Müllerian mimicry in Neotropical butterflies: One mimicry ring to bring them all, and in the jungle bind them

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**Author contributions:**

EP, ME and MD conceived the study and designed the analyses. NR, KK, WOM, BH, JM, JR & KW provided specimens and occurrence data. KK provided the phylogenetic trees. MD aggregated the database. EP curated the database. EP & MD wrote the R scripts. EP & MD carried out the analyses, produced maps, results, and figures. EP & MD led the manuscript writing. All authors contributed to the final manuscript.

## Abstract (238 words)

Understanding the mechanisms underlying species distributions and coexistence is essential to predict and prevent the impacts of global change, particularly in biodiversity hotspots. However, biotic interactions may be challenging to investigate at large spatial scales. Leveraging well-characterized Müllerian mimetic systems in Neotropical butterflies, we investigated spatial patterns of mutualistic mimetic interactions within and between two tribes of aposematic Nymphalid butterflies: the Heliconiini and the Ithomiini. Despite 85 My of independent evolutionary histories, many species share similar warning wing patterns across the Neotropics.

In this study, we show that both tribes display similar biodiversity hotspots with a high prevalence of rare species and mimetic patterns in the tropical Andes. However, we reveal a higher relative richness of heliconiine butterflies than ithomiines in the Amazon basin contrasting with the Andean concentration of ithomiine diversity. Despite this difference in broadscale diversity patterns, we also document large-scale spatial associations among phenotypically similar species within and between tribes, thereby providing new empirical evidence for Fritz Müller’s historical model of mutualistic mimicry at a continental scale. Furthermore, comparative phylogenetic analyses suggest that co-mimetic species within and between tribes have converged towards similar climatic niches as a response to selection favoring co-occurrence.

Our findings illustrate the power of mutualistic interactions in shaping large scale distribution patterns and supporting niche convergence even across evolutionarily distant lineages. Critically, it also emphasizes the pervasive vulnerability of mimetic communities, bound by positive interactions, to disassembly induced by climate change.

**238 words**

**Keywords**

biodiversity hotspots, comparative phylogenetic analyses, heliconiines, ithomiines, Müllerian mimicry, Neotropical butterflies, niche convergence, spatial co-occurrence.

## Significance statement

Significance statement (Direct and Contributed Submissions only)

* + Explain the significance of the research at a level understandable to an undergraduate-educated scientist outside their field of specialty
  + Include no more than 120 words

Not sure how not to simply paraphrase the Abstract…

Müllerian mimicry is a remarkable example of convergent evolution driven by natural selection where coexisting prey species converge in their warning signal advertising their defenses to predators. Heliconiine and ithomiine butterflies found throughout Neotropical rainforests were instrumental in Fritz Müller’s historical model, which provided the mechanism for such resemblance. Leveraging decades of fieldwork observations and museum collections, we show that species with similar color patterns present strikingly similar spatial distributions, regardless of how closely related they are. Such co-occurrence appears reinforced by the evolution of similar climatic requirements among look-alike species. Our findings emphasize the influential role of mutualistic interactions in shaping large-scale patterns of biodiversity and supporting convergence in the niches of species spanning across phylogenetically distant clades.

**119 words**

Cover letter

Dear Editorial Board and Editors,

On behalf of all co-authors, I am pleased to submit a manuscript entitled “Müllerian mimicry in Neotropical butterflies: One mimicry ring to bring them all, and in the jungle bind them” for consideration for publication as an original research article in PNAS.

In this study, we investigate the importance of positive interactions in guiding species niche evolution and shaping biodiversity patterns and community composition at a large spatial scale. We explore this topic using Müllerian mimicry in Neotropical butterflies, an emblematic example of mutualistic interactions between defended prey species, as a textbook case-study. We focus on the highly diverse nymphalid tribes of Heliconiini and Ithomiini, which were instrumental in the discovery and formal description of mimicry by Bates (1862) and Müller (1879), and greatly facilitated the acceptance among the general public of Darwin’s and Wallace’s theory of evolution by means of natural selection. Despite ca. 85 My of independent evolutionary histories, many species in the two tribes share similar warning wing patterns across the Neotropics.

Leveraging decades of fieldwork observations and museum collections, we show that phenotypically similar species present striking broadscale associations in spatial distributions and climatic niche evolution both within and between tribes, thereby providing new empirical support for Müller’s historical model of mutualistic mimicry at a continental scale. Furthermore, our comparative phylogenetic analyses suggest that the similarity in climatic niche among co-mimetic species is caused by evolutionary convergence, likely as a consequence of selection favoring both the phenotypic convergence of sympatric species and the co-occurrence of look-alike species.

Our findings emphasize the traditionally overlooked importance of intraguild positive interactions in ecology and evolution, by illustrating how they can shape large scale distribution patterns and support niche convergence even across evolutionarily distant lineages. As such, we believe our study will appeal to a wide audience interested in community ecology, evolutionary biology, biogeography, and conservation biology, and that it may be suitable for publication in your journal. We thank you for your time and consideration and look forward to hearing from you.

Sincerely yours,

Maël Doré

Editorial Board members (3 to 5)

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**Susan P. Harrison (University of California, Davis)**

* Research in the Harrison lab seeks to understand the processes that shape and maintain plant species diversity at the landscape scale, where small-scale forces such as competition and facilitation interact with large-scale forces such as niche evolution and dispersal. Studying the highly diverse and endemic-rich Californian flora, they found that major patterns in diversity at the species, functional, and phylogenetic scales align with the regions’ strong climatic gradients in a way that suggests an overriding influence for regional biogeographic history. In turn, diversity within local communities strongly reflects these larger-scale regional influences. Working in both northern Californian grasslands and southern Oregon forest understories, they found that plant community diversity has declined in response to the warmer and/or drier climate of recent decades, and that species with functional traits indicating drought-intolerance were especially likely to have been lost. However, these effects of climate on diversity appeared to be weaker in settings where nutrients rather than water are the most limiting resource, and where the physical environment selects for species with stress-tolerant functional traits.

**Simon A. Levin (Princeton University)**

* My principal interests are in understanding how macroscopic patterns and processes are maintained at the level of ecosystems and the biosphere in terms of ecological and evolutionary mechanisms that operated primarily at the level of organisms. Much of my work is concerned with the evolution of diversification, the mechanisms sustaining biological diversity in natural systems, and the implications for ecosystem structure and functioning. The work integrates empirical studies and mathematical modeling, with emphasis on how to extrapolate across scales of space, time, and organizational complexity. The essential mathematical challenge is the development of macroscopic descriptions for the collective behavior of large, heterogeneous ensembles that are subject to continual evolutionary modifications. Specific attention is directed to evolution and ecology of dispersal. Current systems of study include plant communities and marine open-ocean and intertidal systems. I have also been interested in the self-organization and evolution of strain structure in influenza A. I have also been involved in the conservation implications of the basic ecological work, with emphasis on reserve design and on economic linkages.

**Pablo A. Marquet (Pontificia Universidad Catolica de Chile)**

* Marquet, a leading Latin American ecologist, has made seminal contributions to macroecology, complexity theory, metapopulation theory, and conservation of terrestrial and marine ecosystems. He seeks to develop general theory to account for observed patterns in the abundance, distribution, and diversity of species, and to address practical problems of human impacts. Marquet, a leading Latin American ecologist, has made seminal contributions to macroecology, complexity theory, metapopulation theory, and conservation of terrestrial and marine ecosystems. He seeks to develop general theory to account for observed patterns in the abundance, distribution, and diversity of species, and to address practical problems of human impacts.

**Nancy A. Moran (The University of Texas at Austin)**

* Moran is a world leader in the study of the evolutionary aspects of plant-insect interactions. Her work on mutualistic, endosymbiotic associations has revolutionized our view of the nature of coevolutionary interactions and of the adaptation to host plants by insects. My long-term interests are in the evolution of biological complexity, such as that apparent in complex life histories, in intimate interactions among species and in species-diversity of clades and communities. My focus is on symbiosis, particularly that between multicellular hosts and microbes. Symbioses are central in the evolution of complexity; have evolved many times and are critical to the lifestyles of many animals and plants and also to whole ecosystems, in which symbiotic organisms are key players. The primary reason that symbiosis research is suddenly active, after decades at the margins of mainstream biology, is that DNA technology and genomics give us enormous new ability to discover symbiont diversity, and more significantly, to reveal how microbial metabolic capabilities contribute to the functioning of hosts and biological communities. My ongoing projects, mostly collaborations with students and postdoctoral associates, include phylogenetic and genomic studies of previously unstudied insect symbioses, experiments on gene expression of symbionts within hosts, computational reconstruction of the content and arrangement of genes in bacterial ancestors, and experimental investigations of facultative symbioses that are heritable but more labile within host lineages.

**Geerat J. Vermeij (University of California, Davis)**

* My research centers on the question how and in which directions evolution has proceeded as the consequence of competition- and predation-related selection. Although the focus has been on the functional morphology and history of shell-bearing molluscs, I have also worked with plants and crustaceans and have considered patterns in life's history broadly from its beginnings to the ascent of our own species. A secondary interest involves biogeography, where the focus is on how faunal dominance has changed over geological time. I have also explored fundamental parallels between economics and evolution and considered how ecosystems collapse and recover.

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**Daniel Janzen (University of Pennsylvania)**

* I am a tropical ecologist who specializes on animal-plant interactions in Costa Rican tropical dry forest and on biodiversity development and management of large conserved tropical ecosystems. I work as a team with my wife, Winnie Hallwachs, likewise a tropical ecologist. Special research emphasis is given to Lepidoptera larvae (caterpillars), their food plants, and their parasitoids (parasites). This information is processed into user-friendly databases, images and web pages for the public domain available at . Special conservation emphasis is given to seeking ways for decentralized administration of the non-damaging use of large conserved wildlands by society. Examples are biodiversity prospecting, carbon sequestration, ecotourism, biodiversity services to agriculture, and direct field research.

**Paul R. Ehrlich (Stanford University)**

* Ehrlich is best known as one of the originators of the modern concept of coevolution; with P. H. Raven he coined the term, and his work on butterfly-plant interactions has played a key role in documenting the complexities of the process. He has also pioneered in the long-term studies of population structure, demonstrating for example the great importance of limited dispersal in speciation and local extinction. My research interests include genetics, dynamics, and structure of insect populations; coevolution, especially of insects and plants; human ecology, especially the interactions among population growth, resource depletion, environmental deterioration, and social variables; environmental consequences of nuclear war; human crowding; perception; the biology of butterflies, birds, and coral reef fishes; the theory of taxonomy; and butterfly taxonomy.

**Jonathan Losos (Washington University in St. Louis)**

* Jonathan Losos is an evolutionary ecologist whose research take a multi-disciplinary, integrative approach to understanding evolutionary diversification. Focusing on the diversity of lizards in the genus Anolis, Losos combines studies of ecology, behavior, functional morphology and systematics to address why the evolutionary radiation of anoles (400+ species) has been so successful and how particular species adapt to their environments. To address these questions, Losos and colleagues conduct experimental studies of evolution in nature, sequence genomes, observe animals in their natural habitats to study behavior and ecology, and bring lizards into the laboratory for biomechanical, physiological and developmental studies.

**Daniel Simberloff, (The University of Tennessee, Knoxville)**

* Simberloff's studies have altered our understanding of ecological community structure. He blends theory, simulation and empirical work with powerful statistical analysis of biogeographic data to relate microscopic and macroscopic phenomena in community development, especially regarding the role of invasive species. His pioneering work helped launch the field of island biogeography.

Suggested reviewers (3 to 6)

*Between 3 and 6 suggested reviewers are required. Up to 3 non-preferred reviewers are allowed.*

*Should tend to be diverse in gender and origins*

A brief justification for suggested reviewers is welcome

Kimberly S. Sheldon (University of Tennessee, USA): Insect tropical ecology and biogeography. Community disassembly in tropical mountains

Yves Basset (STRI): Entomology, Tropical rainforests, Plant-insect interactions, Insect conservation, Tropical Ecology

Lucia G. Lohmann (Universidad de Sao Paulo, Brazil): Biogeography, SDM, Systematics of Neotropical Flora

Guillaume Chomicki (University de Sheffield, UK): Evolution in tropical Andes (plants), evolution of mutualism

Jan Beck (University of Colorado, USA): Macroecology and Biogeography of Tropical Lepidoptera

**Intro = 1075**

**R = 1659**

**D = 1966**

**MM = 1590**

**I+MM+R+D = 6,290 words**

## Introduction (1075 words)

Biotic interactions are known to structure ecological communities (Bascompte, 2009) but their impact on biodiversity patterns remains difficult to quantify, especially at large spatial scales (Gaüzère et al., 2022; Windsor et al., 2023). There is a large diversity of biotic interactions, typically characterized by their effects on the fitness of interacting partners. These 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 a similar resource, 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 on Earth (Bascompte, 2009).

Extensive theoretical and empirical evidence supports the role of negative intraguild interactions in driving spatial and phenotypical divergence among competing species (Brown & Wilson, 1956; Dayan & Simberloff, 2005; Hardin, 1960; Webb et al., 2002). By contrast, intraguild mutualistic interactions remain some of the most understudied (Elias et al., 2009), yet they can also have important consequences for both trait evolution and the geographic distributions of species involved. For instance, selection may favor evolutionary convergence in flowering phenology as well as floral traits which allow different plant species to benefit from attracting a similar group of pollinators (Kantsa et al., 2017; Moeller, 2004; Sakai, 2002; Thomson & Wilson, 2008). Furthermore, facilitation shapes the distribution of plant species allowing the cooccurrence of distantly related species, thus enhancing phylogenetic diversity (Carrión et al., 2017; Valiente-Banuet & Verdú, 2007). However, such potentially broadscale effects of intraguild mutualistic interactions 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 on species niche evolution and community composition at large spatial and phylogenetic scales. Müllerian mimicry occurs between coexisting prey species that have evolved similar warning patterns advertising their defenses to predators (Ruxton et al., 2004; Sherratt, 2008). Such intraguild interactions are mutualistic because species displaying the same warning pattern benefit from sharing the mortality cost of educating naive predators among a larger set of individual prey (Müller, 1879). Müllerian mimicry has been described in many organisms, including birds, insects, snakes, fishes, and amphibians (Alexandrou et al., 2011; Dumbacher & Fleischer, 2001; Motyka et al., 2021; Muñoz-Ramírez et al., 2016; Symula et al., 2001; Williams, 2007; Wilson et al., 2015). Numerous independent origins across distantly related taxa reinforce the idea that Müllerian mimicry represents a selective advantage for defended prey (Mallet & Barton, 1989; Müller, 1879; Sherratt, 2008). Unlike many ecological interactions, Müllerian mimicry is relatively straightforward to characterize: in a given community, defended prey species sharing a common warning signal form groups called ‘mimicry rings’ underlying mutualistic interactions (Joron & Mallet, 1998; Papageorgis, 1975; Weismann, 1904), while species harboring different signals do not interact through mimicry.

Two diverse tribes of Neotropical nymphalid butterflies, the Heliconiini Swainson, 1822 and Ithomiini Godman & Salvin, 1879, provide an excellent study system to assess the effect of Müllerian mimicry on species distributions and ecological niches between two distantly related clades (**Fig. 1.b;** Chazot, et al., 2019b). Both tribes were instrumental in the discovery (Bates, 1862) and formalization of Müllerian mimicry (Müller, 1879), a pivotal finding that provided both empirical and theorical supports for the then young theory of evolution by the means of natural selection formulated concomitantly by Charles Darwin and Alfred Russel Wallace (Darwin, 1859; Wallace, 1858). All species in Heliconiini and Ithomiini tribes are considered to be chemically defended to varying degrees, thereby unpalatable to predators (Arias et al., 2016; Brown Jr, 1984; McCauley, 2006; 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 synthesize *de novo* compounds from amino-acids (Engler-Chaouat & Gilbert, 2007), whereas ithomiines mostly derive toxic compounds from feeding on decaying Boraginaceae and Asteraceae flowers as adults (Brown Jr, 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 (Doré et al., 2022; Rosser et al., 2012). Throughout this wide range, many species interact both within and between the tribes via Müllerian mimicry.

The tribe Heliconiini contains ca. 8 genera, 77 species and 457 subspecies (Jiggins & Lamas, 2017; Kozak et al., 2015, but see Núñez et al., 2022 for recent proposed taxonomic updates). The tribe Ithomiini contains 42 genera, 396 species and 1542 subspecies (Chazot, et al., 2019a; Doré et al., 2022) whose some are known for their partially transparent wings, such as the emblematic glasswing butterfly *Greta morgane oto* (**Fig. 1.a**). Despite having diverged about 85 million years ago (**Fig. 1.b;** Chazot, et al., 2019b), the same distance as humans from flying lemurs (Order: Dermoptera; Upham *et al.* 2019), the two tribes share numerous warning patterns, thus interact through mimicry (**Fig. 1.a**).

A chart of different butterflies

Description automatically generated with medium confidence

**Figure 1. (a) Diversity of wing patterns within and between tribes for Ithomiini and Heliconiini.** The four central subspecies represent examples of subspecies that share similar wing patterns and take part in Müllerian mimicry interactions. 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 elevates elevatus*, *Eueides isabella dissoluta*, *Mechanitis lysimnia utemaia, Tithorea harmonia helicaon*, *Greta morgane oto*. Comprehensive plates of the 39 heliconiine mimetic groups (**Fig. S1**) and 44 ithomiine mimetic groups (**Fig. S2**) are available in **Appendix 1**. **(b) Relative position of Ithomiini and Heliconiini tribes in the Nymphalidae phylogeny.** Extracted from Chazot, et al., (2019b). Tip labels represent butterfly subfamilies except for Danainae and Heliconiinae, which are divided into tribes. The red-dotted line represents the estimated divergence time between Heliconiini and Ithomiini.

Recent work showed that mutualistic interactions have led to large-scale spatial associations and climatic niche convergence between phenotypically similar species in ithomiine butterflies (Doré et al., 2023). Here, we extend that work to investigate the effects of mimicry between the Heliconiini and Ithomiini tribes on large-scale biodiversity patterns. While biogeographic patterns of species richness in heliconiine butterflies are already known (Rosser et al., 2012), no study has yet investigated the biodiversity patterns of both tribes in an integrated framework. An integrative approach encompassing the two most diverse adaptive radiations of Neotropical mimetic butterflies (Doré et al., 2022; Kozak et al., 2015) is crucial to jointly define mimicry rings in local butterfly communities and provides strong statistical support for the co-occurrence of phenotypically similar butterfly species throughout the Neotropics. From an evolutionary perspective, it allows a better understanding of the role of mimetic interactions in shaping large-scale distribution patterns, and niche and trait evolution across phylogenetically distant clades (Page et al., 2024).

Specifically, we aim to:

1. Map multiple facets of Heliconiini biodiversity including species richness, phylogenetic diversity, geographic rarity, and mimicry richness, and test for congruences and disparities with Ithomiini biodiversity patterns described in Doré et al. (2022).
2. Test whether phenotypically similar species co-occur at large spatial scales, supporting pervasive mutualistic interactions between Heliconiini and Ithomiini.
3. Test if mutualistic interactions are associated with the convergence of the climatic niche of phenotypically similar species within and between tribes throughout the Neotropics.

## Results (1659 words)

We classified subspecies into 39 groups of wing pattern similarity forming 'mimetic groups' of phenotypic patterns (**Fig. S1** in **Appendix 1**). Because those groups are based only on phenotypic similarity, members of such groups may not currently be involved in mutualistic interactions as they may not actually co-occur. Each group represents ‘putative’ local mimicry rings (as in Doré *et al.,* 2023). If a significant signal of spatial co-occurrence within a 'mimetic group' is detected, it then qualifies as an ‘effective mimicry ring’, tentatively depicting ecological interactions (Sanders et al., 2006; Wilson et al., 2022). We employed a curated database of 67,563 georeferenced occurrences of heliconiine butterflies to predict subspecies distributions and broadscale biodiversity patterns for Heliconiini. Ithomiini biodiversity patterns used for inter-tribe comparisons were extracted from Doré et al., 2022.

### Congruence and contrasts in biodiversity patterns between tribes

While we found significant correlations in global biodiversity patterns and location of hotspots, we also detected notable regional differences between the two tribes (**Tables S1** in **Appendix 4**; see **Fig. S3** in **Appendix 2** for a map of bioregions). Similar to the pioneering work on heliconiine butterflies (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 species in the group predicted to be found in some 30 km × 30 km grid cells (**Fig. 2.a**; 35 out of 77 species = 45.5%; **Fig. S4.a** in **Appendix 3**). We also detected secondary hotspots of species richness in the Amazon basin and in southern Central America. These broadscale richness patterns are significantly correlated with the predictions for Ithomiini distribution (Spearman’s rho = 0.771, t-stat = 7.9, Clifford’s df = 42.7, Q95% = 1.681, p < 0.001; **Table S1** in **Appendix 4**), which also show a peak of species richness in the Andes and southern Central America (Doré et al., 2022). However, the Ithomiini have proportionally fewer species in the Amazon basin and the Brazilian Atlantic Forest (**Fig. 2.a)**. Finally, Heliconiini are present in the Nearctic region, while Ithomiini are almost not found further north than Mexico (**Figs. S4.a & S5.a** in **Appendix 3**).

Phylogenetic diversity in Heliconiini was highly correlated with species richness (Spearman’s rho = 0.993, t-stat = 32.07, Clifford’s df = 14.6, Q95% = 1.757, p < 0.001; **Table S2** in **Appendix 4**) with the highest values also found in the Andes and around the Amazon River, and with secondary hotspots in Central America and the Brazilian Atlantic Forest (**Fig. 2.b; Fig. S4.b** in **Appendix 3**). However, while Ithomiini phylogenetic diversity was mostly concentrated in the Andes (**Fig. 2.b**; **Fig. S5.b** in **Appendix 3**; Doré et al., 2022), less spatial variance was predicted for Heliconiini (Coefficients of Variation asymptotic test: CVHeliconiini = 0.355, CVIthomiini = 0.633, χ² = 6.02, Clifford’s sample size = 93.7, df = 1, Q95% = 3.841, p = 0.014), with values across the Amazon basin approaching those in the Andean regions (**Fig. S4.b** in **Appendix 3)**.

The Caatinga hosts the highest proportion of heliconiine species with restricted geographical ranges (**Fig. 2.c; Fig. S4.c** in **Appendix 3**) due to the occurrence of taxa restricted to this semi-arid region, though this pattern hinges on a couple of taxa only (Dantas et al., 2021). Meanwhile, geographical rarity scored the 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 are found in the Andes and in Central America (**Fig. 2.c; Fig. S5.c** 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 = -0.014, t-stat = -0.11, Clifford’s df = 57.5, Q95% = 1.672, p = 0.542; **Table S1** in **Appendix 4**).

Spatial patterns of mimicry richness in heliconiines (i.e., the number of ‘mimetic groups’ represented at a given location) were strongly correlated to those of heliconiine species richness (Spearman’s rho = 0.983, t-stat = 7.45, Clifford’s df = 41.1, Q95% = 1.683, p < 0.001; **Table S2** in **Appendix 4**) and mimicry richness in ithomiines (Spearman’s rho = 0.758, t-stat = 7.45, Clifford’s df = 41.1, Q95% = 1.683, p < 0.001; **Table S1** in **Appendix 4**). Both tribes displayed a sharp contrast between the Andes and the rest of the continent. Maximum mimicry richness was reached in the northern Andes, where up to 24 (61.5%) of the 39 Heliconiini mimetic patterns and 29 (65.9%) of the 44 Ithomiini mimetic patterns are predicted to be found in local grid cells (**Fig. 2.d; Fig. S5.d** in **Appendix 3**; Doré et al., 2022). Mimicry richness in the Western Amazon basin stands out much less for Heliconiini than for Ithomiini (**Fig. 2.d; Fig. S4.d** in **Appendix 3**) because of a higher number of local species sharing mimicry patterns compared to the Andes. ‘Mimetic groups’ of Heliconiini in the Amazon comprise between 1.5 to 3 species on average but only up to 1.5 species in the Andes (**Fig. 2.e; Fig. S4.e** in **Appendix 3**). Furthermore, high mimetic geographic rarity indicates the presence of ‘mimetic groups’ with smaller distribution ranges in the Andes compared to the rest of the continent (**Fig. 2.f**). Meanwhile, ithomiines form larger ‘mimetic groups’ in the Andes, the western Amazon, Central America, and the Brazilian Atlantic Forest, with between 3.5 to 7 species per group on average (**Fig. 2.e; Fig. S5.e** in **Appendix 3**; Doré et al., 2022). However, ithomiine and heliconiine ‘mimetic groups’ are fairly similar to each other in terms of geographic rarity (Spearman’s rho = 0.557, t-stat = 5.03, Clifford’s df = 56.2, Q95% = 1.672, p < 0.001; **Table S1** in **Appendix 4**), with widely distributed mimetic patterns in Amazonia and patterns with restricted distributions in the Andes.

A map of the world

Description automatically generated

**Figure 2: Relative patterns of biodiversity in Heliconiini and Ithomiini at the continental scale. (a)** Species richness. **(b)** Faith’s Phylogenetic Diversity (Faith, 1992) **(c)** Mean species geographic rarity. Rarity index based on species ranges. **(d)** Mimicry richness (i.e., number of local ‘mimetic groups’). **(e)** Mean mimetic group size (i.e., mean number of species per local ‘mimetic group’). **(f)** Mean mimicry geographic rarity. Rarity index based on mimetic group ranges. The bivariate color 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. Blue areas reflect higher relative diversity/rarity for Ithomiini while yellow areas reflect higher relative diversity/rarity for Ithomiini. Dark 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 **Figs. S4 & S5** in **Appendix 3**.

### Mimicry promotes broadscale 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 Bray-Curtis (BC) index to quantify dissimilarities in large-scale spatial patterns of species. We compared the observed mean BC within ‘mimetic groups’ against BC obtained from random permutation of phenotypic patterns between species as a null hypothesis depicting the absence of relationship between phenotypic patterns and spatial distributions of species. We detected that Heliconiini (Permutation test: BCobs = 0.726, BCnull Q5% = 0.869, p ≤ 0.001), Ithomiini (Permutation test: BCobs = 0.896, BCnull 5% = 0.946, p ≤ 0.001; Doré et al., 2023) and ‘inter-tribe mimetic groups’ (Permutation test: BCobs = 0.886, BCnull Q5% = 0.934, p ≤ 0.001) all display significantly lower mean spatial dissimilarities than at random (**Fig. S6** in **SI Appendix 5)**. As such, we detected a significant congruence of large-scale spatial distributions among phenotypically similar species, within and between tribes.

Tests were also carried out for each ‘mimetic group’ with at least two species. We observed that 15 out of 31 (48.4%) ‘mimetic groups’ displayed 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%) ‘mimetic groups’ within the Ithomiini (Doré et al., 2023). For ‘inter-tribe mimetic groups’, 6 out of 8 (75%) showed significant spatial congruence and are thus supported as ‘effective mimicry rings’ (**Table S3** in **Appendix 6**). For instance, the MOTHONE group showed an important and significant overlap between tribes (**Fig. 3.a**; Permutation test: BCobs = 0.731, BCnull Q5% = 0.901, p ≤ 001), with most species found in the Andes. On the contrary, the group MANTINEUS showed no overlap between the two tribes (**Fig. 3.b**; Permutation test: BCobs = 1, BCnull Q5% = 0.945, p = 1), with Ithomiini species only found in the western lowlands across Ecuador and Colombia, and Heliconiini species found in the Brazilian Atlantic Forest, the Caatinga, the lower Amazon and the Guyana Shield. The MAMERCUS group presented a remarkable pattern where Heliconiini species display a disjunct distribution spread between the lower Amazon and several mountain ranges in the Andes that may seem puzzling at first in the context of mimicry. However, their co-mimetic ithomiine species collectively occupy a wide geographical range, from Central America to Argentina, encompassing entirely the disjunct distribution of Heliconiini species, thus effectively acting as mimetic partners for the isolated heliconiine species (**Fig. 3.c**). Despite this important overlap at group level, the non-significance of the spatial congruence test for this ‘mimetic group’ (Permutation test: BCobs = 0.948, BCnull Q5% = 0.929, p = 0.564) was likely due to the small number of Heliconiini taxa (4) with restricted ranges compared to Ithomiini (64), limiting the spatial overlap between most of the pairs between tribes.

A map of the world with a butterfly

Description automatically generated

**Figure 3: Comparative distributions of predicted presence for Heliconiini and Ithomiini ‘mimetic groups’ defined on the basis of phenotypic similarity.** **(a)** MOTHONE group. **(b)** MANTINEUS group. **(c)** MAMERCUS group.

### Mimicry is associated with 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 ‘mimetic 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 SDM. We compared the observed mean climatic niche distance (i.e., MCD) within ‘mimetic 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 ‘mimetic group’ (Heliconiini only: MCDobs = 0.670, MCDnull Q5% = 0.919, p ≤ 001; Ithomiini only: MCDobs = 0.782, MCDnull Q5% = 0.959, p ≤ 001 from Doré et al., 2023; inter-tribe: MCDobs = 0.785, MCDnull Q5% = 0.812, p = 0.029). Therefore, we detected a significant signal for the evolutionary convergence of the climatic niche among phenotypically similar species, both within and between tribes, as species in ‘mimetic groups’ tend to have more similar climatic niches than expected under neutral niche evolution.

Overall, we observed that 9 out of 31 (29.0%) of ‘mimetic groups’ in Heliconiini, and 33 out of 39 (84.6%) ‘mimetic groups’ in Ithomiini (Doré et al., 2023), showed significant niche convergence. For ‘inter-tribe mimetic groups’, niche convergence was supported for 2 out of 8 (25.0%) groups (**Table S4** in **Appendix 6**).

## Discussion (1966 words)

Our study highlights the power of mutualistic interactions to shape large scale distribution patterns and to support species niche convergence across evolutionarily distant lineages. Specifically, we showed how Müllerian mimicry shapes large-scale spatial distributions and niche evolution within and between two emblematic tribes of unpalatable Neotropical butterflies that diverged from a common ancestor roughly 85 million years ago.

Both heliconiine and ithomiine butterflies display a high diversity and concentration of species and mimicry patterns in the tropical Andes, with an important proportion displaying 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, we provided further evidence that mimicry is associated with large scale spatial congruences among phenotypically similar species, both within and between tribes. This finding provides new empirical evidence for the unfolding of the prediction of Müller’s mimicry model at a macroecological scale and across large phylogenetic spans. Furthermore, comparative phylogenetic analyses suggested that mimetic interactions support the evolutionary convergence of the climatic niche of phenotypically similar species within and even across tribes as a consequence of selection favoring both the phenotypic convergence of sympatric species and the co-occurrence of look-alike species.

### Biogeographic history, topographic heterogeneity, and host plant distributions may explain global biodiversity patterns

Our analyses predict species richness and phylogenetic diversity of Heliconiini to be particularly high in the Amazon basin and in the tropical Andes (**Fig. 2**), in accordance with previous investigations (Rosser et al., 2012, 2021). Ithomiini also exhibit high specific and phylogenetic diversity patterns in these regions, especially in the tropical Andes (Chazot, Willmott, Freitas, Lisa De Silva, et al., 2016; Doré et al., 2022; **Fig. S5** in **Appendix 3**). Those congruent biodiversity patterns are similar to those observed in other taxa, including angiosperms (Ter Steege et al., 2003), beetles (Pearson & Carroll, 2001), birds (Orme et al., 2005), mammals (Kaufman & Willig, 1998), reptiles (Roll et al., 2017), and amphibians (Hutter et al., 2017). As such, the tropical Andes are the richest biodiversity hotspot on Earth (Hutter et al., 2017; Myers et al., 2000). This outstanding biodiversity can mostly be explained by geological and climatic factors. The topographical complexity of recent mountain regions such as the tropical Andes facilitates fine-scale spatial variation of environmental conditions and provides more opportunities for parapatric and allopatric speciation fueling regional adaptive radiations (Bouchenak-Khelladi et al., 2015; Rangel et al., 2018; Särkinen et al., 2012). Moreover, the tropical Andes and the Amazon basin have benefited from a relative historical climatic stability thought to reduce species extinction rate (Colinvaux & De Oliveira, 2001; Fine, 2015) and allowing for the long-term persistence of high levels of species diversity and endemism (Araújo et al., 2008; Harrison & Noss, 2017; Rull & Carnaval, 2020; Svenning et al., 2015). Noticeably, the Brazilian Atlantic Forest, although far away from the other hotspots, harbors a relatively high diversity for both Heliconiini and Ithomiini. This disjunct pattern could be explained by multiple independent colonization events resulting from changing connectivity with Amazonia (Brown Jr, 1982; Chazot, et al., 2019a; Lisa De-Silva et al., 2017), followed by local diversification in the Brazilian Atlantic Forest facilitated by an adequate environment of dense complex forests.

While broadscale 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 appears strikingly concentrated in the tropical Andes (Chazot, et al., 2016b; Doré et al., 2022), while heliconiines harbor high richness in the Amazon basin too, not far-off of what can be encountered in the Andes (**Fig. 2.a**). Such contrast could be explained by the different geographic origin of the tribes. While the Ithomiini are predicted to originate from the Central Andes (Chazot, et al., 2019a), formal historical biogeographic reconstructions at the tribe level are still lacking for Heliconiini (Merrill et al., 2015). Given more time to speciate and accumulate lineages regionally, species richness patterns hint for a possible Amazonian origin of the Heliconiini tribe, contrasting with the Andean origin of Ithomiini. Perhaps more notably, both tribes are composed of specialized species that typically feed on a small number of larval host plant species (Benson et al., 1975; Willmott & Mallet, 2004). However, heliconiines and ithomiines are specialized on two distinct families of plants, the Passifloraceae and the Solanaceae, with which they are respectively suspected to have tightly coevolved (Chazot, Willmott, Freitas, de Silva, et al., 2016b; Jiggins & Lamas, 2017; Willmott & Mallet, 2004). Thus, differences in biogeographic histories and species richness patterns of the two host plant lineages (Dupin et al., 2017; Hunziker, 2001; Muschner et al., 2012) could partly explain the current dissimilarities observed in biodiversity patterns between the two butterfly tribes.

Beyond taxonomic and phylogenetic patterns, both tribes exhibit contrasting mimetic characteristics between the Andean and Amazonian communities. A few large-range and species-rich ‘mimetic groups’ dominate mimetic butterfly communities in the Amazon basin (**Fig. 2.d-f**). This suggests a pervasive wing pattern convergence between distant lineages and/or high degree of phenotypic conservatism within local radiations acting along a 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 ‘mimetic groups’ have a smaller distribution area and are composed of fewer species, there is a higher diversity of mimetic patterns per grid cell (**Fig. 2.d-f**). This is likely explained by strong environmental gradients and geographic barriers present in these mountainous regions. These abiotic features favor partitioning of predator and prey communities across space, which incurs selection on mimicry patterns at a scale smaller than our 30 km × 30 km grid cells, thereby driving the partitioning of species among more ‘mimetic groups’ (Gompert et al., 2011).

### Large-scale spatial congruence of phenotypically similar species

Despite showing some minor disparities in global biodiversity patterns, the two tribes are strongly linked through mimetic interactions. An important proportion of the ‘mimetic groups’ identified within and between both tribes show significant large-scale spatial congruence (e.g., MOTHONE pattern in **Fig. 3.a**) and thus likely represent ‘effective mimicry rings’ as groups of species involved in mutualistic interactions in local communities.

Our study also highlighted the importance of accounting for multiple members of the mimetic community when investigating how mutualistic interactions shape the distribution of species, even when those are distantly related. For example, when studying the Heliconiini group MAELUS, we found no evidence of co-occurrence nor climatic niche convergence among species for this ‘mimetic group’, likely because of low sample size (**Table S3** in **Appendix 6**). Yet, once accounting for the Ithomiini members in the ‘inter-tribe mimetic group’, we detected an overall significant signal for spatial congruence and niche convergence (**Tables S3 & S4** in **Appendix 6**). Similarly, the Heliconiini group MAMERCUS presented a disjunct distribution pattern (**Fig. 3.c**) that seemed hardly coherent at first sight. Yet, once studied in relation to its Ithomiini counterpart, it formed a continuous range since the distribution of co-mimetic ithomiine species encompasses the different geographic patches of heliconiines belonging to this ‘mimetic group’ (**Fig. 3.c**).

Despite a high proportion of species with a similar wing pattern showing significant spatial co-occurrence, and thus likely representing current mimetic interactions, in some rare cases similar-looking species displayed disjunct distribution areas (i.e., MANTINEUS group in **Fig 3.b**). In these cases, the similarity of patterns could tentatively be explained by co-occurrence in the past that led to local pattern convergence followed by different dispersal trajectories leading to current disjunct areas. However, this is unlikely for the MANTINEUS group considering the important geographic distances and topographic barriers separating the two components. Thus, the similarity in phenotypes may have arisen by chance (i.e., genetic drift).

### Climatic niche associations over 85 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 behavior (Page et al., 2024), and for ecological dimensions acting at local scales, such as nocturnal roosting habitat height (Mallet & Gilbert, 1995), flight height (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 convergence can arise for niche dimensions (i.e., climatic niche) that directly affect large scale biodiversity patterns and link the fate of two tribes that, despite being separated by over 85 My of independent evolution, are currently sharing highly similar phenotypes, spatial distributions and associated climatic niches.

Such strong adaptive bonding 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 competition (Aubier & Elias, 2020), and fueling higher local richness (Aubier et al., 2017; Gross, 2008). 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 harboring unknown phenotypes in the newly colonized areas (Langham, 2004; Mallet & Barton, 1989). 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 (Sheldon et al., 2011; Svenning et al., 2015; Toby Kiers et al., 2010). Finally, the effects of climate change on biotic factors that affect local abundance, such as host plants (Hamann et al., 2021; Schweiger et al., 2008) and parasitoids (Gentry, 1998; Longino, 1984), may also differ among interacting species, impeding even more their abilities to cope with climate change as tightly coevolved assemblages tied by positive interactions (Tylianakis et al., 2008).

### Limitations and perspectives

We found a statistical support for climatic niche convergence within ‘mimetic groups’ of phenotypically similar species, within and between tribes. However, our analyses do not allow to disentangle whether this evolutionary association of species climatic niche and aposematic patterns resulted from selection favoring the phenotypic convergence of sympatric species or the co-occurrence and associated niche convergence of look-alike species. In practice, both mechanisms are likely involved (Doré et al., 2023). Besides favoring 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 colonization of new environments shared with their mimetic partners resulting in niche convergence. In the peculiar case of frequency-dependent Müllerian mimicry, such evolution likely occurs through advergence rather than gradual convergence with the rarest species evolving towards the more abundant, thus better numerically defended, species (Turner, 1984). Most likely in our system, heliconiine have been adverging towards ithomiines both because of color pattern ancestry, such as heliconiine subspecies of *Heliconius numata* mimicking different ithomiine species of *Melinaeae* (Joron et al., 1999), and greater numerical abundances in ithomiines (Bates, 1862; Beccaloni, 1997a).

While ithomiines and heliconiines form the bulk of butterfly mimetic communities in the Neotropics (Beccaloni, 1997a; Poole, 1970), they also interact with a wide range of other mimetic butterflies and moths, such as the chemically defended Dioptinae (Notodontidae; DeVries, 1994) and Pericopina (Erebidae; Brown Jr, 1979), numerous presumed innoxious Batesian mimics such as Dismorphiinae butterflies (Pieridae; Poulton, 1898) and even damselflies (Corral-lopez et al., 2021; Outomuro et al., 2013). 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 on this research topic may aim to enlarge the taxonomic scope and shed light on the importance of mimetic interactions in shaping large spatial biodiversity patterns across evolutionary distantly related lineages.

## Materials and Methods (1590 words)

### Mimicry classification

We classified heliconiine subspecies into 39 groups of wing pattern similarity forming 'mimetic groups' of phenotypic patterns (**Fig. S1** in **Appendix 1**) representing ‘putative’ local mimicry rings (as in Doré *et al.* 2023). Because those groups are 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 ' mimetic group' is detected, it then qualifies as an ‘effective mimicry ring’, tentatively depicting true ecological interactions (Sanders et al., 2006; Wilson et al., 2022). We collected at least one image of dorsal wing patterns for 436 out of 457 subspecies of Heliconiini, taken from museum and private collection specimens. We visually clustered all Heliconiini images based on perceived similarity in their dorsal wing color, pattern, and shape. Geographic distributions of taxa were not considered during this process. For Ithomiini, we used the currently accepted classification of mimicry patterns (Doré et al., 2022), built using a similar rationale of phenotypic similarity, independent from geographical distributions. Then, we matched the identity of ‘mimetic groups’ associated with a pattern represented in the two tribes and labeled them as ‘inter-tribe mimetic groups’. The comprehensive phenotypic-based classification of heliconiine subspecies is available in an online archive ([10.5281/zenodo.10903197](file:///D:\Mael_D\Articles\Heliconiini%20diversity%20patterns\10.5281\zenodo.10903197)).

### 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 by records from museum collections available for the most part on <https://heliconius-maps.github.io/> (accessed on November 2020). We updated the taxonomic identity of records in agreement with the literature up to June 2021 (Jiggins & Lamas, 2017; Kozak et al., 2015, but see Núñez et al., 2022 for recent proposed taxonomic splits). This database covering 73 out of 77 species of the tribe (94.8 %) and 439 out of 457 subspecies (96.1 %) is available in [10.5281/zenodo.10906853](https://doi.org/10.5281/zenodo.10906853).

We employed the Heliconiini phylogeny of Kozak *et al.* (2015) encompassing 67 of the 77 recognized species (87 %) in the tribe to estimate indices of phylogenetic diversity and evaluate niche convergence. However, we repeated the Bayesian calculation of divergence times between Heliconiini updating the secondary calibration points in accordance with recent estimates for Papilionoidea (Chazot *et al.*, 2019a): Heliconiini-Acraeini (31.9-43.9 Mya); Podotricha-Philaethria (14.2-21.1 Mya), Heliconius-Eueides (11.6-20.3 Mya). 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 the Ithomiini tribe, we used the Ithomiini phylogeny of Chazot *et al.* (2019b) that encompasses 339 of the 396 species (85.6 %). Divergence time used to bind the two tribes' phylogenies were estimated at 84.49 My following Chazot *et al.* (2019a).

### Species Distribution Modeling (SDM)

To predict spatial distributions, we performed Species Distribution Modeling (SDM) for each subspecies of Heliconiini independently. Modeling was carried out at subspecies level because some species are polymorphic, thus may belong to several ‘mimetic groups’. The output of the SDM process was a single consensus model (ensemble model) for each subspecies that provides a proxy of likelihood 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. Temperatures 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 Jr, 1997) are important factors shaping heliconiine butterfly distribution. We extracted annual mean temperature, mean diurnal range, annual precipitation levels, and precipitation seasonality from WorldClim bioclimatic variables dataset (v2.1, accessed 02/2021; Fick & Hijmans 2017) and forest cover from the Landsat Tree Cover Continuous Fields dataset (Sexton et al., 2013) aggregated at a quarter-degree cell resolution (i.e., pixel of ca. 30 km × 30 km).

We modelled each subspecies using three different algorithms (Random Forest, Gradient Tree Boosting and Artificial Neural Network) crossed with three independent sets of pseudo-absences and three spatially structured cross-validation blocks. We calculated the median 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). OMUs are defined as all individuals of a unique species, including those spread among several subspecies, 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 ‘co-mimetic species’ and ‘phenotypically similar species’ in the text to refer to the subspecies and OMUs sharing the same mimicry pattern.

All distribution maps are available in [10.5281/zenodo.10903661](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 7**. 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.

### Diversity indices

We computed a series of indices for each community (represented by 30 km × 30 km grid cell) and mapped them throughout the whole distribution range of the two tribes:

- Species and mimicry richness, computed as the number of predicted species/mimetic group per community.

- Faith's Phylogenetic Diversity (Faith, 1992), computed as the sum of branch lengths of the phylogenetic tree including all taxa found in a community.

- Mean species & mimetic group geographic rarity (Leroy et al., 2012), computed as the weighted proportion of species or mimetic group with small geographical range per community. These indices inform on the areas where species/mimetic groups with the smallest range are concentrated.

- Mean mimetic group size, computed as the mean number of species per mimetic group for each community. This index provides insights on the degree of pattern convergence in the community as a high mean mimetic group size implies a high number of species harboring the same mimetic patterns locally.

To compare the index values between Heliconiini and Ithomiini, we mapped them together with a two-dimensional color scale, scaled by the maximum of each index for each tribe, thus describing relative patterns of biodiversity (**Fig. 2**). Additionally, we computed spatial correlation tests across all communities for each index, between the two tribes (**Table S1** in **Appendix 4**), and within Heliconiini biodiversity patterns (**Table S2** in **Appendix 4**). We ran Spearman’s rank correlation tests using 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 & Miller, 1996).

### Test for spatial association among co-mimetic species

In order to detect effects of mimetic group membership, and thus of mutualistic interactions, on the spatial distribution of Heliconiini and Ithomiini, we investigated the degree of co-occurrence of phenotypically similar species (species of the same mimetic group used as a ‘putative’ mimicry ring) across grid cells. We computed pairwise Bray-Curtis dissimilarities (Bray & Curtis, 1957), an index that quantifies differences between the distribution of two entities, in our case between pairs of OMUs. Thus, we calculated the mean Bray-Curtis dissimilarity of all OMUs within ‘mimetic 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 mimetic group membership has no effect on co-occurrence. Therefore, for each permutation, we randomized the phenotypic pattern between all OMUs to investigate whether phenotypically similar species co-occur more than expected at random, globally, and within each ‘mimetic group’. As such, an observed BC 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 labeled as ‘inter-tribe’ in subsequent analyses (**Fig. S6** in **Appendix 5**; **Table S3** in **Appendix 6**).

### Test for niche evolution among co-mimetic species

In order to investigate whether mimicry led to niche convergence between phenotypically similar species (i.e, Heliconiini only and inter-tribe groups), 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 occurrences using bioclimatic variables employed during niche modeling (i.e., annual mean temperature, mean diurnal range, annual precipitation levels, precipitation seasonality).

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 implementing additional Pagel’s lambda or/and Pagel’s kappa parameters accounting respectively for 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 0.791.

We used mean climatic distances (MCD) as the pairwise Euclidean distances between niche centroids in the climatic space to estimate the similarity of climatic niches between OMUs. To test for an 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 (**Fig. S7** in **Appendix 5**; **Table S4** in **Appendix 6**).

### Data availability

All R scripts used to conduct the analyses and generate the figures are available on GitHub (https://github.com/**XXX**) and Zenodo (https://doi.org/**XXX**). Mimicry classification, occurrences data, and maps of the distribution of subspecies, OMUs, species, and mimetic groups produced and used in this study are available from Zenodo (Occurrences data: [10.5281/zenodo.10906853](https://doi.org/10.5281/zenodo.10906853); Distribution maps: [10.5281/zenodo.10903661](https://doi.org/10.5281/zenodo.10903661); Mimicry classification: [10.5281/zenodo.10903197](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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**Supplementary Information for**

Müllerian mimicry in Neotropical butterflies: One mimicry ring to bring them all, and in the jungle bind them

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**This PDF file includes:**

* Supporting Information as Appendix 1 to 7.
* Figures S1 to S9.
* Tables S1 to S4.

Appendix 1: Mimetic groups in Heliconiini and Ithomiini

We classified subspecies of Heliconiini butterflies into 39 'mimetic groups' based on wing pattern similarity (**Fig. S1**) and representing ‘putative’ local mimicry rings (as in Doré *et al.* 2023). Because those groups are 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 ' mimetic group' is detected, it then qualifies as an ‘effective mimicry ring’, tentatively depicting true ecological interactions (Sanders et al., 2006; Wilson et al., 2022).

We labeled each ‘mimicry group’ following the rationale of a taxonomic nomenclature. For each group, we defined a ‘type’ taxon whose name was used to identify the ‘mimicry group’ and associated wing pattern. The hierarchical criteria used to select the ‘type taxa’ were as follows:

* 1/ Avoid selecting a taxon whose name is associated with a polymorphic clade. This criterion aims to prevent confusion by forbidding the labeling of ‘mimetic groups’ with a name associated with multiple patterns. For instance, among taxa with large white bands on both hindwings and forewings, the most widely spread taxa are *Heliconius cydno cydno* and *Heliconius sapho sapho*. However, both *Heliconius cydno* and *Heliconius sapho* are polymorphic species. Therefore, we selected instead *Heliconius cydno chioneus* as the ‘type taxon’, and labeled the ‘mimetic group’ CHIONEUS, preventing any confusion potentially arising from a CYDNO or SAPHO group whose names refer to species with a diversity of wing patterns.
* 2/ Selecting a taxon within the clade of highest taxonomic rank that shows pattern homogeneity (i.e., within which all taxa display patterns belonging to the same ‘mimetic group’). In such case, use the higher rank name to label the ‘mimetic group’. For instance, all *Philaethria* taxa fall within the same mimetic group (i.e., share the same wing pattern). Thus, the ‘type taxon’ was selected among *Philaethria* (i.e., *Philaethria dido dido*), but the ‘mimetic group’ was labeled PHILAETHRIA rather than DIDO.
* 3/ Selecting the taxa with the broadest geographic range, and/or the most abundant, and/or the most widely known. The idea here is to favor the selection of the most widely recognized taxa among similar-looking taxa as the type. For instance, among taxa displaying a black background with a red band on the forewings, the most widespread and best-known taxon is *Heliconius erato hydara*, which is common throughout all the north of South America. Thus, we referred to this ‘mimetic group’ as HYDARA. However, we also retained the historical label of 'RED BAND' as a synonym to ensure compatibility with the previous literature.
* 4/ Select the taxa with the oldest name, when multiple taxa are equivalent according to the previous criteria. For instance, *Heliconius pachinus* and *Heliconius hewitsoni* display similar triple white banded patterns and are found in similar areas across Central America. Since *Heliconius pachinus* was named in 1871, while *Heliconius hewitsoni* was named in 1875, we selected *Heliconius pachinus* as the ‘type taxon’ and labeled the ‘mimetic group’ PACHINUS.

The comprehensive mimetic classification of all 436 heliconiine subspecies for which we retrieved a picture is available in the online archive, alongside pictures of the ‘type taxon’ of each ‘mimicry group’ (see [10.5281/zenodo.10903197](https://doi.org/10.5281/zenodo.10903197)).

For Ithomiini, we used the currently accepted classification of mimicry patterns (**Fig. S2,** Doré et al., 2022), built using a similar rationale of phenotypic similarity, independent from geographical distributions. Then, we matched the identity of ‘mimetic groups’ associated with a pattern represented in the two tribes and labeled them as ‘inter-tribe mimetic groups’ (dash frames in **Figs. S1 & S2**). As a special case, we considered both ithomiine mimetic groups PAVONII and HUMBOLDT to be mimetic of the heliconiine group ELZUNIA. Because ‘ithomiine mimetic groups’ were defined prior to ‘heliconiine mimetic groups’, the ‘inter-tribe mimetic groups’ retained their initial name based on an ithomiine ‘type taxon’ (see [10.5281/zenodo.5497876](https://doi.org/10.5281/zenodo.5497876)).

A group of butterflies with different colors

Description automatically generated

**Figure S1: Mimetic groups in Heliconiini. ‘**Type taxon’ of each heliconiine ‘mimetic group’ representing the pattern shared by all members of such groups used in this sutdy. Groups are designed based on phenotypic similarity in shape, patterns, and colors. Labels of the group were chosen to reflect the name of the selected ‘type taxon’, yet we kept the historical labels such as ‘RED BAND’, ‘DENNIS-RAY’, and ‘POSTMAN’, as synonyms to ensure compatibility with the literature. Groups shown within the dash frame are ‘inter-tribe mimetic groups’ shared with ithomiine butterflies. They are labeled after ithomiine type taxon (Doré et al., 2022, 2023). Photo credit: C. Jiggins.

A group of butterflies with different colors

Description automatically generated

**Figure S2: Mimetic groups in Ithomiini.** Type taxon of each ithomiine ‘mimetic group’ representing the pattern shared by all members of such groups. Groups are designed based on phenotypic similarity in shape, patterns, and colors. Groups shown within the dash frame are ‘inter-tribe mimetic groups’ shared with heliconiine butterflies. Both PAVONII and HUMBOLDT groups are considered mimetic of the ELZUNIA group. Figure adapted from Doré *et al.*, 2023. Photo credit: K. Willmott.

Appendix 2: Map of bioregions

**A map of the south and south america

Description automatically generated**

**Figure S4: Map of bioregions.** Bioregions used throughout the study to describe biodiversity patterns are based on the aggregation of provinces defined in Morrone et al., (2022). White lines represent geopolitical boundaries between countries.

Appendix 3: Heatmaps of biodiversity patterns

A group of maps of different continents

Description automatically generated

**Figure S4: Heliconiini biodiversity patterns.** **(a)** Species richness. **(b)** Faith’s Phylogenetic Diversity (Faith, 1992). **(c)** Mean species geographic rarity. Rarity index based on species ranges. **(d)** Mimicry richness (i.e., number of local ‘mimetic groups’). **(e)** Mean mimicry geographic rarity. Rarity index based on mimetic group ranges. **(f)** Mean mimetic group size (i.e., mean number of species per local ‘mimetic groups’).

A group of maps of different colors

Description automatically generated

**Figure S5: Ithomiini biodiversity patterns.** Modified from Figure 3 in Doré et al., (2022). **(a)** Species richness. **(b)** Faith’s Phylogenetic Diversity (Faith, 1992). **(c)** Mean species geographic rarity. Rarity index based on species ranges. **(d)** Mimicry richness (i.e., number of local ‘mimetic groups’). **(e)** Mean mimicry geographic rarity. Rarity index based on mimetic group ranges. **(f)** Mean mimetic group size (i.e., mean number of species per local ‘mimetic groups’).

Appendix 4: Tables for spatial correlation tests

**Table S1: Tests for spatial correlation of biodiversity indices between Heliconiini and Ithomiini tribes. N = 18,006 grid cells. Rho = Spearman's rank correlation coefficient. Df adjusted with Clifford's correction (Clifford et al., 1989). Q95 = Threshold value for α = 0.05. Significance levels: \* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.001.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Index** | **Rho** | **T-stat** | **Adjusted df** | **Q95** | **p-value** |
| Species richness | 0.771 | 7.91 | 42.7 | 1.681 | < 0.001 \*\*\* |
| Phylogenetic diversity | 0.78 | 8.45 | 46 | 1.679 | < 0.001 \*\*\* |
| Mean species geographic rarity | -0.014 | -0.11 | 57.5 | 1.672 | 0.542 |
| Mimicry richness | 0.758 | 7.45 | 41.1 | 1.683 | < 0.001 \*\*\* |
| Mean mimetic group size | 0.626 | 5.87 | 53.5 | 1.674 | < 0.001 \*\*\* |
| Mean mimetic group geographic rarity | 0.557 | 5.03 | 56.2 | 1.672 | < 0.001 \*\*\* |

**Table S2: Tests for spatial correlation between Heliconiini species richness and other biodiversity indices. N = 26,539 grid cells. Rho = Spearman's rank correlation coefficent. Df adjusted with Clifford's correction (Clifford et al., 1989).** **Q95 = Threshold value for α = 0.05. Significance levels: \* = p < 0.05; \*\* = p < 0.01; \*\*\* = p < 0.001.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Index** | **Rho** | **T-stat** | **Adjusted df** | **Q95** | **p-value** |
| Phylogenetic diversity | 0.993 | 32.07 | 14.6 | 1.757 | < 0.001 \*\*\* |
| Mean species geographic rarity | 0.499 | 2.2 | 14.6 | 1.756 | 0.022 \* |
| Mimicry richness | 0.983 | 20.23 | 14.3 | 1.759 | < 0.001 \*\*\* |
| Mean mimetic group size | 0.909 | 8.4 | 14.8 | 1.754 | < 0.001 \*\*\* |
| Mean mimetic group geographic rarity | 0.844 | 6.69 | 18.1 | 1.734 | < 0.001 \*\*\* |

Appendix 5: Global tests for spatial congruence and niche convergence

A group of graphs showing different types of data

Description automatically generated

**Figure S6: Null distributions for spatial congruence tests within ‘mimetic groups’. (a)** Heliconiini **(b)** Ithomiini adapted from (Doré et al., 2023) **(c)** Inter-tribe mimetic groups. Permutation tests with 1000 randomizations. Bray-Curtis (BC) indices quantify the degree of dissimilarity in spatial distribution between pairs of OMUs. An observed mean BC value lower than the 5% quantile (Q5%) of the null distribution supports the overall spatial congruence of phenotypically similar species.

A group of graphs showing different types of data

Description automatically generated with medium confidence

**Figure S7: Null distributions for niche convergence tests within ‘mimetic groups’. (a)** Heliconiini **(b)** Ithomiini adapted from (Doré et al., 2023) **(c)** Inter-tribe mimetic groups. Phylogenetic comparative tests with 1000 simulations of neutral niche evolution (Brownian Motion model with Pagel’s lambda = 0.791). Standardized Mean pairwise Climatic Distances (MCD) quantify the degree of dissimilarity in niche centroids between pairs of OMUs. An observed mean MCD value lower than the 5% quantile (Q5%) of the null distribution supports the overall niche convergence of phenotypically similar species.

Appendix 6: Mimetic group-level tests for spatial congruence and niche convergence

**Table S3: Tests for spatial congruence within each mimetic group.** Bray-Curtis (BC) indices quantify the degree of dissimilarity in spatial distribution between pairs of OMUs within a ‘mimetic group’. An observed mean BC value lower than the 5% quantile (Q5%) of the null distribution supports the spatial congruence of phenotypically similar species within a ‘mimetic group’. Mimetic groups are listed by tribes. Tests for Ithomiini are extracted from Doré et al., (2023) for comparison. Tests for inter-tribe mimetic groups are carried out between pairs of OMUs from different tribes. BCobs = Observed mean pairwise BC. BCQ50 = Median of the null distribution. BCQ5 = Quantile 5% of the null distribution = statistical significance threshold for α = 0.05. P-value for the spatial congruence test is based on the rank of the BCobs among the null distribution obtained through random permutation of mimetic group membership (N = 1000): \* = p < 0.05; \*\* = p < 0.01; \*\*\* = p ≤ 0.001.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **MIMETIC GROUP** | **N units** | **N pairs** | **BC**obs | **BC**Q50 | **BC**Q5 | **p-value** |
| **Heliconiini tribe** | | | | | | |
| AGRAULIS | 5 | 10 | 0.867 | 0.897 | 0.747 | 0.338 |
| AMALFREDA | 8 | 28 | 0.425 | 0.901 | 0.793 | 0.001\*\*\* |
| CHARITHONIA | 5 | 10 | 0.938 | 0.903 | 0.762 | 0.741 |
| CHESTERTONII | 1 | 0 |  |  |  |  |
| CHIONEUS | 2 | 1 | 0.437 | 0.97 | 0.514 | 0.029\* |
| CRETACEA | 1 | 0 |  |  |  |  |
| CYDNIDES | 4 | 6 | 0.905 | 0.914 | 0.708 | 0.458 |
| CYRBIA | 2 | 1 | 0.172 | 0.968 | 0.491 | 0.003\*\* |
| DRYAS | 5 | 10 | 0.515 | 0.901 | 0.75 | 0.001\*\*\* |
| ELZUNIA | 2 | 1 | 0.43 | 0.981 | 0.476 | 0.035\* |
| HERMATHENA | 1 | 0 |  |  |  |  |
| HERMIAS | 6 | 15 | 0.733 | 0.9 | 0.781 | 0.014\* |
| HEURIPPA | 1 | 0 |  |  |  |  |
| HYDARA | 3 | 3 | 0.724 | 0.928 | 0.684 | 0.076 |
| JUDITH | 1 | 0 |  |  |  |  |
| LEUCE | 5 | 10 | 0.77 | 0.903 | 0.766 | 0.057 |
| LONGARENA | 1 | 0 |  |  |  |  |
| LYBIA | 4 | 6 | 0.889 | 0.905 | 0.713 | 0.404 |
| MAELUS | 2 | 1 | 0.997 | 0.972 | 0.483 | 0.608 |
| MAMERCUS | 4 | 6 | 0.973 | 0.91 | 0.716 | 0.813 |
| MANTINEUS | 3 | 3 | 0.71 | 0.916 | 0.696 | 0.056 |
| MESSENE | 1 | 0 |  |  |  |  |
| MOTHONE | 1 | 0 |  |  |  |  |
| NOTABILIS | 2 | 1 | 0.182 | 0.983 | 0.471 | 0.003\*\* |
| OCTAVIA | 2 | 1 | 1 | 0.979 | 0.478 | 1 |
| ORESTES | 5 | 10 | 0.652 | 0.908 | 0.76 | 0.007\*\* |
| PACHINUS | 2 | 1 | 0.277 | 0.981 | 0.499 | 0.005\*\* |
| PAVANA | 3 | 3 | 0.971 | 0.915 | 0.673 | 0.717 |
| PHILAETHRIA | 6 | 15 | 0.897 | 0.904 | 0.778 | 0.441 |
| PHYLLIS | 4 | 6 | 0.81 | 0.911 | 0.718 | 0.165 |
| RICINI | 7 | 21 | 0.93 | 0.902 | 0.793 | 0.693 |
| SILVANA | 4 | 6 | 0.881 | 0.903 | 0.714 | 0.4 |
| SUPERIORIS | 6 | 15 | 0.768 | 0.904 | 0.768 | 0.048\* |
| TELESIPHE | 2 | 1 | 0.148 | 0.98 | 0.478 | 0.002\*\* |
| THELXIOPE | 18 | 153 | 0.719 | 0.895 | 0.832 | 0.001\*\*\* |
| VULCANUS | 2 | 1 | 0.263 | 0.971 | 0.479 | 0.009\*\* |
| WALLACEI | 9 | 36 | 0.67 | 0.895 | 0.796 | 0.003\*\* |
| XENOCLEA | 2 | 1 | 0.395 | 0.978 | 0.505 | 0.021\* |
| ZULEIKA | 4 | 6 | 0.75 | 0.91 | 0.725 | 0.068 |
| **Ithomiini tribe** | | | | | | |
| ACRISIONE | 1 | 0 |  |  |  |  |
| AGNOSIA | 85 | 3570 | 0.924 | 0.95 | 0.936 | 0.004\*\* |
| AMALDA | 9 | 36 | 0.849 | 0.956 | 0.889 | 0.009\*\* |
| AURELIANA | 12 | 66 | 0.74 | 0.951 | 0.897 | 0.001\*\*\* |
| BANJANA-M | 45 | 990 | 0.899 | 0.95 | 0.927 | 0.002\*\* |
| CONFUSA | 20 | 190 | 0.843 | 0.953 | 0.914 | 0.001\*\*\* |
| DERCYLLIDAS | 1 | 0 |  |  |  |  |
| DILUCIDA | 40 | 780 | 0.844 | 0.951 | 0.927 | 0.001\*\*\* |
| DOTO | 15 | 105 | 0.922 | 0.952 | 0.909 | 0.127 |
| DUESSA | 4 | 6 | 0.96 | 0.965 | 0.836 | 0.477 |
| DUILLIA | 3 | 3 | 0.829 | 0.992 | 0.781 | 0.093 |
| EGRA | 11 | 55 | 0.872 | 0.955 | 0.902 | 0.014\* |
| EURIMEDIA | 35 | 595 | 0.906 | 0.95 | 0.923 | 0.007\*\* |
| EXCELSA | 18 | 153 | 0.844 | 0.952 | 0.913 | 0.001\*\*\* |
| HEMIXANTHE | 7 | 21 | 0.543 | 0.957 | 0.871 | 0.001\*\*\* |
| HERMIAS | 53 | 1378 | 0.918 | 0.95 | 0.931 | 0.006\*\* |
| HEWITSONI | 30 | 435 | 0.807 | 0.95 | 0.921 | 0.001\*\*\* |
| HUMBOLDT | 1 | 0 |  |  |  |  |
| ILLINISSA | 6 | 15 | 0.585 | 0.958 | 0.86 | 0.001\*\*\* |
| LERIDA | 66 | 2145 | 0.925 | 0.95 | 0.933 | 0.015\* |
| LIBETHRIS | 21 | 210 | 0.901 | 0.952 | 0.915 | 0.022\* |
| LYSIMNIA | 5 | 10 | 0.787 | 0.965 | 0.841 | 0.017\* |
| MAELUS | 16 | 120 | 0.662 | 0.952 | 0.911 | 0.001\*\*\* |
| MAMERCUS | 64 | 2016 | 0.916 | 0.951 | 0.933 | 0.002\*\* |
| MANTINEUS | 5 | 10 | 0.315 | 0.962 | 0.857 | 0.001\*\*\* |
| MESTRA | 14 | 91 | 0.741 | 0.953 | 0.906 | 0.001\*\*\* |
| MOTHONE | 14 | 91 | 0.802 | 0.953 | 0.903 | 0.001\*\*\* |
| OCNA | 13 | 78 | 0.902 | 0.955 | 0.909 | 0.036\* |
| ORESTES | 16 | 120 | 0.695 | 0.953 | 0.91 | 0.001\*\*\* |
| OZIA | 19 | 171 | 0.894 | 0.952 | 0.916 | 0.014\* |
| PANTHYALE | 39 | 741 | 0.908 | 0.951 | 0.926 | 0.005\*\* |
| PARALLELIS | 7 | 21 | 0.694 | 0.958 | 0.88 | 0.001\*\*\* |
| PAVONII | 2 | 1 | 1 | 1 | 0.656 | 1 |
| POLITA | 10 | 45 | 0.877 | 0.954 | 0.89 | 0.03\* |
| PRAESTANS | 1 | 0 |  |  |  |  |
| PRAXILLA | 9 | 36 | 0.768 | 0.955 | 0.889 | 0.001\*\*\* |
| QUINTINA | 6 | 15 | 0.88 | 0.958 | 0.871 | 0.066 |
| SINILIA | 9 | 36 | 0.883 | 0.957 | 0.895 | 0.028\* |
| SUSIANA | 20 | 190 | 0.829 | 0.952 | 0.913 | 0.001\*\*\* |
| THABENA-F | 11 | 55 | 0.875 | 0.954 | 0.899 | 0.018\* |
| THEUDELINDA | 8 | 28 | 0.686 | 0.956 | 0.886 | 0.001\*\*\* |
| TICIDA-M | 8 | 28 | 0.285 | 0.957 | 0.886 | 0.001\*\*\* |
| UMBROSA | 3 | 3 | 0.876 | 0.993 | 0.781 | 0.162 |
| VESTILLA | 1 | 0 |  |  |  |  |
| **Inter-tribe mimetic groups** | | | | | | |
| HERMIAS | 59 | 318 | 0.872 | 0.946 | 0.927 | 0.001\*\*\* |
| HUMBOLDT | 3 | 2 | 0.529 | 0.95 | 0.769 | 0.004\*\* |
| MAELUS | 18 | 32 | 0.774 | 0.947 | 0.908 | 0.001\*\*\* |
| MAMERCUS | 68 | 256 | 0.948 | 0.946 | 0.929 | 0.564 |
| MANTINEUS | 8 | 15 | 1 | 0.945 | 0.863 | 1 |
| MOTHONE | 15 | 14 | 0.731 | 0.95 | 0.901 | 0.001\*\*\* |
| ORESTES | 21 | 80 | 0.761 | 0.943 | 0.906 | 0.001\*\*\* |
| PAVONII | 4 | 4 | 0.693 | 0.948 | 0.816 | 0.006\*\* |

**Table S4:** **Tests for niche convergence within each mimetic group.** Standardized Mean pairwise Climatic Distances (MCD) quantify the degree of dissimilarity in niche centroids between pairs of OMUs. An observed mean MCD value lower than the 5% quantile (Q5%) of the null distribution obtained through simulation of the neutral evolution of the niche supports the niche convergence of phenotypically similar species within a ‘mimetic group’. Mimetic groups are listed by tribes. Tests for Ithomiini are extracted from Doré et al., (2023) for comparison. Tests for inter-tribe mimetic groups are carried out between pairs of OMUs from different tribes. MCDobs = Observed MCD. BCQ50 = Median of the null distribution. BCQ5 = Quantile 5% of the null distribution = statistical significance threshold for α = 0.05. P-value for the spatial congruence test is based on the rank of the MCDobs among the null distribution obtained through neutral evolution of the niche (N = 1000): \* = p < 0.05; \*\* = p < 0.01; \*\*\* = p ≤ 0.001.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **MIMETIC GROUP** | **N units** | **N pairs** | **MCD**obs | **MCD**Q50 | **MCD**Q5 | **p-value** |
| **Heliconiini tribe** | | | | | | |
| AGRAULIS | 5 | 10 | 0.752 | 0.978 | 0.555 | 0.239 |
| AMALFREDA | 8 | 28 | 0.226 | 1.006 | 0.702 | 0.001\*\*\* |
| CHARITHONIA | 5 | 10 | 1.127 | 0.999 | 0.61 | 0.694 |
| CHESTERTONII | 1 | 0 |  |  |  |  |
| CHIONEUS | 2 | 1 | 0.336 | 0.985 | 0.266 | 0.079 |
| CRETACEA | 1 | 0 |  |  |  |  |
| CYDNIDES | 4 | 6 | 0.892 | 0.959 | 0.523 | 0.425 |
| CYRBIA | 2 | 1 | 0.223 | 0.929 | 0.222 | 0.051 |
| DRYAS | 5 | 10 | 0.336 | 1.072 | 0.661 | 0.001\*\*\* |
| ELZUNIA | 2 | 1 | 0.929 | 0.929 | 0.24 | 0.5 |
| HERMATHENA | 1 | 0 |  |  |  |  |
| HERMIAS | 6 | 15 | 0.534 | 0.968 | 0.651 | 0.012\* |
| HEURIPPA | 1 | 0 |  |  |  |  |
| HYDARA | 3 | 3 | 0.261 | 0.928 | 0.435 | 0.008\*\* |
| JUDITH | 1 | 0 |  |  |  |  |
| LEUCE | 5 | 10 | 1.101 | 0.963 | 0.594 | 0.687 |
| LONGARENA | 1 | 0 |  |  |  |  |
| LYBIA | 4 | 6 | 0.613 | 0.921 | 0.261 | 0.267 |
| MAELUS | 2 | 1 | 0.42 | 0.884 | 0.248 | 0.144 |
| MAMERCUS | 4 | 6 | 1.353 | 0.985 | 0.553 | 0.882 |
| MANTINEUS | 3 | 3 | 0.549 | 0.987 | 0.434 | 0.103 |
| MESSENE | 1 | 0 |  |  |  |  |
| MOTHONE | 1 | 0 |  |  |  |  |
| NOTABILIS | 2 | 1 | 0.427 | 0.913 | 0.229 | 0.153 |
| OCTAVIA | 2 | 1 | 1.19 | 0.92 | 0.24 | 0.671 |
| ORESTES | 5 | 10 | 0.633 | 1.001 | 0.623 | 0.054 |
| PACHINUS | 2 | 1 | 0.291 | 0.907 | 0.269 | 0.061 |
| PAVANA | 3 | 3 | 0.676 | 0.947 | 0.418 | 0.219 |
| PHILAETHRIA | 6 | 15 | 0.747 | 0.93 | 0.562 | 0.221 |
| PHYLLIS | 4 | 6 | 0.695 | 0.946 | 0.512 | 0.198 |
| RICINI | 7 | 21 | 1.141 | 1.003 | 0.653 | 0.726 |
| SILVANA | 4 | 6 | 0.803 | 0.941 | 0.5 | 0.326 |
| SUPERIORIS | 6 | 15 | 0.602 | 0.984 | 0.667 | 0.024\* |
| TELESIPHE | 2 | 1 | 0.097 | 1.096 | 0.28 | 0.005\*\* |
| THELXIOPE | 18 | 153 | 0.585 | 1.006 | 0.808 | 0.001\*\*\* |
| VULCANUS | 2 | 1 | 0.853 | 0.921 | 0.22 | 0.452 |
| WALLACEI | 9 | 36 | 0.689 | 0.993 | 0.695 | 0.048\* |
| XENOCLEA | 2 | 1 | 0.053 | 0.916 | 0.218 | 0.004\*\* |
| ZULEIKA | 4 | 6 | 1.623 | 1.025 | 0.541 | 0.96 |
| **Ithomiini tribe** | | | | | | |
| ACRISIONE | 1 | 0 |  |  |  |  |
| AGNOSIA | 85 | 3570 | 0.913 | 0.954 | 0.864 | 0.239 |
| AMALDA | 9 | 36 | 0.439 | 0.915 | 0.66 | 0.002\*\* |
| AURELIANA | 12 | 66 | 0.657 | 1.005 | 0.755 | 0.008\*\* |
| BANJANA-M | 45 | 990 | 0.673 | 0.933 | 0.809 | 0.001\*\*\* |
| CONFUSA | 20 | 190 | 0.867 | 0.975 | 0.788 | 0.17 |
| DERCYLLIDAS | 1 | 0 |  |  |  |  |
| DILUCIDA | 40 | 780 | 0.366 | 0.985 | 0.849 | 0.001\*\*\* |
| DOTO | 15 | 105 | 0.616 | 1.081 | 0.832 | 0.001\*\*\* |
| DUESSA | 4 | 6 | 0.823 | 0.968 | 0.433 | 0.339 |
| DUILLIA | 3 | 3 | 0.159 | 0.884 | 0.411 | 0.002\*\* |
| EGRA | 11 | 55 | 0.319 | 1.038 | 0.746 | 0.001\*\*\* |
| EURIMEDIA | 35 | 595 | 0.947 | 0.976 | 0.823 | 0.387 |
| EXCELSA | 18 | 153 | 0.588 | 1.049 | 0.823 | 0.001\*\*\* |
| HEMIXANTHE | 7 | 21 | 0.14 | 1.144 | 0.708 | 0.001\*\*\* |
| HERMIAS | 53 | 1378 | 0.771 | 1.052 | 0.927 | 0.001\*\*\* |
| HEWITSONI | 30 | 435 | 0.404 | 0.95 | 0.798 | 0.001\*\*\* |
| HUMBOLDT | 1 | 0 |  |  |  |  |
| ILLINISSA | 6 | 15 | 0.31 | 1.178 | 0.764 | 0.001\*\*\* |
| LERIDA | 66 | 2145 | 1.014 | 0.951 | 0.854 | 0.827 |
| LIBETHRIS | 21 | 210 | 0.733 | 0.898 | 0.733 | 0.051 |
| LYSIMNIA | 5 | 10 | 0.481 | 1.161 | 0.629 | 0.013\* |
| MAELUS | 16 | 120 | 0.628 | 1.135 | 0.873 | 0.002\*\* |
| MAMERCUS | 64 | 2016 | 0.867 | 1.078 | 0.953 | 0.003\*\* |
| MANTINEUS | 5 | 10 | 0.286 | 0.941 | 0.543 | 0.001\*\*\* |
| MESTRA | 14 | 91 | 0.42 | 0.918 | 0.714 | 0.001\*\*\* |
| MOTHONE | 14 | 91 | 0.532 | 1.047 | 0.781 | 0.001\*\*\* |
| OCNA | 13 | 78 | 0.535 | 0.917 | 0.696 | 0.001\*\*\* |
| ORESTES | 16 | 120 | 0.428 | 1.107 | 0.871 | 0.001\*\*\* |
| OZIA | 19 | 171 | 0.62 | 0.911 | 0.711 | 0.006\*\* |
| PANTHYALE | 39 | 741 | 0.574 | 0.947 | 0.817 | 0.001\*\*\* |
| PARALLELIS | 7 | 21 | 0.478 | 1.081 | 0.727 | 0.003\*\* |
| PAVONII | 2 | 1 | 0.63 | 0.81 | 0.229 | 0.339 |
| POLITA | 10 | 45 | 0.583 | 0.879 | 0.63 | 0.019\* |
| PRAESTANS | 1 | 0 |  |  |  |  |
| PRAXILLA | 9 | 36 | 0.357 | 0.868 | 0.622 | 0.002\*\* |
| QUINTINA | 6 | 15 | 0.349 | 1.029 | 0.632 | 0.001\*\*\* |
| SINILIA | 9 | 36 | 0.234 | 1.13 | 0.787 | 0.001\*\*\* |
| SUSIANA | 20 | 190 | 0.489 | 0.898 | 0.719 | 0.001\*\*\* |
| THABENA-F | 11 | 55 | 0.502 | 0.962 | 0.705 | 0.001\*\*\* |
| THEUDELINDA | 8 | 28 | 0.098 | 0.993 | 0.676 | 0.001\*\*\* |
| TICIDA-M | 8 | 28 | 0.114 | 0.989 | 0.684 | 0.001\*\*\* |
| UMBROSA | 3 | 3 | 0.595 | 0.781 | 0.358 | 0.233 |
| VESTILLA | 1 | 0 |  |  |  |  |
| **Inter-tribe mimetic groups** | | | | | | |
| HERMIAS | 59 | 318 | 0.782 | 0.75 | 0.492 | 0.559 |
| HUMBOLDT | 3 | 2 | 0.638 | 0.832 | 0.39 | 0.233 |
| MAELUS | 18 | 32 | 0.453 | 0.754 | 0.486 | 0.021\* |
| MAMERCUS | 68 | 256 | 0.876 | 0.727 | 0.439 | 0.754 |
| MANTINEUS | 8 | 15 | 0.793 | 0.825 | 0.622 | 0.418 |
| MOTHONE | 15 | 14 | 0.71 | 0.705 | 0.43 | 0.514 |
| ORESTES | 21 | 80 | 0.491 | 0.795 | 0.577 | 0.003\*\* |
| PAVONII | 4 | 4 | 0.888 | 0.837 | 0.463 | 0.574 |

Appendix 7: ODMAP

Overview

Authorship

**Authors:** Eddie Pérochon, Neil Rosser, Krzysztof Kozak, W. Owen McMillan, Blanca Huertas, James Mallet, Jonathan Ready, Keith Willmott, Marianne Elias, Maël Doré.

**Contact:** Maël Doré ; [mael.dore@gmail.com](mailto:mael.dore@gmail.com)

**Title:** Müllerian mimicry in Neotropical butterflies: One mimicry ring to bring them all, and in the jungle bind them

Model objective

**Model objectives:** Mapping and interpolation. We mapped current potential distribution of subspecies of heliconiine butterflies.

**Target output:** Meeting our objectives required several steps in the post-processing of model outputs. (i) We obtained environmental suitability maps depicting potential distributions from SDM for each subspecies. (ii) We aggregated predictions to derive distributions for Operational Mimicry Units (OMUs; Doré et al., 2022), species and mimetic groups as likelihood of presence of at least one subspecies from the OMU/species/mimetic group. (iii) We obtained richness maps as stacked-SDMs from species and mimetic group maps. (iv) We computed various taxonomic, phylogenetic and mimicry diversity and rarity indices from the previous richness maps.

Focal Taxon

**Focal Taxon:** Our study group was the longwing butterfly tribe Heliconiini Swainson, 1822 (Nymphalidae: Heliconiinae). This clade contains ca. 8 genera, 77 species and 457 subspecies (Jiggins & Lamas, 2017; Kozak et al., 2015, but see Núñez et al., 2022 for recent proposed taxonomic splits). Our study includes the 439 subspecies (96.1 %) with available georeferenced occurrences.

Location

**Location:** Americas, from Argentina to Canada, including the Caribbean region, encompassing the whole range of the Heliconiini tribe. Most diversity falls within the Neotropics with only a few lineages venturing in the Nearctic region.

Scale of Analysis

**Spatial extent:** Longitude 130° E - 30° E, Latitude 38° S – 50° N

**Spatial resolution:**

Community boundaries were defined as grid cell of 0.25° x 0.25° = 27.8km x 27.8km.

**Temporal extent:** Field surveys were conducted in the last decades. The dataset is complemented with historical records that span from the 19th century to present, with the majority within the last 30 years.

**Temporal resolution:** We modeled distributions under current environmental conditions: we retrieved bioclimatic data for the 2000’s decade, and forest cover data for the year 2010.

Biodiversity data

**Observation type:** Georeferenced occurrences from field surveys and museum collections

**Response data type:** A curated set of 67,563 subspecies-locality records as presence data were screened to yield 18,841 subspecies-grid-cell records after removing duplicate records from single grid cells. We drew pseudo-absences from those occurrences in a target group strategy. See details in Data.

Predictors

**Predictor types:** bioclimatic, topographic (elevation), and habitat (forest cover)

Hypotheses

**Hypotheses:**

Heliconiini species inhabit either forests or savannah across Americas (Jiggins & Lamas, 2017). Thus, their distribution is expected to be widely influenced by the local availability of forest cover. Likewise, elevation has been shown to shape the broadscale patterns of Heliconiini diversity (Rosser et al., 2012). We also used climatic layers as predictors in an exploratory way because climate is known to be an important driver of species distributions at a continental scale in general (Thomas et al., 2004).

Assumptions

**Model assumptions:** We assumed that (i) relevant ecological drivers (or proxies) of species distributions are included, (ii) detectability does not change across environmental gradients, (iii) predictor measurements are free of error, (iv) the species are at equilibrium with their environment, (v) sampling is sufficient and representative, and (vi) environmental suitability outputs are valuable proxies to estimate potential distributions.

Algorithms

**Modelling techniques:** We employed three different machine learning algorithms: Random Forest (RF), Generalized Boosted Models (GBM) also known as Boosted Regression Trees (BRT), and Artificial Neural Networks (ANN).

**Model complexity:** We kept model settings to the default settings in *biomod2* v.3.4.6, keeping a balance between flexibility of the response curves and overfitting (Merow et al., 2014). The only exceptions were the minimum size of leaves that was lowered to two instead of five, and the fraction of observations used at each step (0.7 instead of 0.5) to allow tentative runs in GBM for OMUs with low sample size.

**Model ensembles:** We stacked all models meeting our validation thresholds to produce a single “ensemble” model per subspecies. We computed the ensemble as the median rather than the mean to limit the influence of models with extreme outputs. We did not use a weighting scheme since we considered our evaluation metric (i.e., Jaccard index) a suitable metric to discard low quality models, but not adequate to rank best models in the context of pseudo-absences data (Leroy et al., 2018).

Workflow

**Model workflow:** We fitted SDMs for 364 subspecies (91.4 %) representing 75 species (97.4%), for which we had at least six occurrences available. We included the remaining 75 subspecies in stacks as binary raster of presence-absences. Workflow also differed between the 196 subspecies with restricted sample size (6 ≤ N < 30) and the 168 subspecies with large sample size (N ≥ 30). For restricted sample size, we kept all occurrences for calibration and validation and draw 10 independent pseudo-absences sets. For large sample sizes, we drew three independent pseudo-absences sets combined with 3-fold spatial block cross-validation to assess predictive model performance. We selected valid models for ensemble based on maximized Jaccard indices and plausibility checks. Ensemble predictions were derived using ensemble medians. We clipped final outputs with subspecies-specific buffered alpha-hulls and Andean region masks to constrain the extent of possible distributions to reasonable areas. We derived OMU, species and mimetic group maps from the subspecies maps as the likelihood to find at least one of the related subspecies in the community. Final post-processing step consisted in the computation of six diversity and rarity indices based directly on the species or mimetic group maps. This workflow is depicted in as a chart adapted from Doré et al., (2022) in **Figure S8**.

**A diagram of a model

Description automatically generated**

**Figure S8: SDM workflow chart** **depicting the different steps of the analysis performed in this study.** Depending on sample size, modeling steps and settings differed. Clipping step to constrain SDM projections to plausible distribution ranges is not shown on the chart. Algo = algorithms used in the study, namely random forest (RF), gradient boosting models (GBM), and artificial neural networks (ANN); PAs = pseudo-absences sets; CV = cross-validation folds. Modified from ODMAP in Doré et al. (2022).

Software

**Software:** R version 3.6.2 (R Core Team, 2019) with packages *raster* 3.0-12(Hijmans, 2020), *biomod2* 3.4.6(Thuiller et al., 2020), *sf* 0.9-0 (Pebesma, 2018), *blockCV* 2.1.1 (Valavi et al., 2019), *alphahull* 2.2(Pateiro-Lopez & Rodriguez-Casal, 2019)*,* and others.

**Code availability:** All scripts are provided on GitHub at https://github.com/XXX

**Data availability:** Occurrences data and mimetic group delimitation used for modeling are available from Zenodo at [10.5281/zenodo.10906853](https://doi.org/10.5281/zenodo.10906853) and [10.5281/zenodo.10903197](https://doi.org/10.5281/zenodo.10903197). All subspecies/OMU/species/mimetic group distribution maps are available from Zenodo at [10.5281/zenodo.10903661](https://doi.org/10.5281/zenodo.10903661).

Data

Biodiversity data

**Taxon names:** Heliconiini tribe. All subspecies are listed in the mimicry classification available in [10.5281/zenodo.10903197](https://doi.org/10.5281/zenodo.10903197).

**Taxonomic reference system:** Current names in use as listed in Jiggins & Lamas (2017).

**Ecological level:** Subspecies, and species in case of taxa with a unique or no subspecies described.

**Data sources:** Dataset of georeferenced occurrences is a compilation of fieldwork data from N. Rosser (Harvard University, USA), J. Mallet (Harvard University, UK), K. Kozak (STRI, Panama) and O. McMillan (STRI, Panamá) obtained over the past decades.

Additionally, the dataset comprises records from museums and private collections compiled by N. Rosser. Data sources are summarized in Table 1 in Rosser et al. (2012). The main contributors (>3000 records each) are the Florida Museum of Natural History, Gainesville (FLMNH), the Natural History Museum, London (NHMUK), the Tropical Andean Butterfly Diversity Project, CONABIO, Mexico, and the Museo de Historia Natural, Lima (MHN).

The dataset of the curated 67,563 subspecies-locality records used for distribution modeling is available from Zenodo at [10.5281/zenodo.10906853](https://doi.org/10.5281/zenodo.10906853).

**Sample size:** Sample size for each subspecies, after spatial filtering, varied widely from 1 to 565. We employed a different modeling scheme for subspecies falling into different sample size categories. We classified the 75 subspecies (17.0%) with sample size lower than six as “rasterized” and did not go through the SDM process. We labelled as “restricted” the 196 subspecies (44.6%) with sample size between 6 and 29. We modeled these “restricted” subspecies without cross-validation. The 168 subspecies (38.3%) with sample size greater or equal to 30 underwent the full SDM process. See workflow in **Fig. S8** above.

**Scaling:** We removed spatial duplicates by applying spatial filtering on a 0.25° x 0.25° grid used as final modeling resolution whose pixels defined our virtual communities. As a consequence we obtained 18,841 subspecies-grid-cell records.

**Cleaning:** We examined the presence of geographic and environmental outliers prior to modeling. We considered as geographic outliers all occurrences of a specific subspecies with no other neighboring points in a 1000km buffer area. These outliers were further scrutinized to decide case by case to retain or discard those points from the dataset if considered erroneous or not.

We automatically removed occurrences with significant Mahalanobis distance (Mahalanobis, 1936) from other points in the environmental space. Those points could be either errors, or real abnormal occurrences, caused by temporary migration of individuals following an extreme climatic event (e.g., individuals migrating temporarily up mountain slopes following an extreme heat event). In any case, those occurrences cannot be considered helpful to model the global species distribution based on the local average climate and were therefore discarded.

**Pseudo-absence data:** We generated pseudo-absences using a target-group strategy (Mateo et al., 2010), employing sampling sites where other subspecies have been detected but not the targeted subspecies as a pool for drawing pseudo-absences. In doing so, we increased the likelihood for the targeted subspecies to be effectively not present in our pseudo-absence sites, a critical aspect in order to produce quantities that approach the actual probability of occurrence of the entity modeled as output, as we intended to do (Guillera-Arroita et al., 2015). This approach also allowed us to use confidently the Jaccard index as an evaluation metric to discard poorly performing models from the ensemble models despite this measurement being based on confusion matrix, thus designed primarily for presence-absence data.

Additionally, in order to minimize even more the risk of assigning wrongly a pseudo-absence in an actual occupied site we applied a minimum buffer of 1° (111.32km at the equator) to discard all sites within this minimum range of a presence point from the potential pseudo-absence pool. Finally, to prevent selecting pseudo-absences too far from any presence points while avoiding having to decide a global arbitrary maximum threshold, we weighted the probability for sites to be selected by their inverse distance to any presence point. Therefore, we ensure our pseudo-absences were likely to represent real absences, while at the same time avoiding to extensively sample too far beyond the range of a species, where absences are likely to occur because of non‐bioclimatic reasons (e.g., Biber et al., 2020).

Following recommendations from Barbet-Massin et al. (2012) for machine-learning algorithms, we drew a number of new pseudo-absences equal to the number of presences recorded for the target subspecies, for each run. For each subspecies with a restricted sample size (6 ≤ N < 30), we ran ten independent replicates for each algorithm leading to a total of 30 models per subspecies. For each subspecies with a large enough sample size (N ≥ 30), we ran three independent replicates for each algorithm leading to a total of 27 models per subspecies (i.e., 3 algorithms \* 3 pseudo-absence sets \* 3 CV-folds), once the 3-fold spatial blocks CV was applied.

Data partitioning

**Validation data:** We split data between training set and validation sets only for subspecies with sample size ≥ 30.

For models with limited sample size (6 ≤ N < 30), we decided to keep all data points in our calibration set in order to yield better estimates from SDMs with low sample size. Using a partition scheme would have left fewer points for calibration, decreasing the already scarce information available to yield proper SDMs, and even fewer for validation which would have become meaningless (Hallman & Robinson, 2020). Thus, we evaluated model performances with the same dataset used for calibration (« resubstitution » in Roberts et al., 2017). To compensate for non-independence between our calibration sets and validation sets, we used conservative high thresholds to select models with valid performance to keep for the final ensemble.

For models with sufficient sample size (N >= 30), we applied a 3-folds cross-validation (CV) strategy with spatial blocks to define our calibration and validation sets. Spatial blocks CV allows to partition dataset into spatially independent blocks that ensure the predictive error of the model is not underestimated because of spatial autocorrelation between calibration and validation sets (Roberts et al., 2017). We defined our folds for each subspecies dataset of presences combined with each independent draw of pseudo-absences using the *spatialBlock* function in the R package *blockCV* 2.1.1 (Valavi et al., 2019).

**Test data:** No truly independent dataset was available.

Predictor variables

**Predictor variables:**

Climate is known to widely influence large-scale patterns of species distribution (McGill, 2010). We selected as predictors four bioclimatic variables among the 19 available in the WorldClim 2.1 online database (Fick & Hijmans, 2017): mean annual temperature, mean diurnal range, total annual precipitation, and precipitation seasonality. We selected this subset of climate predictors following two aims: (1) representativity of the whole variance in our study region, and (2) ease of ecological interpretations. Each variable was included in a different group of intercorrelated variables when performing hierarchical clustering. Within each group, we selected the most adequate variables for ease of ecological interpretation of effects of climate on species distribution.

We used elevation as it has been shown to shape the broadscale patterns of Heliconiini diversity (Rosser et al., 2012).

We used percentage of forest cover as our habitat/land use type predictor since Heliconiini species are known to be found either in forests or savannah across Americas (Jiggins & Lamas, 2017).

**Data sources:**

Bioclimatic predictors were obtained from WorldClim v2.1 (Fick & Hijmans, 2017) for the latest period available at the time of our modeling process (1970-2000).

We retrieved elevation from the SRTM Dataset v.4.1 (Farr et al., 2007; <http://srtm.csi.cgiar.org/>, accessed on 03/26/2019).

We extracted the percentage of land cover per pixel from the Landsat Tree Cover Continuous Fields dataset (Sexton et al., 2013) for the year 2010, accessible through Google Earth Engine (GLCF: Landsat Tree Cover Continuous Fields in the Earth Engine Data Catalog, accessed on 03/26/2019). The GLCF tree cover layers contain estimates of the percentage of horizontal ground covered by woody vegetation.

**Spatial extent:** We clipped all rasters to our study area: Longitude 130° E - 30° E, Latitude 38° S – 50° N.

**Spatial resolution:** We obtained GLCF and WorldClim data at a resolution of 5min of arc, while SRTM had a resolution of 90m. We aggregated all predictor variables to our final model resolution (0.25°) prior to modeling.

**Coordinate reference system:** Data were retrieved under WGS84 (EPSG:4326). All rasters were projected to Mollweide projections (ESRI:54009) priori to modeling in order to ensure grid cells represented similar areas.

**Temporal extent:**

We downloaded WorldClim data averaged for the 1970-2000 decades, and GLCF for the year 2010.

**Data processing:** We aggregated all predictor variables to our final model resolution (0.25°) prior to modeling. We harmonized final predictor rasters to display missing data in pixels where at least one predictor was lacking information to avoid modeling points with partial environmental information.

**Dimension reduction:** We selected four bioclimatic variables among the 19 bioclimatic variables available in WorldClim in order to reduce multicollinearity among bioclimatic predictors, and limit the complexity of the models to a reasonable number of predictors (six in total).

We selected bioclimatic variables as the results of a hierarchical agglomerative clustering on Spearman’s rho correlation coefficients, using a complete linkage method with the function *hclust* in R base package. We applied a cutoff of |ρ| > 0.7 (Brun et al., 2020; Dormann et al., 2013) on the resulting dendrogram to highlight groups of multicorrelated variables. Then, we selected only one variable in each group. Selection criteria for retaining variables were (1) their ease to interpret as an ecological factor (e.g., “mean temperature” rather than the “mean temperature of the driest quarter”) and (2) their high correlation with the axis of a global PCA run on all 19 variables. The final four variables included in the models were mean annual temperature, mean diurnal range, total annual precipitation, and precipitation seasonality.

Transfer data

We interpolated our final maps of environmental suitability depicting potential distributions with the same environmental rasters as the one used for modeling. Thus, the transfer data is the same as the predictors.

Model

Variable pre-selection

See Dimension reduction in Data section.

Multicollinearity

See Dimension reduction in Data section.

Model settings

**Model complexity:** We kept model settings to the default settings in *biomod2* v.3.4.6, since models with intermediate levels of complexity have been shown to perform best (Brun et al., 2020), keeping a balance between flexibility of the response curves and overfitting (Merow et al., 2014). The only exceptions to default settings were the minimum size of leaves that was lowered to two instead of five, and the fraction of observations used at each step (0.7 instead of 0.5) to allow tentative runs in GBM for subspecies with low sample size.

**BRT/GBM settings:** distribution (bernoulli), nTrees (2500), interactionDepth (7), shrinkage (0.001), bagFraction (0.7), trainFraction (1), n.minobsinnode (2), CV.folds (3)

**randomForest settings:** ntree (500), mtry (2), maxnodes (n.obs), sampsize (n.obs), replace (TRUE)

**ANN settings:** nbCV (5), maxit (200)

size = 2, 4, 6, or 8. Optimized by CV for best AUC.

decay = 0.001, 0.01, 0.05, or 0.1. Optimized by CV for best AUC.

**Model extrapolation:** Extrapolation was possible but remained limited since we constrained final outputs inside the buffer around known presence points.

Model estimates

**Variable importance:** We assessed variable importance for each calibrated model within the R package *biomod2* 3.4.6 (Thuiller et al., 2020) by looking at the correlation between predictions obtained from the real data and predictions from data with randomized values for each variable evaluated.

Model selection - model averaging - ensembles

**Model selection:** We discarded all models that did not reach our thresholds for model quality prior to ensemble (See Performance statistics in Assessment section for details on evaluation metric choice). We set our threshold to a minimum Jaccard index of 0.6 for complete models (N >= 30), and 0.95 for restricted models (6 ≤ N < 30). The threshold for subspecies with “restricted” sample size was more conservative since they were evaluated on the calibration set, while complete models were evaluated on spatially independent validation sets. We chose those thresholds since they ensured each subspecies retained at least 5 models for the ensemble, while keeping quality standard to a high value. We conducted additional plausibility checks by inspecting the response curves of each variable for each model following an automatic procedure, completed with manual checks (See plausibility checks in Assessment for details). We discarded from the ensemble models holding at least one response curve with a non-ecologically plausible shape.

**Model ensembles:** We stacked all models meeting our validation thresholds to produce a single “ensemble” model per subspecies. We computed the ensemble as the median rather than the mean to limit the influence of models with extreme outputs. We did not use a weighting scheme since we considered our evaluation metric (i.e., Jaccard index) a suitable metric to discard low quality models, but not adequate to rank best models in the context of pseudo-absence data (Leroy et al., 2018).

Analysis and Correction of non-independence

**Spatial autocorrelation:** We applied spatial blocks CV to account for spatial autocorrelation among calibration and validation sets for models with sufficient sample size (N >= 30).

Threshold selection

**Threshold selection:** We did not apply a threshold on the final continuous outputs prior stacking since it has been proven that thresholding could introduce bias leading to overestimation of species richness (Calabrese et al., 2014). For instance, we simply estimated species richness as the sum of species environmental suitability maps depicting potential distributions as proxies of occurrence probabilities.

Assessment

Performance statistics

**Metric choice:** In order to evaluate model performance, we chose to use the Jaccard index, an ecological index of similarity which can be directly interpreted as the spatial overlap between the observed distribution (valid predicted presences as true positives (TP), and missed presences as false negatives (FN)) and predicted distribution (valid predicted presences as true positives (TP), and erroneous predicted presences as false positives (FP)). Thus, for each model we retained the maximum Jaccard index obtained for a model specific optimized threshold, and computed as TP/(TP + FN + FP). Contrary to the TSS, the Jaccard index prevents overestimation of model performance caused by the inflation of true negatives based on pseudo-absences drawn far from presences, and appeared to be not biased by prevalence (Leroy et al., 2018).

Additionally, despite being primarily designed for presence-absence data, we used the Jaccard index as evaluation metric because: (1) we did not have enough occurrence data to use presence-only evaluation metrics such as the Boyce index (Hirzel et al., 2006) for most of our subspecies; (2) we carefully selected our pseudo-absences in a target-group strategy (Mateo et al., 2010) to maximize the probability for our pseudo-absences to be real absences, thus we are confident the Jaccard index remains informative to discard poorly performing models.

**Performance on training data:** We set to a high 0.95 the threshold to meet required quality for “restricted” models evaluated directly on the calibration set because of low sample size.

**Performance on validation data:** We set to 0.6 the threshold to meet required quality for “complete” models (N >= 30) evaluated using spatial CV-blocks.

Following our criteria, we retained 87.3% of sub-models run with Random Forest algorithms, 96.0% of Gradient Boosted Models, and 56.7% of Artificial Neural Networks (**Fig. S9**). All ensemble models retained at least five sub-models, allowing to provide final predictions based on ensemble models accounting for uncertainties associated with modeling choices.

A diagram of a diagram

Description automatically generated

**Figure S9: Evaluation of sub-model performances based on Jaccard indices.** Sub-models are grouped by type of algorithms: Random Forest (RF), Gradient Boosted Models (GBM), and Artificial Neural Networks (ANN). Two distinct thresholds (dashed lines) were used to discard from ensemble models the sub-models with insufficient performance depending on the type of evaluation set used: 0.95 when evaluated on the training set data (“restricted models”, in blue), 0.6 when evaluated on a validation set designed from spatial CV-blocks (“complete models”, in red).

Plausibility check

**Response shapes:** We designed an automatic procedure to check for multimodality and positive quadratic relationships in the response curve of all variables for all models since such relationships would have low ecological plausibility. We assessed multimodality through Hartigan’s dip test using the R package *diptest* 0.75-7 (Maechler, 2016). We inspected case by case the response curves highlighted by the automatic procedure and then manually removed models holding non-plausible response curves based on expert judgement.

Prediction

Prediction output

**Prediction unit:** Models produced environmental suitability maps depicting potential distribution for each subspecies.

**Clipping:** We clipped all final ensemble model per unit using a subspecies-specific buffer.

We clipped all final ensemble models to constrain the extent of possible distribution of each subspecies to a reasonable area accordingly to the limited migration abilities of our butterflies, and the degree of certainty we had about the range of the species based on the spread of occurrence points. Thus, we computed alpha-hulls (α = 1000 km) using the function *ahull* from the R package *alpha-hull* 2.2 (Pateiro-Lopez & Rodriguez-Casal, 2019) encompassing all occurrence points for each subspecies in order to design a smooth surface able to engulf occurrences points but that could also generate automatically disjointed distributions when needed. We choose an alpha parameter of 1000 km (diameter of the circles used to draw the alpha-hull) to be coherent with our threshold for detection of outliers. In parallel, we computed the 80% quantile for the distance to the closest occurrence points among occurrence points of each subspecies. This measure is to be seen as a measurement of how confident we are that our records cover extensively the range of the subspecies studied. The rationale is that a subspecies with a clustered set of occurrences is more likely to describe accurately the global range of this subspecies, while a subspecies with a more dispersed set of occurrence points could signal a lack of information, or a subspecies with a wide range. Therefore, we added to our alpha-hull a buffer corresponding to the max value between this subspecies-specific parameter and a distance of 1° assumed to represent a conservative limit for Heliconiini dispersion abilities. We used these final polygons to restrict our SDMs predictions for each subspecies.

In the specific case of the Andean region, strong environmental gradients can be found following the slopes, leading to potentially suitable areas on both sides of the Cordilleras across limited distances. To avoid false predictions of subspecies known with reasonable confidence to be restricted to one side of the Cordilleras, we cropped the final maps applying a set of two polygons corresponding respectively to each side of the Andean mountain ranges. We built those polygons by aggregating watersheds retrieved from a Digital Elevation Model in ArcGIS. In practice, if a subspecies presented occurrences falling only in one of the two polygons, we used the other to crop out the final map of this subspecies.

**Aggregating to higher level:** Exploiting the 439 environmental suitability maps depicting potential distributions for each subspecies, we built potential distribution maps at OMU, species and mimetic group levels.

We assumed outputs from SDMs relate to likelihood of presence of each subspecies. Then, for each community, the likelihood of presence of an OMU, a species, or a mimetic group was computed as the likelihood to find at least one of the related subspecies in the community such as

(1)

where po/s/m is the likelihood of presence of the OMU, species or mimetic group, and pi the likelihood of presence of each subspecies of this OMU, species or mimetic group.

**Index computation:** A final post-processing step consisted in the computation of six diversity and rarity indices based directly on the species or mimetic group maps. For all computation, we used the continuous outputs from SDM since binarization to presence-absences usually degrades inference and can introduces bias in community richness evaluation (Calabrese et al., 2014; Guillera-Arroita et al., 2015).

Uncertainty quantification

**Algorithmic uncertainty:** We accounted for algorithmic uncertainty by applying an ensemble approach averaging over three different SDM algorithms.

**Input data uncertainty:** We accounted for uncertainty in input data by applying an ensemble approach averaging over three (for subspecies with additional spatial blocks CV) or ten (for subspecies without CV) different pseudo-absences draws.

**Novel environments:** Predictions to novel environments were limited since we interpolate maps inside a buffer encompassing known presence points.

Online Archive

**Mimetic classification of subspecies**

[10.5281/zenodo.10903197](file:///D:\Mael_D\Articles\Heliconiini%20diversity%20patterns\10.5281\zenodo.10903197)

**Distribution maps: All subspecies, OMUs, species, mimetic groups**

[10.5281/zenodo.10903661](https://zenodo.org/doi/10.5281/zenodo.10903661)

**Occurrence data of heliconiine butterflies**

[10.5281/zenodo.10906853](https://zenodo.org/doi/10.5281/zenodo.10906853)