Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Müllerian Mimicry in Neotropical Butterflies: One Mimicry Ring to Bring Them All and in the Jungle Bind Them

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Received: 3 March 2025 | **Revised:** 25 August 2025 | **Accepted:** 8 September 2025

Handling Editor: Andres Baselga

Funding: This work was supported by Agence Nationale de la Recherche, CLEARWING (ANR-16-CE02-0012). Human Frontier Science Program, RGP0014/2016. Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, PhD Grant - ED 227.

Keywords: biodiversity hotspots | comparative phylogenetic analyses | heliconiines | ithomiines | Lepidoptera | Müllerian mimicry | Neotropics | niche convergence | spatial co-occurrence

ABSTRACT

Aim: Uncovering the effects of Müllerian mimetic interactions on the evolution of species niches and geographic distributions at a continental scale.

Location: Neotropics and part of Nearctic.

Time Period: 19th century to present, with most data collected within the last 30 years.

Major Taxa Studied: Heliconiini (Heliconiinae) and Ithomiini (Danainae) butterfly tribes.

Methods: We leveraged a dataset of 67,563 geolocalized occurrences from fieldwork observations and museum collections to map broad-scale biodiversity patterns of heliconiine butterflies. We tested for congruences and disparities with known Ithomiini biodiversity patterns, a group from which they diverged 86.5 My ago, yet share numerous warning wing colour patterns. We used phylogenetic comparative analyses to test for both the spatial co-occurrence of species with similar aposematic wing patterns and the convergence of their climatic niche within and between tribes.

Results: Both tribes exhibit wide overlap in biodiversity hotspots across the Neotropics, including a high prevalence of rare species and mimetic patterns in the tropical Andes. Ithomiine species dominate Andean communities, while the Amazon basin hosts a higher relative richness of heliconiines. Phenotypically similar species within and between tribes share climatic niches as a result of selection favouring both co-occurrence of look-alike species and convergence of warning signals within local communities.

Main Conclusions: We documented continental-scale spatial and evolutionary associations among species sharing warning signals both within and between tribes separated by 86.5 My of independent evolutionary history. Our results provide empirical evidence for the pervasive effects of mutualistic interactions on biodiversity patterns. Critically, they also emphasise the vulnerability of mimetic communities, bound together by positive interactions, to disassembly induced by climate change.

1 | Introduction

Biotic interactions are known to structure ecological communities (Bascompte 2009), but their impact on biodiversity patterns remains difficult to quantify, especially in large geographic areas (Gaüzère et al. 2022; Windsor et al. 2023). Biotic interactions include negative interactions such as exploitative competition for resources, positive interactions such as pollination and asymmetrical interactions such as predation. Ecologists also distinguish intraguild interactions occurring between species in the same ecological guild, such as competition for similar resources, from interguild interactions between species in different ecological guilds, such as predators and prey. As such, interactions underlie numerous complex ecological and evolutionary processes and involve virtually all life forms (Bascompte 2009).

Extensive theoretical and empirical evidence supports the role of negative intraguild interactions in driving spatial and phenotypical divergence among competing species (Brown and Wilson 1956; Hardin 1960; Webb et al. 2002; Dayan and Simberloff 2005). By contrast, intraguild mutualistic interactions remain some of the most understudied, yet they can also have important consequences for both trait evolution and the geographic distributions of species involved (Elias et al. 2009). For instance, selection may favour evolutionary convergence in flowering phenology as well as floral traits that allow different plant species to benefit from attracting a similar group of pollinators (Sakai 2002; Moeller 2004; Thomson and Wilson 2008; Kantsa et al. 2017). Furthermore, facilitation shapes the distribution of plants, allowing the co-occurrence of distantly related species, thus enhancing phylogenetic diversity (Valiente-Banuet and Verdú 2007; Carrión et al. 2017). However, the potential effects of intraguild mutualistic interactions at broad scales remain largely overlooked outside of plants and microorganisms (Bruno et al. 2003; Koffel et al. 2021).

In this study, we investigate the consequences of Müllerian mimicry for species niche evolution and community composition at large spatial and phylogenetic scales. Müllerian mimicry occurs between coexisting defended prey species that have evolved similar aposematic patterns advertising their defences to predators (Ruxton et al. 2004; Sherratt 2008). Such intraguild interactions are mutualistic because sets of species with the same warning pattern benefit from sharing the mortality cost of educating naïve predators (Müller 1879). Müllerian mimicry has been described in many organisms, including birds, insects, snakes, fishes and amphibians (Dumbacher and Fleischer 2001; Symula et al. 2001; Williams 2007; Alexandrou et al. 2011; Wilson et al. 2015; Muñoz-Ramírez et al. 2016; Motyka et al. 2021). Numerous independent origins across distantly related taxa reinforce the idea that Müllerian mimicry represents a selective advantage for defended prey (Müller 1879; Mallet and Barton 1989; Sherratt 2008). Unlike many ecological interactions, Müllerian mimicry is relatively straightforward to characterise: in a given community, defended prey species sharing a common warning signal form groups called 'mimicry rings' underlying mutualistic interactions (Weismann 1904; Papageorgis 1975; Joron and Mallet 1998), while species harbouring different signals do not interact through mimicry.

Two diverse tribes of Neotropical nymphalid butterflies, the Heliconiini Swainson, 1822 and Ithomiini Godman and Salvin, 1879, provide an excellent study system to assess the effects of Müllerian mimicry on species distributions and ecological niches between two distantly related clades (Figure 1b; Chazot, Wahlberg, et al. 2019). Both tribes were instrumental in the discovery (Bates 1862) and formalisation of Müllerian mimicry (Müller 1879), a pivotal finding that provided support for the then nascent theory of evolution by means of natural selection formulated concomitantly by Charles Darwin and Alfred Russel Wallace (Wallace 1858; Darwin 1859). All species in Heliconiini and Ithomiini are considered to be chemically defended to varying degrees, and are thereby unpalatable to predators (Brown 1984; McCauley 2006; Arias et al. 2016; McClure et al. 2019). Heliconiine butterflies sequester toxic chemical compounds from their Passifloraceae host plants (de Castro et al. 2019; Sculfort et al. 2020) and/or can synthesise *de novo* compounds from amino acids (Engler-Chaouat and Gilbert 2007), whereas ithomiines mostly derive toxic compounds from feeding on decaying leaves or flowers of Boraginaceae and Asteraceae as adults (Brown 1984; Trigo et al. 1996). Both tribes are widely distributed across the American continent, from Canada (Heliconiini) and Mexico (Ithomiini) to northern Argentina and from the Pacific to the Atlantic and Caribbean coasts (Rosser et al. 2012; Doré et al. 2022). Throughout this wide range, many species interact both within and between the tribes via Müllerian mimicry.

The tribe Heliconiini includes 8 genera, ca. 77 species and 457 subspecies (Jiggins 2017; Kozak et al. 2015; but see Núñez et al. 2022 for recent proposed taxonomic updates). The tribe Ithomiini comprises 42 genera, 396 species and 1542 subspecies (Chazot, Willmott, et al. 2019; Doré et al. 2022), with many having partially transparent wings, such as the emblematic Glasswing butterfly *Greta morgane oto* (Figure 1a). Despite having diverged 86.5 million years ago (Figure 1b; Chazot, Wahlberg, et al. 2019), about the same time that humans split from flying lemurs (Order: Dermoptera; Upham et al. 2019), the two tribes share numerous warning patterns and thus interact through mimicry (Figure 1a).

Recent work showed that mutualistic interactions have led to extensive spatial associations and climatic niche convergence between phenotypically similar species in ithomiine butterflies (Doré et al. 2023). Here, we extend that scope to investigate the effects of mimicry between the distantly related tribes Heliconiini and Ithomiini on their biodiversity patterns at a continental scale. While biogeographic patterns of species richness in ithomiine and heliconiine butterflies are already known (Rosser et al. 2012; Doré et al. 2022), other facets of the biodiversity of heliconiine butterflies such as phylogenetic diversity and geographic rarity remain unknown. Moreover, studying the two most diverse adaptive radiations of Neotropical mimetic butterflies (Kozak et al. 2015; Doré et al. 2022) in a single

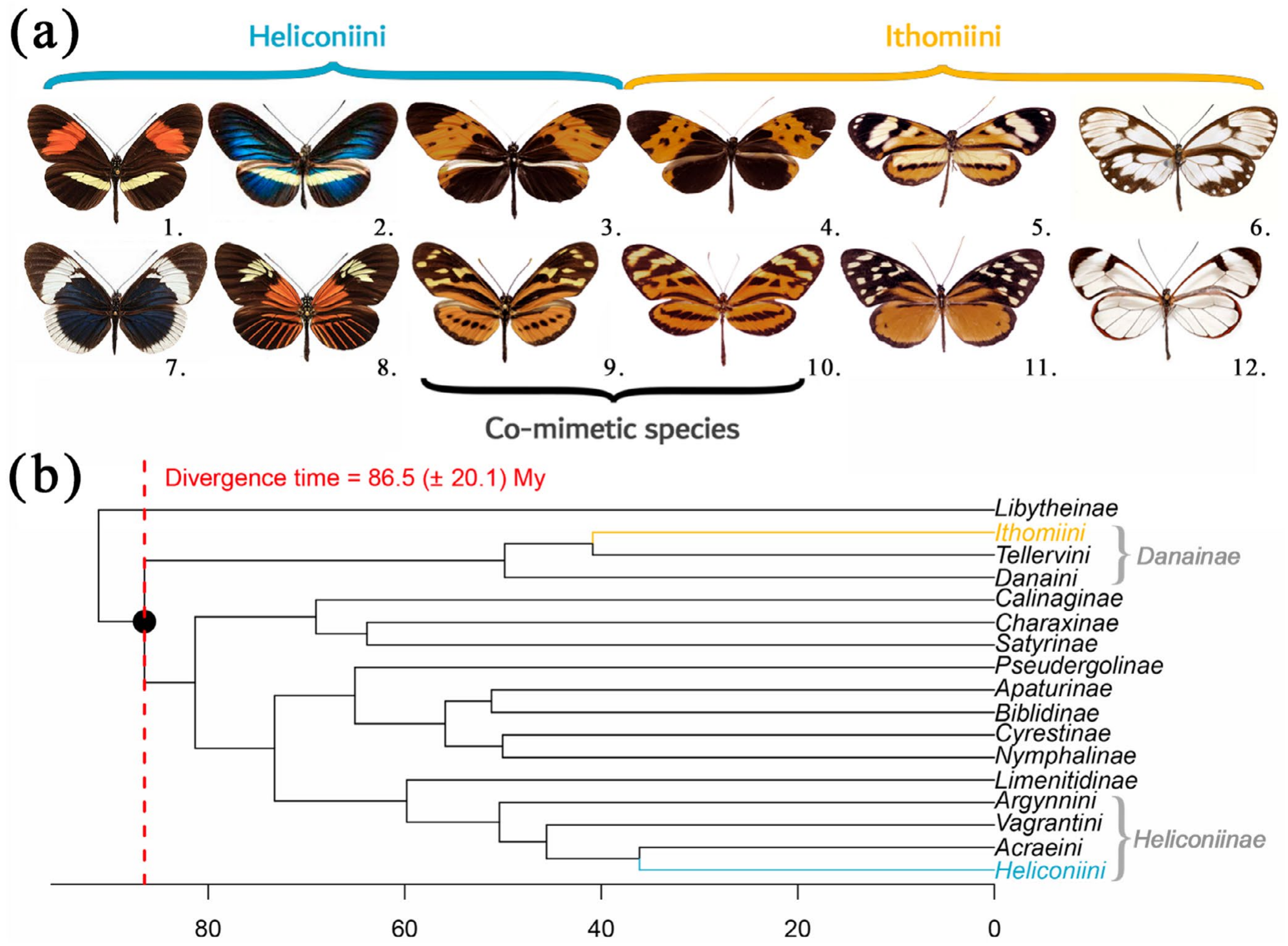

FIGURE 1 | (a) Diversity of wing patterns within and between tribes in Ithomiini and Heliconiini. The pairs 3 and 4 and 9 and 10 exemplify distantly related subspecies from different subfamilies that share similar wing patterns and take part in co-mimetic mutualistic interactions through Müllerian mimicry. From 1 to 12: *Heliconius melpomene amaryllis*, *Heliconius erato chestertonii*, *Heliconius numata bicoloratus, Melinaea isocomma simulator*, *Hypothyris ninonia daeta*, *Veladyris pardalis christina*, *Heliconius sapho sapho*, *Heliconius elevatus elevatus*, *Eueides isabella dissoluta*, *Mechanitis lysimnia utemaia, Tithorea harmonia helicaon*, *Greta morgane oto*. Comprehensive plates of the 38 heliconiine phenotypic groups (Figure S1) and 44 ithomiine phenotypic groups (Figure S2) are available in Appendix 1. (b) Relative position of Ithomiini and Heliconiini tribes in the Nymphalidae phylogeny. Extracted from Chazot, Wahlberg, et al. (2019). Tip labels represent butterfly subfamilies except for Danainae and Heliconiinae, which are divided into tribes. The *x*-axis represents the time distances between clades in millions of years (My). The red-dotted line represents the estimated divergence time between Heliconiini and Ithomiini.

integrated framework allows us to jointly define mimicry rings in local butterfly communities, produce standardised comparisons of mimetic diversity and provide statistical support for the co-occurrence of phenotypically similar butterfly species throughout the Neotropics. From an evolutionary perspective, it enables a better understanding of the role of mimetic interactions in shaping continental-scale distribution patterns and niche and trait evolution across phylogenetically distant clades (Page et al. 2024).

Specifically, we aim to:

1. Predict heliconiine subspecies distributions, map continental-scale biodiversity patterns of Heliconiini including species richness, phylogenetic diversity, geographic rarity and phenotypic richness, and test for congruences and disparities with known Ithomiini biodiversity patterns
2. Examine whether phenotypically similar species co-occur at the continental scale, supporting pervasive mutualistic interactions between Heliconiini and Ithomiini
3. Test if mutualistic interactions are associated with convergence in the climatic niche of phenotypically similar species within and between tribes throughout the Neotropics

2 | Materials and Methods

2.1 | Phenotypic Classification of Wing Colour Patterns

We classified heliconiine subspecies into 38 groups of wing colour pattern similarity forming phenotypic groups (Figure S1 in Appendix 1) representing 'putative' local mimicry rings (as in Doré et al. 2022, 2023 for Ithomiini). Since those groups are formed based only on phenotypic similarity, members of such groups may not currently be involved in mutualistic interactions as they may not actually co-occur. If a significant signal of spatial co-occurrence within a phenotypic group is detected, it then qualifies as an 'effective mimicry ring', tentatively reflecting true ecological interactions (Sanders et al. 2006; Wilson et al. 2022). We collected at least one digital image of the dorsal wing patterns for 436 out of 457 known subspecies of Heliconiini (Heliconiinae), taken from specimens held in museums and private collections. We clustered all Heliconiini images based on visual similarity by eye in their dorsal wing colour, pattern and shape. Geographic distributions of taxa were not considered during this process. We chose this classification to maintain tractability with previous studies (Doré et al. 2022, 2023). Automated approaches (e.g., deep learning or pattern recognition tools) were not used, as they rely on equally subjective methodological choices (e.g., neural network architecture, training sets, colour scheme selection, pattern alignment method) and fail to reliably capture biologically meaningful phenotypic clusters in this kind of complex system. For Ithomiini (Danainae), we used the currently accepted classification of mimicry patterns (Doré et al. 2022), built using a similar rationale of phenotypic similarity. Then, we matched the identity of phenotypic groups associated with a pattern represented in the two tribes and labelled them as inter-tribe phenotypic groups. In order to ensure the robustness of our results to alternative classifications, we also designed higher level groups encompassing multiple initial phenotypic groups. We carried out analyses for the two most extreme choices for the classification: the most 'split' with the 38 initial phenotypic groups as shown in the main text, and the most 'lumped' with 20 phenotypic groups (see Appendix 7). This design ensures that any intermediate choice in the phenotypic classification would lead to similar results, as long as results of the two extreme options lead to similar conclusions. The comprehensive phenotypic-based classification of heliconiine subspecies is available in an online archive (https://doi.org/10.5281/zenodo.10903197).

2.2 | Occurrence Database and Phylogenies

In order to map biodiversity patterns of heliconiine butterflies, we curated a database of 67,563 georeferenced occurrences collected during multiple fieldwork campaigns and complemented with records from museum collections available for the most part on https://heliconius-maps.github.io/ (accessed on November 2020; Rosser and Mallet 2024). We updated the taxonomic identity of records in agreement with the literature up to June 2021 (Jiggins 2017; Kozak et al. 2015; but see Núñez et al. 2022 for recent proposed taxonomic splits). This database covering 73 of 77 species of the tribe (94.8%) and 439 of 457 subspecies (96.1%) is available in https://doi.org/10.5281/zenodo.10906853.

We employed the phylogeny of the tribe Heliconiini in Kozak et al. 2015 encompassing 67 of the 77 recognised species (87%) to estimate indices of phylogenetic diversity and evaluate niche convergence. However, we repeated the Bayesian estimations of divergence times between Heliconiini, updating the secondary calibration points in accordance with recent estimates for Papilionoidea (Chazot, Wahlberg, et al. 2019): Heliconiini–Acraeini (31.9–43.9 My ago); *Podotricha–Philaethria* (14.2–21.1 My ago), *Heliconius–Eueides* (11.6–20.3 My ago). We ran four independent analyses of 100 million cycles each in BEAST v2.6, resulting in divergence estimates in line with those generated previously based on the same alignment (Kozak et al. 2015), as well as an independent estimate from genome-wide data (Cicconardi et al. 2023). For Ithomiini, we used the phylogeny of Chazot, Willmott, et al. 2019 that encompasses 339 of the 396 species (85.6%). The divergence time used to bind the two tribes' phylogenies was estimated at 86.5 My following Chazot, Wahlberg, et al. (2019).

2.3 | Species Distribution Modelling (SDM)

To predict spatial distributions, we performed Species Distribution Modelling (SDM) for each subspecies of Heliconiini independently. Modelling was carried out at the subspecies level because many species are polymorphic, thus may belong to several phenotypic groups. The output of the SDM process was a single consensus model (ensemble model) for each subspecies that provides a proxy of the probability of presence of each subspecies in each 30 km × 30 km grid cell (i.e., community).

As predictors of subspecies distributions, we used environmental variables that are relevant to butterfly ecology, according to the literature. Temperature and precipitation are known to influence the development of host plants for butterflies (Boggs et al. 2003), while elevation (Chazot et al. 2014; Montejo-Kovacevich et al. 2020) and forest cover (Brown 1997) are important factors shaping heliconiine butterfly distribution. We extracted annual mean temperature, mean diurnal range, annual precipitation levels, and precipitation seasonality from the WorldClim bioclimatic variables dataset (v2.1 accessed 02/2021; Fick and Hijmans 2017), elevation from the SRTM Dataset (http://srtm.csi.cgiar.org/; v.4.1 accessed on 03/2019; Farr et al. 2007), and forest cover from the Landsat Tree Cover Continuous Fields dataset (accessed on 03/2019; Sexton et al. 2013) aggregated at a quarter-degree cell resolution (i.e., pixel of ca. 30 km × 30 km).

We modelled each subspecies' geographic distribution using three different algorithms (Random Forest, Gradient Tree Boosting and Artificial Neural Network) applied across three independent sets of pseudo-absences and three spatially structured cross-validation blocks. We calculated the median predicted habitat suitability of all models that passed our quality evaluation process to create an ensemble model for each subspecies. We cropped each subspecies' predicted distribution to a relevant area according to its occurrences using a taxon-specific buffered alpha-hull mask. Finally, we merged ensemble models to acquire predicted distribution maps for species, mimetic groups and Operational Mimicry Units (OMUs). The latter are defined as all subspecies of a species that belong to the same mimetic group (Doré et al. 2022). Despite the downstream analyses being carried out at the OMU level, for the sake of simplicity we used 'phenotypically similar species' or 'look-alike species' in the text to refer to the OMUs sharing the same phenotypic pattern. We did not perform a binarisation step on our SDM outputs in order to retain the maximum of information available (Guillera-Arroita et al. 2015). Therefore, all distribution maps are continuous rasters with SDM scores ranging from 0 to 1.

All distribution maps are available in https://doi.org/10.5281/zenodo.10903661. More details about the modelling process are available in the ODMAP form (Zurell et al. 2020) in Appendix 8. Similar models were already performed for Ithomiini at the OMU level in Doré et al. (2022). These predictions were used to compare diversity patterns and investigate spatial associations between the two tribes.

2.4 | Diversity Indices

We computed and mapped a series of spatial biodiversity metrics (in 30 km x 30 km grid cells) using the putative mimicry ring assignments, information on phylogenetic distances and the inferred geographic distributions of each Ithomiini and Heliconiini subspecies:

- Species and phenotypic richness, computed as the number of predicted species/phenotypic groups per grid cell.
- Standardised effect-size of phylogenetic diversity (SES-PD), calculated by comparing the observed Faith's Phylogenetic Diversity (PD; Faith 1992) in each grid cell to a null distribution of PD values generated from 999 random permutations of species identity. SES-PD is expressed as a standardised Z-score: the difference between the observed PD and the mean of the null distribution, divided by the standard deviation of the null values. This index accounts for the dependence of PD on species richness and assesses whether communities are more or less phylogenetically diverse than expected by chance.
- Mean species and phenotypic geographic rarity, computed as the weighted proportion of species or phenotypic groups with small geographical ranges per grid cell. For each species, range size was estimated as the number of grid cells predicted as occupied. An exponential transformation was then applied to map range size to a continuous rarity weight, with a threshold calibrated such that approximately 25% of species were considered rare across all communities (Leroy 2015). Mean rarity is then computed as the mean rarity weight of species present in each grid cell.
- Mean phenotypic group size, computed as the mean number of species per phenotypic group within each grid cell. This index provides insight into the degree of pattern convergence in a community. A high mean phenotypic group size indicates that many species in an area have the same wing pattern.

To compare these indices of Heliconiini with those of Ithomiini, we mapped them together with a two-dimensional colour scale, scaled by the minimum and maximum of each index for each tribe (Figure 2). Additionally, we computed spatial correlation tests across all communities for each index, between the two tribes (Table S1 in Appendix 4) and between Heliconiini biodiversity patterns (Table S2 in Appendix 4). Specifically, we used Spearman's rank correlation tests with Clifford's sample size correction to account for positive spatial autocorrelation across grid cell values (Clifford et al. 1989). Lastly, we evaluated differences in spatial heterogeneity of biodiversity patterns between the two tribes using an asymptotic test to compare Coefficients of Variation (CV; Feltz and Miller 1996).

2.5 | Test for Spatial Association Among Look-Alike Species

To detect the effects of phenotypic group membership, and thus of mutualistic interactions, on the spatial distribution of Heliconiini and Ithomiini, we investigated the degree to which phenotypically similar species (i.e., OMUs) co-occur across grid cells. We computed pairwise Schoener's dissimilarities (SCD) as 1—Schoener's D (Schoener 1970), an index that quantifies mean absolute differences between the distribution of two entities on a grid cell, in our case between continuous SDM scores of pairs of OMUs. This index is especially suitable to quantify niche overlap in the geographical space (Rödder and Engler 2011; Broennimann et al. 2012), accounting for both differences in ranges (i.e., nestedness) and differences in SDM scores within the overlap area (i.e., turnover). Thus, we calculated the mean Schoener's dissimilarities of all OMUs within phenotypic groups, globally and individually, representing the average degree of spatial co-occurrence of phenotypically similar units. To test the significance of these statistics, we used permutation tests under the null hypothesis that phenotypic group membership (i.e., wing colour patterns) has no effect on co-occurrence. Therefore, for each permutation, we randomised the wing pattern between all OMUs to investigate whether phenotypically similar species co-occur more than expected at random, globally and within each phenotypic group. As such, an observed SCD lower than 95% of the null distribution of obtained values indicates a significant signal for spatial congruence. These analyses were performed for Ithomiini and Heliconiini independently and for pairs of phenotypically similar OMUs formed between the two tribes labelled as 'inter-tribe' in subsequent analyses (Figure S6 in Appendix 5; Table S3 in Appendix 6).

2.6 | Test for Niche Evolution Among Look-Alike Species

In order to investigate whether mimicry led to an evolutionary association between climatic niches and wing colour patterns, we performed comparative phylogenetic analyses as was previously done for Ithomiini in Doré et al. (2023). Climatic niche was described as the centroid of OMU's climatic space using bioclimatic variables employed during niche modelling (i.e., annual mean temperature, mean diurnal range, annual precipitation levels, precipitation seasonality). While niche centroids are derived from realised niches based on occurrence data, they have been shown to be less sensitive to mismatches between realised and fundamental niches than other niche descriptors (Gouveia et al. 2014). Thus, they offer a robust proxy for comparing climatic niche evolution when physiological data are unavailable.

First, we fit multivariate neutral evolution models to explain the distribution of niche centroid values on the phylogeny. We compared AICc of a Brownian motion model with models

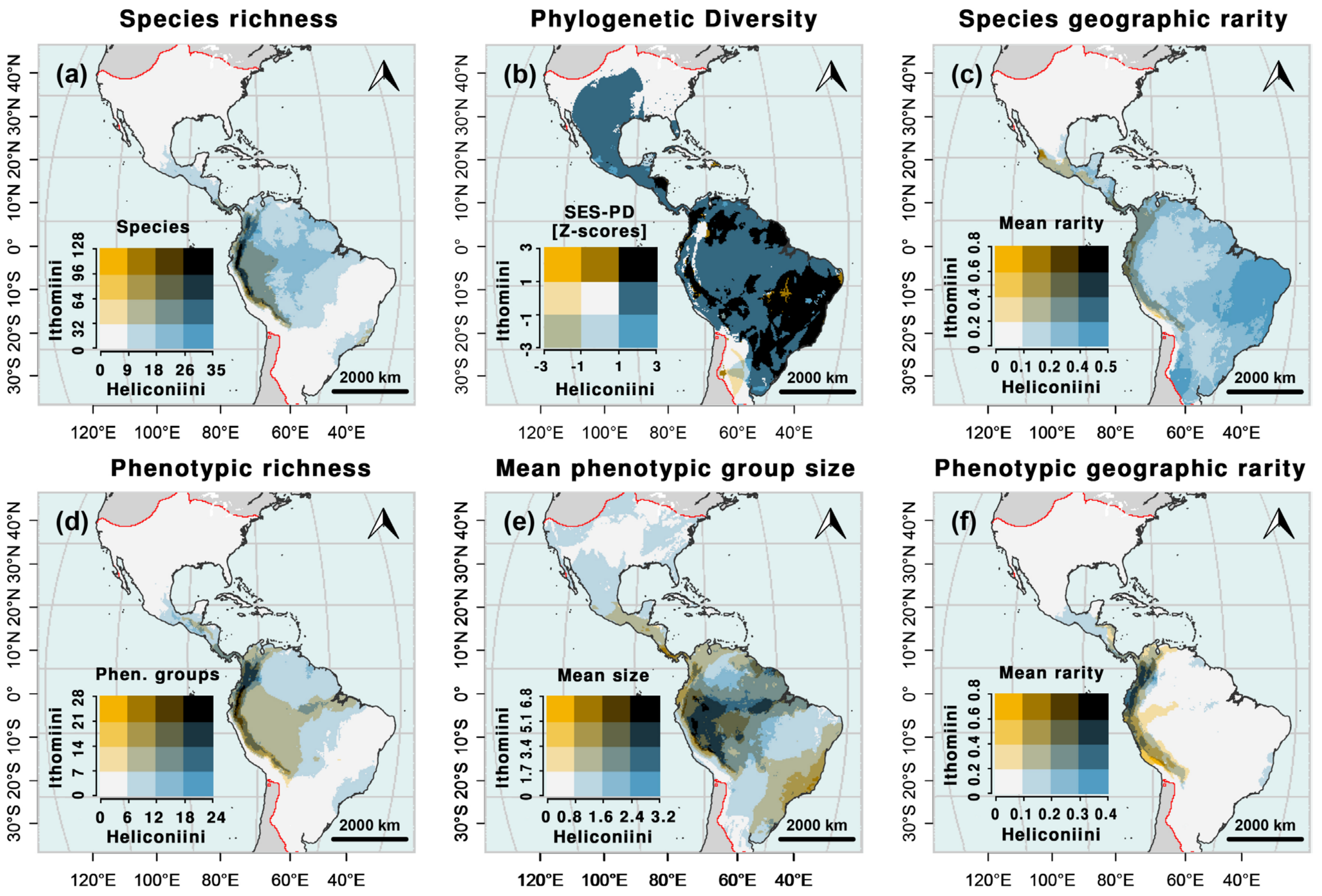

FIGURE 2 | Relative patterns of biodiversity in Heliconiini and Ithomiini at the continental scale. (a) Species richness. (b) Standardised effect size of phylogenetic diversity (SES-PD). (c) Mean species geographic rarity. Rarity index based on species ranges. (d) Phenotypic richness (i.e., number of local phenotypic groups). (e) Mean phenotypic group size (i.e., mean number of species per local phenotypic group). (f) Mean phenotypic geographic rarity. Rarity index based on phenotypic group ranges. The bivariate colour scale represents the scaled values of each index in the two tribes. Values are scaled by the maximum value for each tribe; thus, they describe relative patterns of biodiversity. Z-scores (b) were not scaled as they are already standardised. Blue areas reflect higher relative diversity/rarity for Ithomiini while yellow areas reflect higher relative diversity/rarity for Ithomiini. Darker areas represent shared hotspots of diversity/rarity. Ithomiini patterns are extracted from Doré et al. (2022). Absolute patterns of Heliconiini and Ithomiini biodiversity can be found in Figures S4 and S5 in Appendix 3.

implementing additional Pagel's lambda and/or Pagel's kappa parameters accounting respectively for the presence of phylogenetic signal and punctuated evolution associated with cladogenesis (Pagel 1994, 1999), to select for the best fitted option. At the end, we selected an evolution model with a Pagel's lambda of 0.798.

We used mean climatic distances (MCD) computed as the pairwise Euclidean distances between niche centroids in the climatic space to estimate the similarity of climatic niches between pairs of OMUs. To test the effect of mimicry on climatic niche evolution, we simulated the evolution of the climatic niche under the selected neutral evolutionary model ($n = 999$) to obtain a null distribution for the mean MCD between phenotypically similar OMUs. As such, an observed MCD lower than 95% of null statistics indicates a significant signal for niche convergence (Figure S7 in Appendix 5; Table S4 in Appendix 6).

Importantly, this phylogenetic comparative framework addresses a different biological question than our tests for spatial co-occurrence. While geographic overlap implies that species experience similar environmental conditions, shared climatic niches do not necessarily entail spatial proximity, especially in regions with strong biogeographic barriers. The two tests are therefore complementary. Moreover, our convergence tests rely on comparisons to a neutral evolutionary model, while spatial association was assessed against a null spatial model. As such, niche convergence is only inferred when phenotypically similar species are in more similar niches than expected given their evolutionary relatedness.

3 | Results

3.1 | Congruence and Contrasts in Biodiversity Patterns Between Tribes

We found significant correlations in continental biodiversity patterns and the location of diversity hotspots between the two tribes (Table S1 in Appendix 4). However, we also detected notable regional differences (Figure 2; see Figure S3 in Appendix 2 for a map of bioregions). Similar to Rosser et al. 2012, we found a peak of species richness in the eastern slopes of the Andes, with up to nearly half of the Heliconiini species predicted to be found in some 30 km × 30 km grid cells (Figure 2a; 35 out of 77 species = 45.5%; Figure S4a in Appendix 3). We also detected secondary hotspots of species richness in the Amazon basin and in southern Central America. These patterns are significantly correlated with those of Ithomiini species richness (Spearman's rho = 0.771, t-stat = 7.91, Clifford's df = 42.7, Q95% = 1.681, $p < 0.001$; Table S1 in Appendix 4), which also peak in the Andes and southern Central America (Doré et al. 2022). However, Ithomiini have proportionally fewer species than Heliconiini in the Amazon basin and the Brazilian Atlantic Forest (Figure 2a). Finally, Heliconiini are present in the Nearctic region, while Ithomiini are only barely found north of Mexico (Figures S4a and S5a in Appendix 3).

Standardised phylogenetic diversity (SES-PD) is positive across much of the Heliconiini distribution, indicating that many regions harbour lineages more phylogenetically dispersed than expected by chance. As these are moderately correlated with Ithomiini SES-PD patterns (Spearman's rho = 0.313, t-stat = 4.06, Clifford's df = 151.3, Q95% = 1.655, $p < 0.001$; Table S1 in Appendix 4), they highlight distinct zones of phylogenetic diversity within each clade. Notably, Heliconiini are more diverse than expected from local species richness in the Amazon Basin and in Central America (Figure 2c; Figures S4c and S5c in Appendix 3). In both tribes, the Central Andes and the Brazilian Atlantic Forest (Mata Atlântica) emerged as hotspots of phylogenetic overdispersion. By contrast, northern Andean regions presented more neutral SES-PD values for both tribes.

The Caatinga, a habitat with semi-arid tropical vegetation in Northeast Brazil, has the highest proportion of heliconiine species with restricted geographical ranges (Figure 2b; Figure S4b in Appendix 3). However, this pattern is produced by few taxa that are restricted to this region (Dantas et al. 2021). Meanwhile, geographical rarity is lowest in the Nearctic, which also hosts only a few species, but with wide geographical distributions, such as *Dryas iulia* and *Agraulis vanillae* (but see Núñez et al. 2022 for recent proposed taxonomic splits). By contrast, the highest proportion of Ithomiini species with restricted ranges is found in the Andes and in Central America (Figure 2b; Figure S5b in Appendix 3; Doré et al. 2022), leading to a lack of significant correlation in broadscale patterns of geographic rarity between the two tribes (Spearman's rho = −0.042, t-stat = −0.34, Clifford's df = 64.7, Q95% = 1.669, $p = 0.632$; Table S1 in Appendix 4).

Spatial patterns of phenotypic richness in heliconiines (i.e., the number of 'phenotypic groups' represented at a given location) strongly correlated with those of heliconiine species richness (Spearman's rho = 0.978, t-stat = 18.0, Clifford's df = 14.7, Q95% = 1.755, $p < 0.001$; Table S2 in Appendix 4) and phenotypic richness in ithomiines (Spearman's rho = 0.762, t-stat = 7.60, Clifford's df = 41.8, Q95% = 1.682, $p < 0.001$; Table S1 in Appendix 4). Patterns of diversity and mimicry in both tribes were strikingly different in the Andes compared to the rest of the continent. Maximum phenotypic richness was reached in the northern Andes, where up to 24 (63.2%) of the 38 Heliconiini colour patterns and 29 (65.9%) of the 44 Ithomiini patterns are predicted to be found in local grid cells (Figure 2d; Figure S5d in Appendix 3; Doré et al. 2022). Phenotypic richness in the Western Amazon basin stands out much less for Heliconiini than for Ithomiini (Figure 2d; Figure S4d in Appendix 3), because of a higher number of local species sharing similar colour patterns compared to the Andes. Phenotypic groups of Heliconiini in the Amazon comprise between 1.5 and 3 species on average, but only up to 1.5 species in the Andes (Figure 2e; Figure S4e in Appendix 3). Furthermore, high phenotypic geographic rarity reflects the presence of phenotypic groups with smaller distribution ranges in the Andes compared to the rest of the continent (Figure 2f). Meanwhile, ithomiines form larger phenotypic groups in the Andes, the western Amazon, Central America and the Brazilian Atlantic Forest, with between 3.5 and 7 species per group on average (Figure 2e; Figure S5e in Appendix 3; Doré et al. 2022). However, ithomiine and heliconiine phenotypic groups are fairly similar to each other in terms of geographic rarity of mimicry patterns (Spearman's rho = 0.625, t-stat = 5.71, Clifford's df = 50.9, Q95% = 1.675, $p < 0.001$; Table S1 in Appendix 4), with widely distributed patterns in Amazonia and patterns with narrow distributions in the Andes.

3.2 | Mimicry Promotes Broad Scale Spatial Congruence of Phenotypically Similar Species

To explore whether mutualistic interactions can shape the co-occurrence of phenotypically similar species, within and between tribes, we used the Schoener's dissimilarities (SCD) to quantify dissimilarities in spatial patterns of species. We compared the observed mean SCD within phenotypic groups against SCD obtained from random permutation of patterns between species as a null hypothesis depicting the absence of a relationship between colour patterns and spatial distributions of species. We detected that Heliconiini (Permutation test $SCD_{obs} = 0.738$, SCD_{null} Q5% = 0.887, $p \leq 0.001$), Ithomiini (Permutation test: $SCD_{obs} = 0.900$, SCD_{null} 5% = 0.946, $p \leq 0.001$; similar to Doré et al. 2023) and inter-tribe phenotypic groups (Permutation test: $SCD_{obs} = 0.886$, SCD_{null} Q5% = 0.936, $p \leq 0.001$) all had significantly lower mean spatial dissimilarities than at random (Figure S6 in Appendix 5). As such, we detected significant spatial congruence among the distributions of phenotypically similar species at a continental scale, both within and between tribes.

Tests were also carried out for each phenotypic group with at least two species. We observed that 15 out of 29 (51.7%) groups had significant signal for spatial congruence within the Heliconiini, supporting their qualification as 'effective mimicry rings' representing current mutualistic interactions. This proportion rises to 32 out of 39 (82.1%) groups within the Ithomiini (as in Doré et al. 2023). For colour patterns shared between the two tribes, 9 out of 11 (81.8%) were significantly spatially congruent and are thus supported as 'effective mimicry rings' (Table S3 in Appendix 6). These results represent the first statistical support for the co-occurrence of phenotypically similar species across butterfly tribes at a continental scale. For instance, the pattern EXCELSA had an important and significant overlap of distributions between tribes throughout Central America and the Northern Andes (Figure 3a; Permutation test: $SCD_{obs} = 0.826$, SCD_{null} Q5% = 0.903, $p \leq 0.001$). Similarly, the PAVONII pattern appeared confined to the Northern and Central Andes for

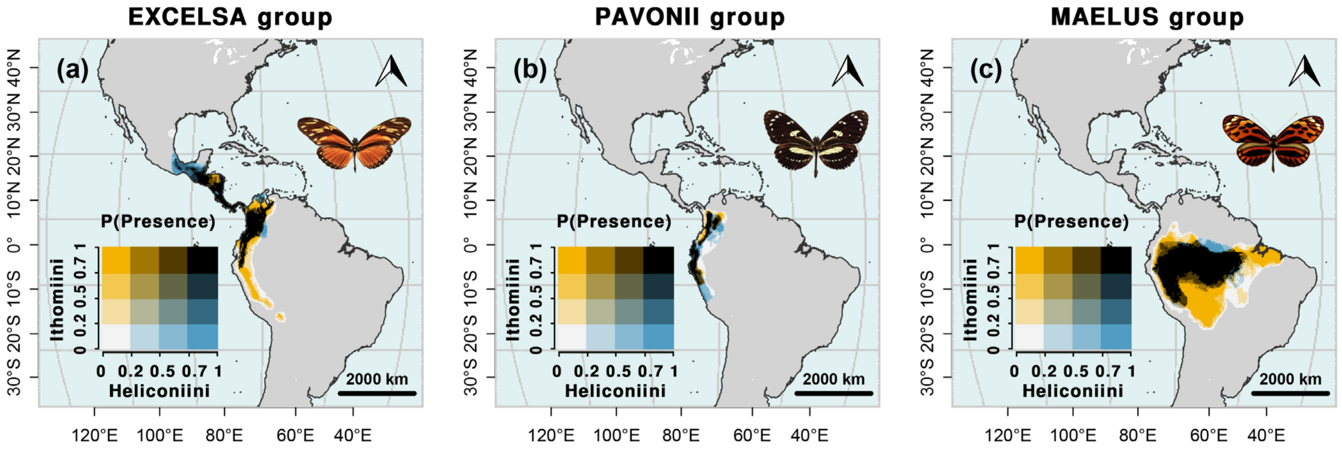

FIGURE 3 | Comparative distributions of predicted presence for Heliconiini and Ithomiini phenotypic groups defined based on phenotypic similarity. (a) EXCELSA group. (b) PAVONII group. (c) MAELUS group.

both tribes (Figure 3b; Permutation test: $SCD_{obs} = 0.667$, SCD_{null} Q5% = 0.834, $p \leq 0.001$), while the heliconiines and ithomiines harbouring the pattern MAELUS had significant overlap in distributions across the Amazon Basin (Figure 3c; Permutation test: $SCD_{obs} = 0.660$, SCD_{null} Q5% = 0.903, $p \leq 0.001$).

3.3 | Mimicry is Associated With Climatic Niche Convergence of Phenotypically Similar Species

Beyond spatial distributions, we investigated the extent and significance of climatic niche convergence between phenotypically similar species for each type of phenotypic group (Heliconiini, Ithomiini, inter-tribe groups). We quantified climatic distances between species as Euclidean distances between the centroids of species occurrences in the bioclimatic space employed for Species Distribution Modelling (SDM). We compared the observed mean climatic niche distance (i.e., MCD) within phenotypic groups against MCD obtained from simulations of neutral evolution of the climatic niche along the phylogeny. The observed MCD was significantly lower for all three types of phenotypic groups (Heliconiini only: $MCD_{obs} = 0.684$, MCD_{null} Q5% = 0.882, $p \leq 0.001$; Ithomiini only: $MCD_{obs} = 0.724$, MCD_{null} Q5% = 0.954, $p \leq 0.001$ adapted from (Doré et al. 2023); inter-tribe: $MCD_{obs} = 0.725$, MCD_{null} Q5% = 0.866, $p \leq 0.001$). Therefore, we detected a significant evolutionary association between climatic niche and colour patterns, both within and between tribes, as species sharing wing patterns tend to have more similar climatic niches than expected under neutral niche evolution.

Overall, we observed that 12 out of 29 (41.4%) phenotypic groups in Heliconiini and 33 out of 39 (84.6%) phenotypic groups in Ithomiini (Doré et al. 2023) had significant niche convergence. For inter-tribe phenotypic groups, niche convergence was supported for 6 out of 10 (60.0%) groups (Table S4 in Appendix 6).

4 | Discussion

Our study highlights the strength of mutualistic interactions to shape biodiversity patterns at a continental scale and to support species niche convergence across evolutionarily distant lineages. Specifically, we showed how Müllerian mimicry shapes spatial congruence in distributions at a continental scale, and is associated with niche convergence within and between two emblematic tribes of unpalatable Neotropical butterflies that diverged from a common ancestor 86.5 million years ago.

The number of heliconiine and ithomiine butterfly species and mimicry rings is particularly dense in the tropical Andes, and many of these have geographically restricted ranges. Although we detected minor differences in regional biodiversity patterns between the two tribes, likely because of differences in host plant distributions and biogeographic origins (see below), we provided further evidence that mimicry is associated with spatial congruence among phenotypically similar species, both within and between tribes across the Neotropics. This finding provides new empirical evidence for the unfolding of the prediction of Müller's mimicry model (Müller 1879) at a macroecological scale and across millions of years of evolution. Furthermore, comparative phylogenetic analyses suggest that mimetic interactions support the evolutionary association between climatic niche and colour pattern evolution within and across tribes as a consequence of selection favouring both the phenotypic convergence of sympatric species and the co-occurrence of look-alike species.

4.1 | Drivers of Continental Biodiversity Patterns

Our analyses predict species richness of Heliconiini to be particularly high in the Amazon basin and in the tropical Andes (Figure 2), in line with previous findings (Rosser et al. 2012, 2021). While both regions harbour high levels of butterfly richness, the Andean diversity is concentrated in a narrower spatial and elevational range compared to the Amazon basin, reflecting a disproportionately species-dense mountainous region. This pattern was recently highlighted for butterflies worldwide (Pinkert et al. 2025) and supports the view that mountain regions act not only as refugia, but also as biodiversity pumps (Rahbek et al. 2019). Similarly, the species richness of Ithomiini is also high in the tropical Andes (Chazot et al. 2016; Doré et al., Doré et al. 2022; Figure S5 in Appendix 3). Those congruent biodiversity patterns are similar in other taxa, including angiosperms (Ter Steege et al. 2003), beetles (Pearson and Carroll 2001), birds (Orme et al. 2005), mammals (Kaufman and Willig 1998), reptiles (Roll et al. 2017) and amphibians (Hutter et al. 2017), reinforcing the position of the tropical Andes as the richest biodiversity hotspot on Earth (Myers et al. 2000; Hutter et al. 2017). This outstanding biodiversity is strongly influenced by geological and climatic factors. The topographical complexity of the tropical Andes facilitates fine-scale spatial variation of environmental conditions and provides more opportunities for parapatric and allopatric speciation, fueling regional adaptive radiations (Särkinen et al. 2012; Bouchenak-Khelladi et al. 2015; Rangel et al. 2018). Moreover, the tropical Andes and the Amazon basin have benefited from a historically stable climate, thought to reduce species extinction rates (Colinvaux and De Oliveira 2001; Fine 2015) and allow for the long-term persistence of high levels of species diversity and endemism (Araújo et al. 2008; Svenning et al. 2015; Harrison and Noss 2017; Rull and Carnaval 2020). Noticeably, the Brazilian Atlantic Forest (Mata Atlântica), although geographically distant from the Andes and the Amazon basin, also harbours a high diversity of both Heliconiini and Ithomiini. This disjunct pattern could be the result of multiple independent colonisation events resulting from changing connectivity with Amazonia (Brown 1982; Lisa De-Silva et al. 2017; Chazot, Willmott, et al. 2019), followed by local diversification in the Brazilian Atlantic Forest. In addition, SES-PD patterns revealed significant phylogenetic overdispersion in both the Brazilian Atlantic Forest and the Central Andes hinting that these regions may have acted as important refugia for ancient and evolutionarily divergent lineages in both tribes. In contrast, northern Andean communities present more neutral SES-PD values, possibly due to a combination of recent radiations and lineage persistence, as previously proposed in Ithomiini (e.g., Chazot, Willmott, et al. 2019).

While broad scale diversity patterns of Heliconiini are significantly correlated with those of Ithomiini (Table S1 in Appendix 4), we also observed minor regional disparities between the two tribes. Ithomiini richness and rarity are concentrated in the tropical Andes (Chazot et al. 2016; Doré et al. 2022), while heliconiines are particularly species-rich in the Andes and Amazon basin (Figure 2a). This difference could be explained by contrasting geographic origins between the tribes. Ithomiini are inferred to have originated in the Central Andes (Chazot, Willmott, et al. 2019), allowing time for speciation and lineage accumulation in this region. Formal historical biogeographic reconstructions at the tribe level are still lacking for Heliconiini (Merrill et al. 2015), but an Amazonian origin of Heliconiini could explain their relative richness in the area. Perhaps more importantly, both tribes encompass numerous species that typically feed on a small number of larval host plants (Benson et al. 1975; Willmott and Mallet 2004). However, they specialise in distinct families of plants, the Passifloraceae for the heliconiines and the Solanaceae for most ithomiines, with which they are suspected to have tightly coevolved (Willmott and Mallet 2004; Jiggins 2017). Thus, differences in biogeographic histories and species richness patterns of the two host plant lineages (Hunziker 2001; Muschner et al. 2012; Dupin et al. 2017) could partly explain the current dissimilarities observed in biodiversity patterns between the two butterfly tribes.

Beyond taxonomic and phylogenetic patterns, both tribes have contrasting mimetic characteristics between Andean and Amazonian communities. A few large-range and species-rich phenotypic groups dominate mimetic butterfly communities in the Amazon basin (Figure 2d–f). This suggests a pervasive wing pattern convergence between distant lineages and/or a high degree of phenotypic conservatism within local radiations, acting alongside relatively strong frequency-dependent selection purging any less common patterns that may arise across the relatively homogeneous climate of the Amazon basin (Michot et al. 2024). Conversely, in the Andes, where phenotypic groups have smaller distributions and are composed of fewer species, there is a higher diversity of wing patterns per grid cell (Figure 2d–f). This is likely explained by strong environmental gradients and geographic barriers present in these mountainous regions. These abiotic features favour partitioning of predator and prey communities across space, which incurs selection on colour patterns through mimicry at a scale smaller than our 30 km × 30 km grid cells, thereby driving the partitioning of species among more phenotypic groups (Chazot et al. 2014).

Together, these results offer the first quantitative comparison of spatial biodiversity patterns across Heliconiini and Ithomiini at the continental scale. By mapping several diversity components within a unified framework, we provide a comprehensive comparative view of how species assemblages are structured across two of the most diverse Neotropical butterfly tribes.

4.2 | Continental-Scale Spatial Congruence of Phenotypically Similar Species

Despite having some minor disparities in continental biodiversity patterns, the two tribes are strongly linked through mimetic interactions. An important proportion of the phenotypic groups identified within each tribe, but also between the two tribes, has significant continental scale spatial congruence. Those groups likely represent 'effective mimicry rings' as sets of phylogenetically distant but phenotypically similar species involved in mutualistic interactions in local communities. However, when studying the Heliconiini group PAVONII, we found no evidence of co-occurrence nor climatic niche convergence among species for this phenotypic group. Only after accounting for the Ithomiini members of this inter-tribe phenotypic group did we detect an overall significant signal for spatial congruence (Figure 3b; Tables S3, S4 in Appendix 6). Therefore, our study highlights the importance of accounting for distinct members of the mimetic community when investigating how mutualistic interactions shape the distribution of species, even when those are distantly related.

4.3 | Climatic Niche Associations Over 86.5 My of Independent Evolution

Beyond similarities in spatial distributions, we found a significant evolutionary association between phenotypic patterns and species climatic niche both within and between tribes. Patterns of trait and niche convergence across co-mimetic species of Neotropical butterflies have already been detected for flight behaviour

(Page et al. 2024), and for ecological dimensions acting at local scales, such as nocturnal roosting habitat height (Mallet and Gilbert 1995), flight height and microhabitat (Beccaloni 1997b; DeVries et al. 1997; Elias et al. 2008; Willmott et al. 2017) and forest structure (Elias et al. 2008; Hill 2010). Here we show that phenotypically similar species tend to share similar climatic niches beyond what is expected from shared ancestry, suggesting a nonrandom association between mimicry and climatic preferences. This convergence can arise for niche dimensions (i.e., climatic niche) that directly affect biodiversity patterns at the continental scale and can link the fate of two tribes that, despite being separated by 86.5 My of independent evolution, currently share highly similar phenotypes, spatial distributions and associated climatic niches. Given the lability of wing pattern evolution (Concha et al. 2019; Van Belleghem et al. 2021) compared to the more conserved nature of climatic niche evolution (Chazot et al. 2014, 2021), it is likely that convergence in wing patterns among co-occurring species is the prominent driver of this association, rather than convergence in niches between looking-alike species favouring spatial co-occurrence, although both mechanisms can act jointly (see Doré et al. 2023).

Such strong coevolution across tens of millions of years of evolution may have significant implications in the face of the ongoing climate change. Indeed, Müllerian mimicry represents interactions that are beneficial for the individuals involved, compensating for the negative effects of resource and habitat competition (Aubier and Elias 2020) and fueling higher local species richness (Gross 2008; Aubier et al. 2017). However, if mutualistic interactions are lost because of species extinction or community disassembly, their disappearance can reduce community stability and potentially trigger cascades of local extinction (Dunn et al. 2009; Vidal et al. 2019). The dispersal abilities of Müllerian mimetic species are impeded by the purifying selection acting on individuals harbouring novel phenotypes in newly colonised areas (Mallet and Barton 1989; Langham 2004). Moreover, despite relatively similar climatic niche optima, tolerance to climate fluctuations and extremes and species dispersal abilities may still differ among co-mimetic species, limiting opportunities for co-dispersal trajectories and leading to community disassembly (Toby Kiers et al. 2010; Sheldon et al. 2011; Svenning et al. 2015). Finally, the effects of climate change on biotic factors that affect local abundance, such as host plants (Schweiger et al. 2008; Hamann et al. 2021) and parasitoids (Longino 1984; Gentry 1998), may also differ among interacting species, impeding even more their abilities to cope with climate change as tightly coevolved assemblages are tied together by positive interactions (Tylianakis et al. 2008).

4.4 | Limitations and Perspectives

We found statistical support for evolutionary associations between species' climatic niches and aposematic colour patterns within and between tribes. However, our niche convergence analyses focus on occurrence-based niche centroids and remain approximations of the fundamental niche. Even if they have been shown to reflect fundamental climatic tolerances accurately (Gouveia et al. 2014), future studies should supplement our findings with analyses based on physiological tolerance data, which are currently missing at such broad taxonomic scales. Moreover, our analyses do not allow us to completely disentangle whether the pattern we found resulted from selection favouring the phenotypic convergence of sympatric species or the niche convergence of look-alike species. In practice, both mechanisms are likely involved (Doré et al. 2023). Besides favouring the phenotypic convergence of sympatric species, the reduced cost of predation associated with Müllerian mimicry (Müller 1879) may enable survival of rare forms within a species and assist the colonisation of new environments shared with their mimetic partners (Aubier et al. 2017), resulting in effective niche convergence. In the case of frequency-dependent Müllerian mimicry, phenotypic evolution likely occurs through advergence (i.e., directional evolution in one lineage towards an unchanging, pre-existing aposematic signal in another) rather than gradual convergence, with the rarest species evolving towards the more abundant, thus better numerically defended, species (Turner 1984). The most likely scenario in our system is advergence of heliconiines towards ithomiines because of colour pattern ancestry, such as recently emerging subspecies of *Heliconius numata* mimicking different species of *Melinaea* harbouring older aposematic patterns (Joron et al. 1999).

While ithomiines and heliconiines form the bulk of butterfly mimetic communities in the Neotropics (Poole 1970; Beccaloni 1997a), they also interact with a wide range of other mimetic butterflies and diurnal moths, such as the chemically defended Dioptinae (Notodontidae; DeVries 1994) and Pericopina (Erebidae; Brown 1979), numerous presumed palatable Batesian mimics such as Dismorphiinae butterflies (Pieridae; Poulton 1898) and even Polythoridae damselflies (Beccaloni 1997a; Outomuro et al. 2013; Corral-lopez et al. 2021). How these relatively less explored, or still undiscovered, components of mimetic communities, and notably the existence of Müllerian and Batesian components, affect the whole distribution and niche evolution of interacting species is virtually unknown (Joshi et al. 2017; Kunte et al. 2021). Thus, future directions in this research topic may aim to enlarge the taxonomic scope and shed light on the importance of mimetic interactions in shaping spatial biodiversity patterns across even more evolutionarily distantly related lineages.

Author Contributions

E.P., M.E. and M.D. conceived the study and designed the analyses. N.R., K.K., W.O.M., B.H., J.M., J.R. and K.W. provided specimens and occurrence data. K.K. provided the phylogenetic trees. M.D. aggregated the database. E.P. curated the database. E.P. and M.D. wrote the R scripts. E.P. and M.D. carried out the analyses, produced maps, results, and figures. E.P. and M.D. led the manuscript writing. All authors contributed to the final manuscript.

Acknowledgements

We gratefully thank all the researchers, field assistants, technicians and students who were involved in the collection of the occurrence data over the past decades. We thank all the local governmental authorities, scientific institutions and communities that supported our research. No specimens were collected within the scope of this research project. All georeferenced data were aggregated from previous research efforts; therefore, the authors declare no funding regarding data collection. E.P.'s research was funded by the Agence Nationale de la Recherche (ANR) under the grant CLEARWING (ANR-16-CE02-0012), and a Human Frontier Science Program grant (RGP0014/2016), both obtained by M.E. K.W. acknowledges the continuing support of the INABIO and Ministerio del Ambiente of Ecuador (MAATE-DBI-CM-2023-0298). M.D. acknowledges funding by the French Ministry of Research (MESRI).

Conflicts of Interest

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.

Data Availability Statement

All R scripts used to conduct the analyses and generate the figures are available on GitHub (https://github.com/EddiePerochon/Heliconiini_Diversity) with all generated files stored on https://doi.org/10.5281/zenodo.14765685. Phenotypic classification, occurrences data and maps of the distribution of subspecies, OMUs, species and phenotypic groups produced and used in this study are available from Zenodo (Occurrences data: https://doi.org/10.5281/zenodo.10906853; Distribution maps: https://doi.org/10.5281/zenodo.10903661; Phenotypic classification: https://doi.org/10.5281/zenodo.10903197). All results reported in this article can be reproduced with the scripts and data provided.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.