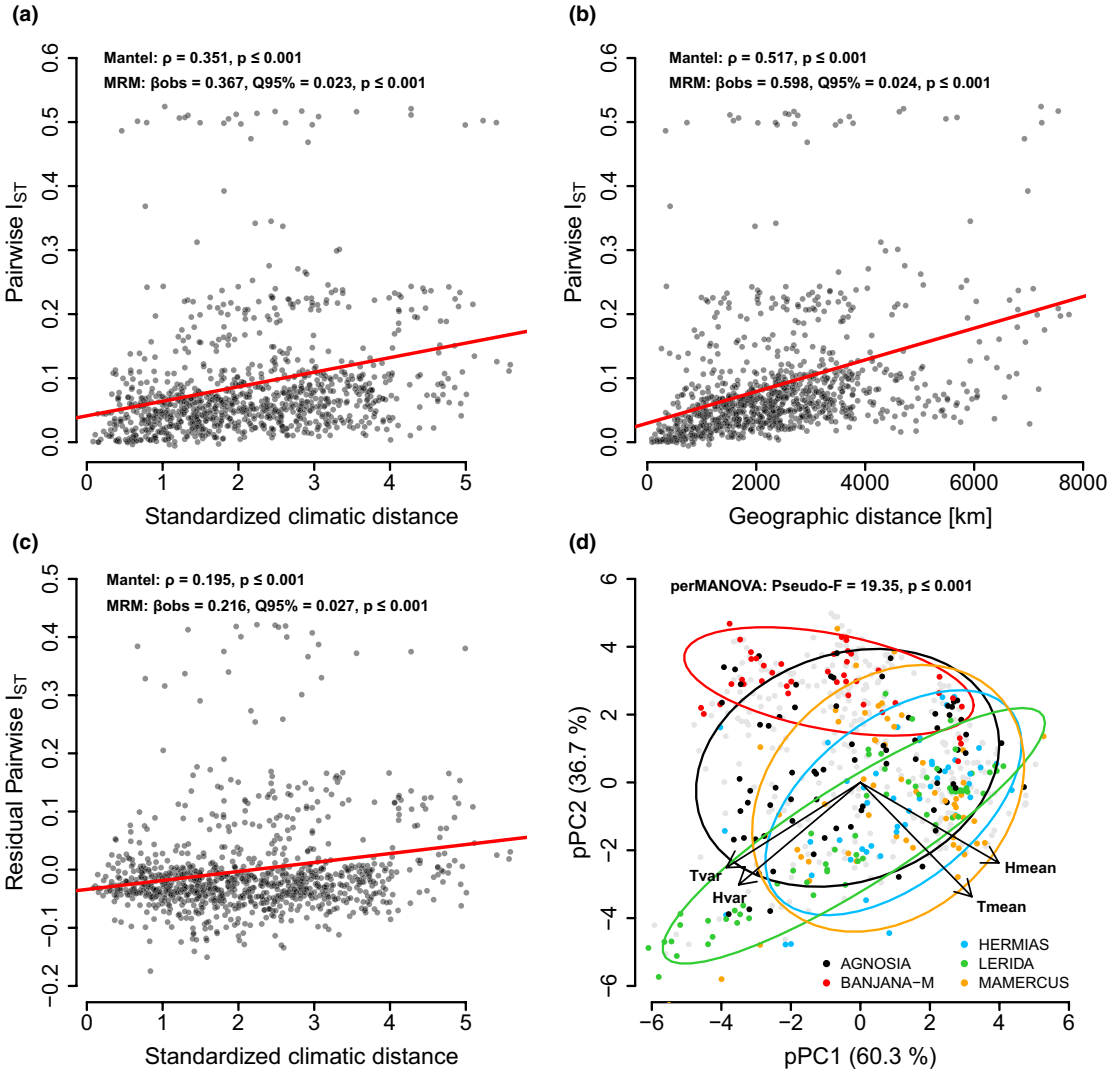


FIGURE 4 Association between climate and mimicry patterns: mimicry turnover explained by climatic and geographic distances across pairs of communities (a–c) relates to the segregation of species climatic niche between mimicry rings (d). Scatter plots display relationship between mimicry turnover and climatic and geographical distances across pairs of communities for a random sample of 1000 distances among the 499,500 distances computed for clarity. ρ = Spearman's rho coefficient for non-parametric correlation associated with p-value from Mantel tests with 999 permutations. βobs = β-coefficient from multiple regression on distance matrices (MRM) with 999 permutations; Q95% = quantile used as threshold for right-tailed significance tests. (a) Mimicry turnover (pairwise I_{ST}) correlates with climatic distances. (b) Mimicry turnover (pairwise I_{ST}) correlates with geographic distances. (c) Mimicry turnover (pairwise I_{ST}) correlates with climatic distances after accounting for the effect of geographic distance. (d) Ordination of species bioclimatic optimum for the five richest mimicry rings in the reduced climatic space resulting from a pPCA (Revell, 2009). AGNOSIA = 74 species (in black); LERIDA = 63 species (in green); MAMERCUS = 56 species (in orange); HERMIAS = 47 species (in blue); BANJANA-M = 43 species (in red). Grey dots represent species belonging to other mimicry rings. Tvar = Temperature seasonality; Hvar = Specific humidity seasonality; Hmean = Mean specific humidity; Tmean = Mean temperature. Ellipses represent normal probability contours (quantile = 0.8) for each mimicry ring.

p-value ≤0.001). All Mantel tests yielded results consistent with MRM (see Tables S2 and S3). Therefore, the significant mimicry turnover across communities was partially explained by differences in local climatic conditions linked to a dissimilarity between the climatic niches of species across mimicry rings.

Species climatic niches are more similar within than between mimicry rings

We tested whether species' realized niches are more similar within than between mimicry rings, regardless of the origin of the similarity/difference (i.e. convergent evolution or shared ancestry). We found a significant association between species climatic niches and their mimicry patterns (Figure 4d; perMANOVA: $R^2 = 0.416$, Pseudo-$F = 19.35$ and $p \leq 0.001$; Figure S6.B). Moreover, perMANOVA post hoc pairwise comparisons of mimicry rings revealed that the vast majority of mimicry ring pairs exhibited significantly different climatic niches (Figure S8: 186 out of 253 pairs [73.5%] with a p-value ≤0.001; 226 [89.3%] with a p-value lower than 0.05). Complementary analyses based on climatic niche overlap rather than niche centroids led to similar results (Figure S9, Table S4).

Müllerian mimicry drives climatic niche convergence

In subsequent analyses, we built upon the phylogeny of the group (Chazot et al., 2019) to disentangle the effects of shared ancestry and evolutionary convergence in niche similarity among co-mimetic species. We found a significant phylogenetic signal in the evolution of mimicry patterns: phenotypically similar species were significantly closer than expected by chance in the phylogeny (MPD obs = 34.43 My, mean MPD null = 37.16 My, CI 5% = 36.73 My, $p \leq 0.001$; see Figure S10.A, Table S5 and Figure S12). In parallel, we observed a weak but significant phylogenetic signal in the evolution of species climatic niche (K_{mult} obs = 0.120, mean K_{mult} null = 0.083, CI 95% = 0.110 and $p = 0.013$; see Figure S10.B). Therefore, the association we revealed between mimicry rings and climatic niche could be at least partly explained by common ancestry (Losos, 2008). However, we found that the association between climatic niche and mimicry patterns was significantly stronger than expected given species evolutionary relationships (Figure S7.A; phylogenetic MANOVA, Wilks' λ obs = 0.271, mean Wilks' λ null = 0.899, CI 5% = 0.844 and $p \leq 0.001$).

To further assess if climatic niches of co-mimetic species are more similar than expected from a process of neutral niche evolution, we computed the standardized mean climatic distance (MCD) among co-mimetic species. The observed value was lower than expected under neutral evolution where climatic niche was allowed to evolve on the phylogeny in any direction of the climatic space (Figure S7.B; MCD obs = 0.782, mean MCD null = 0.984, CI 5% = 0.959 and $p \leq 0.001$), again suggesting an evolutionary association between mimicry and climatic niche that goes beyond the pattern of niche similarity among co-mimetic species. Additionally, 32 out of 39 putative mimicry rings for which the analysis could be performed showed a significant signal for convergence of the climatic niche (Figure 1: mimicry rings associated with 'Cv' symbol in blue; see Table S7 for a detailed statistical summary). No mimicry ring showed a signal of divergence (i.e. MCD higher than expected under neutral climatic niche evolution). Altogether, most mimicry rings (29 out of 44 = 65.9%) exhibited both species spatial congruence and climatic niche convergence all across the Neotropics (Figure 1).

DISCUSSION

In this study, we investigated the impact of positive interactions on the composition of species assemblages and the evolution of species climatic niche in a diverse clade of Neotropical butterflies. We showed that intraguild mutualistic interactions, specifically Müllerian mimicry, drive the large-scale spatial association of interacting species and channel the convergence of species climatic niche across lineages. As such, we showed that the effects of mimicry can outweigh both common ancestry, which promotes similarity among related

species, and potential competition within ecological guilds, which would promote divergence, thereby affecting the global distribution of a highly diverse group at large spatial scales.

From large-scale spatial congruence to fine-scale ecological dimensions

Traditionally, community ecology and biogeography have focused on the interplay between antagonistic interactions such as competition and predation, and common ancestry, to explain community structure and macroecological patterns of biodiversity (Brown & Maurer, 1989; Cardillo, 2011; Pianka, 1981; Webb et al., 2002). Under this paradigm, the importance of positive interactions for shaping large-scale species distribution patterns has remained largely overlooked, despite a growing literature calling attention to their significance for structuring species assemblages and maintaining stability and diversity at the community level (Bastolla et al., 2009; Hale et al., 2020; Pascual-García & Bastolla, 2017). As a case study of the effects of intraguild mutualism, we showed here that phenotypically similar ithomiine species co-occur at large spatial scales more often than expected by chance. This result comforts the idea that similarity of aposematic patterns in ithomiine butterflies largely arose through adaptive convergence induced by Müllerian mimicry. As such, positive interactions, in this case Müllerian mimicry, could outweigh potential effects of competition, notably the geographical overdispersion of phylogenetically close and ecologically similar species (Kunte, 2008; Pianka, 1981; Webb et al., 2002). Co-occurrence among phenotypically similar species of Ithomiini has already been documented at smaller scales, across microhabitats (Beccaloni, 1997b; DeVries et al., 1999; Elias et al., 2008; Hill, 2010; Willmott et al., 2017) and altitudinal gradients (Chazot et al., 2014). Here, we showed that this pattern extends to the entire Ithomiini clade, over its global distribution across the Neotropics, supporting the idea that positive interactions can strongly affect the global spatial distribution patterns of entire diverse groups. Our study provides new empirical evidence at a macroecological scale for the validity of the oldest mathematical model of evolution, namely Müller's prediction of local convergence in warning patterns among toxic aposematic species (Müller, 1879).

Our findings further revealed that mutualistic interactions can lead to the convergence of climatic niches among co-mimetic species, thereby enhancing co-occurrence, and potentially supporting high community diversity (Gross, 2008). In turn, enhanced co-occurrence among phenotypically similar species also potentially increases competition for local resources. Theoretical models showed that while co-mimetic species are expected to use the same trophic resources when these resources are highly segregated across microhabitats, they are instead expected to partition their diet when multiple types of resources are available in their shared microhabitat, thereby lessening the negative effects of competition for resources (Aubier & Elias, 2020). These predictions are partly confirmed in the field, where co-mimetic species sometimes use the same larval host plants, but in other cases do not (Willmott & Mallet, 2004). At these finer scales, mutualistic interactions can therefore still drive convergence, especially in ecological dimensions that favour co-occurrence in the eyes of predators. For example, communities of habitat-specialist predators that select locally for different optimal warning signals can induce the segregation of mimicry rings across microhabitats (Birskis-Barros et al., 2021; Willmott et al., 2017). This fine-scale structuring helps explain the apparent paradox of high local mimicry richness (Joron & Mallet, 1998), with eight or more ithomiine mimicry rings co-occurring in west Amazonian communities (Doré et al., 2022), in the context of Müllerian mimicry predictions of local convergence in colour patterns (Gompert et al., 2011).

Beyond the emblematic case of ithomiine butterflies and Müllerian mimicry, the opposite effects of intraguild positive and negative interactions are found in other biological systems, at multiple spatial scales. For instance, co-mimetic catfish species tend to co-occur at the scale of large river basins, while at local scales diet partitioning, coupled with morphological dissimilarity, appear to be the main factors structuring species assemblages (Alexandrou et al., 2011). Likewise, plants that attract similar pollinators benefit from co-occurrence and facilitative interactions (Moeller, 2004), and may demonstrate convergence for attractive scents and floral morphology (Kantsa et al., 2017; Thomson & Wilson, 2008), while they can also present different mechanisms for pollen deposition (Huang & Shi, 2013) and contrasted phenologies (Armbruster & Herzig, 1984) that limit reproductive interference.

Altogether, the interplay between positive and negative intraguild interactions on community structure and trait evolution may have different outcomes at different spatial scales. At large scales, we found that convergence in climatic niche, strengthening the spatial congruence of the distributions of mutualistic species, seems favoured. At fine scales, the similarity of species' ecological niches may depend on whether the benefits of mutualistic interactions outweigh the effects of competition that otherwise promote niche partitioning.

A scenario for niche convergence in mutualistic communities

Our results hint for an adaptive association between climatic niche and mimicry patterns in Ithomiini species, thereby reinforcing the local co-occurrence of mutualistic species. Indeed, species harbouring the same

mimicry pattern benefit from evolving towards similar climatic niches, since this often results in increased spatial overlap and exposure to the same suite of predators within communities (Sherratt, 2006). However, a pattern of niche similarity within mimicry rings could actually arise from the opposite mechanism: species with a similar climatic niche and living at least partly in sympatry are expected to undergo convergence in their aposematic patterns (Müller, 1879). Both adaptive mechanisms likely act together, as suggested by modelling approaches (Gompert et al., 2011).

A plausible scenario involves an initial partial climatic and spatial overlap of species niches, perhaps guided by the spatial congruence of their respective host plants (Figure 5; Step 1: Initial partial overlap). Thus, in the context of Müllerian mimicry, one may expect those species to converge towards one mimicry pattern, at least in the area of distribution overlap (Figure 5; Step 2: Pattern convergence). Next, the expansion of the range of each species towards areas occupied by co-mimetic species (potentially harbouring different climatic conditions) will be facilitated, since these new areas offer an increased protection against predators, compared to areas where co-mimics are absent (Kapan, 2001; Figure 5; Step 3: Niche expansion). Meanwhile, populations retaining the ancestral pattern, where the co-mimetic partner is absent, experience weaker protection from predators and may sometimes go extinct (Mallet & Barton, 1989; Langham, 2004; Figure 5; Step 4a: Niche thinning). Alternatively, these populations may persist to result in the generation of a polymorphic species with two independent sets of

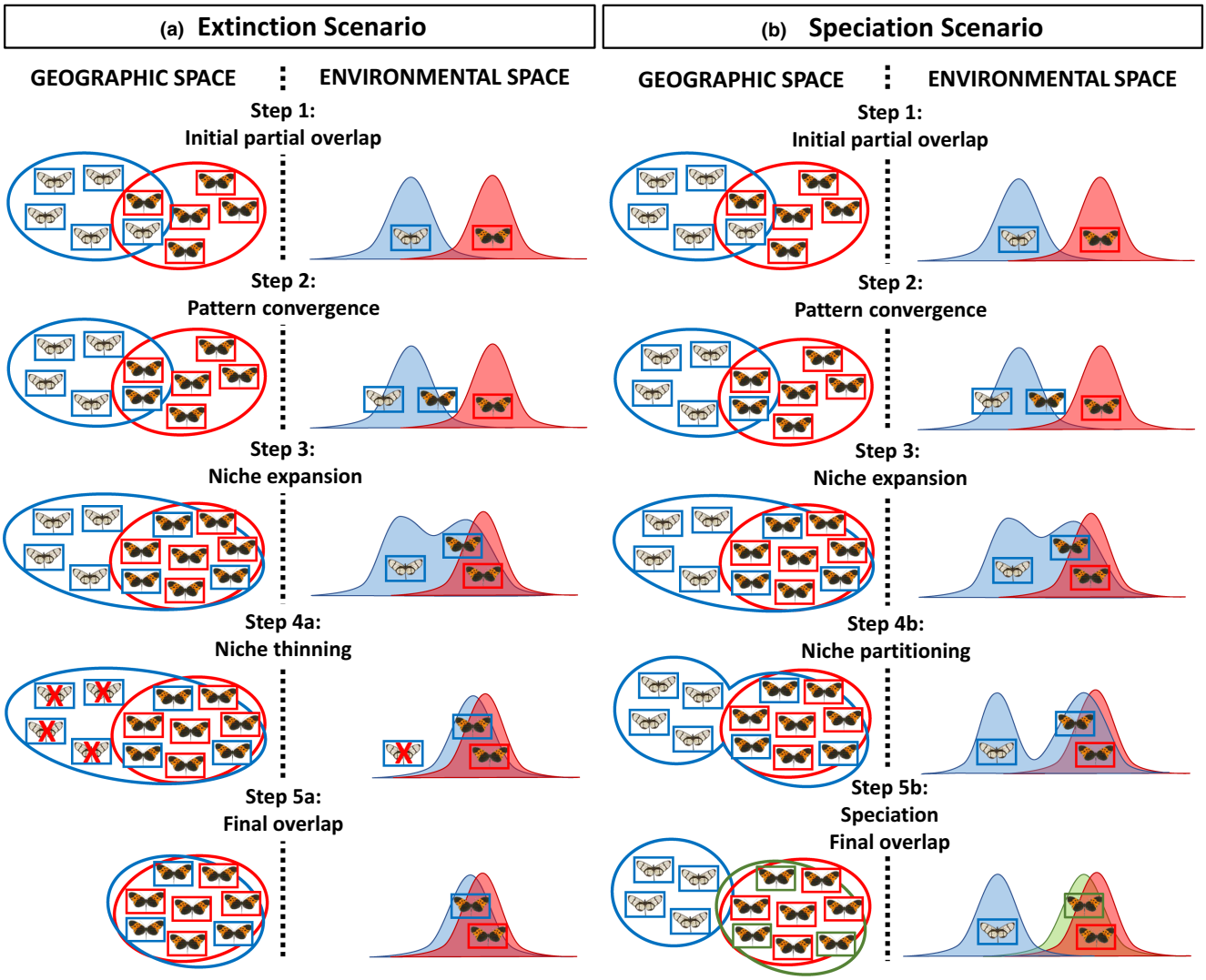


FIGURE 5 Scenarios for niche convergence between co-mimetic species. Five steps to reach spatial and environmental overlap between co-mimetic species leading to the predator-driven adaptive association of environmental niche and mimicry pattern. Scenario A involves the extinction of non-mimetic populations and the convergence of two monomorphic species. Scenario B involves the generation of a polymorphic species leading to speciation. Strictly, instead of convergence these scenarios describe the likely more frequent case of advergence (Mallet, 1999) since the lineage in blue, then green, starts with CONFUSA pattern and adverges to MOTHONE pattern, while the species in red starts with MOTHONE pattern and maintains it over time.

mimetic individuals (i.e. Operational Mimicry Units (OMUs) as in Doré et al., 2022; Figure 5; Step 4b: Niche partitioning). This coexistence generates a spatial mosaic of aposematic patterns bordered by suture zones where hybrids are counter-selected by predation from naïve predators (Mallet & Barton, 1989; Sherratt, 2006; Thompson, 2005). Conveniently, this scenario explains the relatively high prevalence of polymorphism in mutualistic systems, with several OMUs per species. In the long run, these OMUs may diverge enough to be considered as separated species (Figure 5; Step 5b: Speciation) and fuel the high diversity typically observed in mutualistic clades (Aubier et al., 2017; Joron & Mallet, 1998; Motyka et al., 2021). Either way, the distributions of the mimetic populations of the species will gradually increase in overlap, leading to the convergence of climatic niches (Figure 5; Step 5a and 5b: Final overlap). Therefore, both mechanisms of colour pattern and niche convergence likely act jointly to generate the adaptive association of species climatic niche and mimicry patterns we detected for ithomiine butterflies.

Consequences for mutualistic systems in the context of global change

The power of mimicry to shape large-scale community composition and drive species climatic niche convergence illustrates the importance of intraguild mutualistic interactions in shaping both the ecology and evolution of interacting species. In the context of global changes, the fate of those mutualistic communities is even more uncertain due to the positive nature of their interactions. Indeed, climate change and habitat loss force species to migrate at unprecedented rates to follow their climatic niches (Boeye et al., 2013; Pearson, 2006). Mutualistic partners may adapt differently, at different rates, or even impede their respective migration rates (Brooker et al., 2007; Svenning et al., 2014). Such effects may quickly lead to community disassembly and the loss of the positive mimetic interactions, especially in tropical mountainous regions (Sheldon et al., 2011; Uehara-Prado & Freitas, 2009), where distribution ranges are often narrow and most Ithomiini diversity is found (Figure S3).

Mutualistic communities are particularly sensitive to community disassembly because of the long-standing history of co-evolution and interdependency between co-occurring species (Toby Kiers et al., 2010). They are more prone to extinction cascades, since the local disappearance of a species can weaken the network of mutualistic interactions supporting their robustness and resilience to perturbations (Dunn et al., 2009; Vidal et al., 2019). Even if climatic niche similarity between interacting partners, such as co-mimetic species, may limit community disassembly to a certain extent by allowing congruent dispersal trajectories in the face of climate change, climatic niche overlap is hardly ever complete (Figure S9, Table S4). Moreover, despite relatively similar climatic niche optima, tolerance to climate change and extremes, as well as species dispersal abilities, may still differ among species, limiting opportunities for co-dispersal trajectories. Finally, the effects of climate change on biotic factors that affect local abundance, such as hostplants (Willmott & Mallet, 2004) and parasitoids (Gentry, 1998) in the case of Ithomiini butterflies, may also differ among interacting species.

Altogether, mutualistic communities form tightly co-evolved assemblages tied by positive interactions, making them particularly vulnerable to global environmental changes (Tylianakis et al., 2008). Our results stress the need to include species interactions, illustrated here by Müllerian mimicry, in the framework of macroecological and global change studies, as well as in species distribution modelling and conservation assessments (Brooker et al., 2007; Staniczenko et al., 2017; Toby Kiers et al., 2010; Tylianakis et al., 2010; Windsor et al., 2023).

AUTHOR CONTRIBUTIONS

Maël Doré and Marianne Elias conceived the study and designed the analyses. Marianne Elias, Keith Willmott and André V. L. Freitas provided occurrence data. Maël Doré carried out the analyses and led the article writing. All authors critically contributed to the article draft and gave final approval for publication.

ACKNOWLEDGEMENTS

We gratefully thank all the researchers, field assistants, technicians and students who were involved in the collection of the occurrence data from which we predicted our community composition. The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest, or non-financial interest in the subject matter or materials discussed in this article. MD is financed by the French Ministry of Research (MESRI). ME acknowledges funding by the ANR grant CLEARWING (ANR-16-CE02-0012), a Human Frontier Science Program grant (RGP0014/2016), a Leverhulme Trust grant and an ATIP grant. KRW thanks S. Nogales, the INABIO and Ecuadorian Ministerio del Ambiente for arranging permits for research in Ecuador, most recently under the project 'Diversity and Biology of Lepidoptera in Ecuador' (No. 006-19 IC-FLO-FAU-DNB/MA), and the Leverhulme Trust, the Darwin Initiative, the FLMNH Museum Associates, the National Geographic Society (Research and Exploration Grant # 5751-96) and NSF (# 0103746, #0639977, #0639861, #0847582 and #1256742). AVLF thanks FAPESP (2012/50260-6, 2013/50297-0 and 2021/03868-8), the Conselho Nacional de Desenvolvimento Científico e Tecnológico Pq-1A grant (CNPq 304291/2020-0), RedeLep-SISBIOTA-Brasil/CNPq (563332/2010-7) and NSF (DEB 1256742).

Brazilian butterfly species are registered under SISGEN (ADF1F75).

FUNDING INFORMATION

Agence Nationale de la Recherche, Grant/Award Number: CLEARWING (ANR-16-CE02-0012); ATIP; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: CNPq 304291/2020-0; Darwin Initiative; FLMHN Museum Associates; French Ministry of Research (MENSR), Grant/Award Number: PhD Grant in Doctoral School 227; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2012/50260-62013/50297-02021/03868-8; Human Frontier Science Program, Grant/Award Number: RGP0014/2016; INABIO & Ecuadorian Ministerio del Ambiente; Leverhulme Trust; National Geographic Society, Grant/Award Number: 5751-96; NSF, Grant/Award Number: 0103746063997706398610847582125674 2; RedeLep-SISBIOTA-Brasil, Grant/Award Number: CNPq 563332/2010-7

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14198.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://doi.org/10.5281/zenodo.7643679.

DATA AVAILABILITY STATEMENT

All R scripts used to conduct the analyses and generate the figures are available on GitHub (https://github.com/MaelDore/ithomiini_convergence) and Zenodo (https://doi.org/10.5281/zenodo.6277769). Occurrences data, maps of the distribution of Operational Mimicry Units (OMUs) and species, and mimicry classification used in this study are available from Zenodo (Occurrences data: https://doi.org/10.5281/zenodo.4696055; Distribution maps: https://doi.org/10.5281/zenodo.4673446; Mimicry classification: https://doi.org/10.5281/zenodo.5497876). All results reported in this article can be reproduced with the scripts and data provided.

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SUPPORTING INFORMATION

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How to cite this article: Doré, M., Willmott, K., Lavergne, S., Chazot, N., Freitas, A.V.L., Fontaine, C. et al. (2023) Mutualistic interactions shape global spatial congruence and climatic niche evolution in Neotropical mimetic butterflies. *Ecology Letters*, 00, 1–16. Available from: https://doi.org/10.1111/ele.14198