Biodiversity and evolution in Neotropical mimetic butterflies

Maël Doré

PhD Thesis Defense

June 1st 2023

Credit photos: C. Jiggins

MUSÉUM NAL HIST NATURELLE

ISYEB
Institut de Systématique, Evolution, Biodiversité

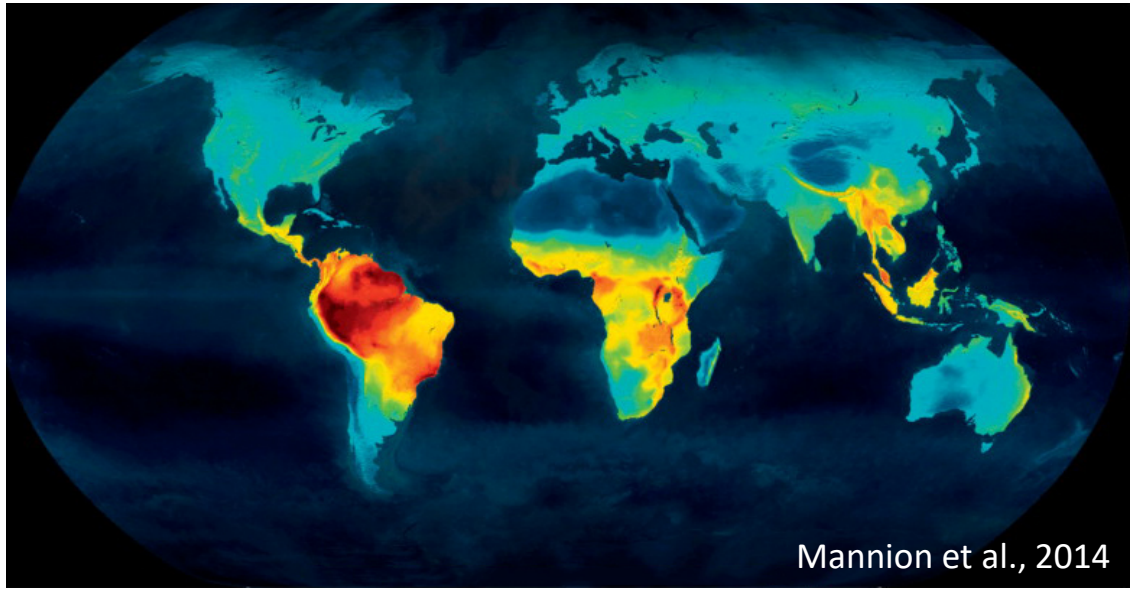
cnrs

CESCO
Centre d'Écologie et des Sciences de la Conservation

Context

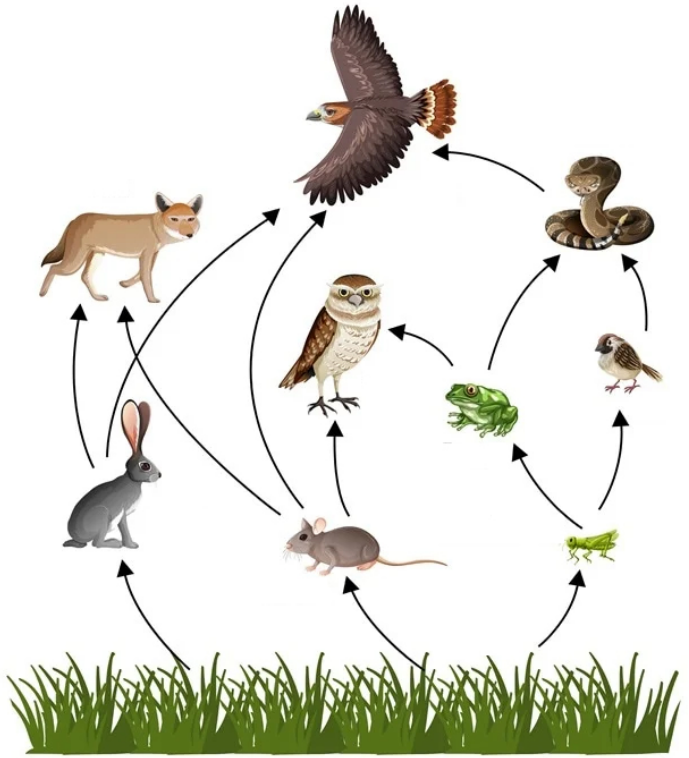
Biodiversity

Biological units



+

Interactions



Credit: Shutterstock.com

Context

Mutualistic interactions:

- Plant facilitation
- Cooperative hunting
- Anti-predatory dilution effect
- Müllerian mimicry

Credits: Amanda R. Liczner

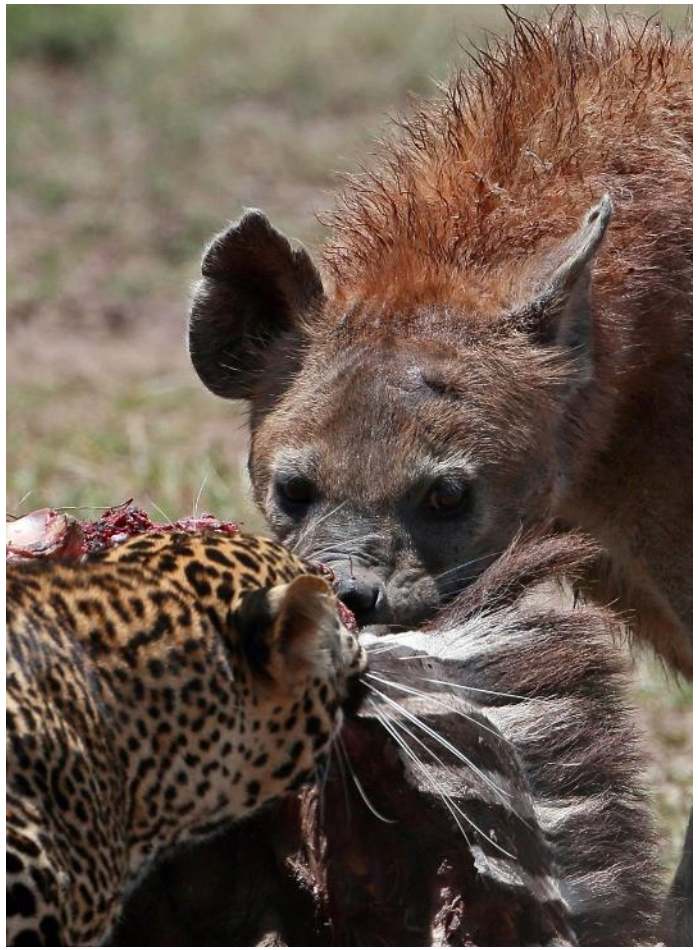
©Thomas Kline ; salmonography.com

Credits: safari-consultants.com

Credits: Jason L. Brown

Context

Credit: Campillo Rafael



Credit: Caters News Agency

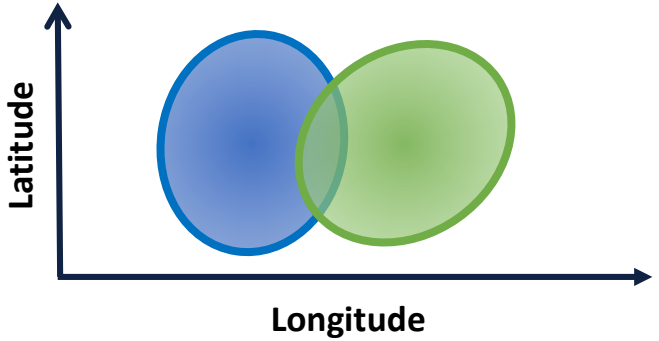
Credits: Anytka Olkova & Larry Myers

Exploitative competition:

- for local resources
- for habitats
- for space

Context

Spatial distribution



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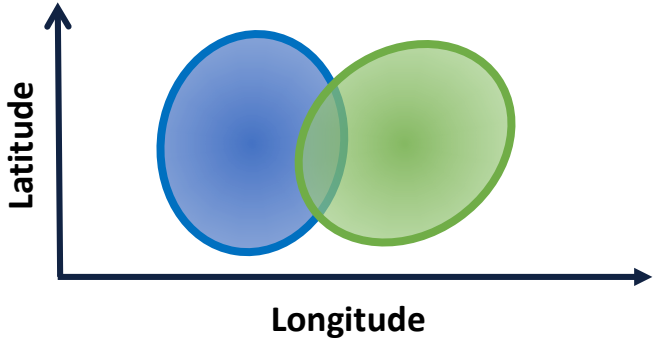

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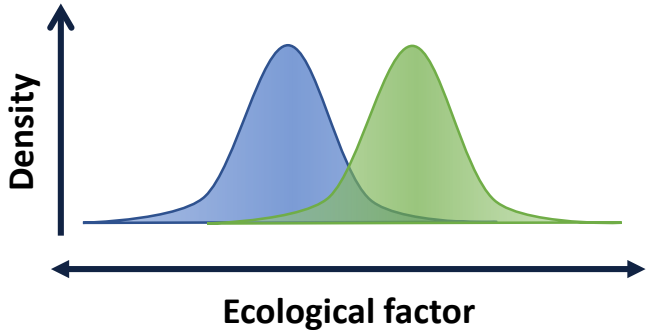
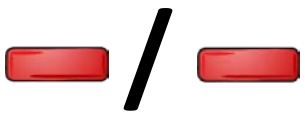
Environmental niche



Context

Competition  **Mutualism** 

Spatial pattern

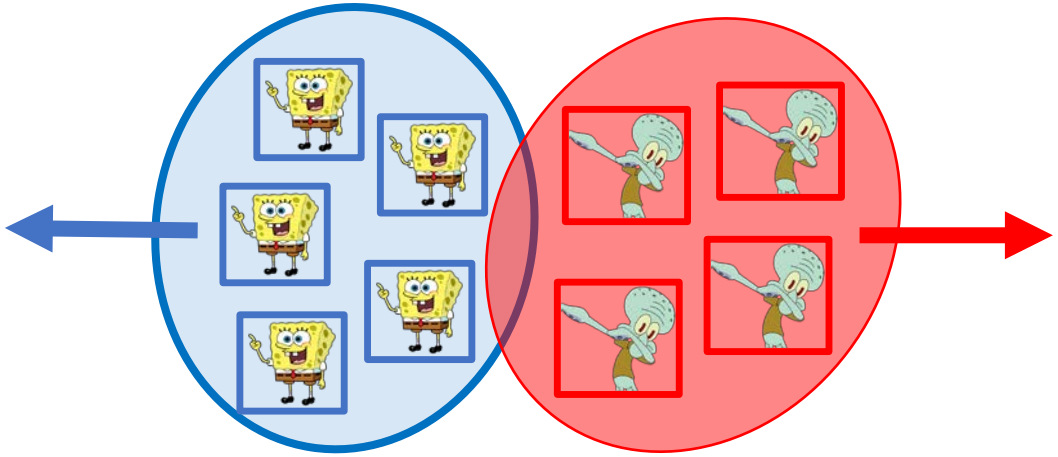
Niche evolution

Context

Competition − / −

Mutualism + / +

Spatial pattern



Niche evolution

Context

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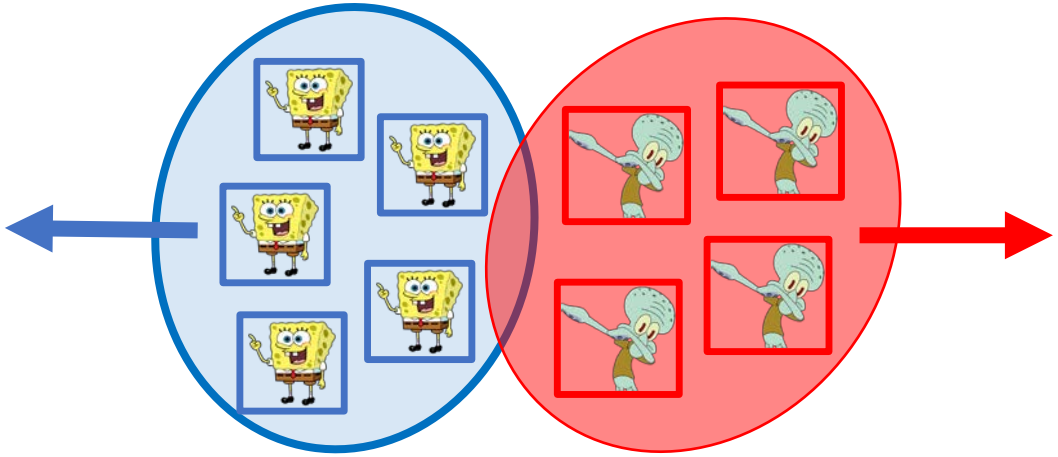

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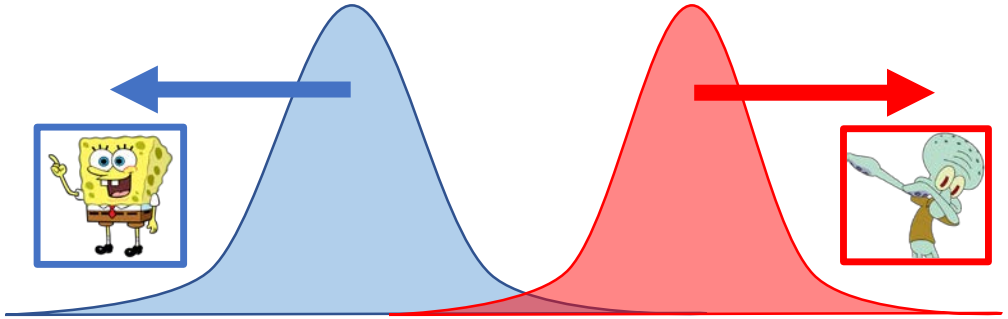

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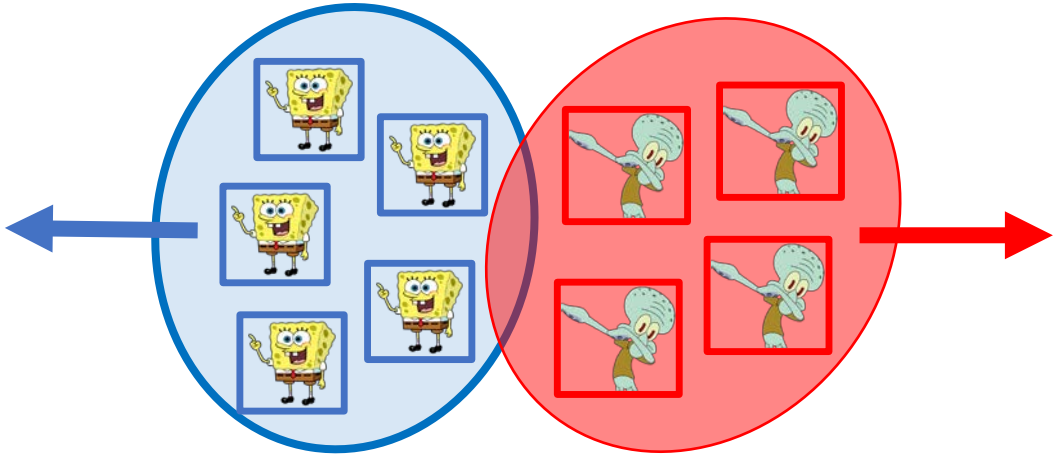

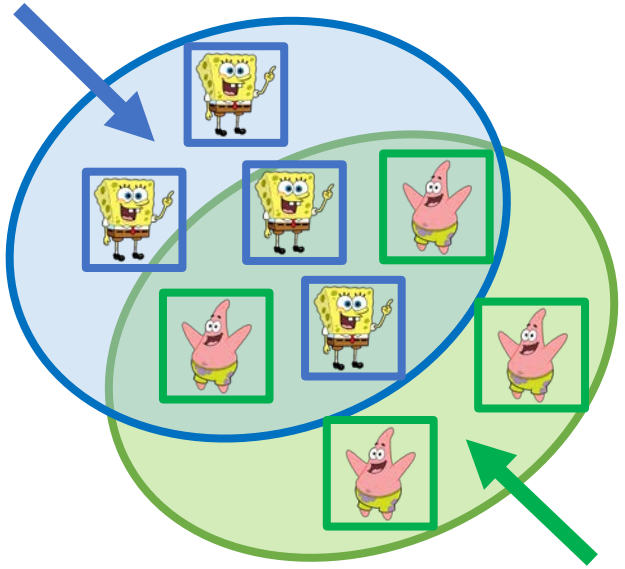

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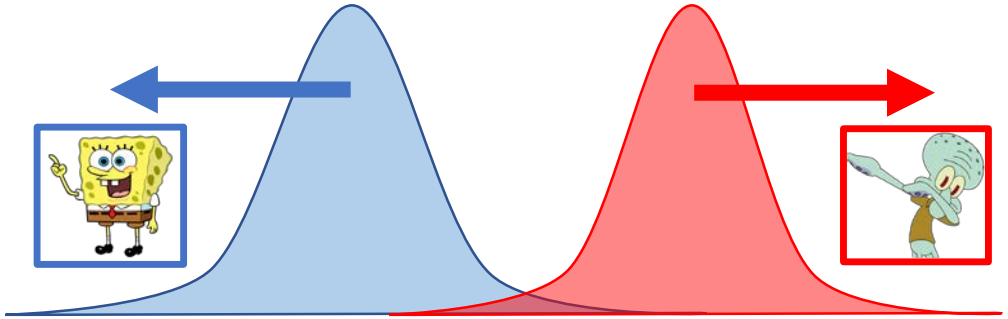

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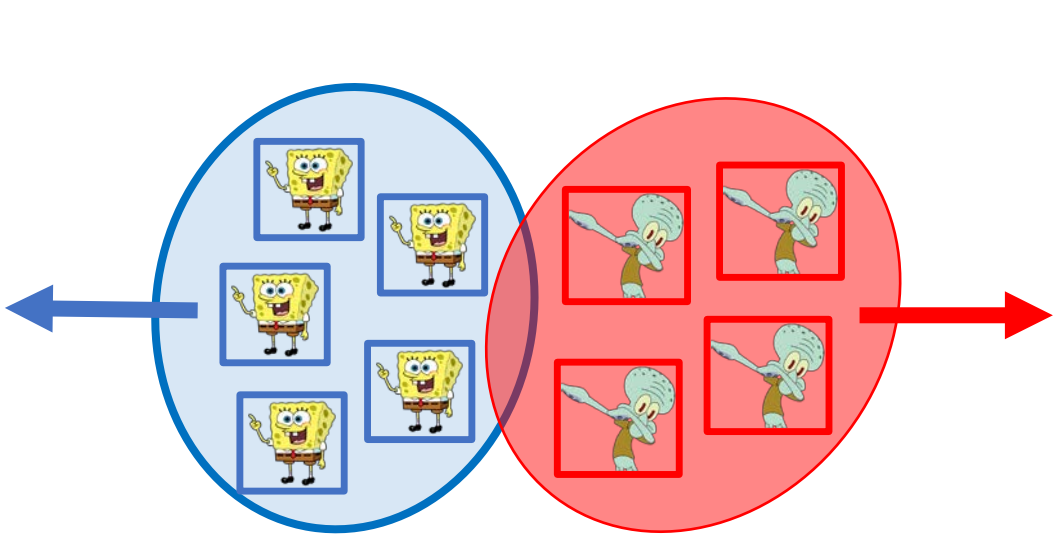

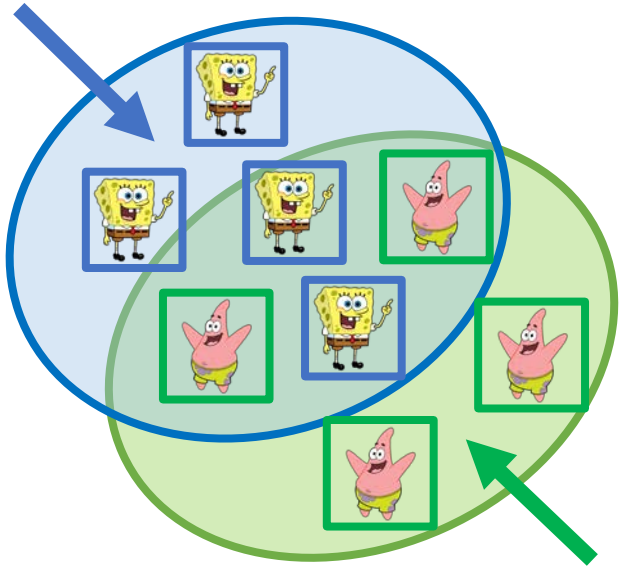

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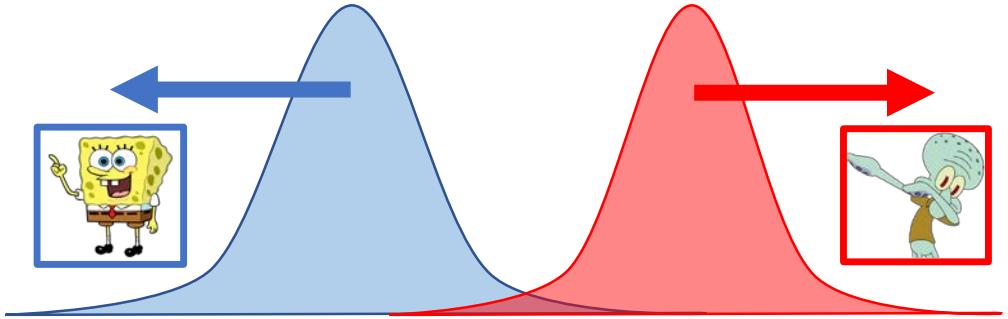

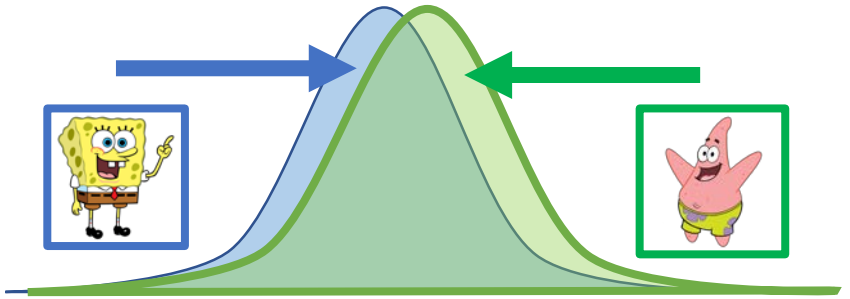

Questions & Hypotheses

Can **mutualistic interactions** outweigh the effects of **competition** 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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Niche evolution

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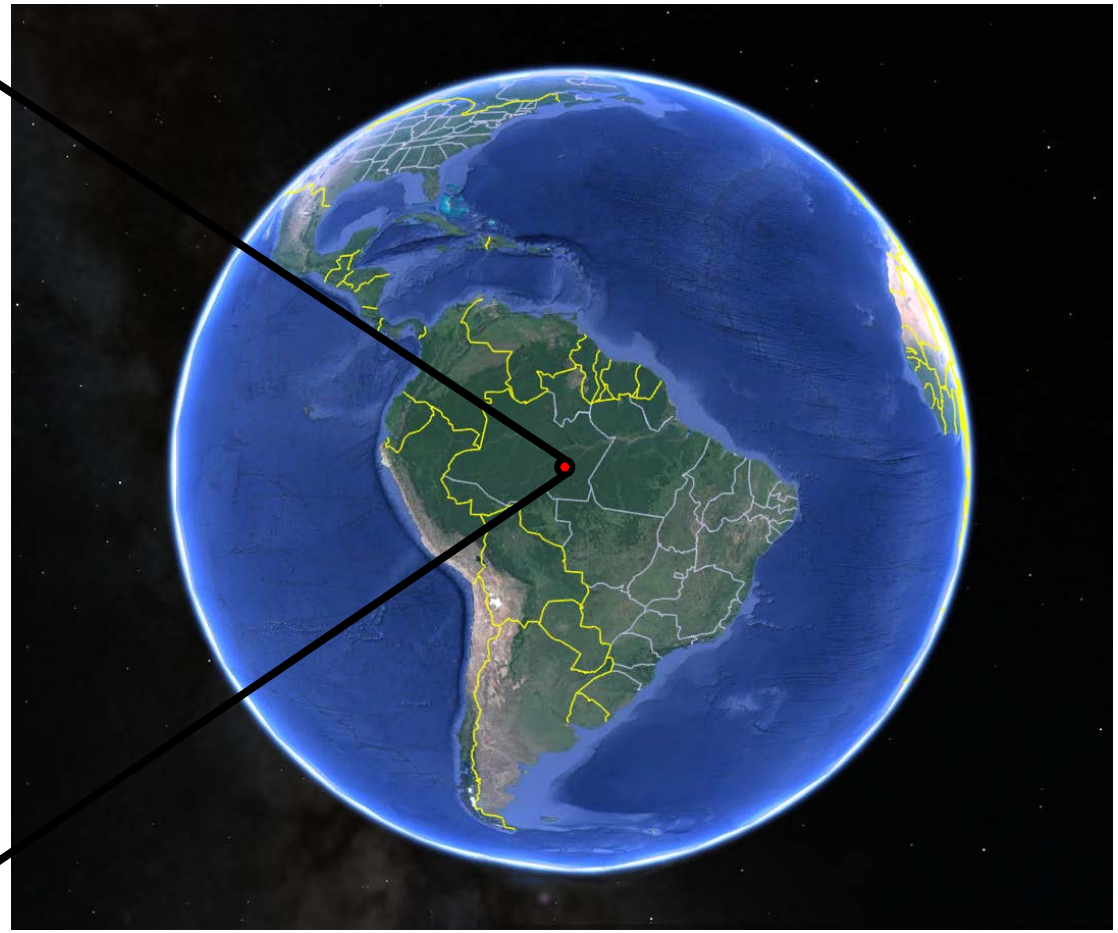
Study system: Müllerian mimicry



Credits: Google Earth

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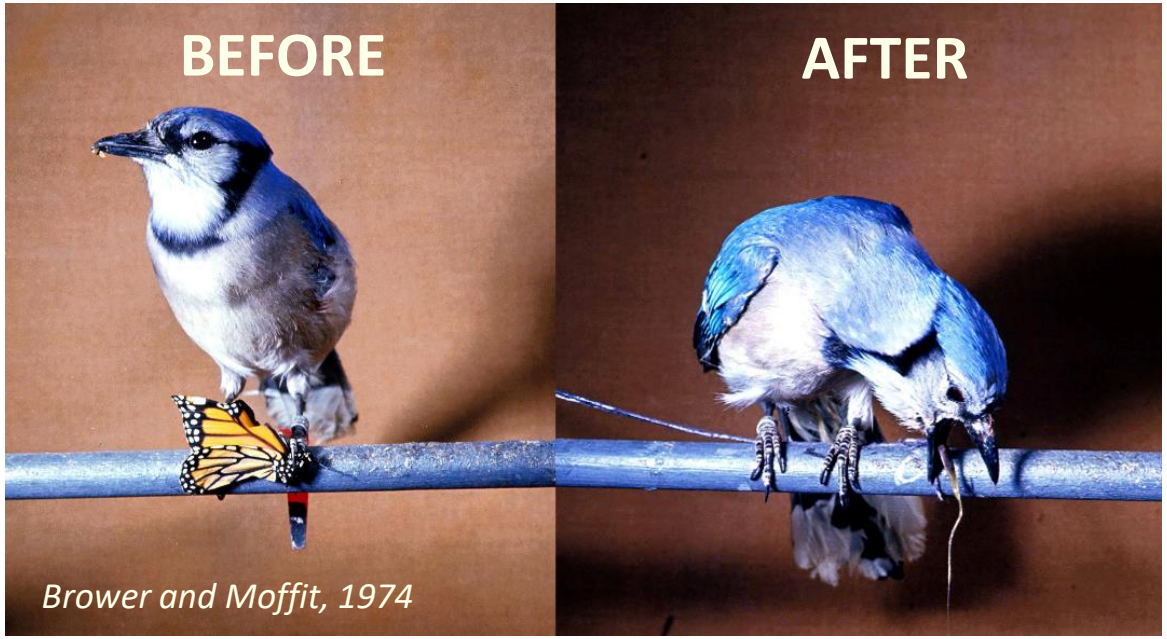

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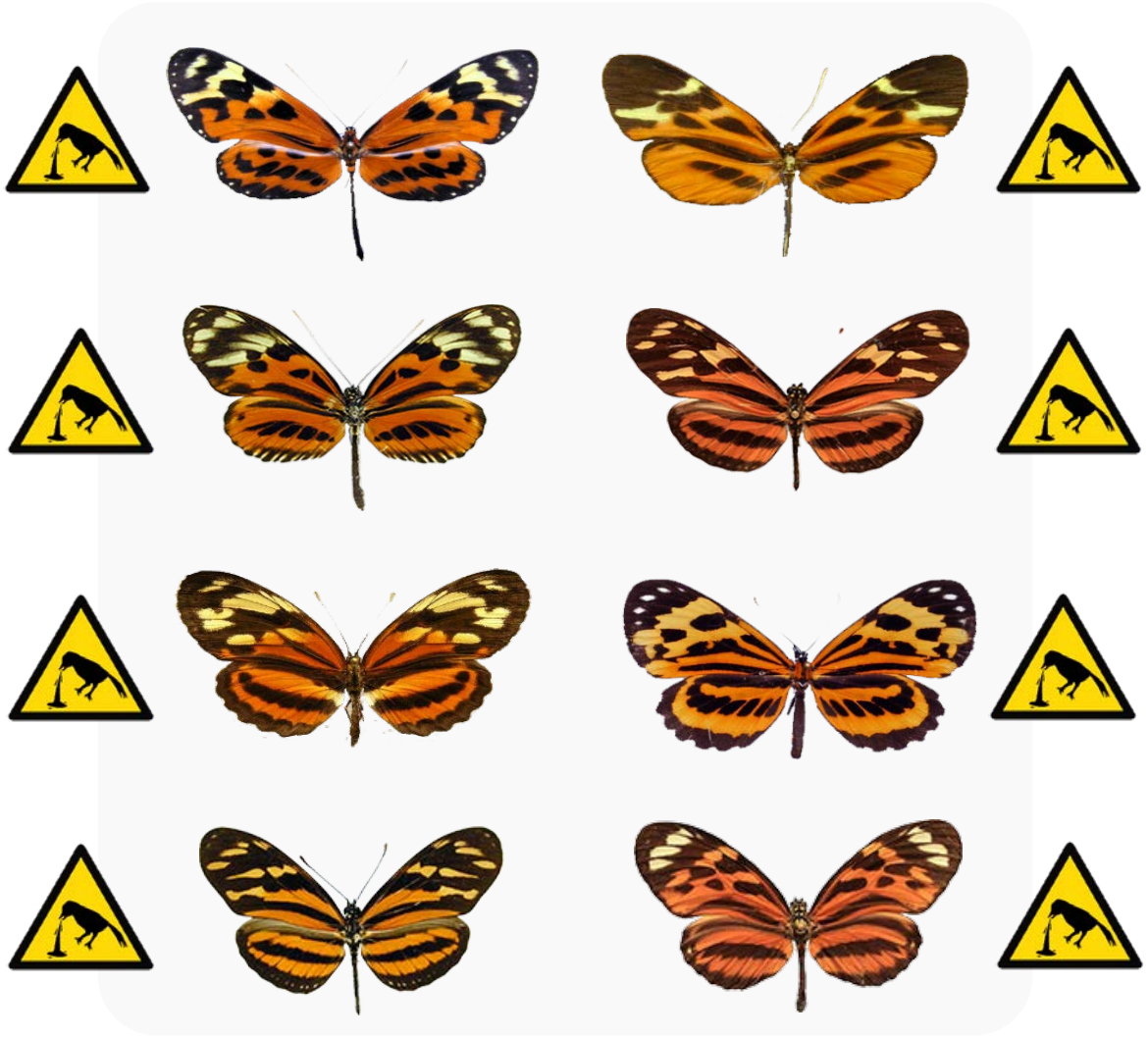
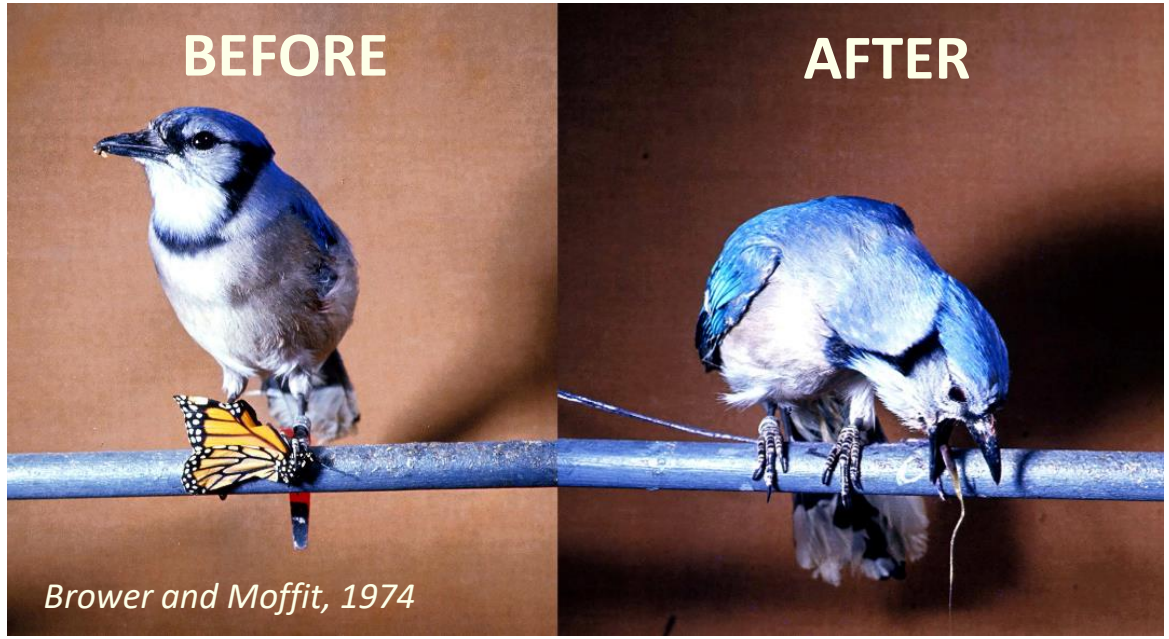




Study system: Müllerian mimicry

† 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

Fritz Müller
(1821 – 1897)

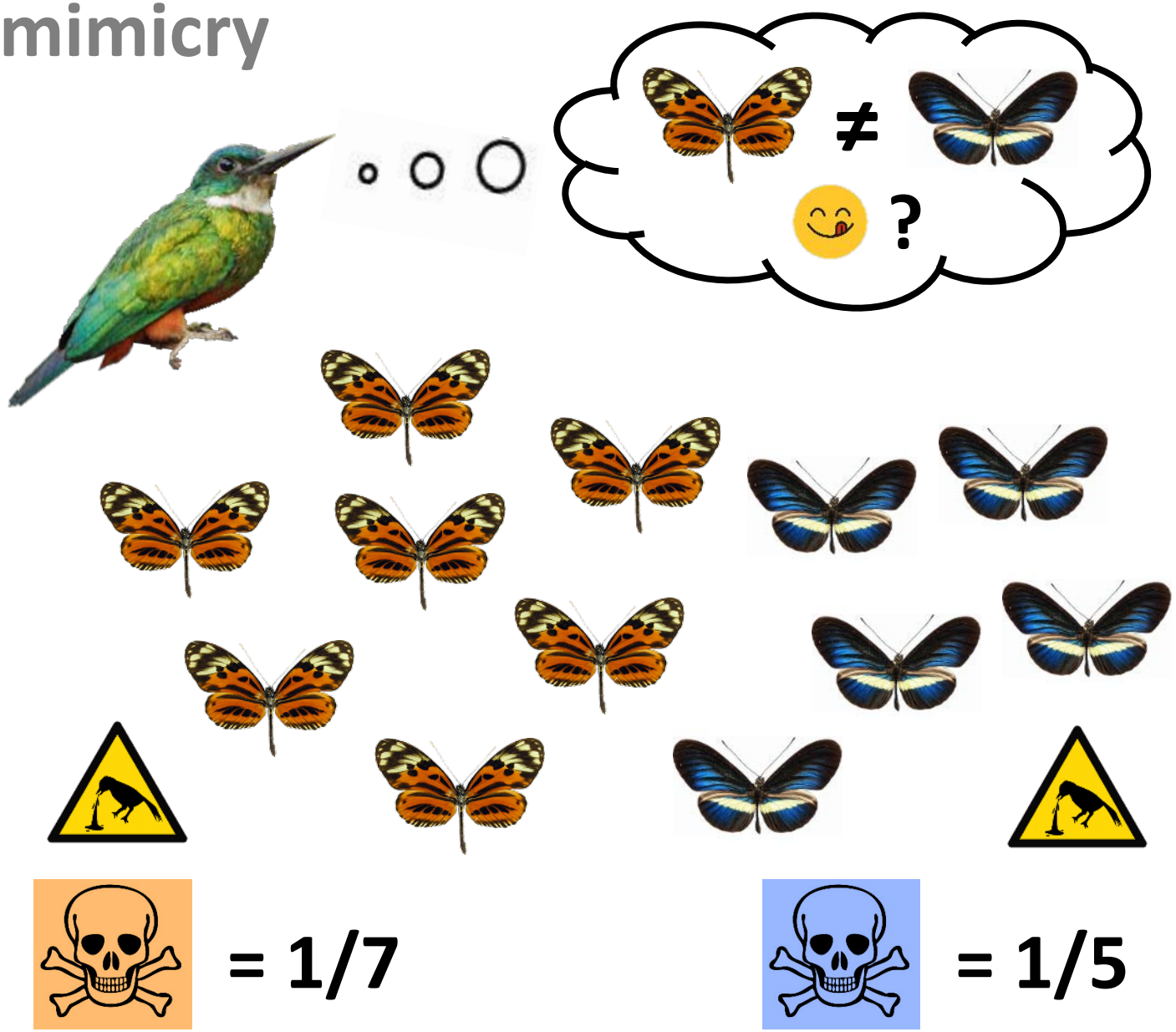
Study system: Müllerian mimicry

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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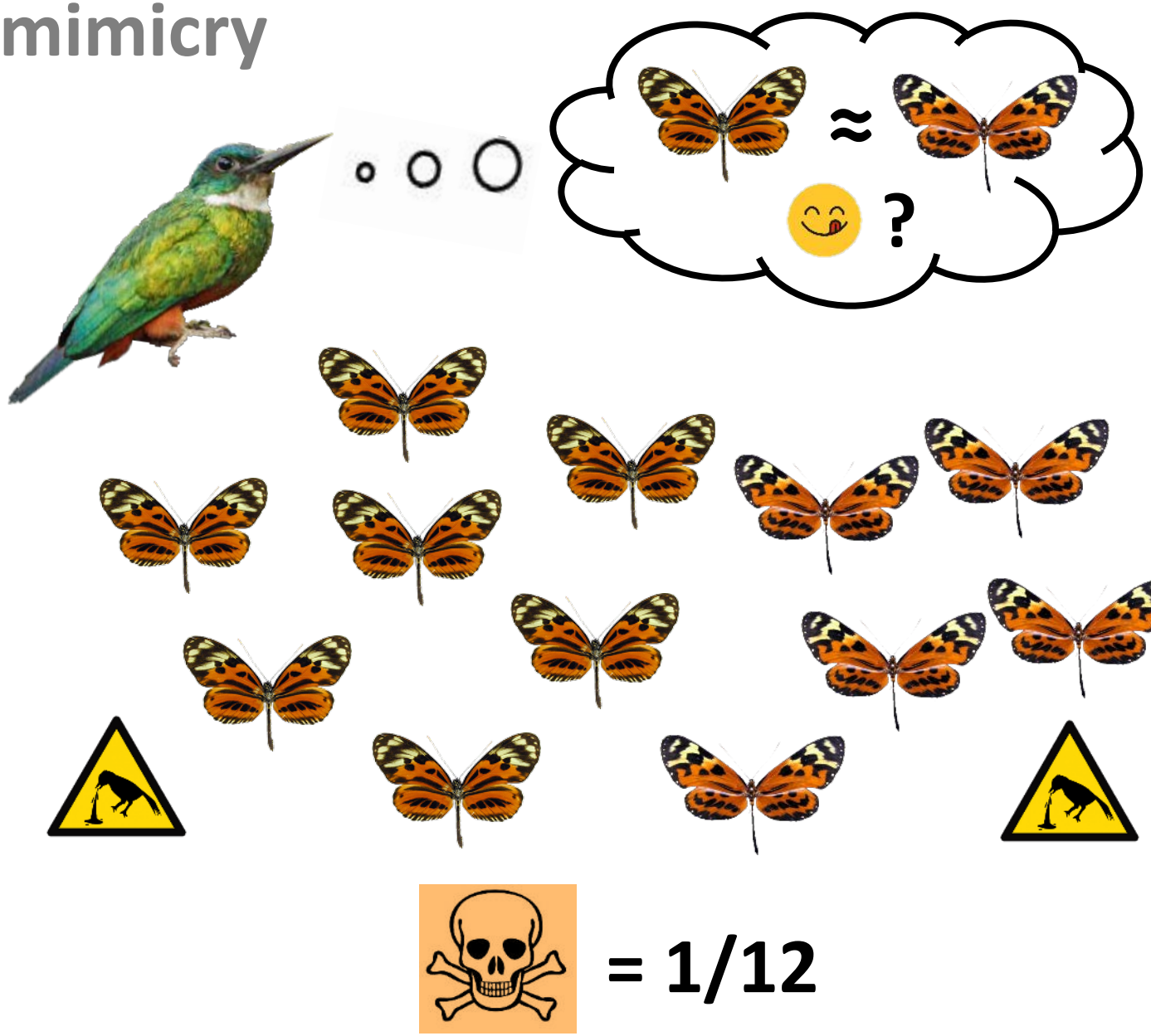

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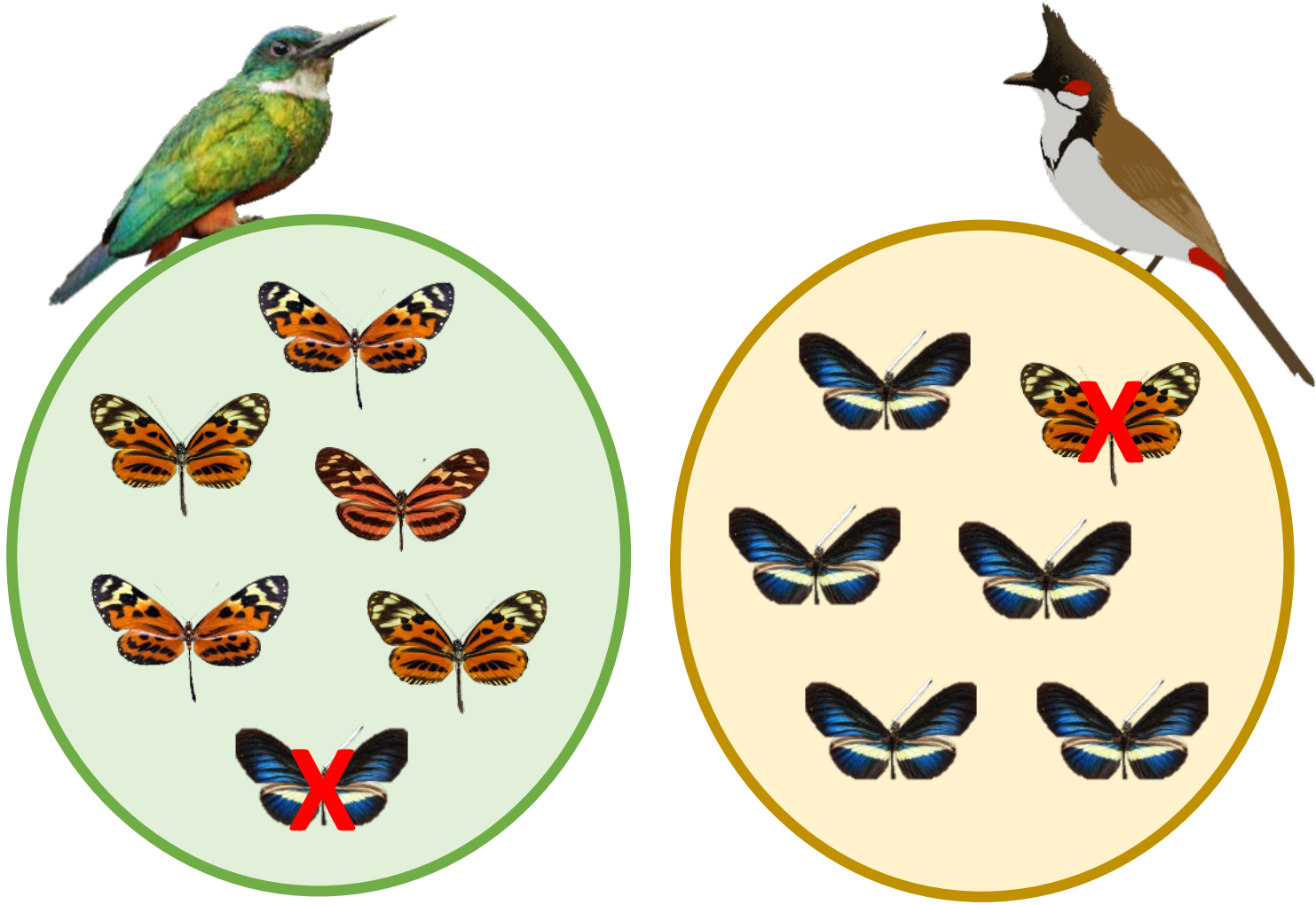


Study system: Neotropical butterflies

Mimicry

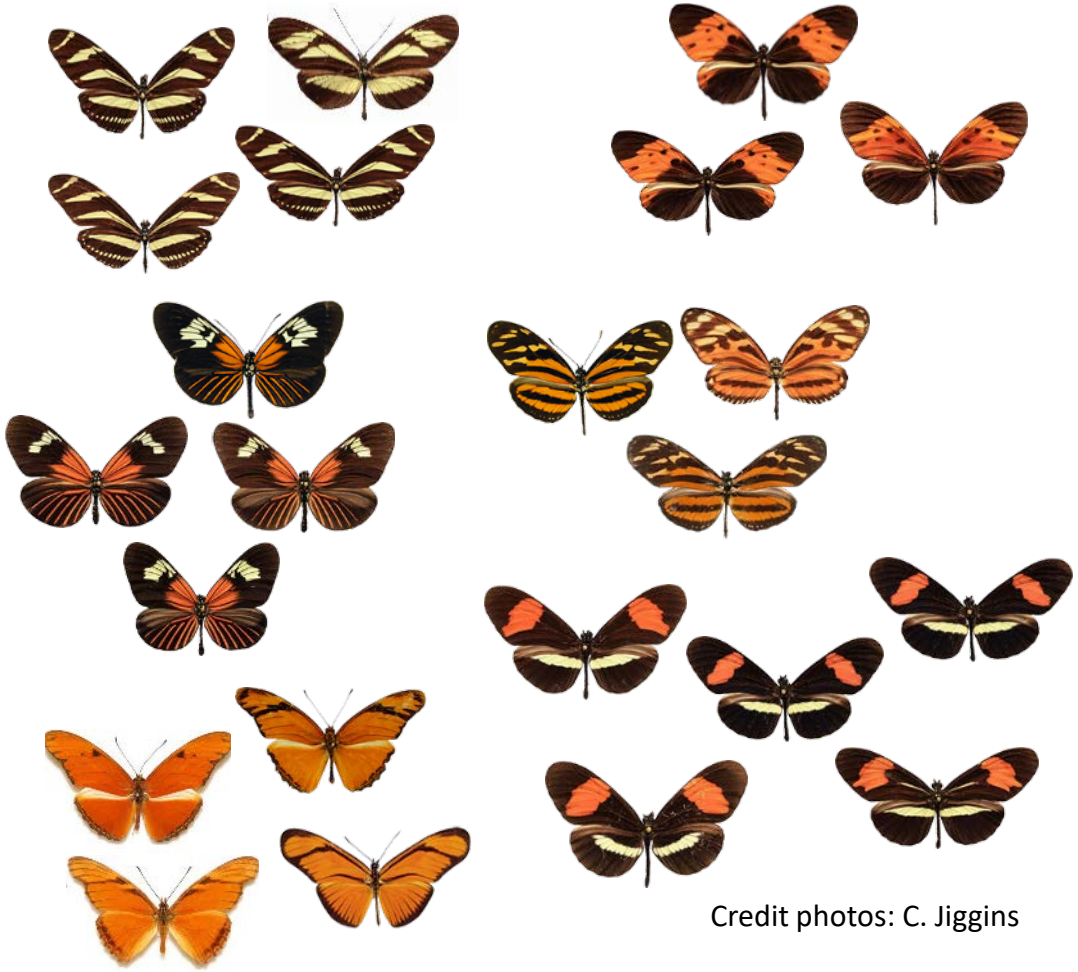
Phylogeny

Geography

Ithomiini tribe

Credit photos: N. Chazot

Heliconiini tribe



Credit photos: C. Jiggins

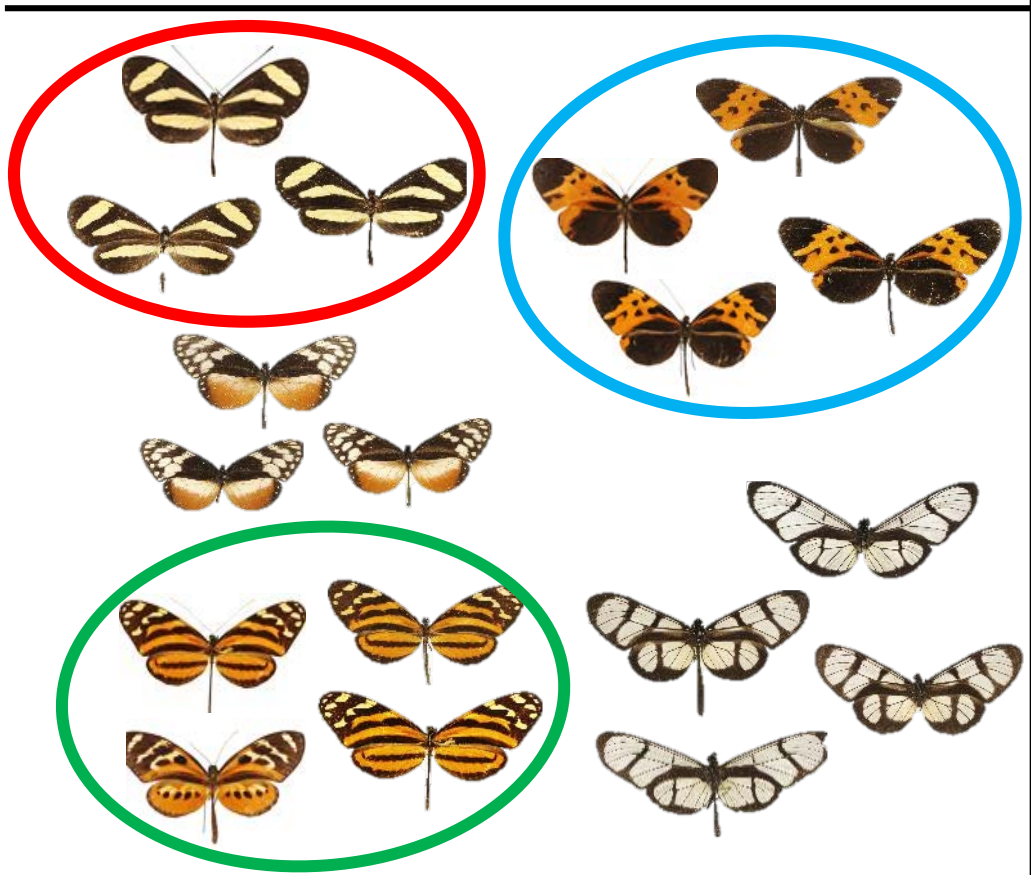
Study system: Neotropical butterflies

Ithomiini tribe | **Heliconiini tribe**

Mimicry

Phylogeny

Geography



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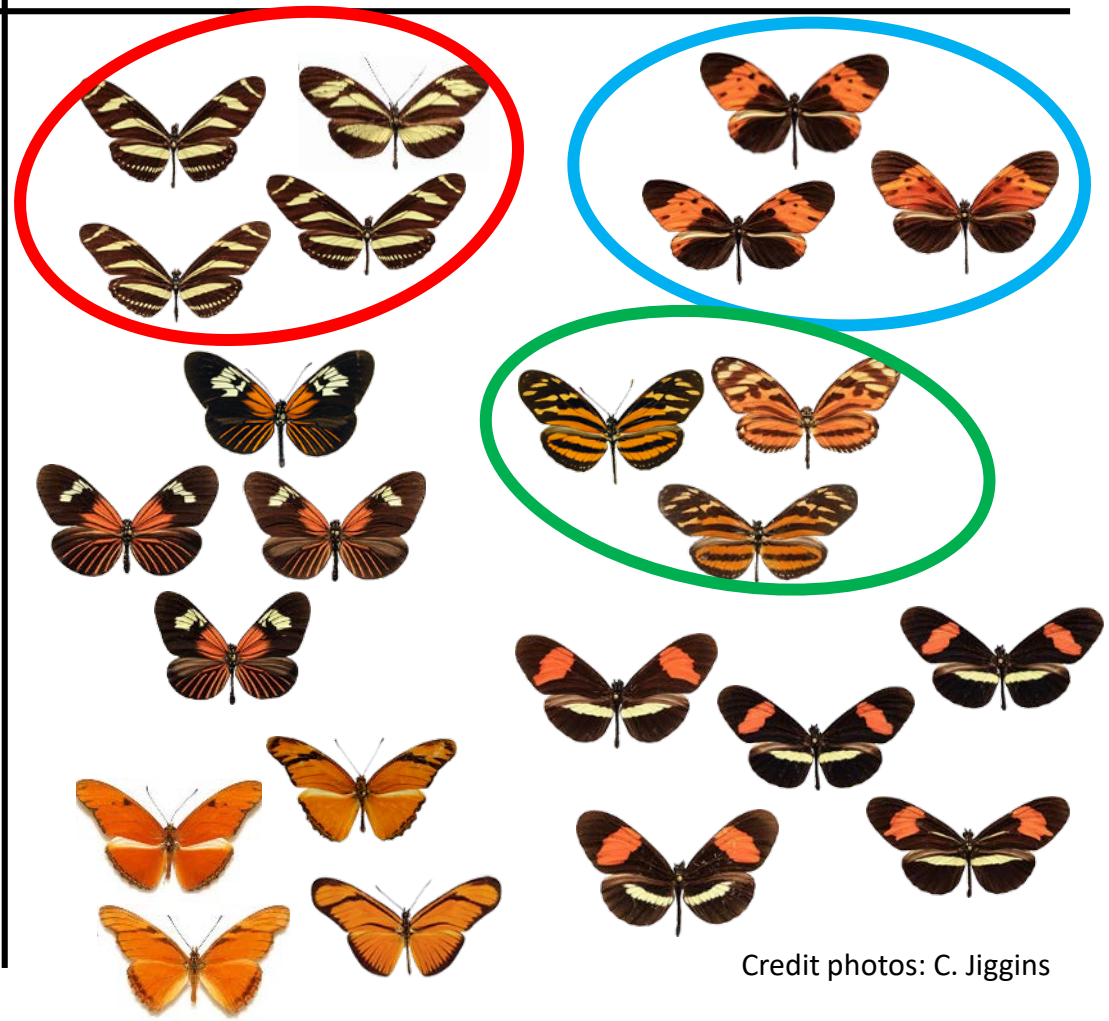

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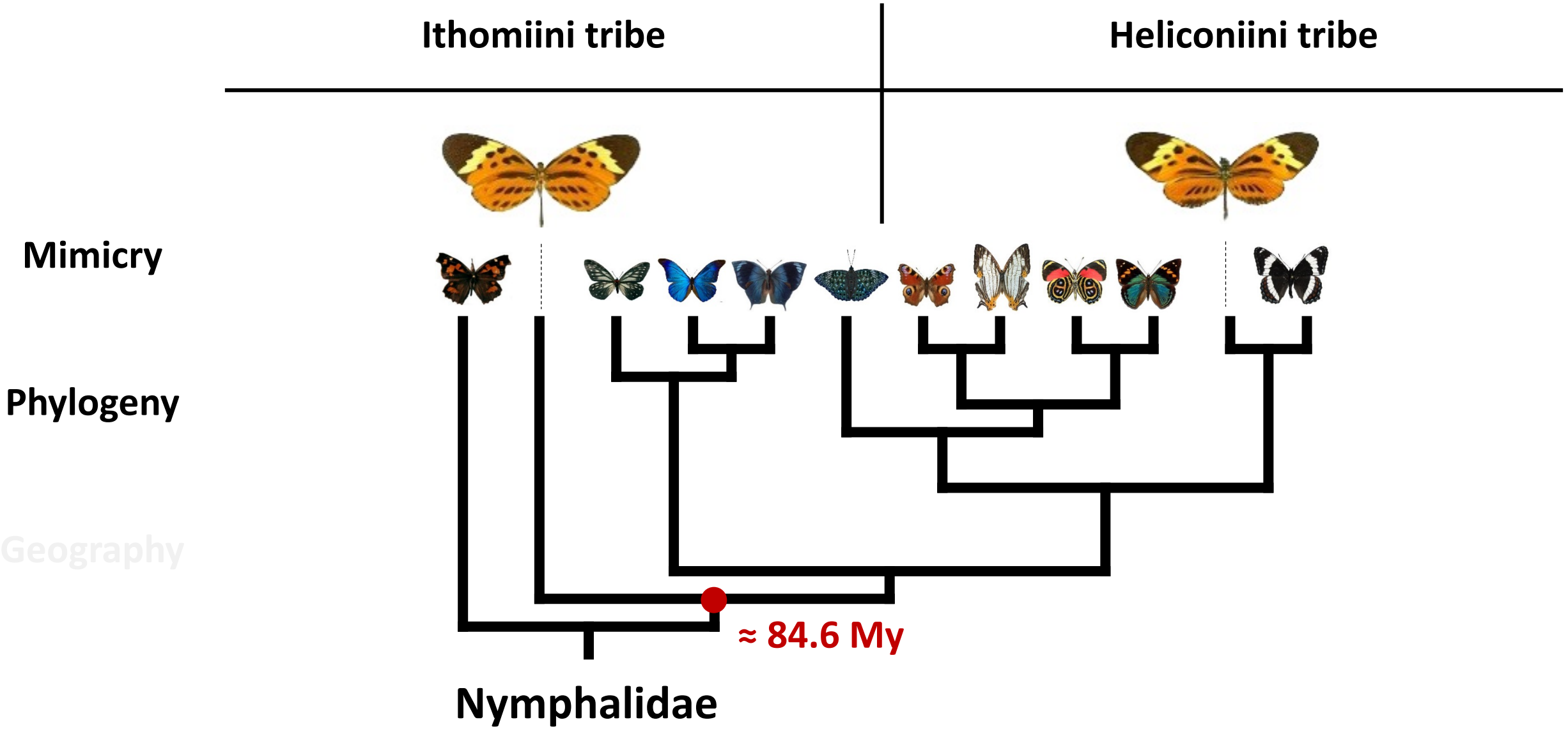

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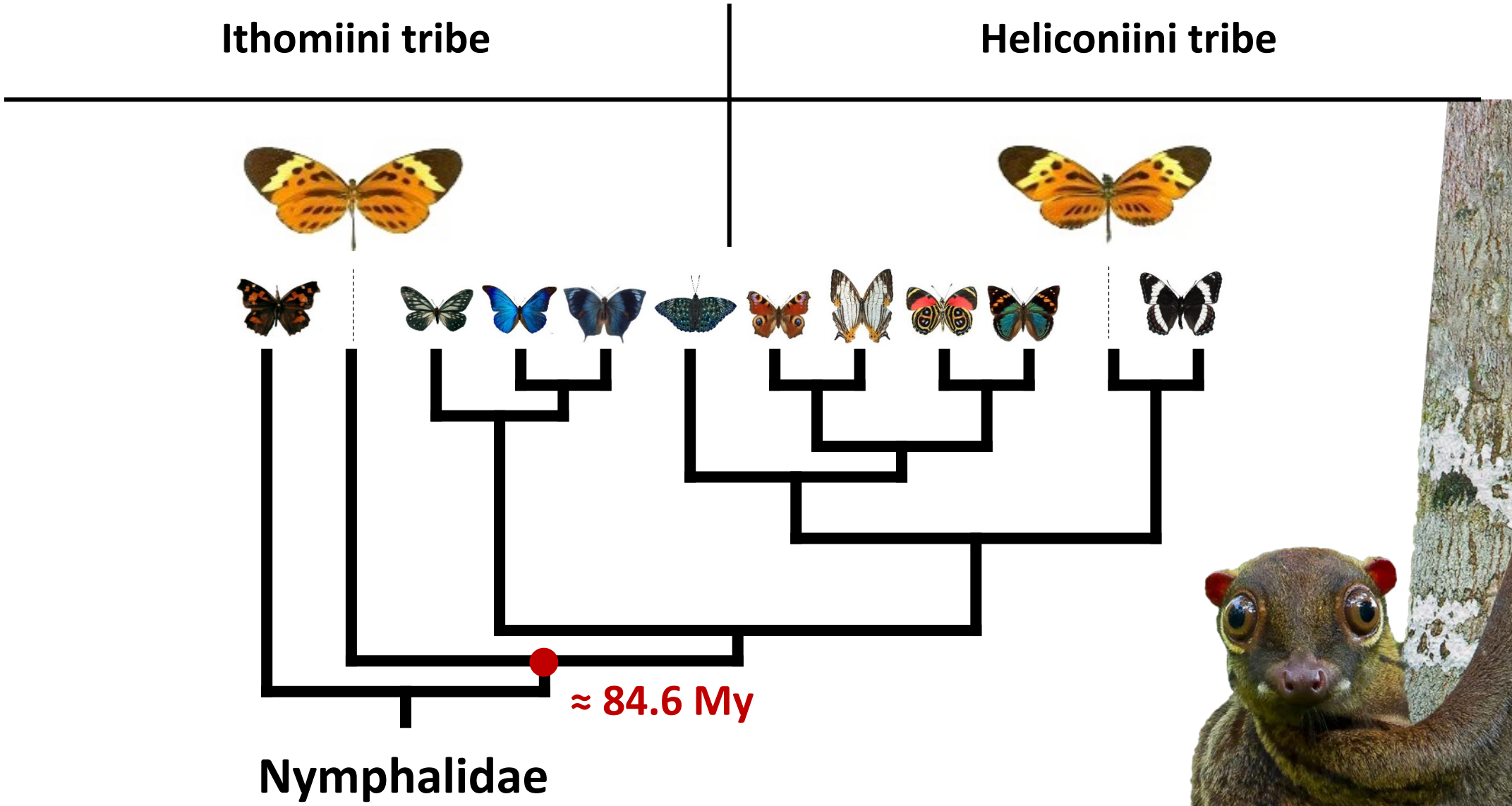
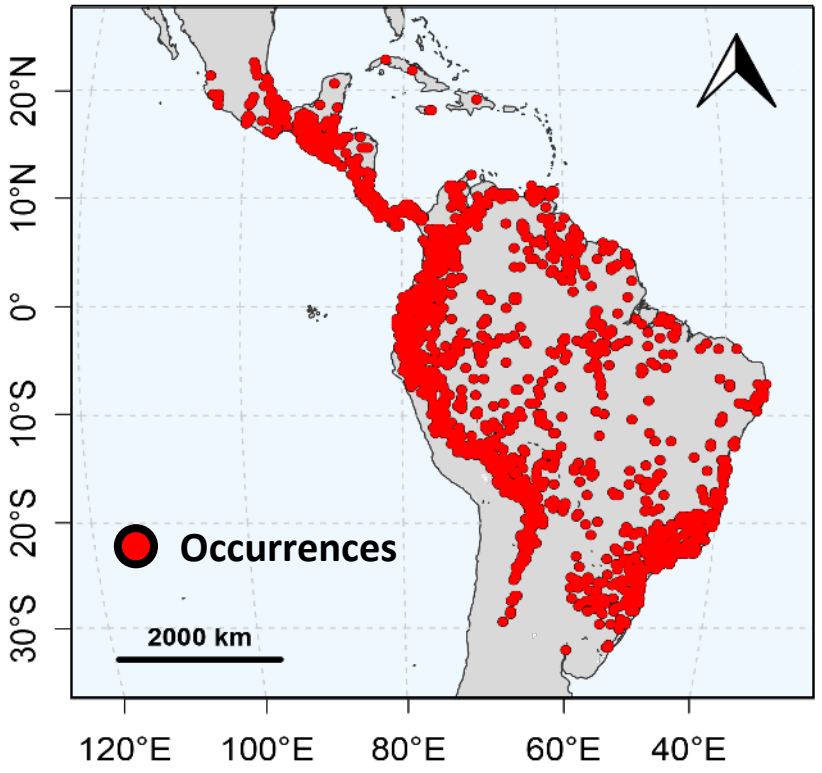
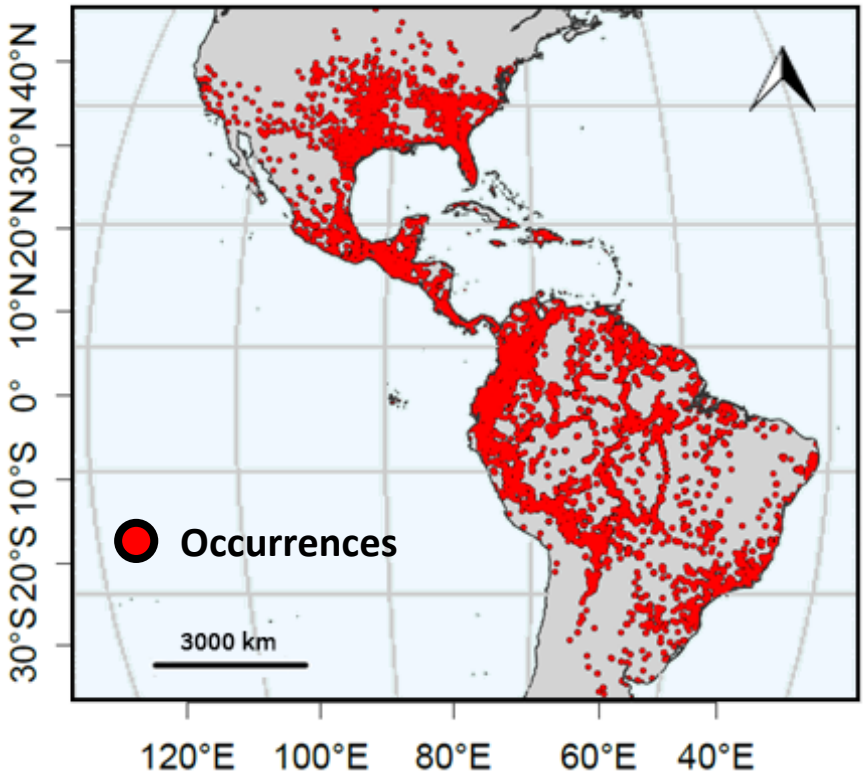


Study system: Neotropical butterflies

	Ithomiini tribe	Heliconiini tribe
Mimicry		
Phylogeny		
Geography	Occurrence map	Occurrence map



Doré et al., 2021



Perochon et al., in prep

Study system: Neotropical butterflies

Ithomiini tribe | **Heliconiini tribe**

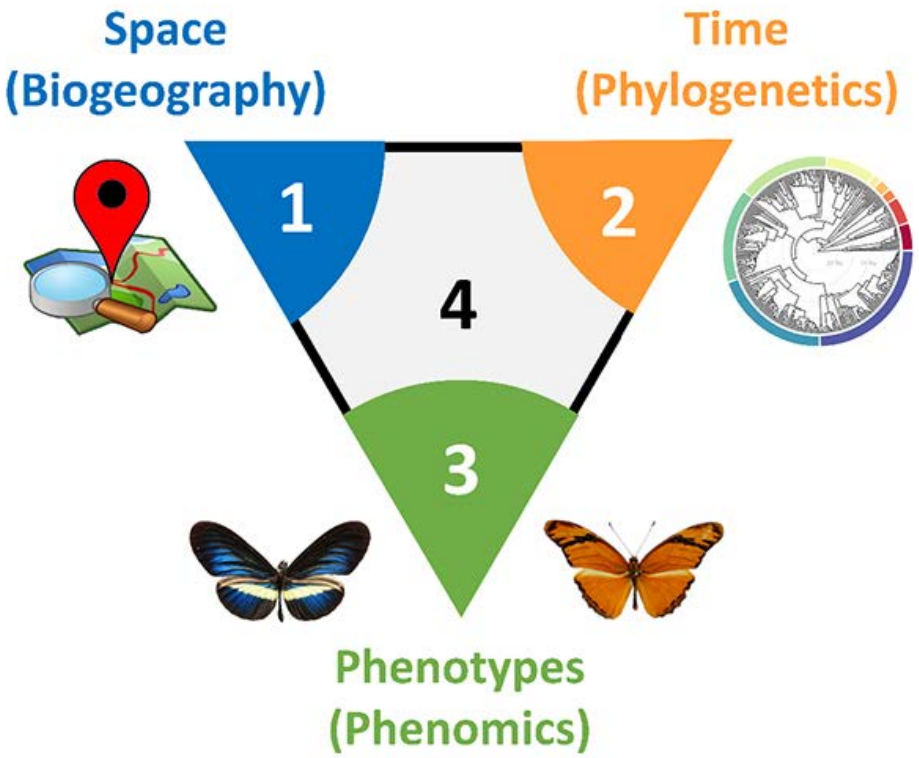
Mimicry

Phylogeny

Geography

Credit Photo: M. Chouteau

Outlines and objectives

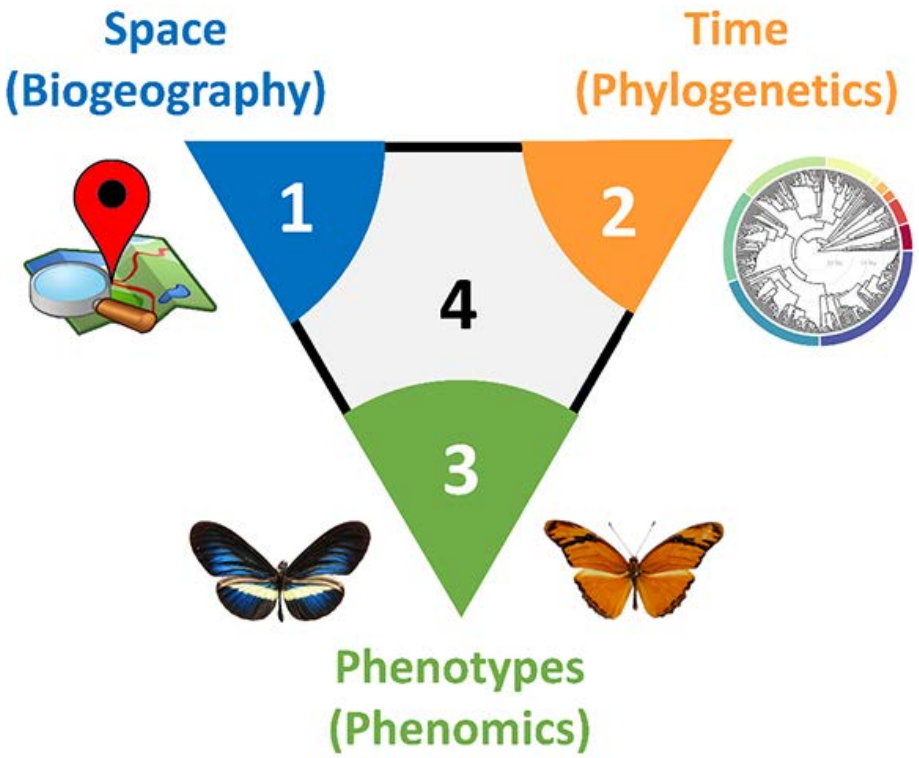


How **mutualistic interactions** affect the **structure** and **evolution** of biodiversity at the **macroecological scale**?

Outlines and objectives

CHAPTER 1

Map **biodiversity patterns**



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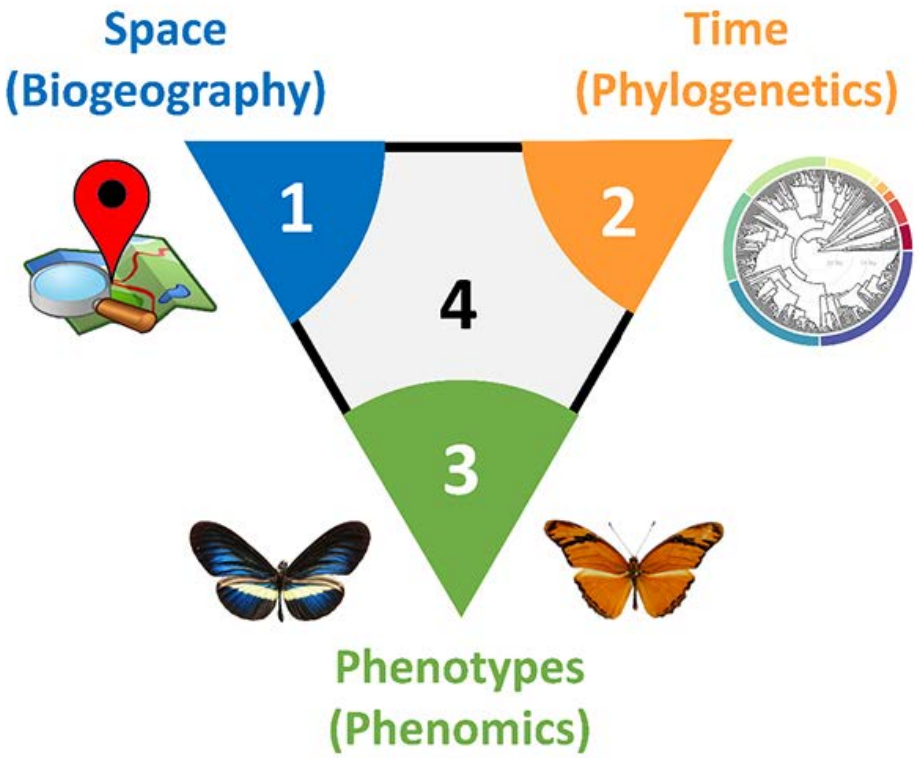

CHAPTER 2

Resolve **deep evolutionary relationships**

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

Outlines and objectives

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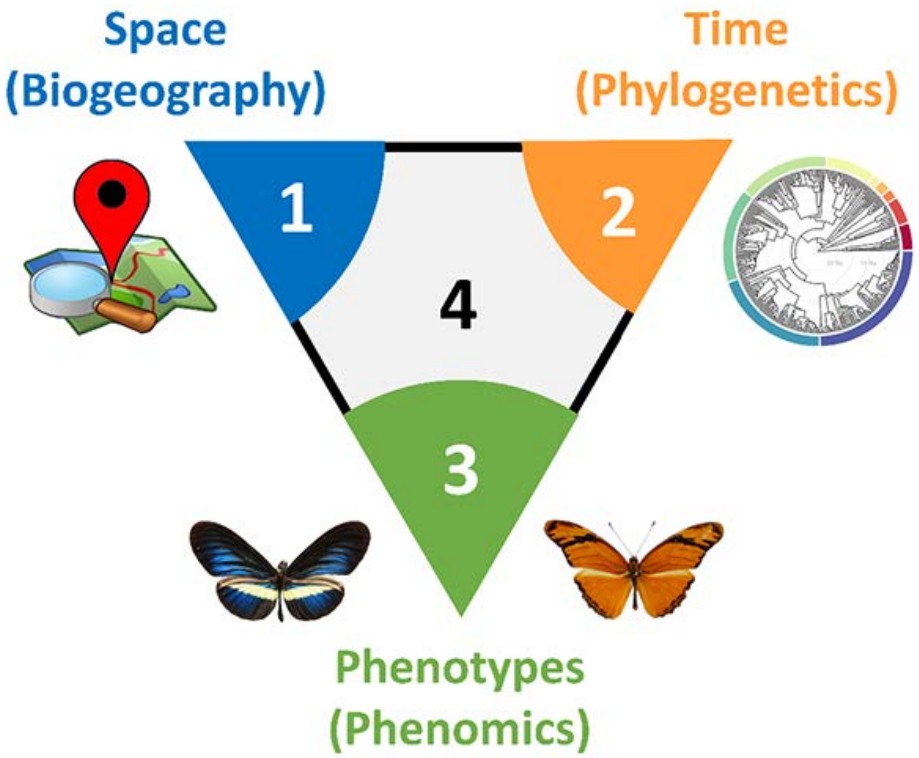

CHAPTER 2

Resolve **deep evolutionary relationships**

CHAPTER 3

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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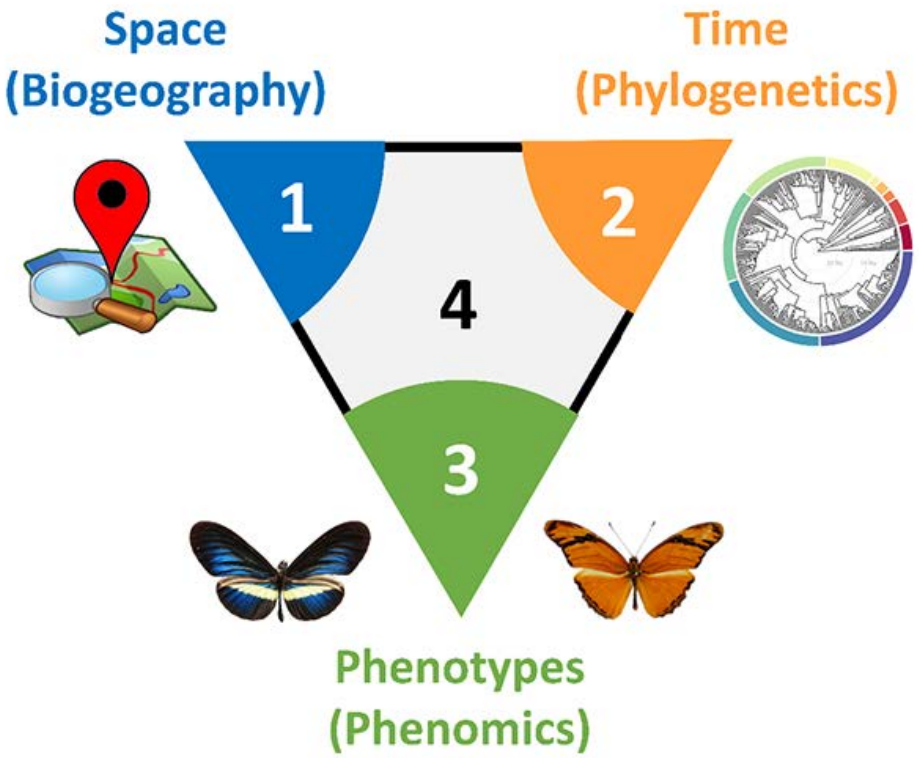
Map **biodiversity patterns**



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CHAPTER 1: Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group

CHAPTER 1

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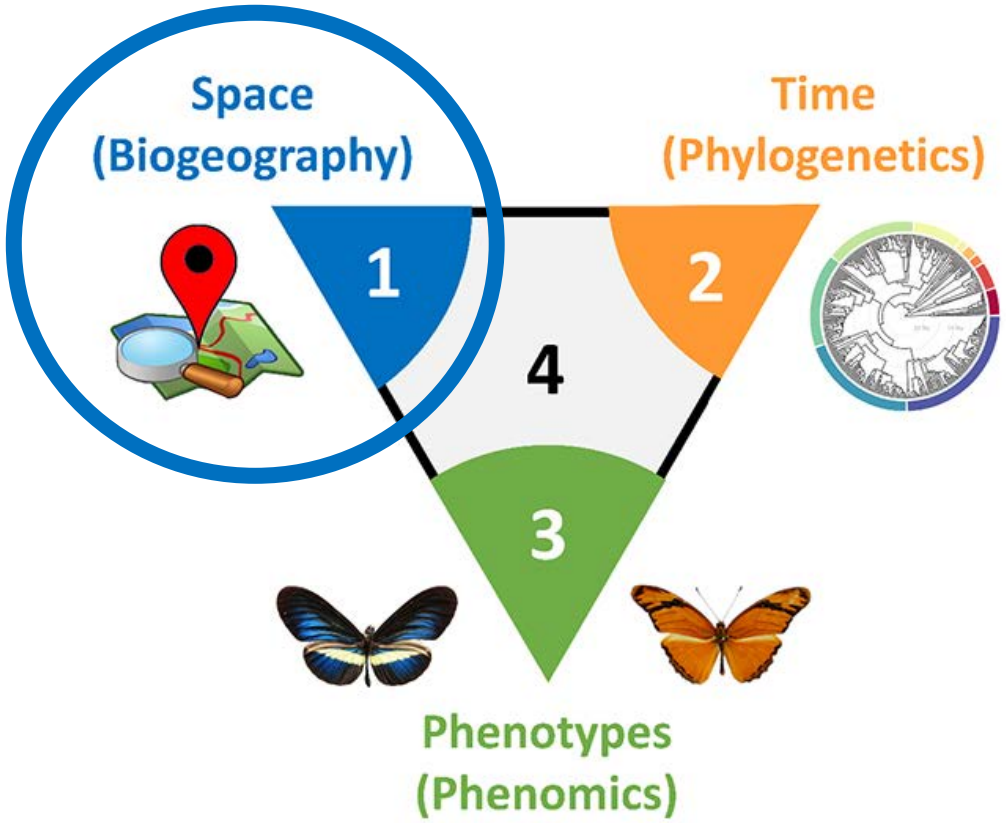

Reference:

Doré, M., Willmott, K., Leroy, B., Chazot, N., Mallet, J., Freitas, A. V. L., Hall, J. P. W., Lamas, G., Dasmahapatra, K. K., Fontaine, C., & Elias, M. (2022). Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. *Diversity and Distributions*, 28(12), 2912–2930. https://doi.org/10.1111/ddi.13455

CHAPTER 1: Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group

CHAPTER 1

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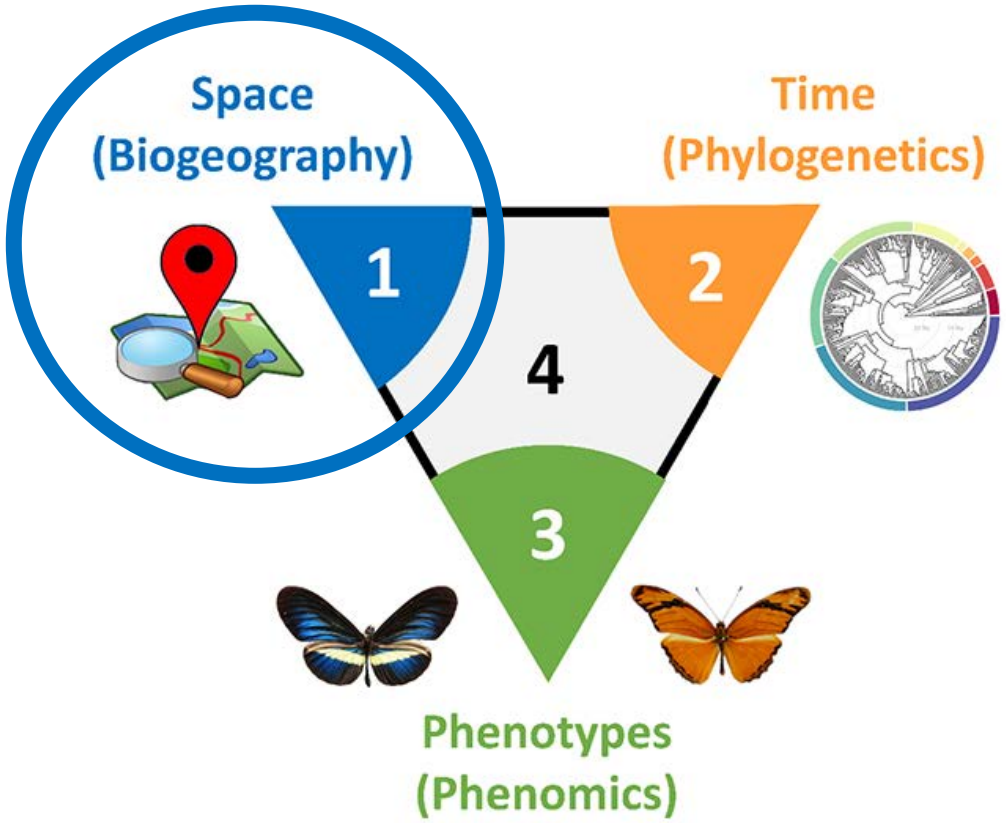


Stage M2: Heliconiini

Eddie Pérochon

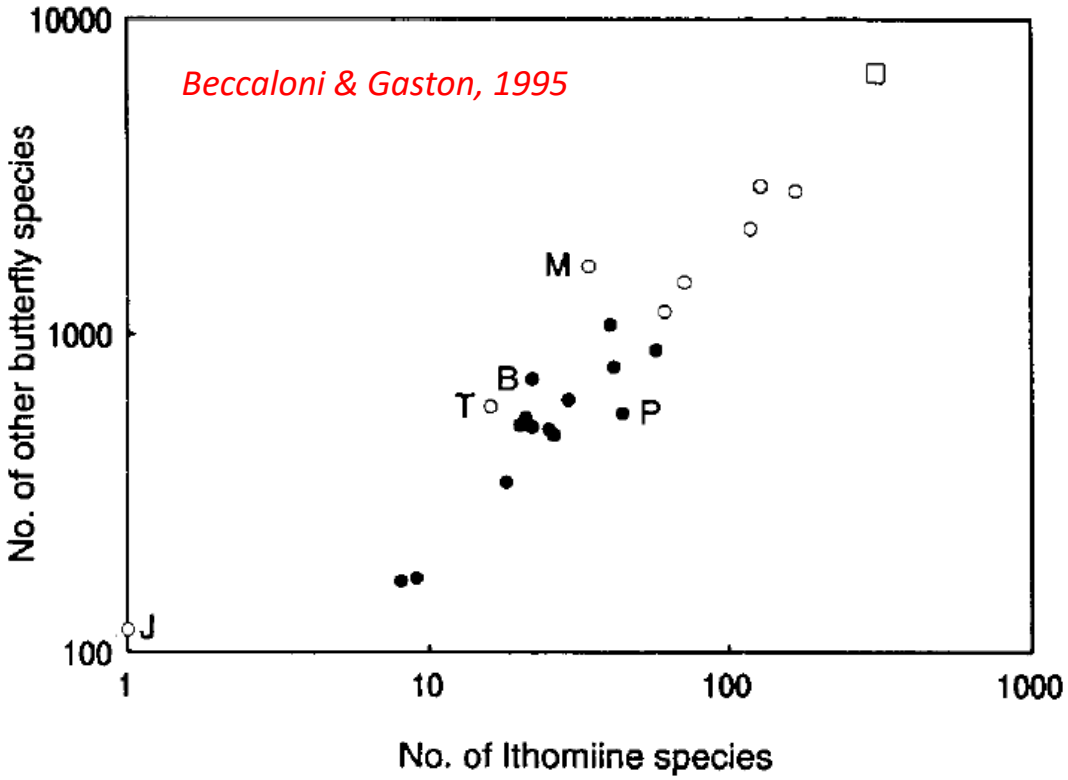
Reference:

Doré, M., Willmott, K., Leroy, B., Chazot, N., Mallet, J., Freitas, A. V. L., Hall, J. P. W., Lamas, G., Dasmahapatra, K. K., Fontaine, C., & Elias, M. (2022). Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. *Diversity and Distributions*, 28(12), 2912–2930. https://doi.org/10.1111/ddi.13455

Context & Objectives

Ithomiini as **indicator species**

- For **forest habitat quality**
  (Brown Jr 1997; Uehara-Prado & Freitas 2009)
- For overall **butterfly diversity**
  (Beccaloni & Gaston, 1995)



Objectives

1/ Map **biodiversity patterns** for ithomiine (and heliconiine)

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

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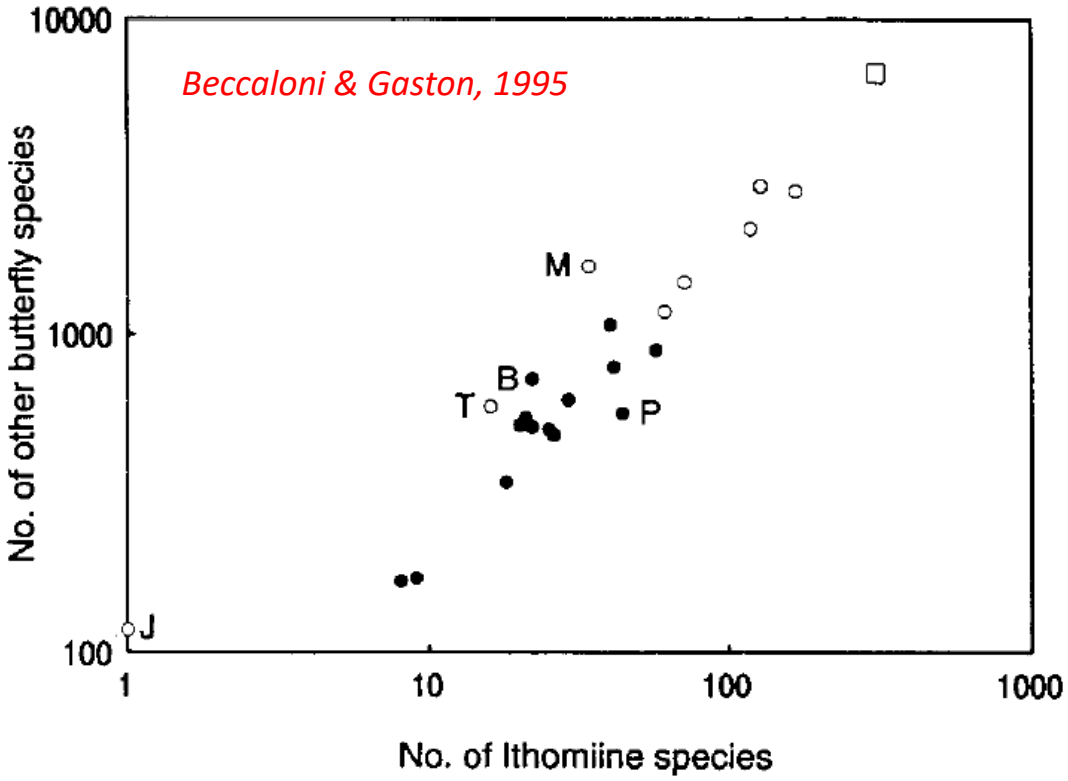

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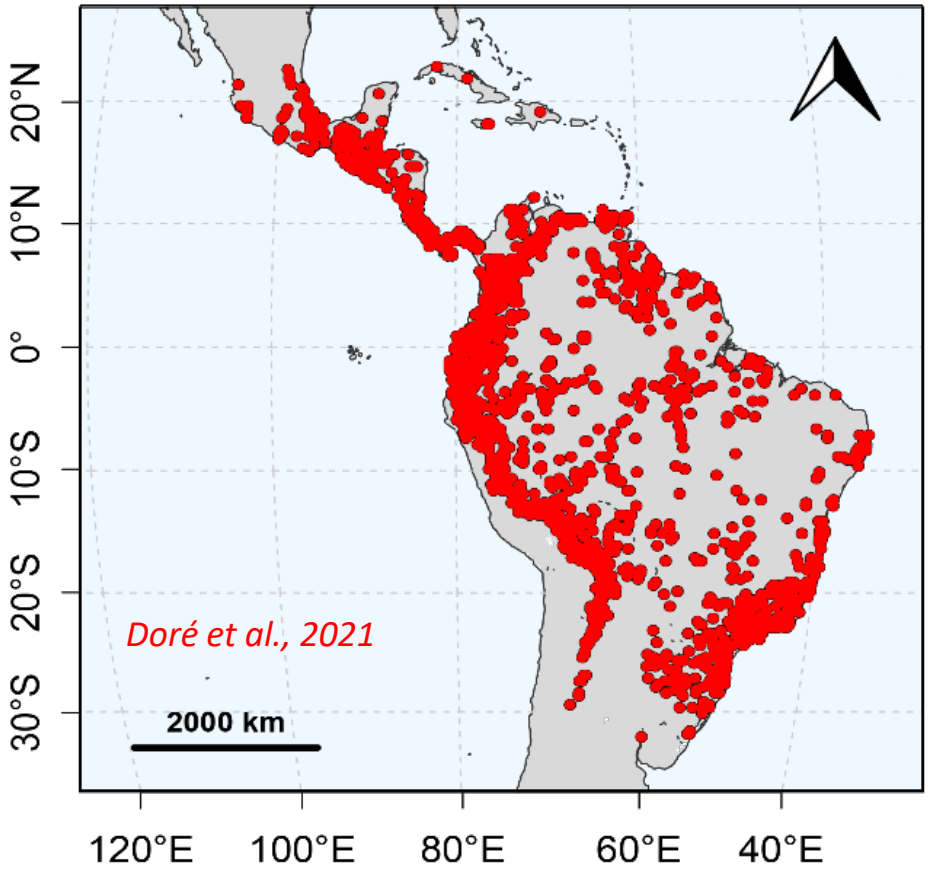
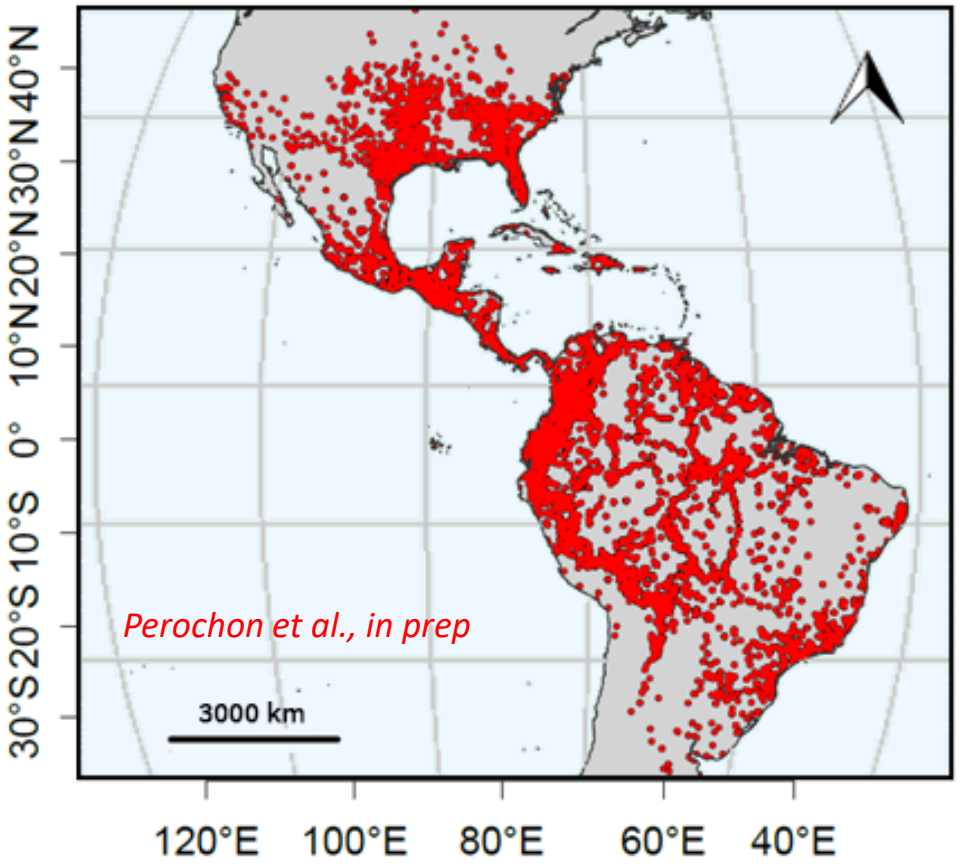
Available data

Ithomiini tribe



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

Heliconiini tribe



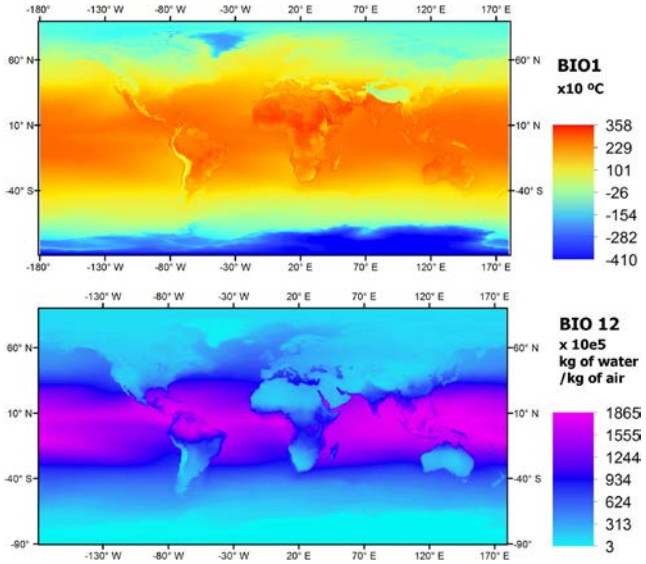
77,577 occurrences across **4,168 sites**

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

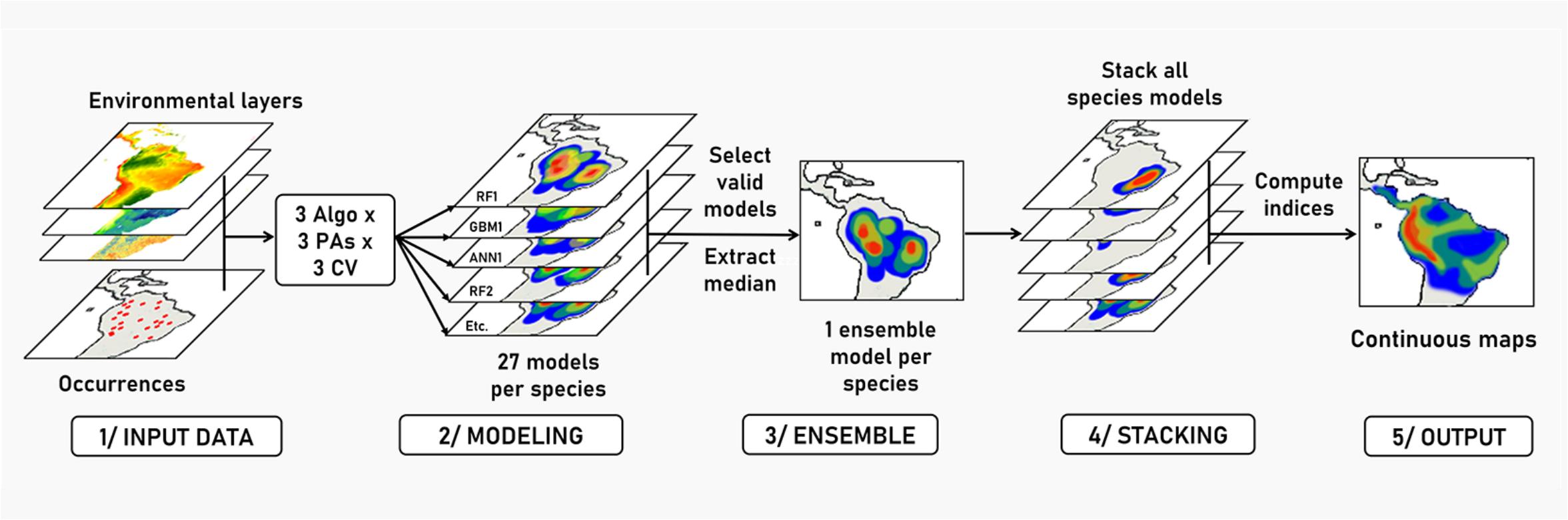
Farr et al., 2007

Vegetation cover

GFCC v.3.0

Sexton et al., 2013

Species Distribution Modeling (SDM)

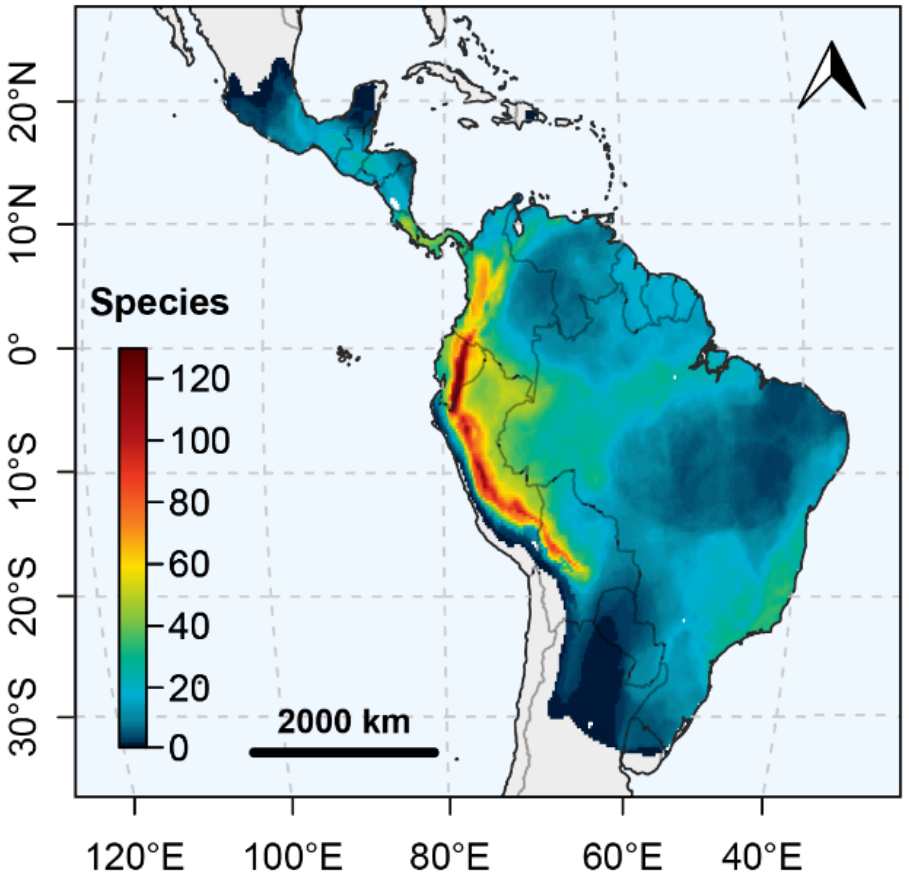


SDM → Species distribution maps → Diversity indices

Biodiversity patterns

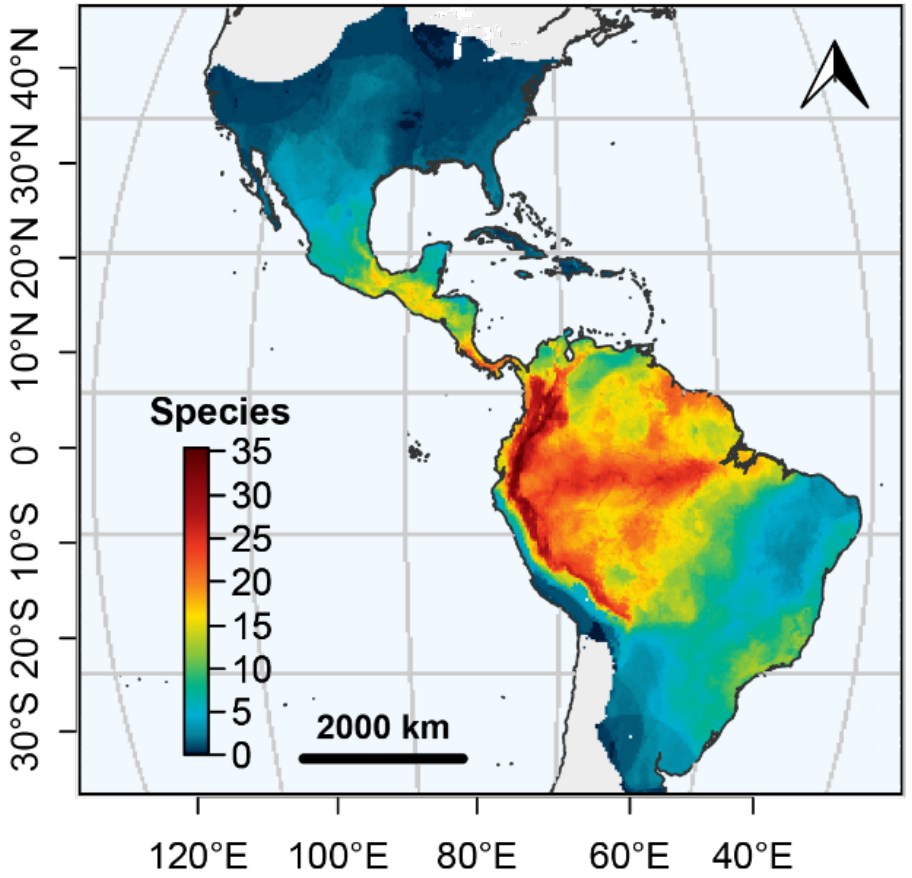
Species richness

Ithomiini



Doré et al., 2021

Heliconiini

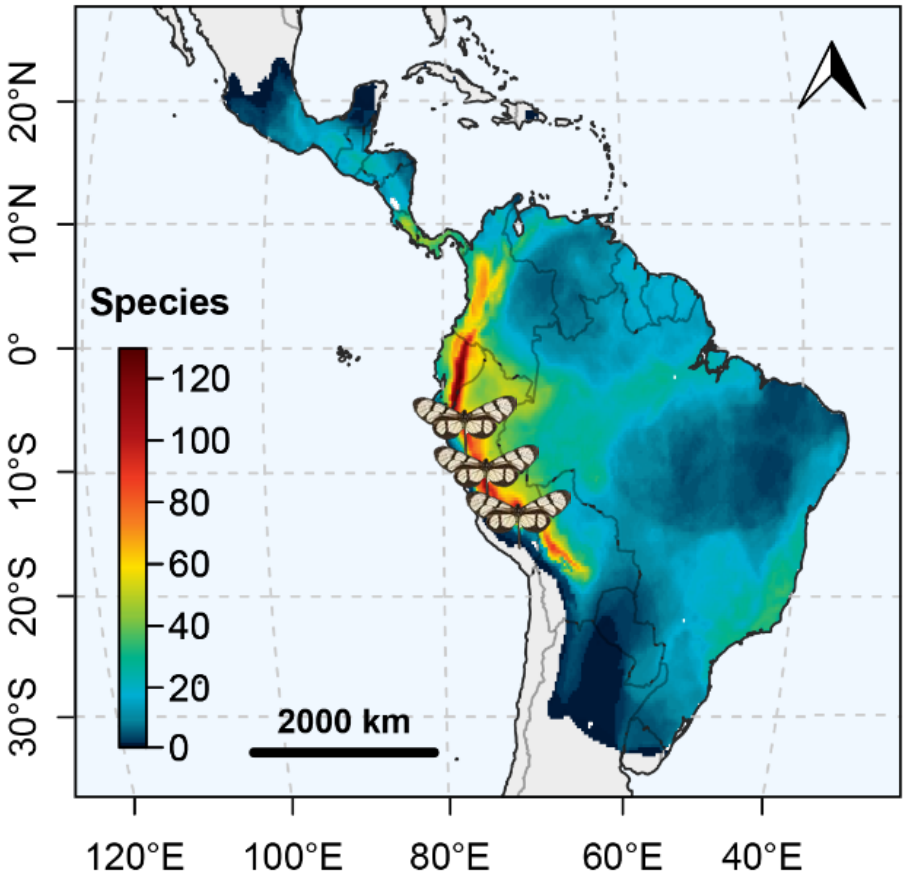


Pérochon et al., in prep

Biodiversity patterns

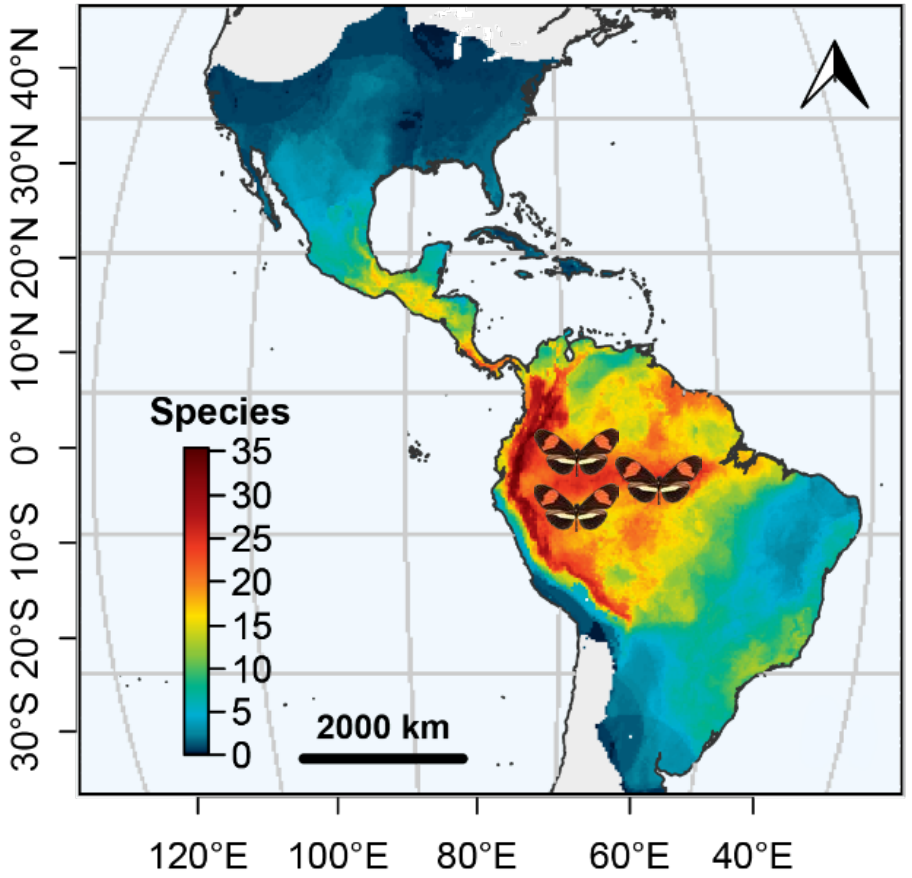
Species richness

Ithomiini



Doré et al., 2021

Heliconiini

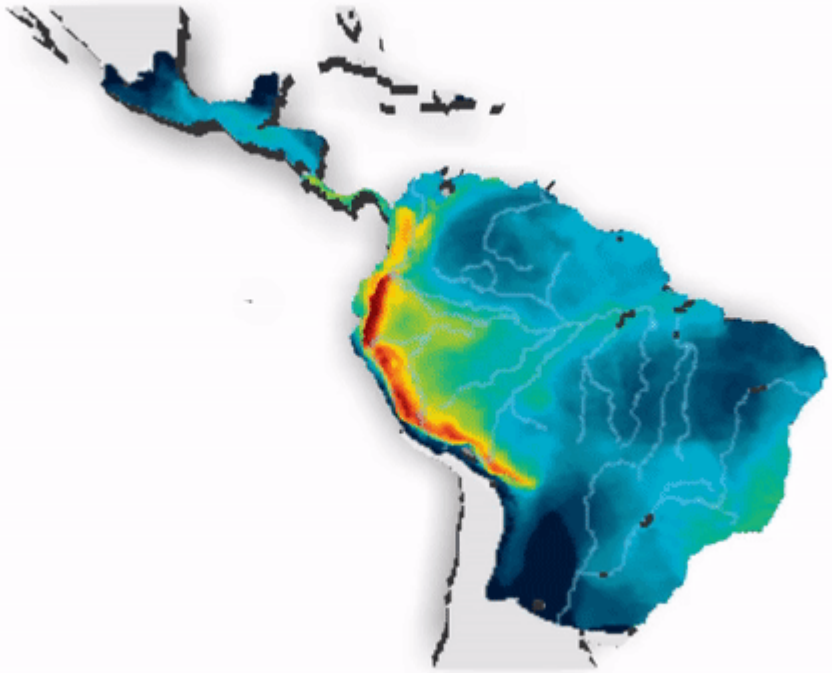


Pérochon et al., in prep

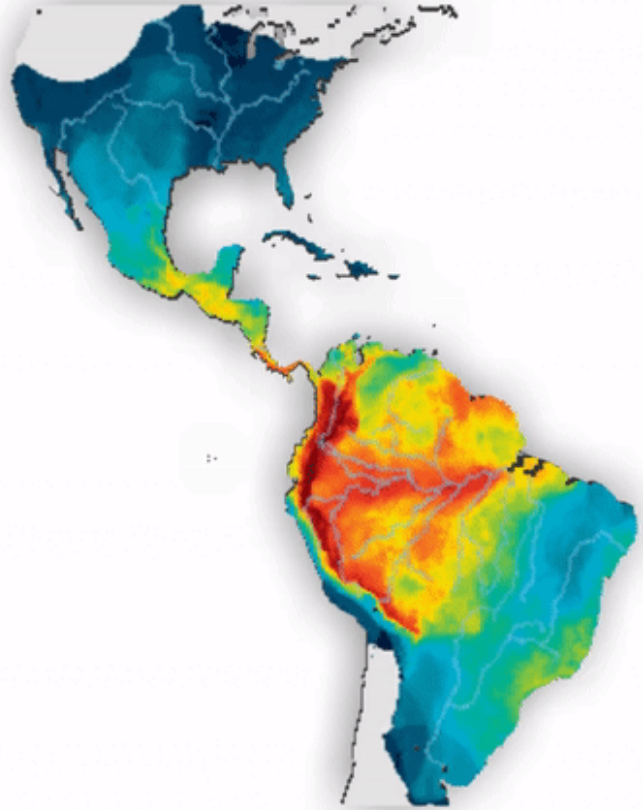
Biodiversity patterns

Species richness

Ithomiini



Heliconiini



Anthropogenic threats

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

Current anthropogenic threats
≈
Human Footprint

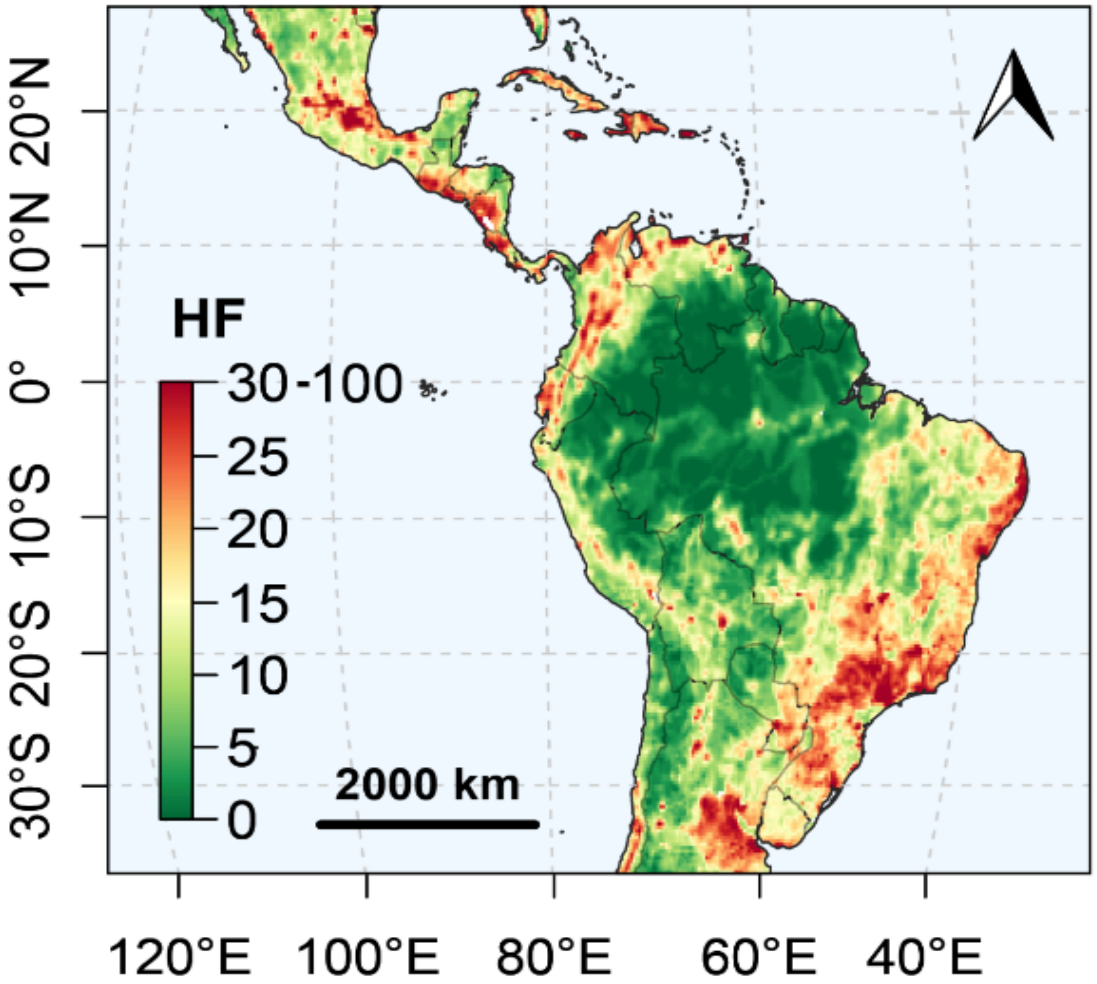
(1) Human population density

(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**

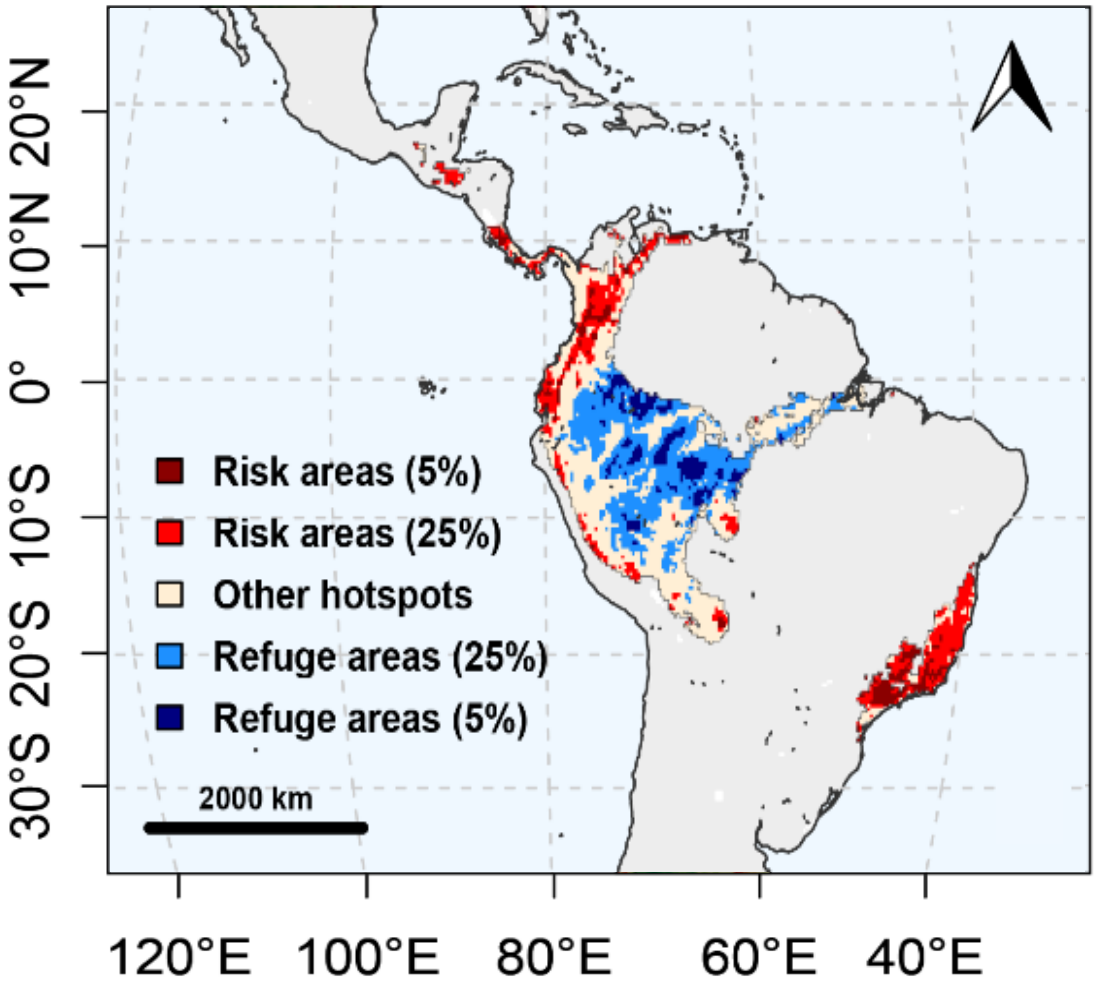
Current anthropogenic threats
≈
Human Footprint

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., 2021

Anthropogenic threats

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Current anthropogenic threats
≈
Human Footprint

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

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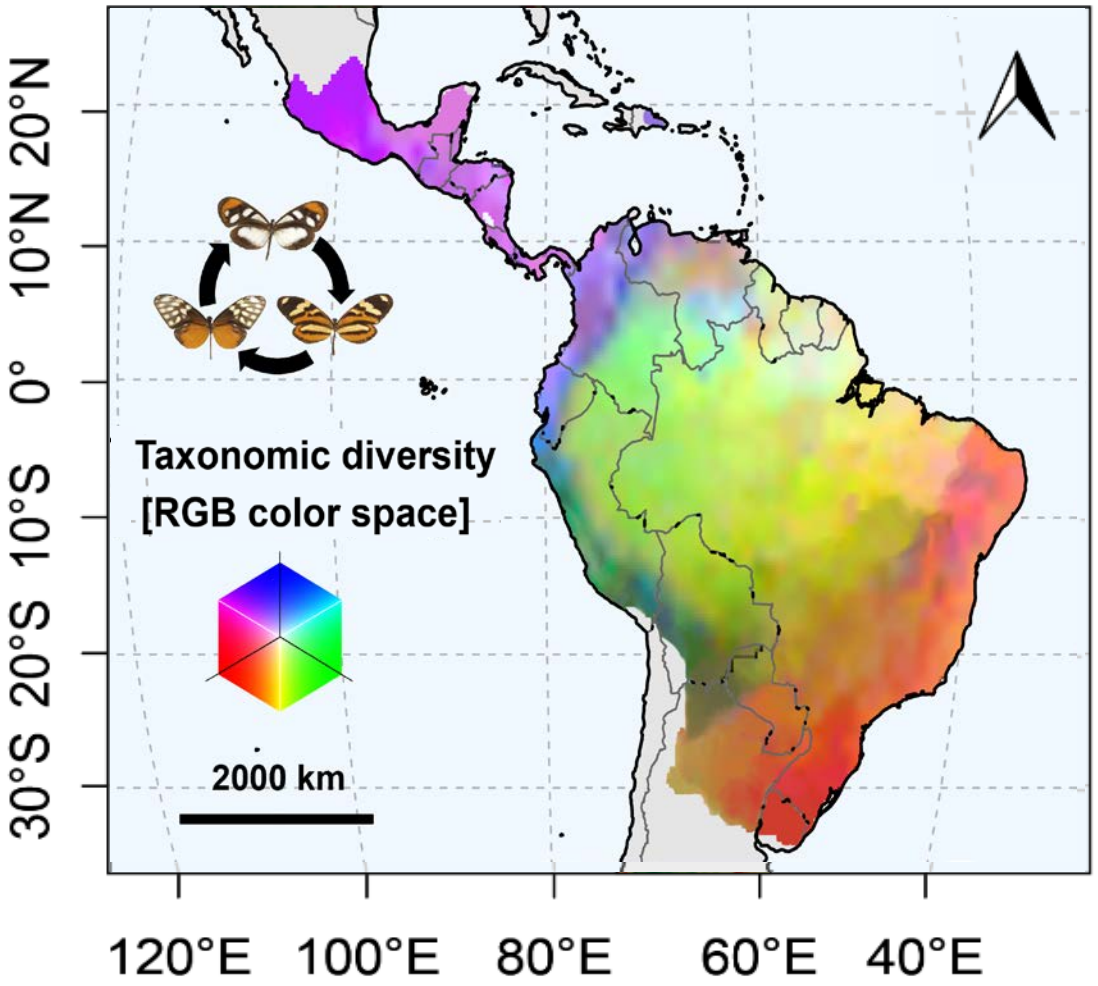
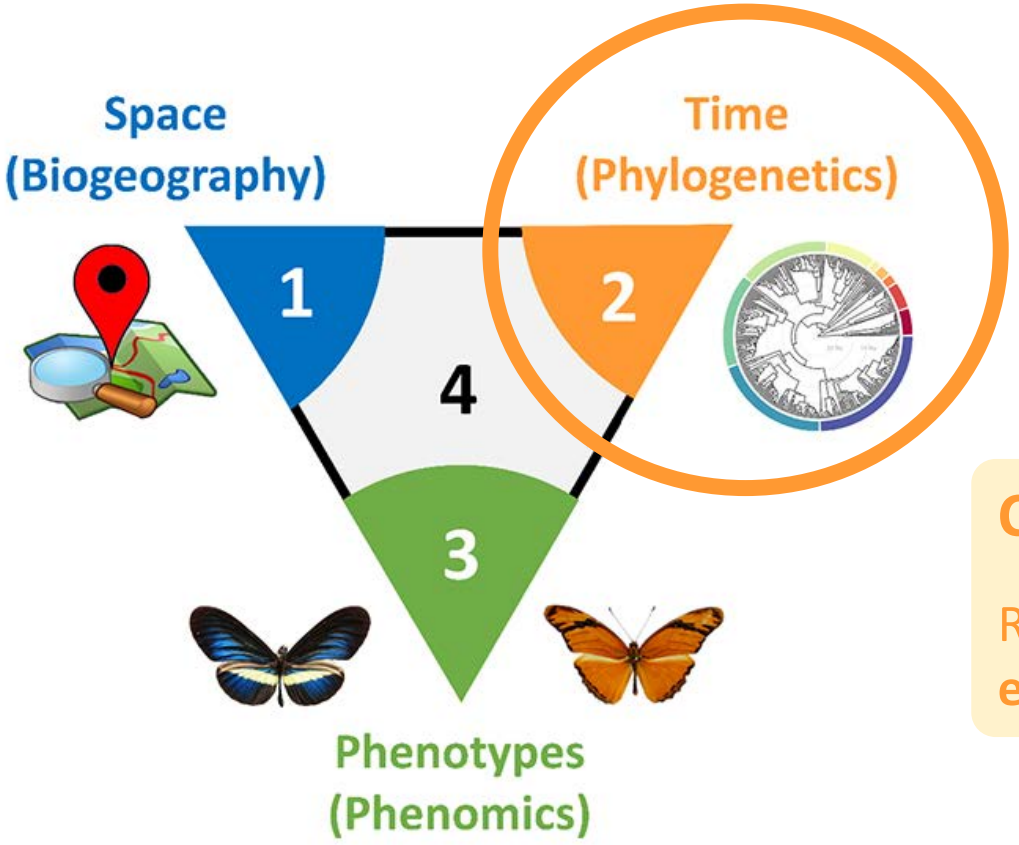
Taxonomic β-Diversity



CHAPTER 2: Phylogenomics resolve deep evolutionary relationships in clearwing butterflies



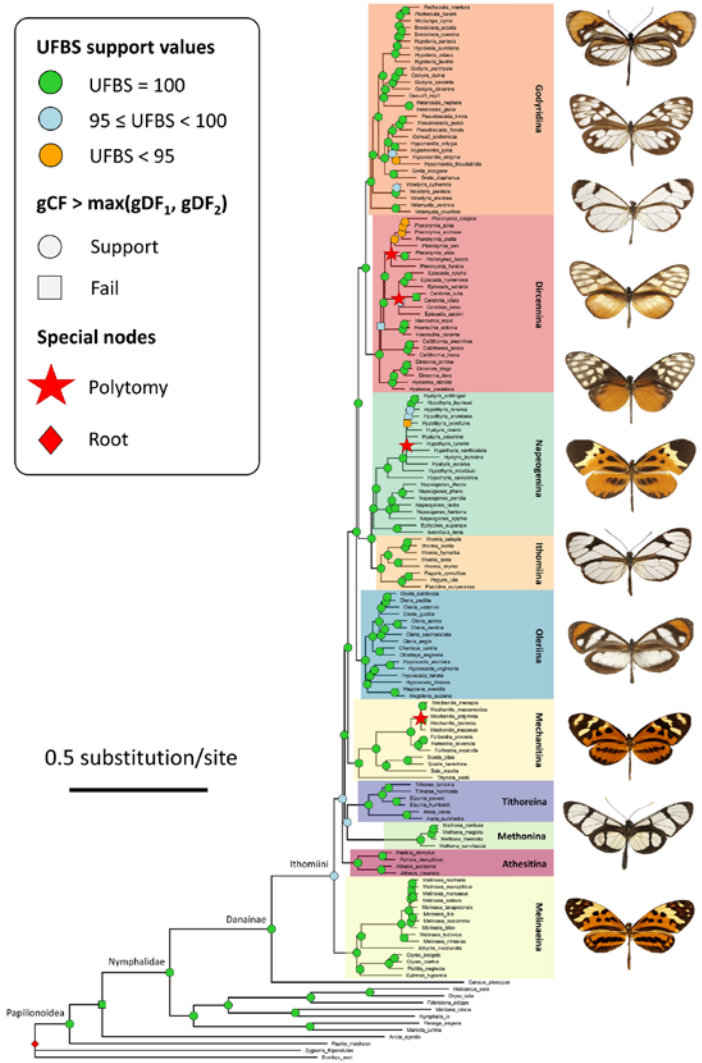
CHAPTER 2

Resolve **deep evolutionary relationships**

Reference:

Doré, M., Gauthier, J., Allio, R., Grishin, N., Meier, J., Chazot, N., Willmott, K., & Elias, M. (2023). Phylogenomics resolve deep evolutionary relationships in clearwing butterflies. *In prep.*

From a WGS-based backbone…



153 ithomiines + 12 outgroups

39 % of extent **species**

100% of extent **genera**

7.8 M sites across **11,012 genes**

… to a comprehensive Time-calibrated phylogeny

356 ithomiines + 12 outgroups

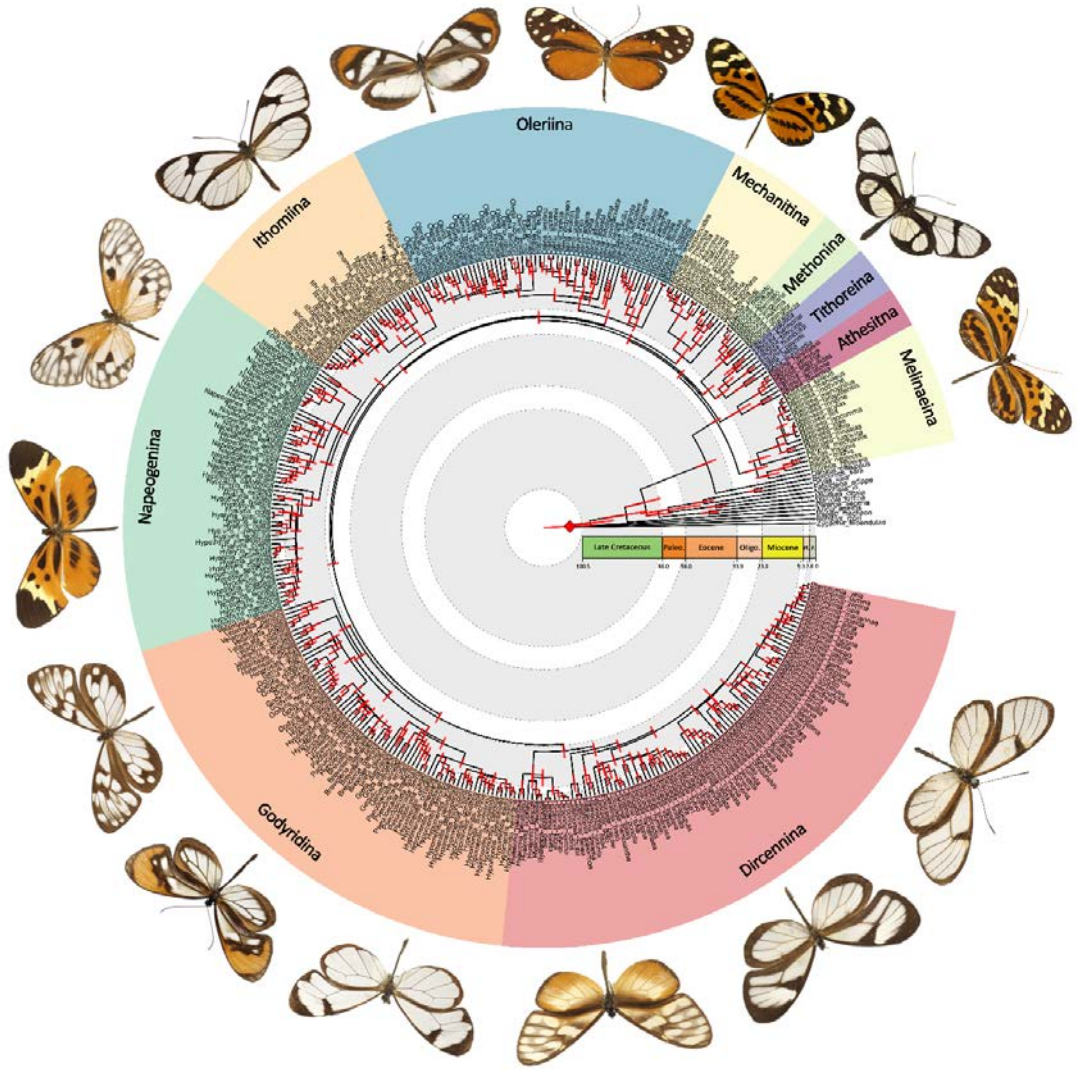
90 % of extent **species**

100% of extent **genera**

9,930 sites across **8 genes**

Fixed backbone from WGS phylogeny

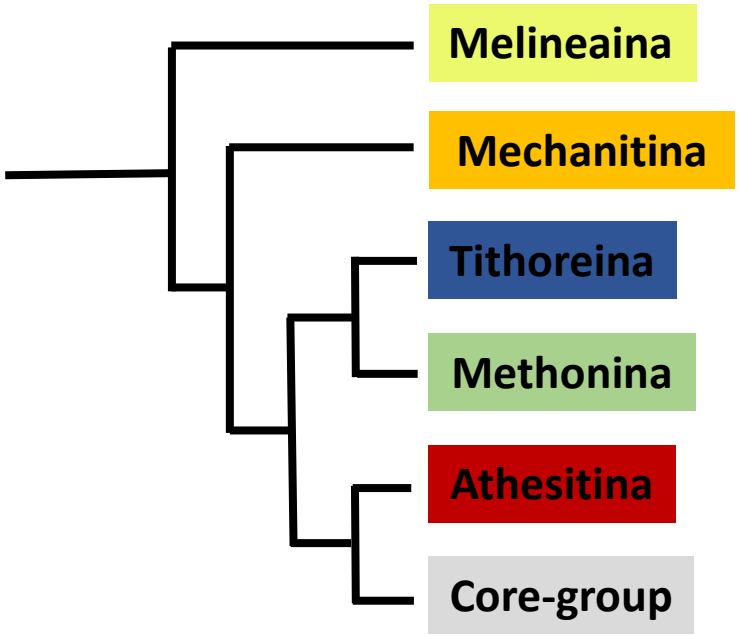
Secondary calibrations
from host-plant ages
and higher-level phylogenies



Phylogenomics resolving conflicts

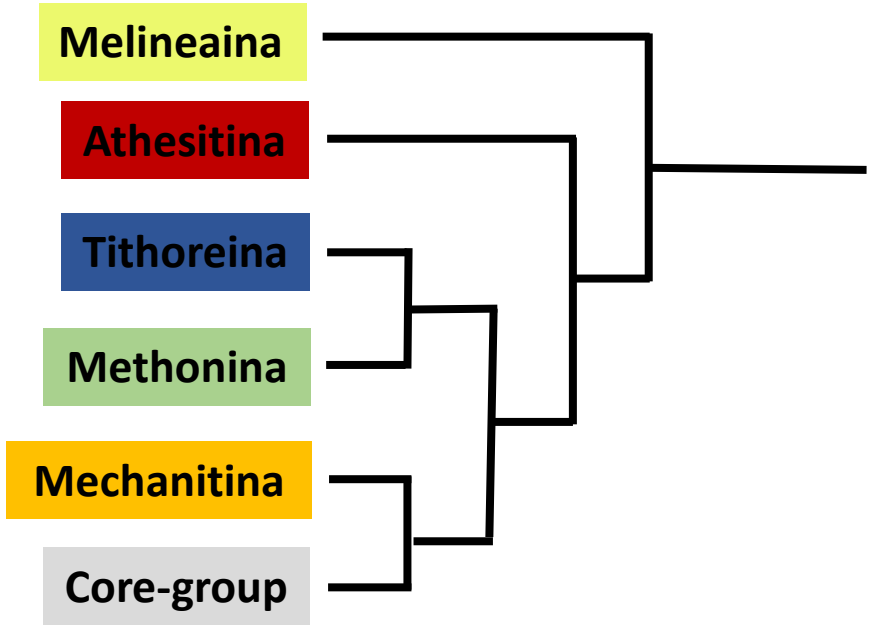
Sanger sequencing

Chazot *et al.*, 2019

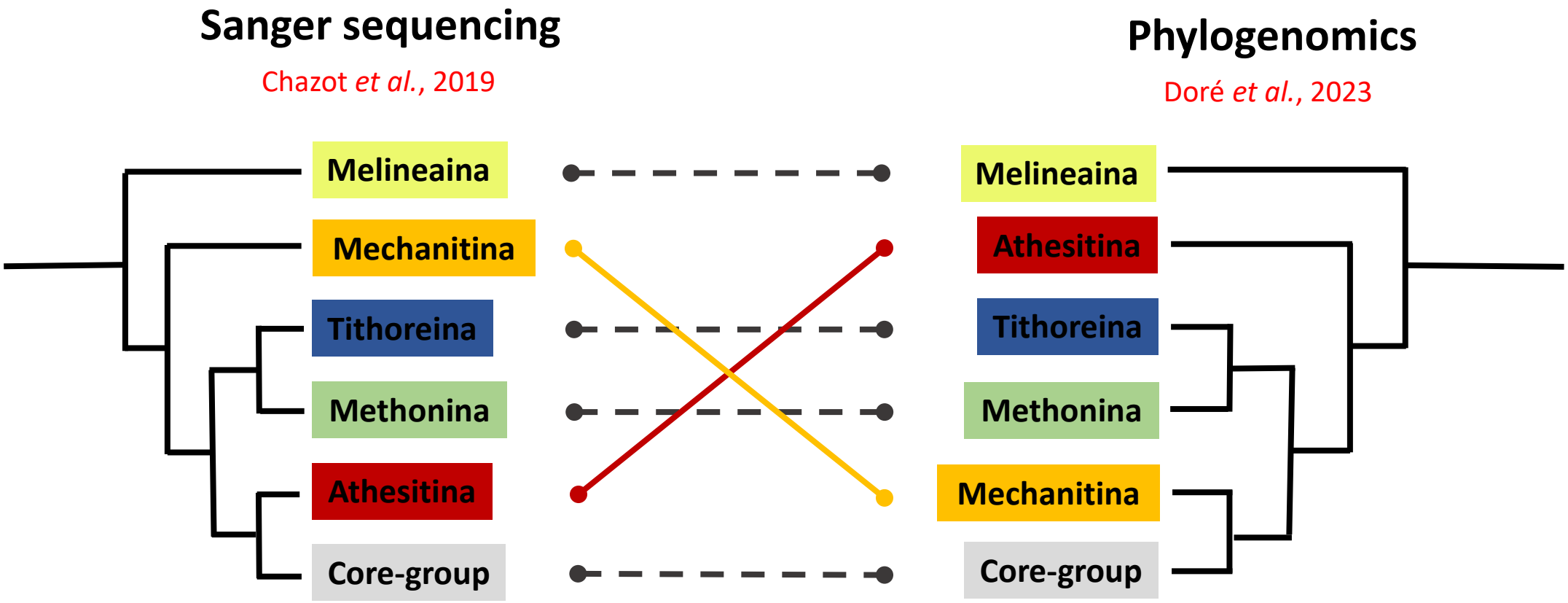


Phylogenomics

Doré *et al.*, 2023



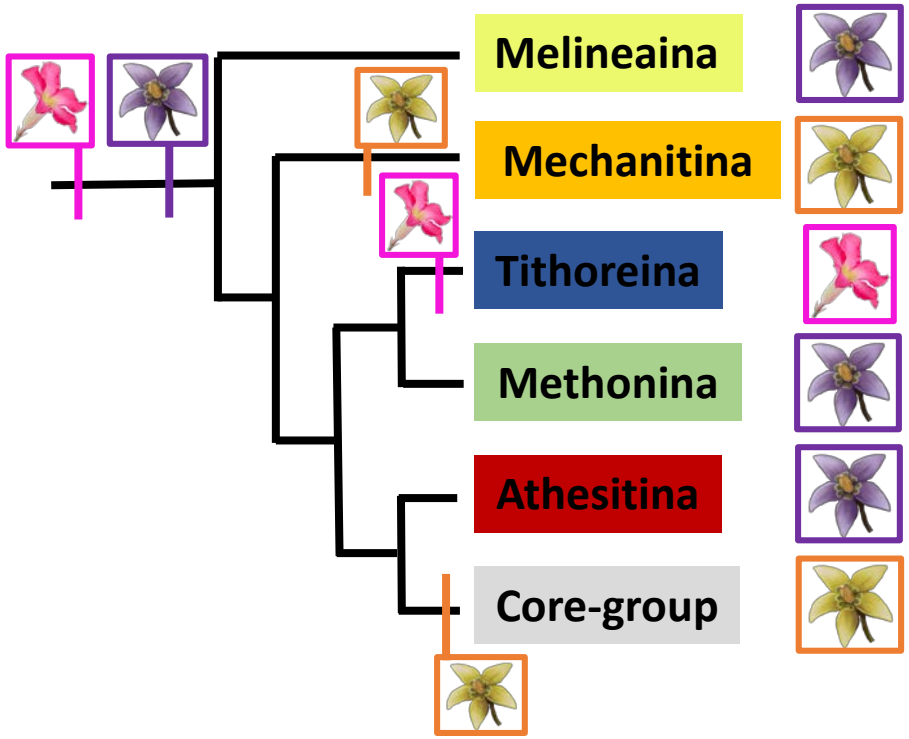
Phylogenomics resolving conflicts



Phylogenomics resolving conflicts

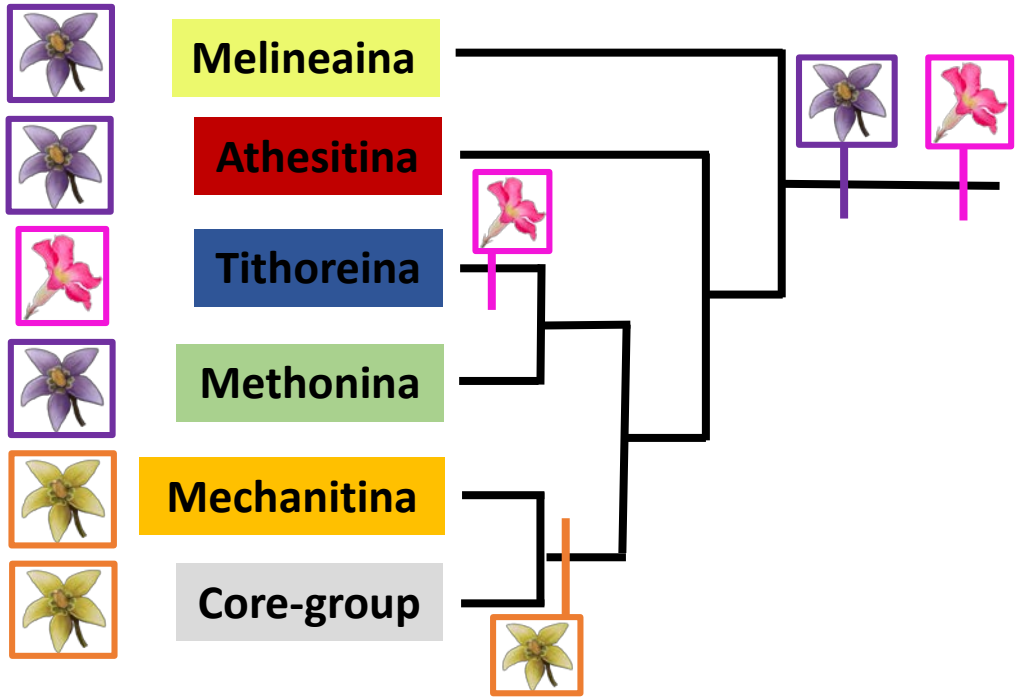
Sanger sequencing

Chazot *et al.*, 2019



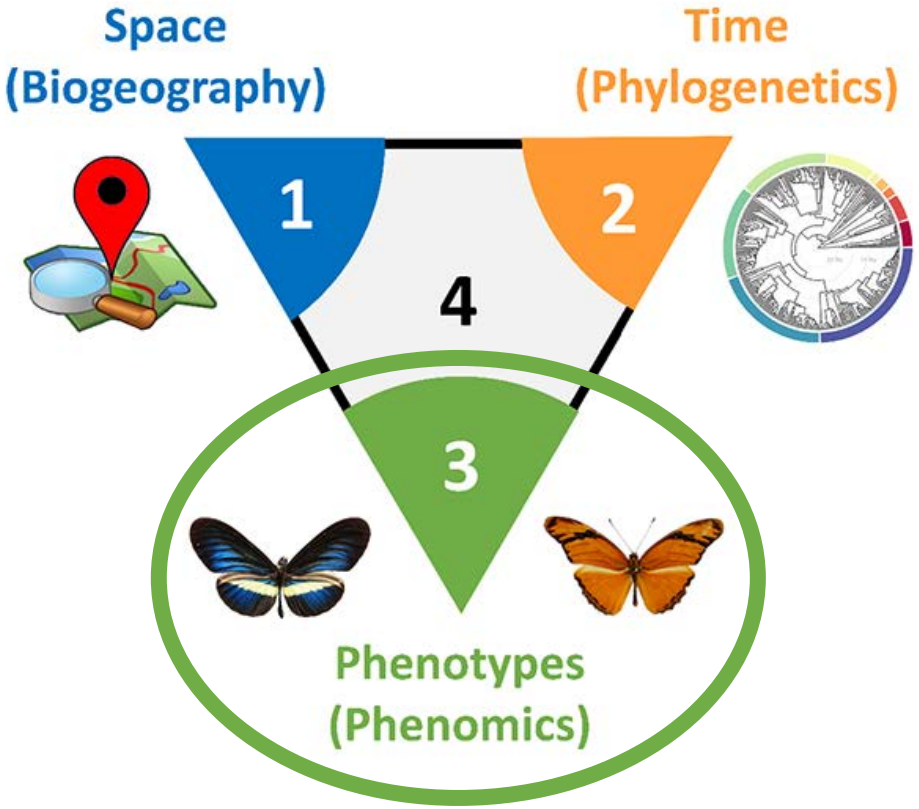
Phylogenomics

Doré *et al.*, 2023



Apocynaceae Solanum Other Solaneaceae

CHAPTER 3: Perceptual maps: a new tool to investigate mimicry patterns from Citizen Science to individual perception



CHAPTER 3

Quantify **phenotypic similarity** in wing patterns

Reference:

Doré, M., Pérochon, E., Aubier, T.G., Joron*, M. & Elias*, M. (2023). Perceptual maps: a new tool to investigate mimicry patterns from Citizen Science to individual perception. *In prep.*

The Heliconiini tribe as study model

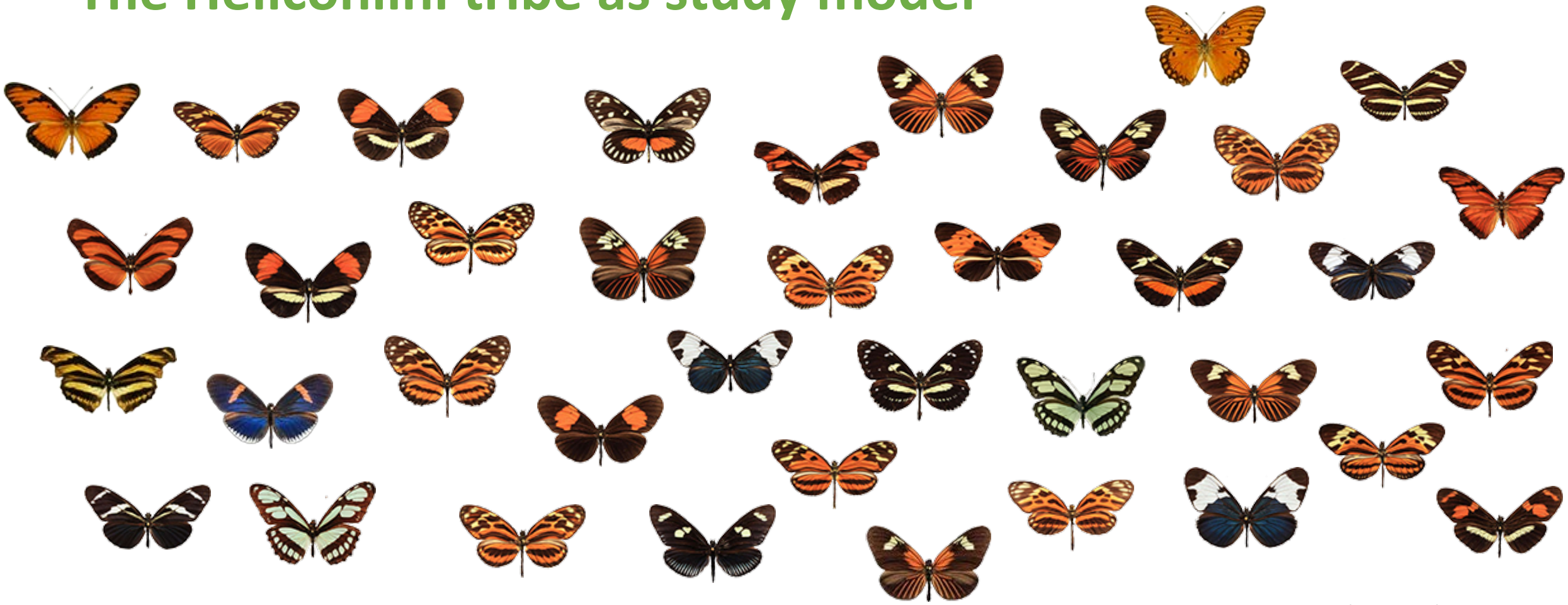


Photo credits: C. Jiggins

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

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

The Heliconiini tribe as study model

Objectives:

1/ **Quantify** phenotypes

2/ **Describe** variation in space

3/ Design a reproducible **mimicry classification**

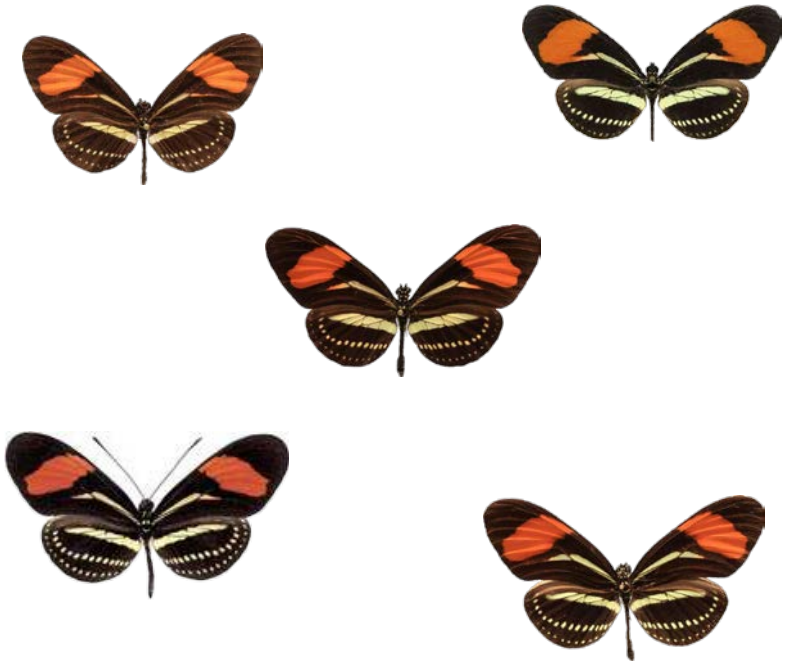
Photo credits: C. Jiggins

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

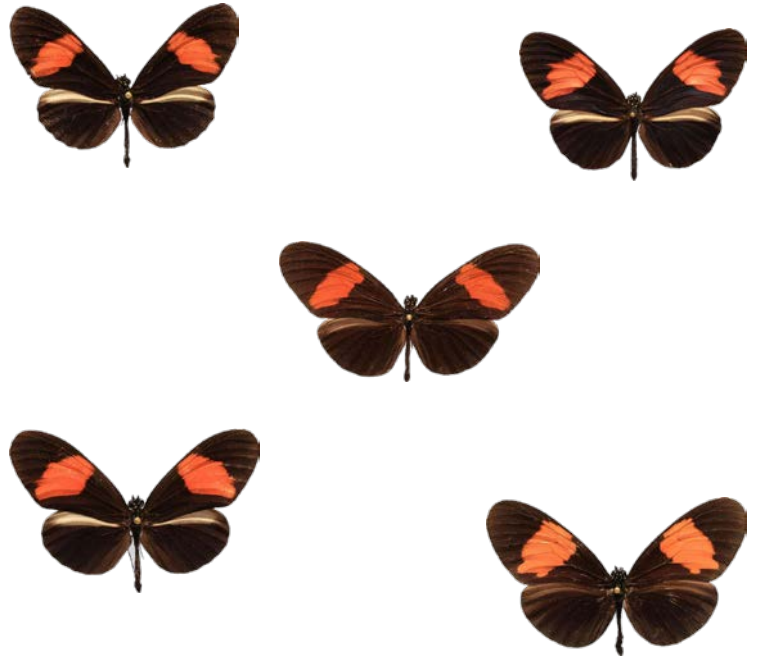
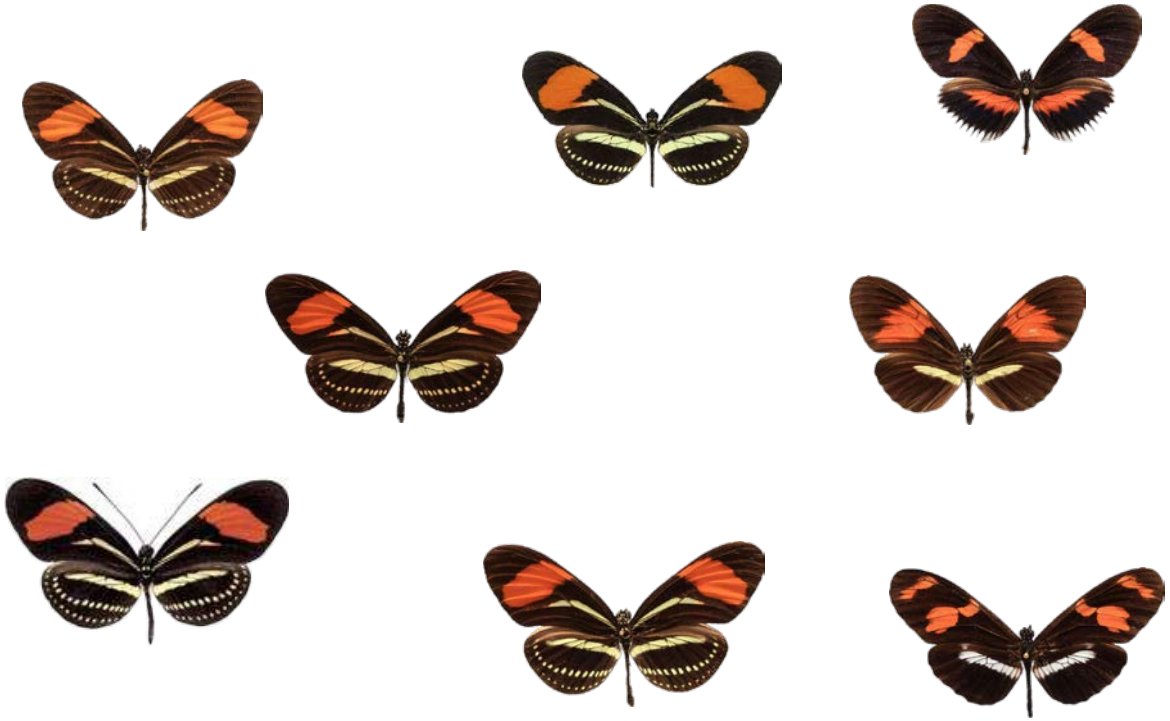


Photo credits: C. Jiggins

How to delineate mimicry rings?

POSTMAN ring



RED BAND ring

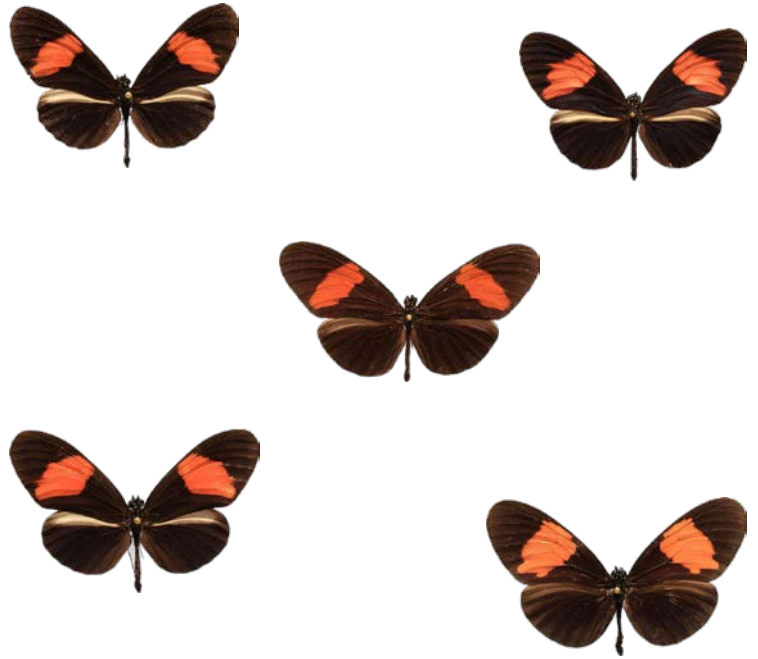
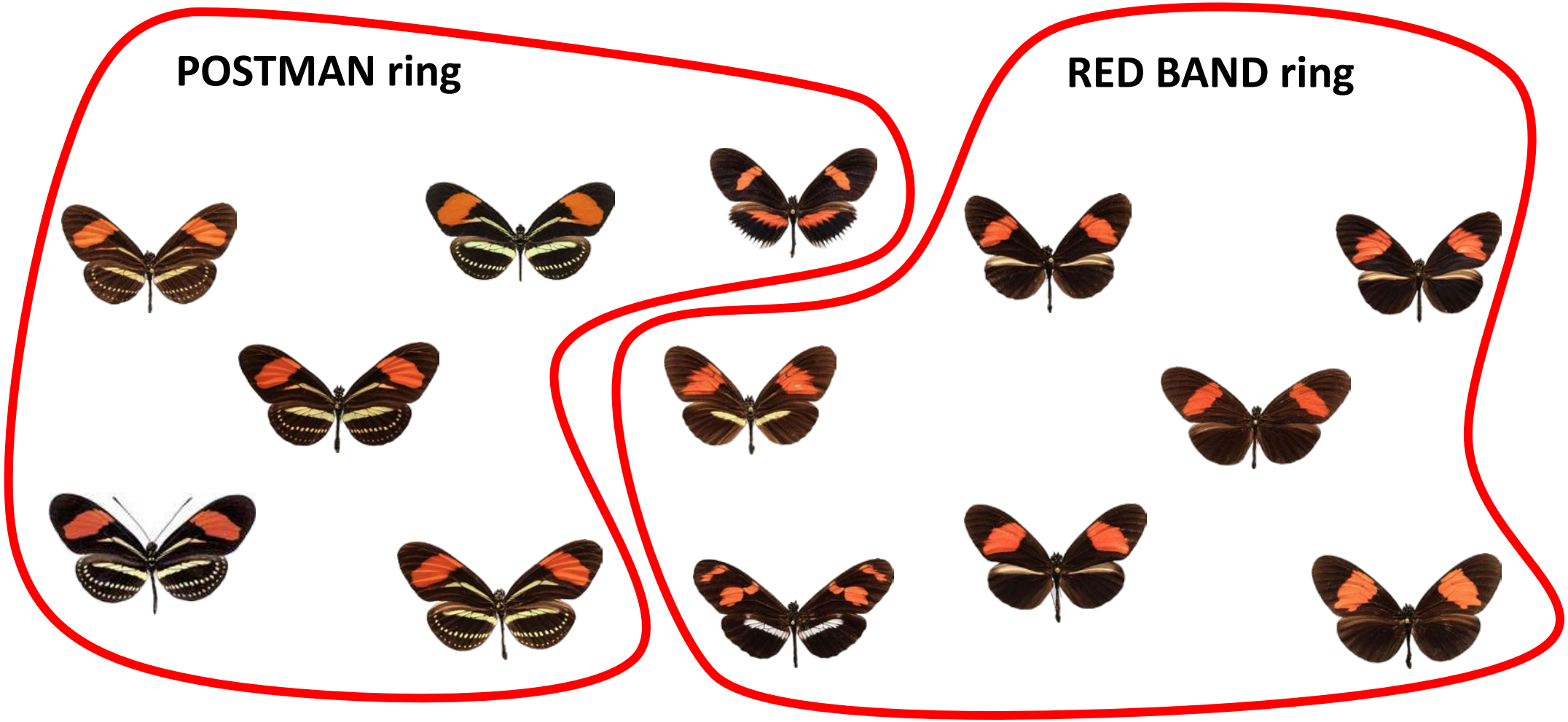


Photo credits: C. Jiggins

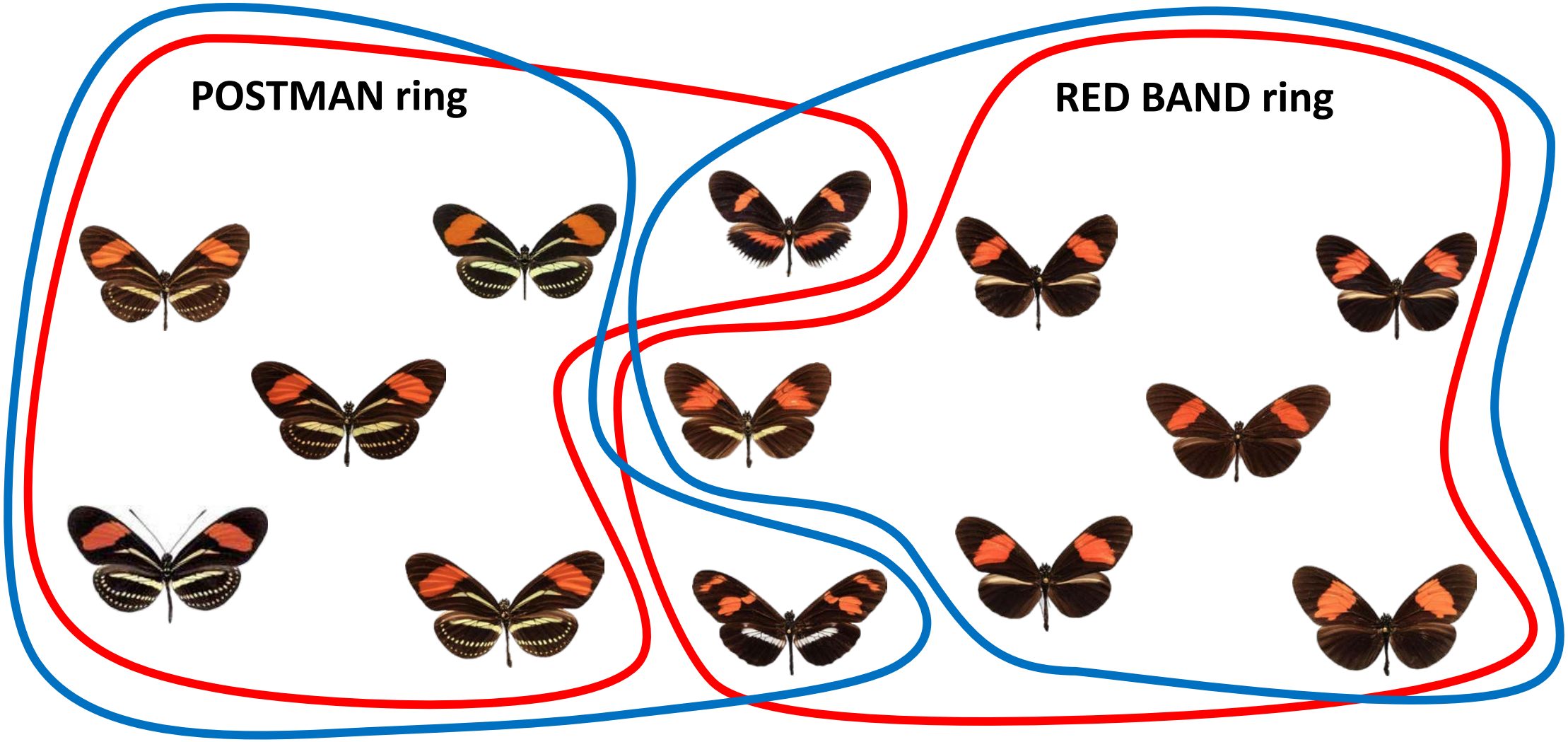
How to delineate mimicry rings?



Article A

Photo credits: C. Jiggins

How to delineate mimicry rings?

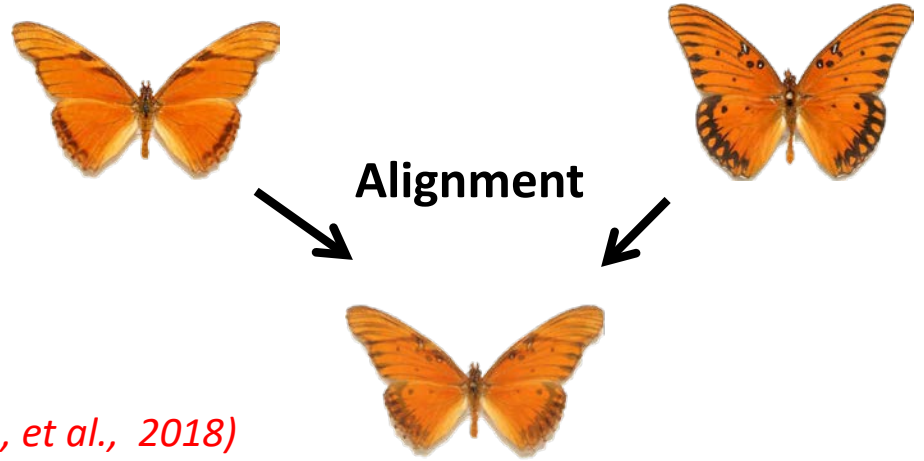


Article A

Article B

Photo credits: C. Jiggins

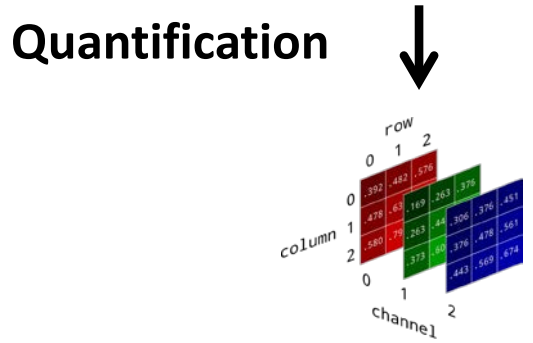
How to delineate mimicry rings?

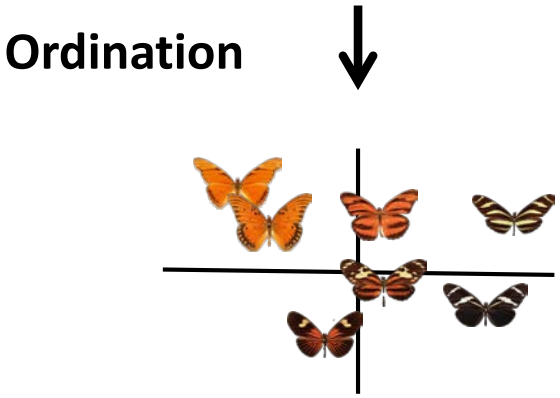


Quantitative approach:

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

Visual signal ≠ Perception of this signal





How to delineate mimicry rings?

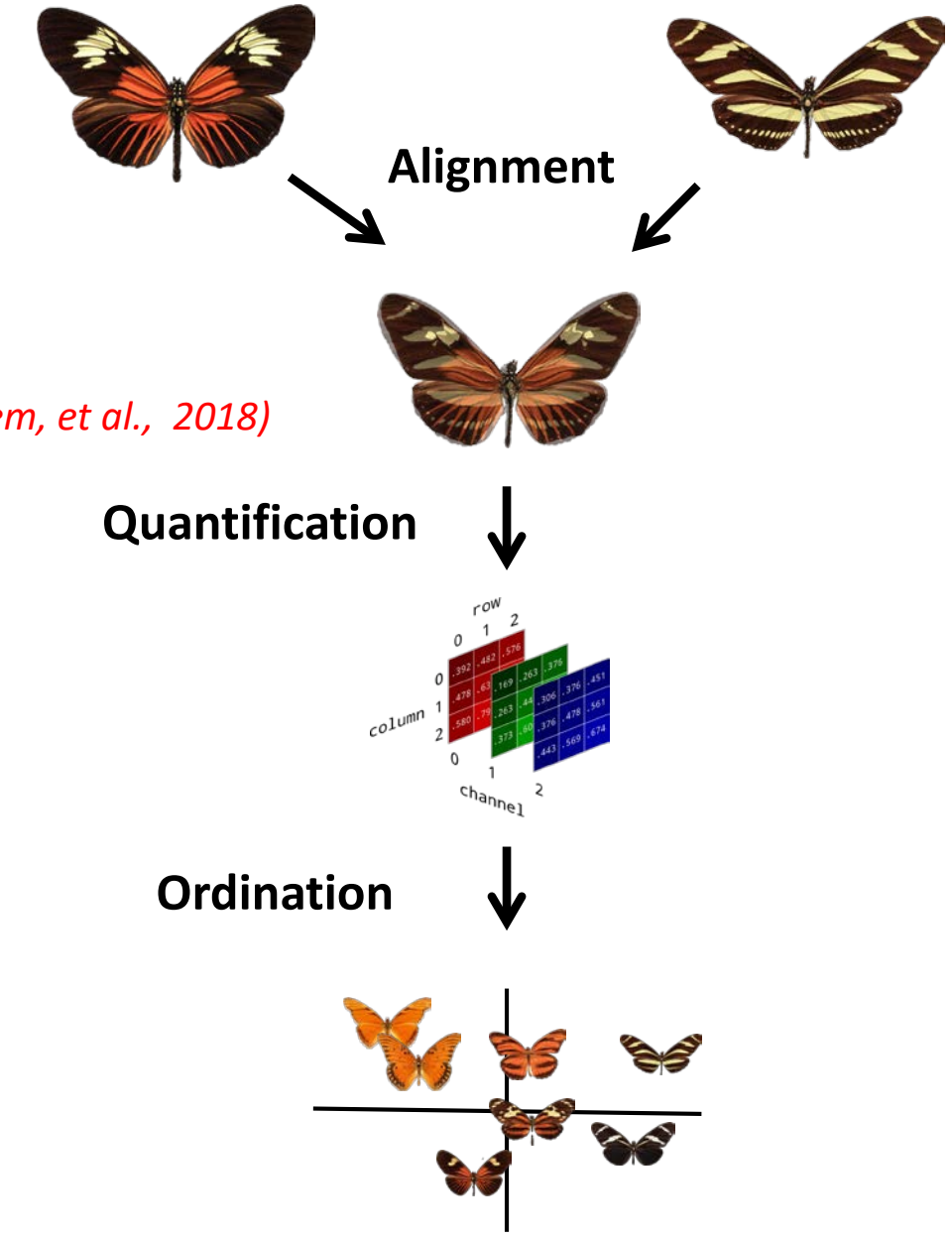


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Photo credits: C. Jiggins

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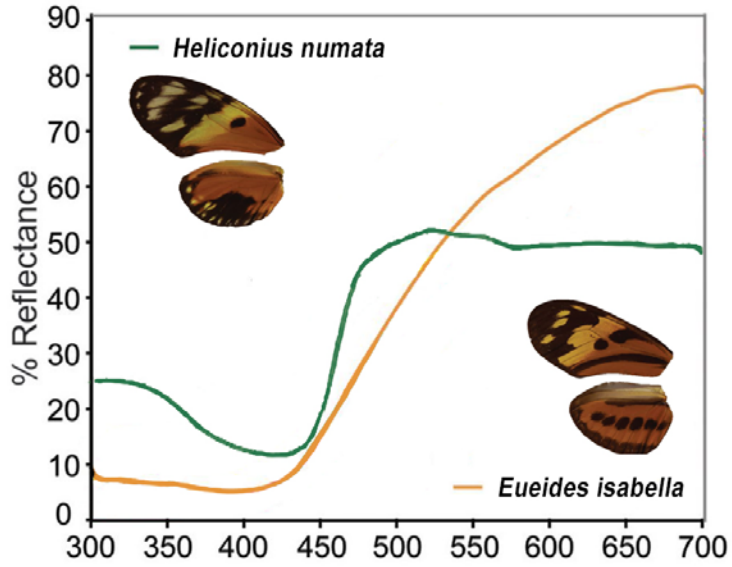
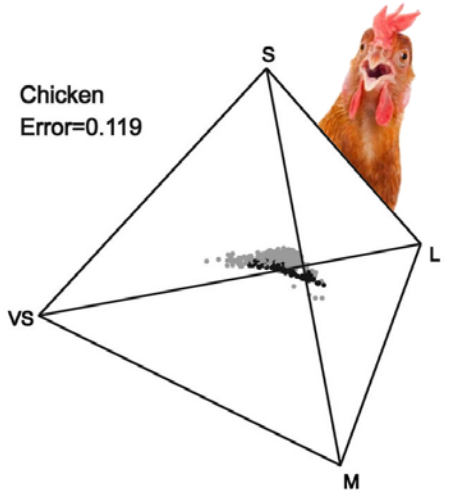
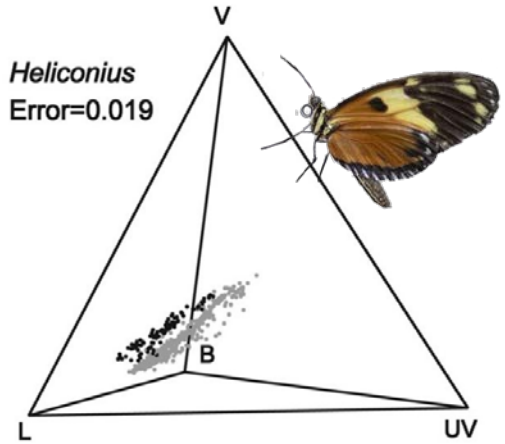




Does NOT discriminate



Discriminate

Adapted from Bybee *et al.* 2012

Limits of quantitative approaches

Photonic approach:
Pixel-to-pixel comparison

( ( , )

Photo credits: C. Jiggins

Limits of quantitative approaches

Perceptual approach:
Cognitive integration

( , ) )

Photo credits: C. Jiggins

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 ( , ) )

.

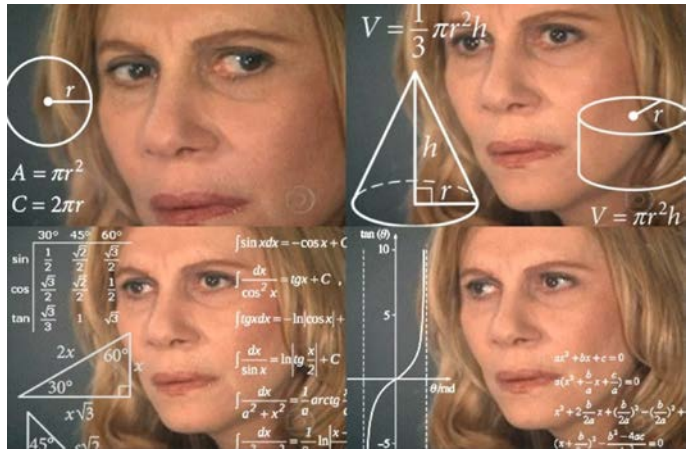
.

.

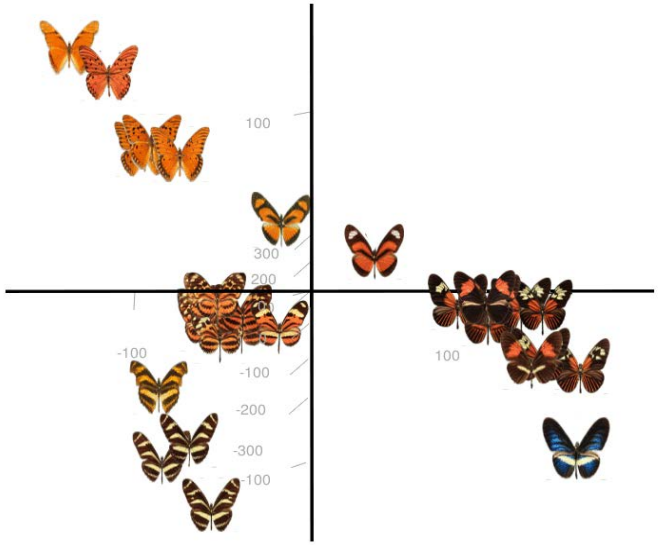
75,240 ( , ) )

Embedding method:
Machine learning algorithm
(t-STE)

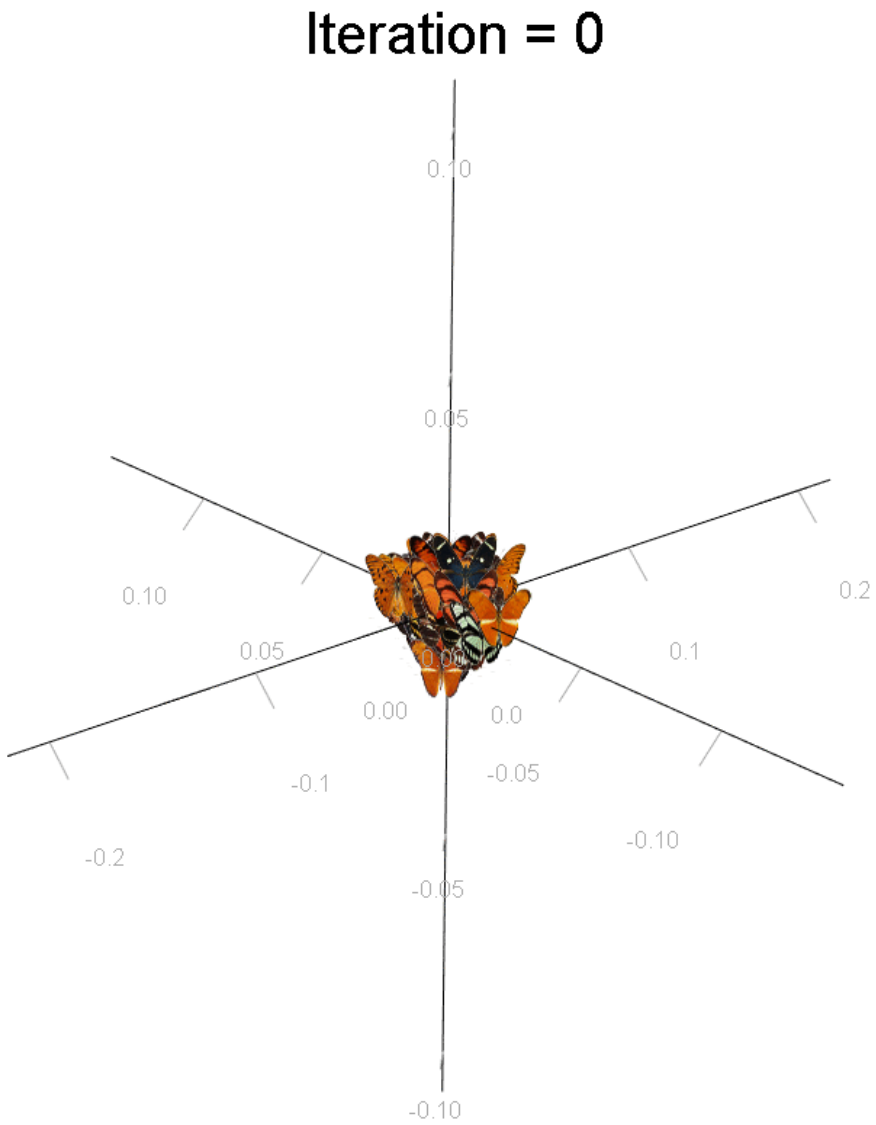
(van der Maaten & Weinberger, 2012)

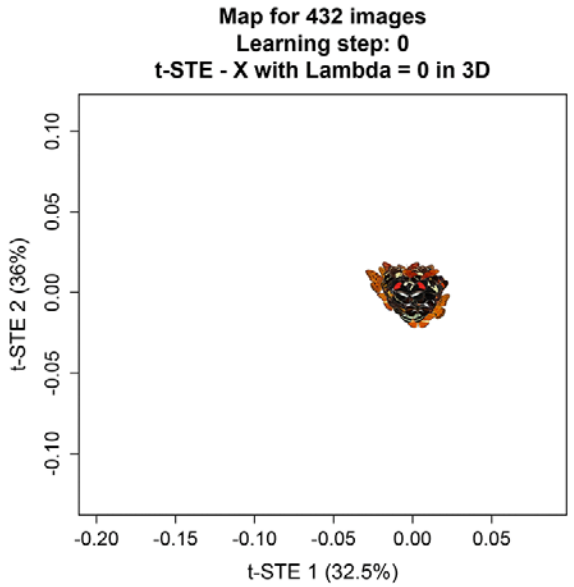


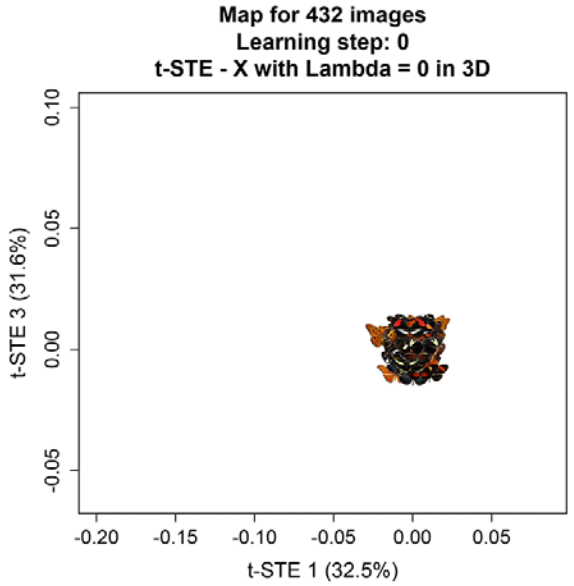
Output = **coordinates** in space of reduced dimensionality
=
Perceptual map

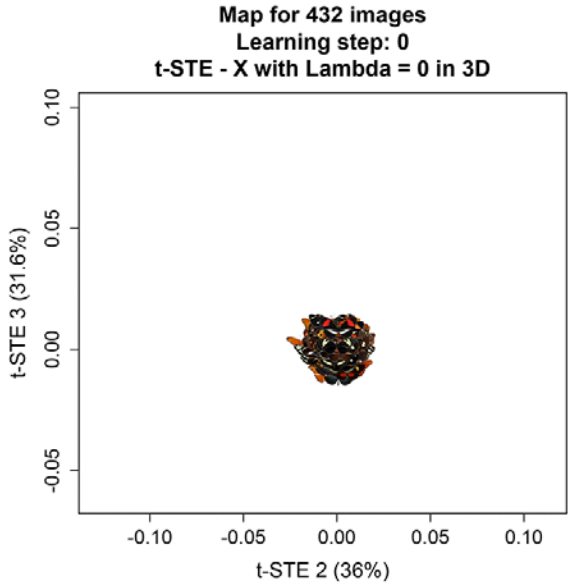


Embedding method: t-STE









Perceptual space

75,240 triplets for **432** images

The spatial scale of mimicry rings

Why do we have a **big potato**?

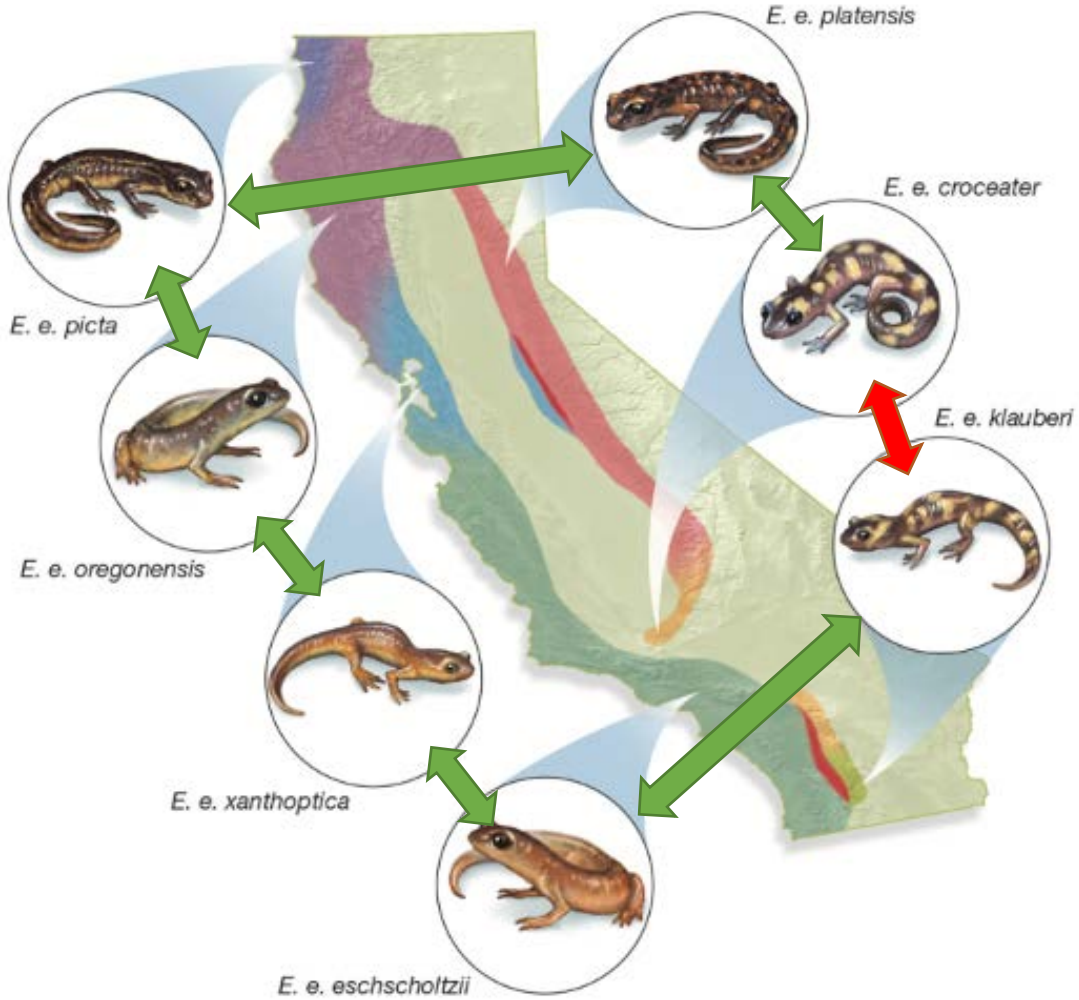
Analogy with **ring species**

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

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 **big potato**?

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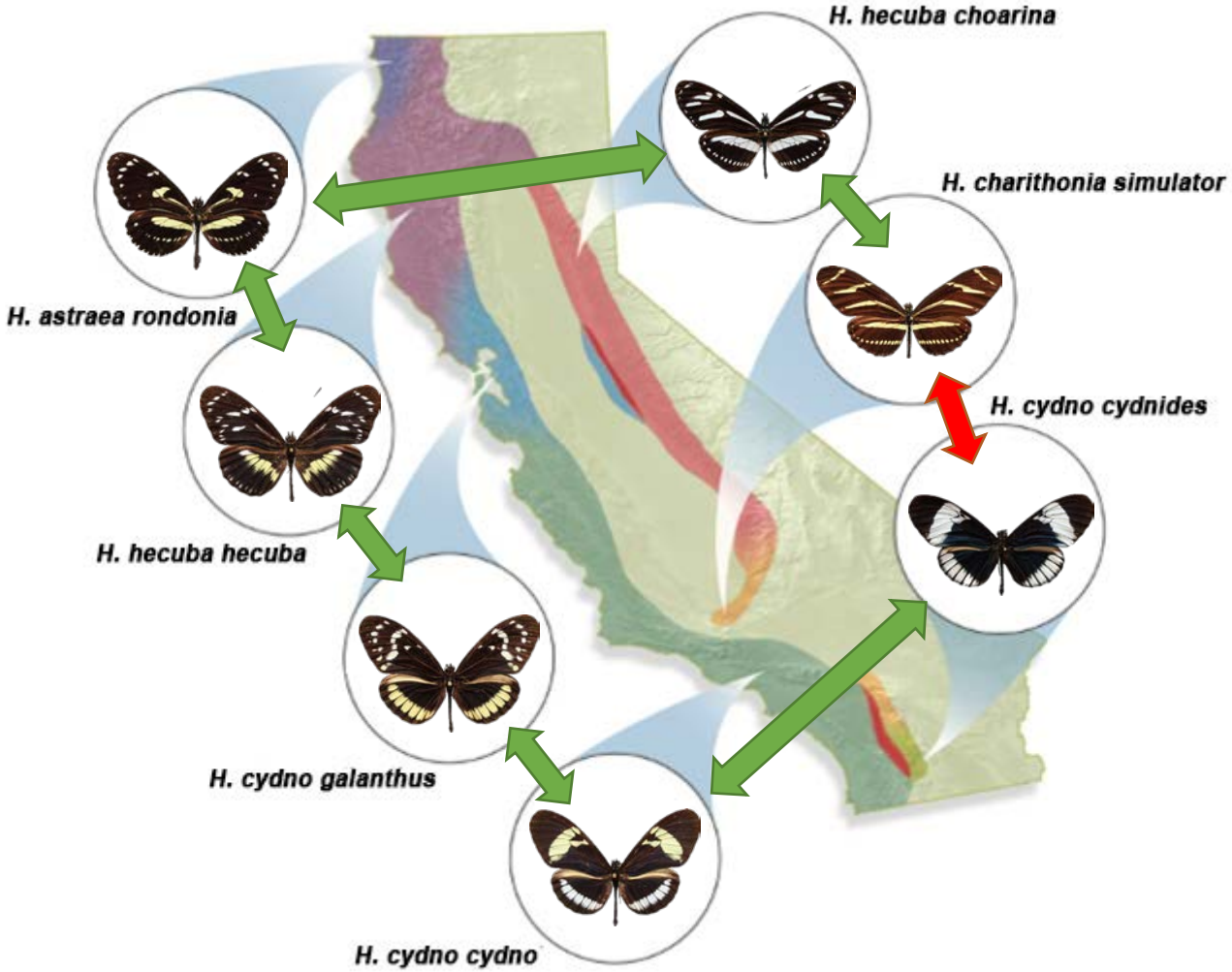

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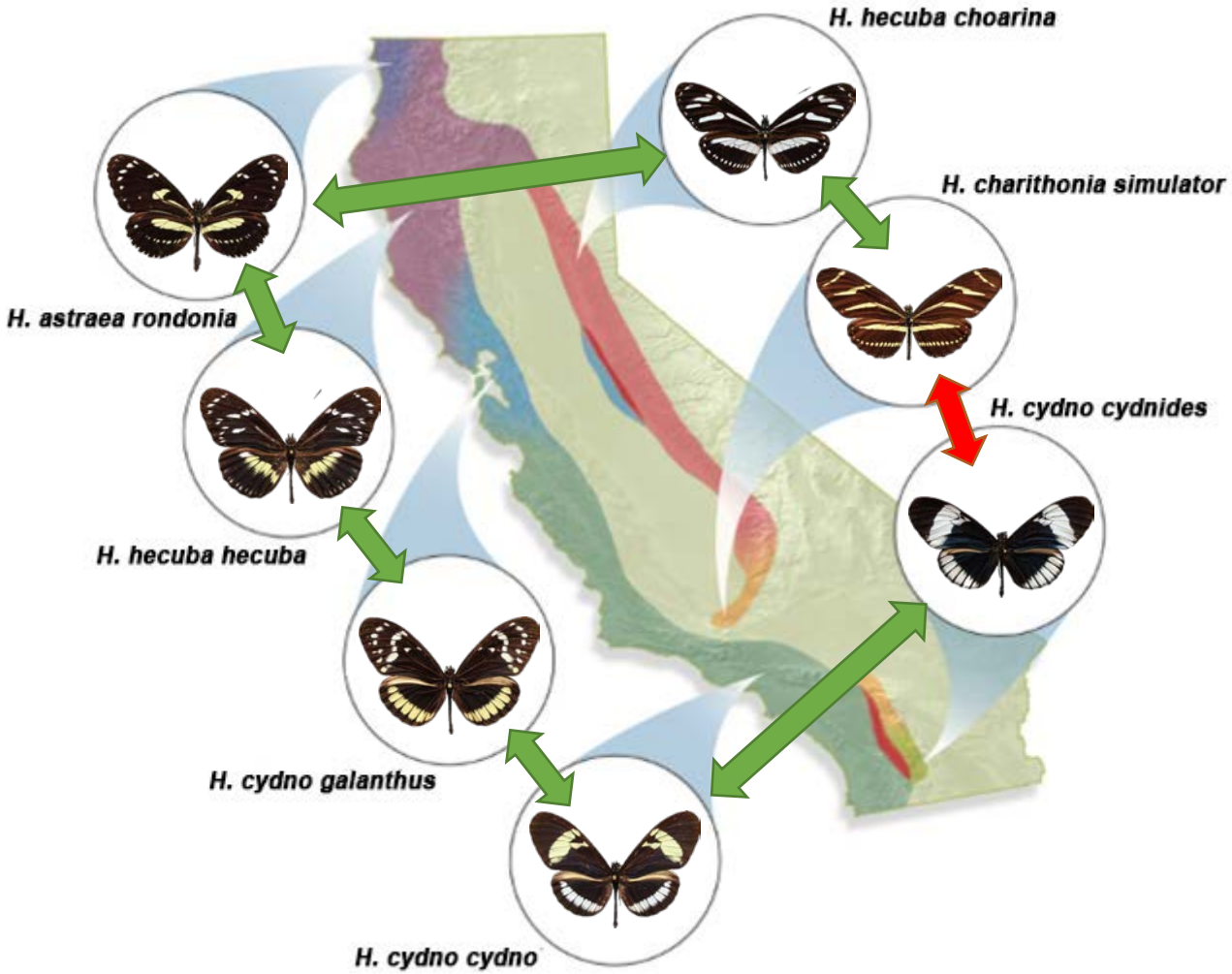
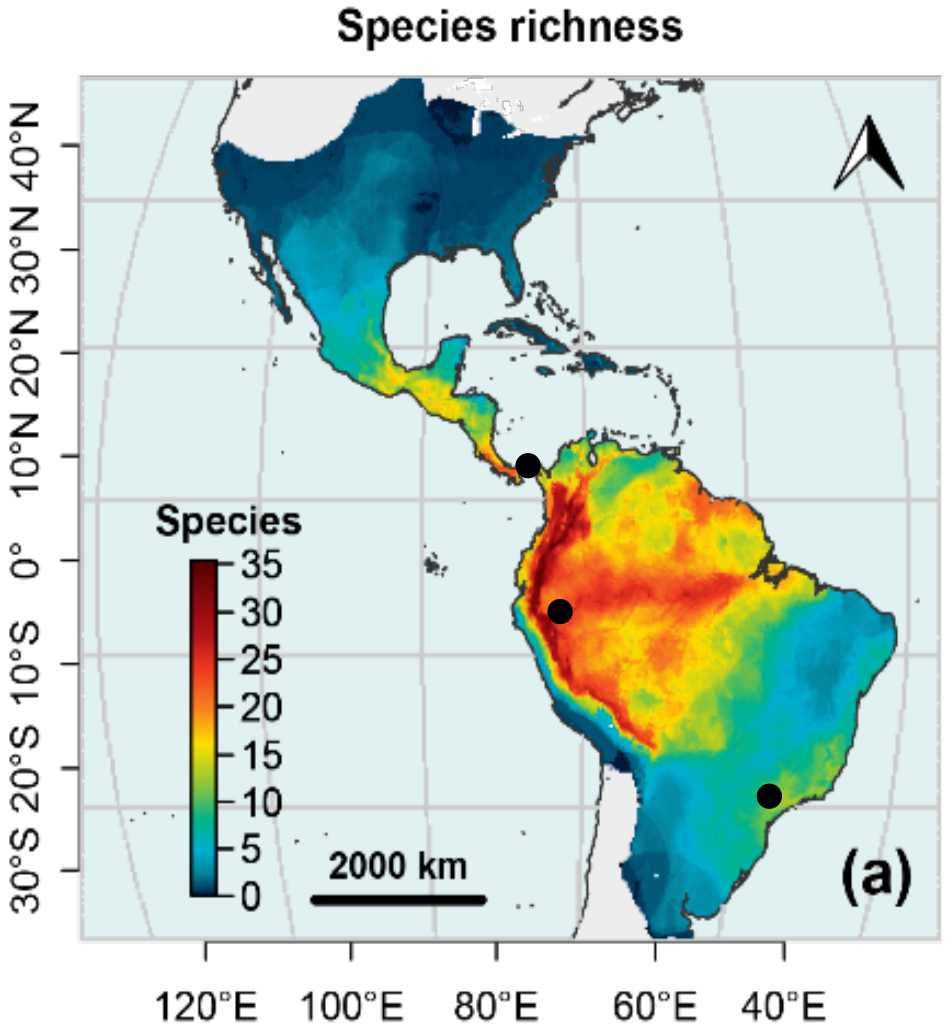
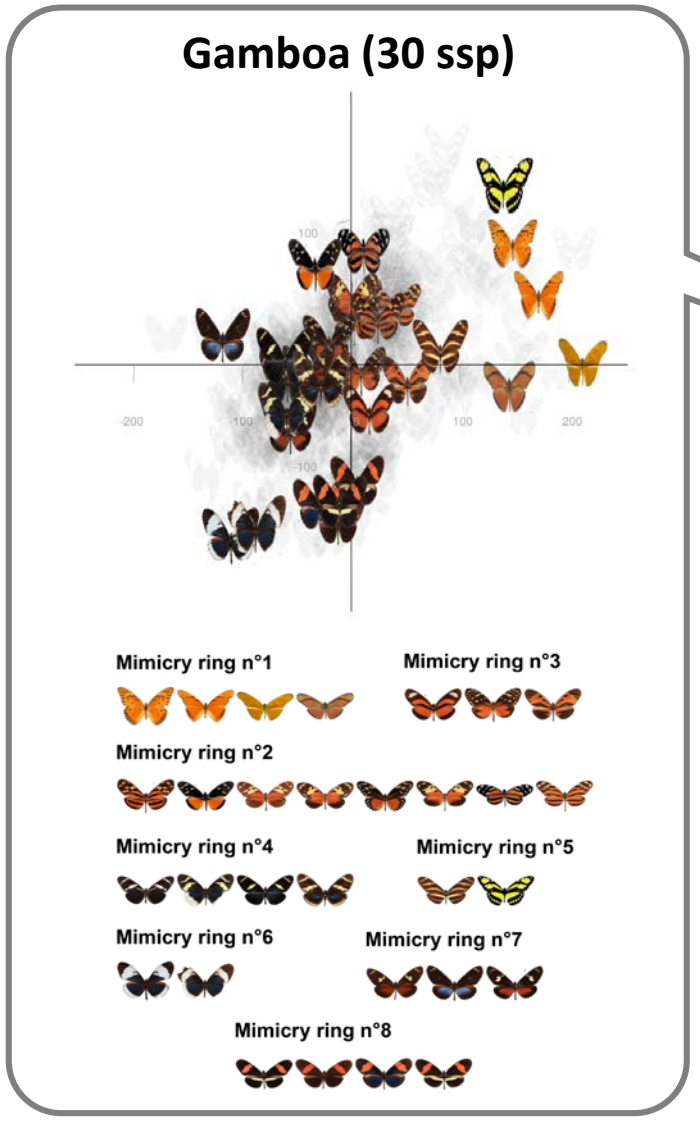


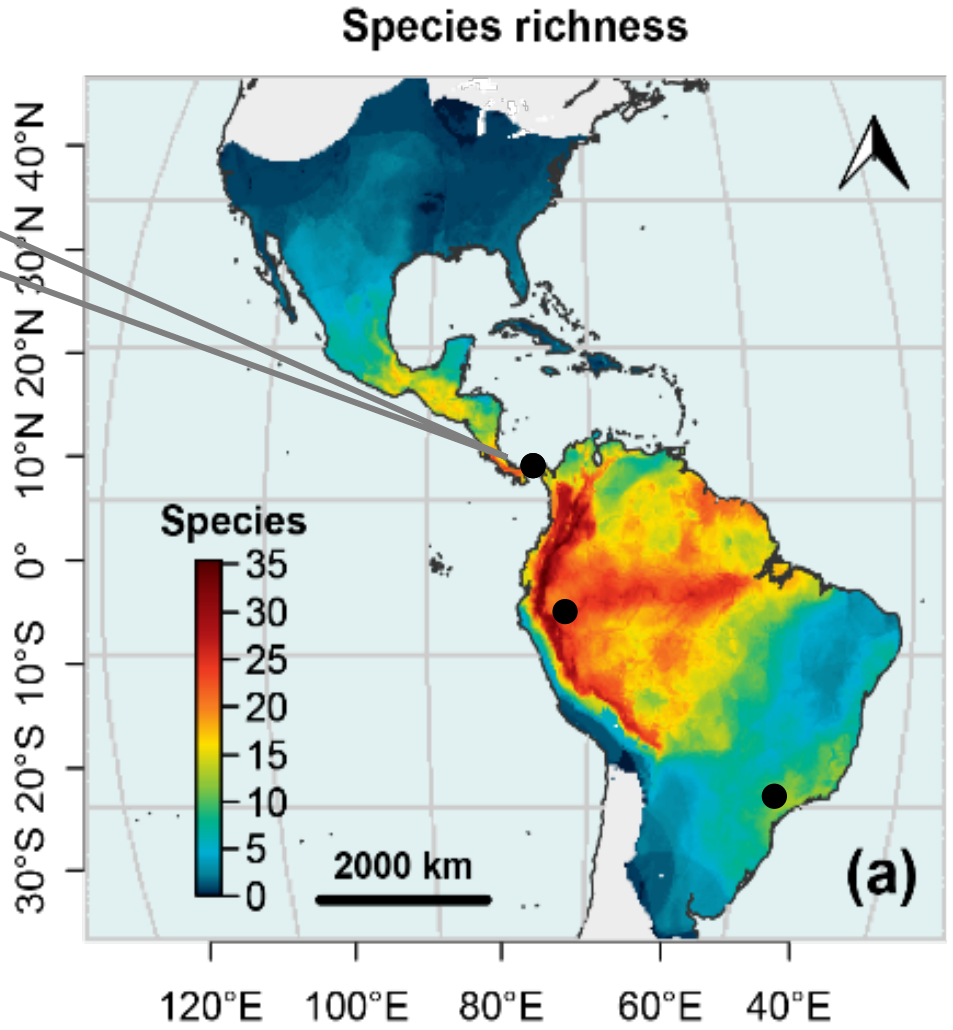
Source: Chegg.com

Interactive map of Müllerian mimicry communities

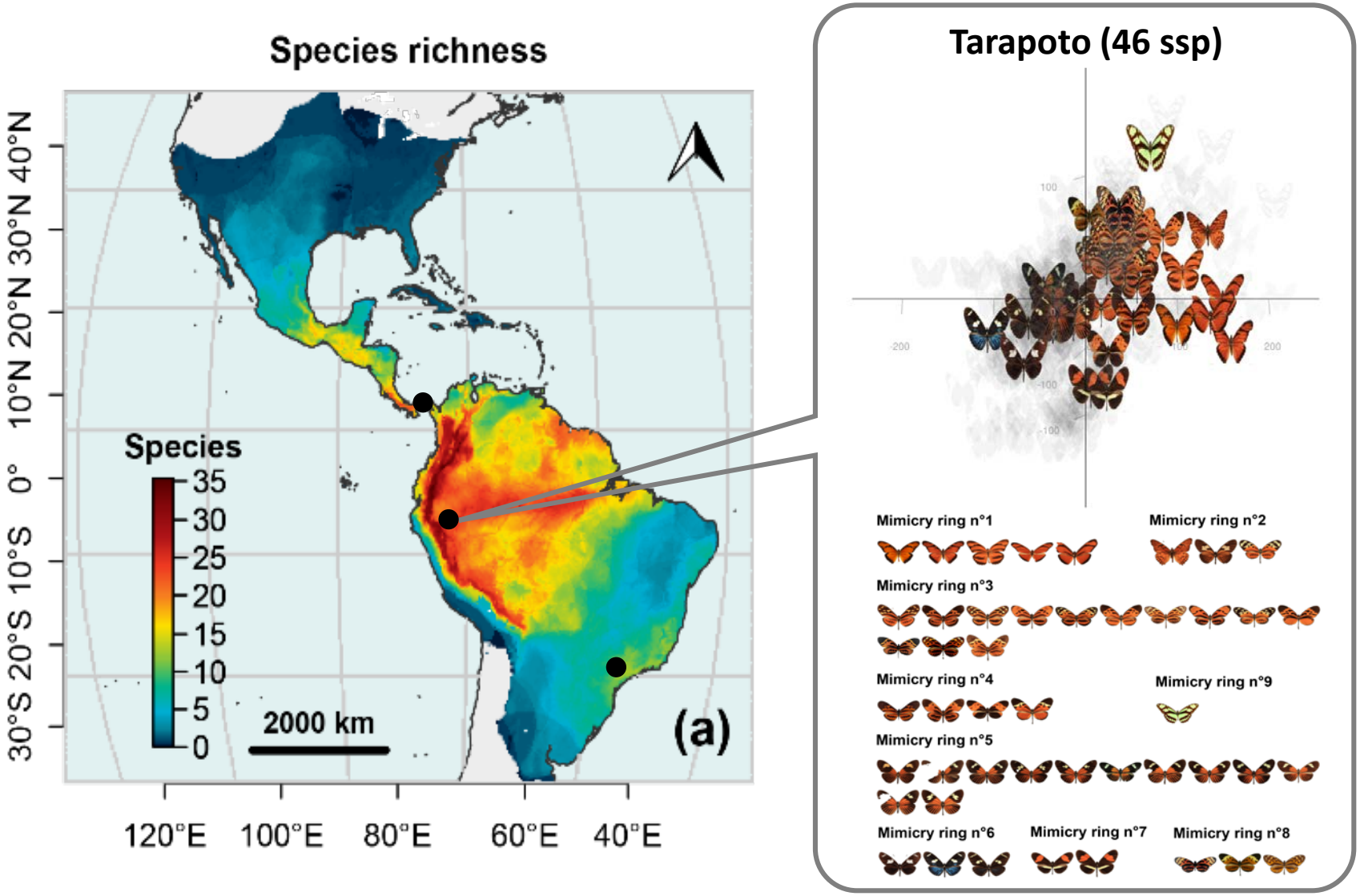


Interactive map of Müllerian mimicry communities

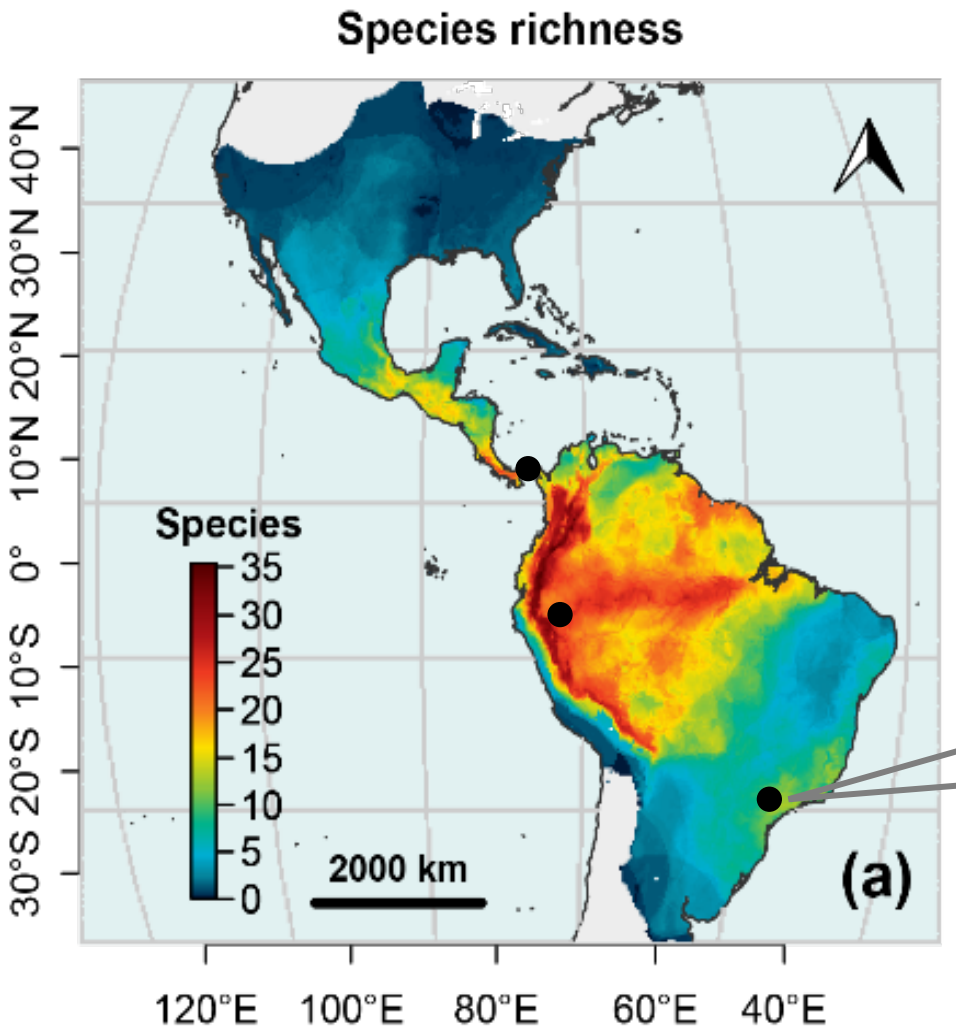


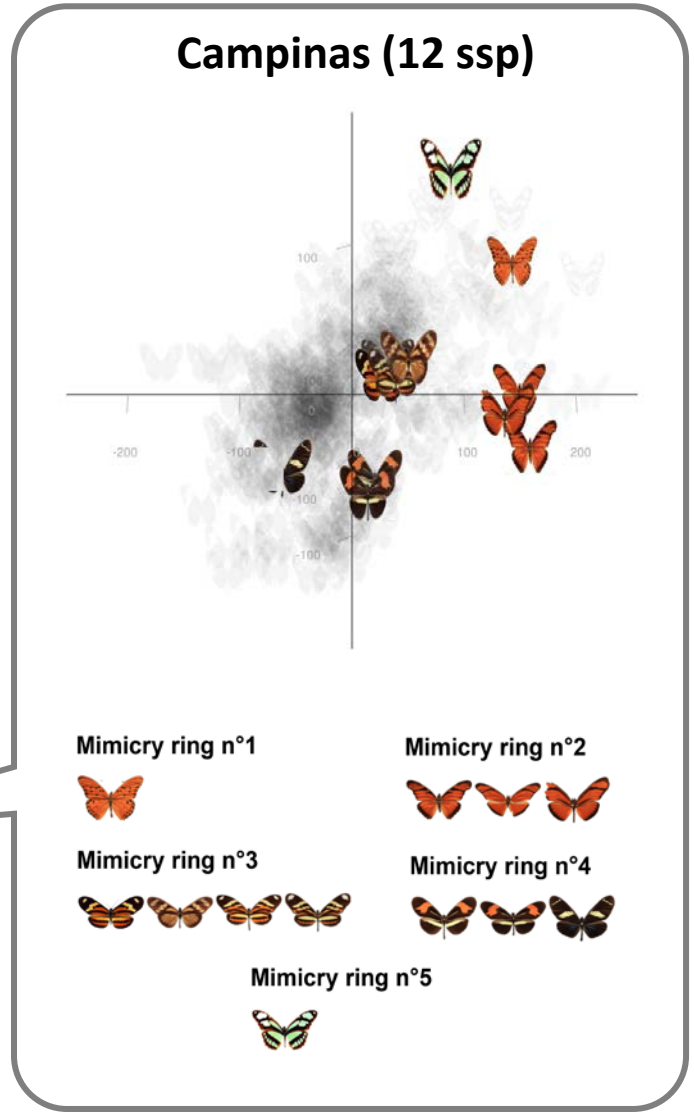


Interactive map of Müllerian mimicry communities



Interactive map of Müllerian mimicry communities

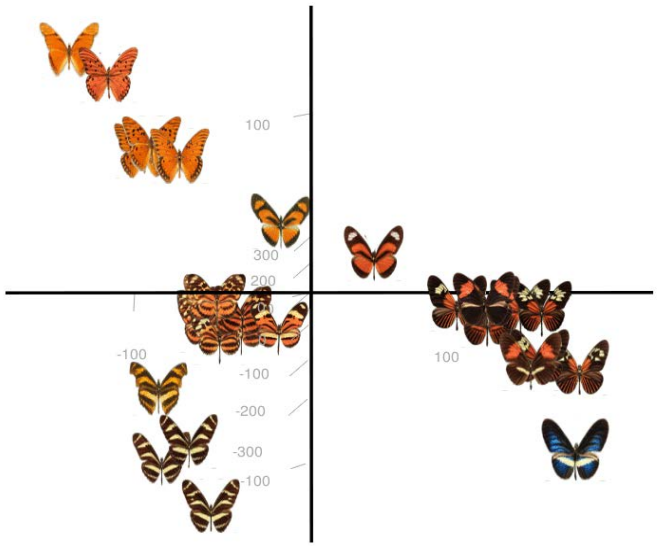




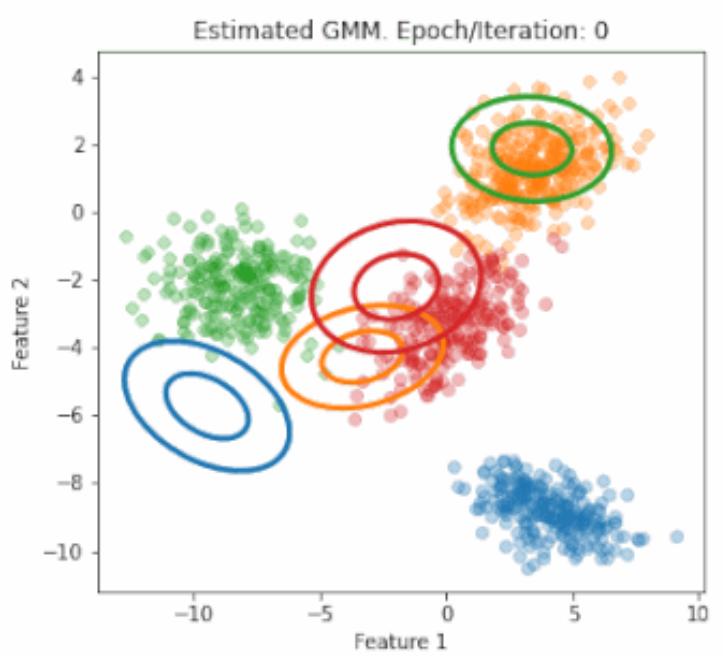
Clustering method

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

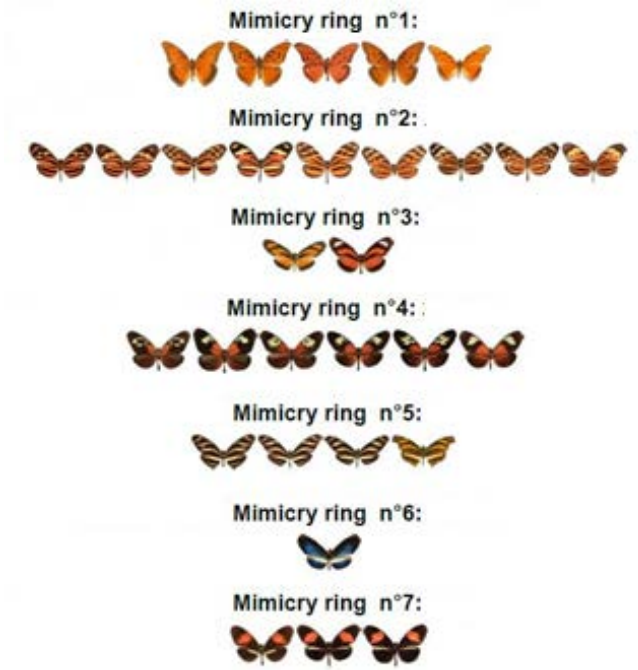
Input = **coordinates**
on the perceptual map



Clustering method:
Gaussian Mixture Models
(GMM)



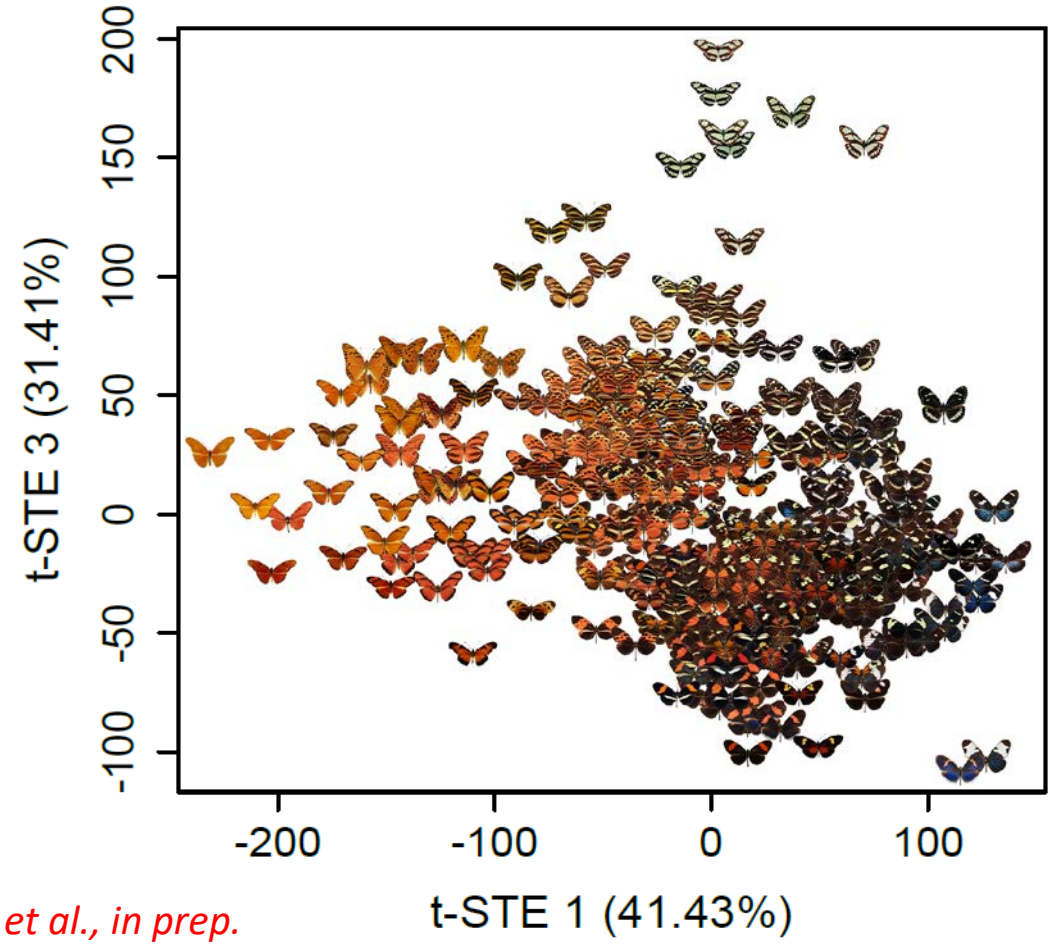
Output = **clusters**
of wing patterns
=
Mimicry rings



Credits: J. Zhang

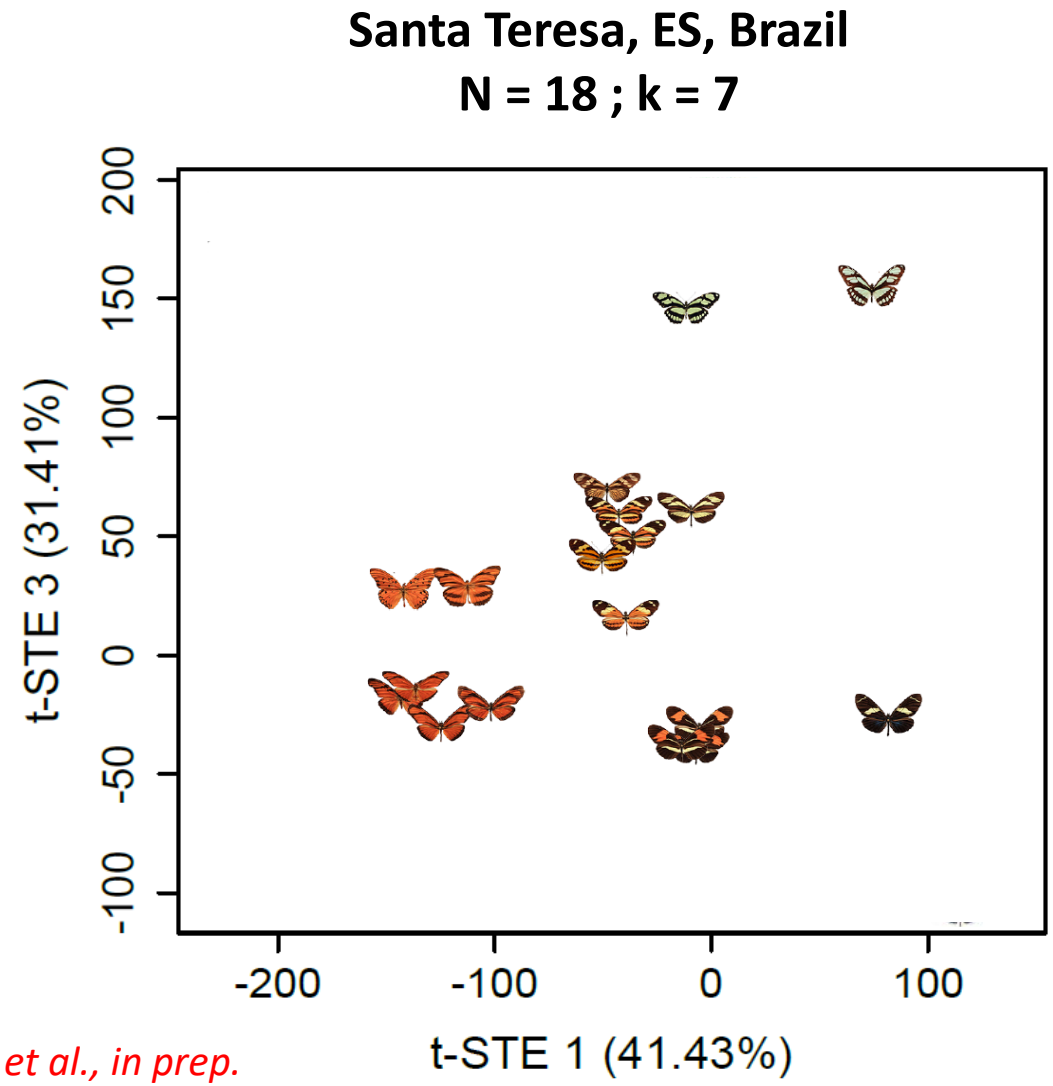
Local perceptual maps

All subspecies
N = 432



Doré et al., in prep.

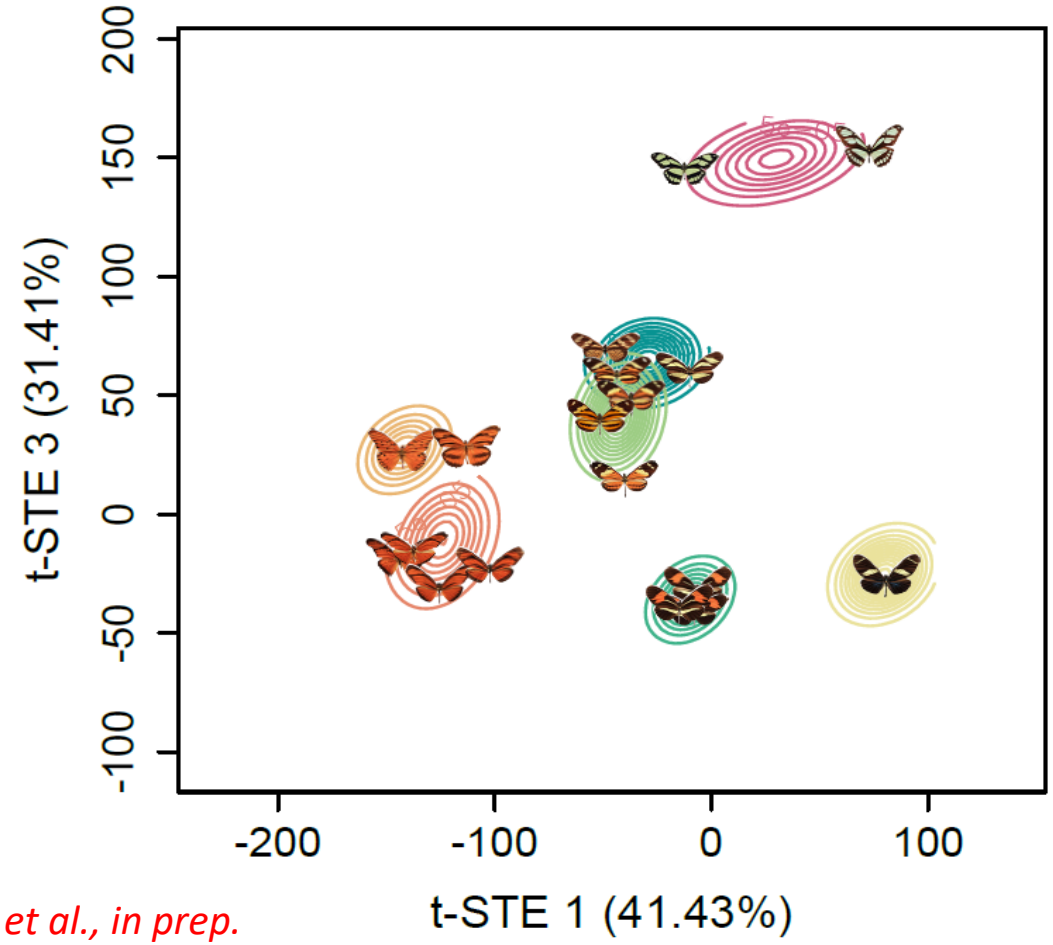
Local perceptual maps



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

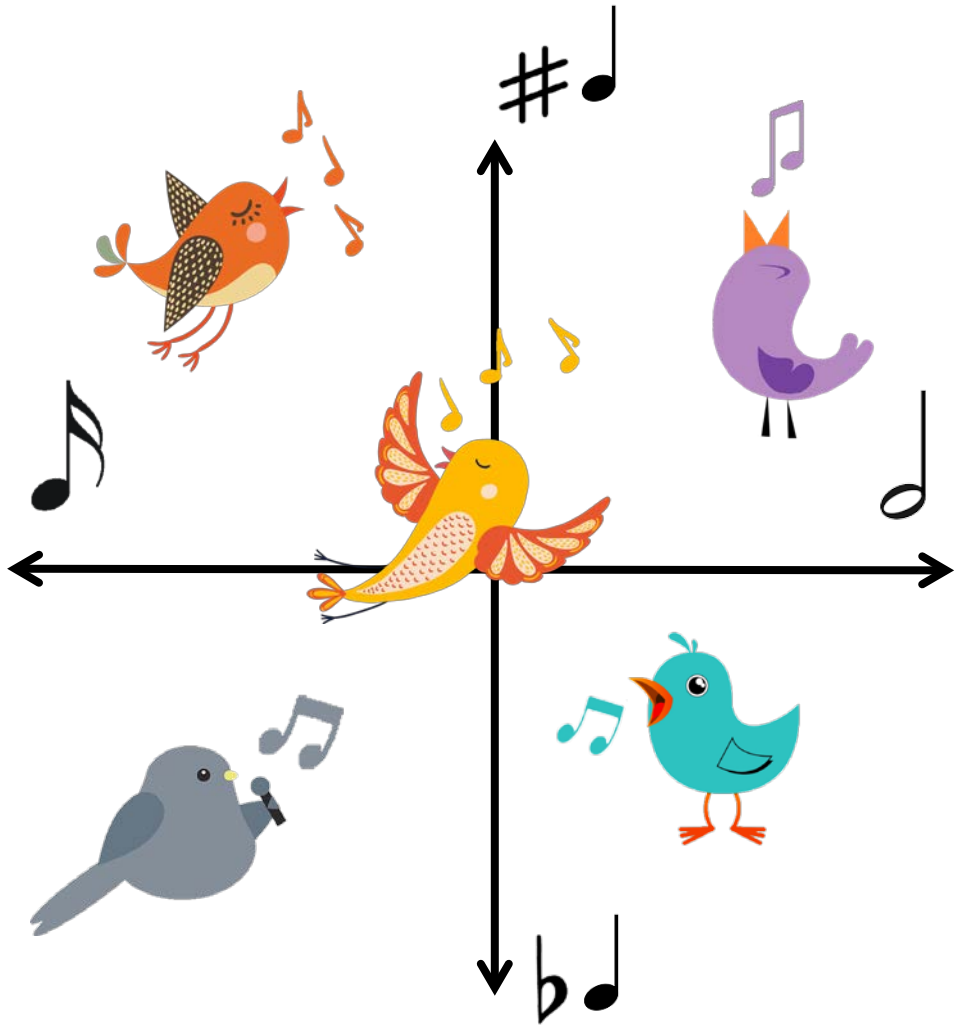
Mimicry ring n°6

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

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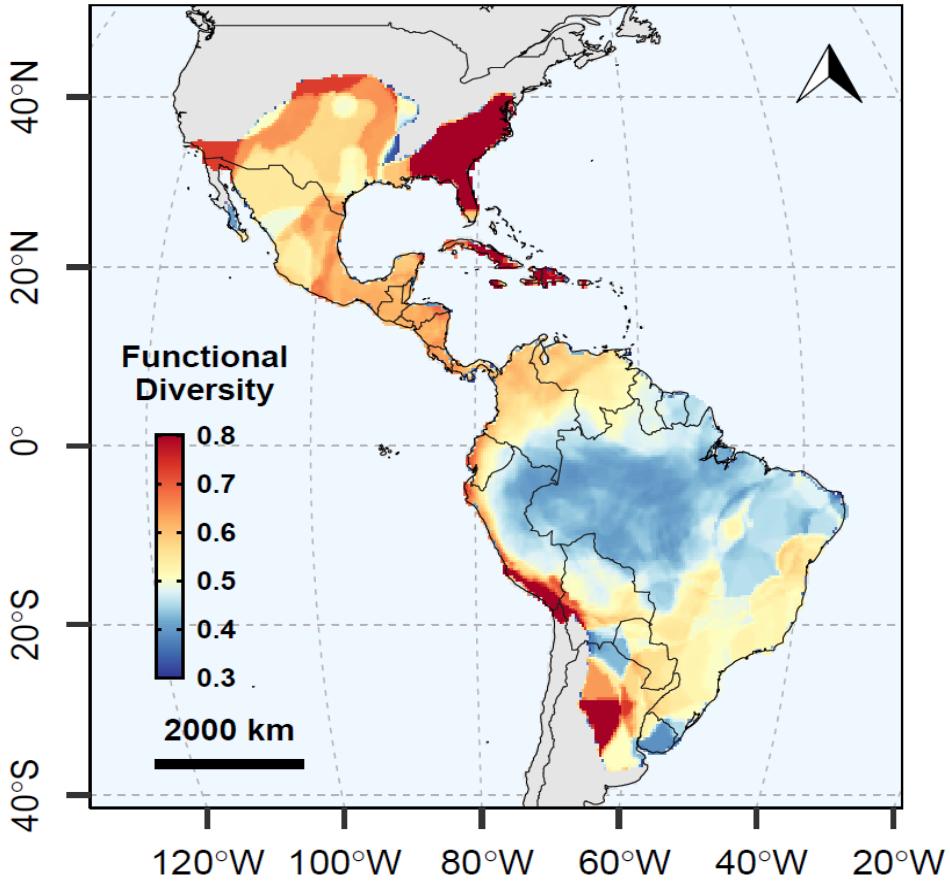

Doré et al., in prep.

Mimetic diversity as clustering in the local perceptual space

Conclusion

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

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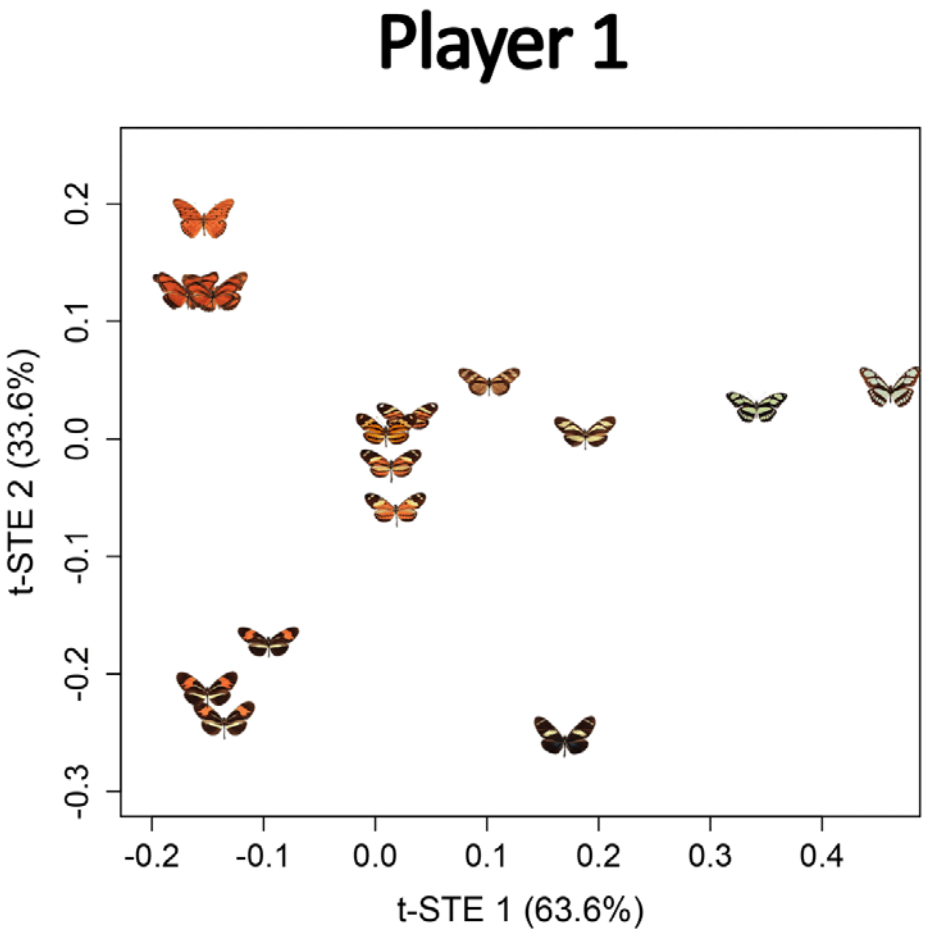


Comparison of indivudal perceptual maps

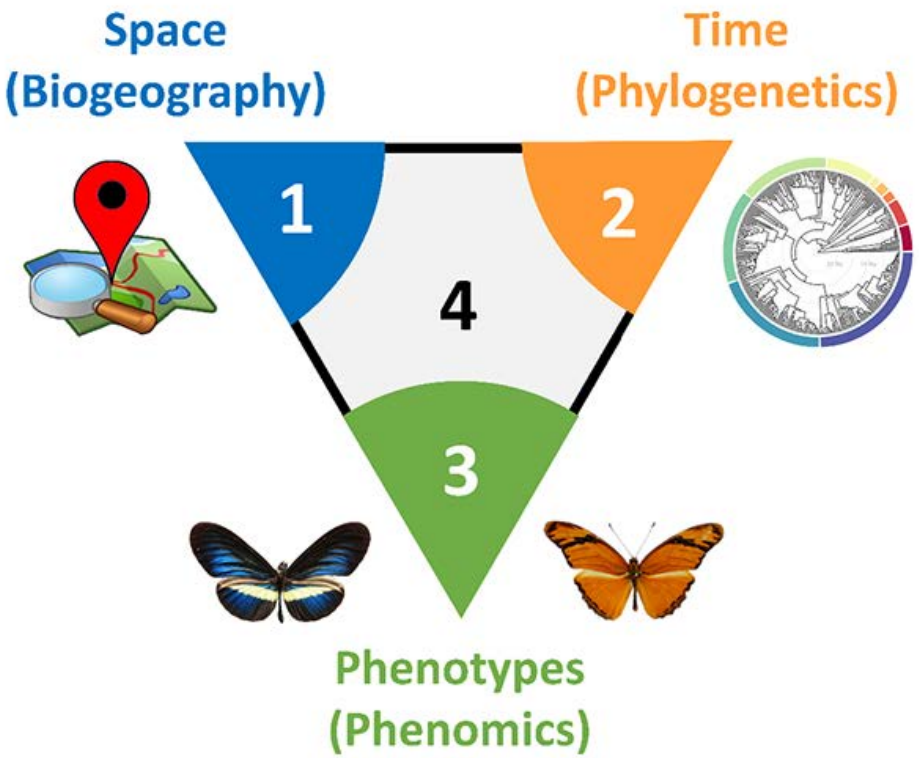
Outlines and objectives

CHAPTER 1

Map **biodiversity patterns**

CHAPTER 3

Quantify **phenotypic similarity** in wing patterns

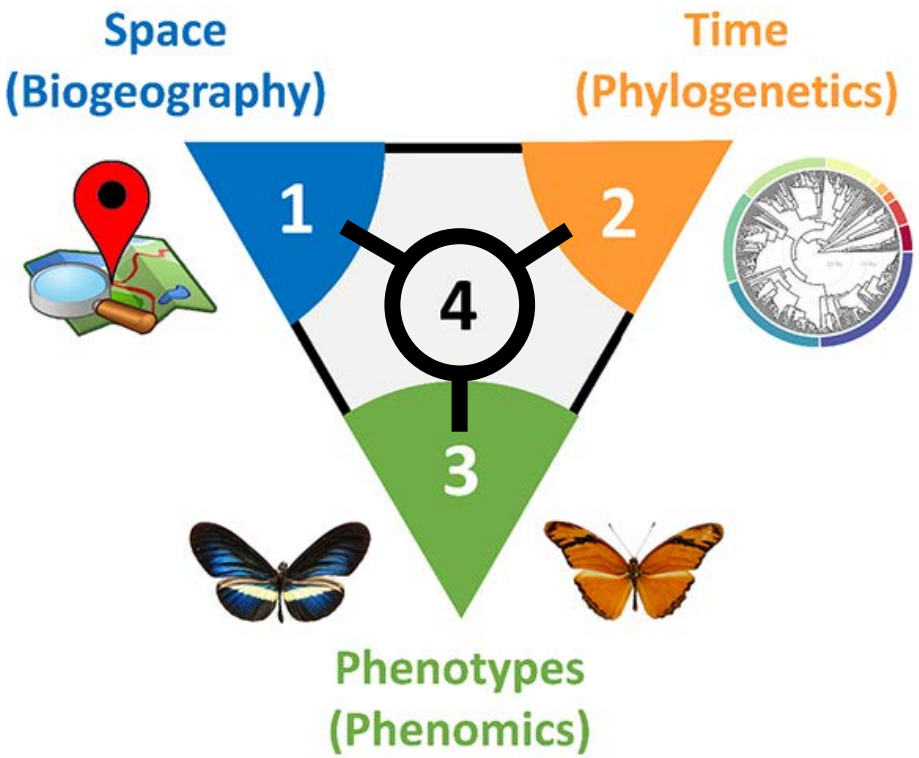


CHAPTER 2

Resolve **deep evolutionary relationships**

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

CHAPTER 4: Mutualistic interactions shape global spatial congruence and climatic niche evolution in Neotropical mimetic butterflies



Reference:

Doré, M., Willmott, K., Lavergne, S., Chazot, N., Freitas, A. V. L., Fontaine, C. & Elias, M. (2023). Mutualistic interactions shape global spatial congruence and climatic niche evolution in Neotropical mimetic butterflies. *Ecology Letters*. In production. https://doi.org/10.1111/ele.14198

Questions & 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

Study system: Neotropical butterflies

Ithomiini tribe

Credits Photo: N. Chazot

8 shared patterns

Heliconiini tribe

Credit photos: C. Jiggins

44 putative mimicry rings

39 putative mimicry rings

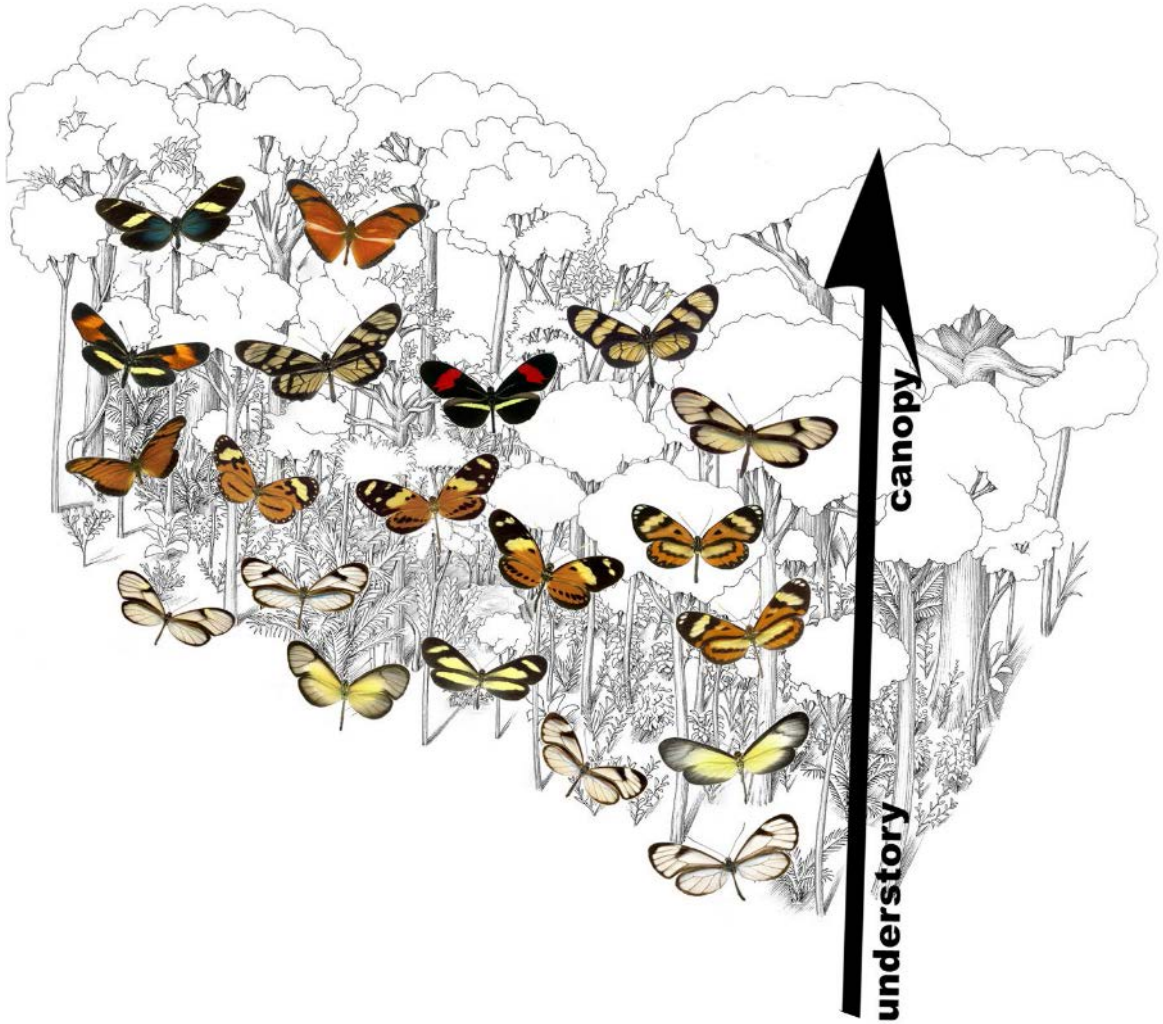
State-of-the-art

Structuration of mimetic communities by:

- **flight height** *(Beccaloni, 1997)*
- **microhabitats** *(Elias et al., 2008)*
- **host plants** *(Willmott & Mallet, 2004)*
- **altitude** *(Chazot et al., 2014)*

Limits :

- **Spatial**: local to regional
- **Taxonomic**: few genera



Adapted from Birskis-Baros et al., 2021

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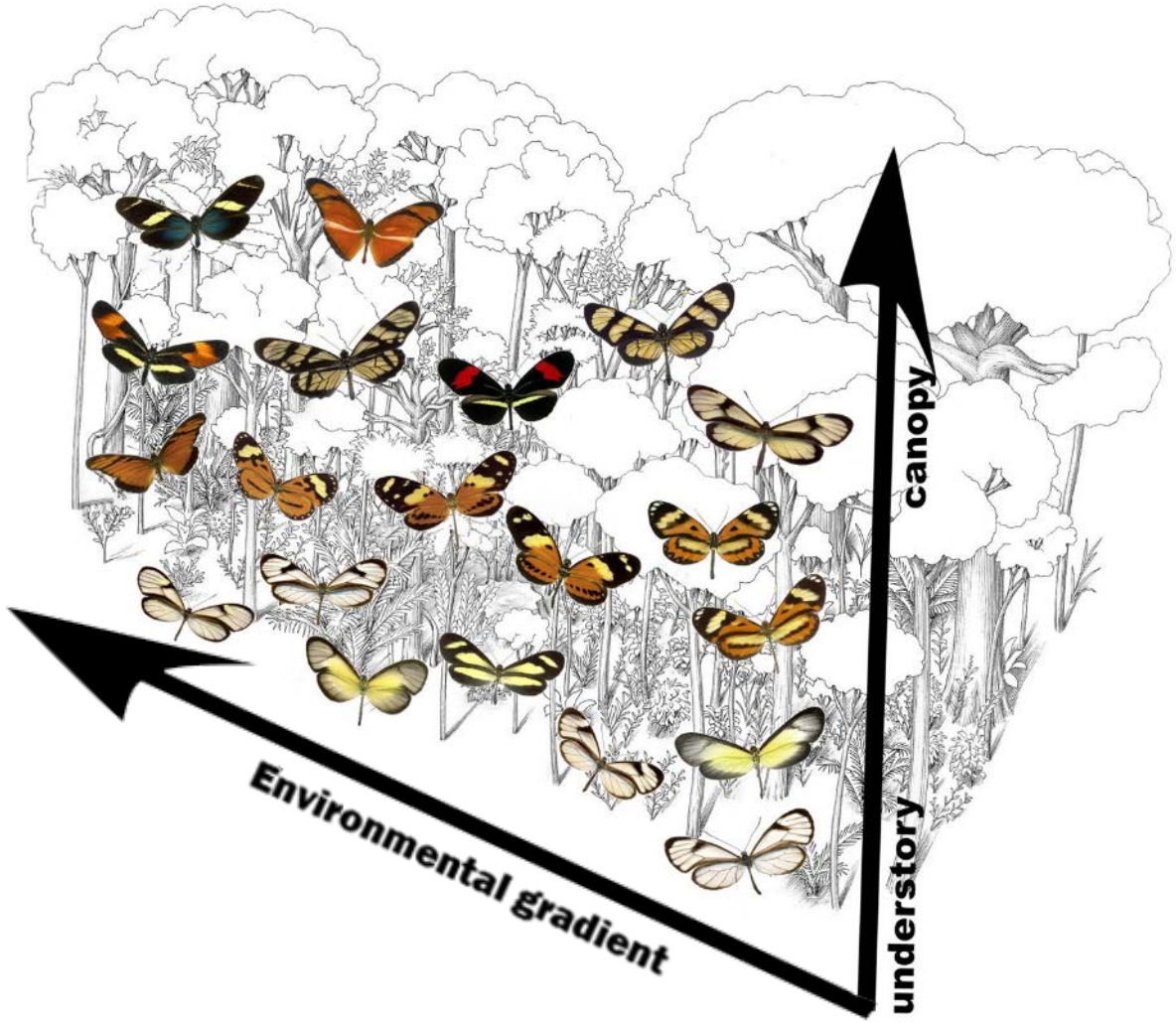

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Credits: Arthur Anker

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This study: **macroecological scale** for the **whole tribes**
Dimensions = **climatic niche**

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Can **mutualistic interactions** outweigh the effects of **competition** at the **macroecological scale**?

1. **Spatial congruence**: Do phenotypically similar species **cooccur** more than expected at random?

2. **Niche similarity**: Do phenotypically similar species have **similar climatic niche**?

3. **Niche convergence**: Is the climatic niche of phenotypically similar species **more similar** than expected from **shared ancestry**?

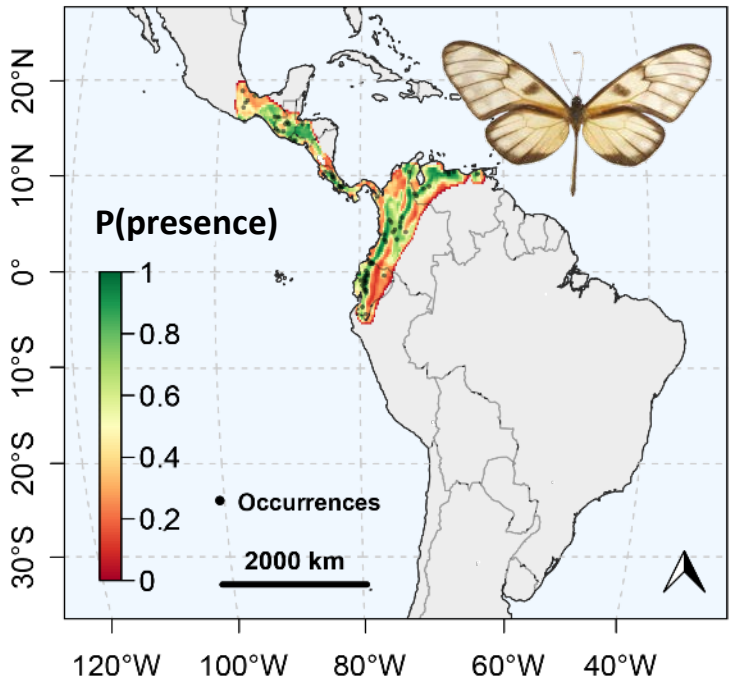
Spatial congruence

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

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

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

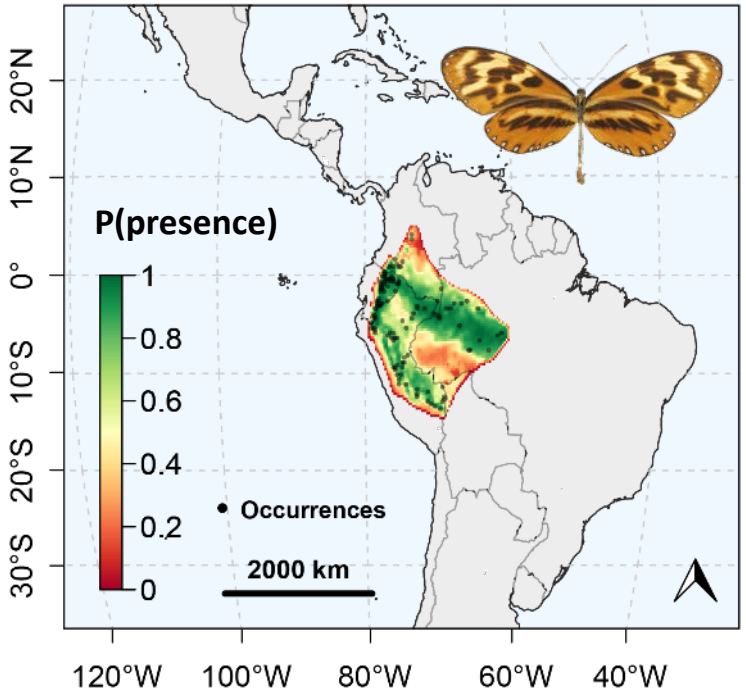
Dircenna jemina **(DILUCIDA)**



No mimicry

BC = 0.9

Mechanitis mazaeus **(MAELUS)**



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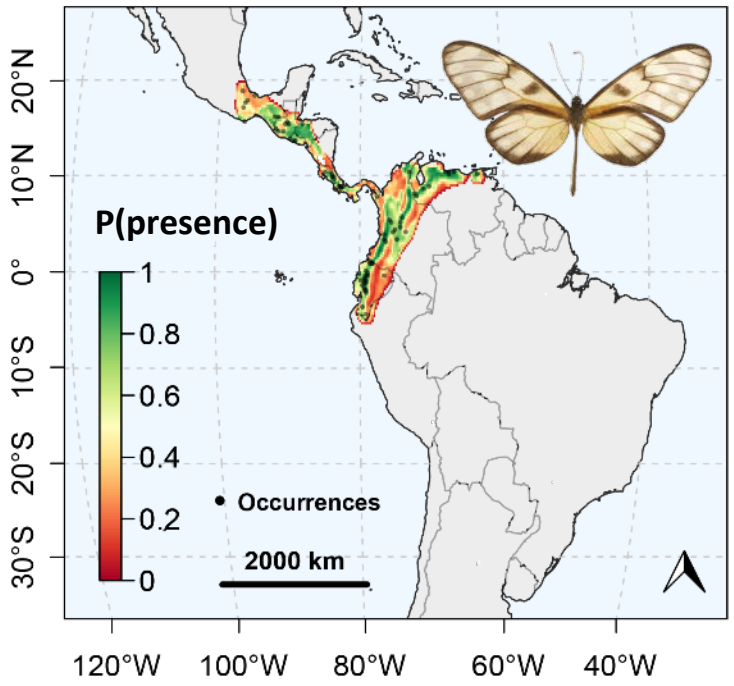
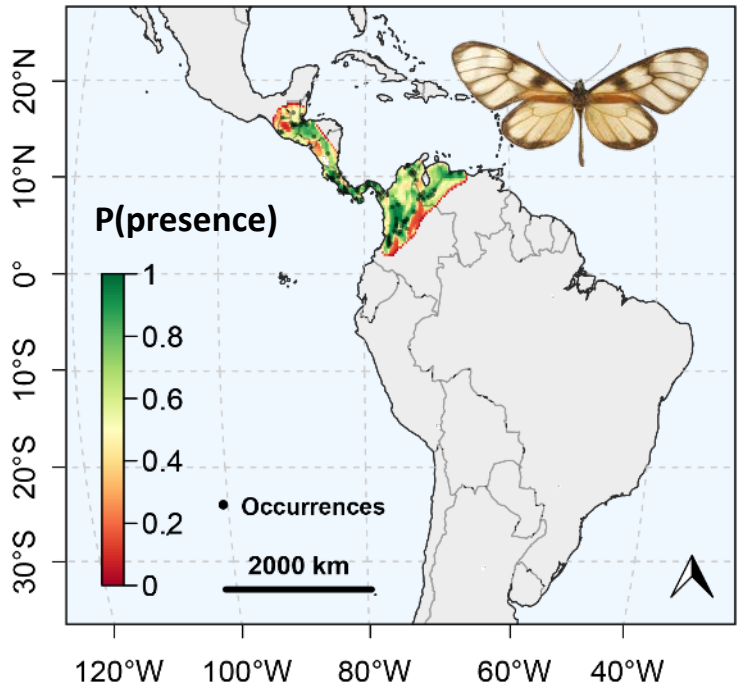


Mimicry

BC = 0.2

Dircenna dero **(DILUCIDA)**



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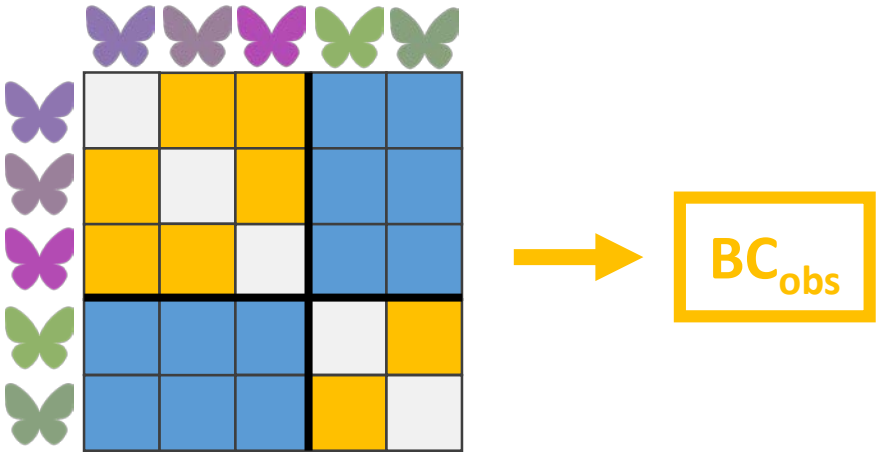
Index: mean BC within **phenotypic groups**

Test: Random permutation of phenotypic group memberships



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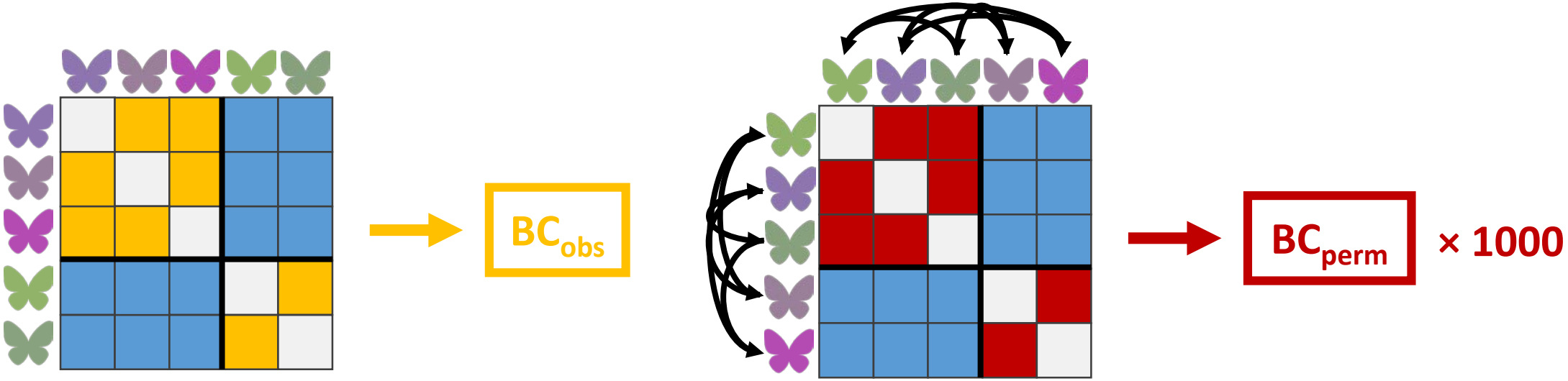


Spatial congruence

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

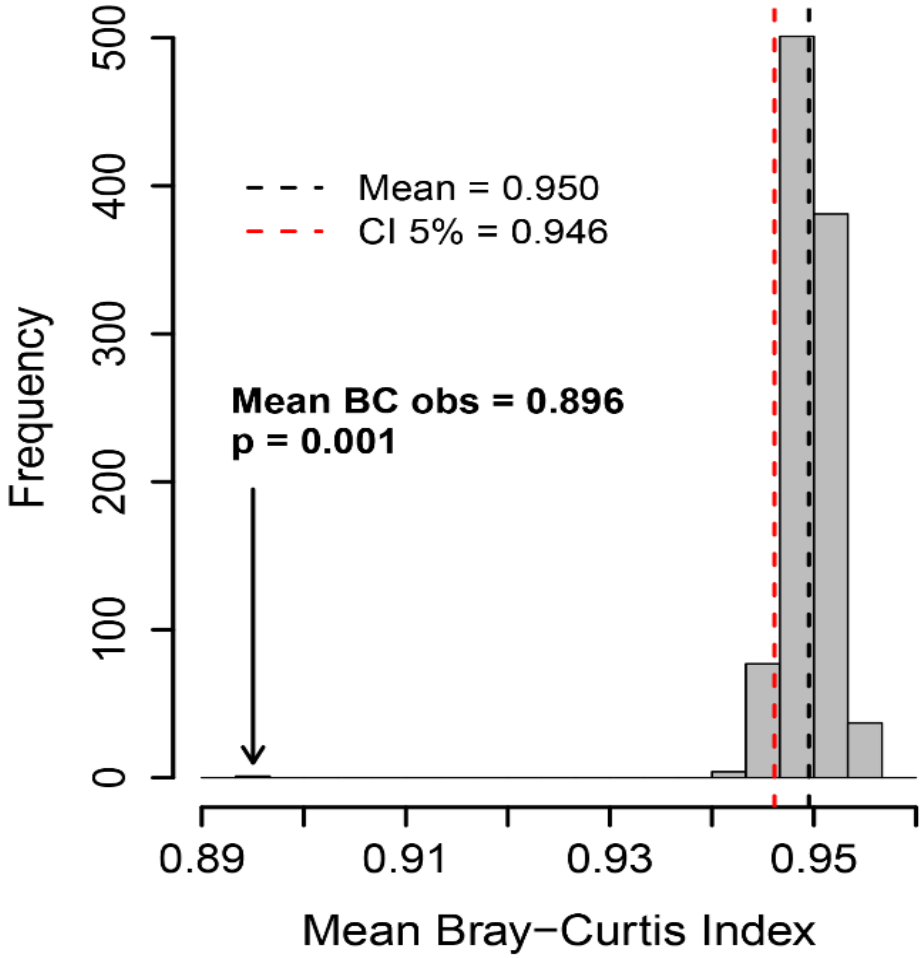
Global: Mean BC_{obs} << Mean BC_{perm}

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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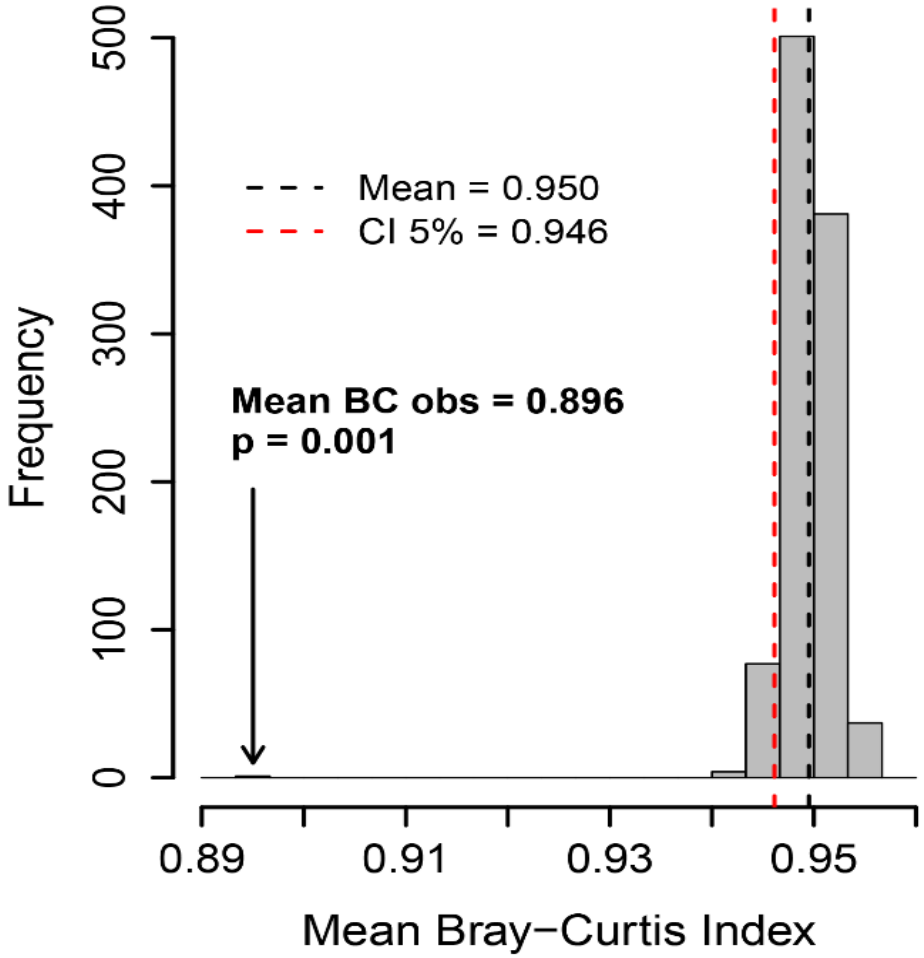

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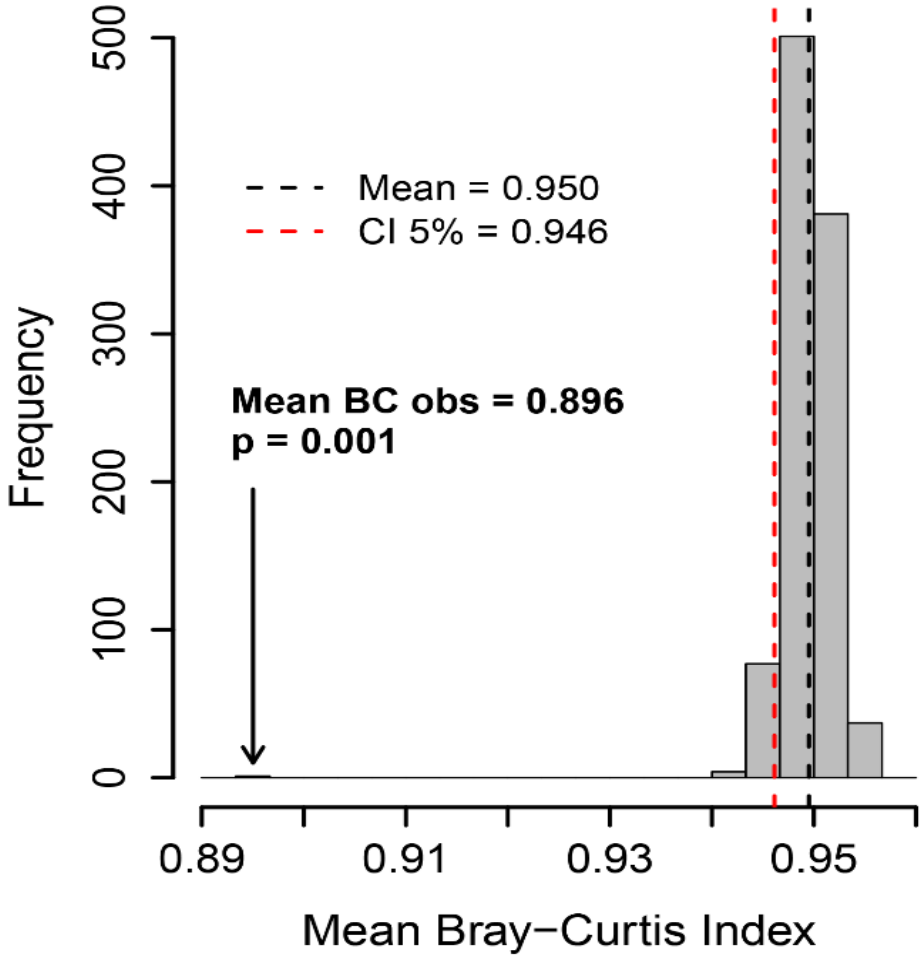
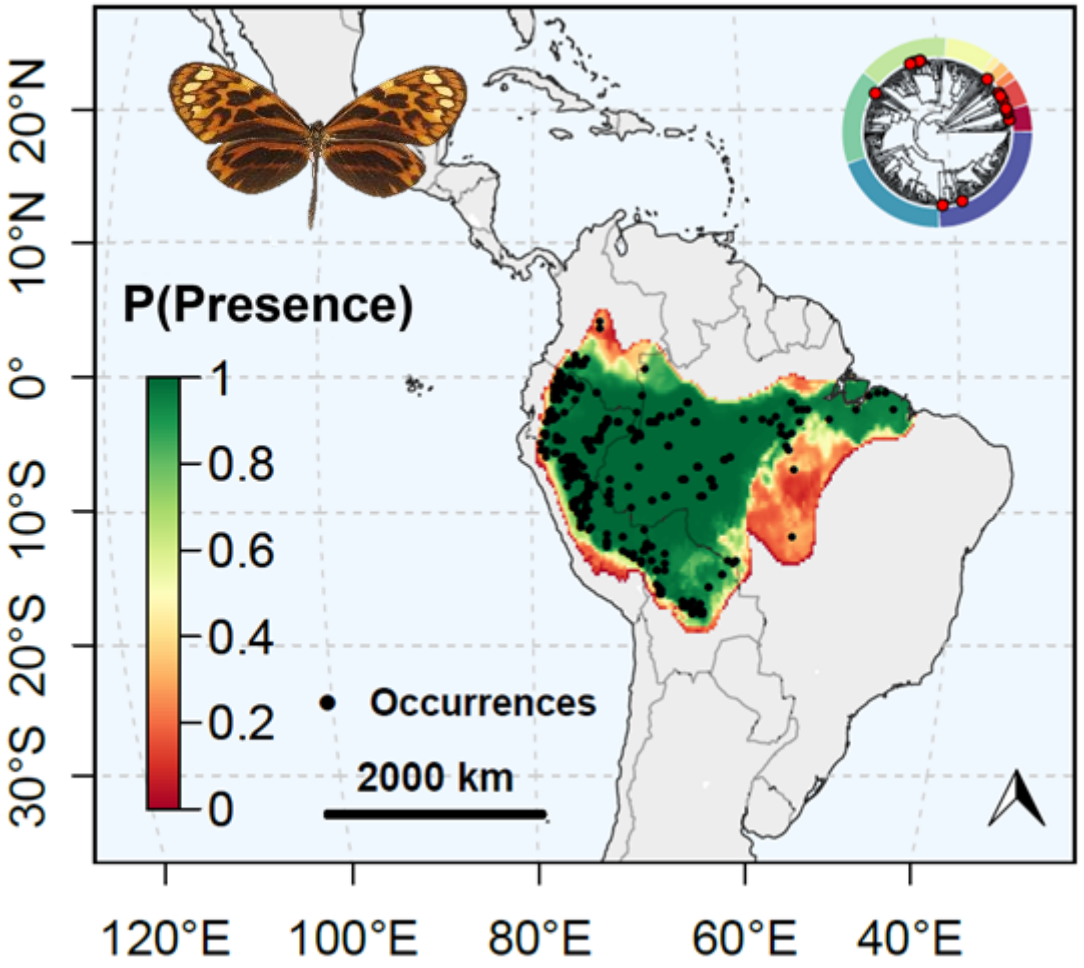
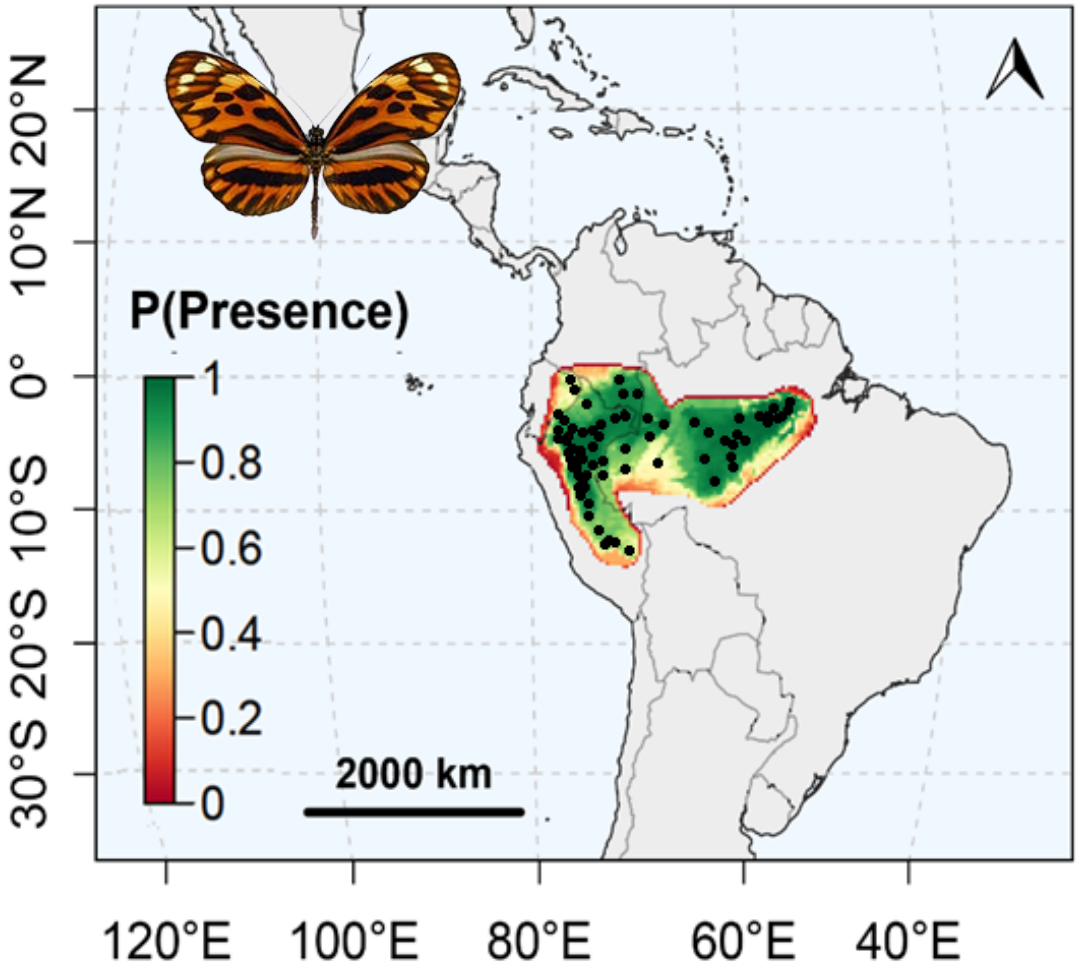


Spatial congruence

Ithomiini: pattern MAELUS
(16 species)

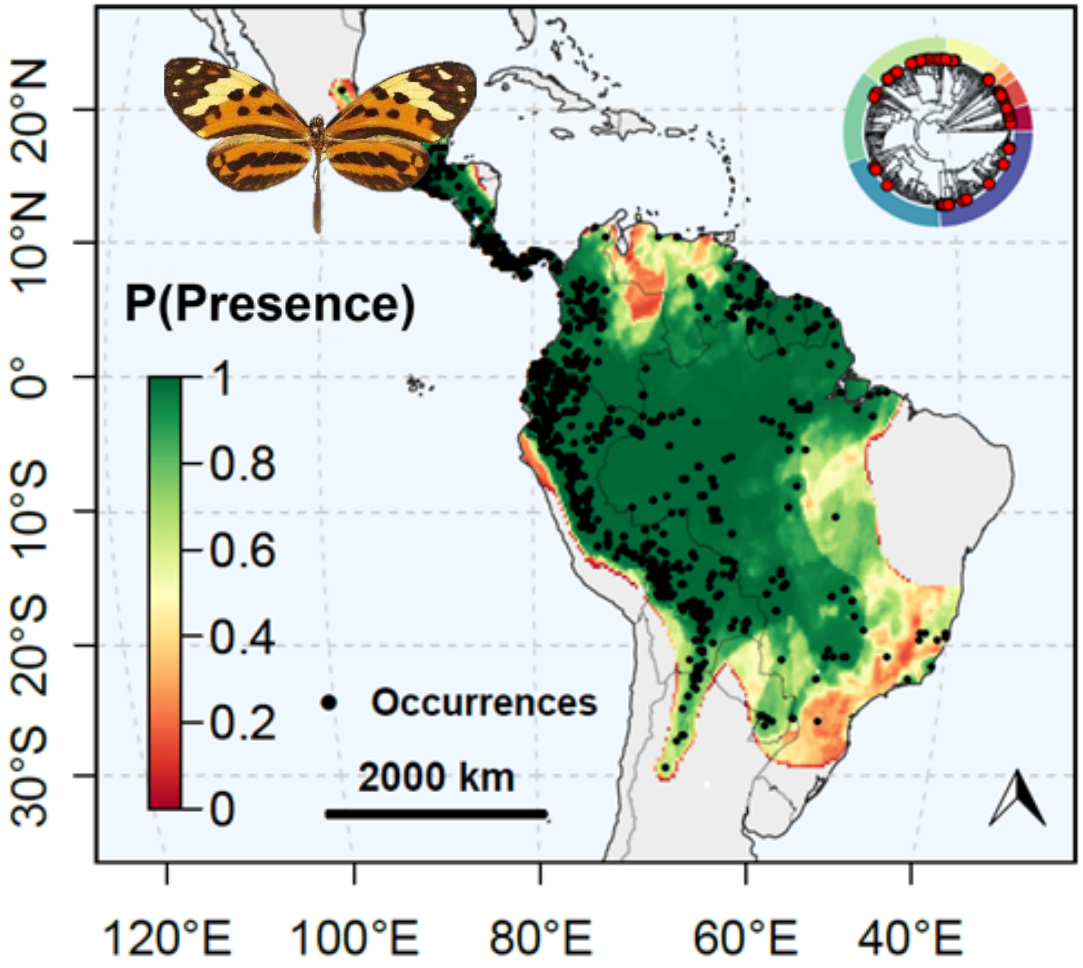


Heliconiini: pattern MAELUS
(5 species)

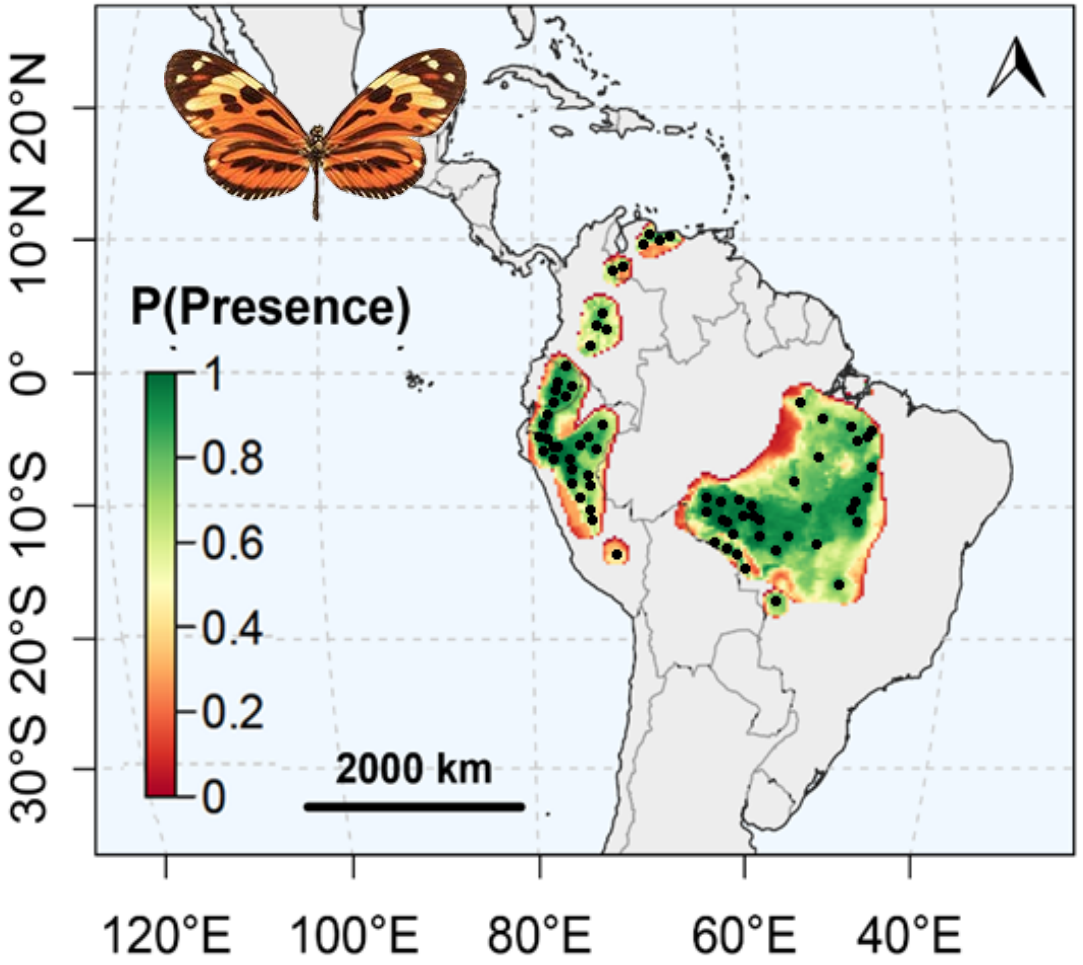


Spatial congruence

Ithomiini: pattern MAMERCUS (64 species)



Heliconiini: pattern MAMERCUS (10 species)



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Climatic niche similarity

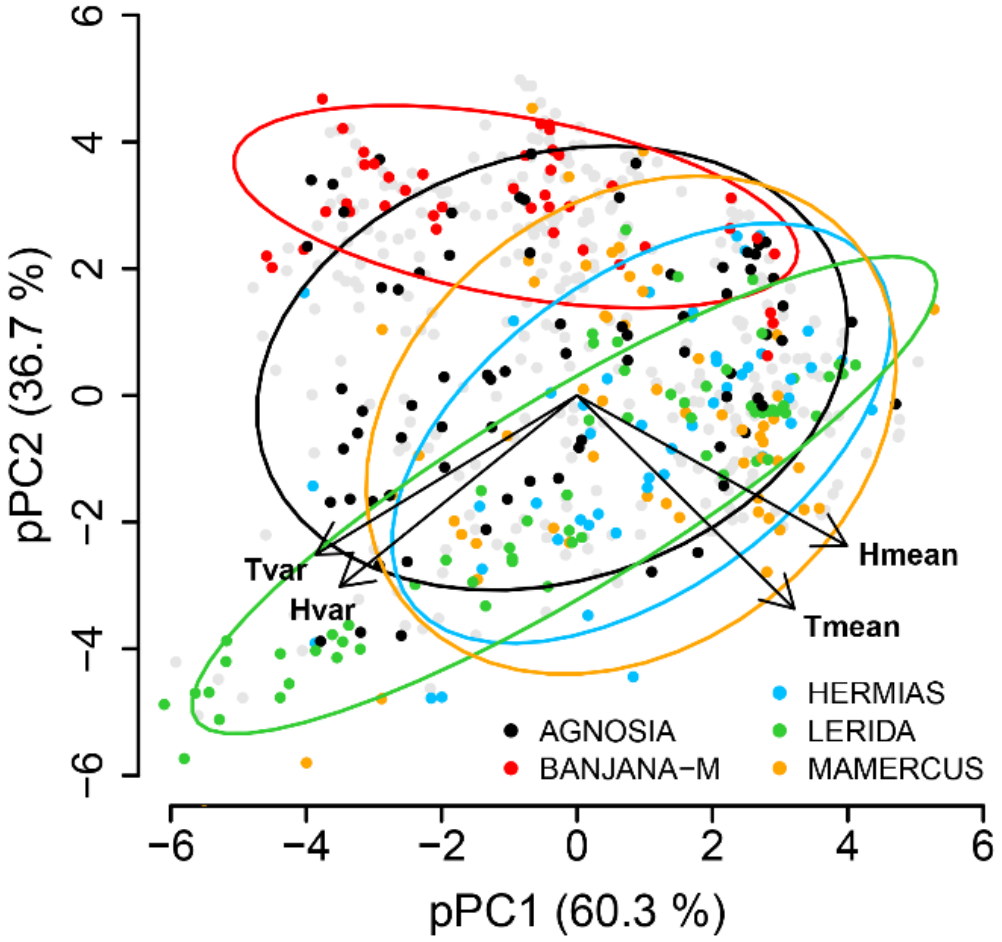
Question: Do **phenotypic groups** occupy different **climatic niche**?

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

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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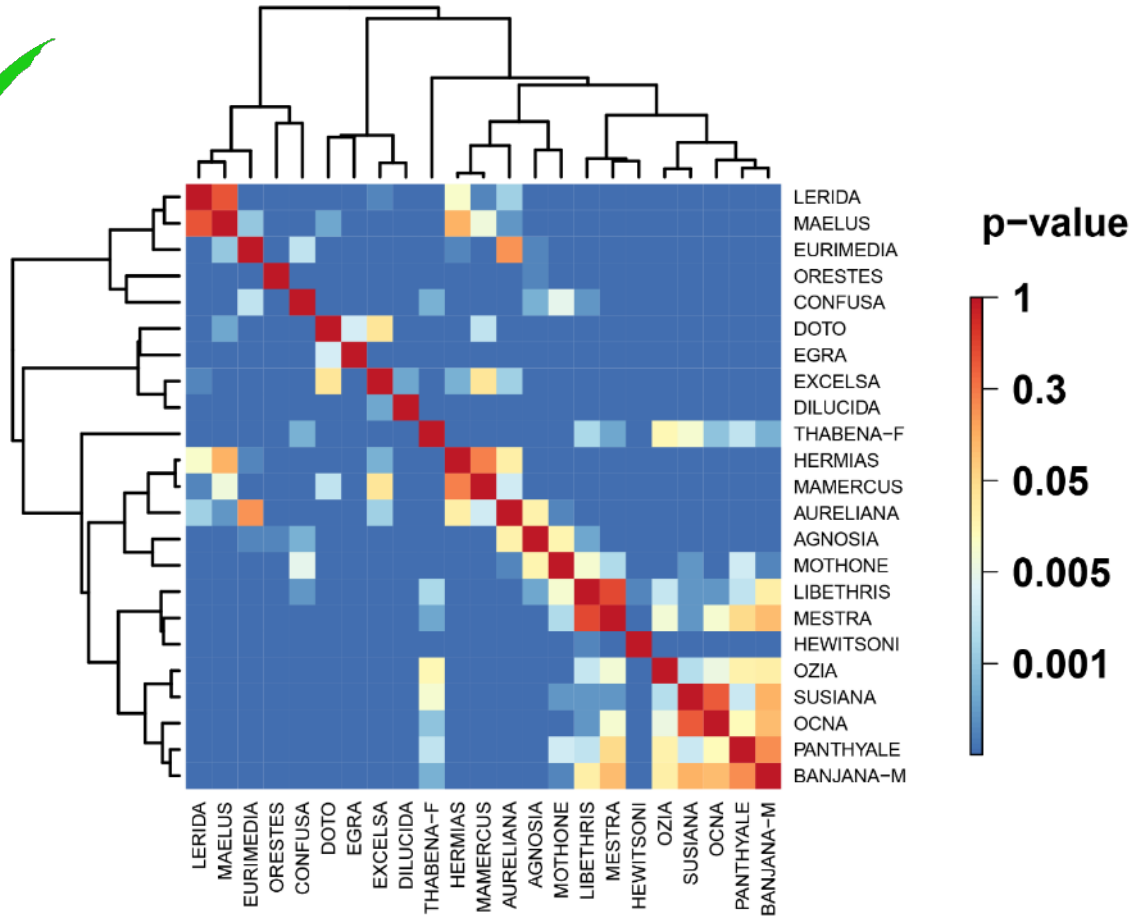

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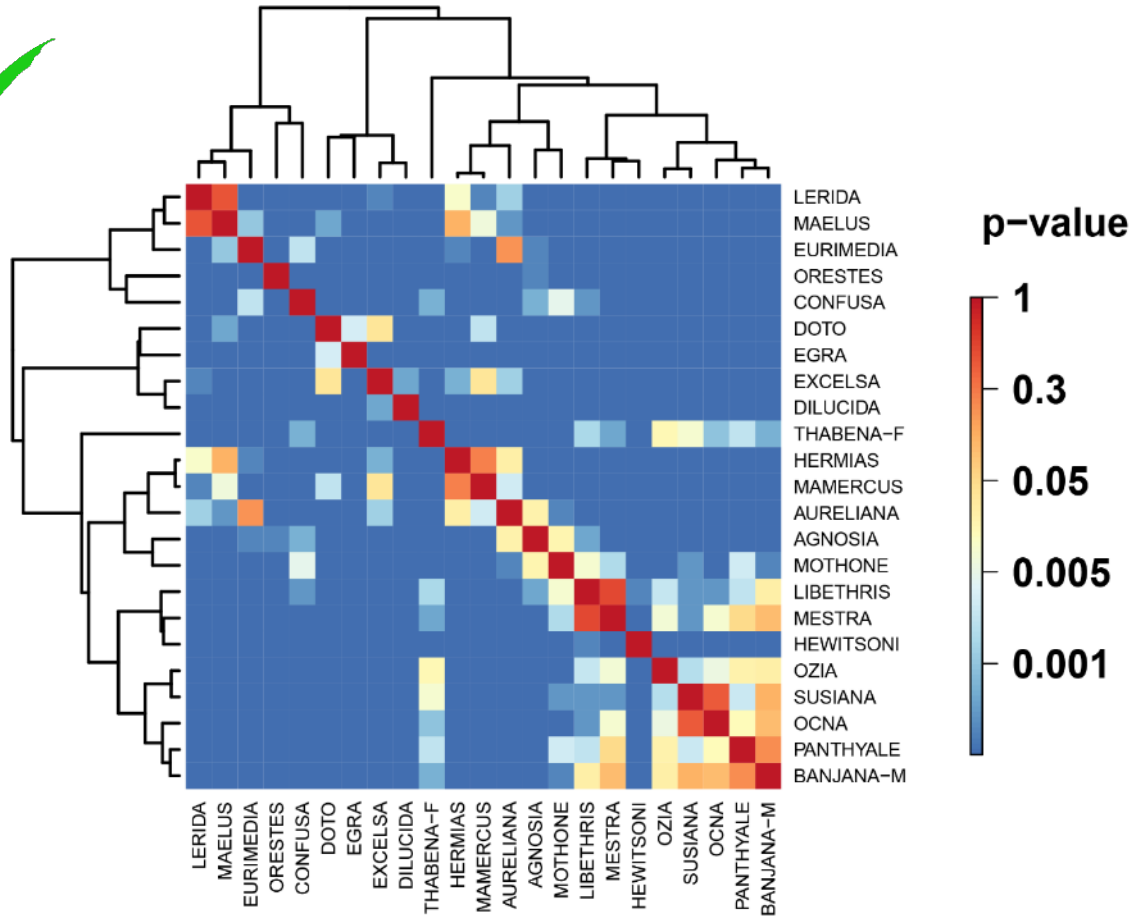

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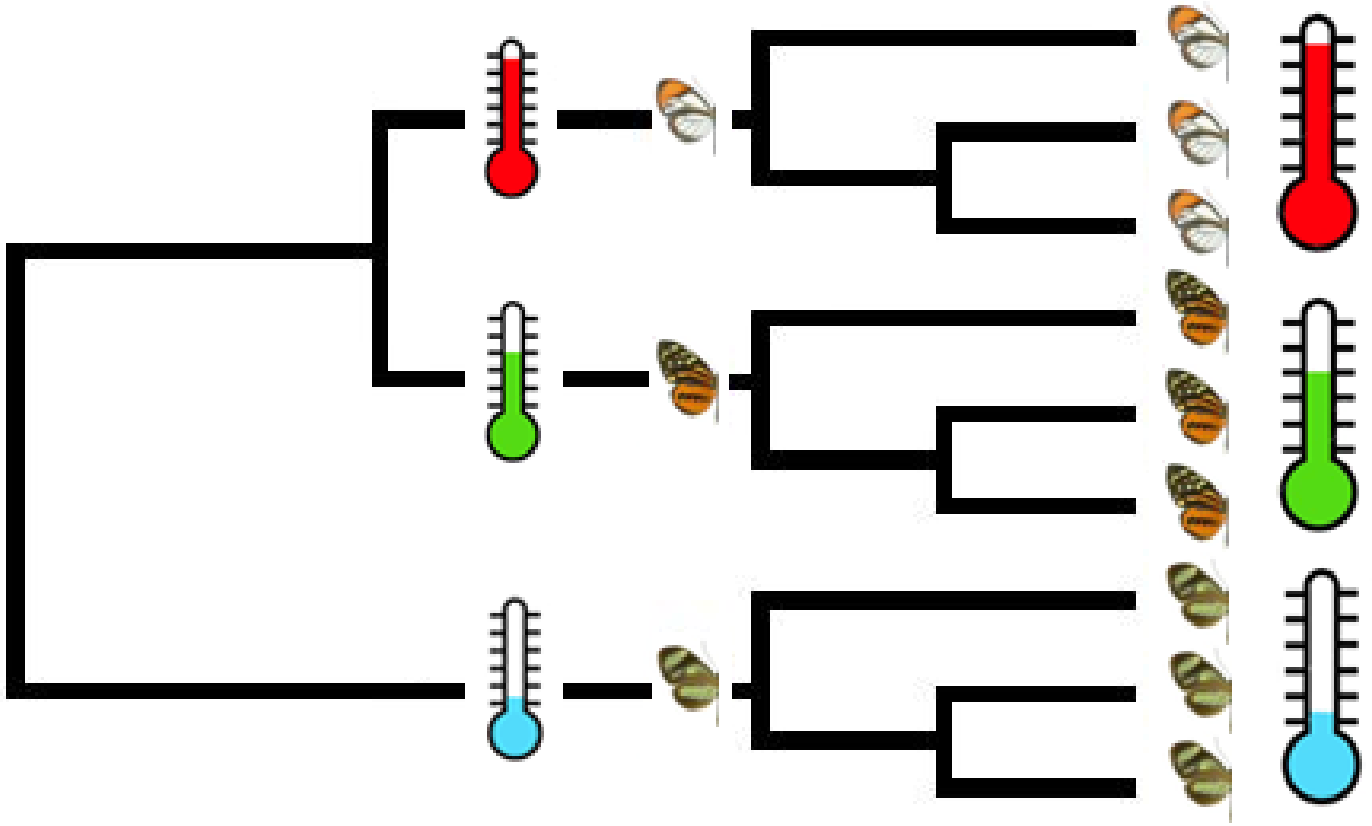
Climatic niche evolution

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



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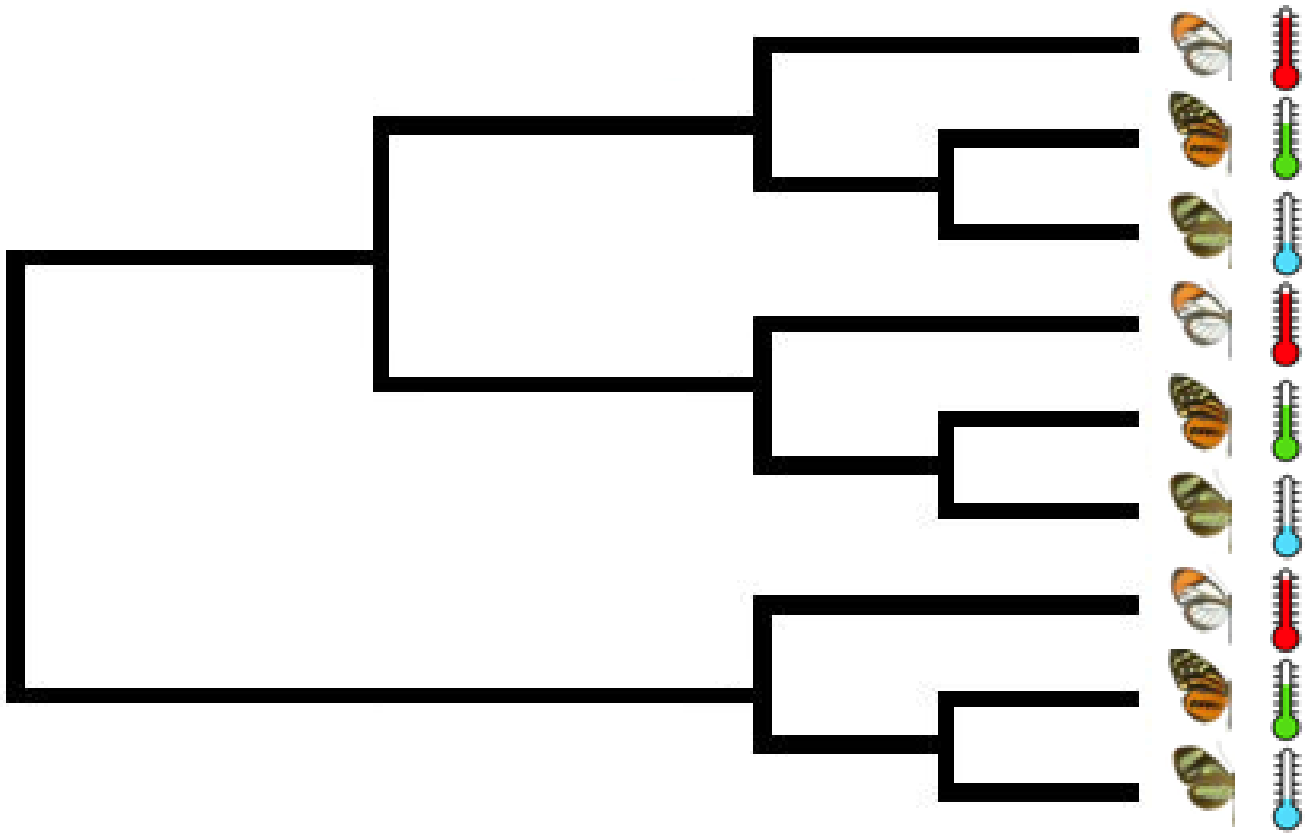


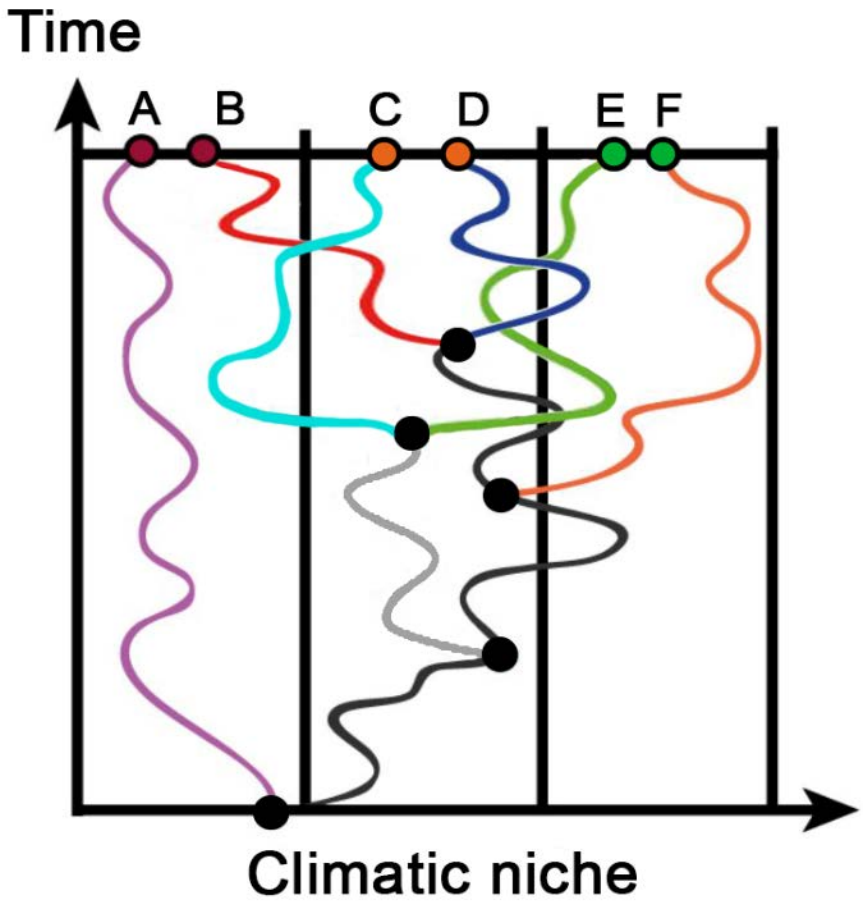
Climatic niche evolution

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 **mimicry patterns**



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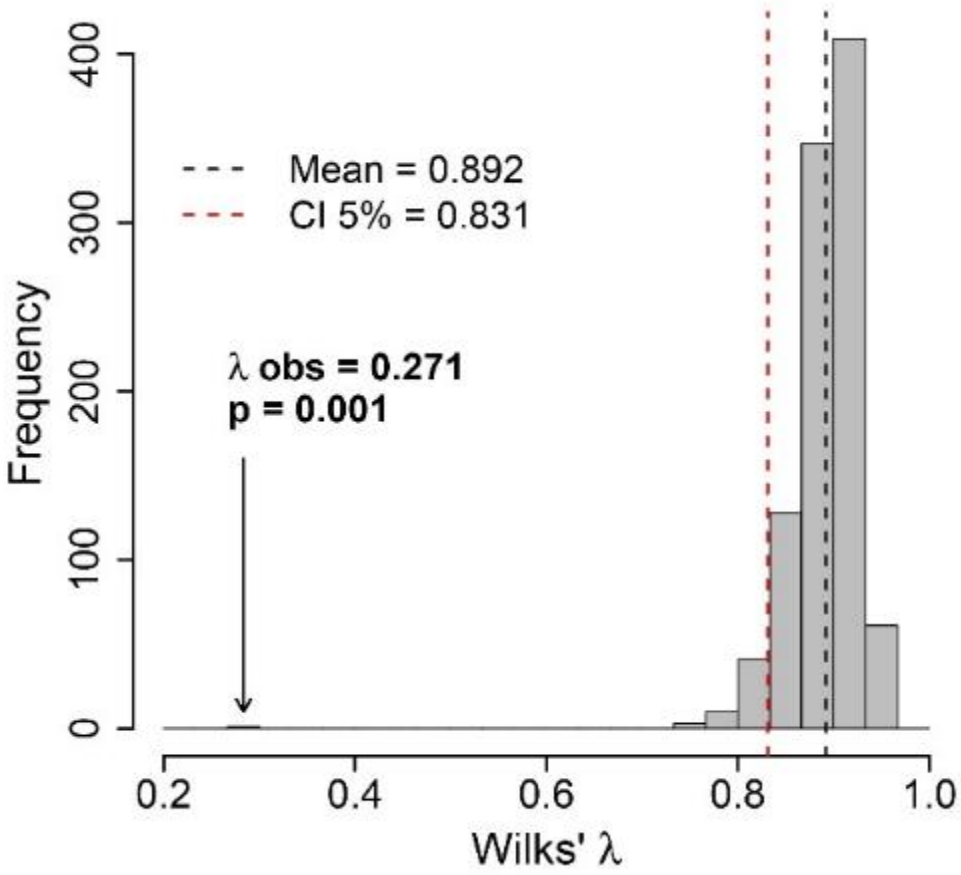

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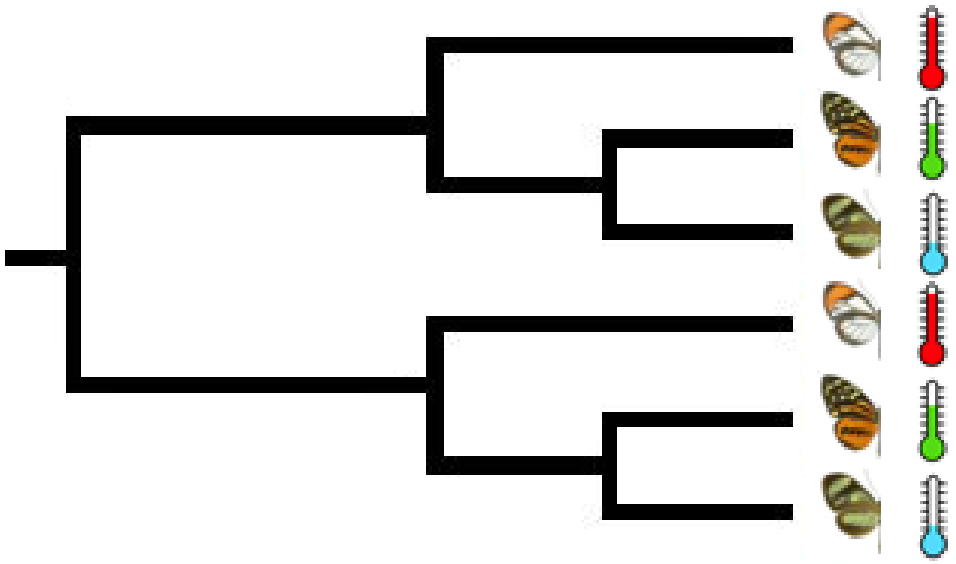
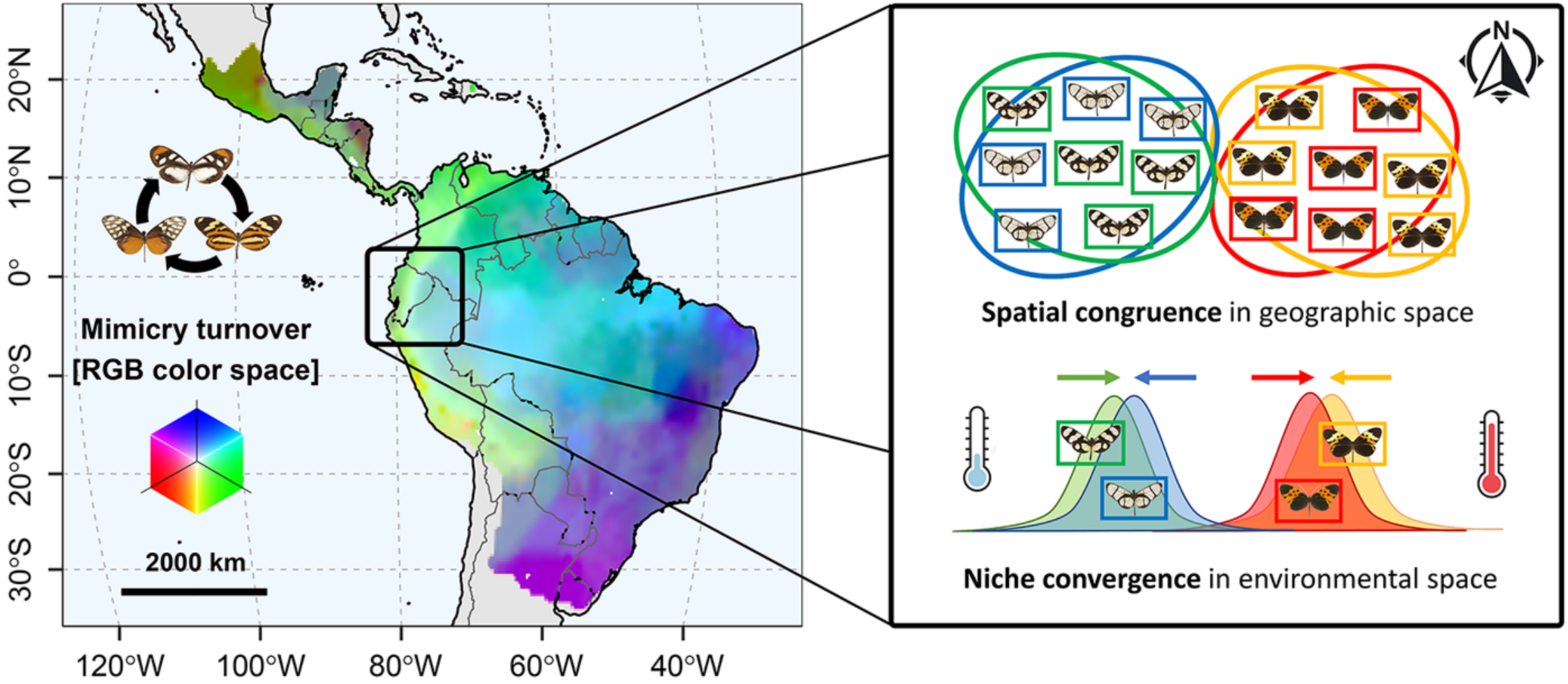
Results: **Evolutionary convergence** between **climatic niche** and **mimicry patterns**

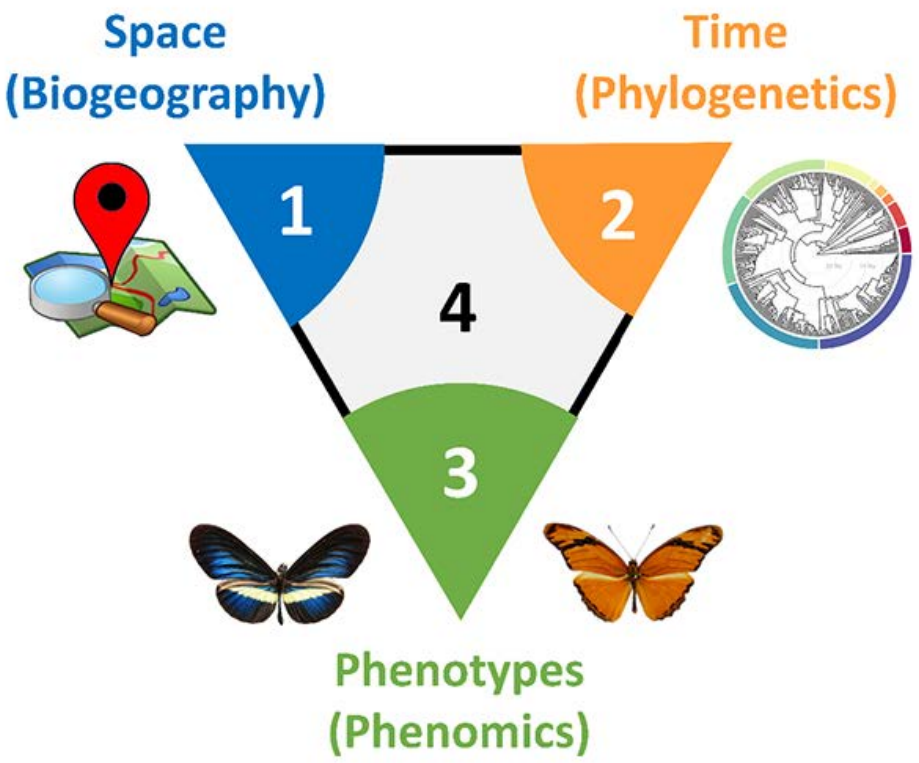
Evolutionary convergence



Conclusion


30°S
20°S
10°S
0°
10°N
20°N
120°W
100°W
80°W
60°W
40°W
Mimicry turnover
[RGB color space]
2000 km
N
Spatial congruence in geographic space
Niche convergence in environmental space

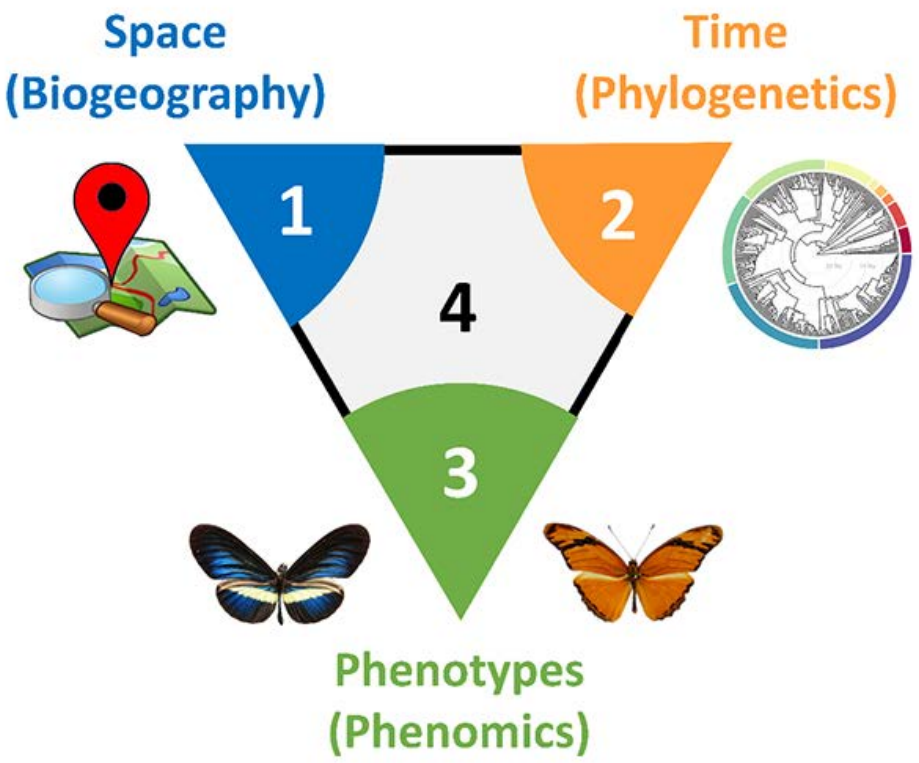
SUMMARY AND PERSPECTIVES



SUMMARY AND PERSPECTIVES

Map **biodiversity patterns** for an **indicator group** in the **Neotropics**

Address the **Wallacean shortfall**



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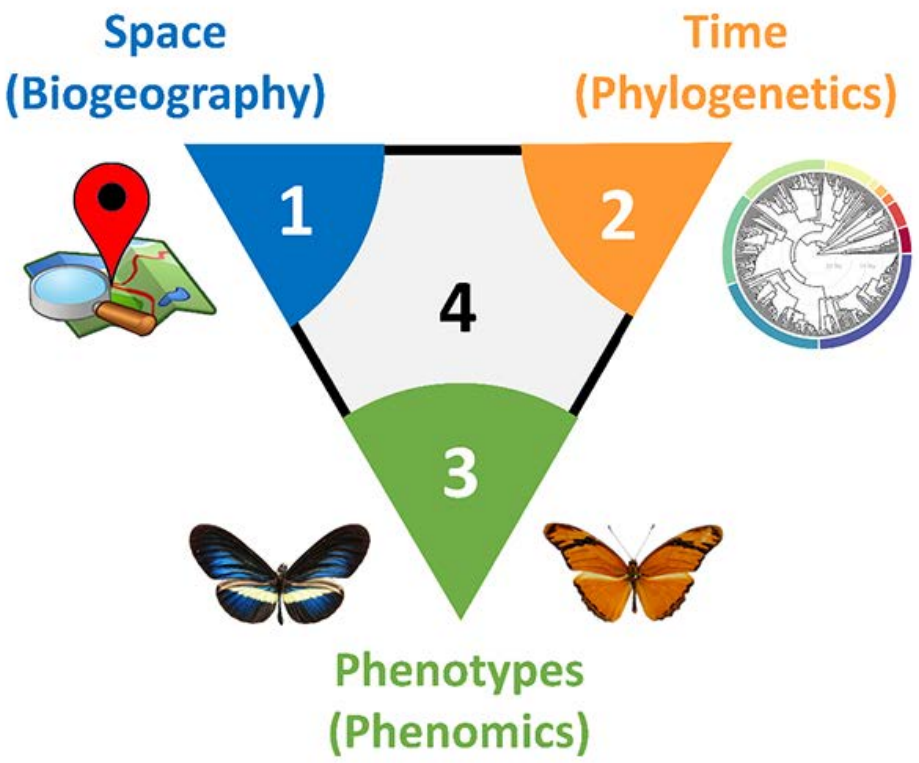

Resolve **deep evolutionary relationships**

New robust phylogeny to test for **macroevolutionary hypotheses**

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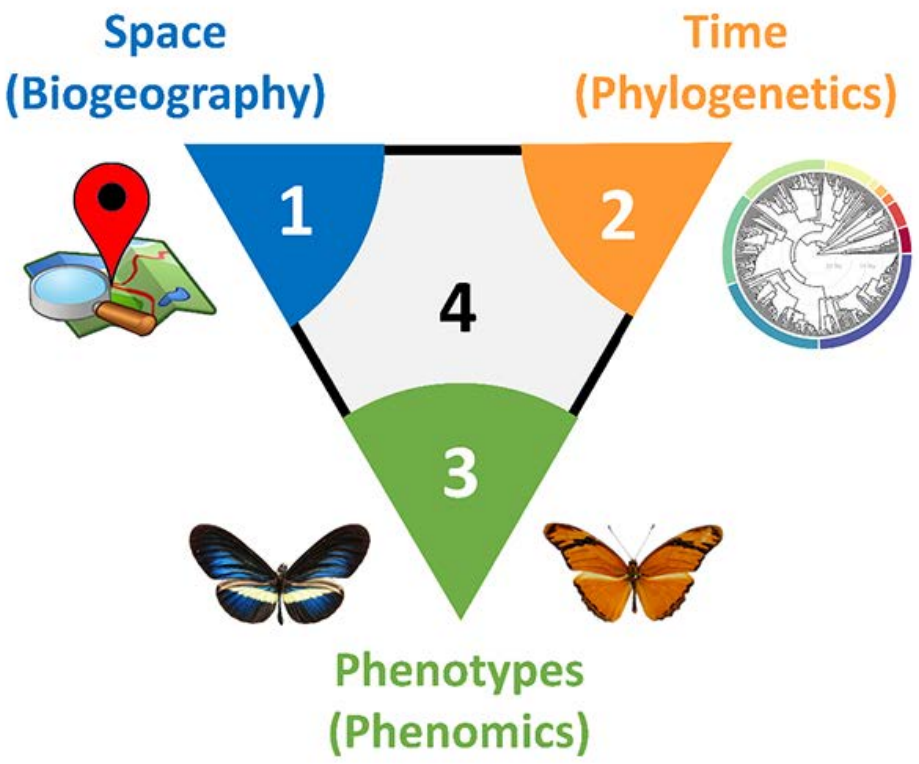
New method to quantify **phenotypic similarity** in any ecological signals

Enable **multi-scale** analyses



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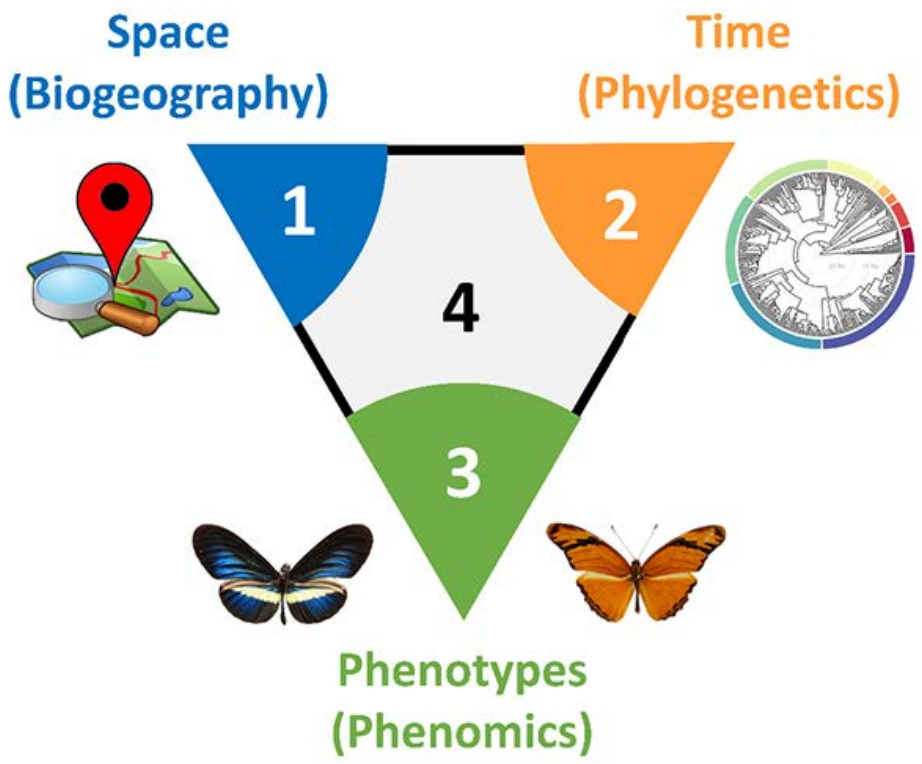


Resolve **deep evolutionary relationships**

New robust phylogeny to test for **macroevolutionary hypotheses**

New empirical evidence for **Müller's model** at a **macroecological scale**

Importance of **ecological interactions** in shaping **species distributions** and **niche evolution**

Inclusion in **conservation assessments** and **global change studies**

Neotropical mimetic butterflies facing climate changes

Specific case of Tropical Andean communities

Long-term **climatic stability**

+

Low diurnal and annual variation

=

Narrow climatic niches

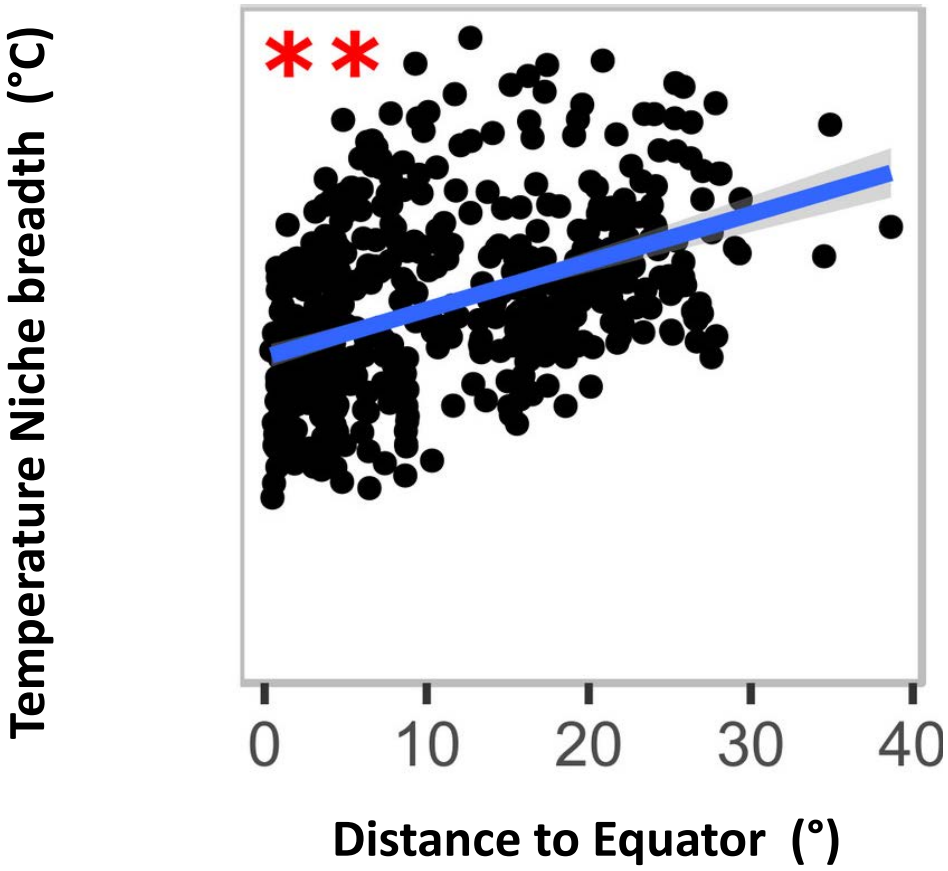
(Trew & Maclean 2021)

Rugged topography

=

Barrier to dispersal + **isolation**

Consequences = **sensitivity to climate change**



(Cuesta et al., 2020)

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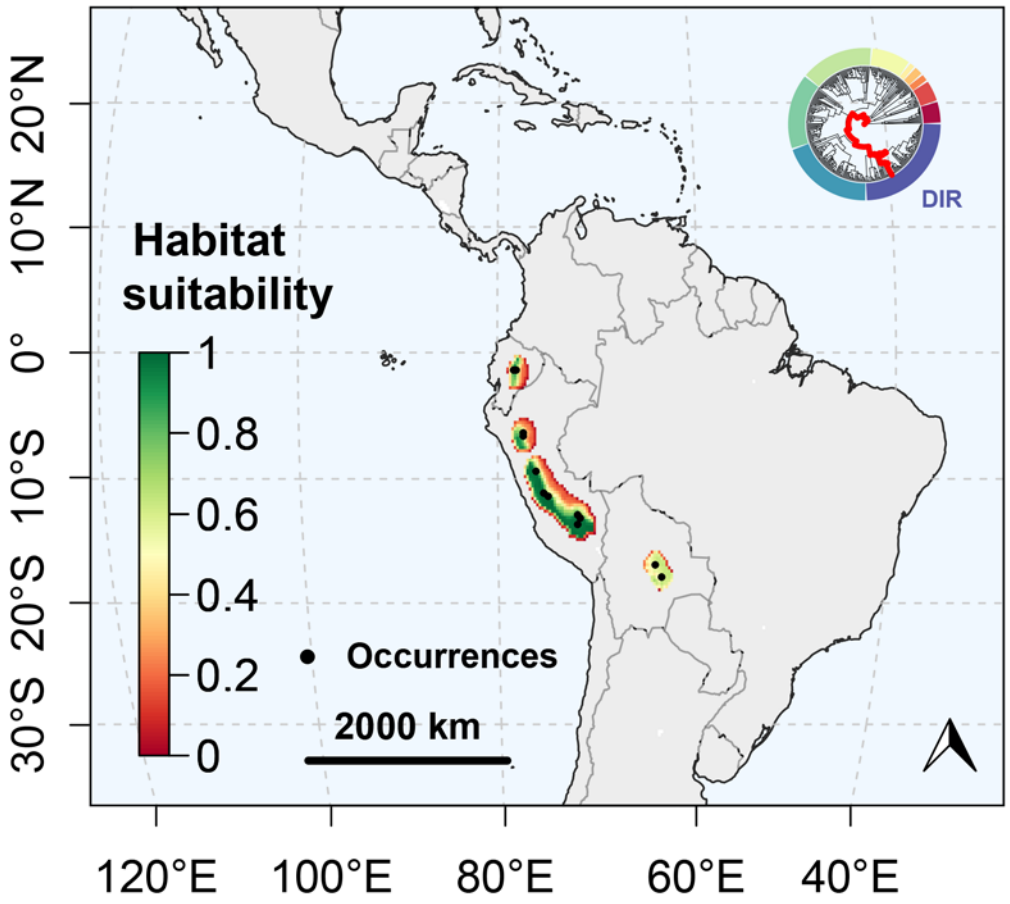
***Episcada hymenaea* (LIBETHRIS)**



(Doré et al., 2021)

Neotropical mimetic butterflies facing climate changes

Mutualistic communities = **adaptive assemblage** of species (patterns + niche)

- Sensitivity to interaction disruption and **cascade of extinctions**

Which response to **climate change**?

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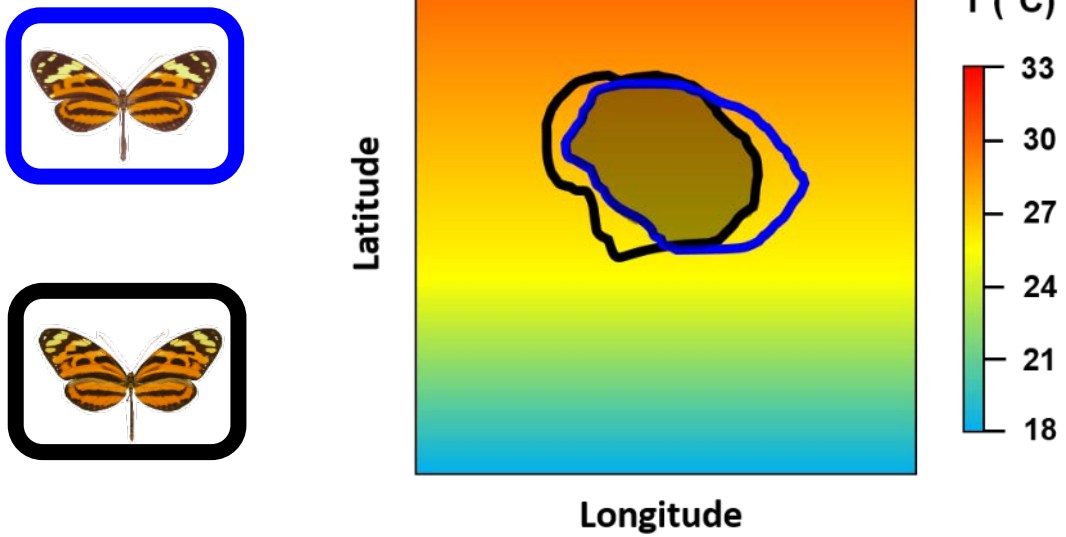

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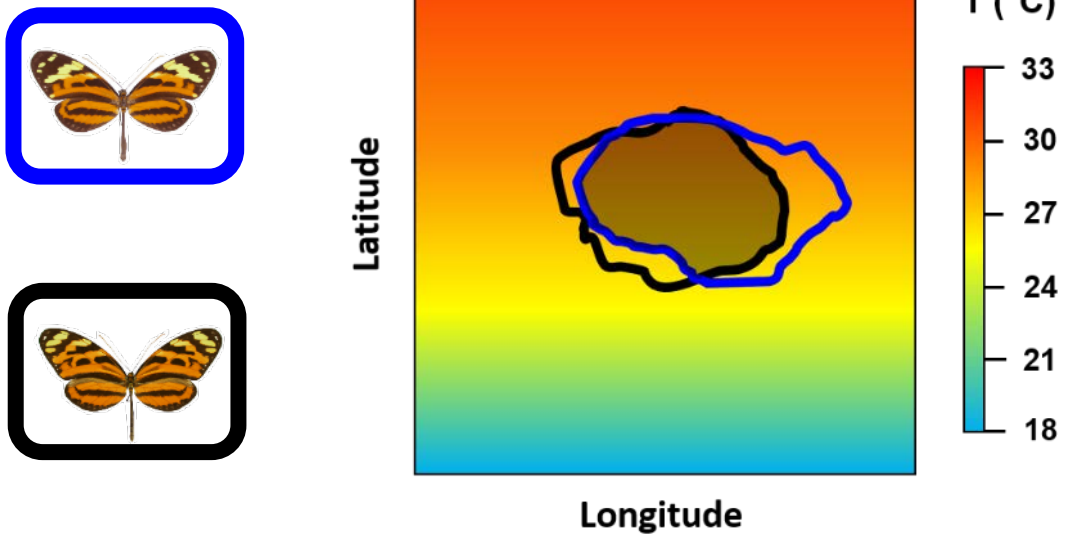

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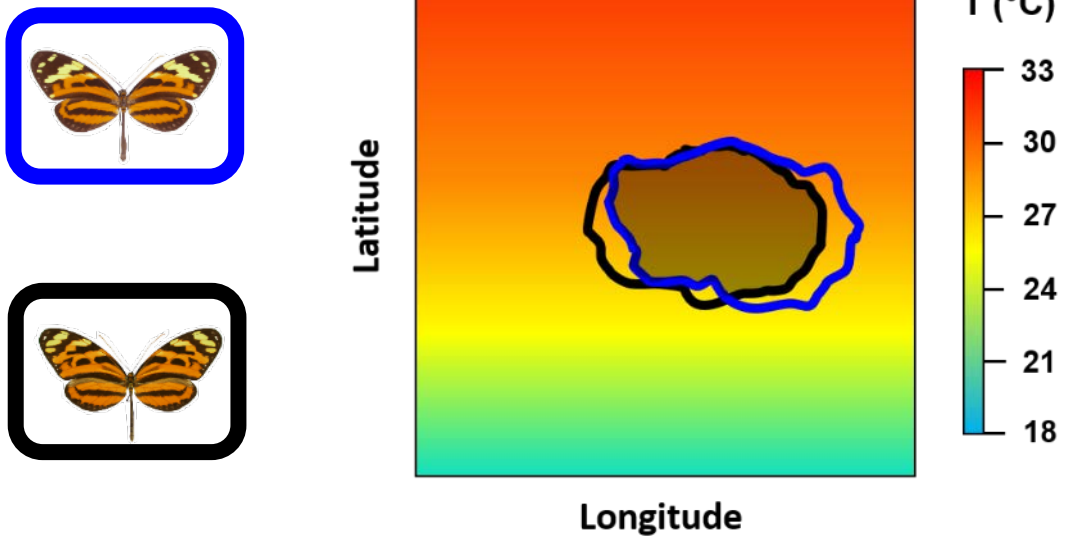

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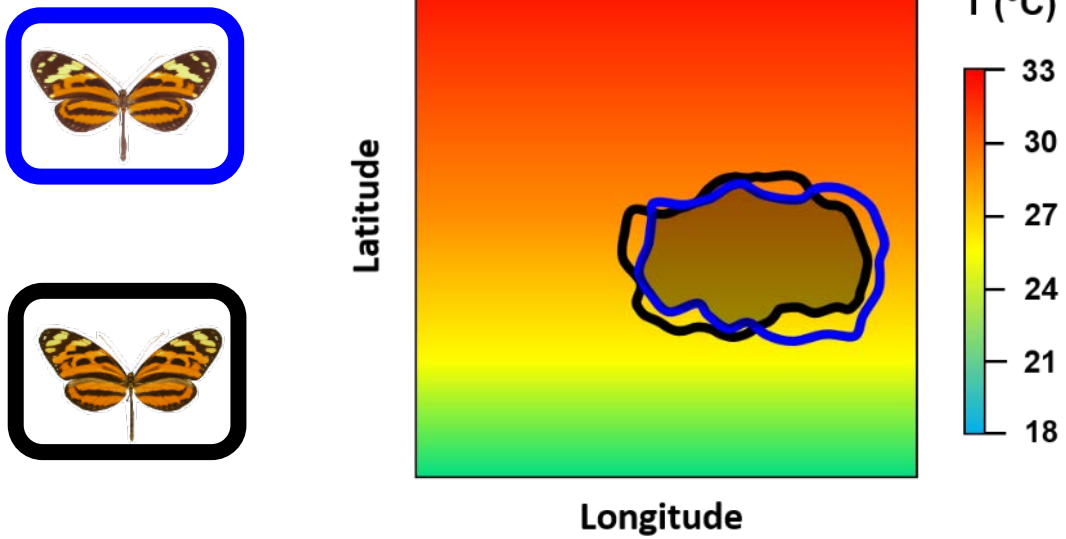

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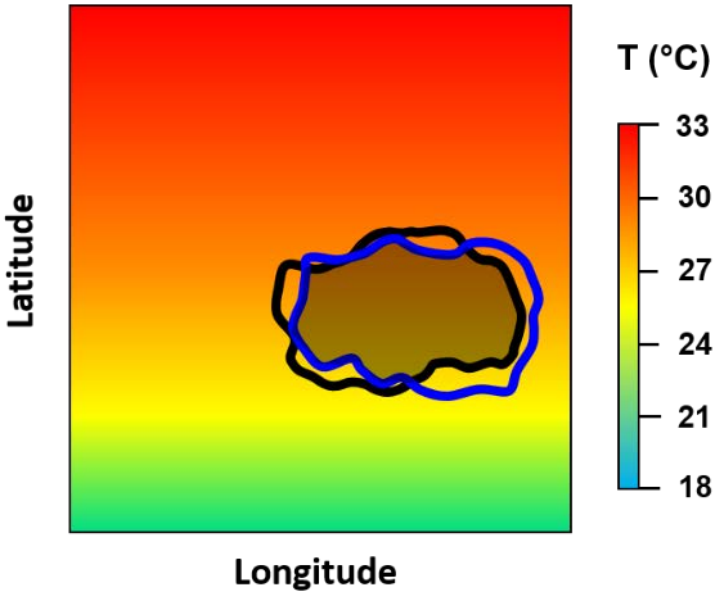
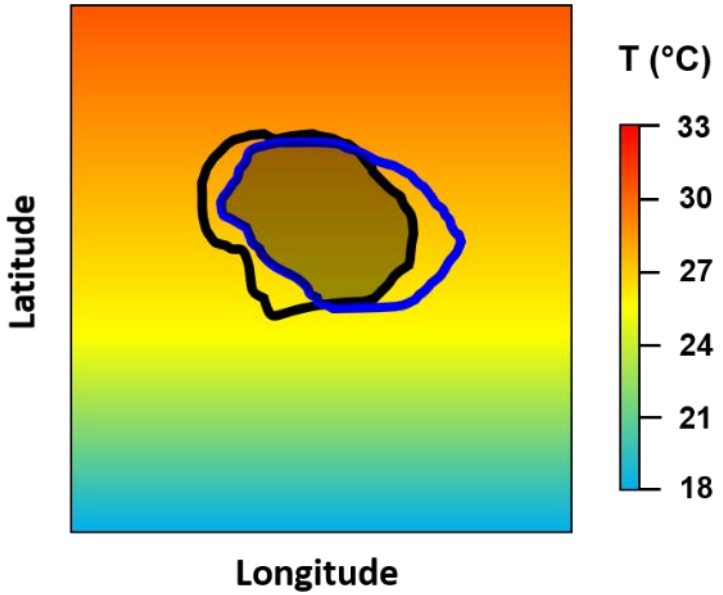


Disassembly?



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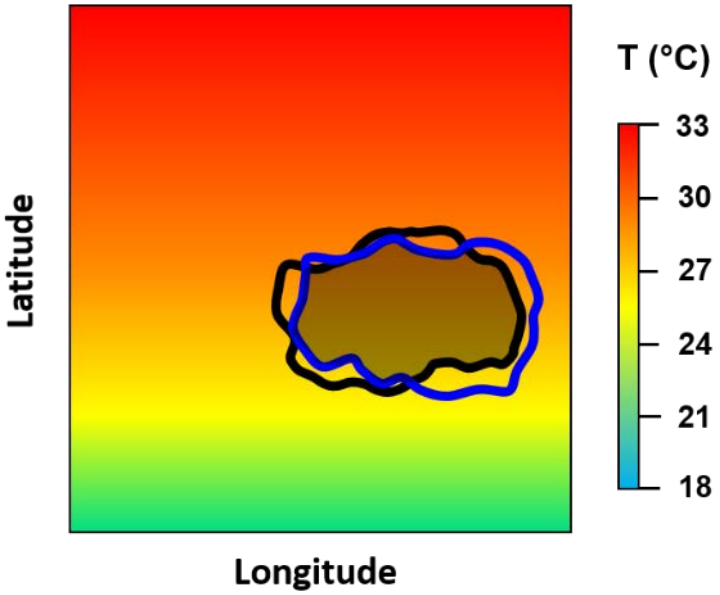

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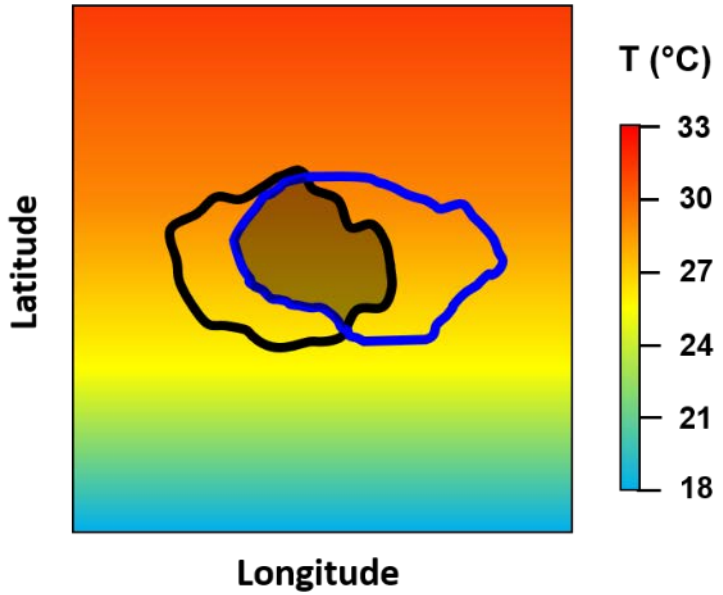

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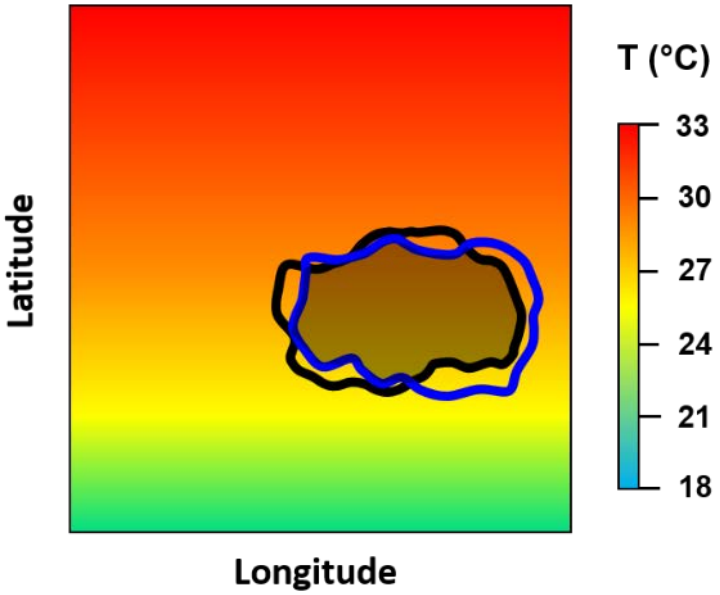

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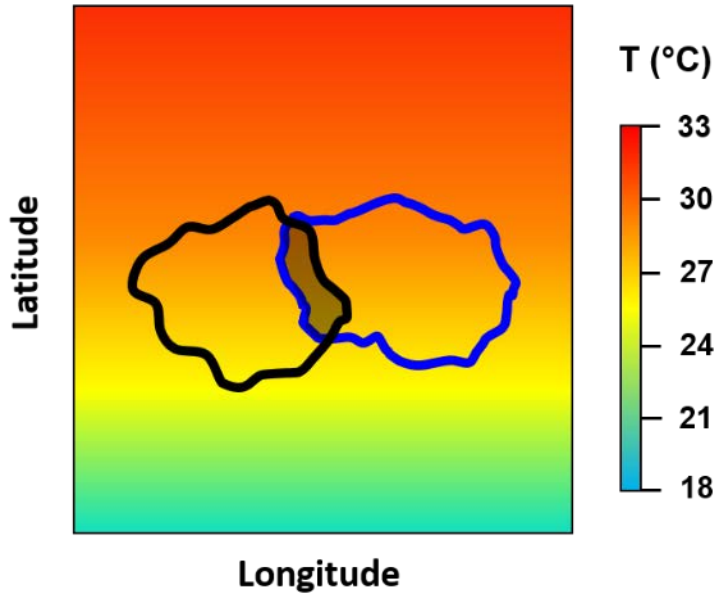

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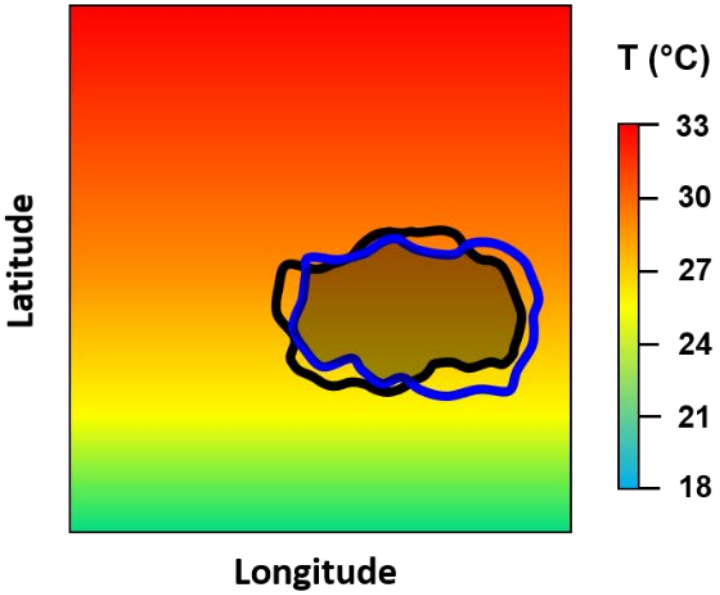

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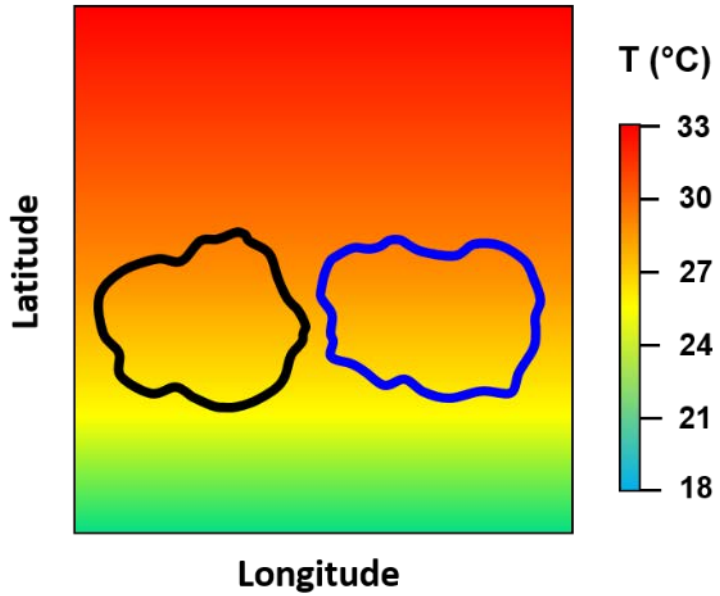
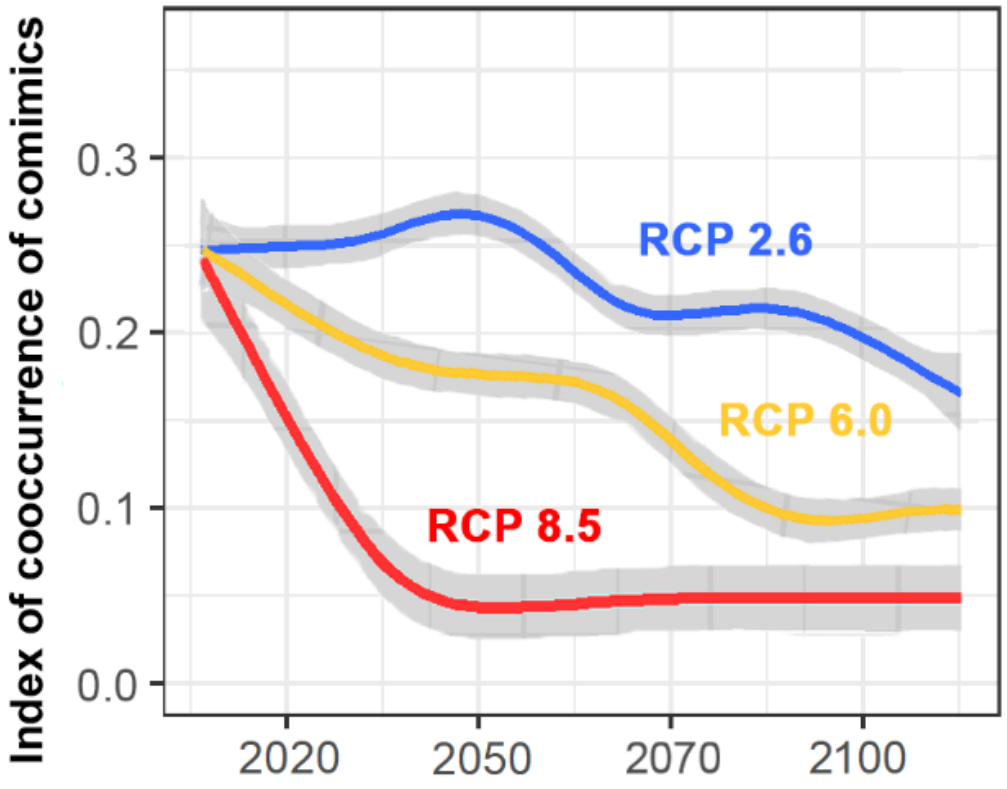
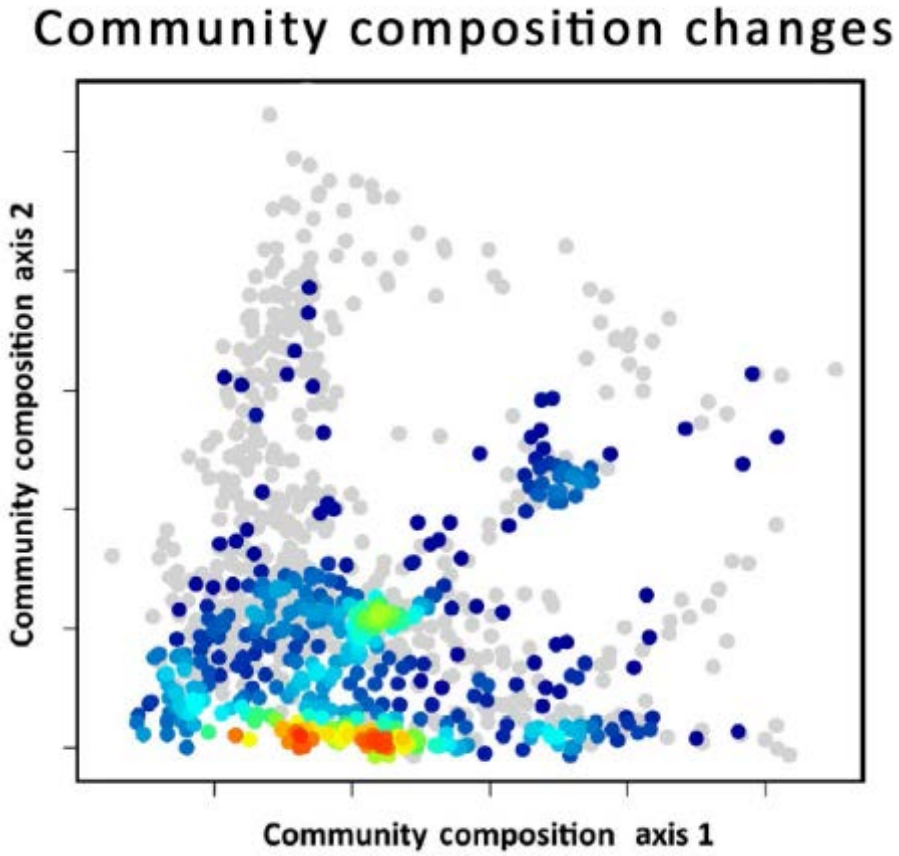


Neotropical mimetic butterflies facing climate changes

Model **future distributions** with **SDM:** changes in **community composition**





Modified from Brown et al., 2020

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SCAN ME

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- Keith Willmott
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- Jérémy Gauthier
- Rémi Allio
- Thomas Aubier
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- James Mallet
- Nicolas Chazot
- Nick Grishin
- Joana Meier
- Sébastien Lavergne
- Neil Rosser
- Krzysztof Kozak

Thanks for your attention

Hypomenitis enigma (Ithomiini). Credits: M. Elias