Beyond Müller's mimicry model:

Perceptual maps support continental-scale convergence in wing patterns of sympatric Neotropical butterflies

Maël Doré

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McGuire Center Seminar

"*Expanding Horizons in Lepidoptera Research*"

Credit photos: C. Jiggins

MUSÉUM NAL HIST NATURELLE

ISYEB
Institut de Systématique, Evolution, Biodiversité

cnrs

CESCO
Centre d'Écologie et des Sciences de la Conservation

History of Mimicry

Bates, 1862

Henry Walter Bates
(1825 – 1892)

History of Mimicry

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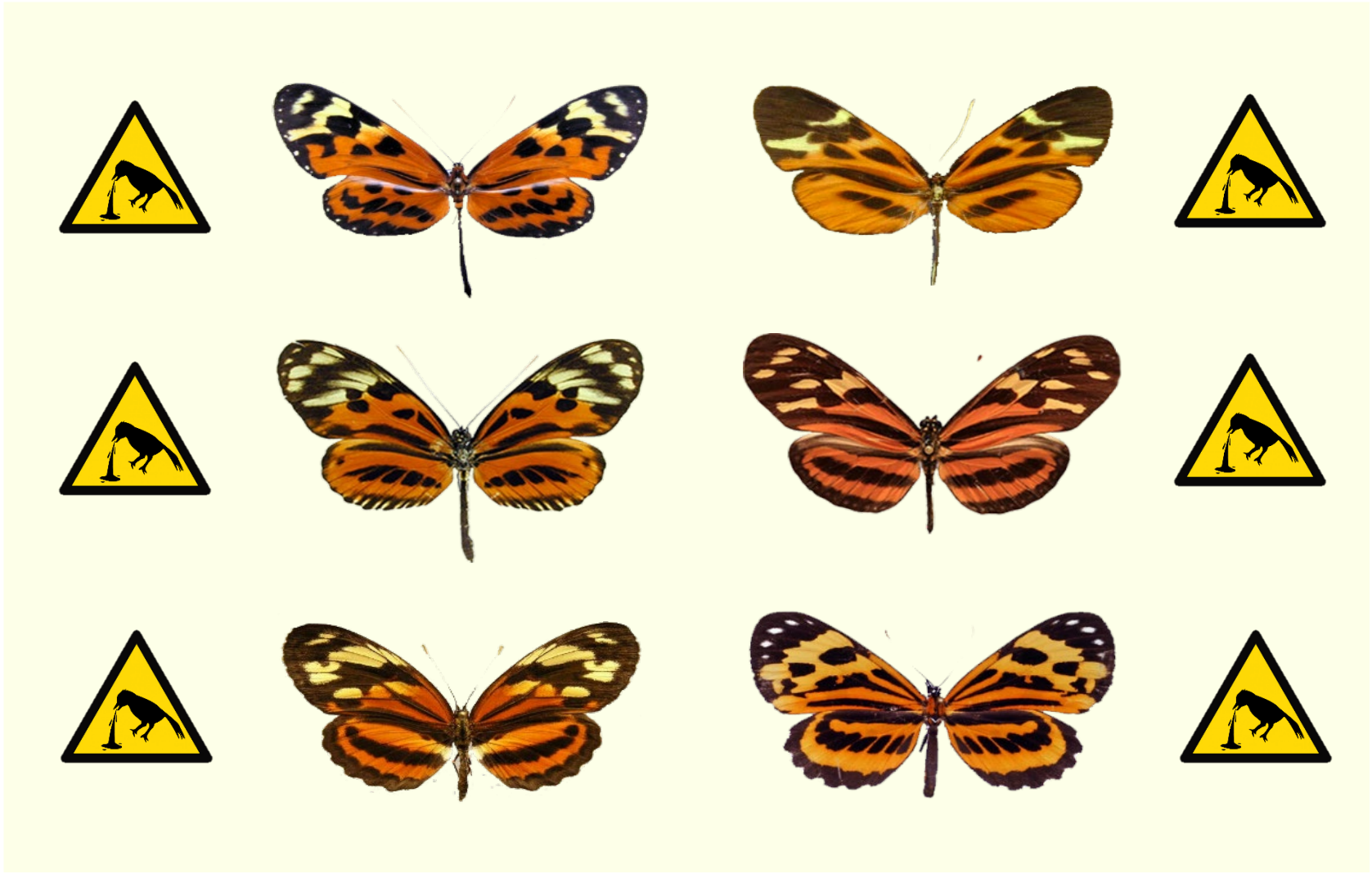
History of Mimicry



Henry Walter Bates
(1825 – 1892)

History of Mimicry

† Let a_1 and a_2 be the numbers of two distasteful species of butterflies in some definite district during one summer, and let n be the number of individuals of a distinct species which are destroyed in the course of a summer before its distastefulness is generally known. If both species are totally dissimilar, then each loses n individuals. If, however, they are undistinguishably similar, then the first loses $\frac{a_1 n}{a_1 + a_2}$, and the second $\frac{a_2 n}{a_1 + a_2}$. The absolute gain by resemblance is therefore for the first species $n - \frac{a_1 n}{a_1 + a_2} = \frac{a_2 n}{a_1 + a_2}$; and in a similar manner for the second, $\frac{a_1 n}{a_1 + a_2}$. This absolute gain, compared with the occurrence of the species, gives for the first, $1_1 = \frac{a_2 n}{a_1 (a_1 + a_2)}$, and for the second species, $1_2 = \frac{a_1 n}{a_2 (a_1 + a_2)}$, whence follows the proportion, $1_1 : 1_2 = a_2^2 : a_1^2$.

Müller, 1879

Henry Walter Bates
(1825 – 1892)

Fritz Müller
(1821 – 1897)

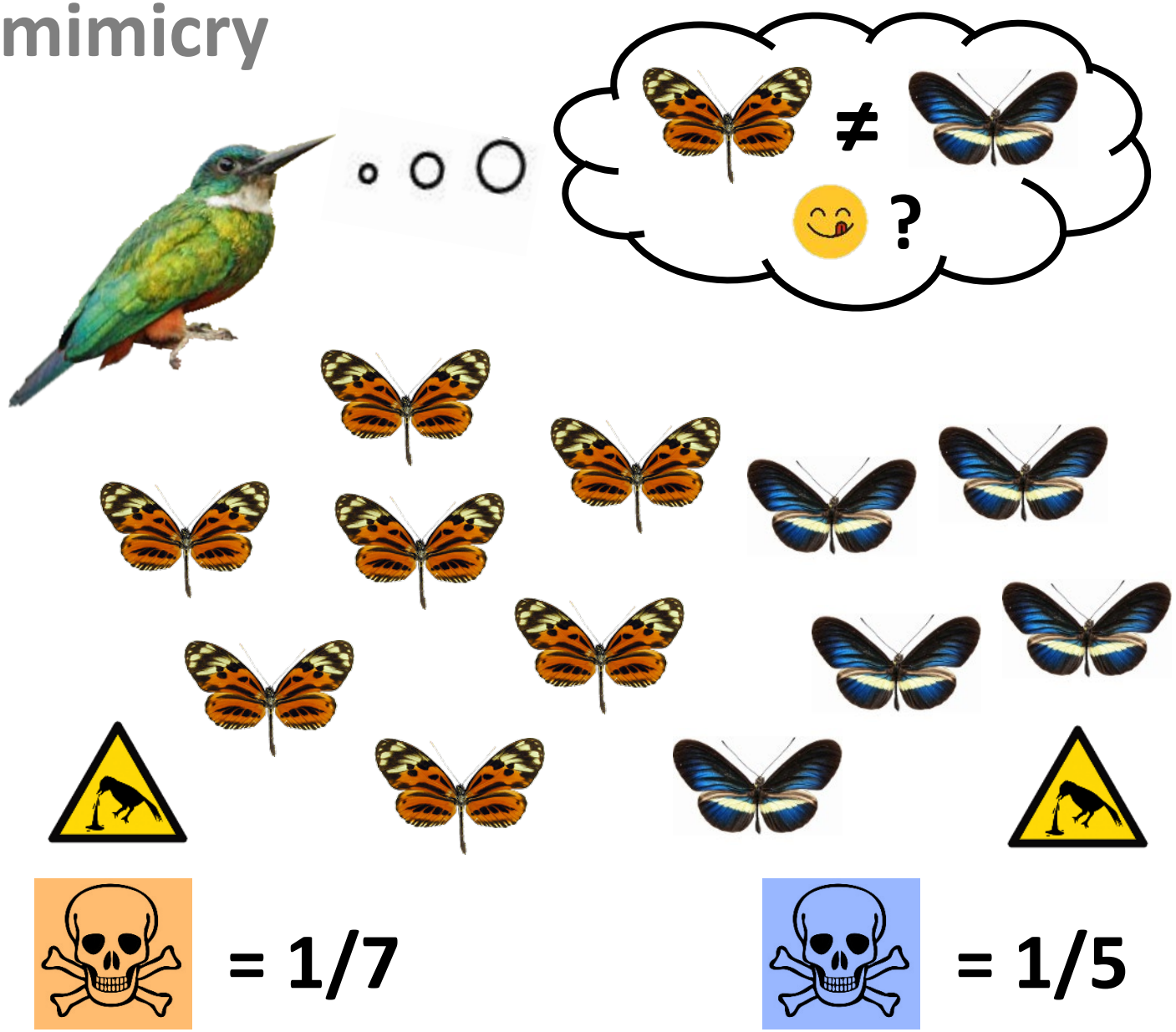
Study system: Müllerian mimicry

1/ **Positive frequence-dependent** selection

2/ Advantage for **similarity**

Consequences:

- Local pattern **convergence** => **mimicry rings**
- Mutual benefit from cooccurrence => **mutualistic interactions**



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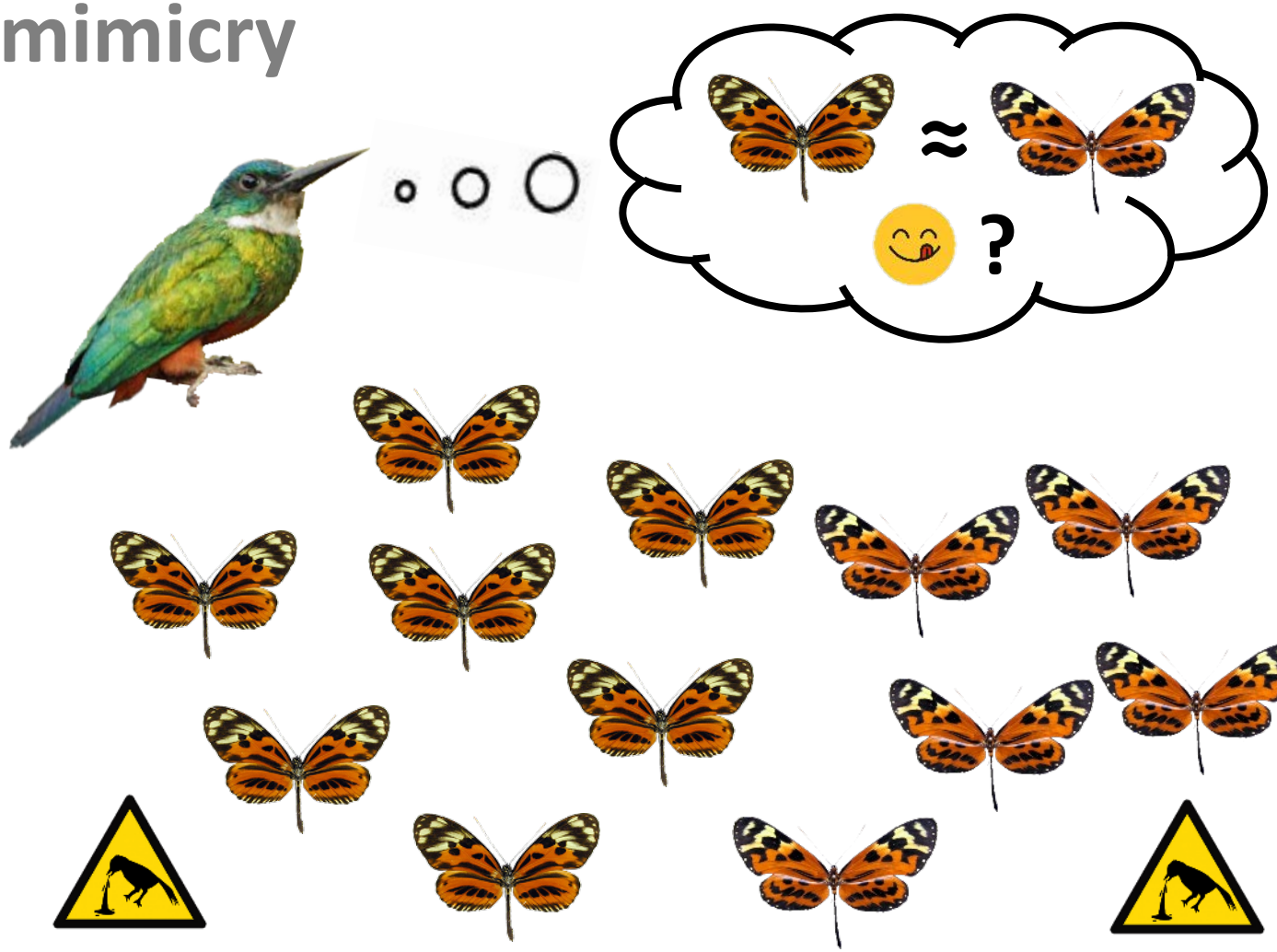

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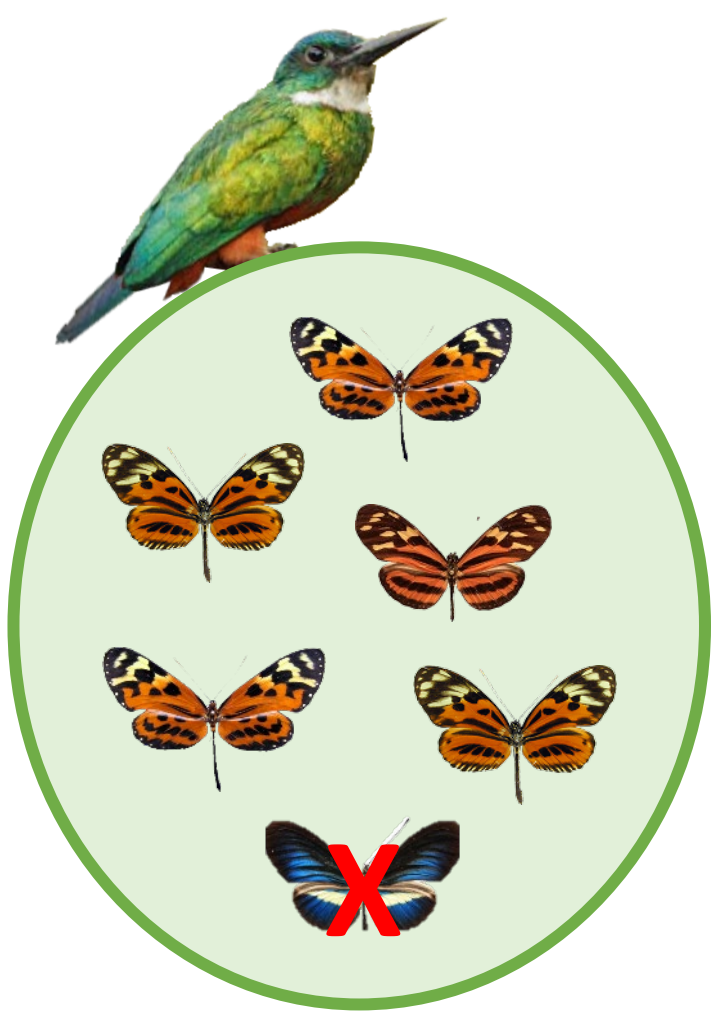


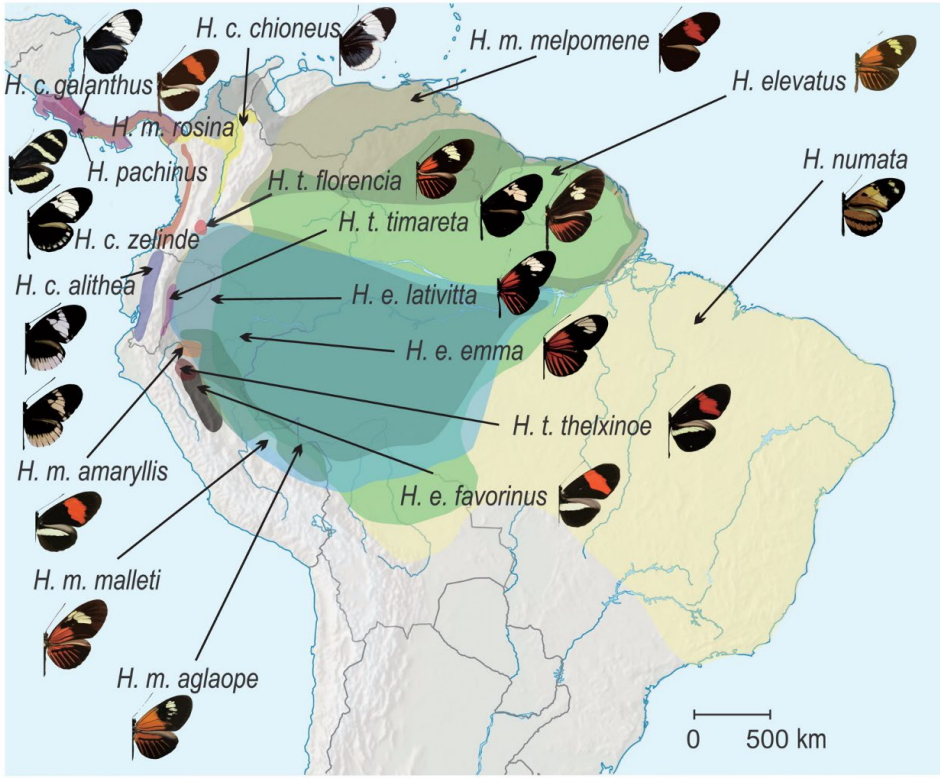
Beyond Müller's model

Consequences of **mimetic interactions:**

- Local pattern convergence **within local communities**

How does it unfold at **large spatial scale**?

- Across the **whole range** of species
- Structuring biodiversity patterns at **continental scale**?



Zhang et al., 2021

How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

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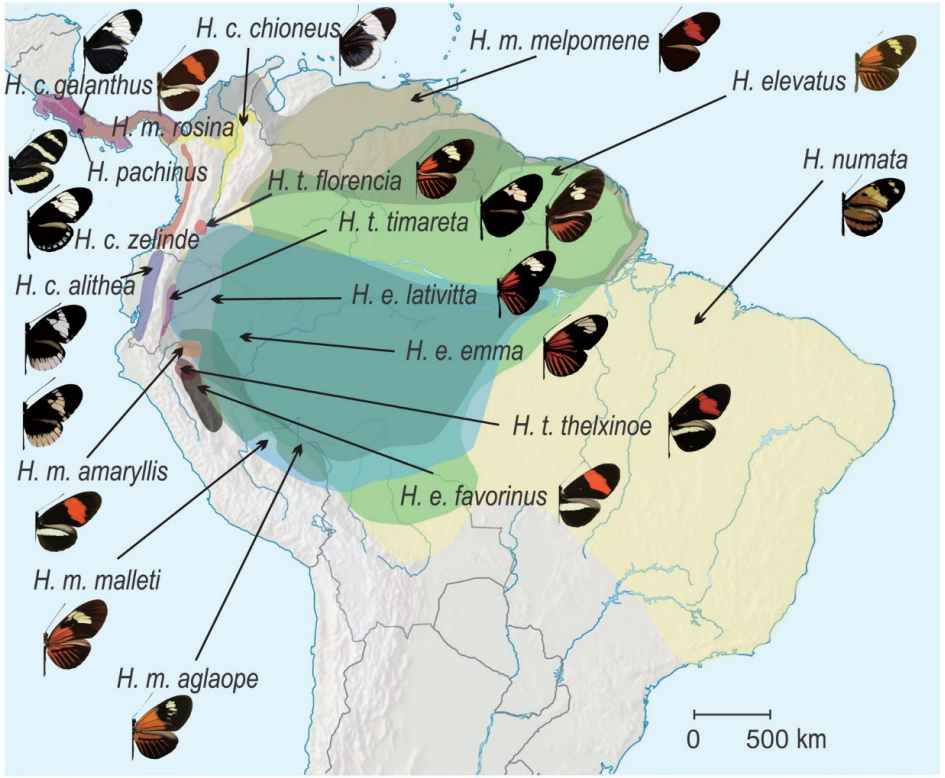

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How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

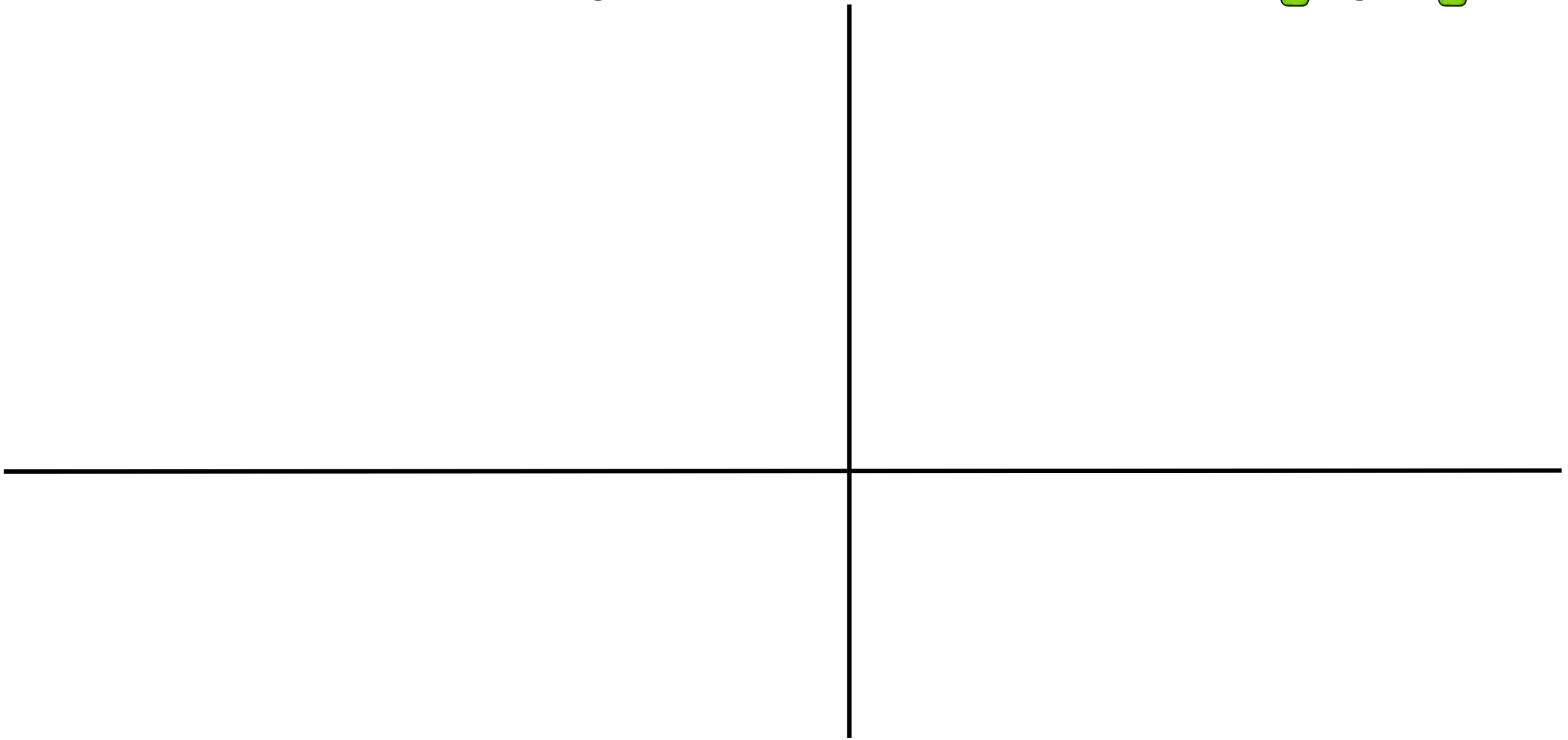
Theoretical context

Competition − / −

Mutualism + / +

Spatial pattern

Niche evolution



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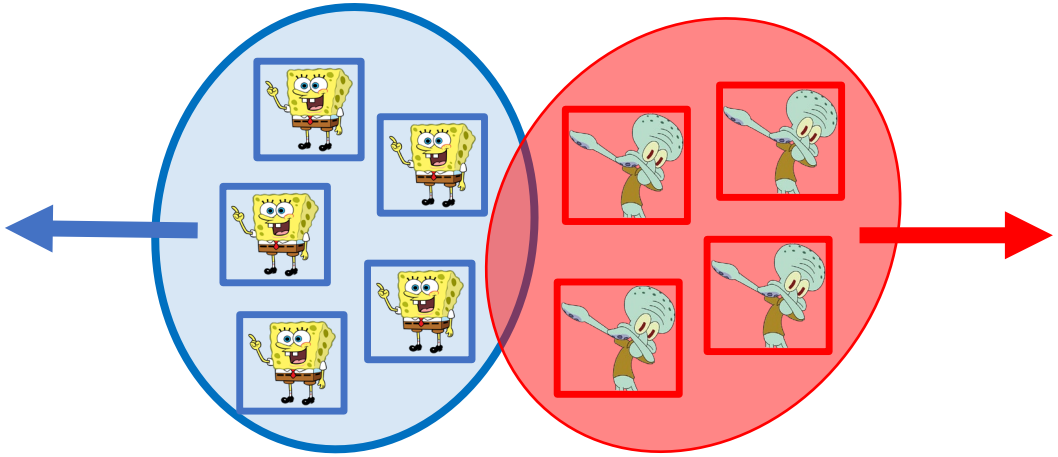

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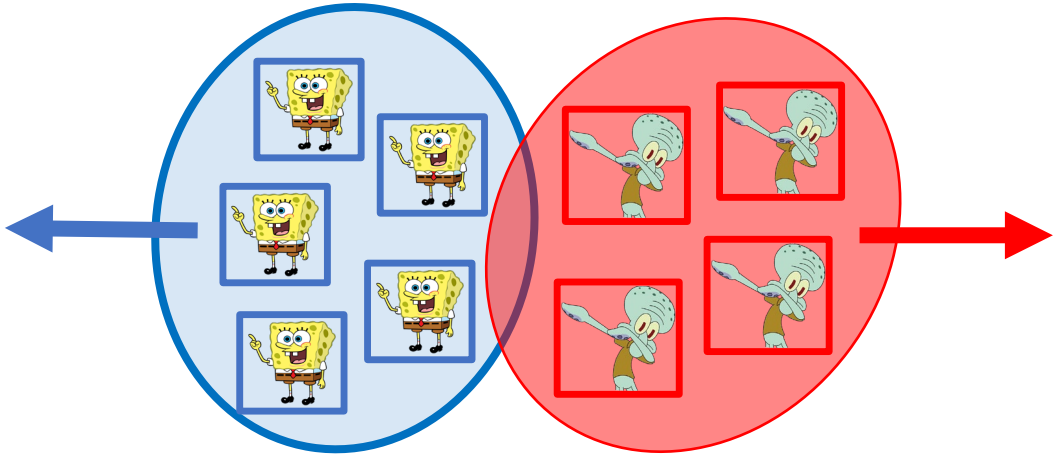

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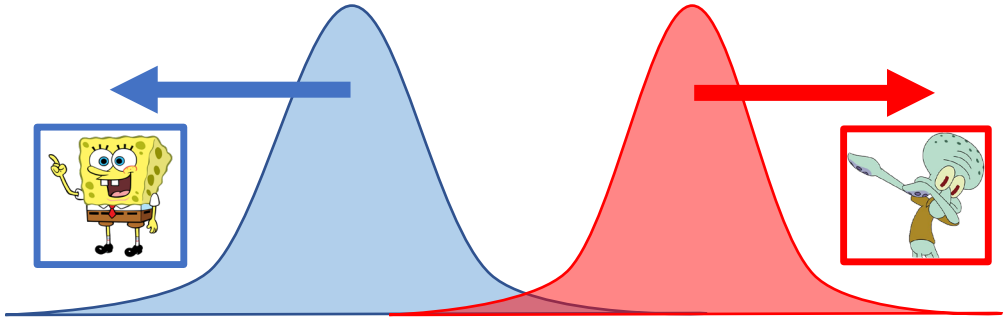

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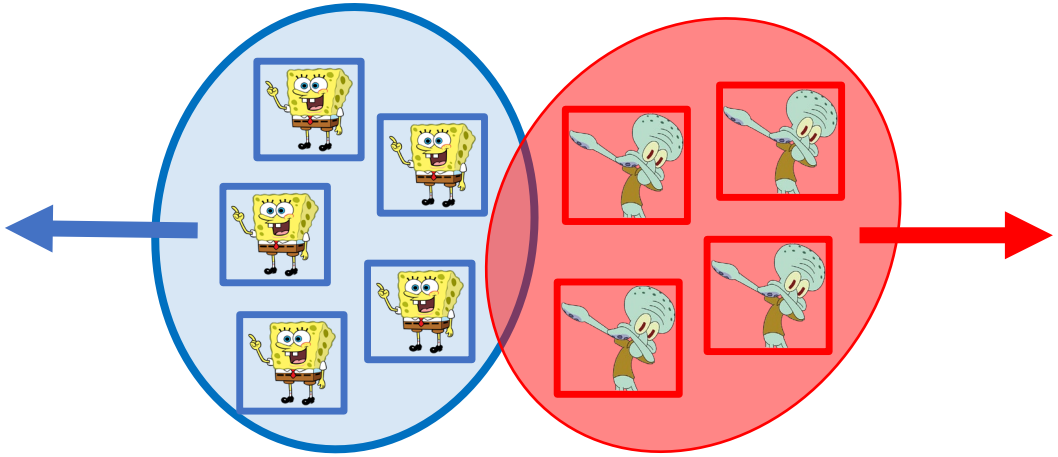

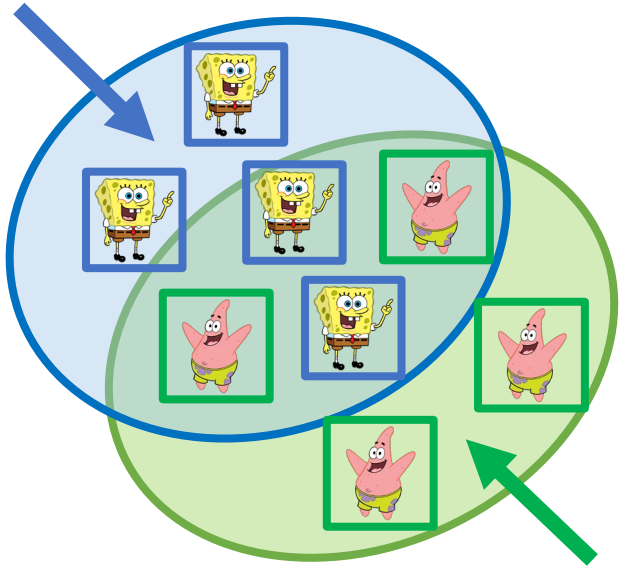

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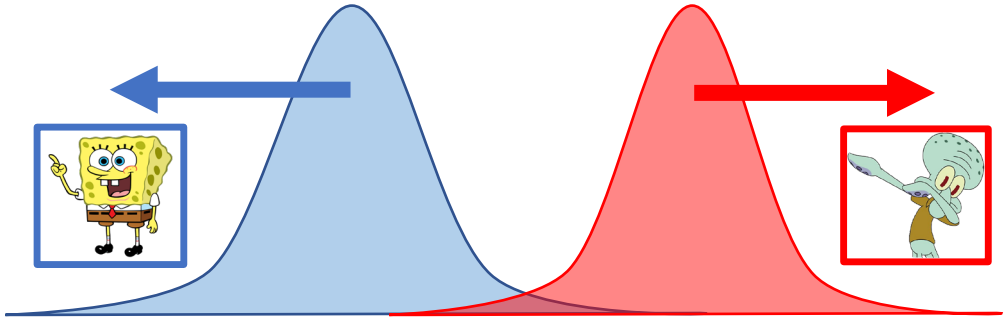

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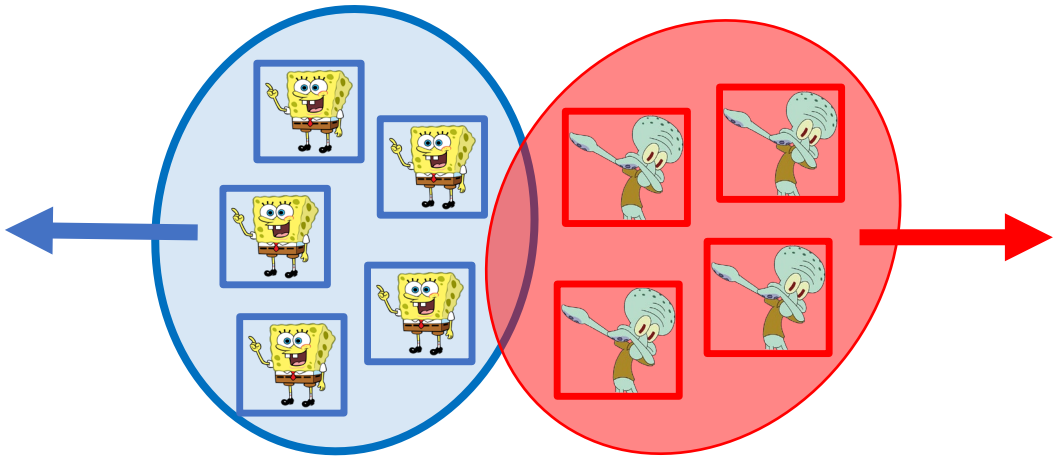

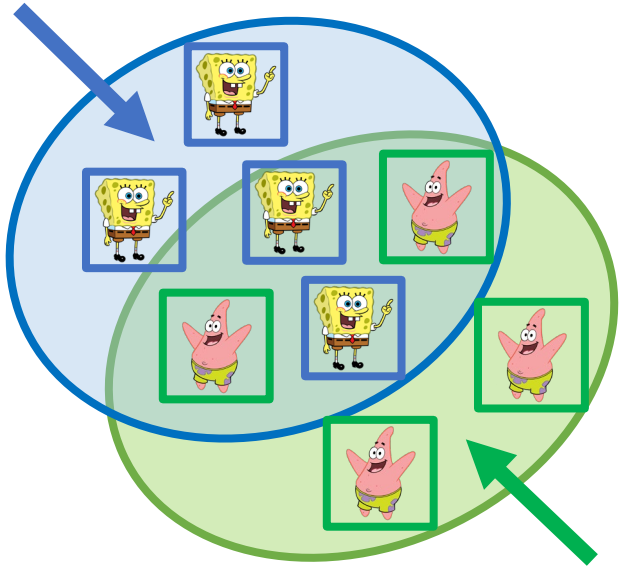

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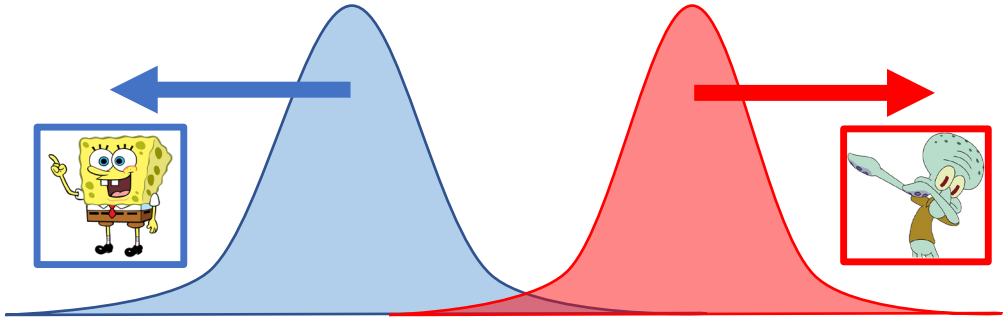

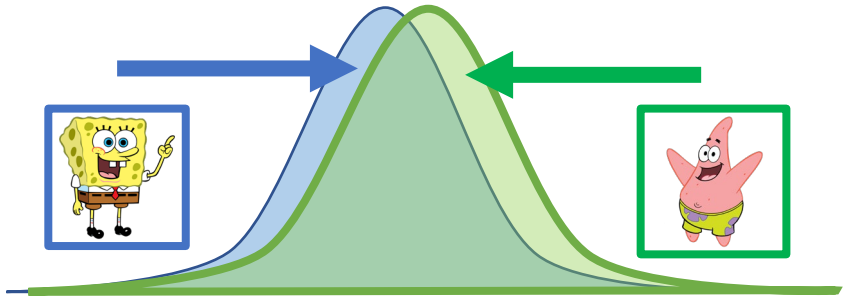

Question & Hypotheses

How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

Spatial pattern

Promote the large-scale **cooccurrence** of mutualistic species

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Niche evolution

Drive the **convergence** of the niche of mutualistic species

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Pattern evolution

Promote the **convergence** of warning signals in sympatric species across whole species range, and at continental scale

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Study system: Neotropical butterflies

Ithomiini tribe

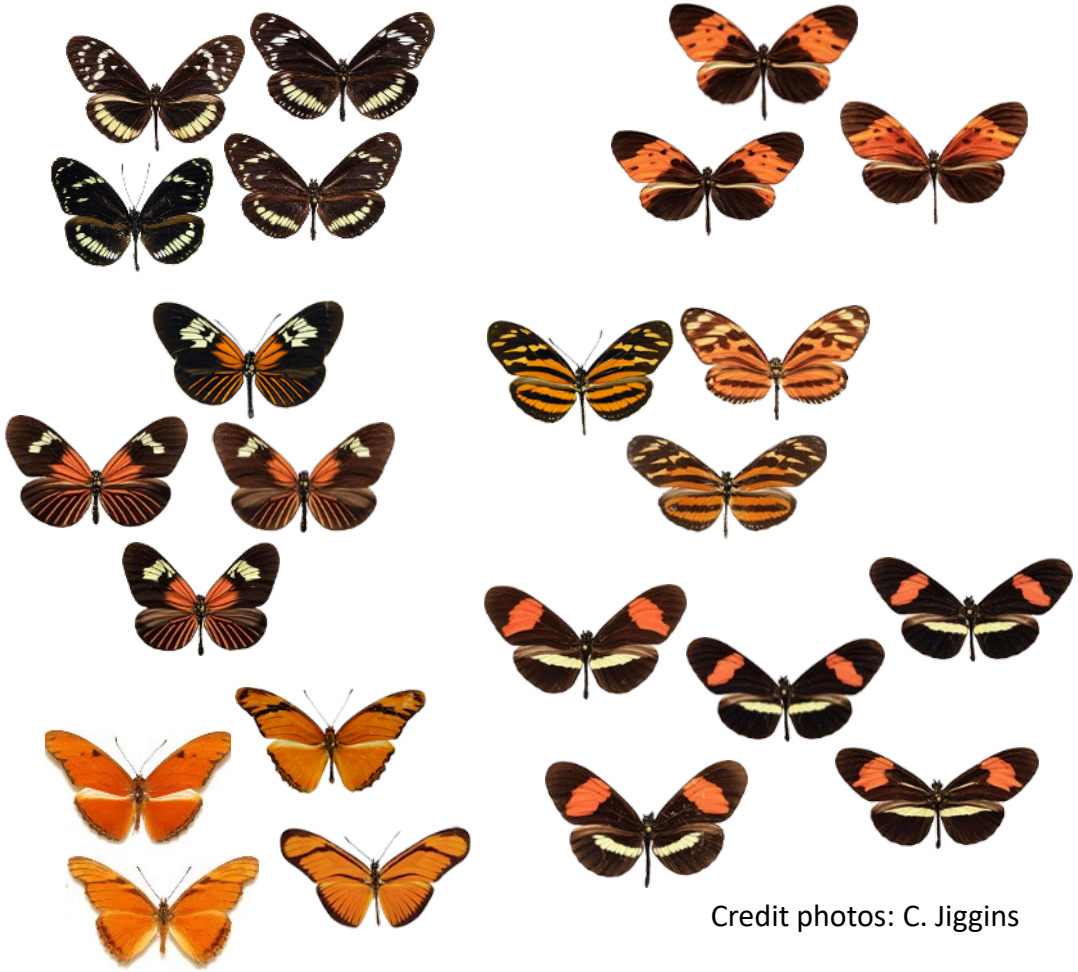
Heliconiini tribe

Mimicry

Phylogeny

Geography

Credit photos: N. Chazot



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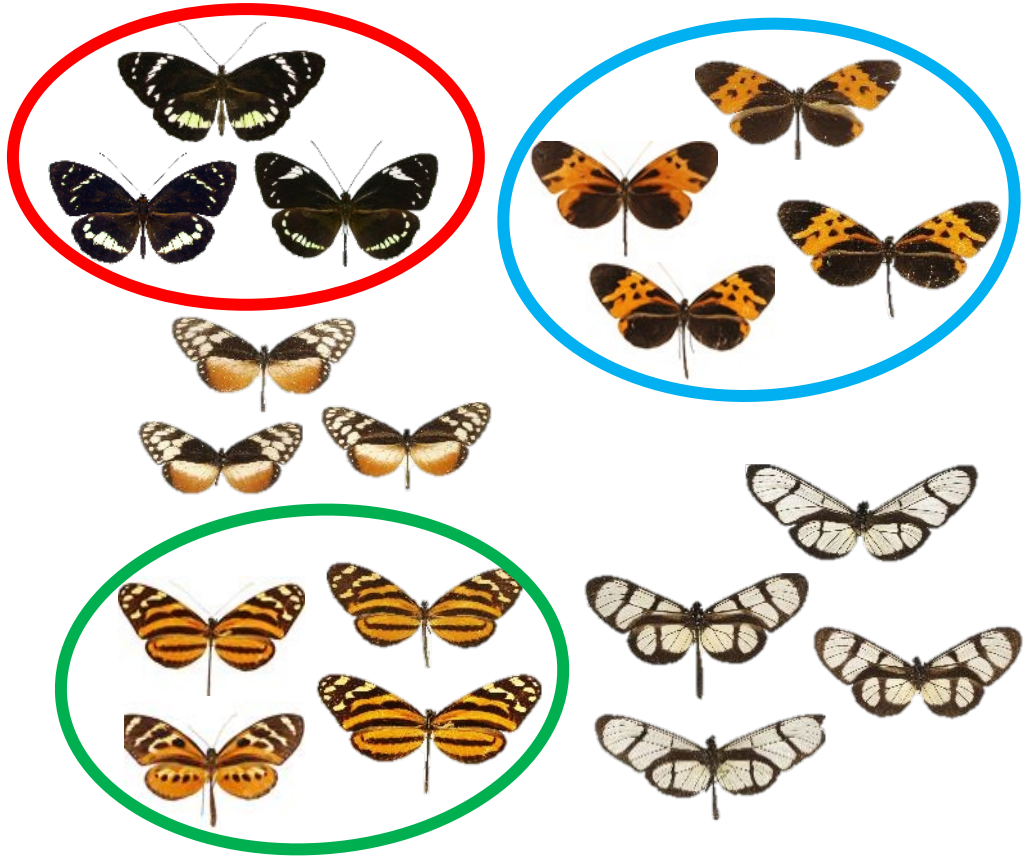

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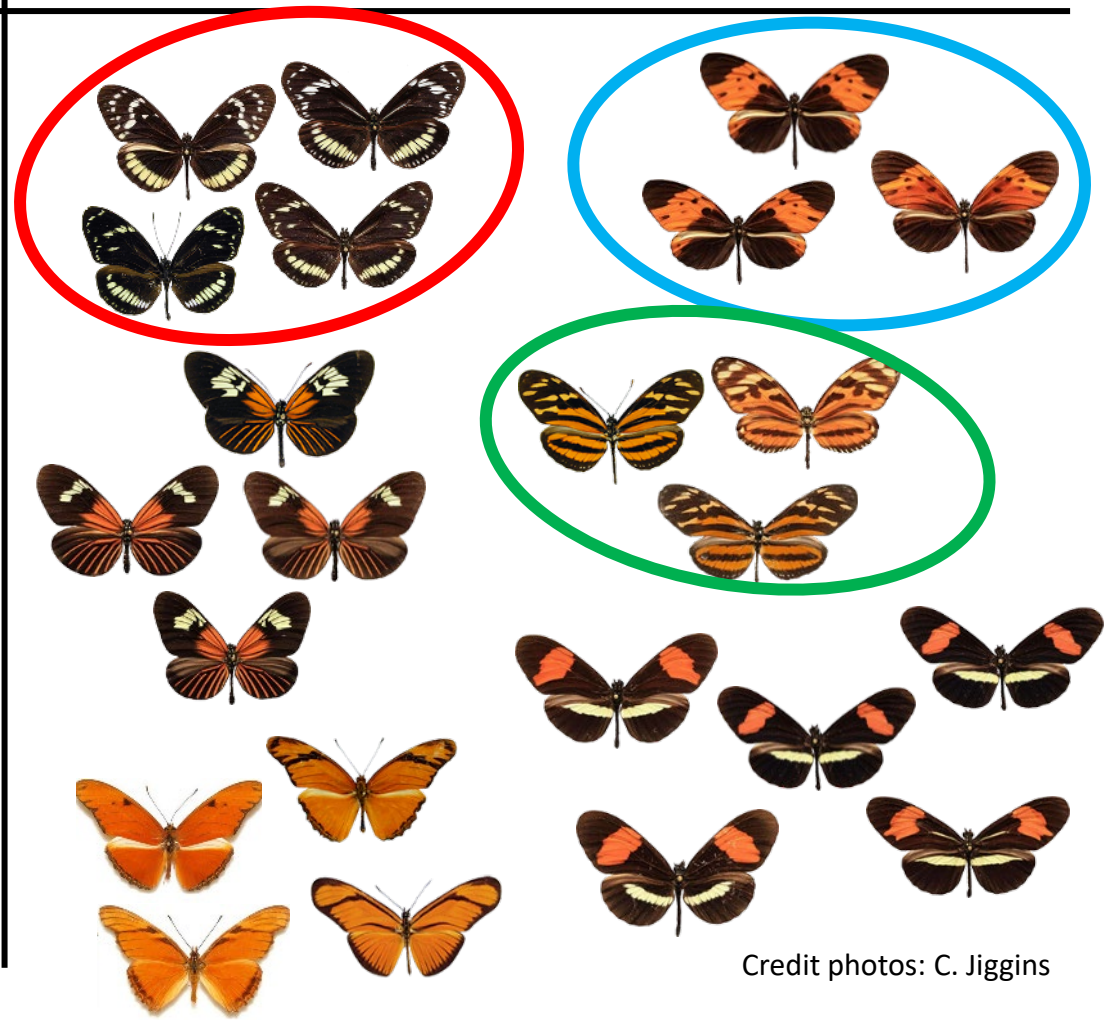

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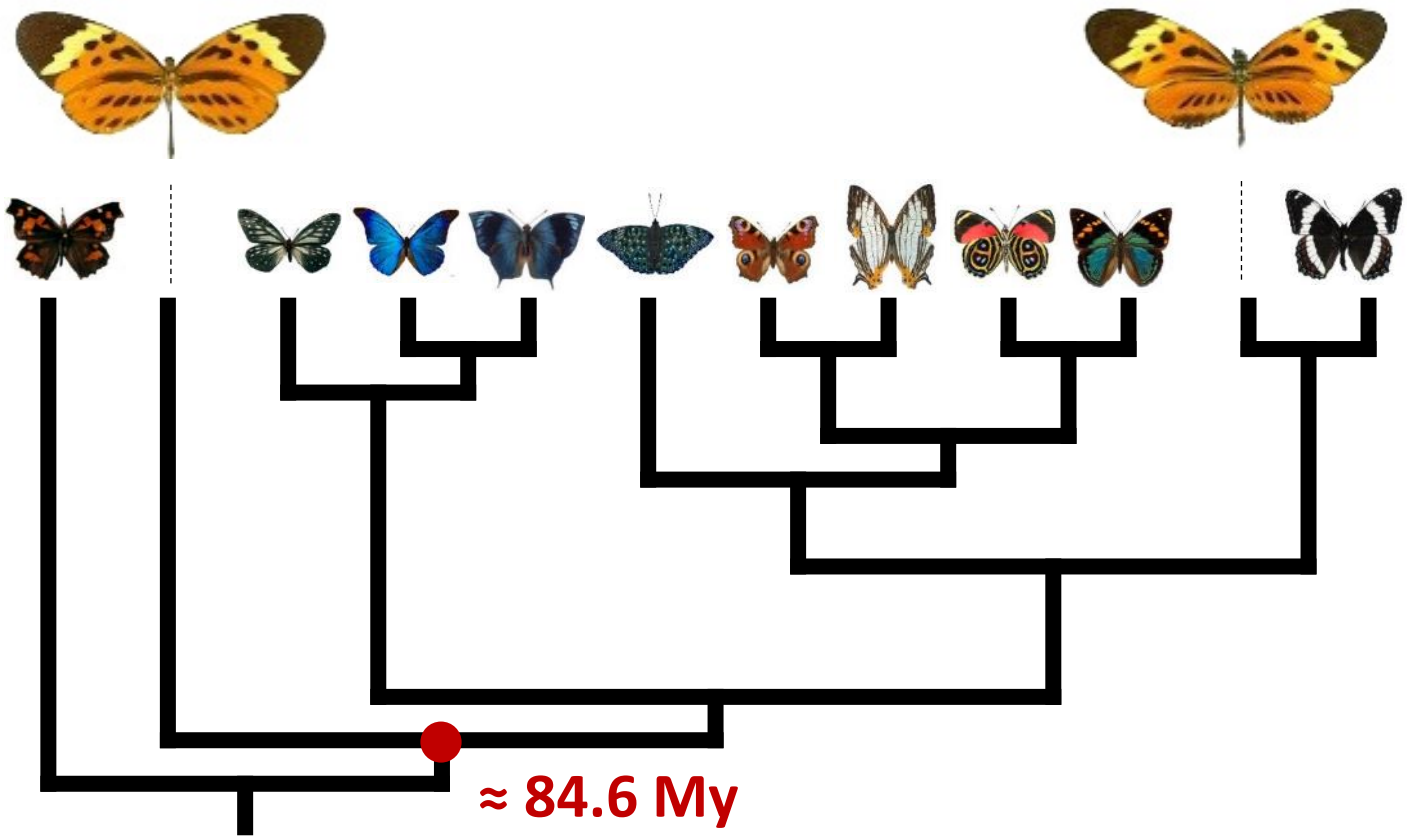

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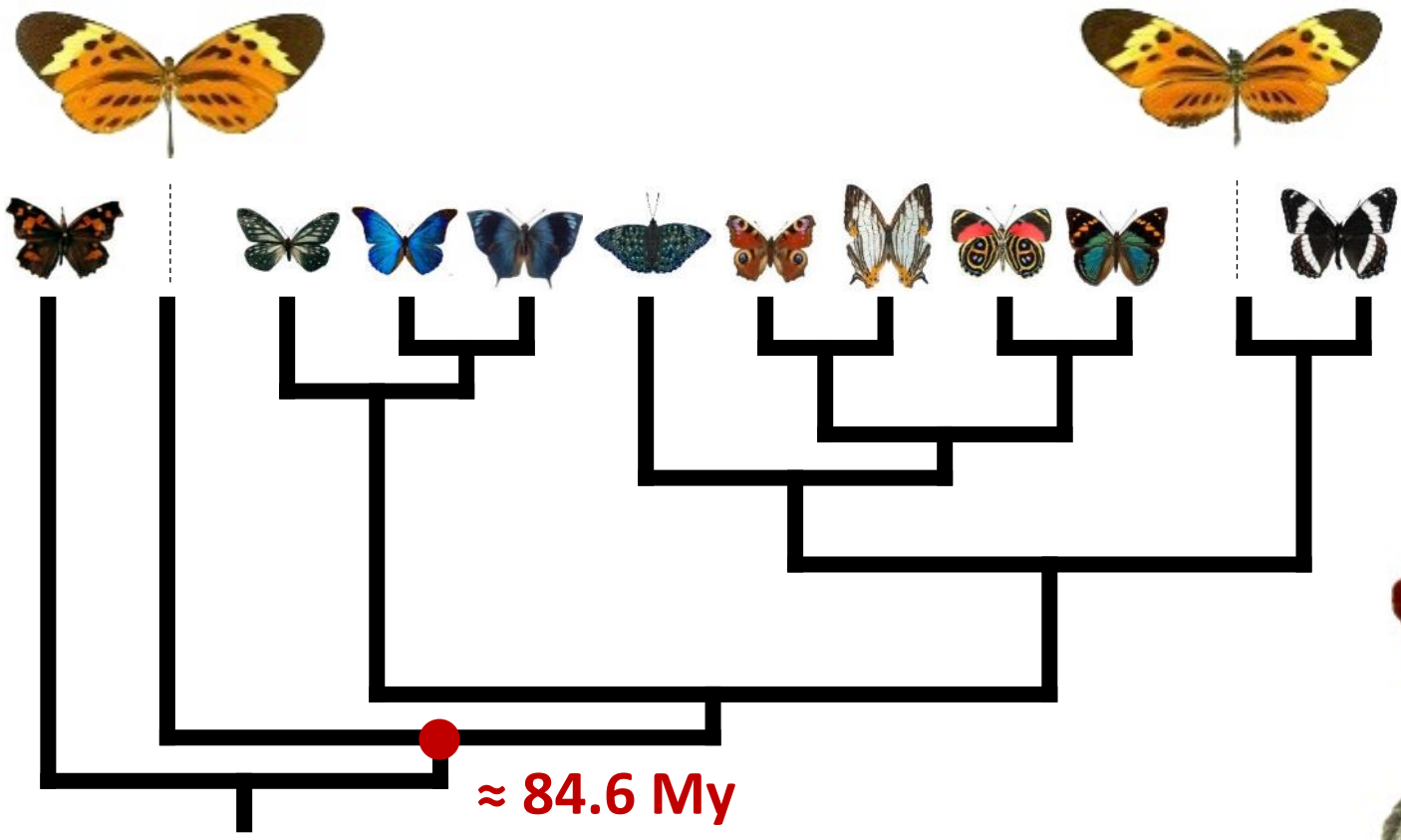
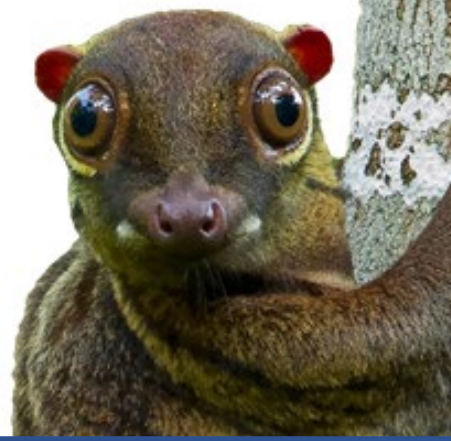


Nymphalidae



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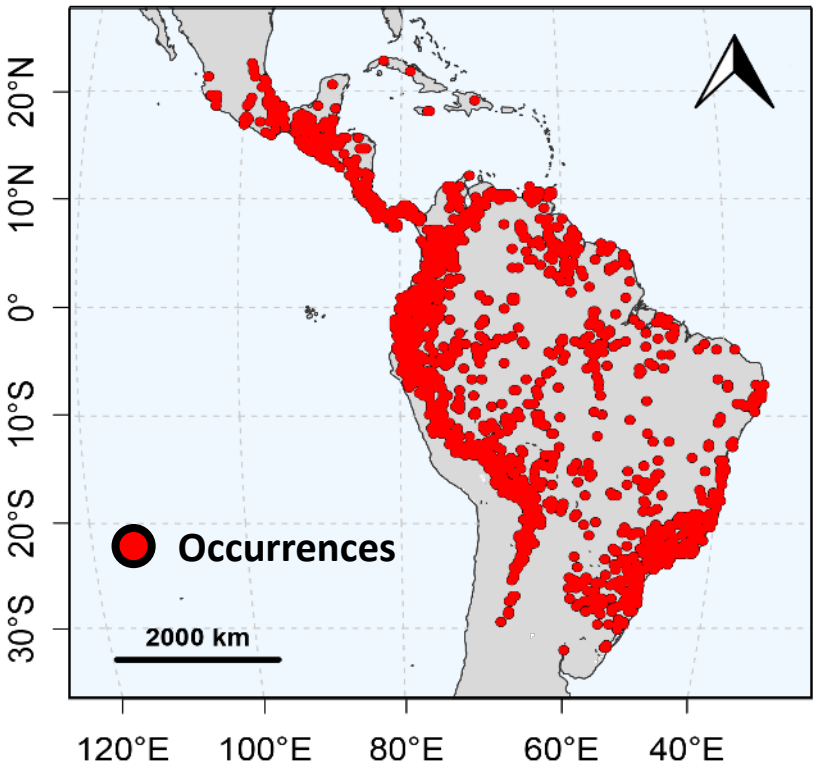
Ithomiini tribe

Occurrence map



Doré et al., 2022

Heliconiini tribe

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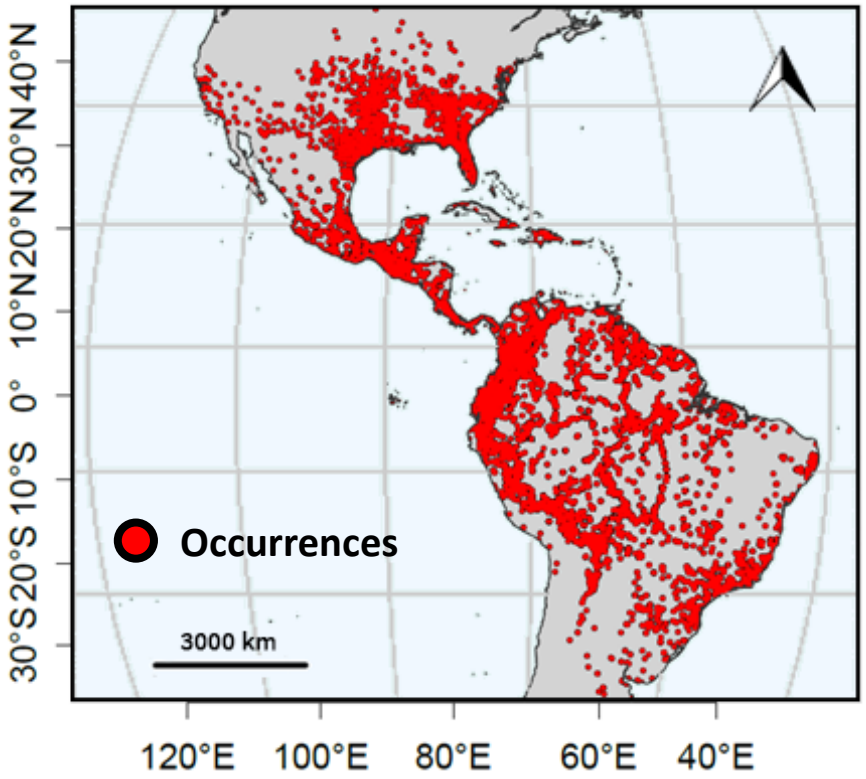

Perochon et al., in prep

Study system: Neotropical butterflies

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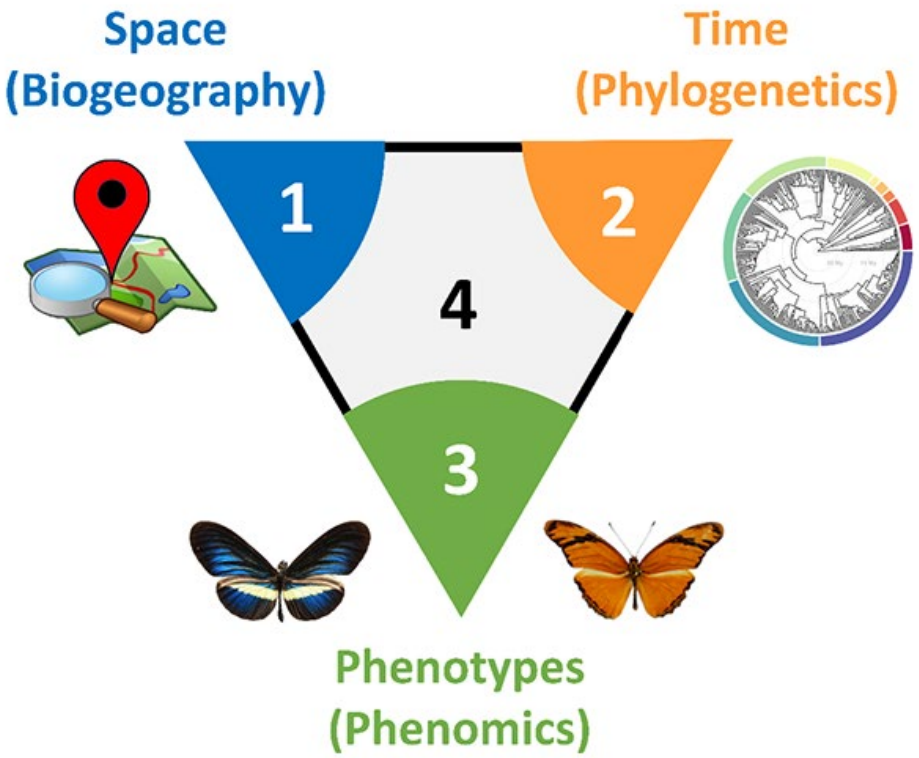
Outlines and objectives



How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

Outlines and objectives

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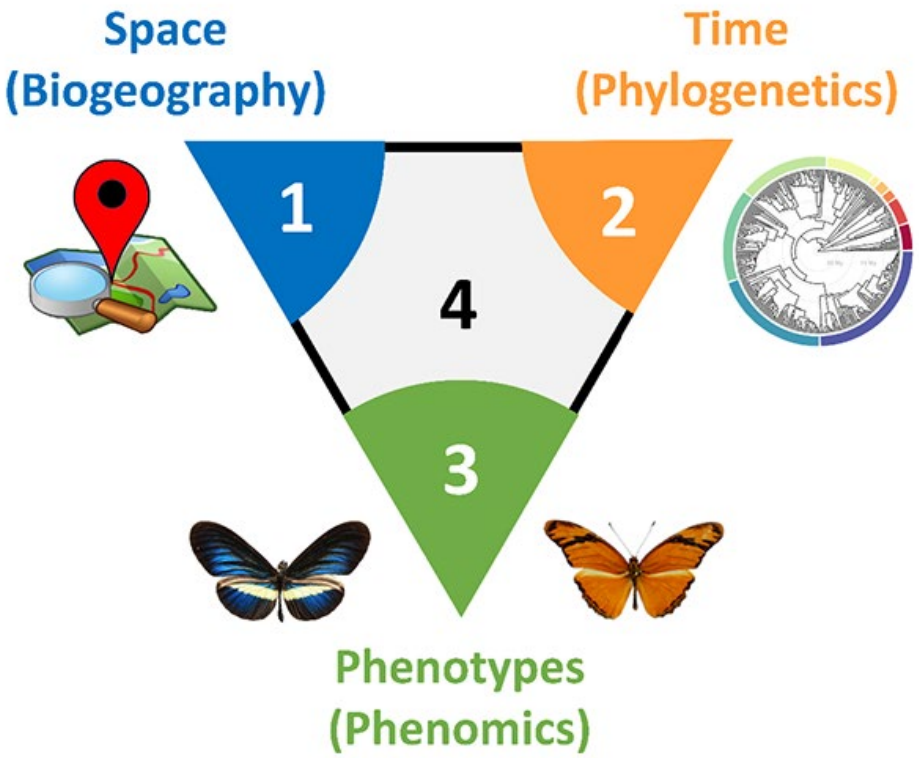
Map **biodiversity patterns**



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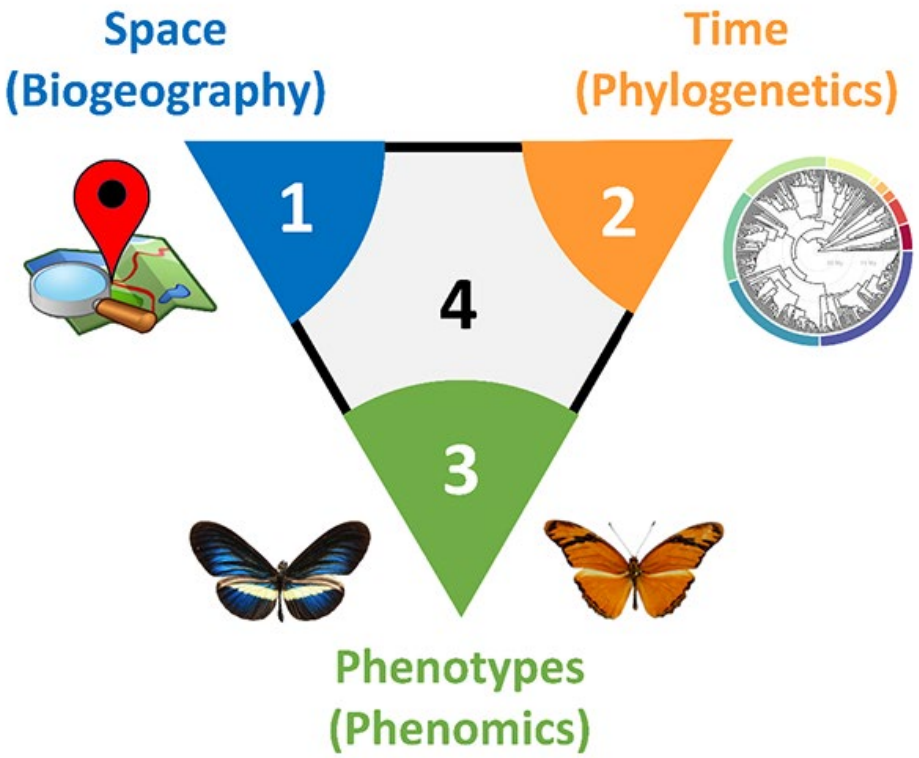

PART 2

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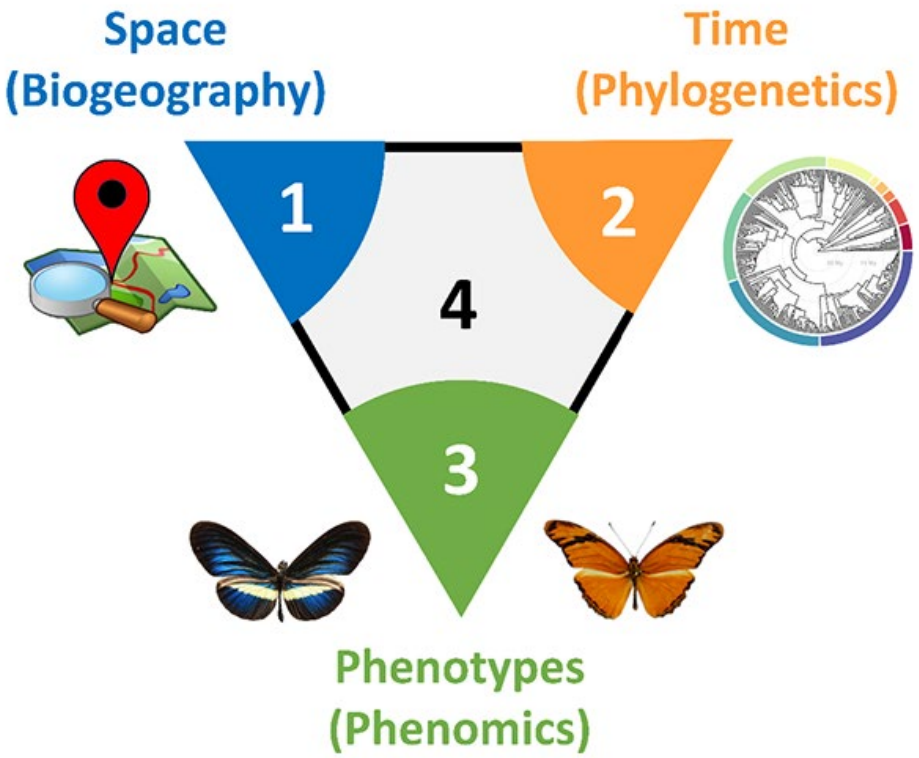

PART 2

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Quantify **phenotypic similarity** in wing patterns

How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

Outlines and objectives

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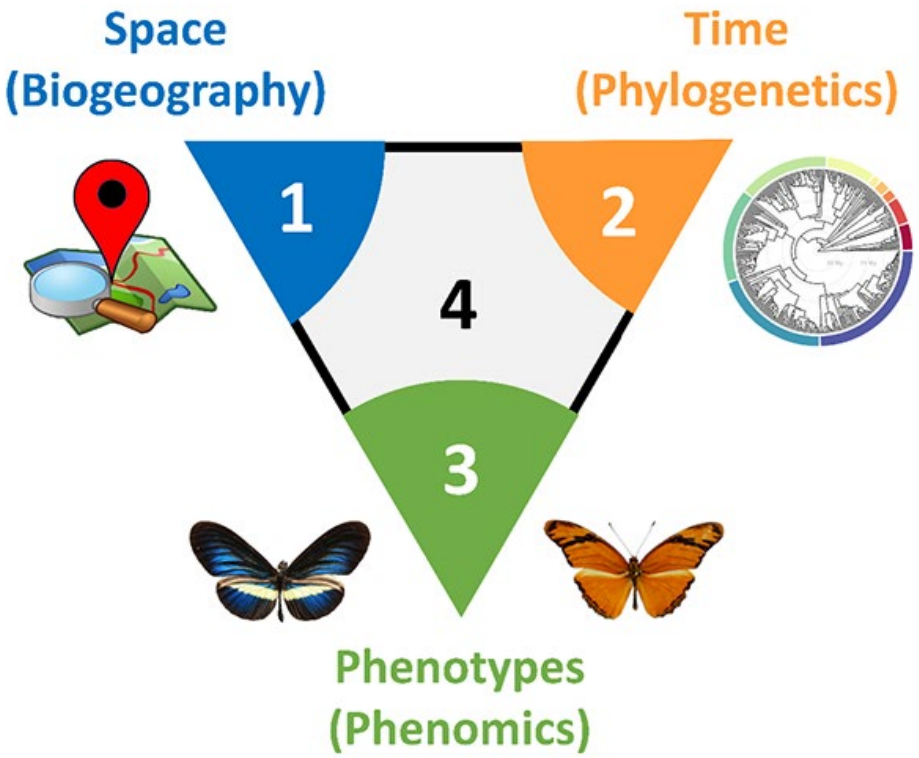

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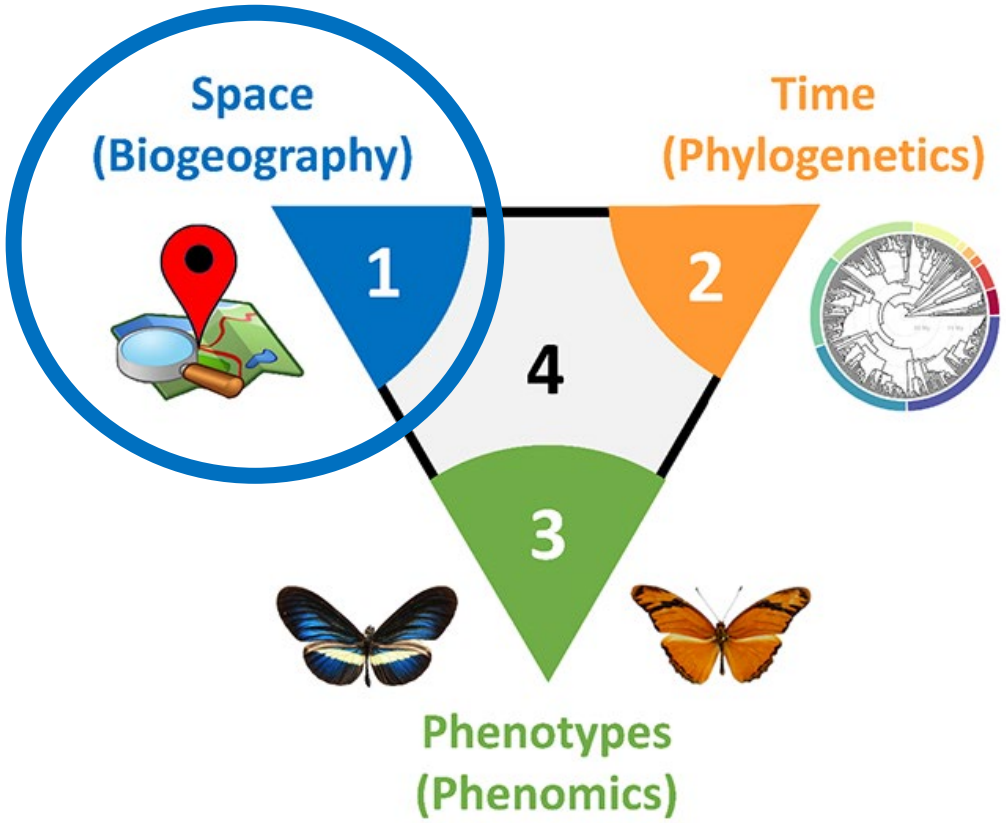
PART 1: Diversity in Space

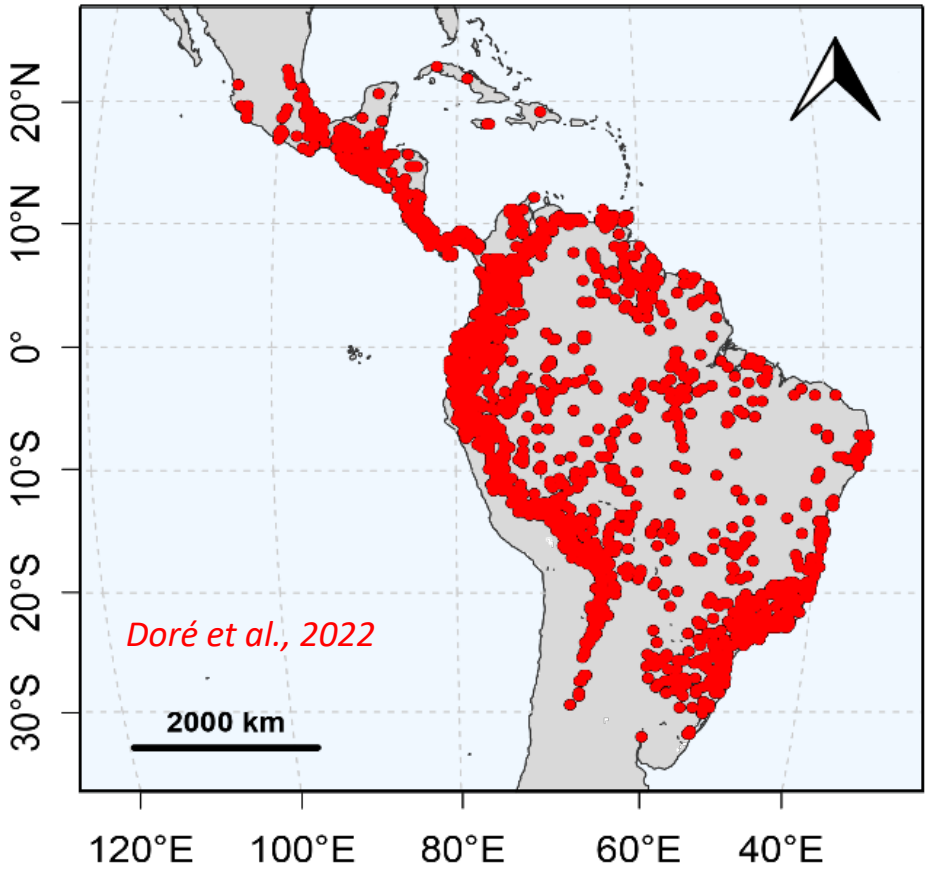
PART 1

Map **biodiversity patterns**



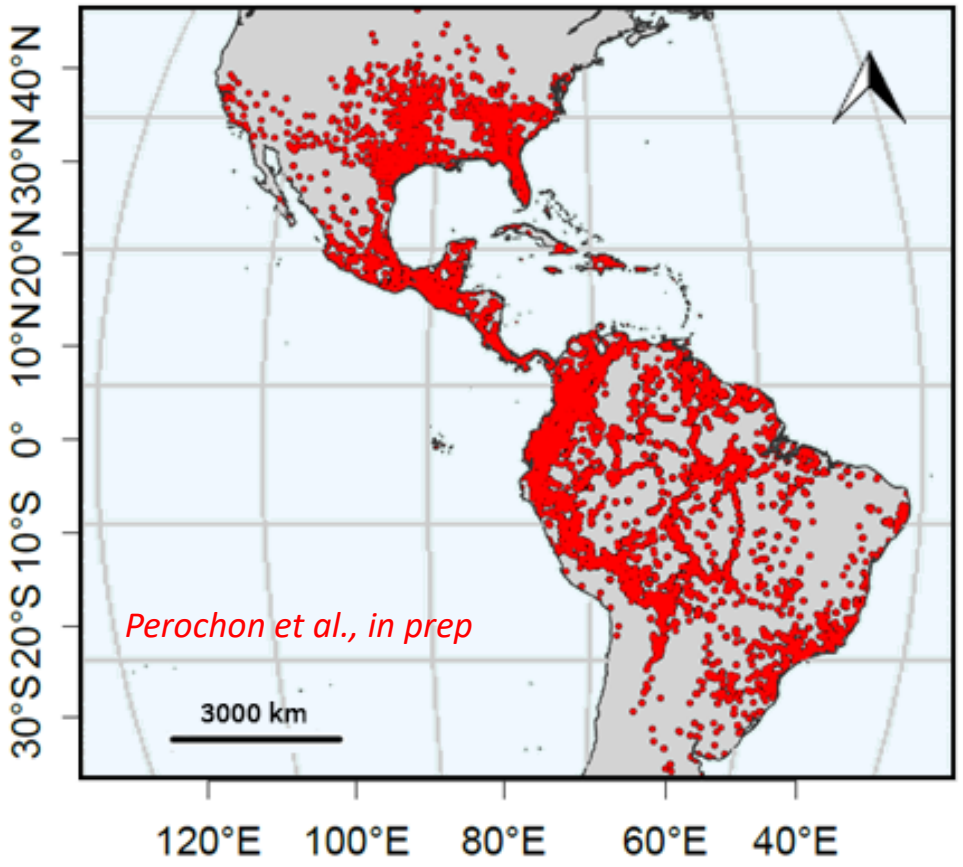
Available data

Ithomiini tribe (396 species)



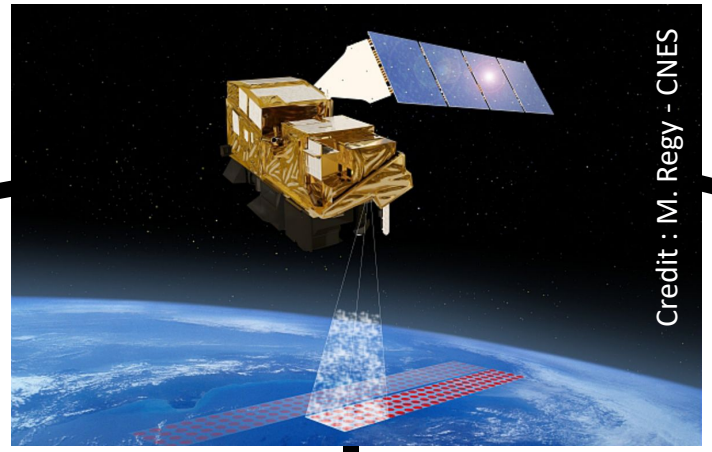
28,986 occurrences across **1,834 sites**

Heliconiini tribe (77 species)



77,577 occurrences across **4,168 sites**

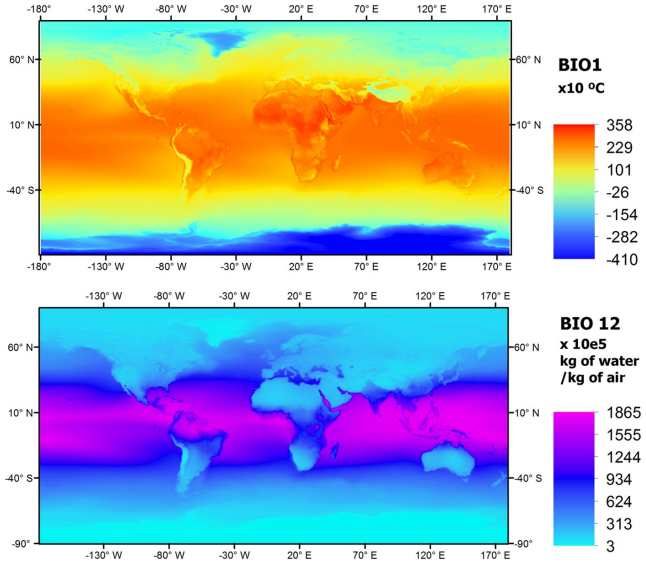
Available data



Climate data

MERRAclim v.2.0

- Annual temperature
- Humidity levels
- Temperature seasonality
- Humidity seasonality



Vega et al., 2017

Elevation

SRTM Dataset v.4.1

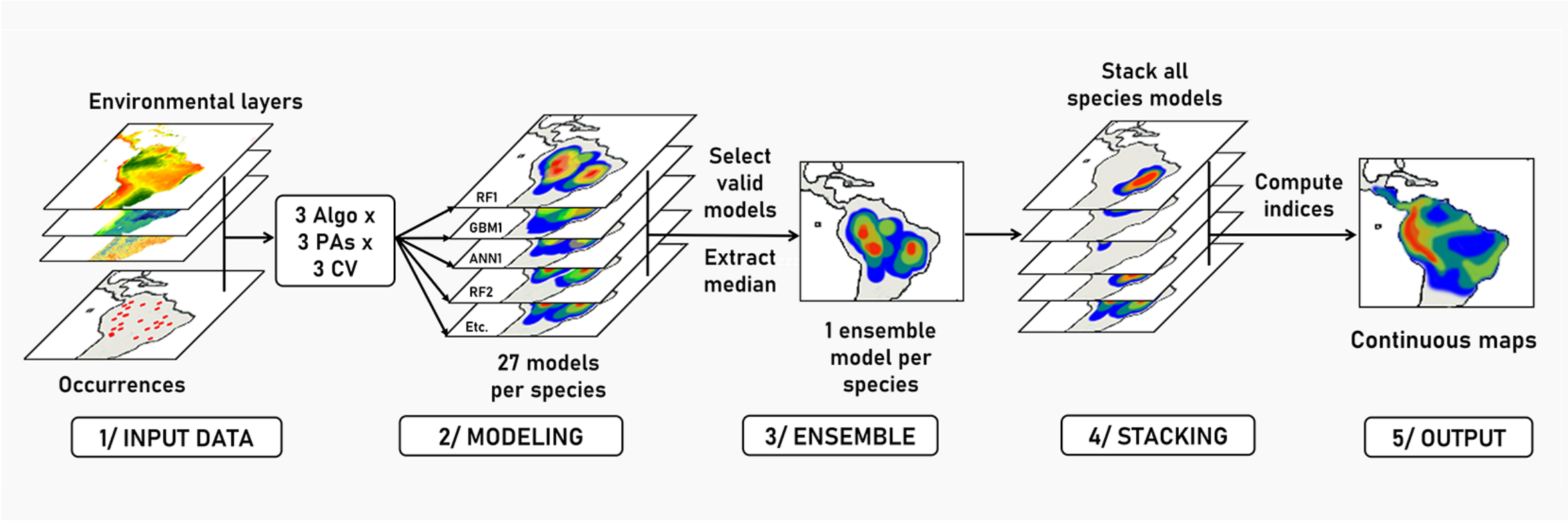
Farr et al., 2007

Vegetation cover

GFCC v.3.0

Sexton et al., 2013

Species Distribution Modeling (SDM)

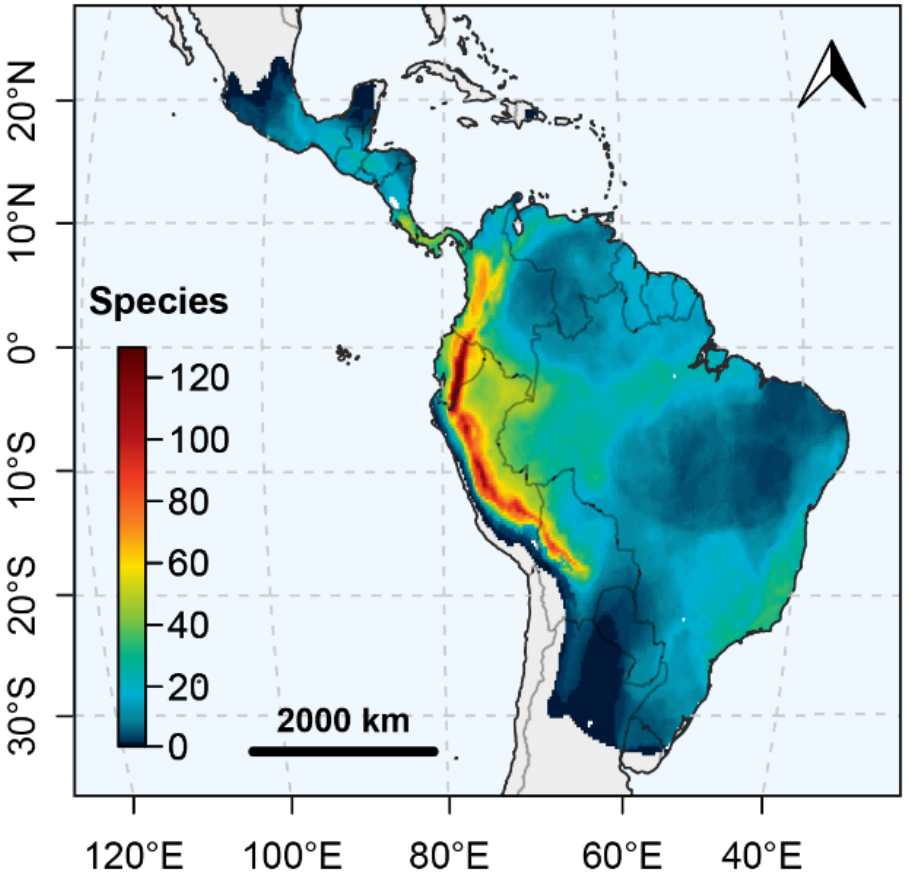


SDM → Species distribution maps → Diversity indices

Biodiversity patterns

Species richness

Ithomiini
(396 species)



Doré et al., 2022

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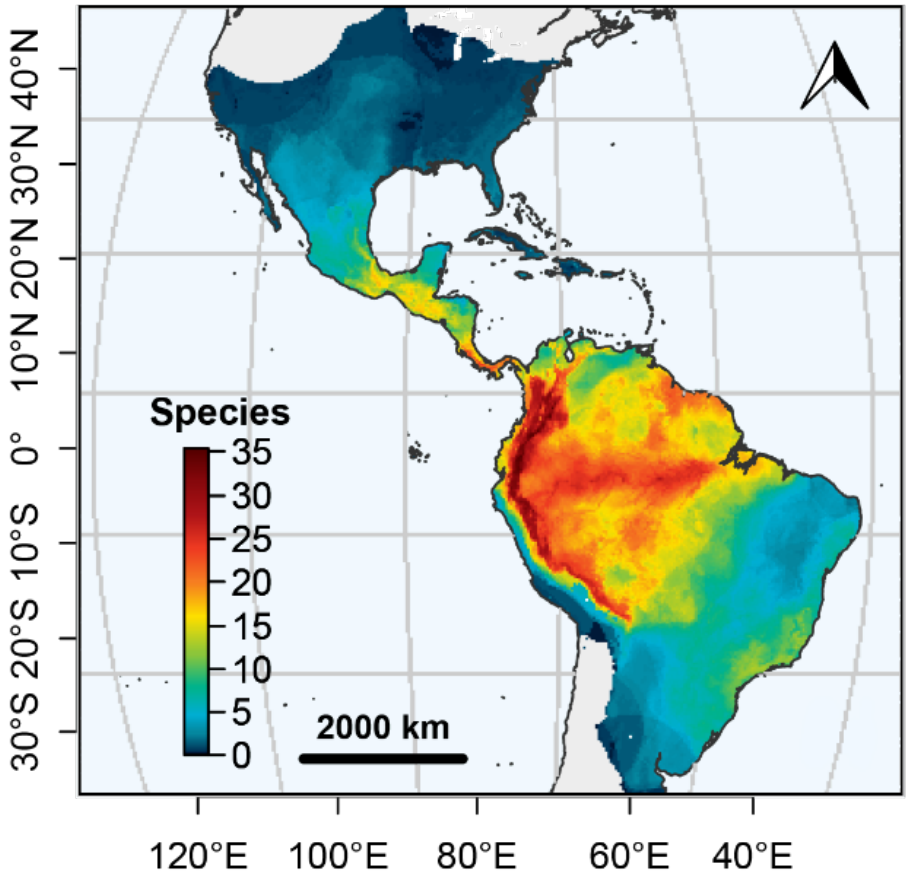

Pérochon et al., in prep

Biodiversity patterns

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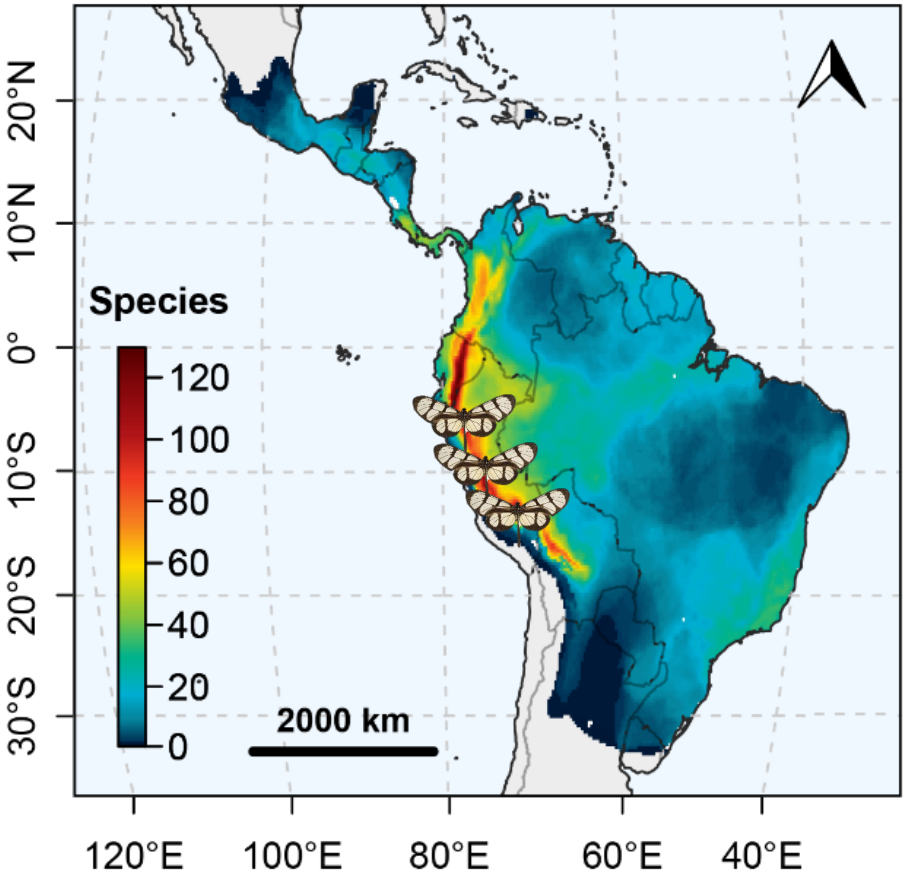

Doré et al., 2022

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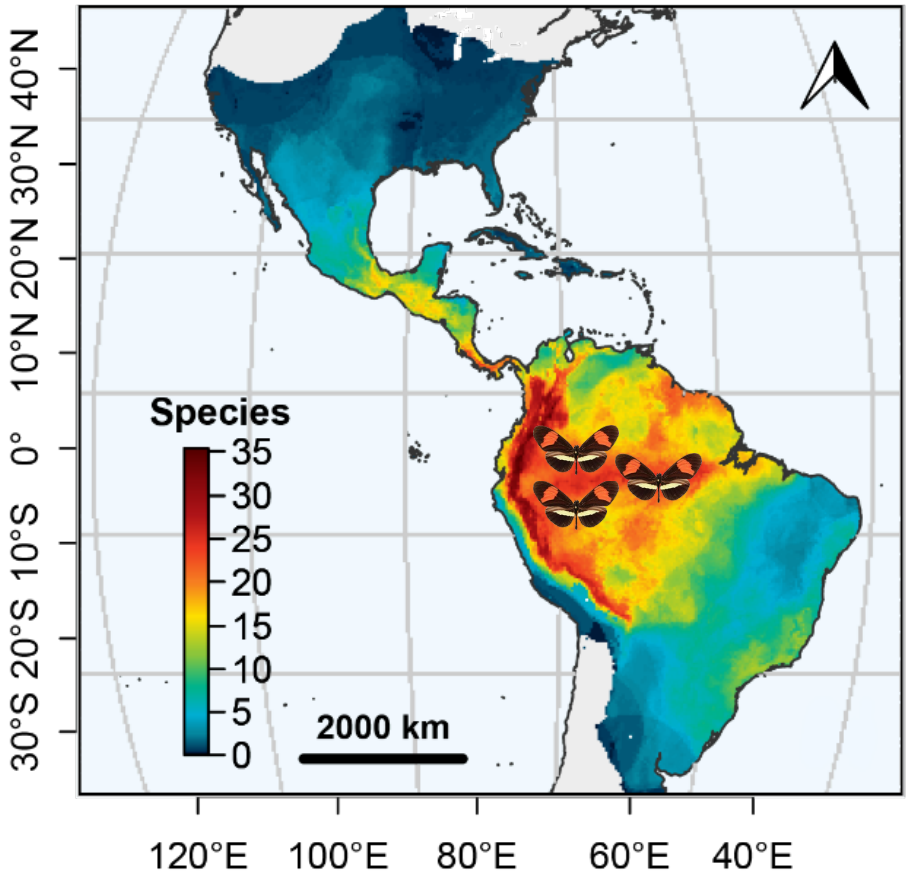

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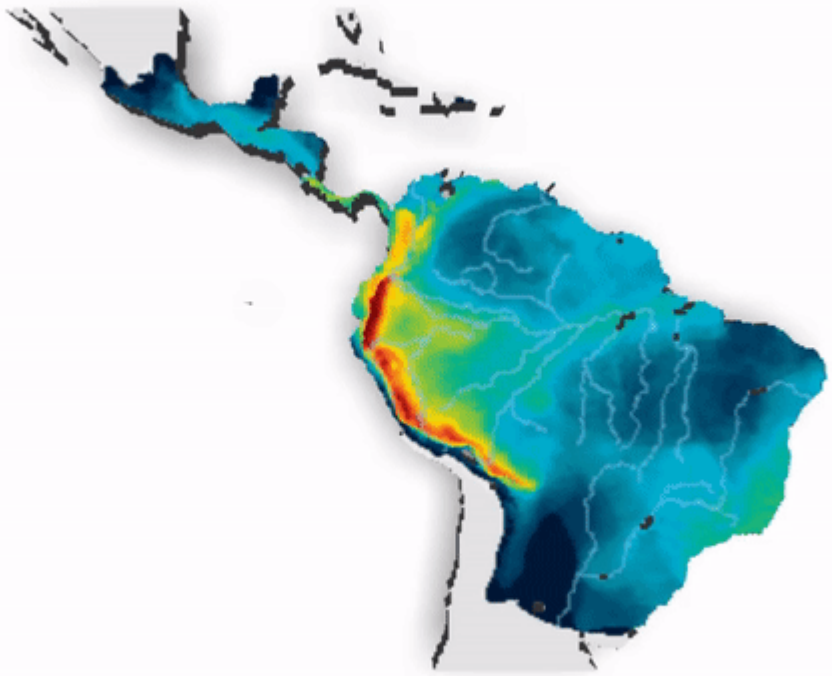

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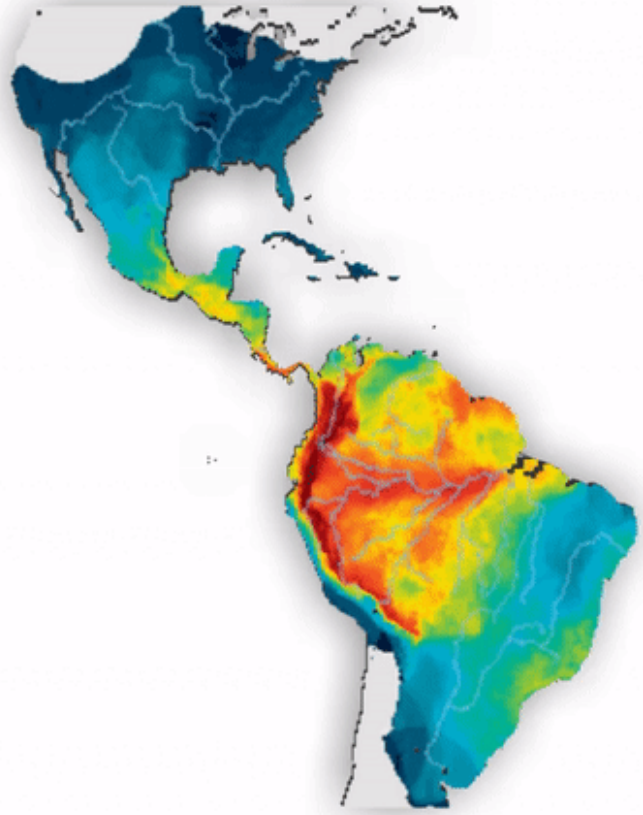


Anthropogenic threats

Identify **risk areas** and **refuge areas** against **anthropogenic threats**

Current anthropogenic threats
≈
Human Footprint

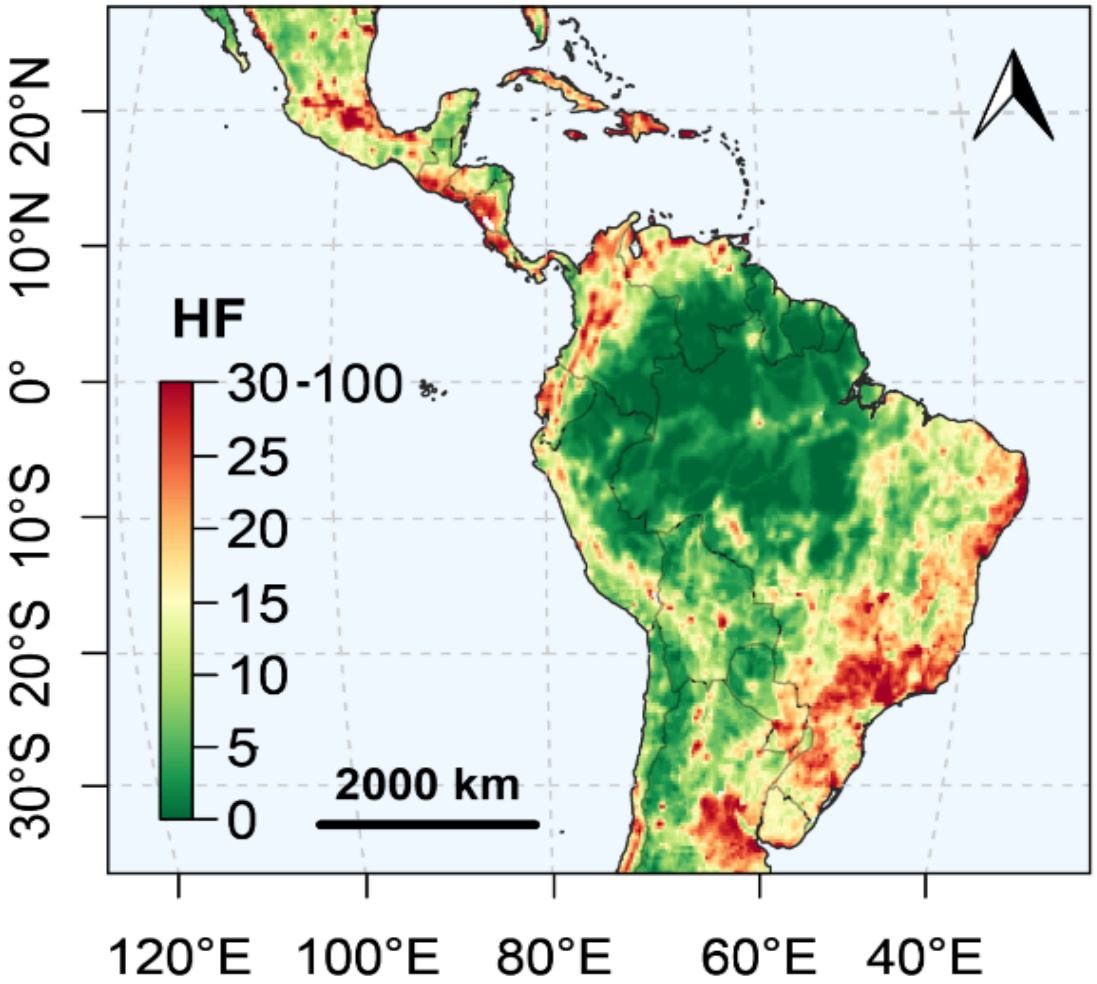
(1) Human population density

(2) Landcover: urban, crop, pasture, wilderness

(3) Proximity to transport infrastructures: railways, major roadways, and navigable waterways

(4) Night-time light pollution

Human Footprint



Venter et al., 2016

Anthropogenic threats

Identify **risk areas** and **refuge areas** against **anthropogenic threats**

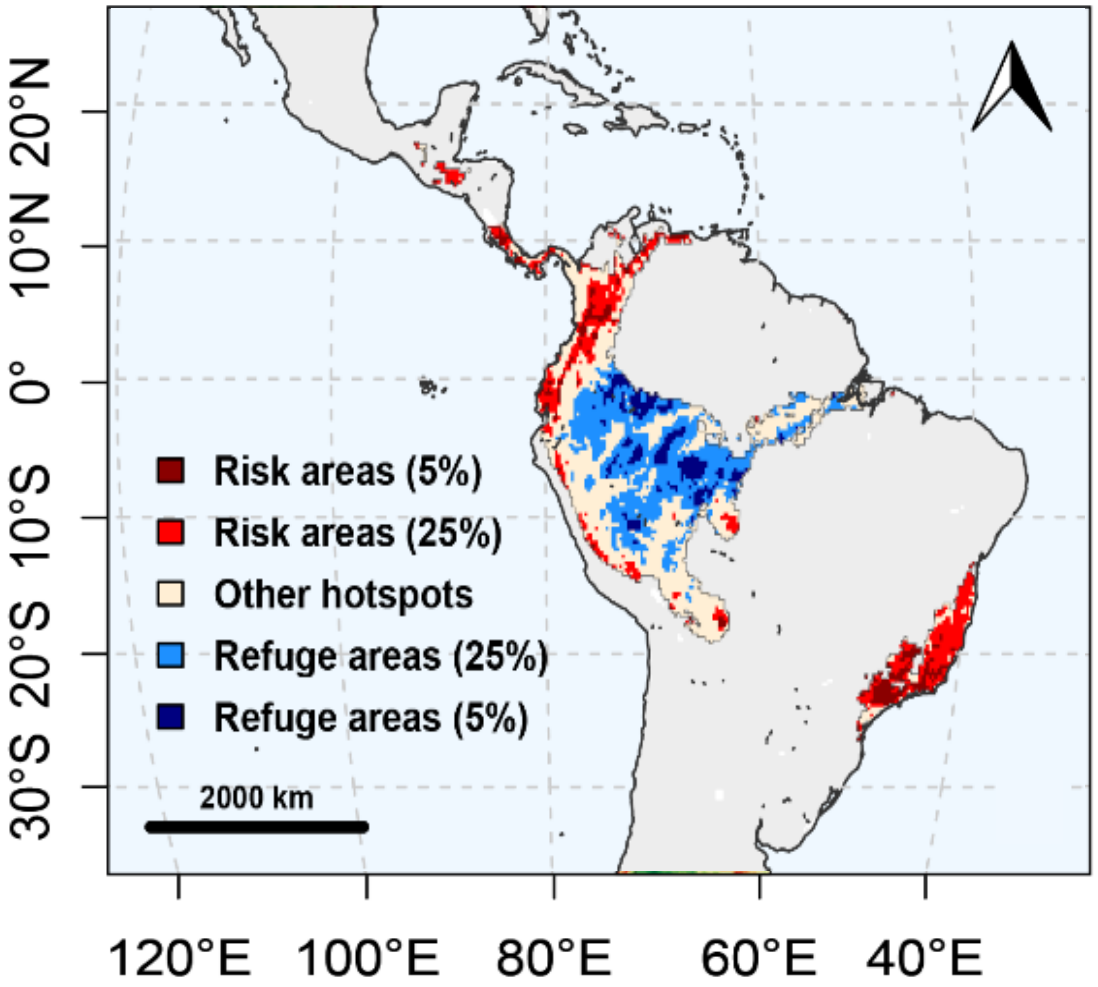
Current anthropogenic threats
≈
Human Footprint

Risk areas: Tropical Andes, Central America, Brazilian Atlantic Forest

Potential **refuge area**: Western Amazon (?)

Limits: **Low redundancy** with other areas
Climate change and **deforestation**

Species richness
Top 25% hotspots



Doré et al., 2022

Anthropogenic threats

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Human Footprint

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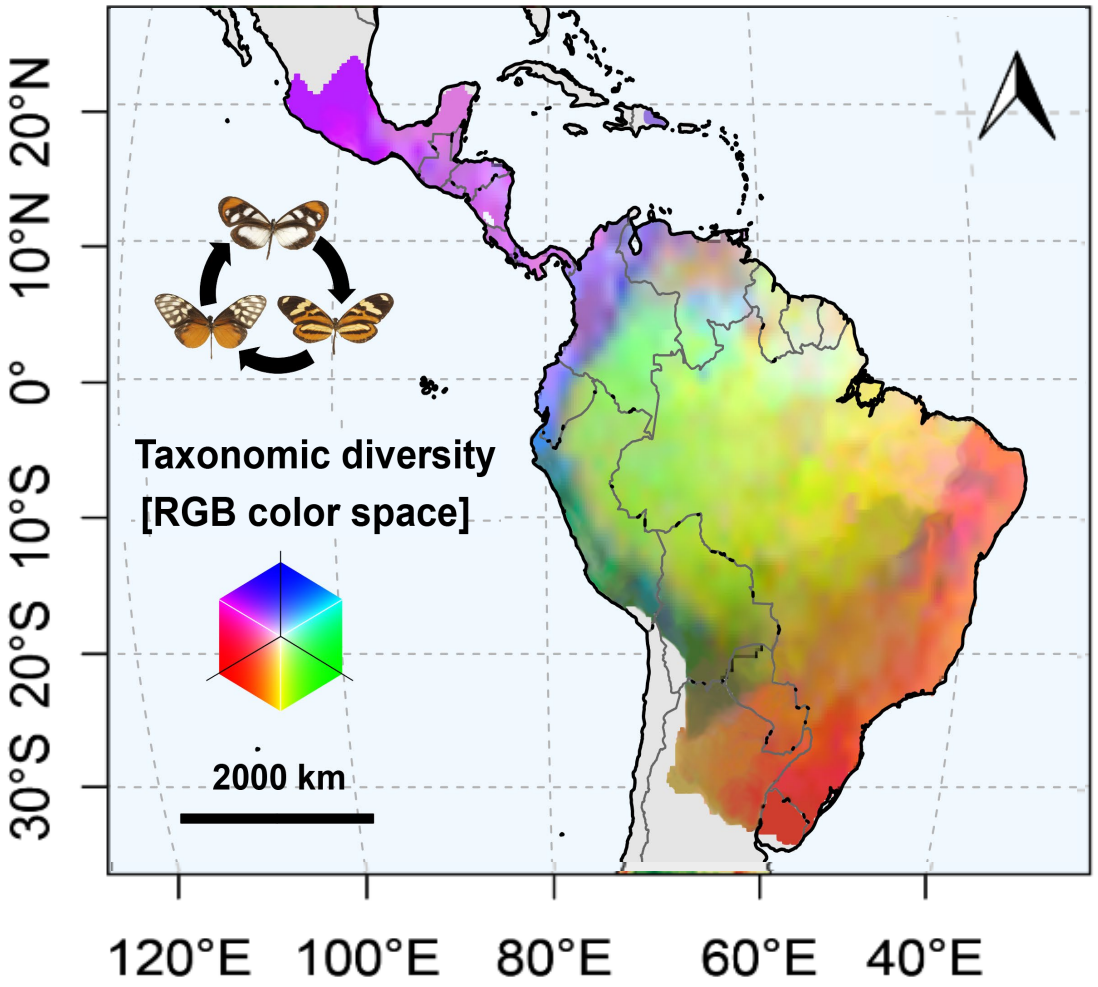
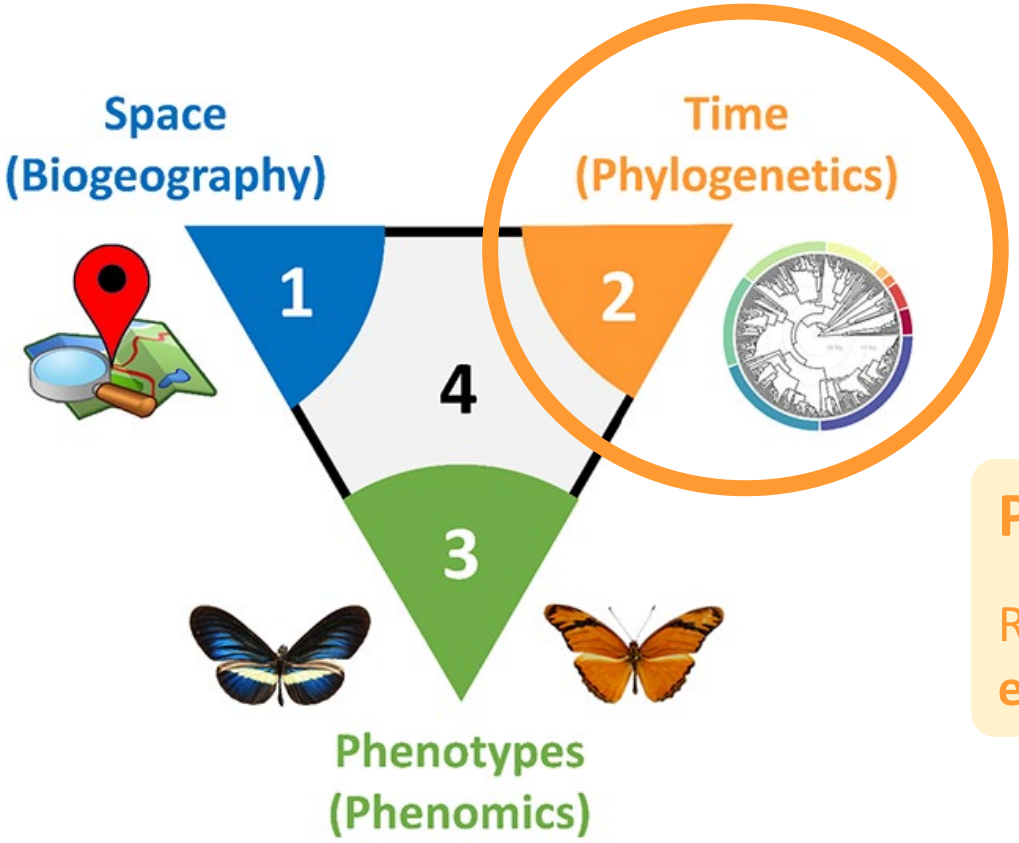
Taxonomic β-Diversity



PART 2: Diversity in Time

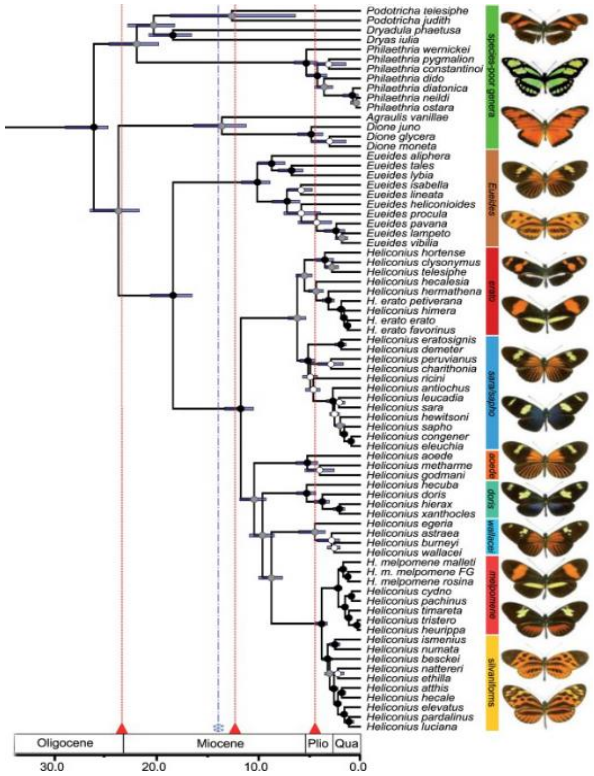


PART 2

Resolve **deep evolutionary relationships**

Comprehensive Time-calibrated phylogenies

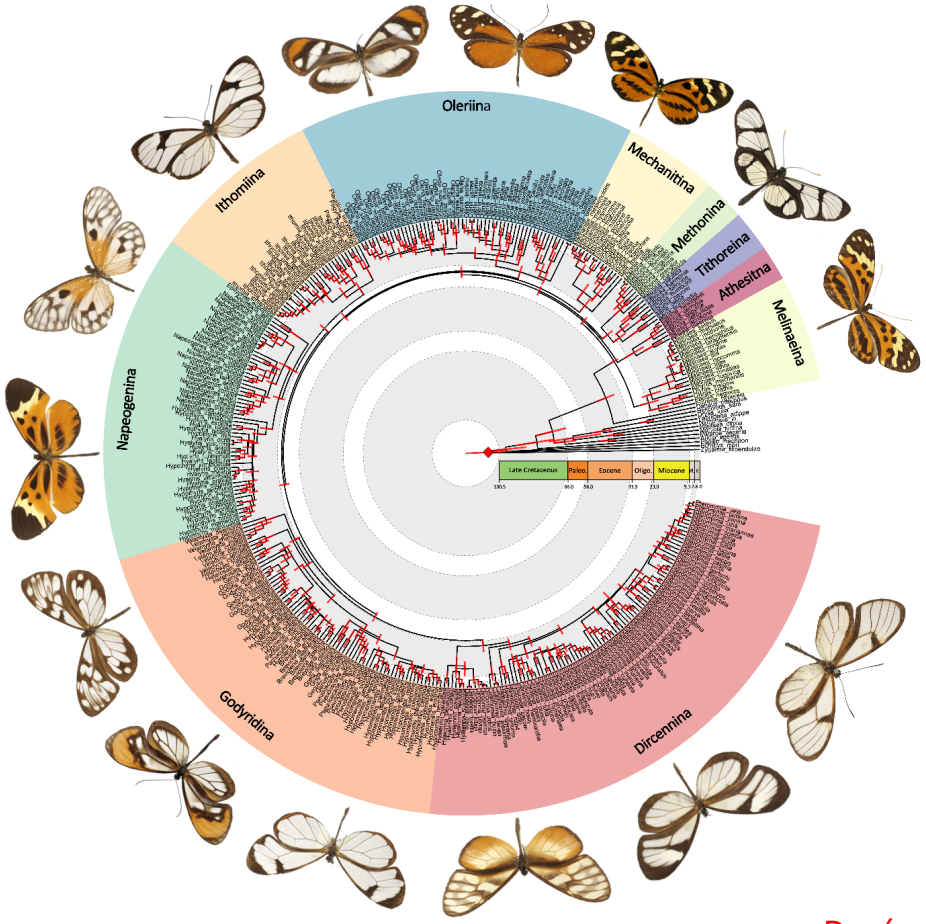
Heliconiini tribe



Kozak et al., 2015

Sanger-based phylogeny with 22 loci and 71 species (92%)

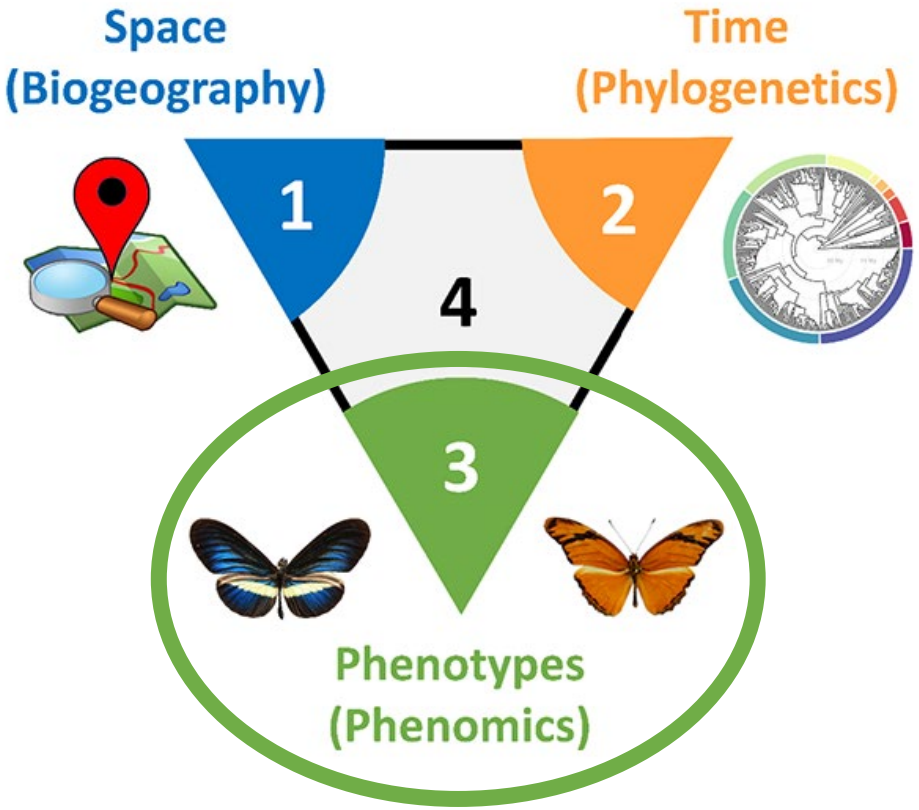
Ithomiini tribe



WGS-based phylogeny with 11,012 loci and 356 species (89.9%)

Doré et al., in prep.

PART 3: Diversity in Phenotypes



PART 3

Quantify **phenotypic similarity** in wing patterns

Pattern diversity in Heliconiini

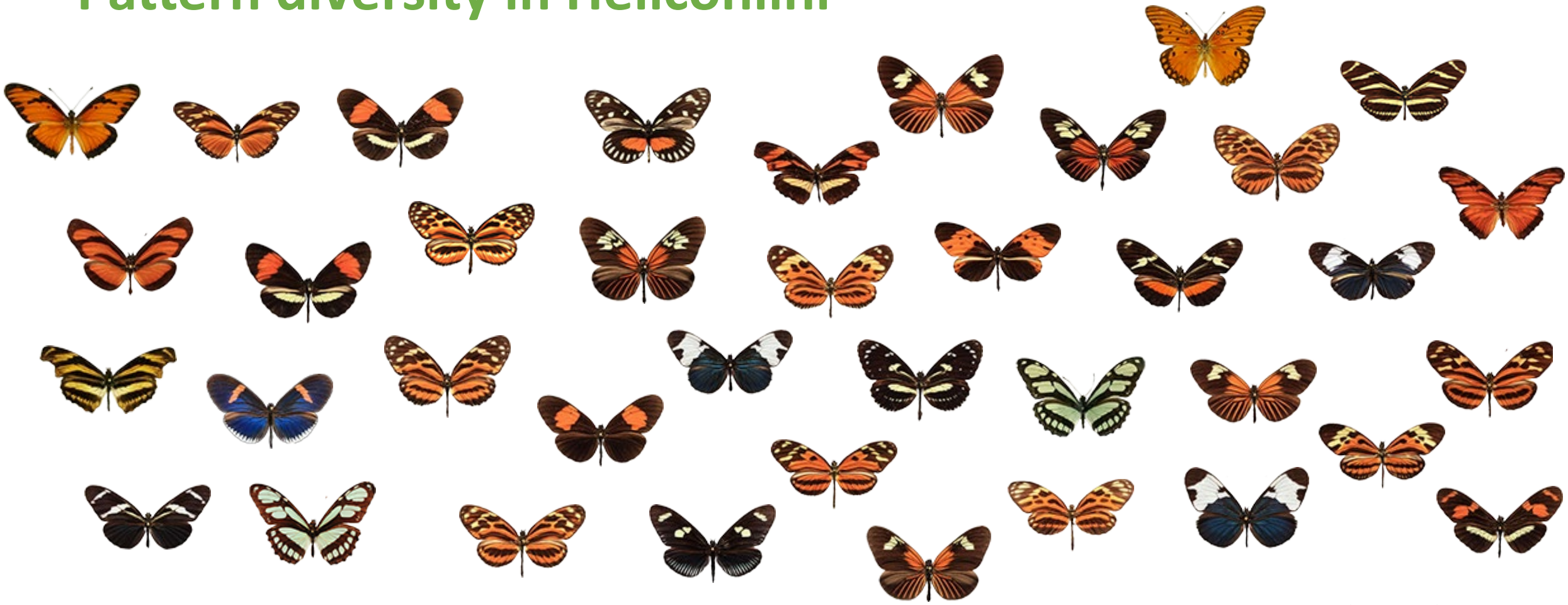


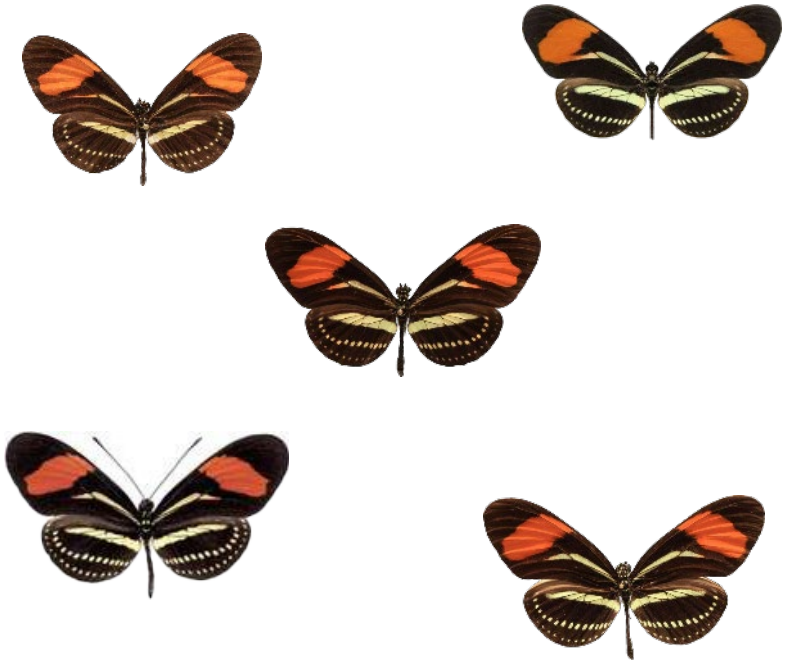
Photo credits: C. Jiggins

Model for the study of **genetics of color patterns** and **convergent evolution**

Yet… no standardized definition of **mimicry rings** in the group!

How to delineate mimicry rings?

POSTMAN ring



RED BAND ring

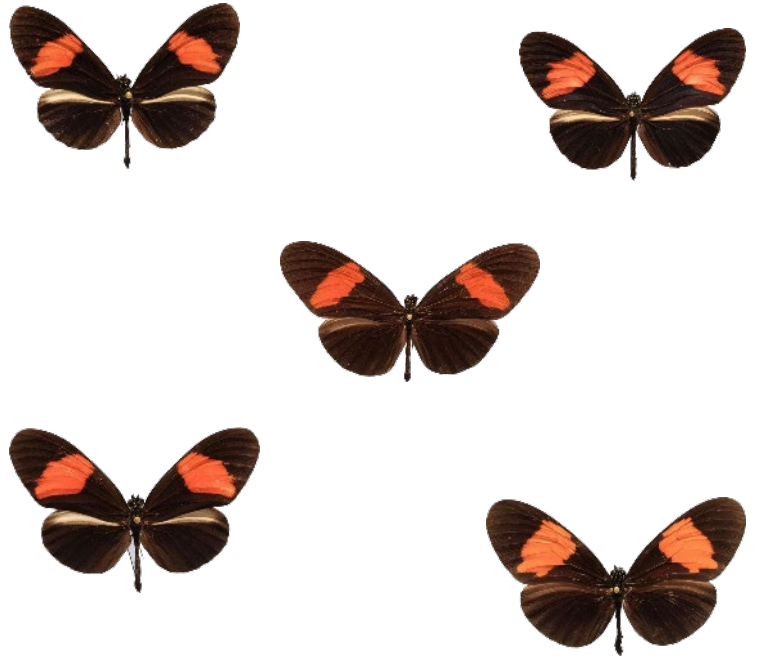


Photo credits: C. Jiggins

How to delineate mimicry rings?

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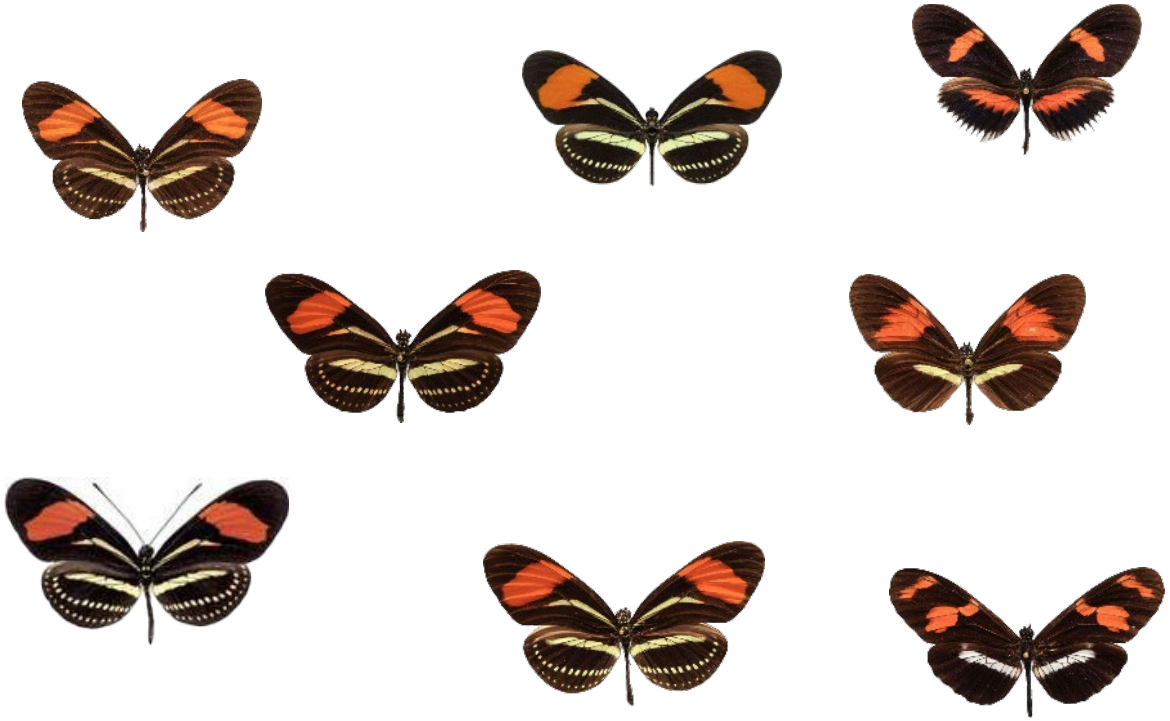


RED BAND ring

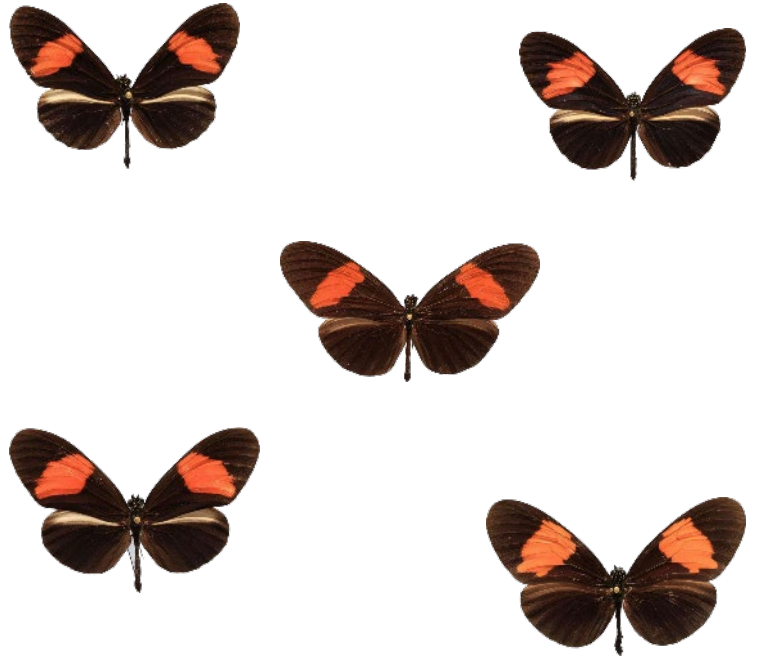
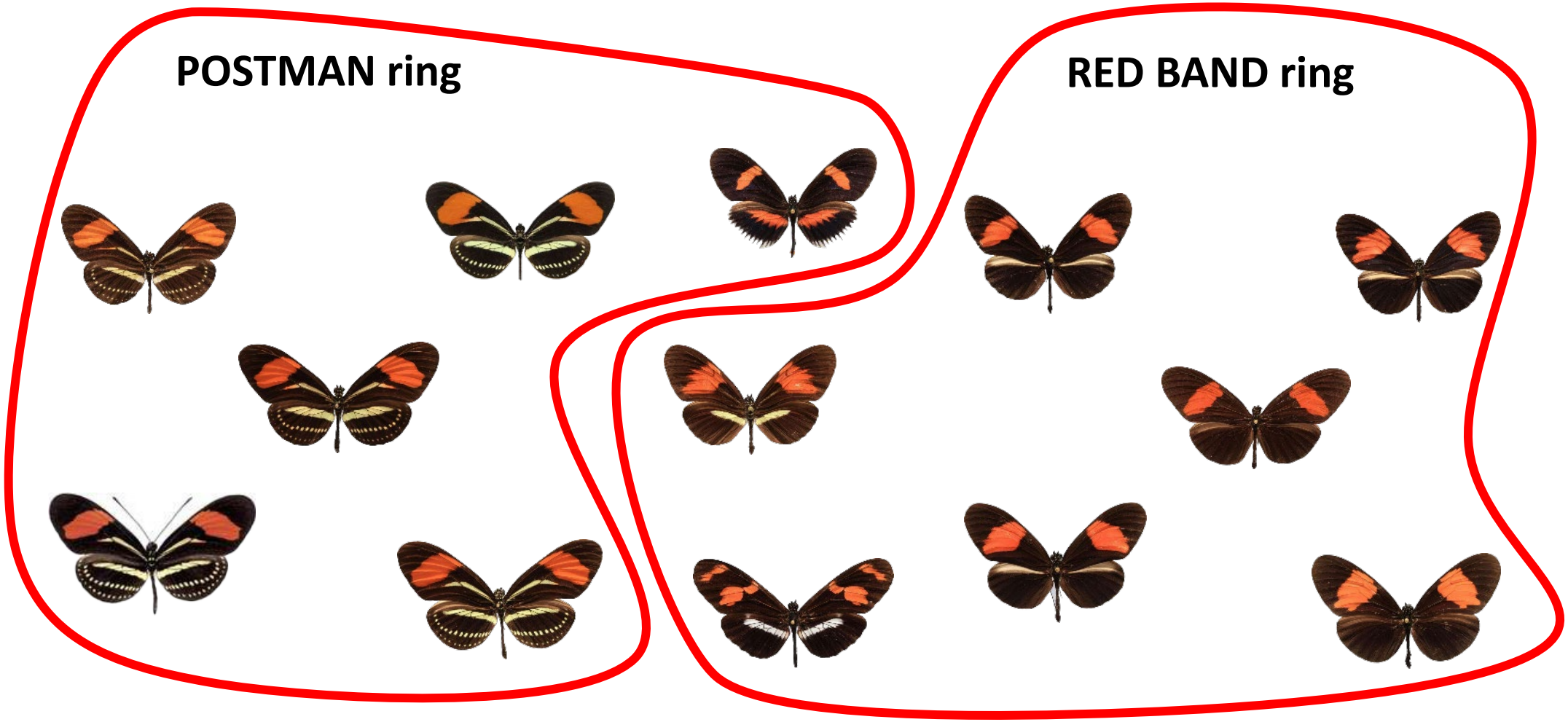


Photo credits: C. Jiggins

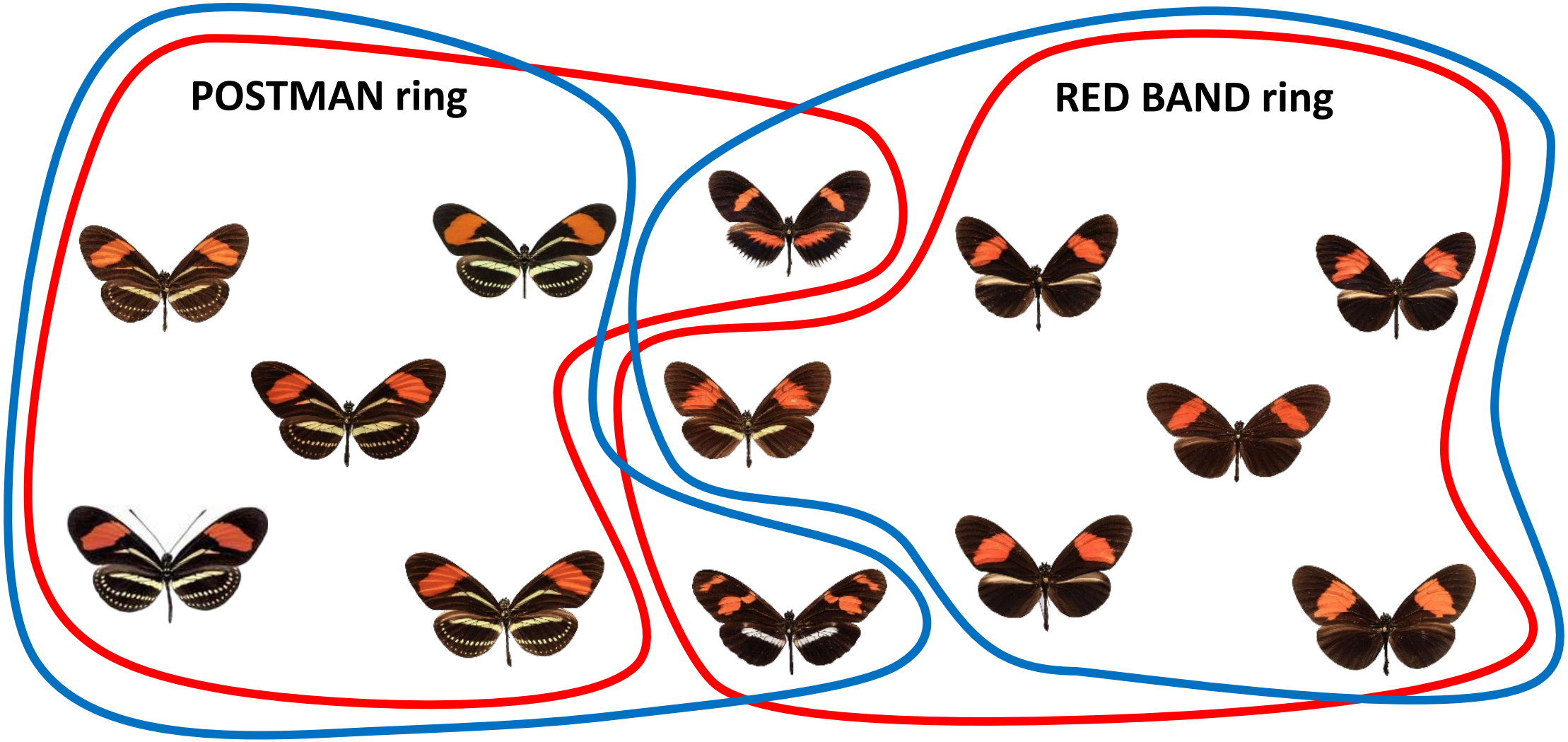
How to delineate mimicry rings?



Article A

Photo credits: C. Jiggins

How to delineate mimicry rings?

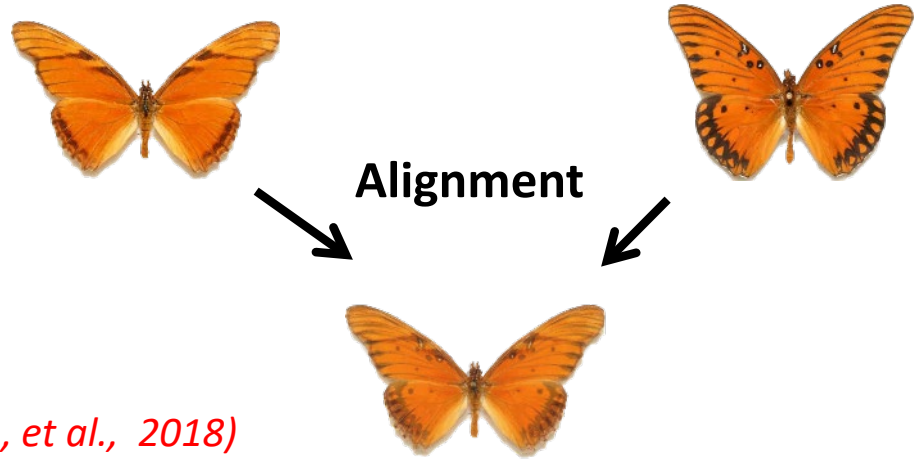


Article A

Article B

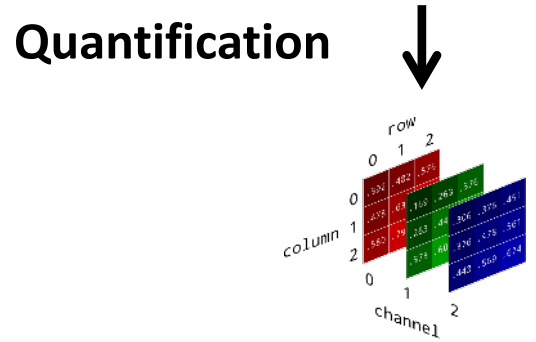
Photo credits: C. Jiggins

How to delineate mimicry rings?



Quantitative approach:

- Quantify **visual signal** => ***patternize*** *(Van Belleghem, et al., 2018)*
- Issues : **alignment** of pattern and outlines in case of high diversity



Photonic signal ≠ **Perception** of this signal

How to delineate mimicry rings?

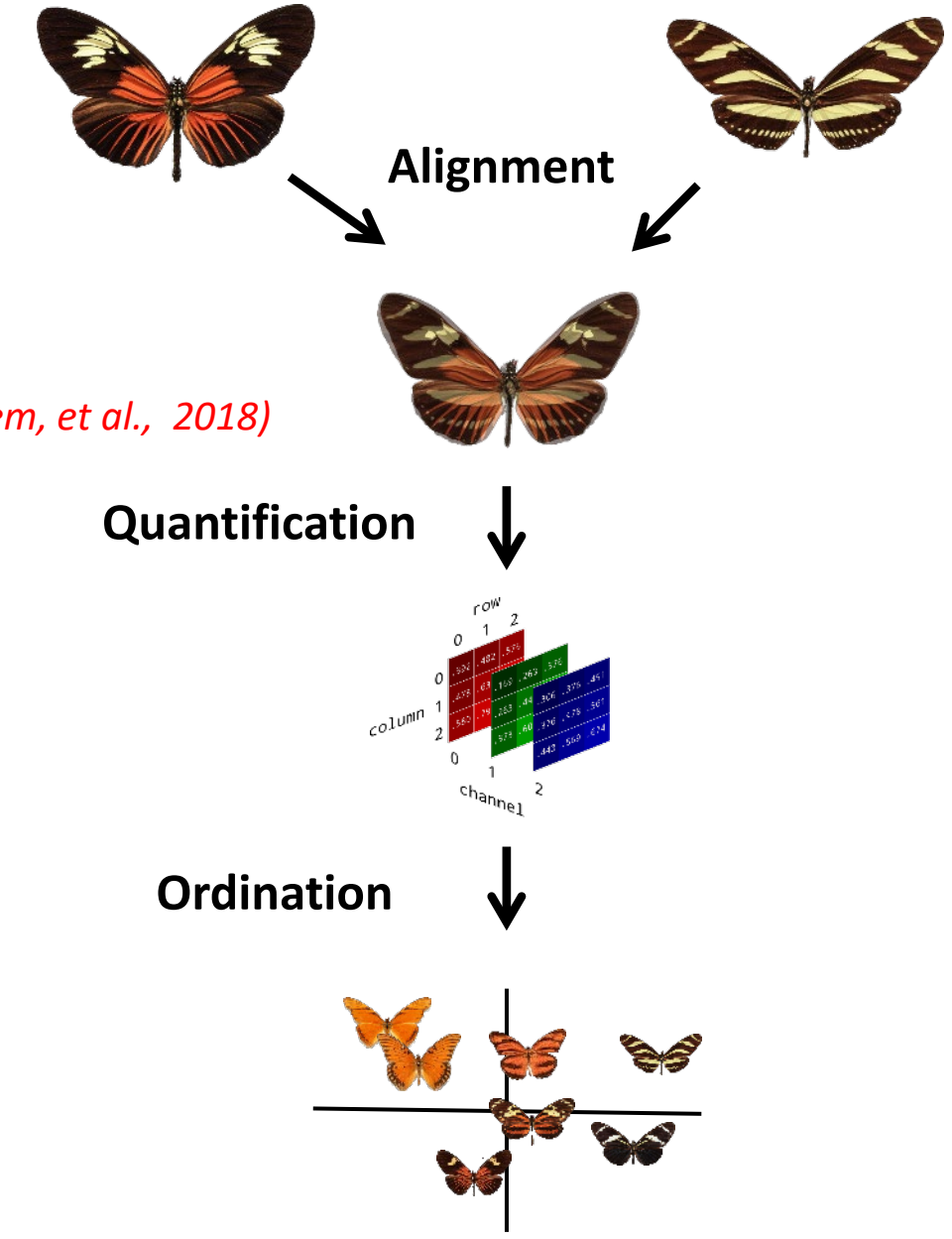


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Photo credits: C. Jiggins

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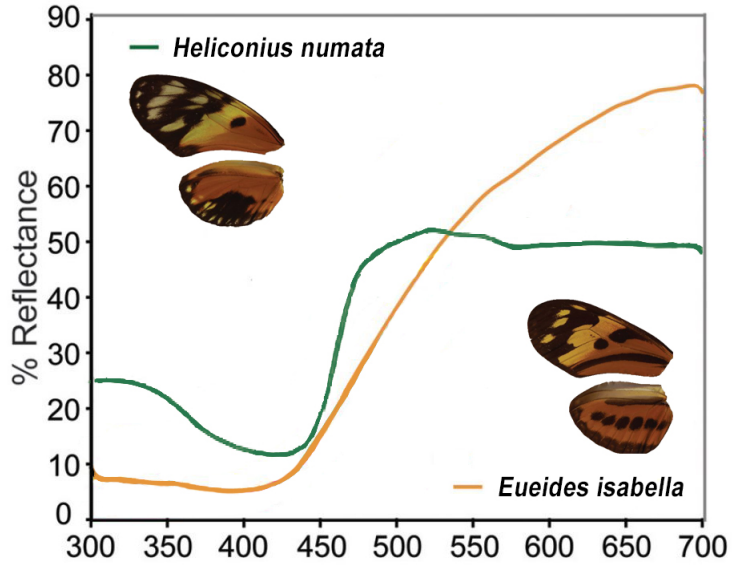
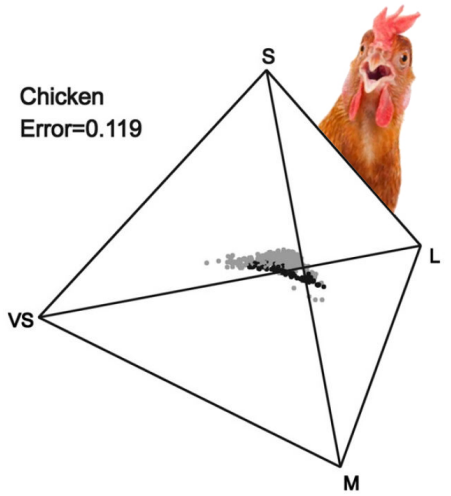
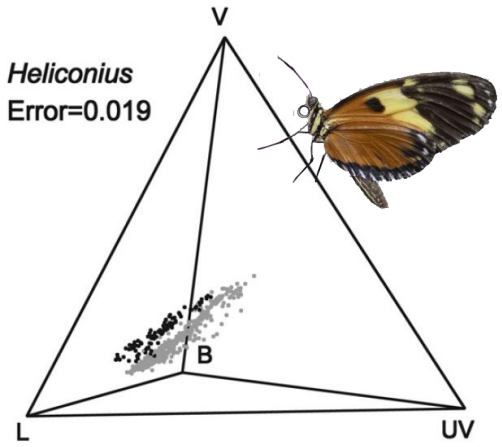






Does NOT discriminate **Discriminate**

Adapted from Bybee *et al.* 2012

Perceptual approach

Online survey to evaluate **perception** of similarity across **image triplets** :

http://memometic.cleverapps.io/

Input: triplet of pictures with a **reference**

Output: list of triplets with **relative distances**

Quality control: 3 **control triplets** for 30 items

Embedding method: t-STE

Goal = obtain a **perceptual map** that reflect the **perceptual distances** between images

Input = **relative triplet distances**

1 ( , ) )

2 ( , ) )

3 ( , ) )

.

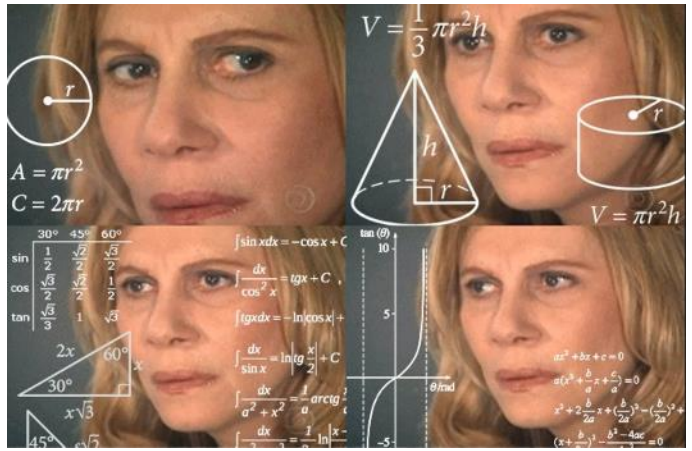
.

.

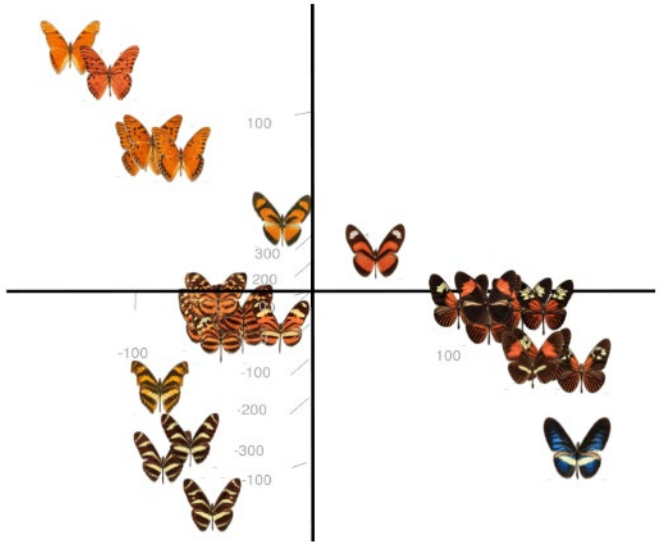
75,240 ( , ) )

Embedding method:
Machine learning algorithm
(t-STE)

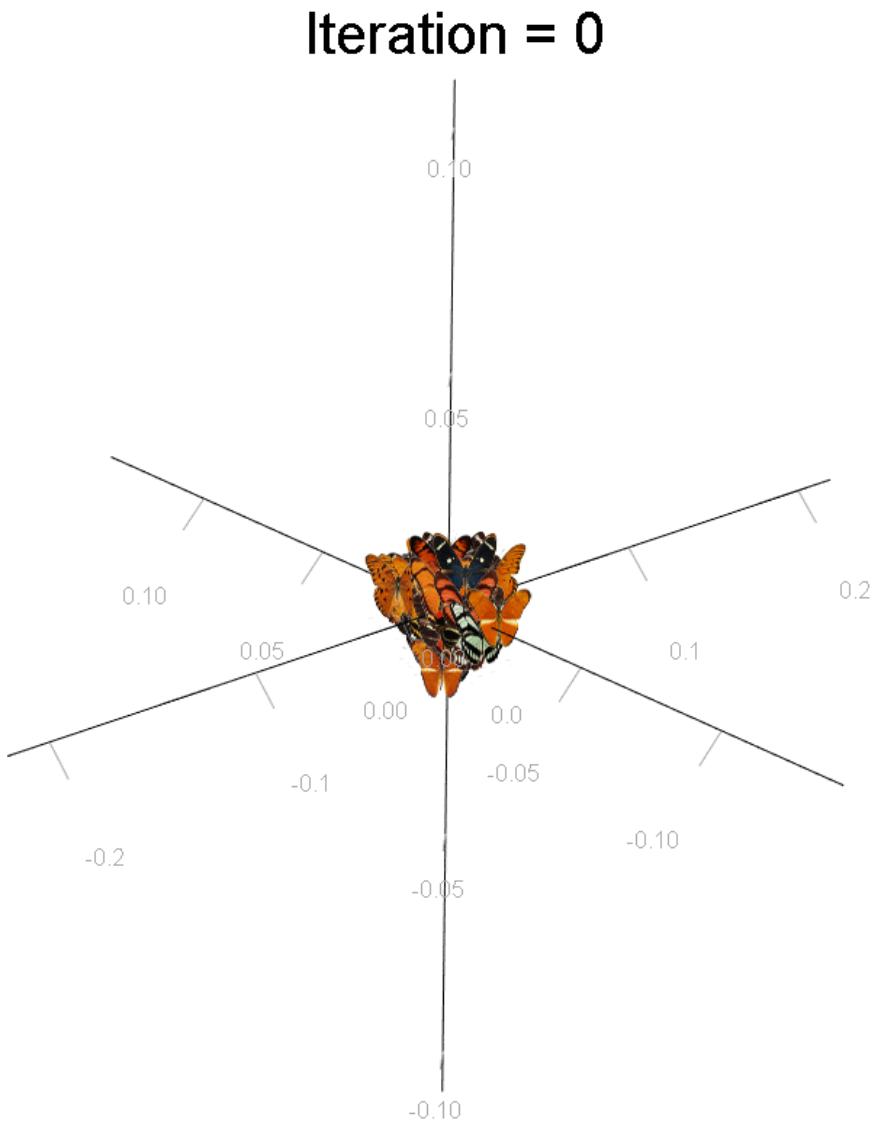
(van der Maaten & Weinberger, 2012)

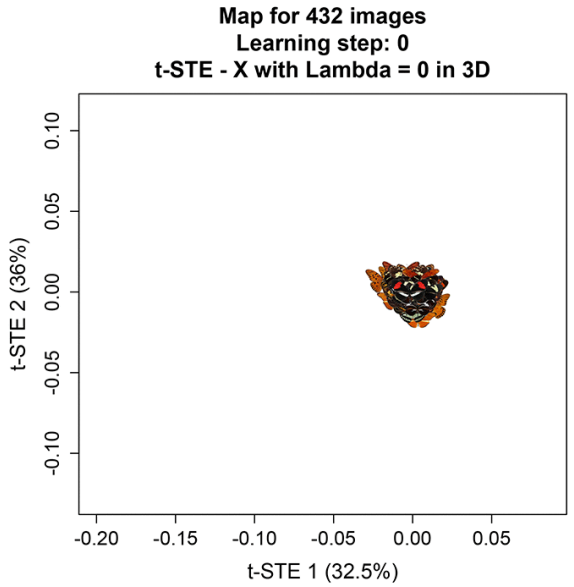


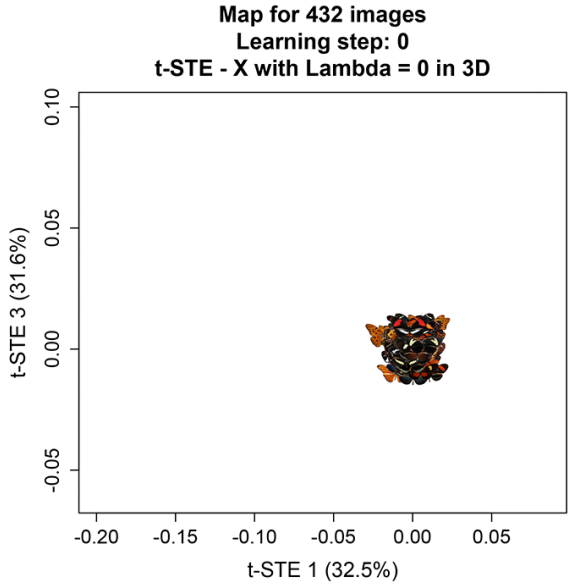
Output = **coordinates** in space of reduced dimensionality
=
Perceptual map

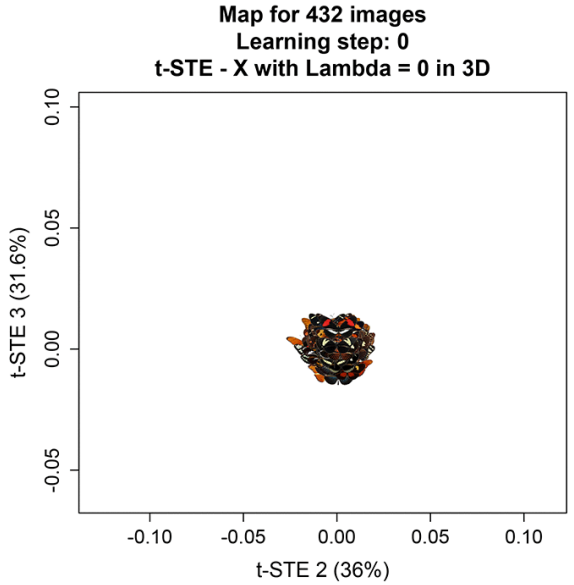


Embedding method: t-STE









Perceptual space

75,240 triplets for **432** images

The spatial scale of mimicry rings

Why do we have a **continuum**?

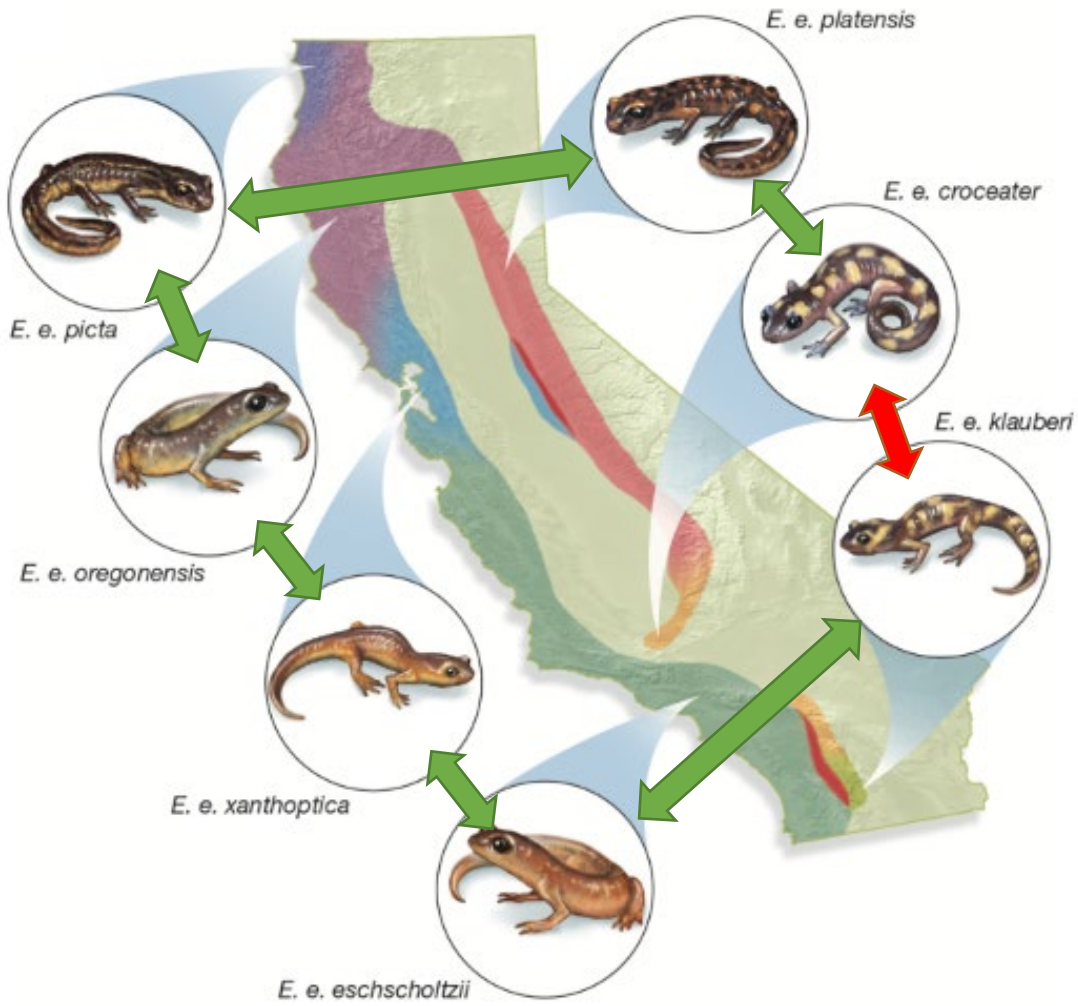
Analogy with **ring species**

- **Hybridization** at local scale
- **Incompatibility** at large distances
- **Continuum** at large scale

Conclusion:

- Expected to find a **continuum** at the **global scale**
- Mimicry rings should be defined at **community-level?**

Next step: Apply the perceptual map approach at **community-level**



Source: Chegg.com

The spatial scale of mimicry rings

Why do we have a **continuum**?

Analogy with **ring species**

- **Mimicry** at local scale
- **Dissimilarity** at large distances
- **Continuum** at large scale

Conclusion:

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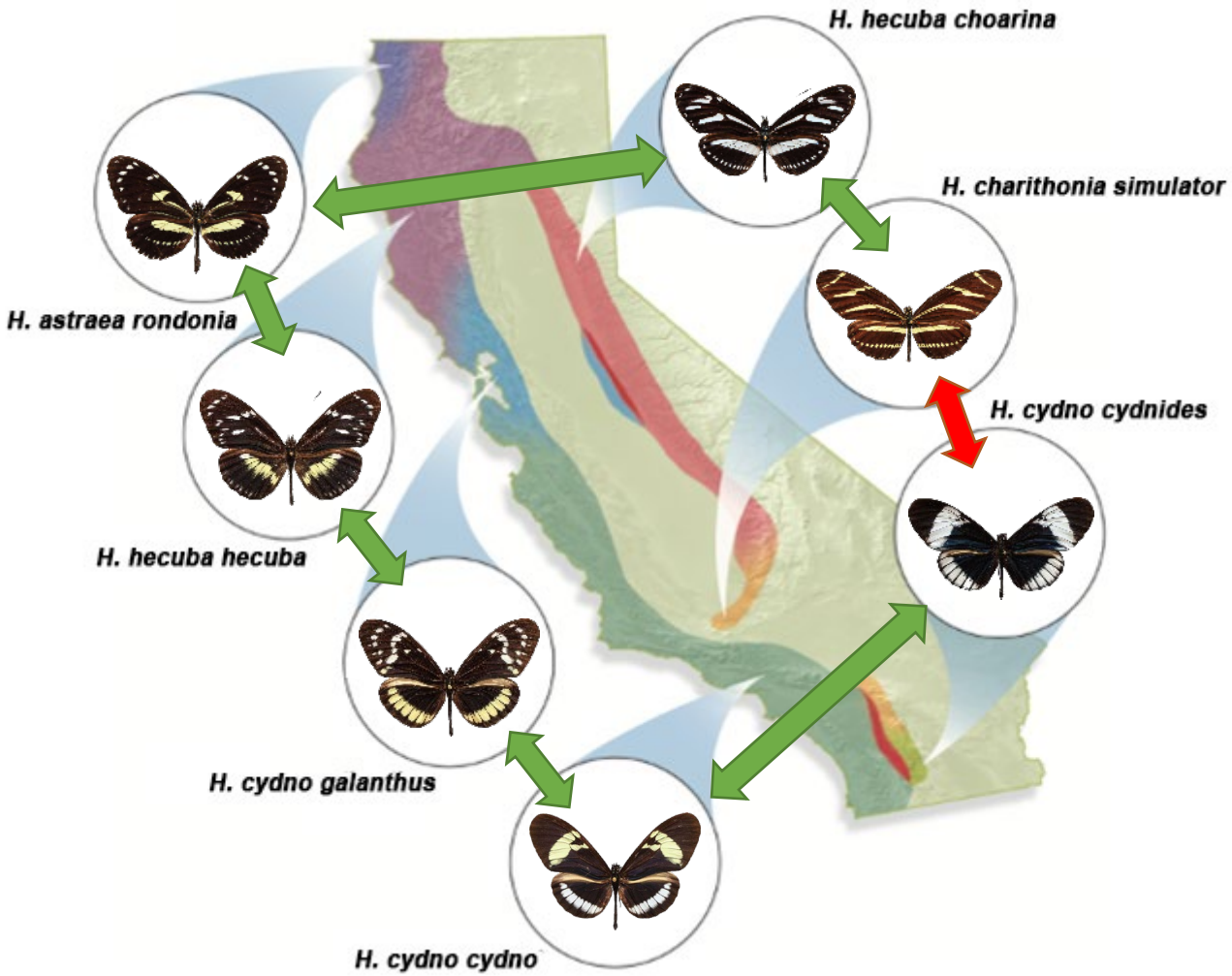
Next step: Apply the perceptual map approach at **community-level**



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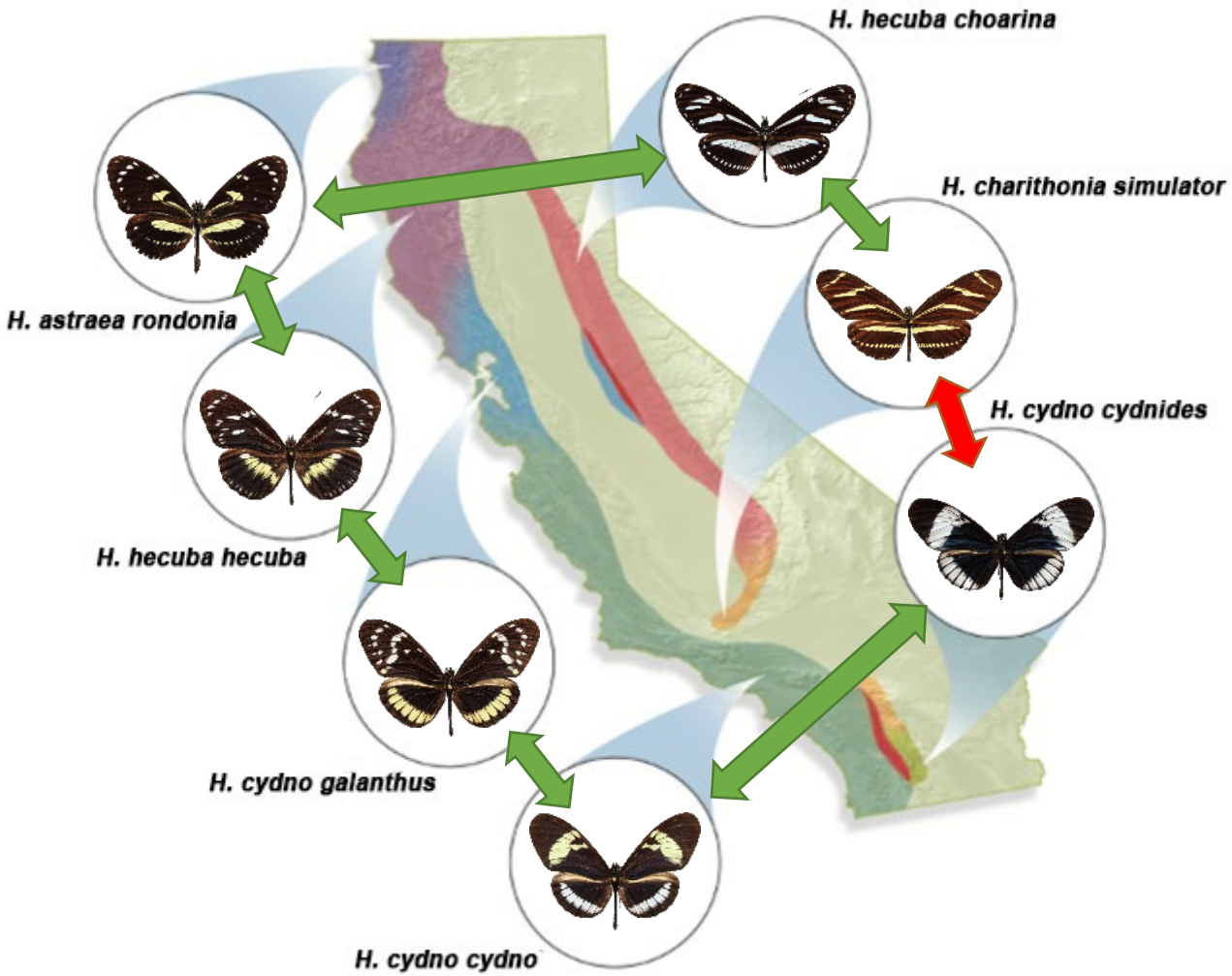
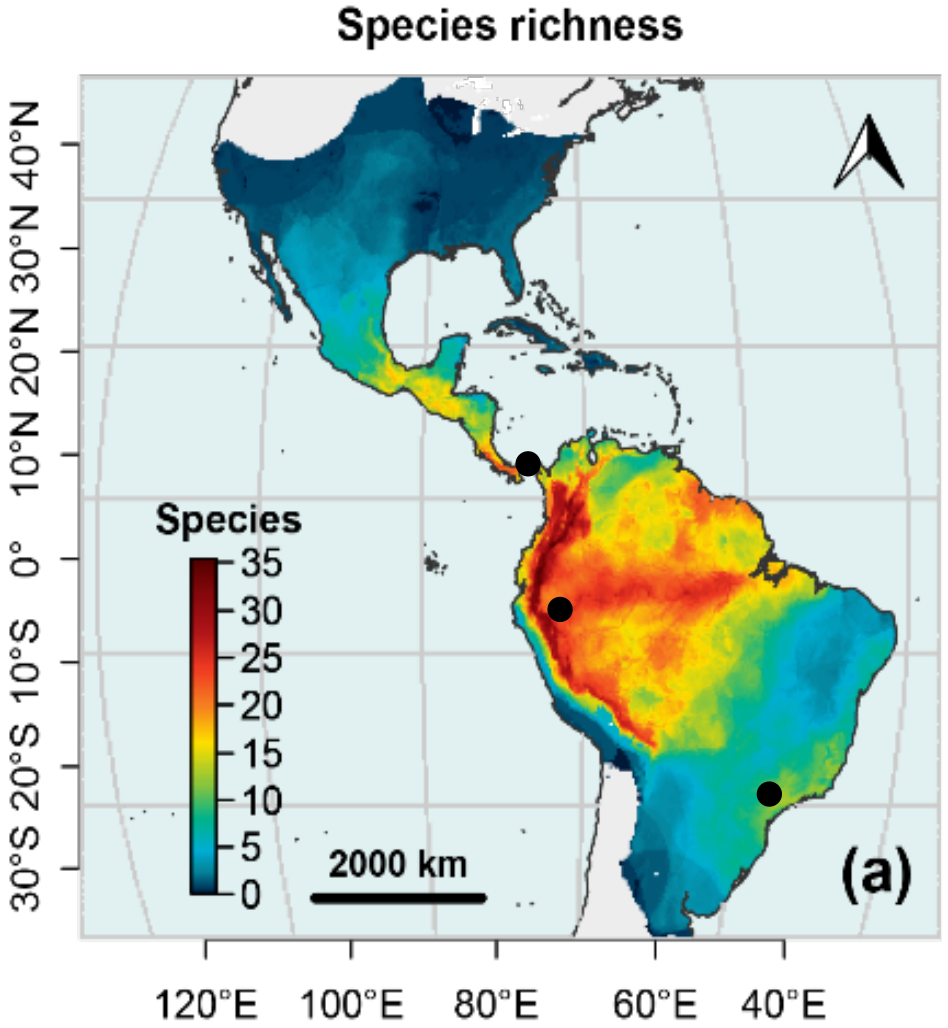


Source: Chegg.com

Interactive map of Müllerian mimicry communities



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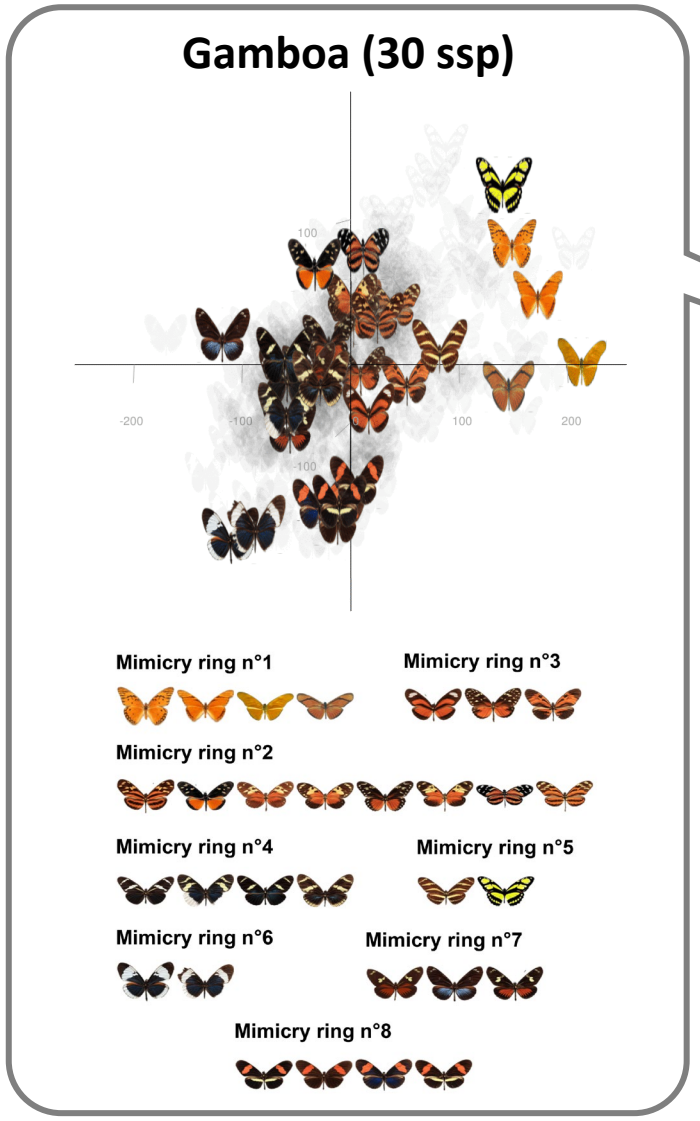

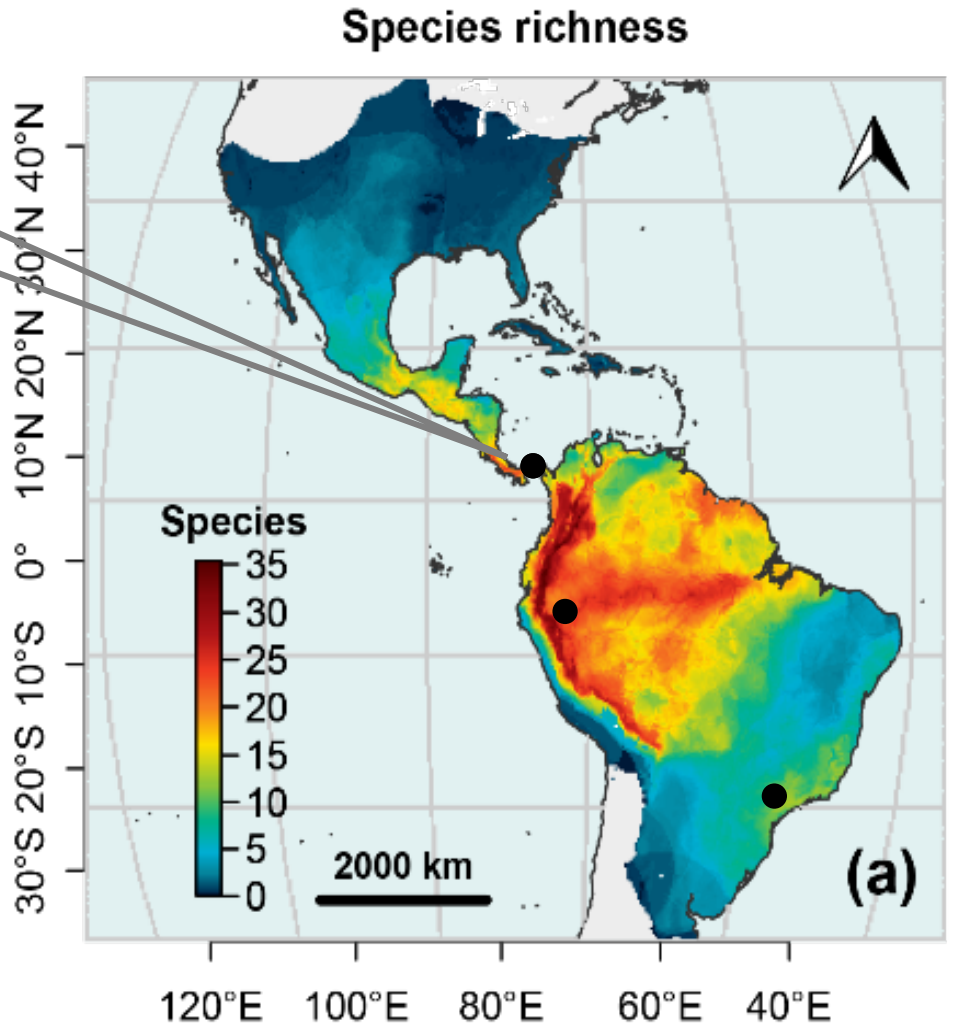

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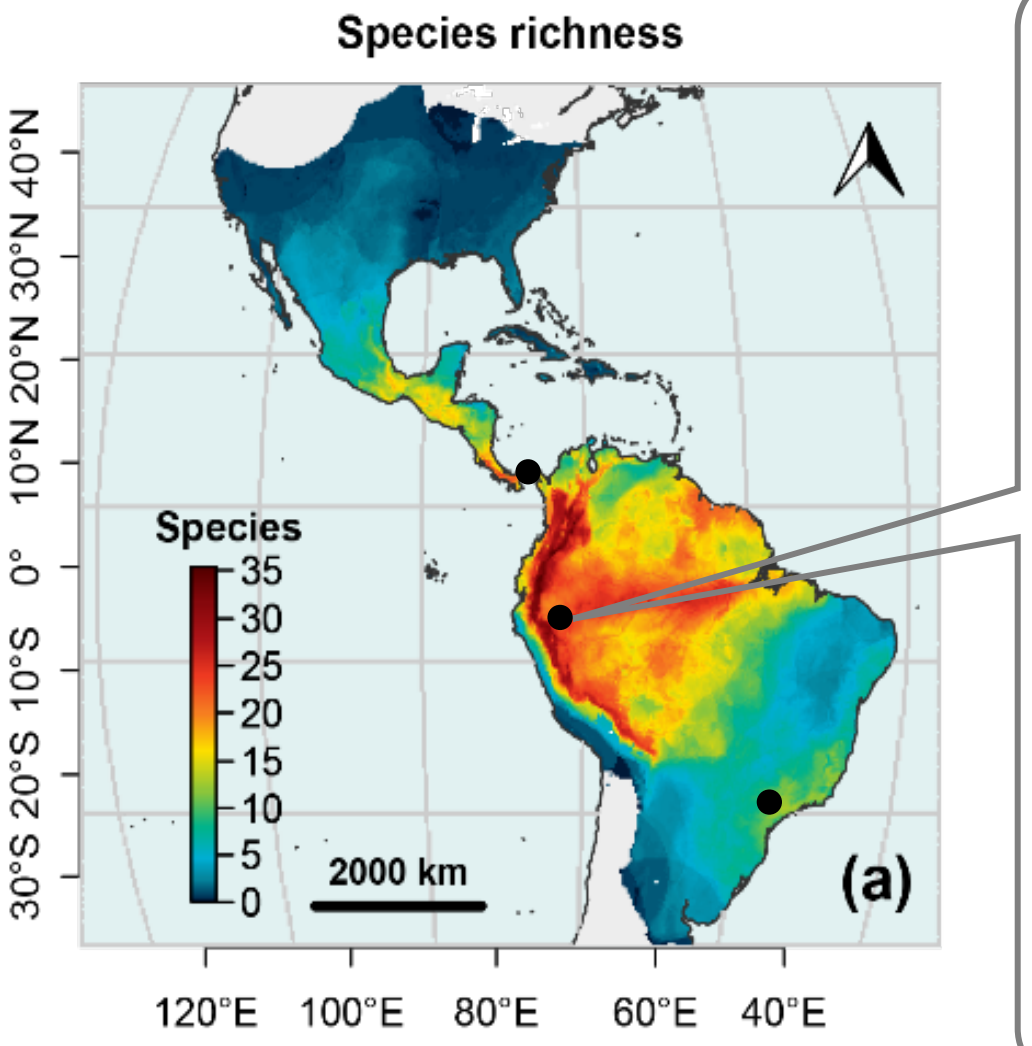

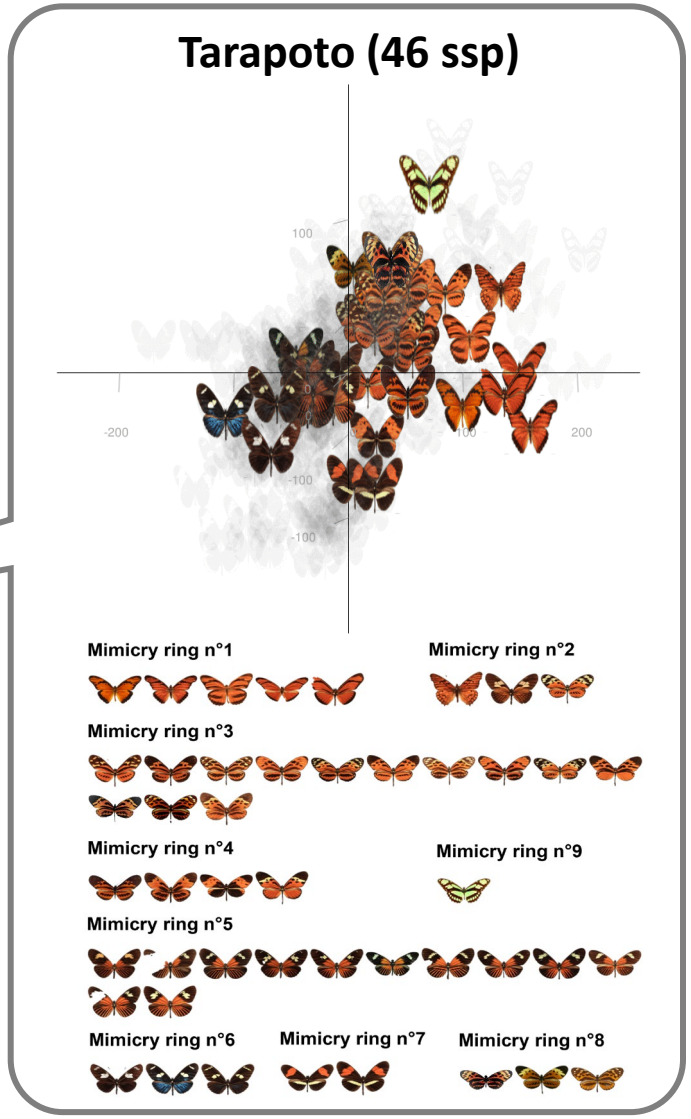

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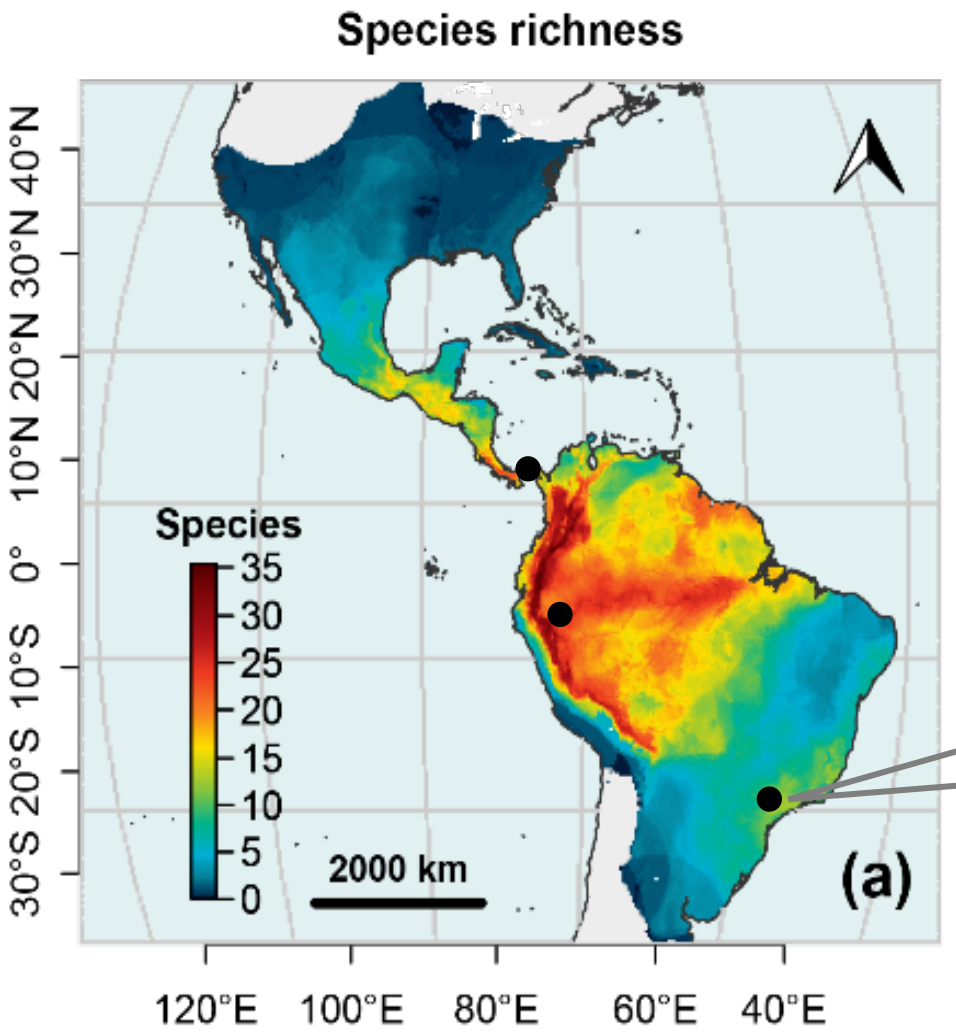

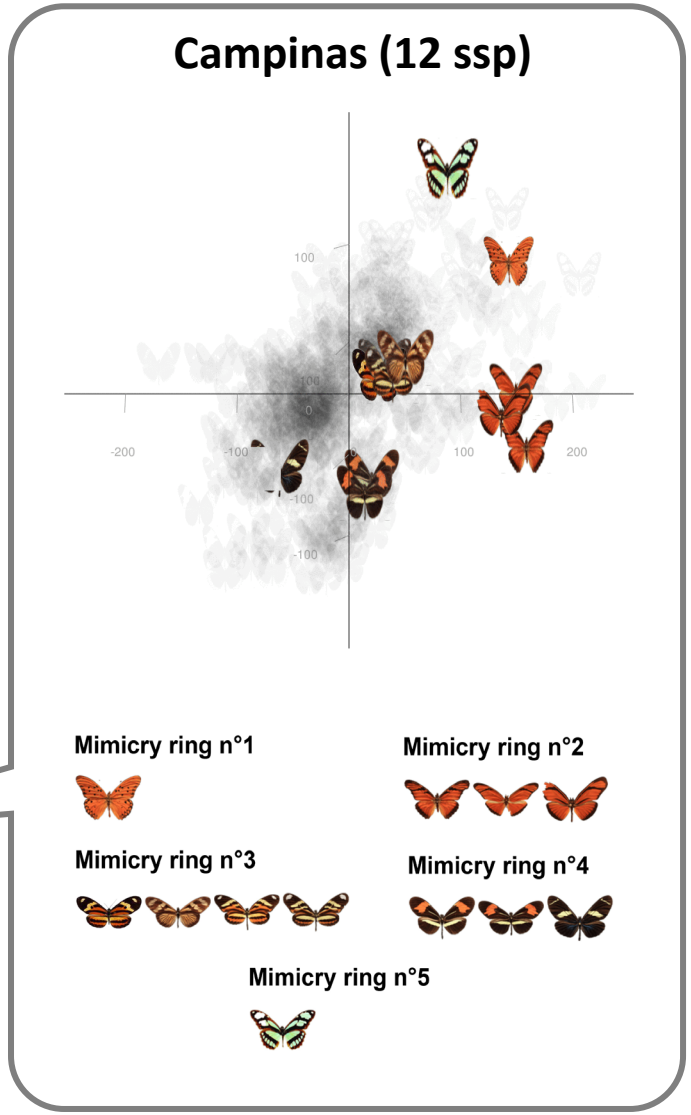

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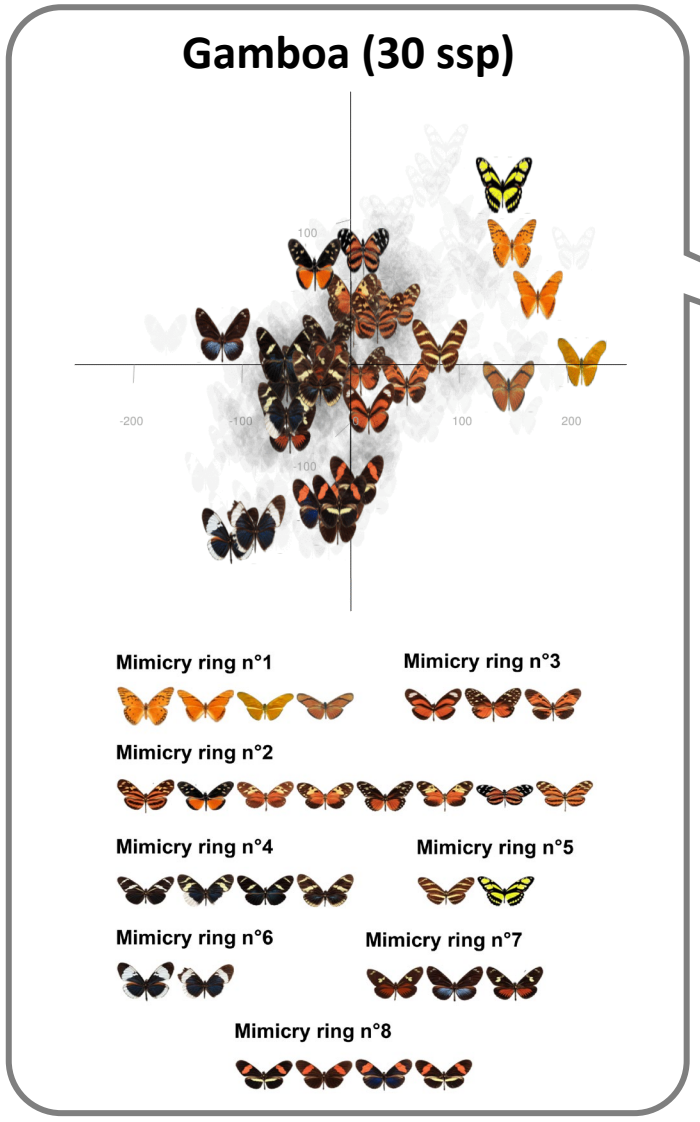
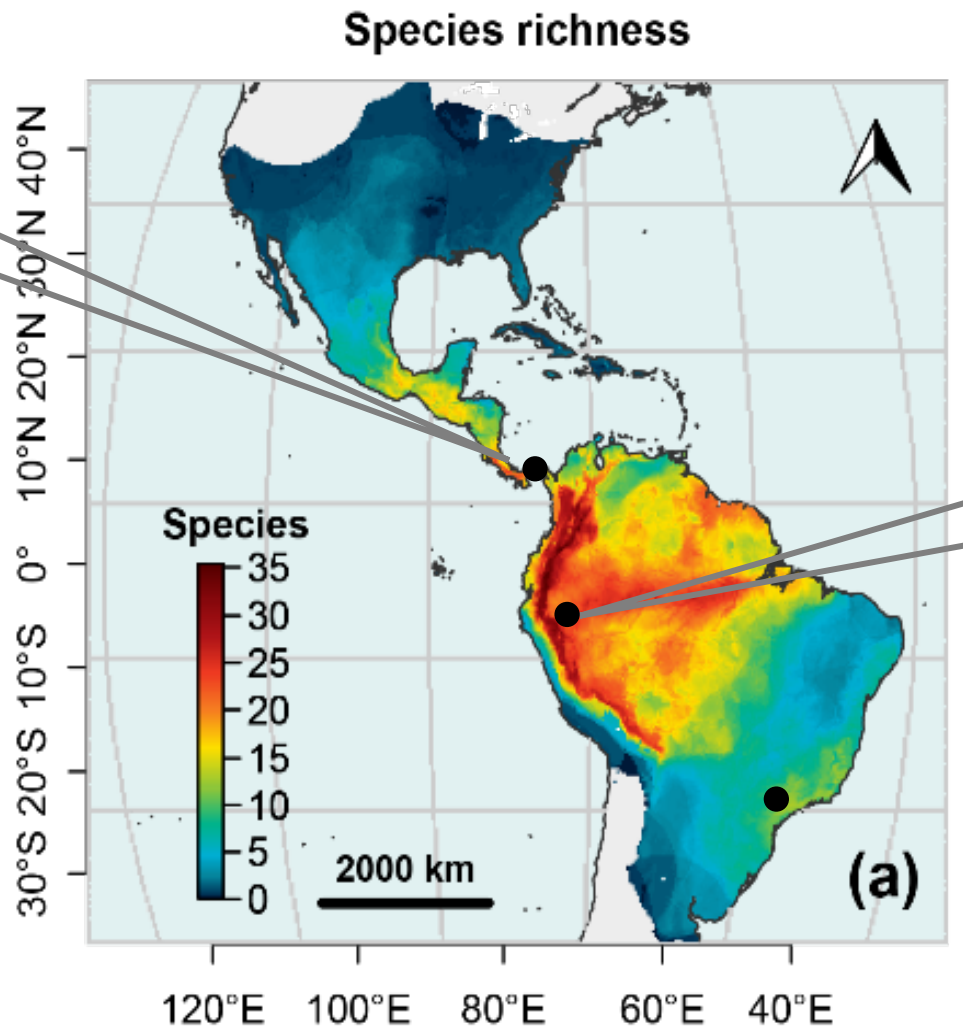
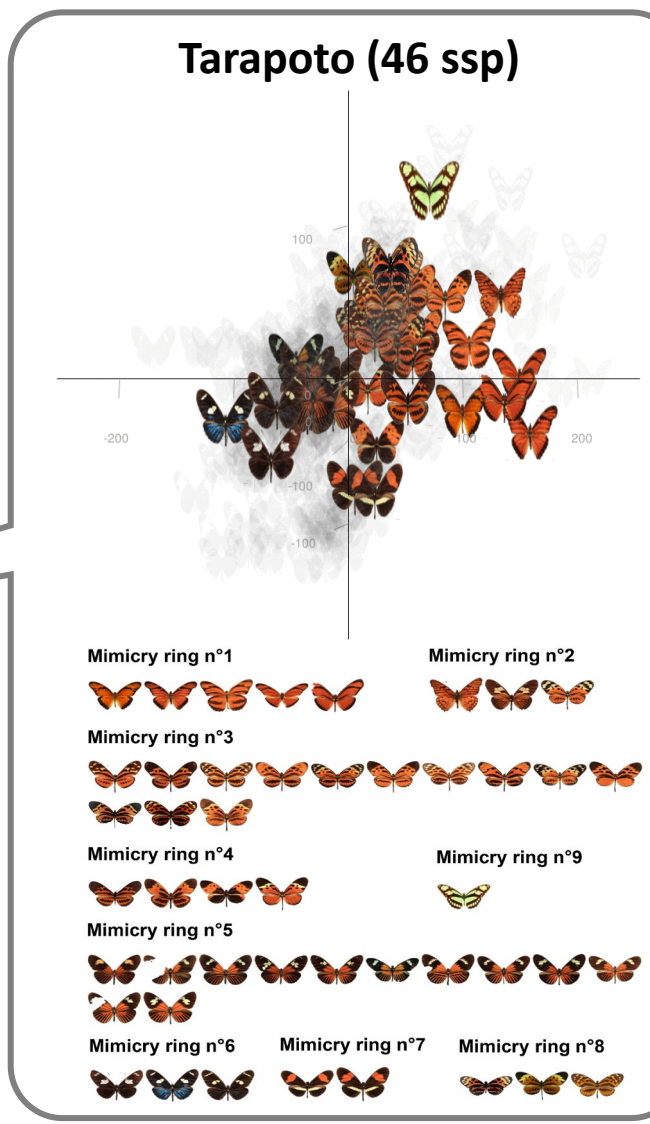
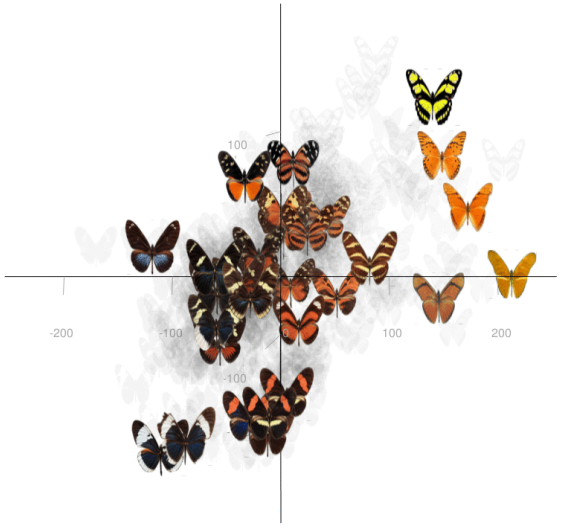






Interactive map of Müllerian mimicry communities

Gamboa (30 ssp)



Mimicry ring n°1

Mimicry ring n°3

Mimicry ring n°2

Mimicry ring n°4

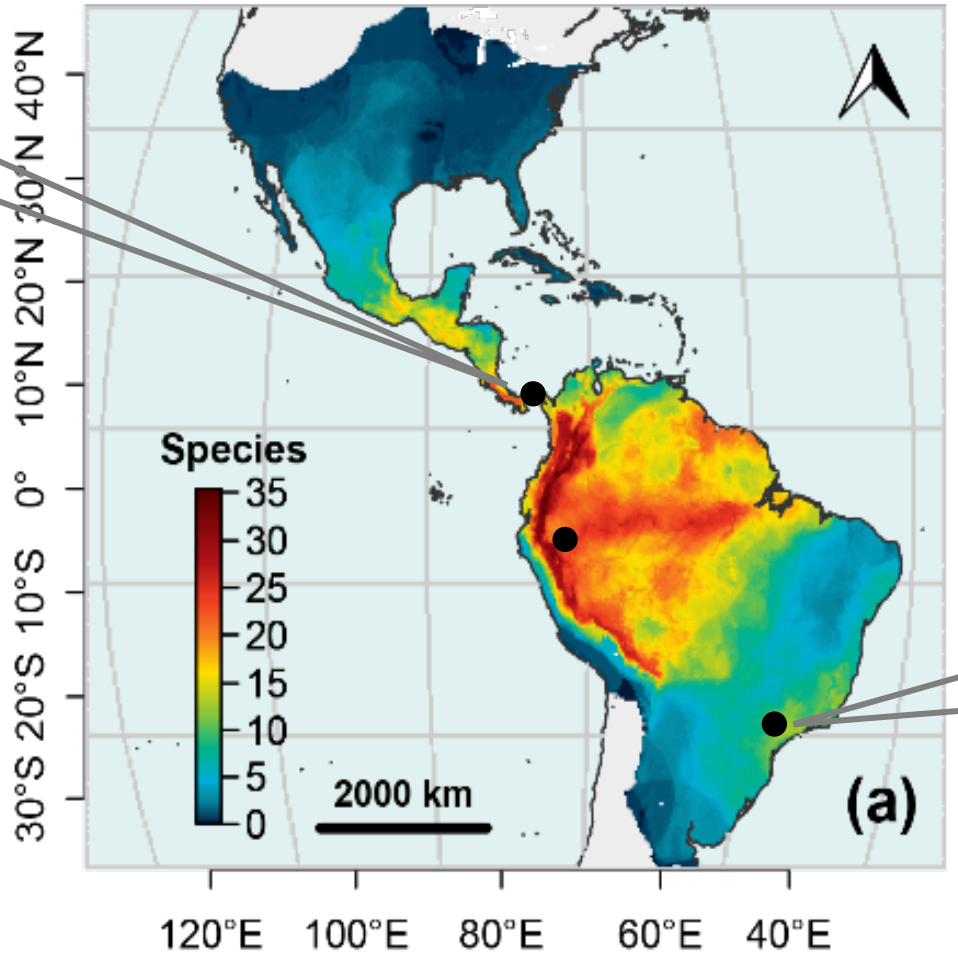
Mimicry ring n°5

Mimicry ring n°6

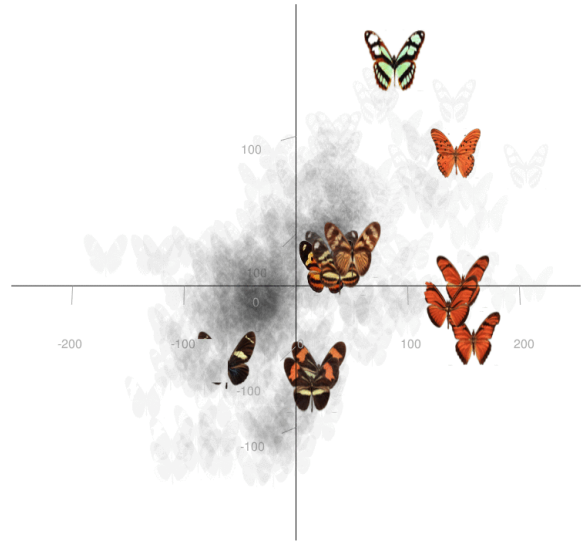
Mimicry ring n°7

Mimicry ring n°8

Species richness



Campinas (12 ssp)



Mimicry ring n°1

Mimicry ring n°2

Mimicry ring n°3

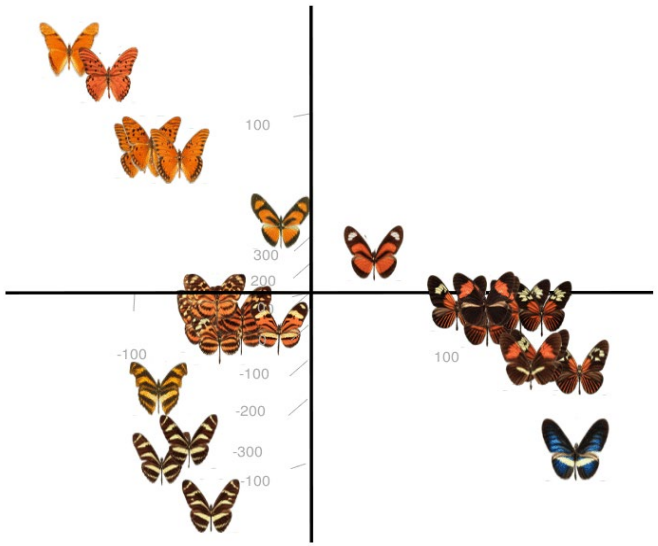
Mimicry ring n°4

Mimicry ring n°5

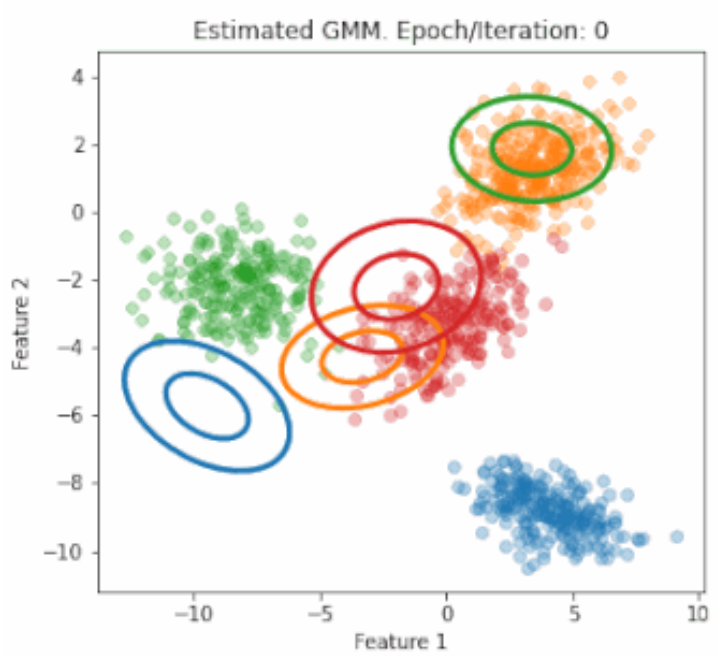
Clustering method

Goal = delineate groups of patterns (**mimicry rings**) in the **local perceptual space**

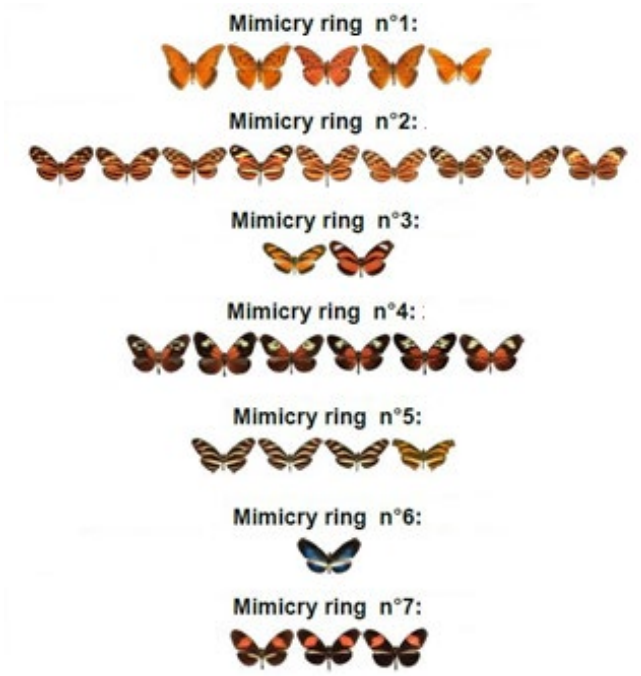
Input = **coordinates**
on the perceptual map



Clustering method:
Gaussian Mixture Models
(GMM)



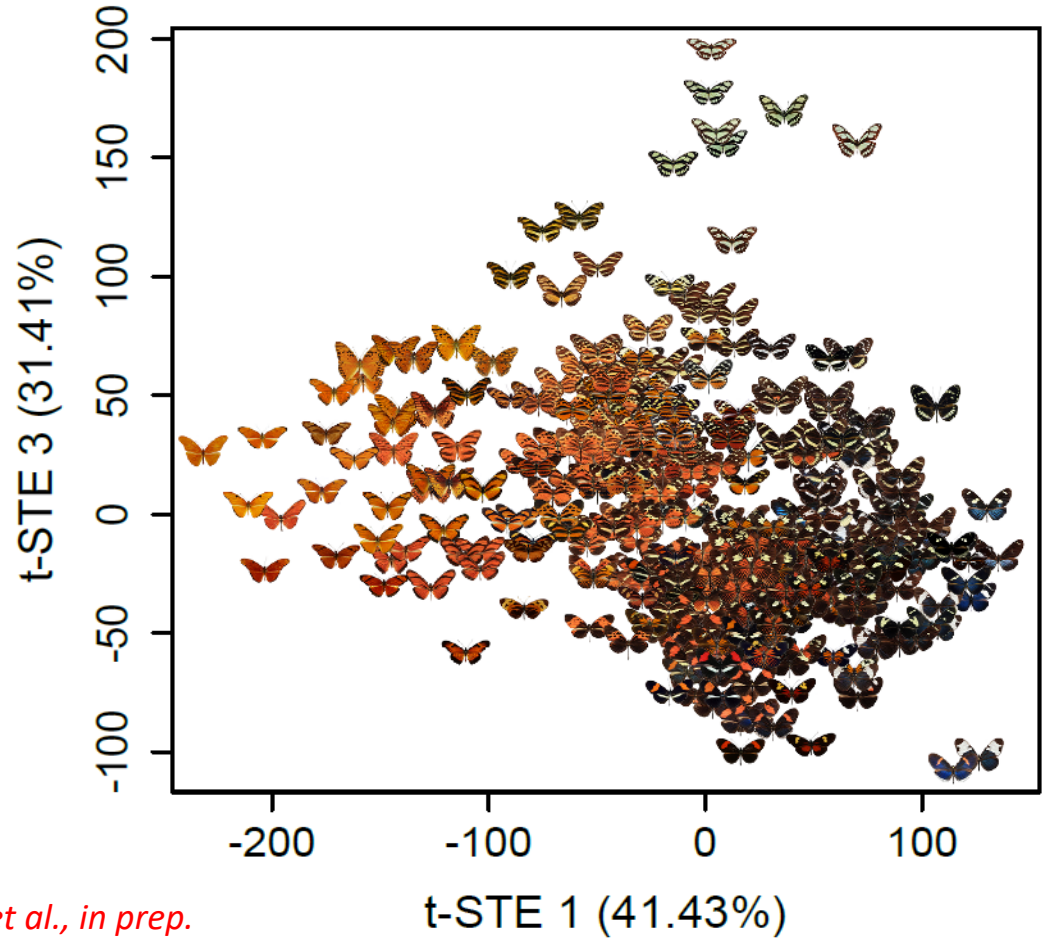
Output = **clusters**
of wing patterns
=
Mimicry rings



Credits: J. Zhang

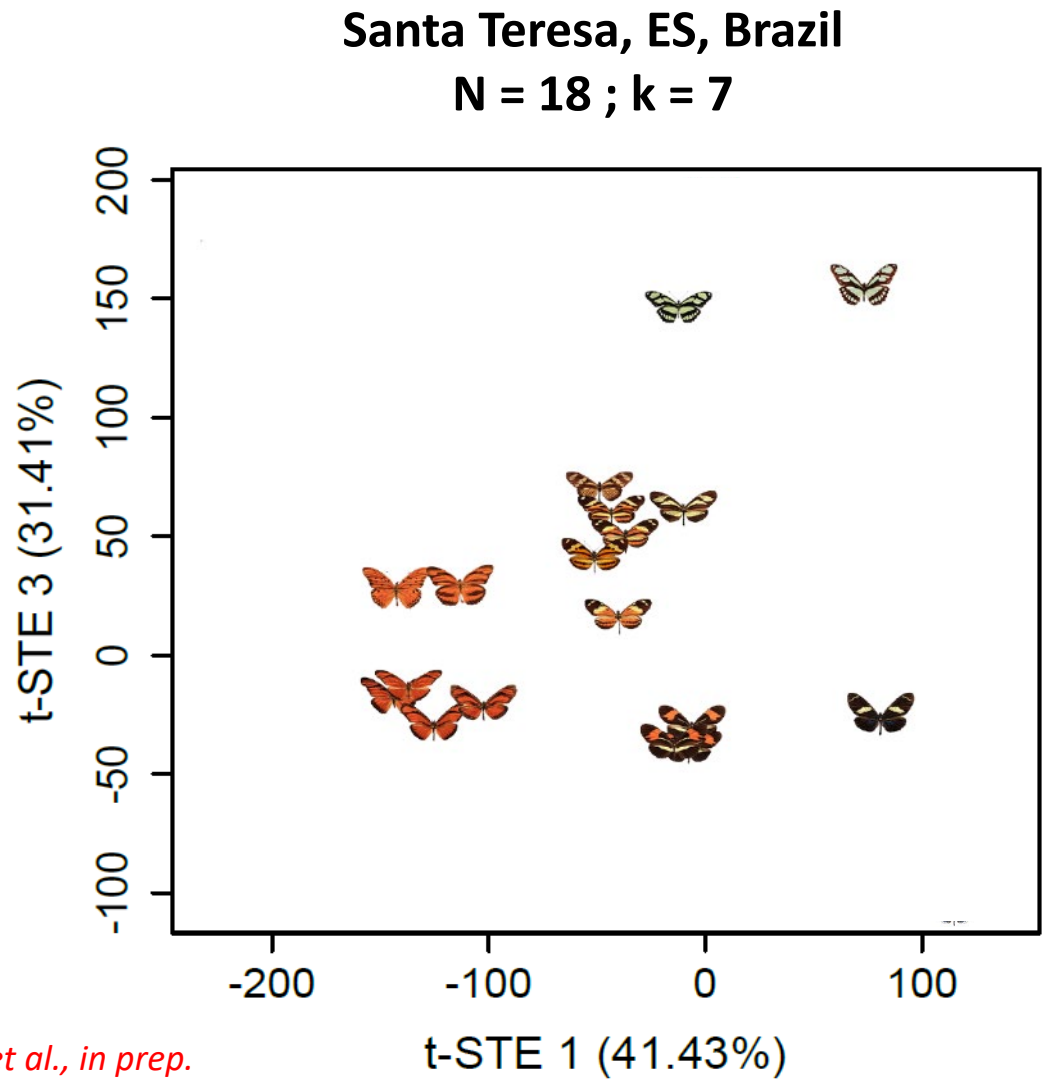
Local perceptual maps

All subspecies
N = 432



Doré et al., in prep.

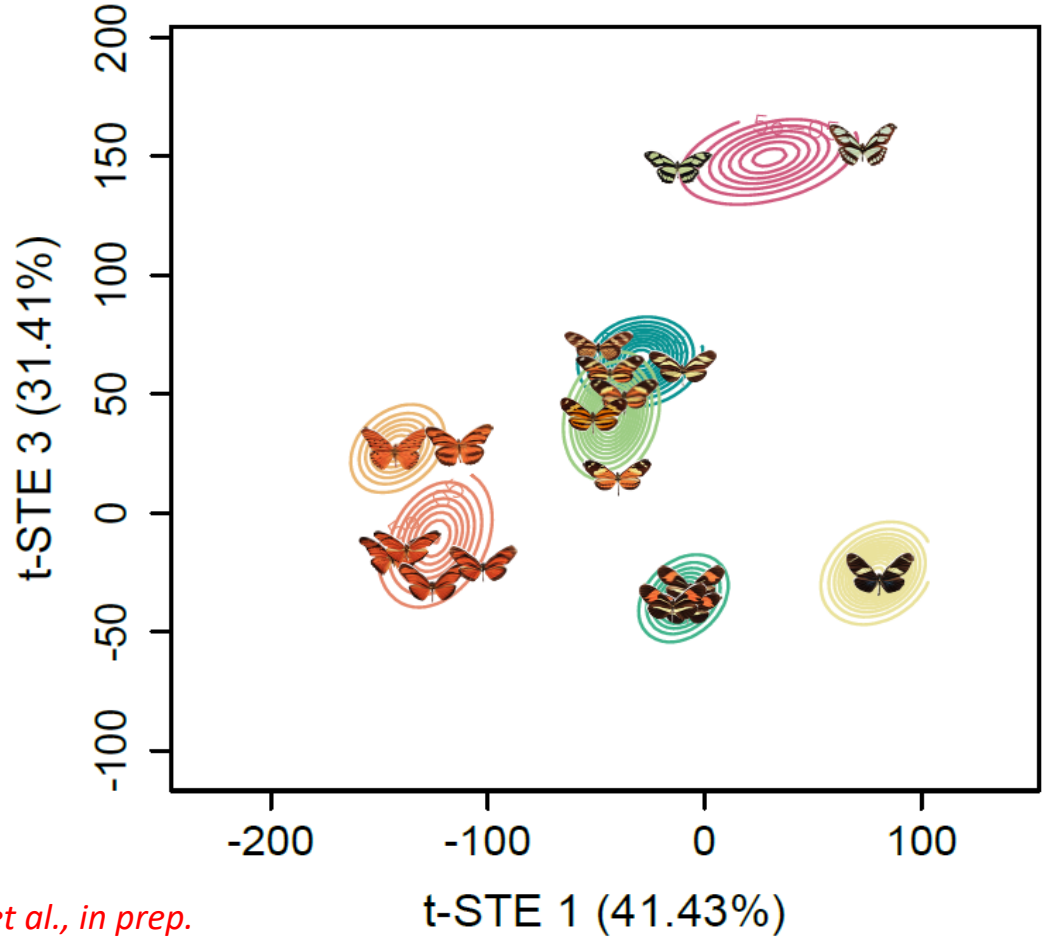
Local perceptual maps



Doré et al., in prep.

Local perceptual maps

Santa Teresa, ES, Brazil
N = 18 ; k = 7



Doré et al., in prep.

Mimicry ring n°1

Mimicry ring n°7

Mimicry ring n°2

Mimicry ring n°3

Mimicry ring n°4

Mimicry ring n°5

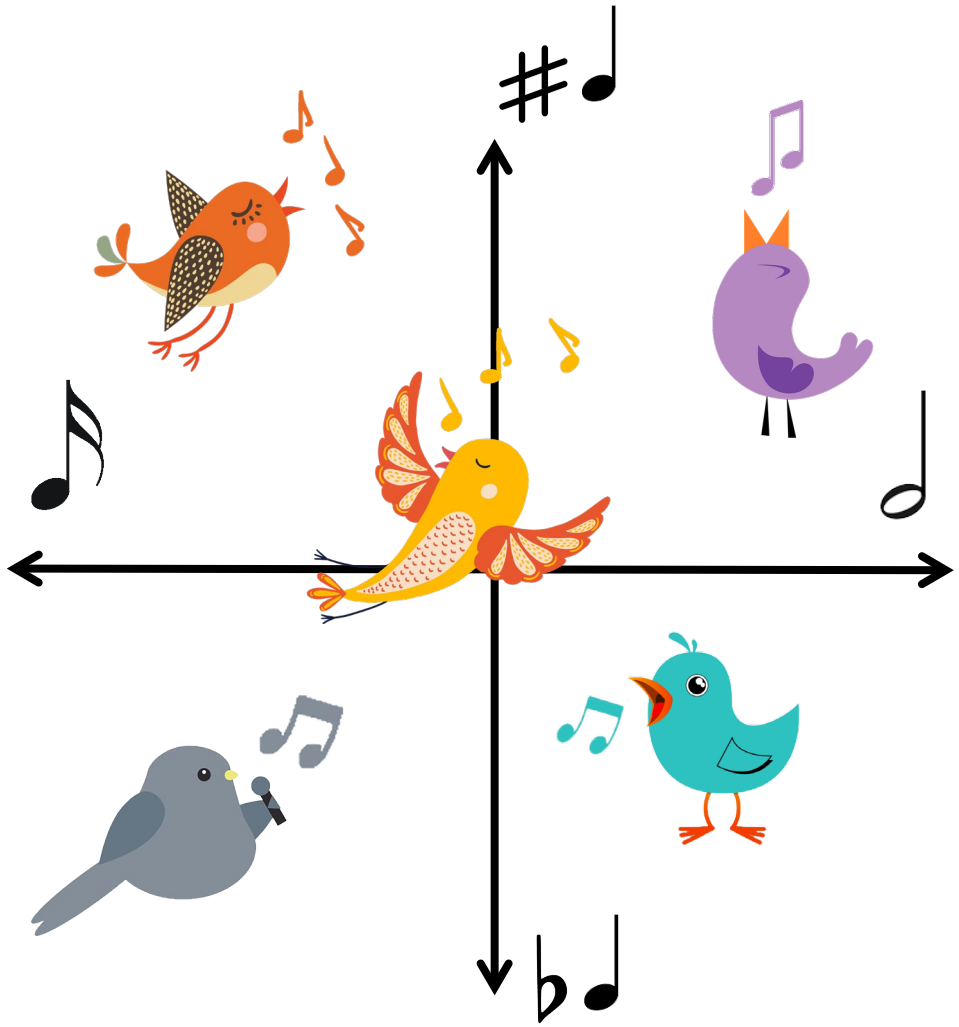
Mimicry ring n°6

Conclusion

Perceptual space = a new tool to quantify any **ecological signals** through perception: colors, shapes, songs, smells, behaviors, etc.

Allow to explore phenotypic patterns at **large spatial and taxonomic scale** in context of **high phenotypic diversity**

Study **differences in perception** across individuals/social groups



Perceptual space of bird songs

Conclusion

Perceptual space = a new tool to quantify any **ecological signals** through perception: colors, shapes, songs, smells, behaviors, etc.

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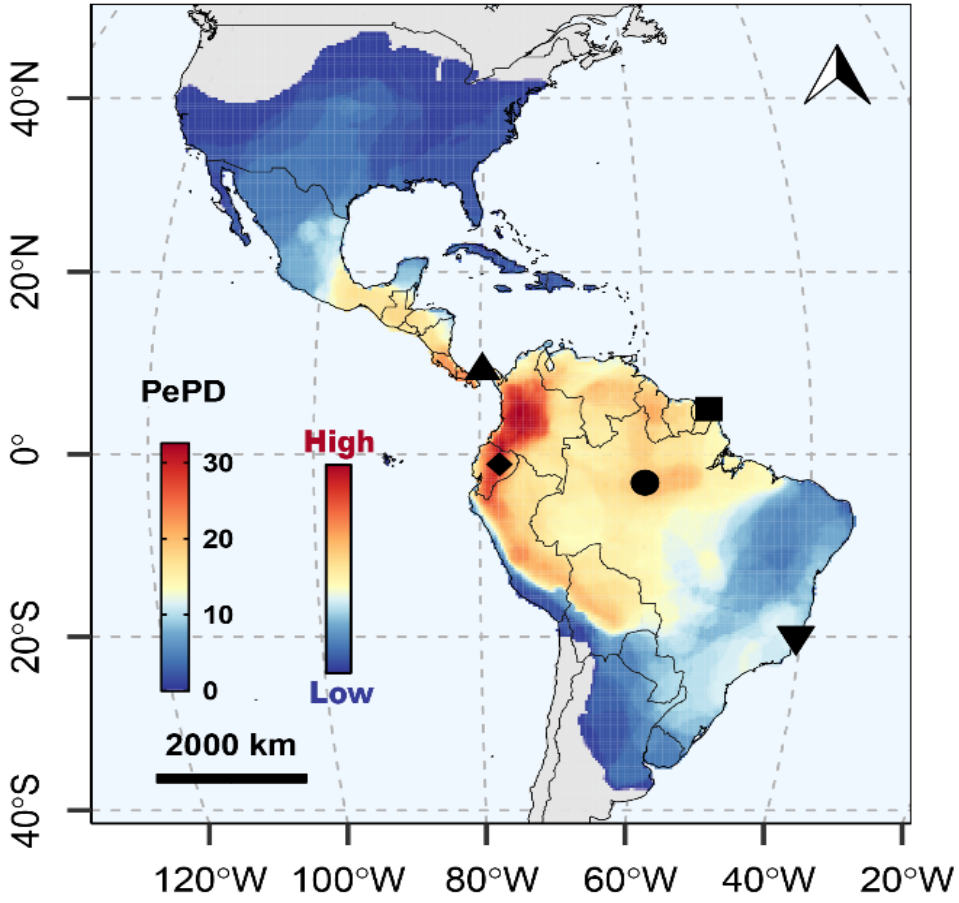

Doré et al., in prep.

Mimetic diversity as density of local phenotypes in the perceptual space

Conclusion

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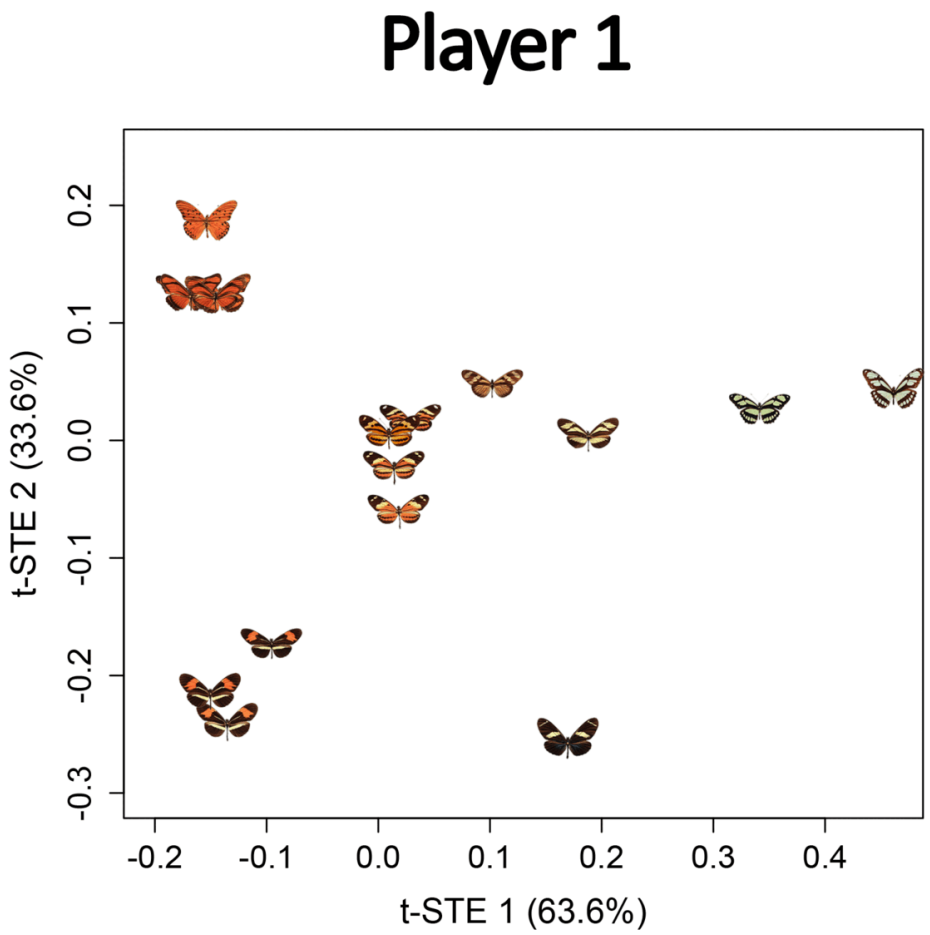


Comparison of indivudal perceptual maps

Collaborations are welcomed ☺

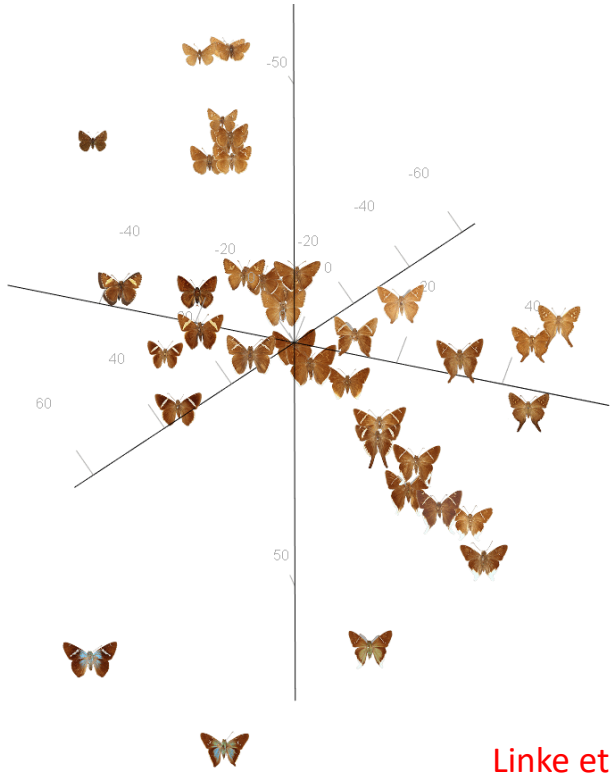
Method can be implemented at **multiple scale**:

- **Individual** perceptual maps
- **Expert-based** projects
- **Citizen Science** surveys

Website for **online surveys** currently available

R package in progress

Perceptual map of Cecropterus (Hesperiidae)



Linke et al., *in prep.*

Publications *in prep.*:

Doré, M., Pérochon, E., Aubier, T.G., Joron, M. & Elias, M. Perceptual maps: a new tool to investigate mimicry patterns from Citizen Science to individual perception. *In prep.*

Doré, M., Pérochon, E., Aubier, T.G., Joron, M. & Elias, M. Beyond Müller's mimicry model: Perceptual maps support continental-scale convergence in wing patterns of sympatric Neotropical butterflies. *In prep*.

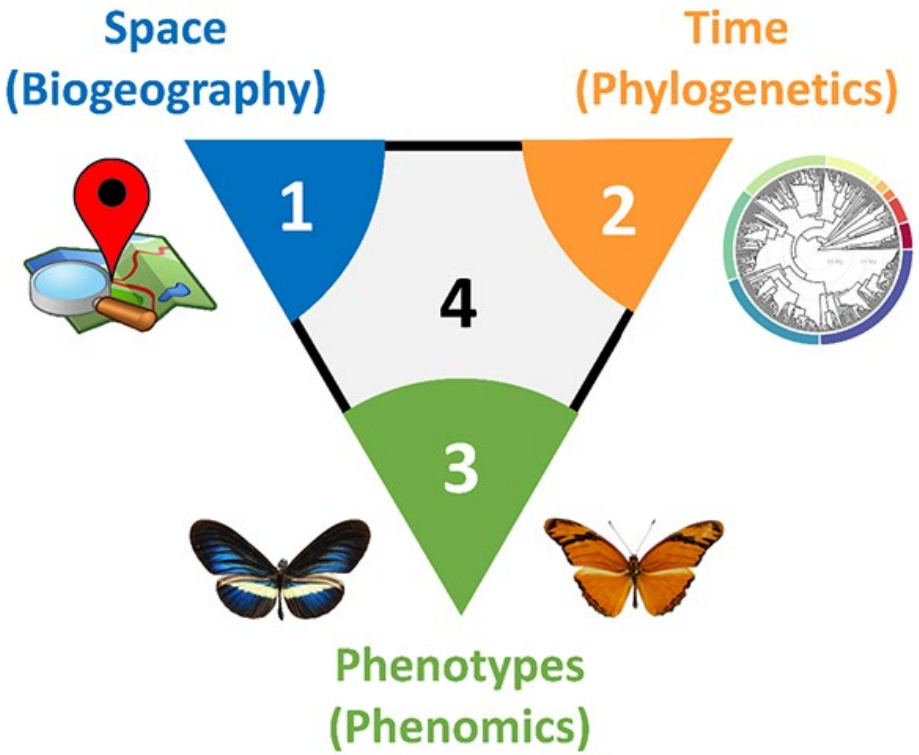
Outlines and objectives

PART 1

Map **biodiversity patterns**

PART 3

Quantify **phenotypic similarity** in wing patterns



PART 2

Resolve **deep evolutionary relationships**

Outlines and objectives

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Map **biodiversity patterns**

PART 3

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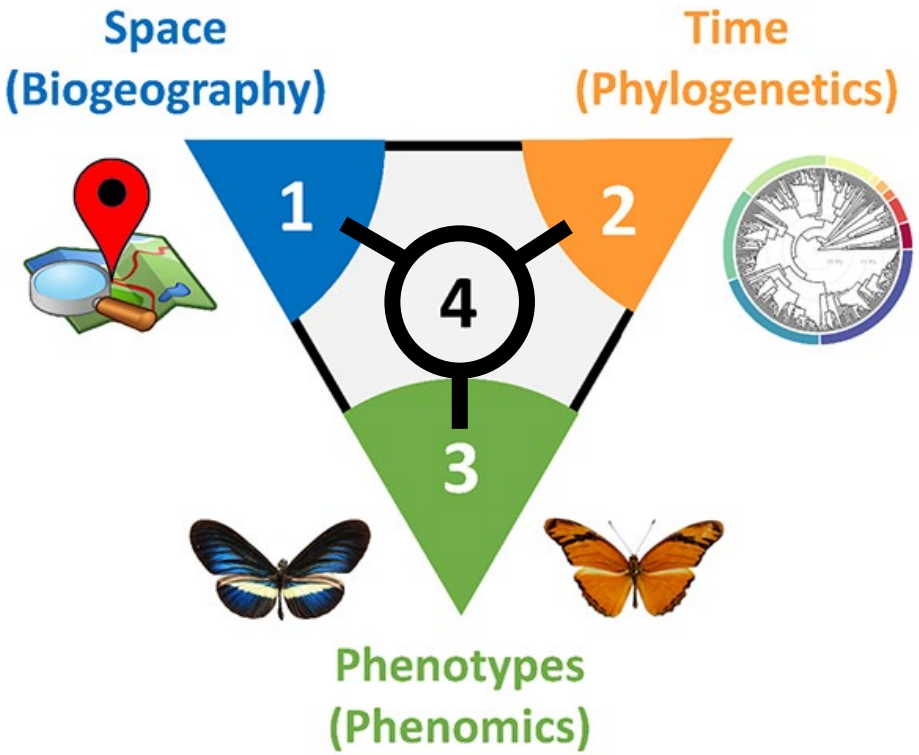

PART 2

Resolve **deep evolutionary relationships**

How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

Question & Hypotheses

How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

Spatial pattern	Promote the large-scale **cooccurrence** of **mutualistic** species
Niche evolution	Drive the **convergence** of the niche of **mutualistic** species
Pattern evolution	Promote the **convergence** of warning signals in **sympatric** species at continental scale

Study system: Neotropical butterflies

Ithomiini tribe

Credits Photo: N. Chazot

8 shared patterns

Heliconiini tribe

Credit photos: C. Jiggins

44 phenotypic groups / putative mimicry rings

39 phenotypic groups / putative mimicry rings

Question & Hypotheses

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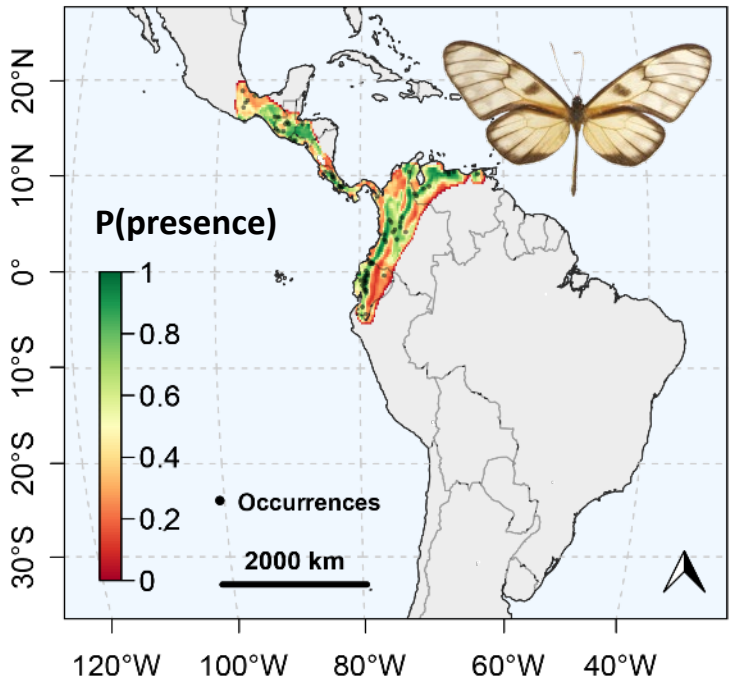
Spatial congruence

Question: Do phenotypically similar species **cooccur** more than expected at **random**?

Hypothesis: Lower **spatial dissimilarity** for comimetic species

$$BC_{ij} = 1 - \frac{2\sum \min(P_i, P_j)}{\sum P_i + P_j}$$

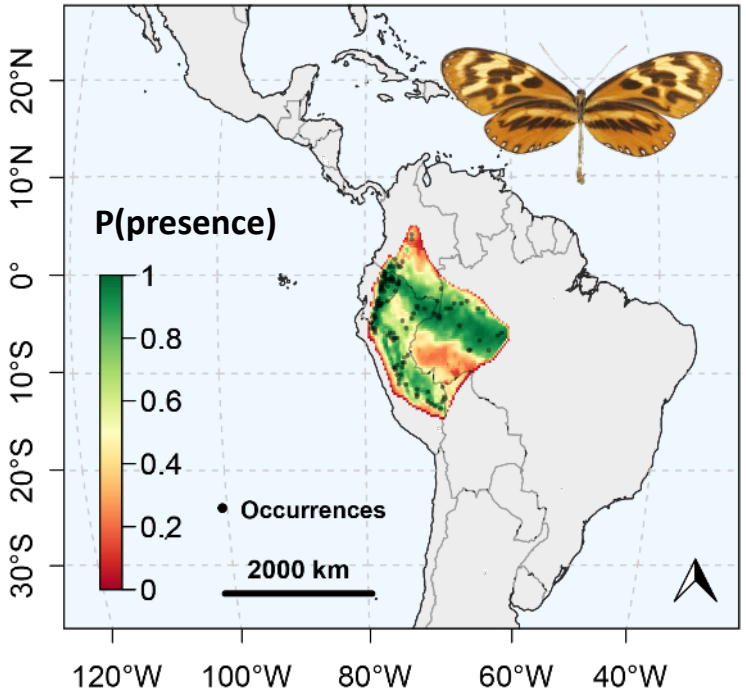
Dircenna jemina **(DILUCIDA)**



No mimicry

BC = 0.9

Mechanitis mazaeus **(MAELUS)**



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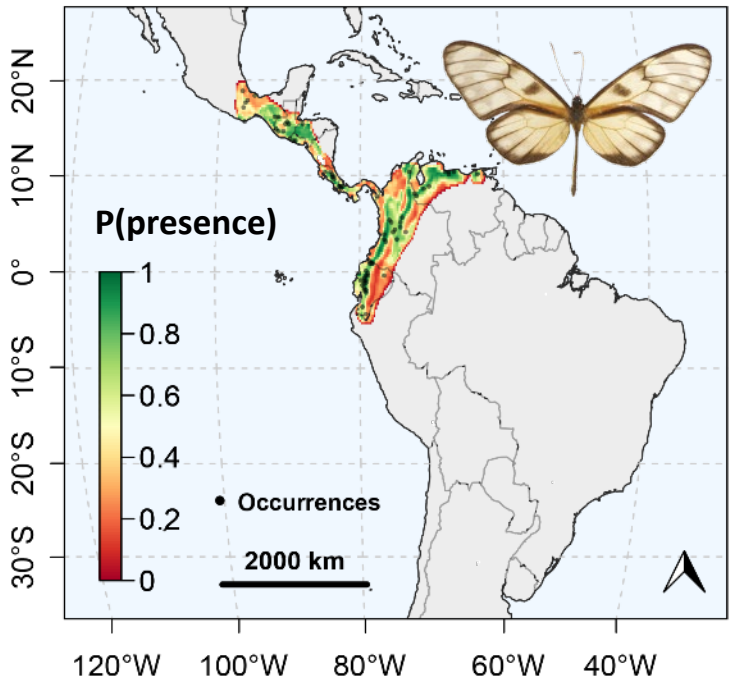
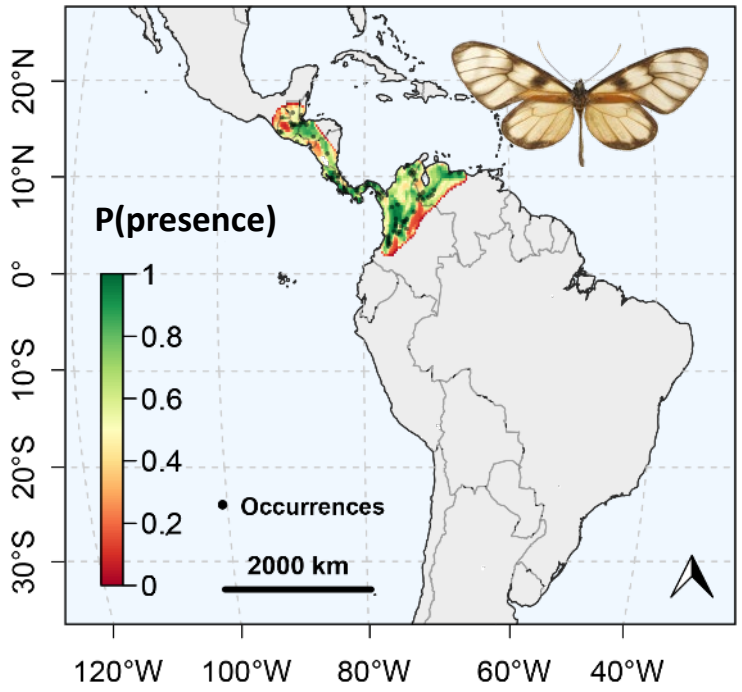


Mimicry

BC = 0.2

Dircenna dero **(DILUCIDA)**



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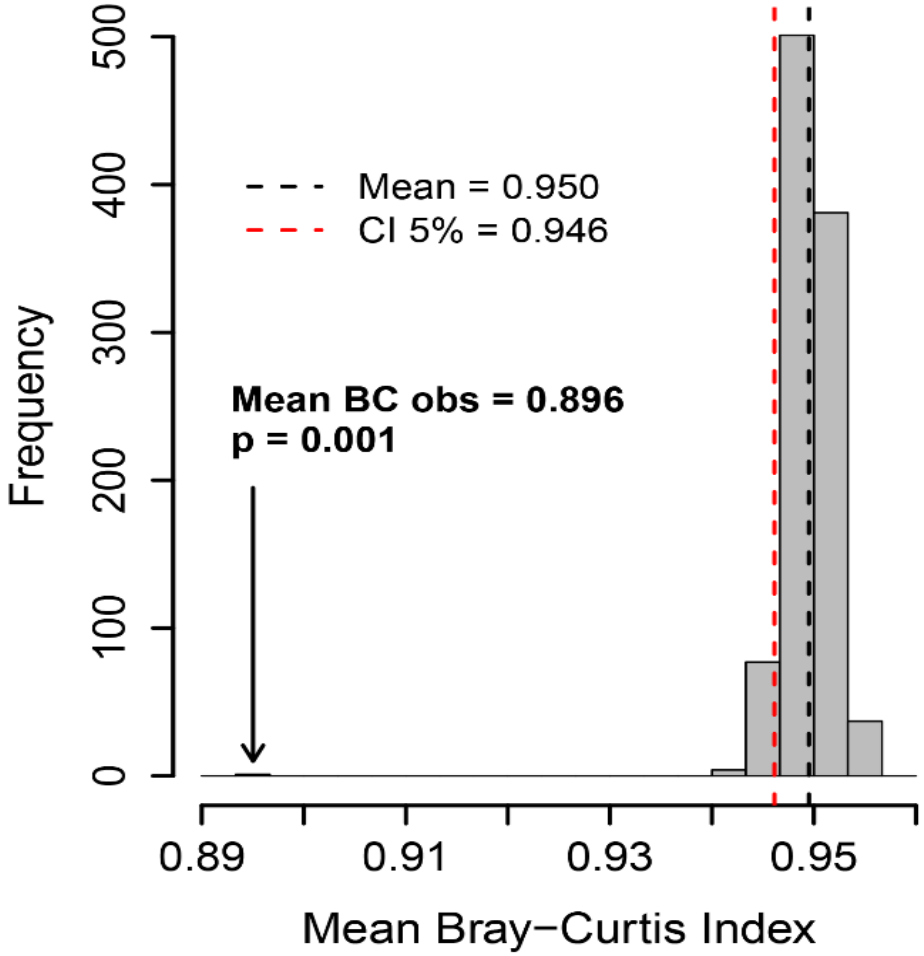
Global: Mean BC_{obs} << Mean BC_{perm} ✓

Per ring: Significant for 85% of rings in Ithomiini

- Non-significant rings = low N

Results: Mimicry promotes the **spatial congruence** of phenotypically similar species at **large-scale**

Next: What happens between **tribes**?



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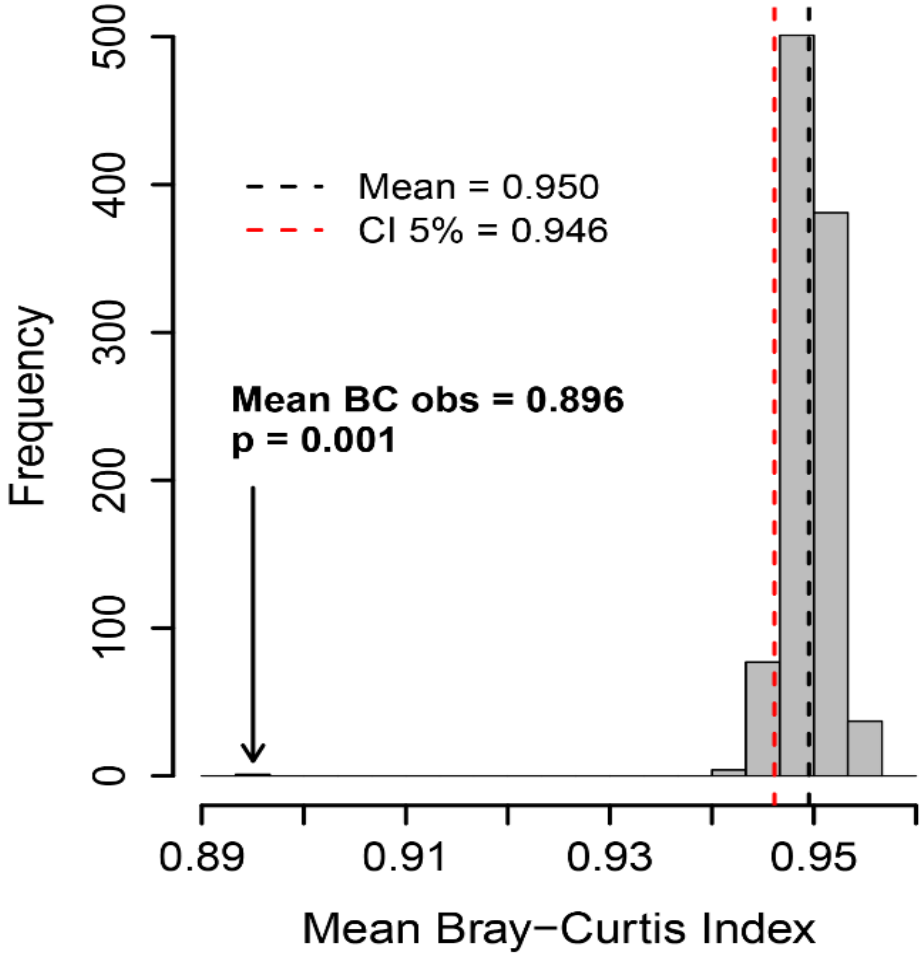

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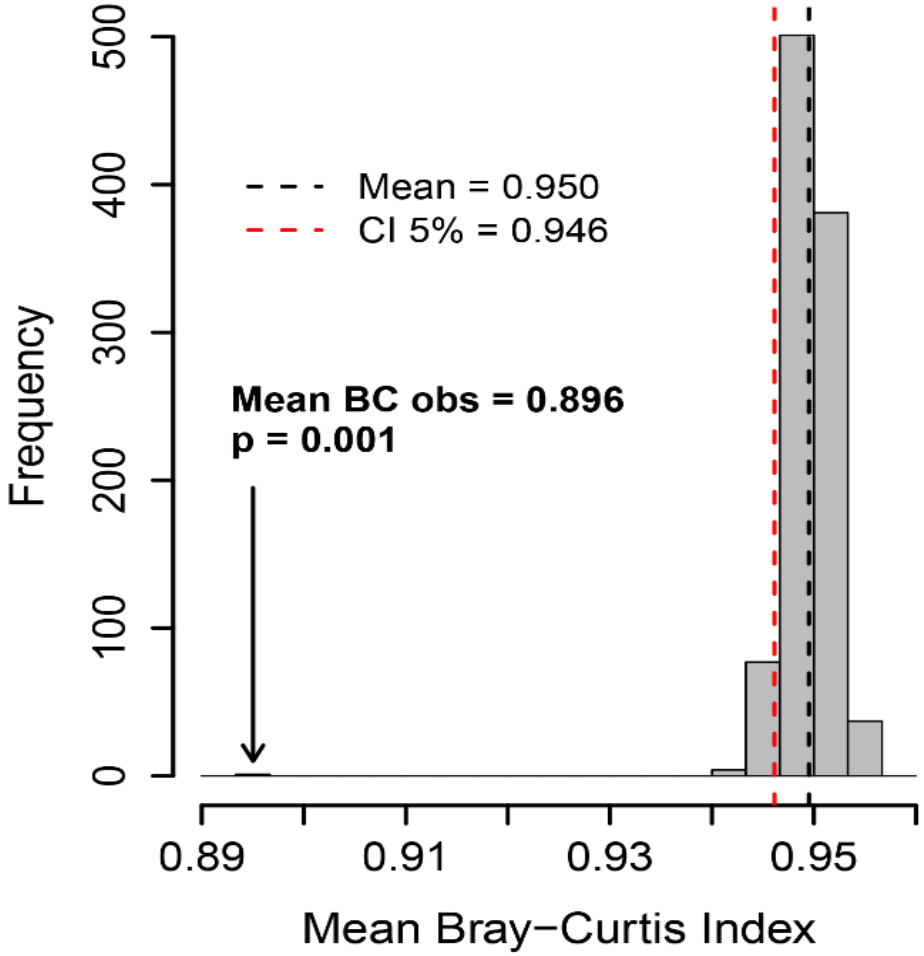
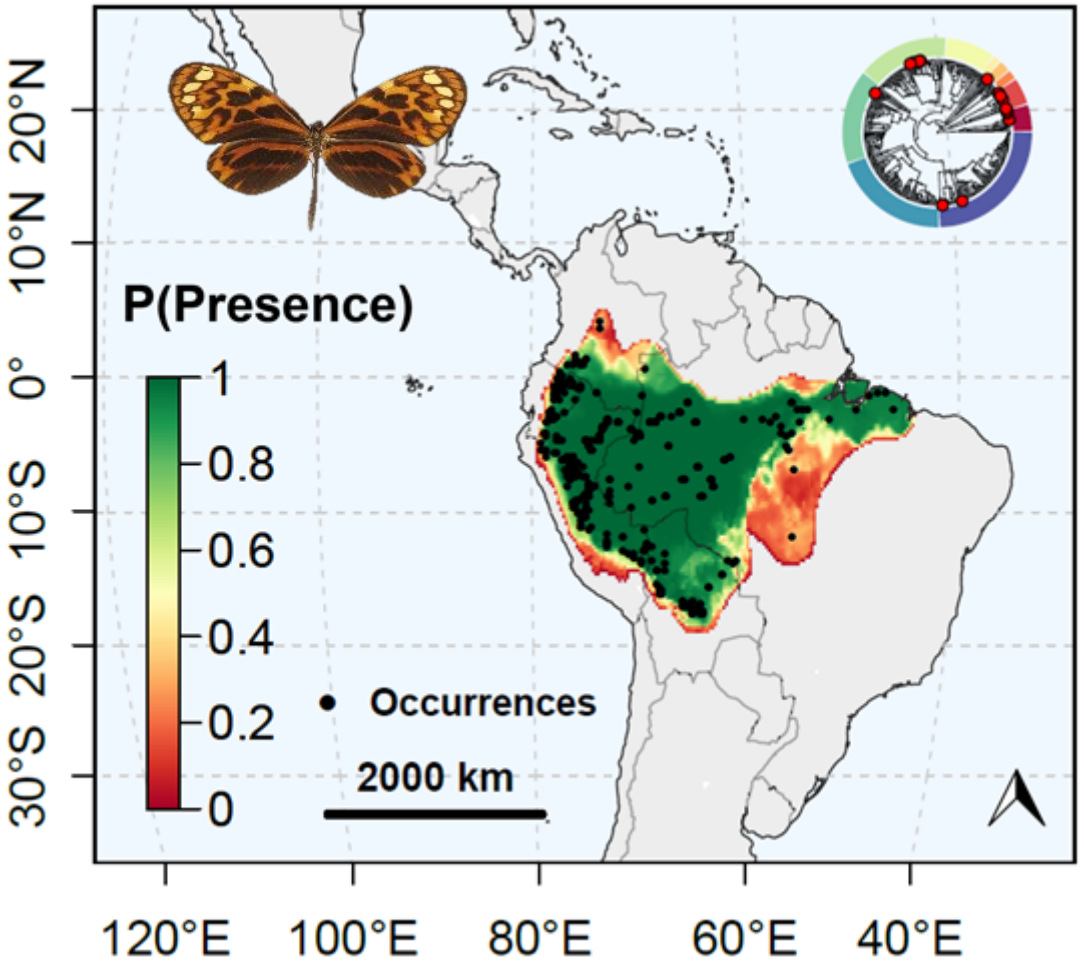
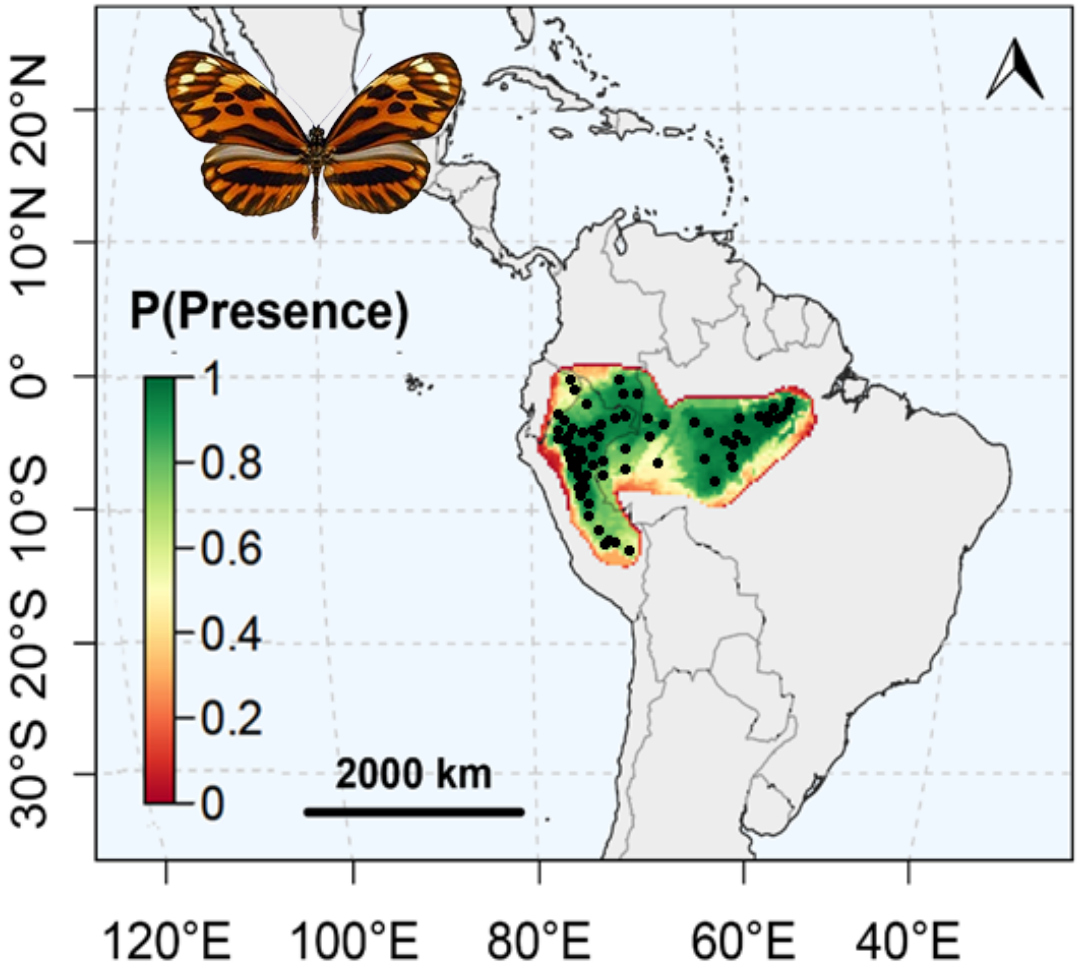


Spatial congruence

Ithomiini: pattern MAELUS
(16 species)

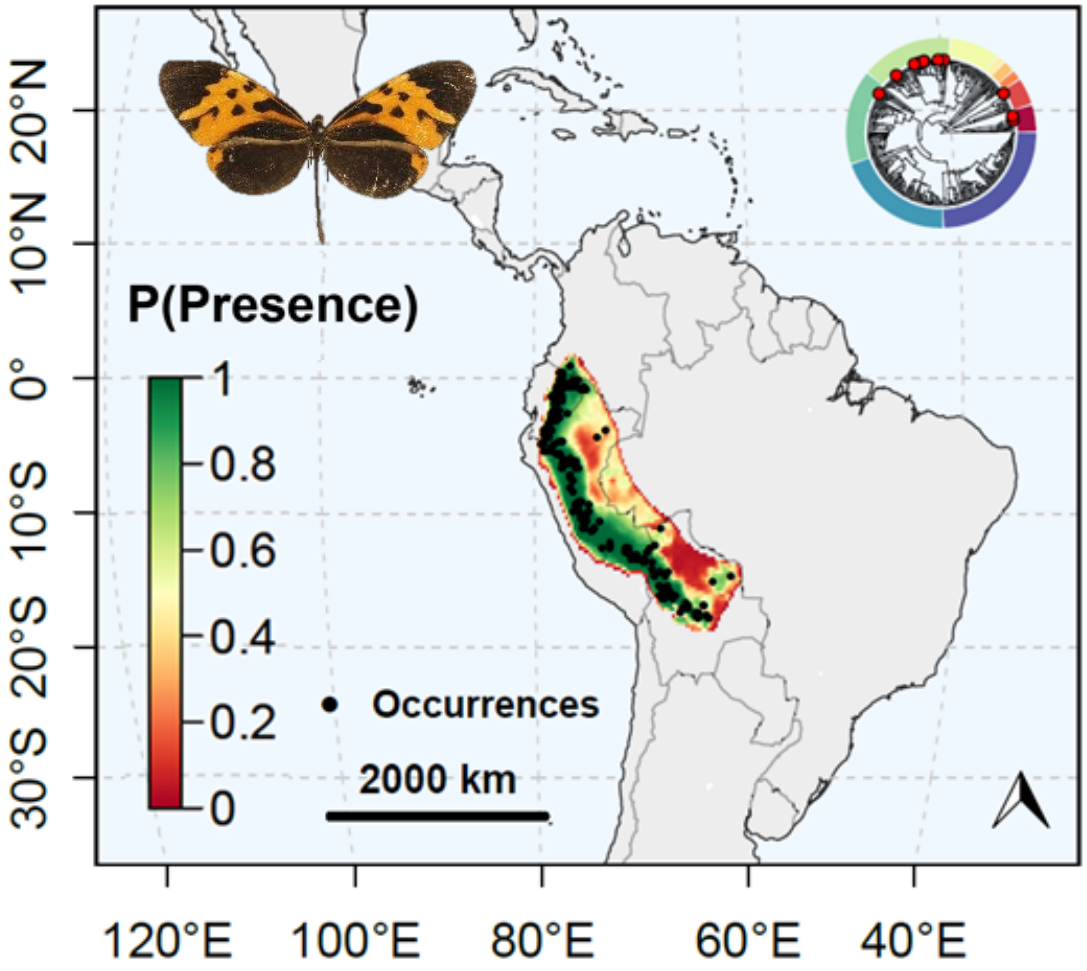


Heliconiini: pattern MAELUS
(5 species)

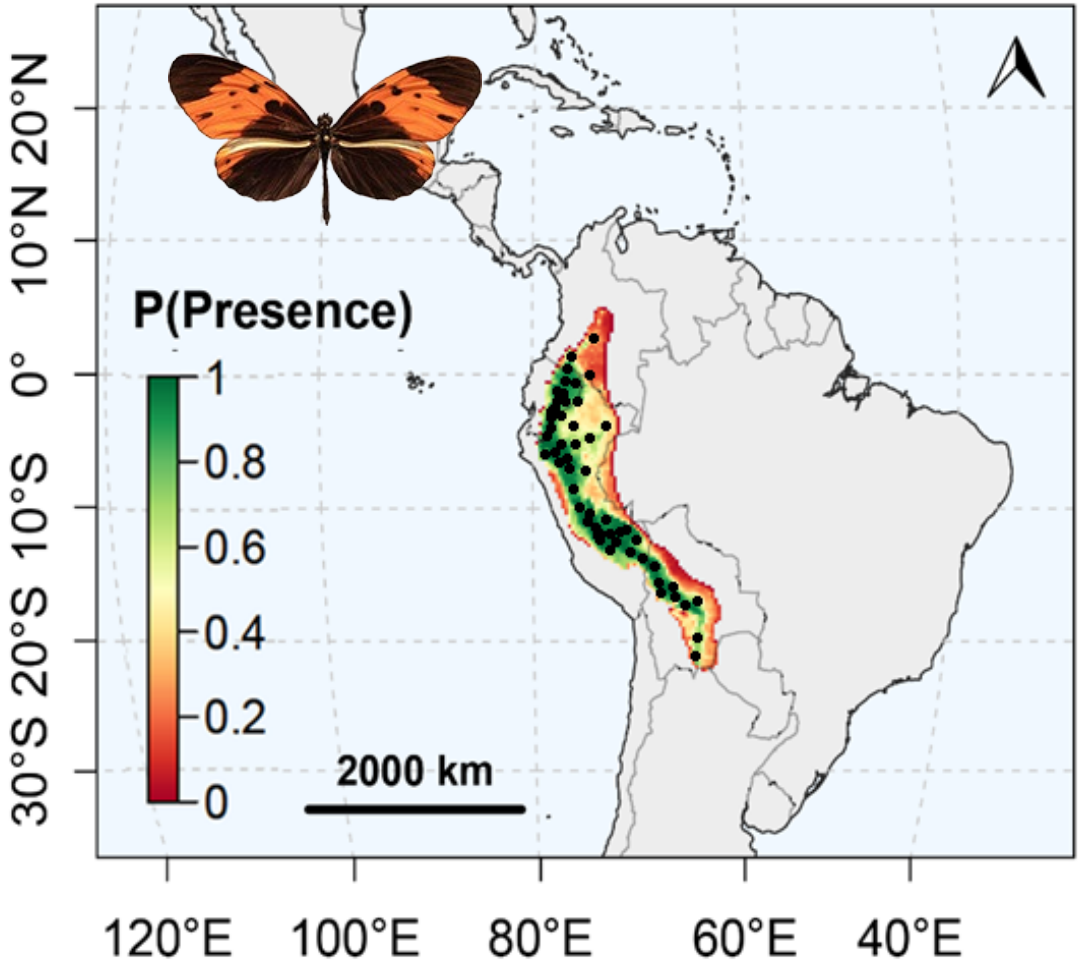


Spatial congruence

Ithomiini: pattern MOTHONE
(14 species)

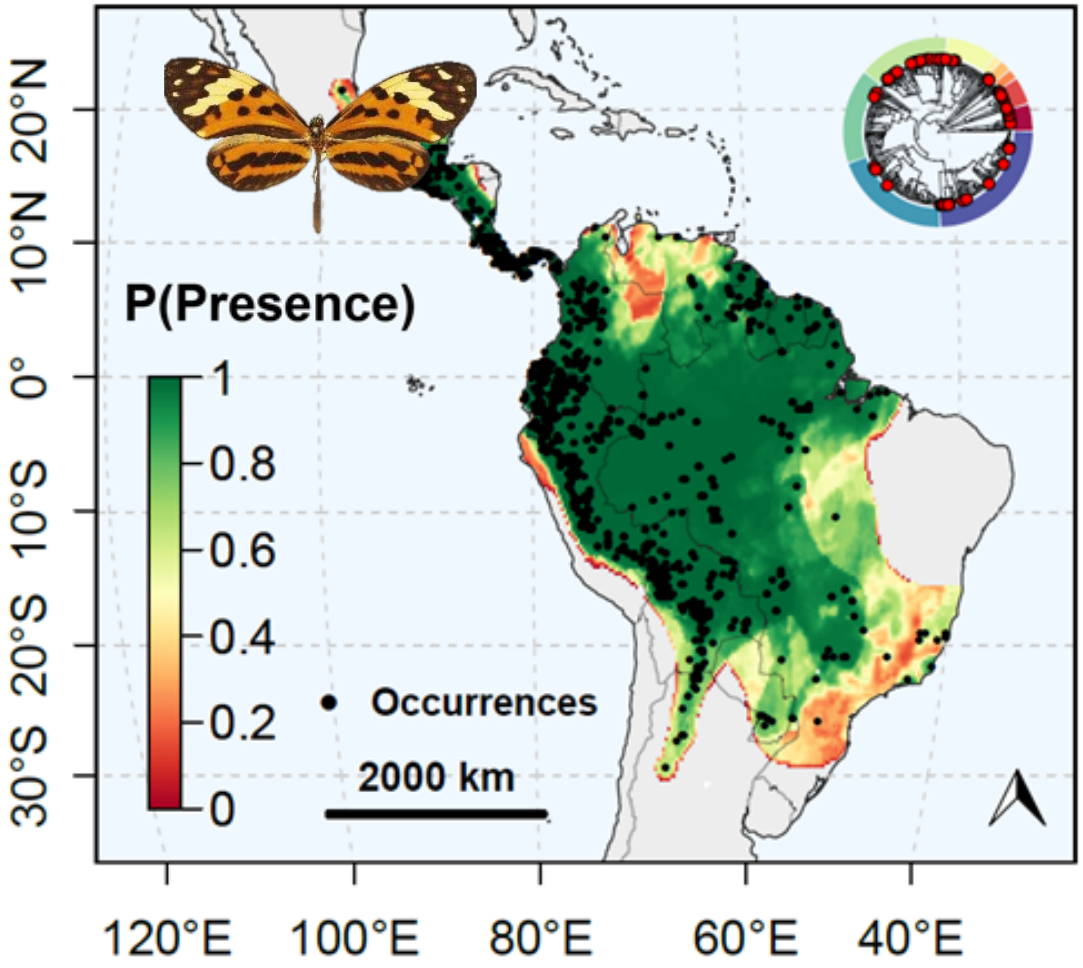


Heliconiini: pattern MOTHONE
(3 species)

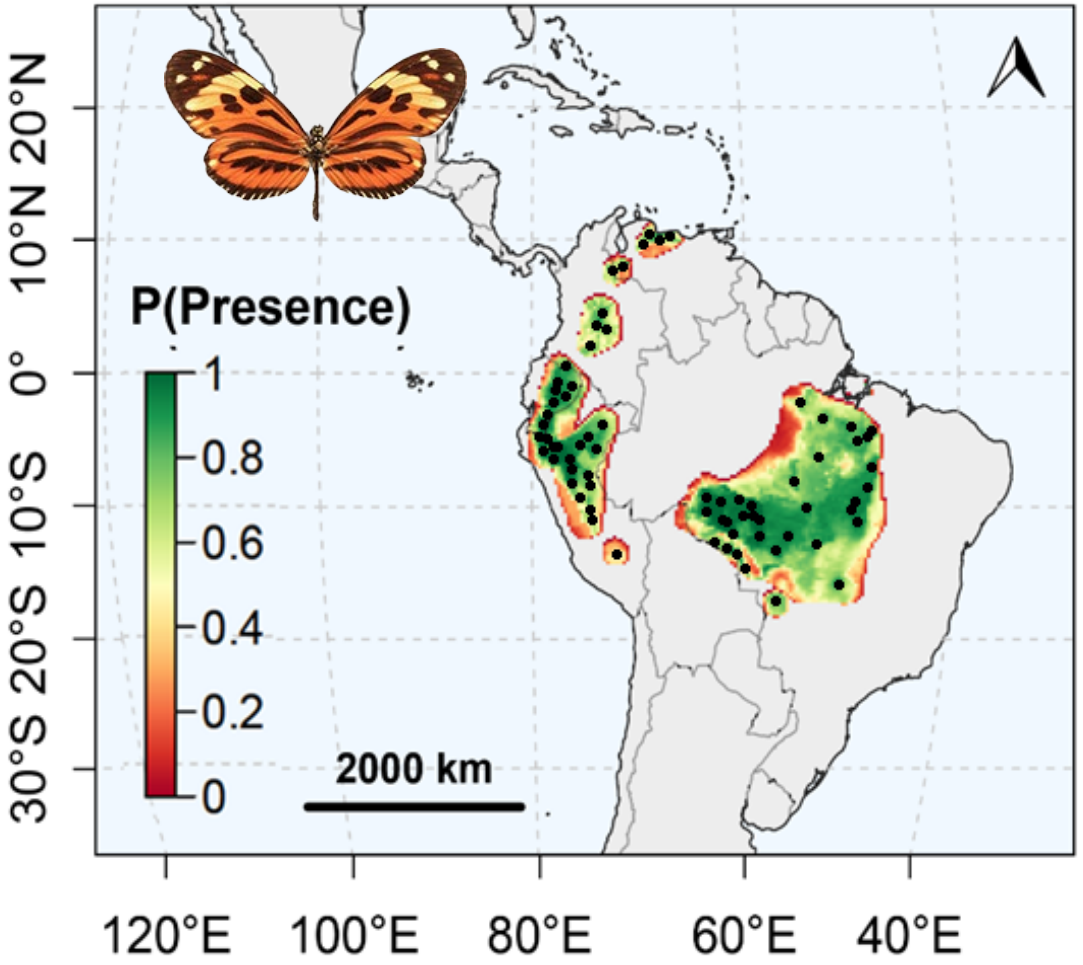


Spatial congruence

Ithomiini: pattern MAMERCUS (64 species)



Heliconiini: pattern MAMERCUS (10 species)



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Spatial pattern

Promote the large-scale **cooccurrence** of **mutualistic** species

---

Niche evolution

Drive the **convergence** of the niche of **mutualistic** species

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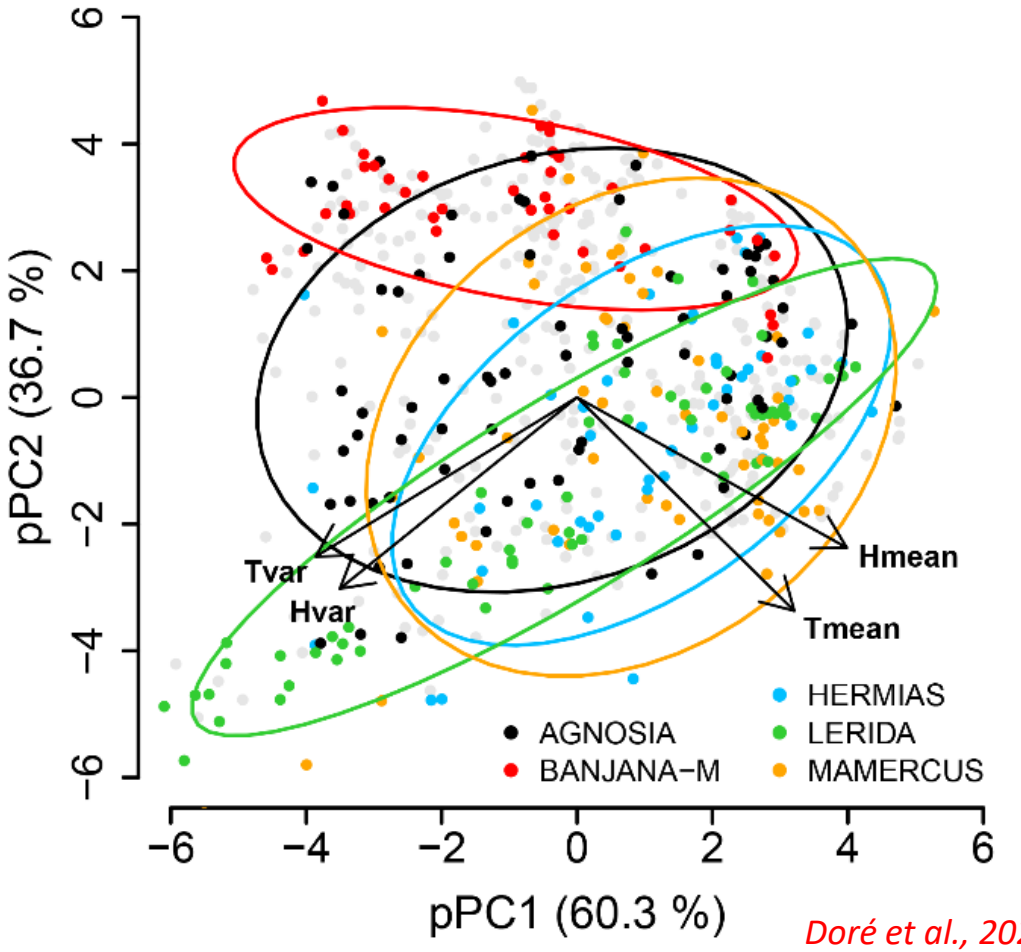
Pattern evolution

Promote the **convergence** of warning signals in **sympatric** species at continental scale

Climatic niche similarity

Question: Do **phenotypic groups** occupy different **climatic niche**?

Global: perMANOVA, $R^2 = 0.41$, $p = 0.001$



Doré et al., 2023

Per phenotypic group:

- 81.0% pairs with $p < 0.05$
- 66.4% pairs with $p < 0.001$

Next: Is this pattern due to **shared ancestry** or **evolutionary convergence**?

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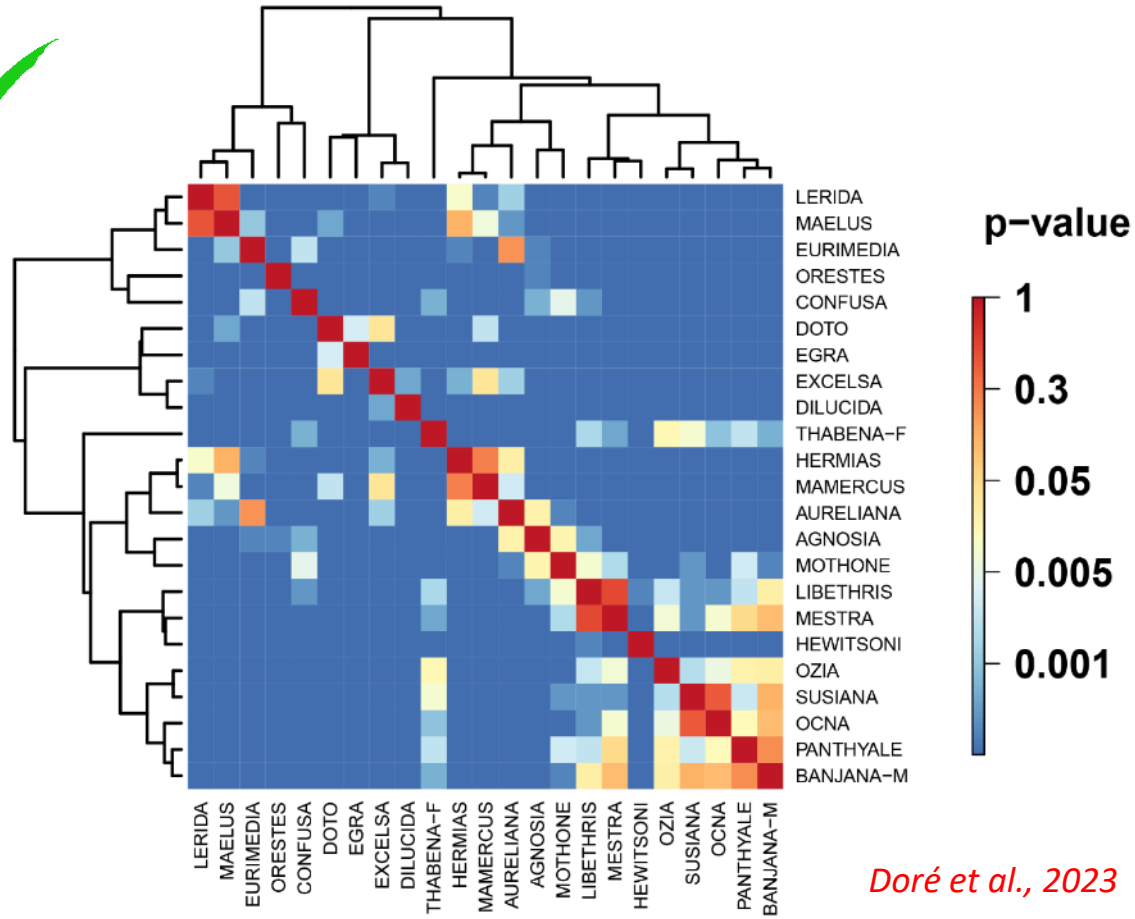

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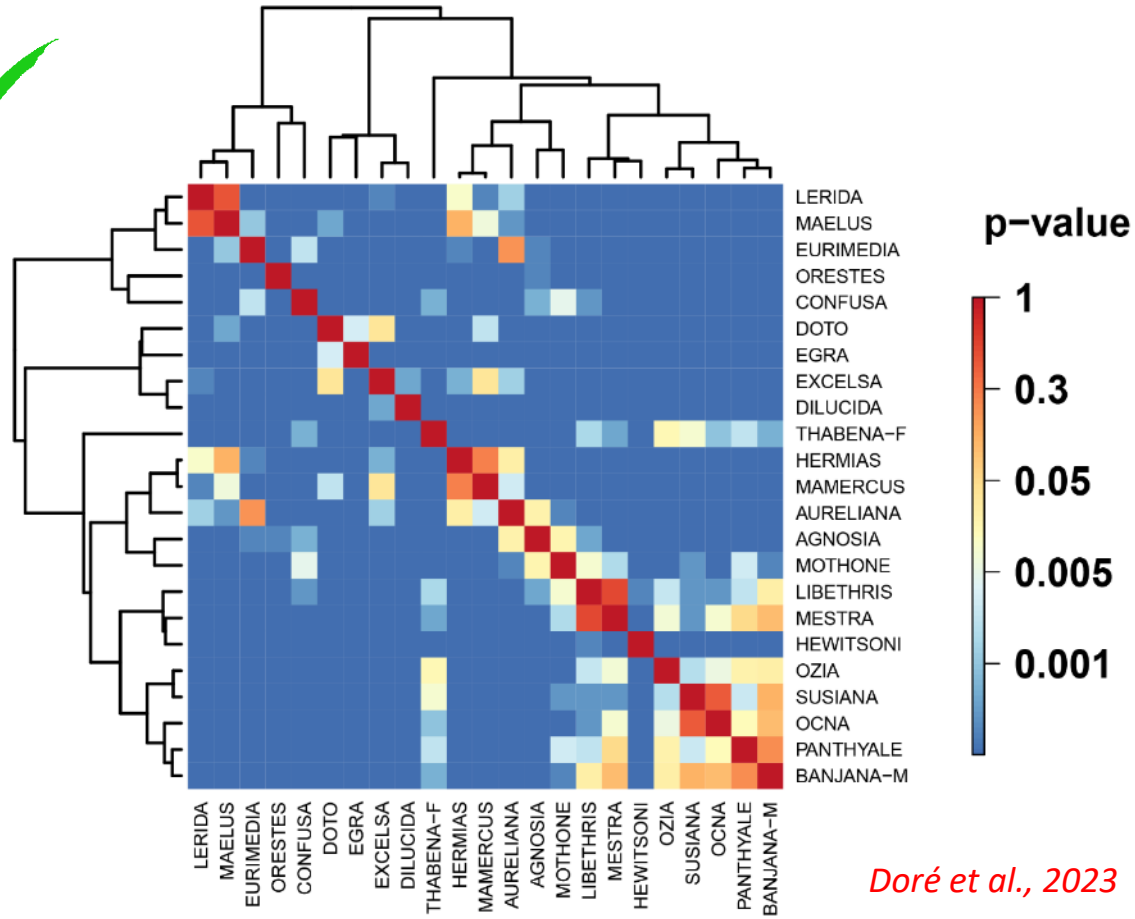

Doré et al., 2023

Comparative phylogenetic analyses

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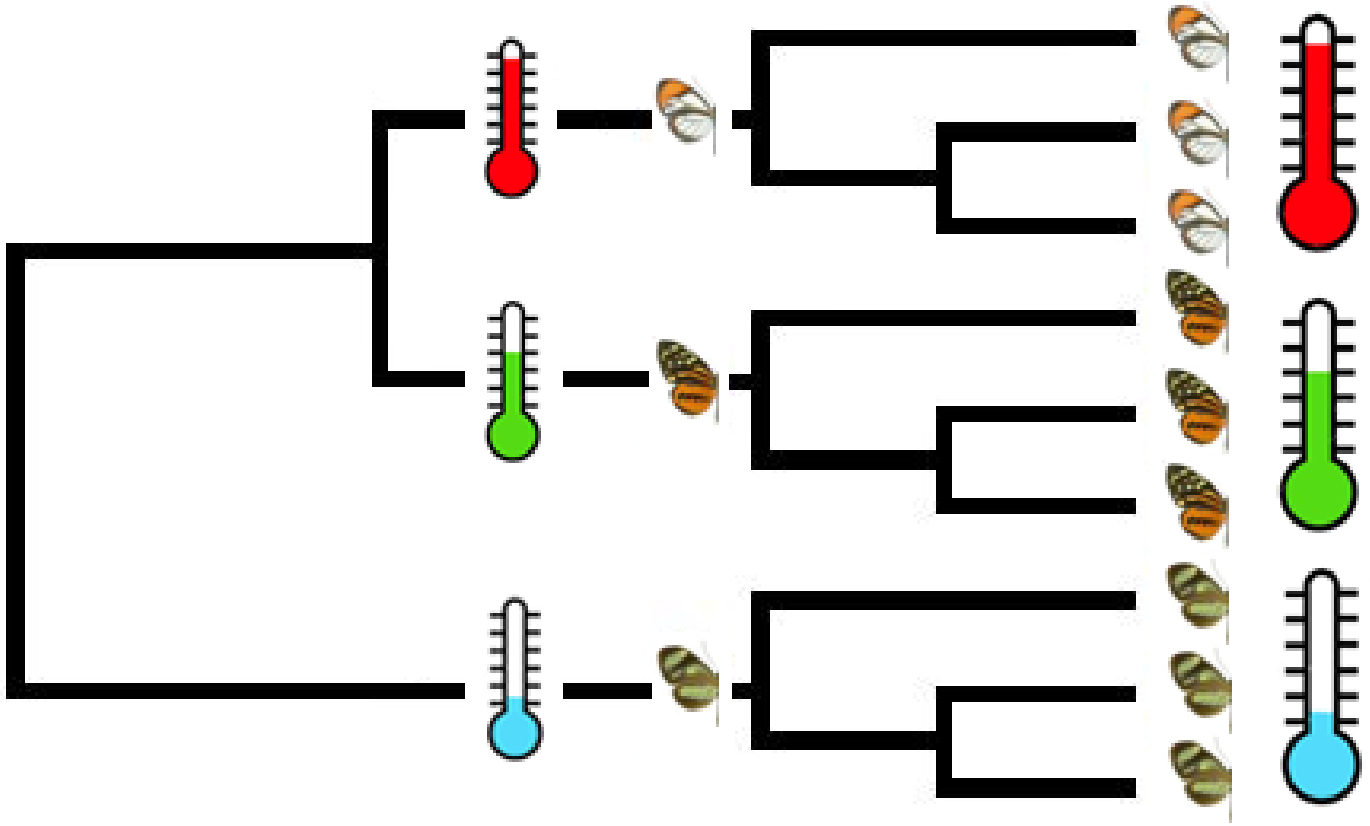

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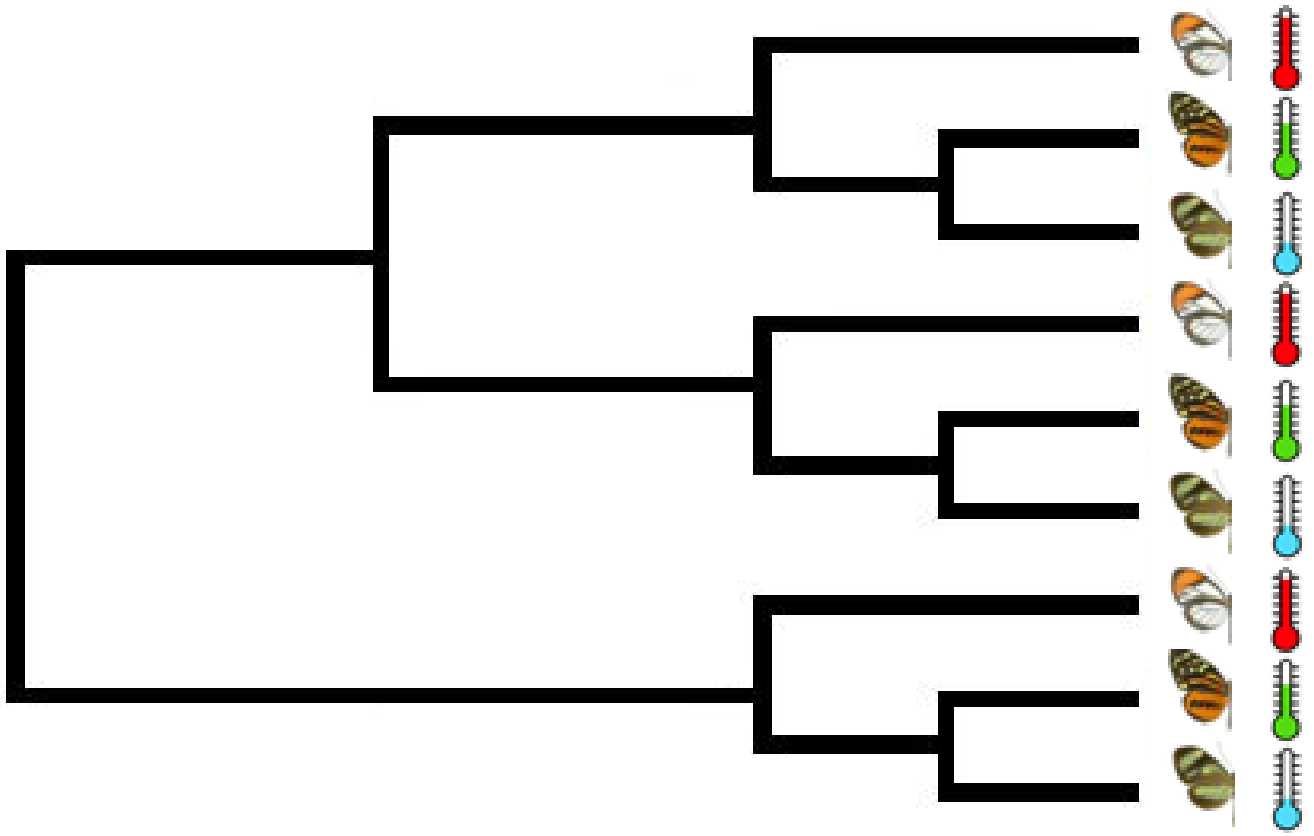


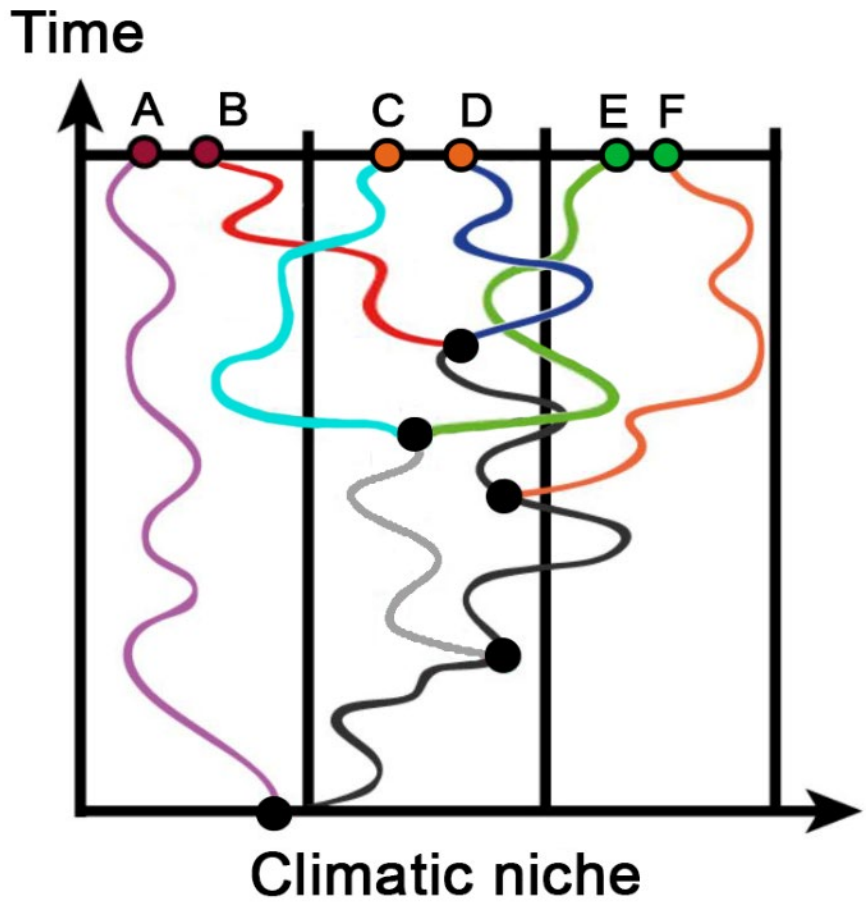
Climatic niche evolution

Question: Is the **climatic niche** of phenotypically similar species more similar than expected from the **phylogeny**?

Simulate the evolution of climatic niche under multivariate **neutral evolutionary model**

phyloMANOVA: $\lambda_{obs} << \lambda_{simul}$

Results: Evolutionary association between **climatic niche** and **wing patterns**



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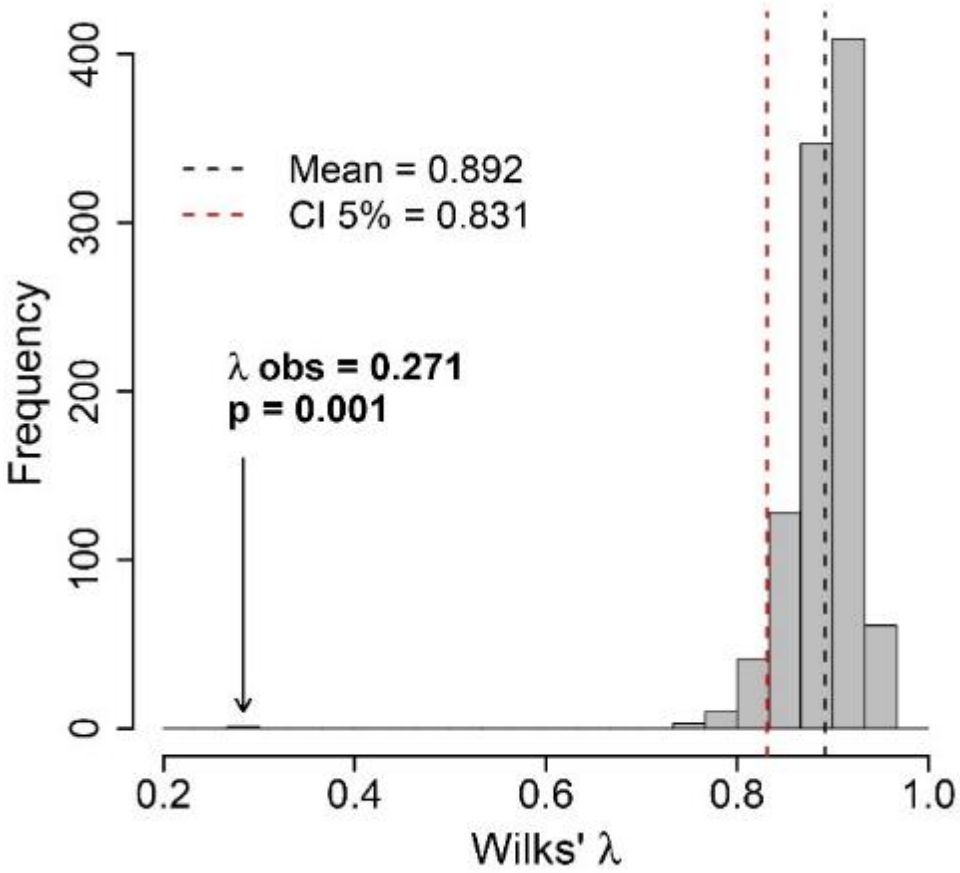

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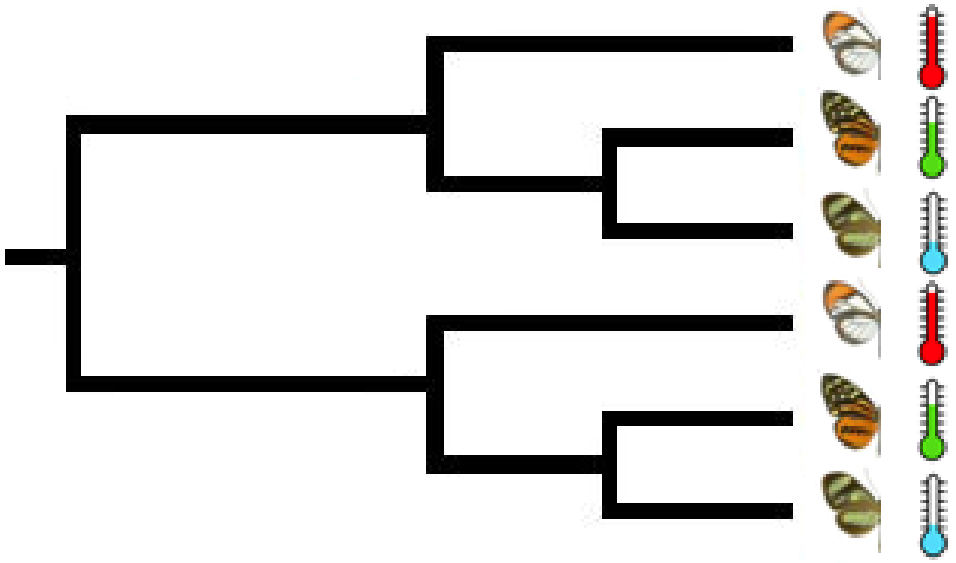
Results: **Evolutionary convergence** between **climatic niche** and **wing patterns**

Evolutionary convergence



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Pattern convergence

Question: Does mimicry promote the **convergence** of warning signals in **sympatric** species at continental scale?

Data: Perceptual space x Distribution maps

Index: Perceived Phenotypic Diversity = PePD

Test: Compare to **neutral evolution** of phenotypes

- Brownian Motion in the perceptual space
- Local tests for **Müller's model**
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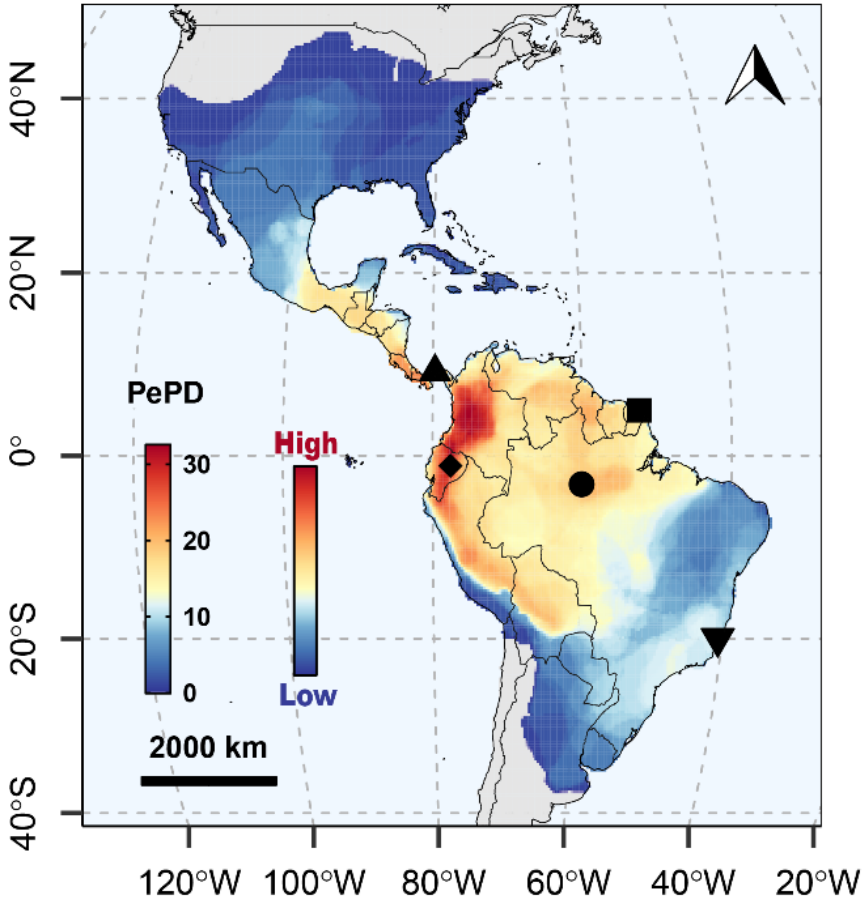
Results: Continental-scale convergence

Conclusion: Perceptual maps support continental-scale convergence in wing patterns of sympatric heliconiines



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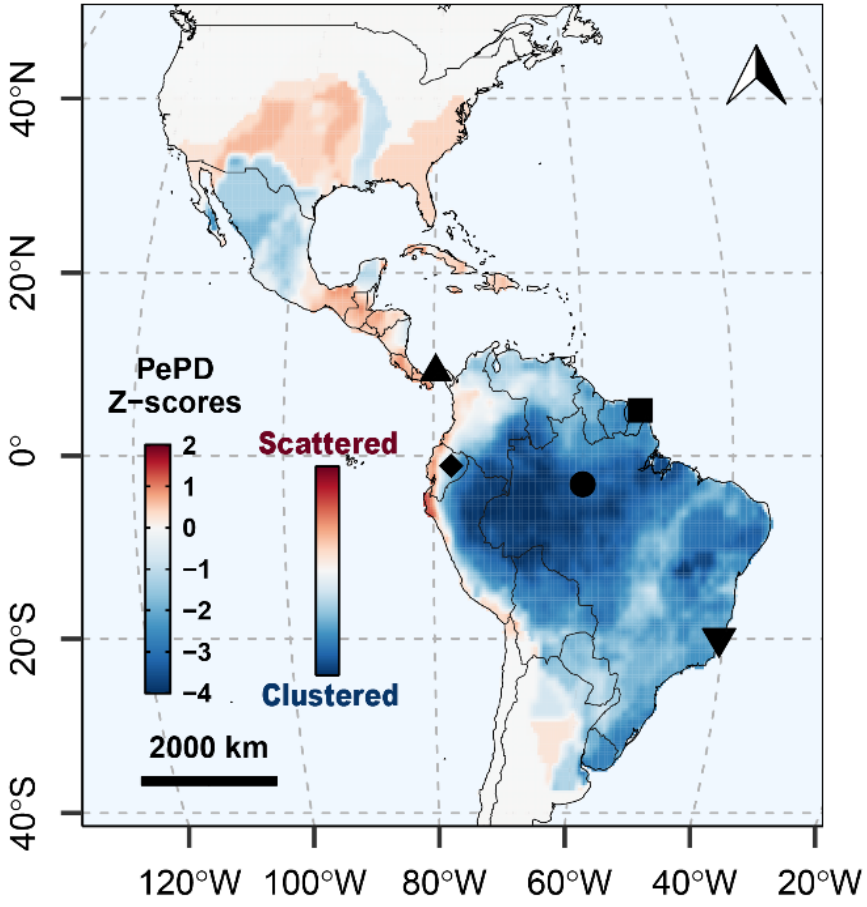

Doré et al., in prep.

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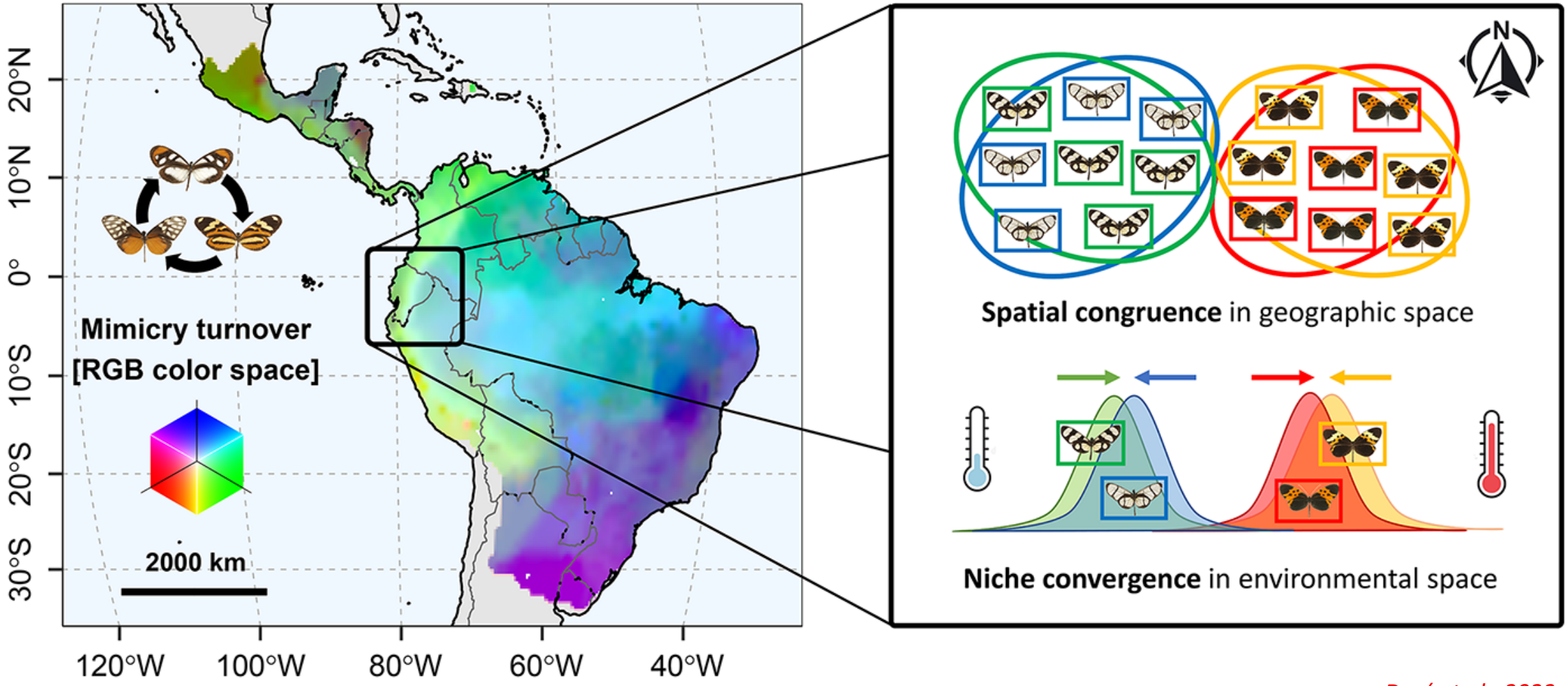

Doré et al., 2023

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SCAN ME

Main collaborators:

- Eddie Pérochon
- Keith Willmott
- Boris Leroy
- Jérémy Gauthier
- Rémi Allio
- Thomas Aubier
- Mathieu Joron
- André VL Freitas
- James Mallet
- Nicolas Chazot
- Nick Grishin
- Joana Meier
- Sébastien Lavergne
- Neil Rosser
- Krzysztof Kozak

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Thanks for your attention

Hypomenitis enigma (Ithomiini). Credits: M. Elias