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

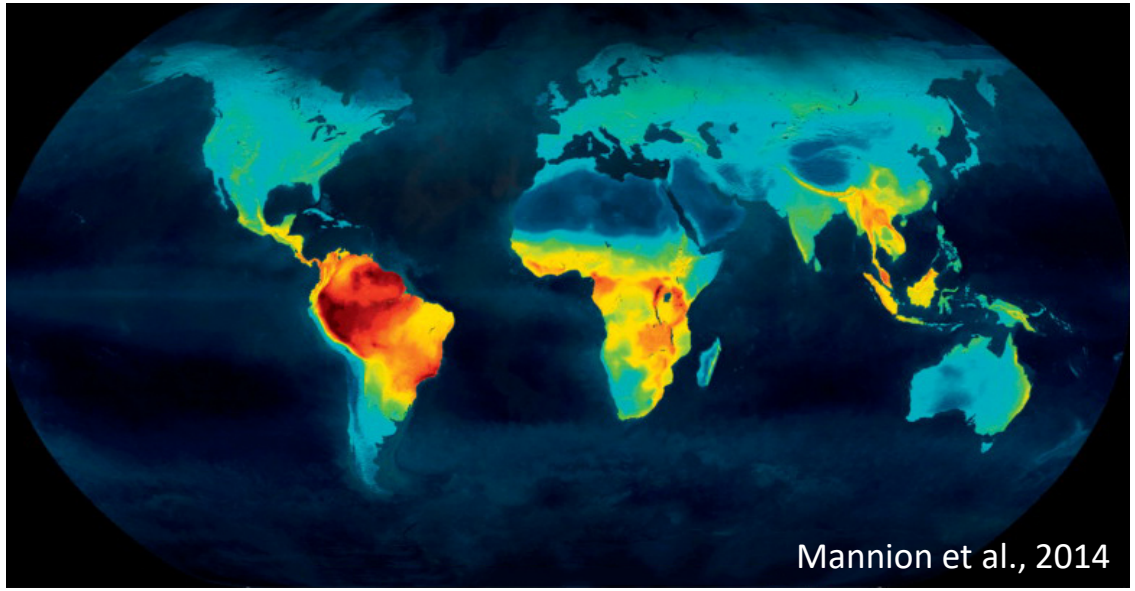
cnrs

CESCO
Centre d'Écologie et des Sciences de la Conservation

Context

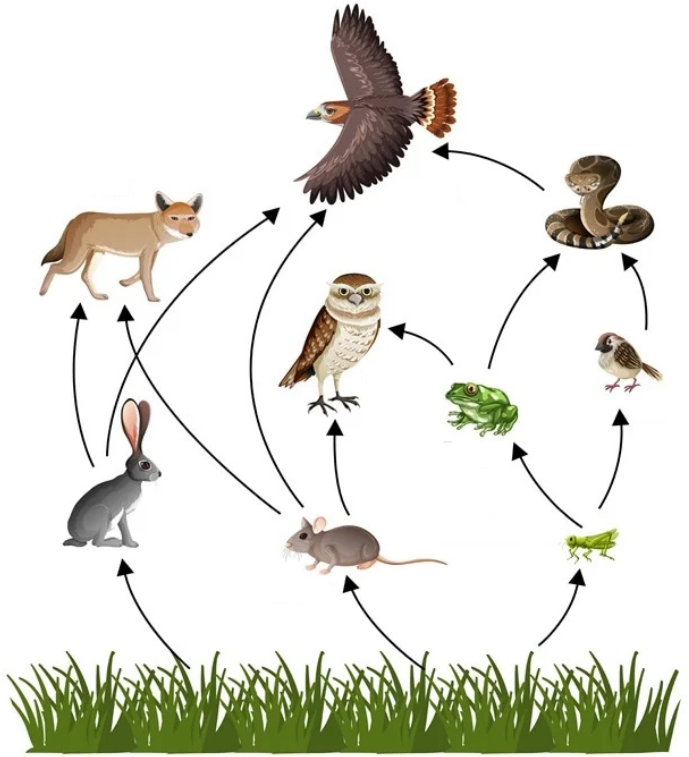
Biodiversity

Biological units



+

Interactions



Credit: Shutterstock.com

Context

Mutualistic interactions:

- Cooperative hunting
- Plant facilitation
- Müllerian mimicry

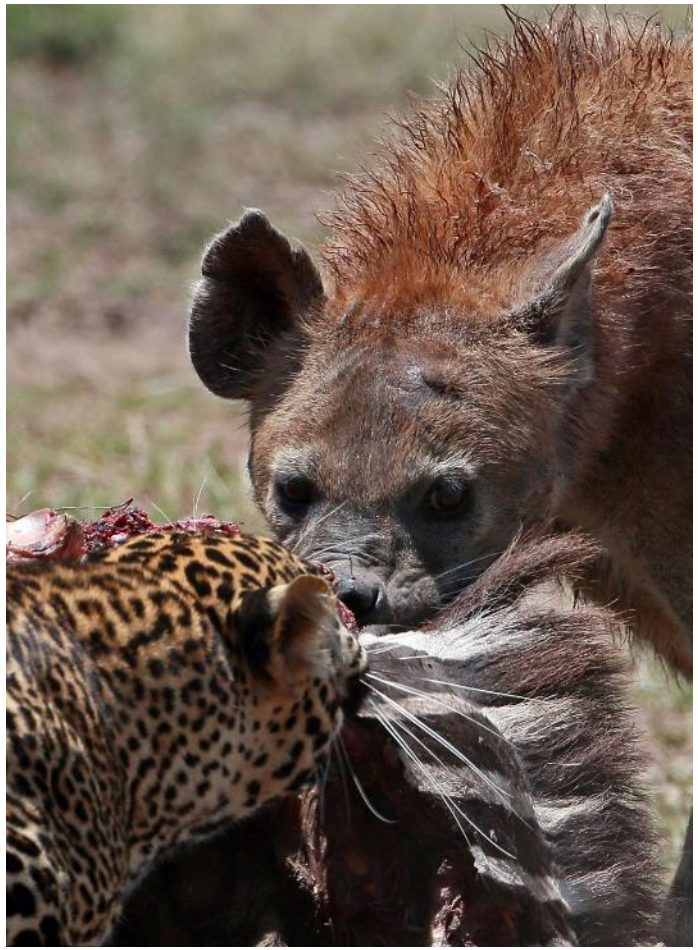
Credits: Thomas Kline

Credits: Amanda R. Liczner

Credits: Jason L. Brown

Context

Credit: Campillo Rafael



Credit: Caters News Agency

Credits: Anytka Olkova & Larry Myers

Exploitative competition:

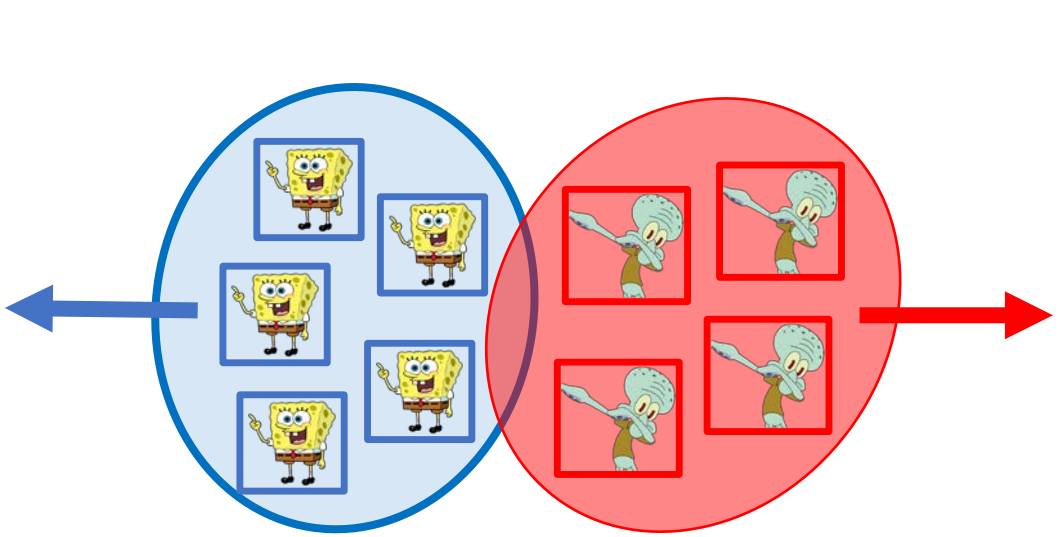
- for local resources
- for habitats
- for space

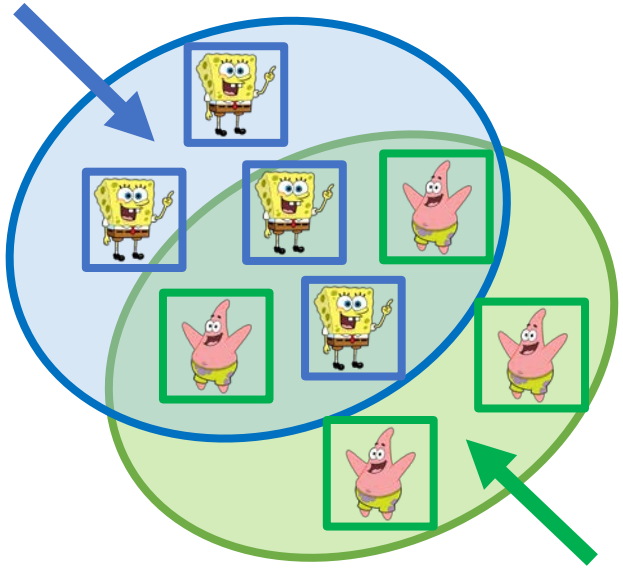
Context

Competition − / −

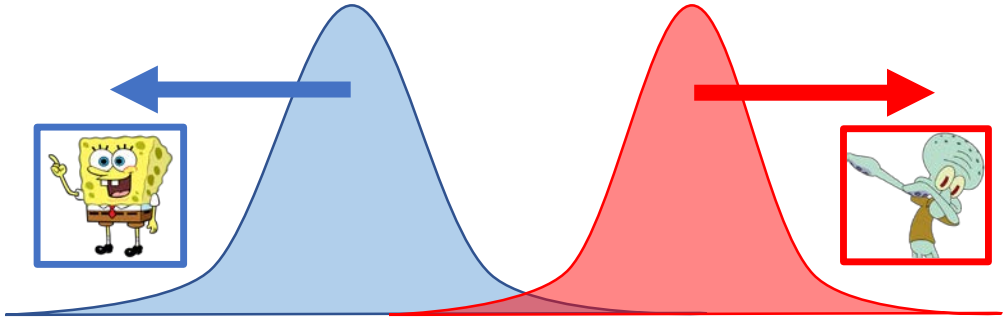
Mutualism + / +

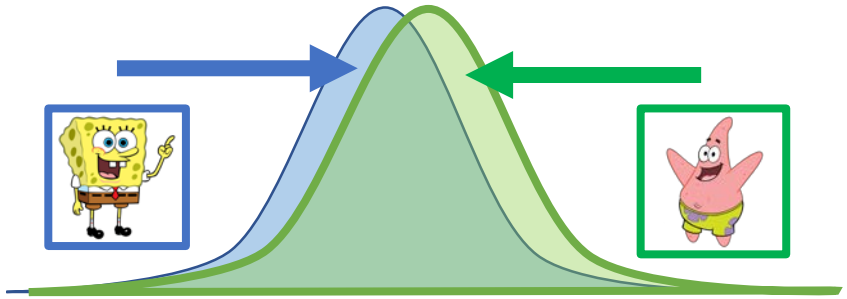
Spatial pattern





Niche evolution





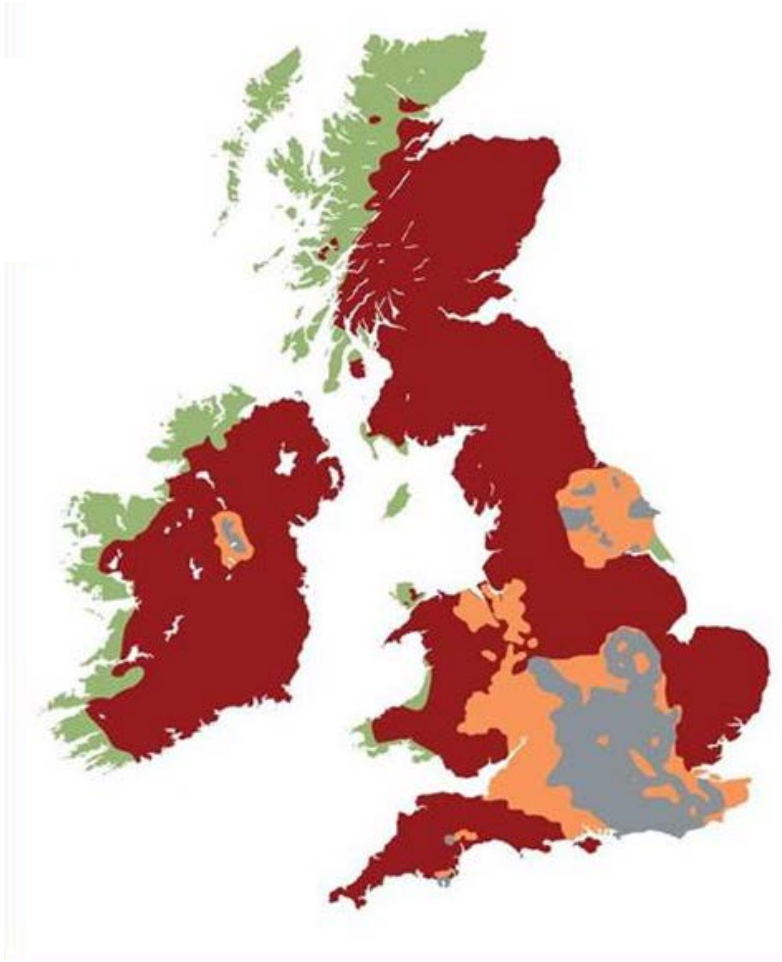
Context

Grey squirrel
Sciurus carolinensis

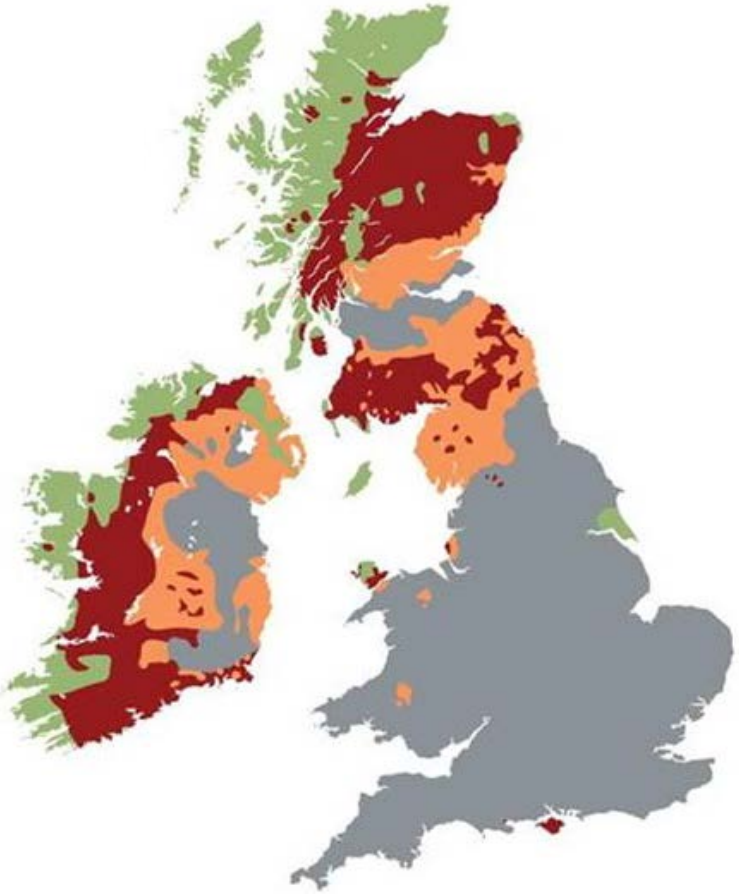
Both species

Red squirrel
Sciurus vulgaris

Year 1945



Year 2010



Source: WTSWW

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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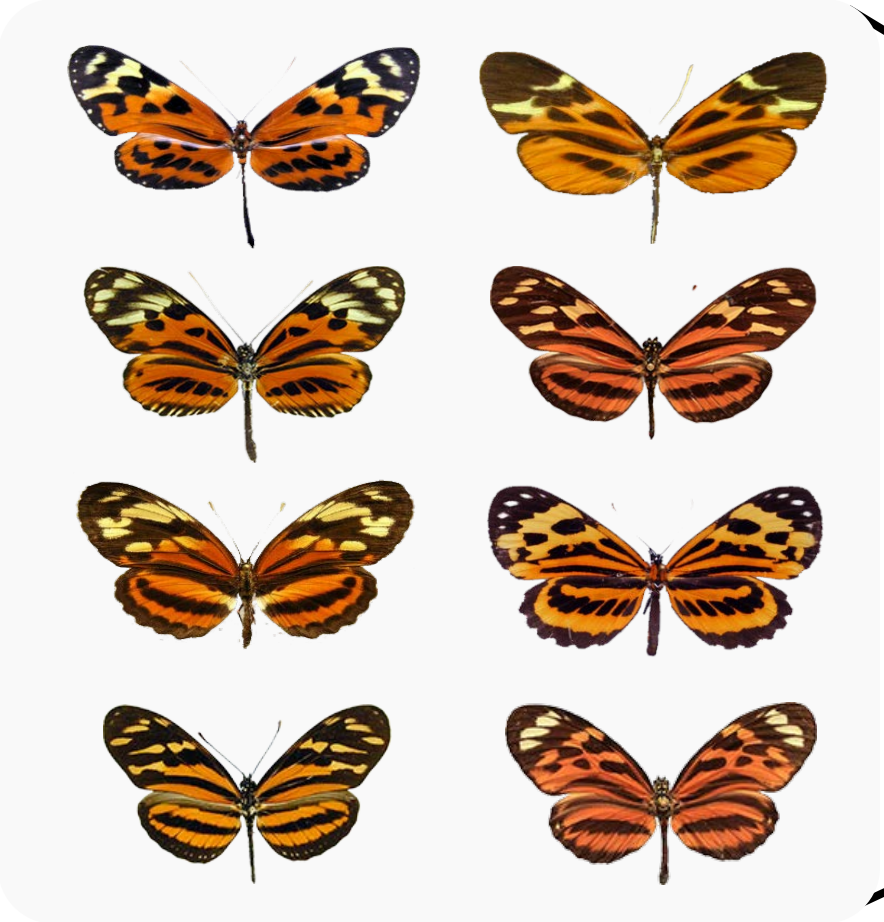
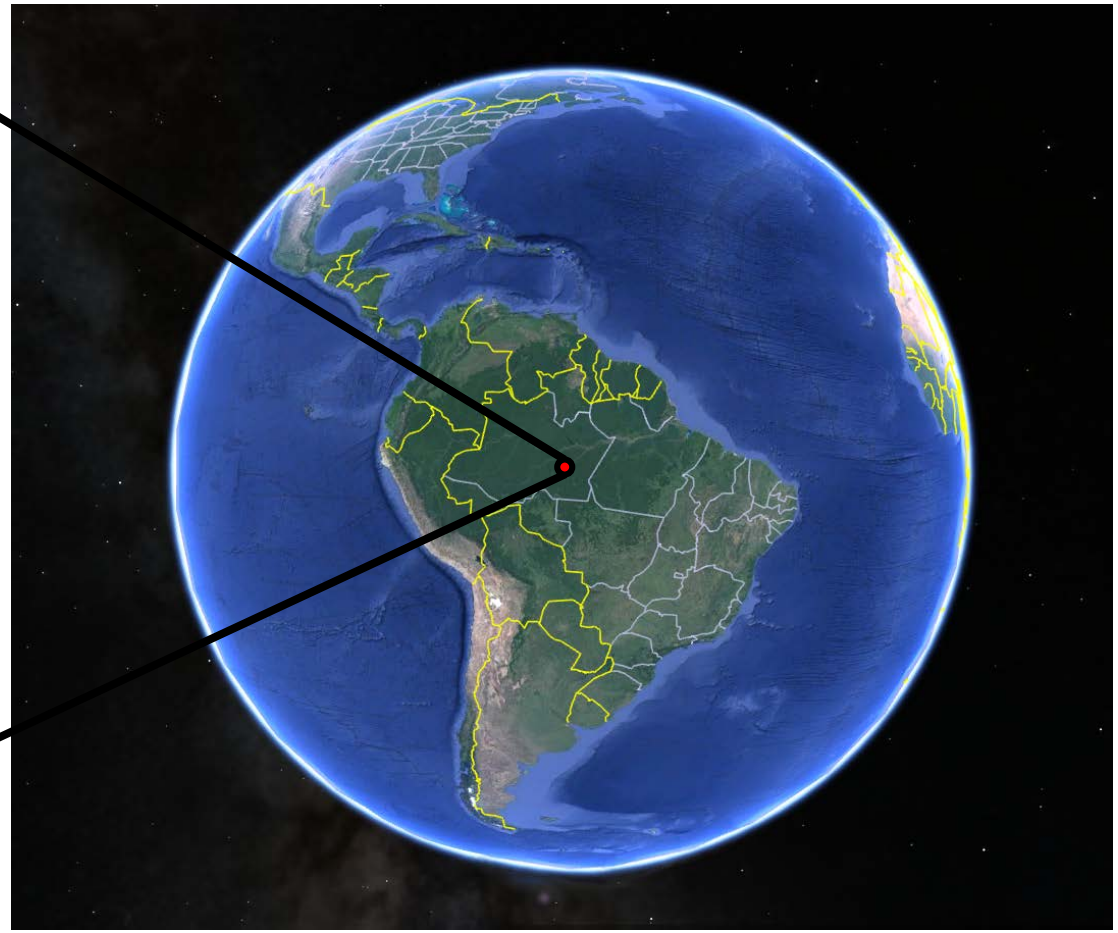
Niche evolution

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

Study system: Müllerian mimicry

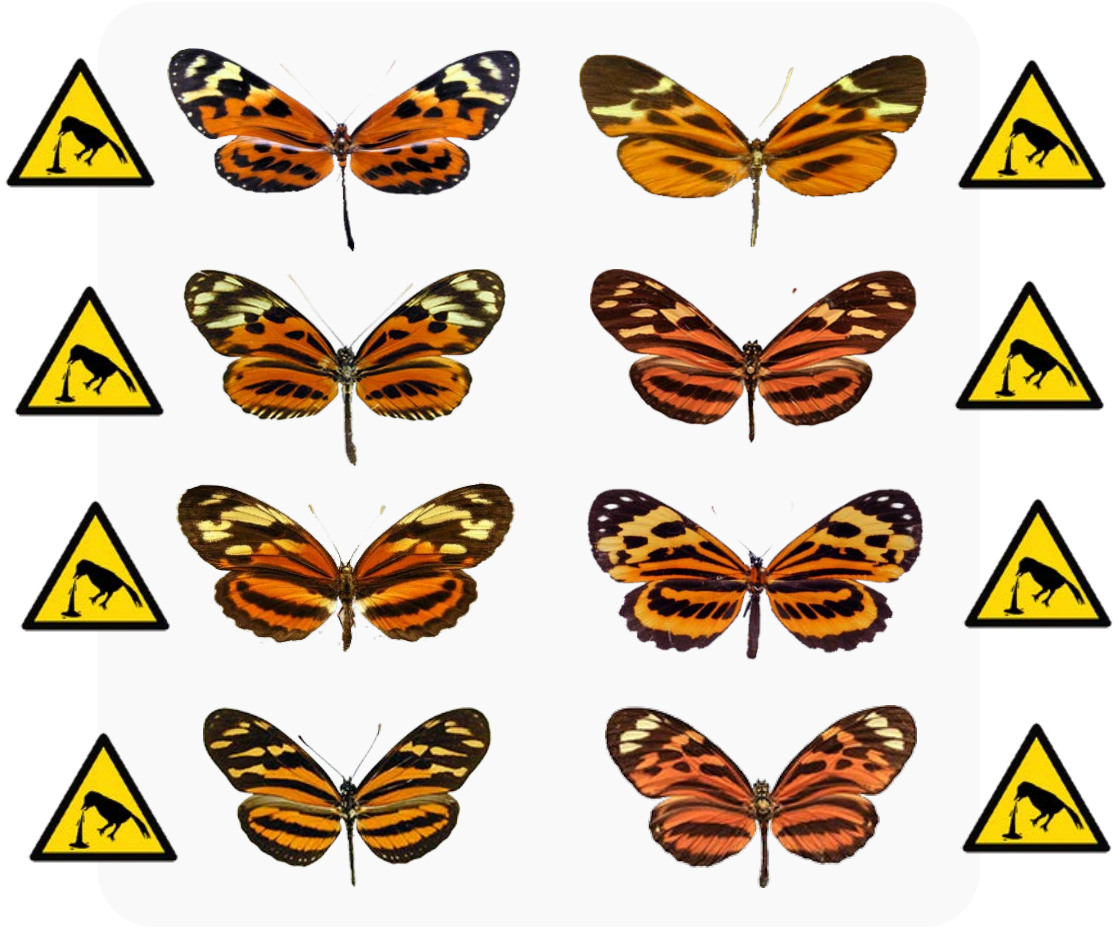


A mimicry ring

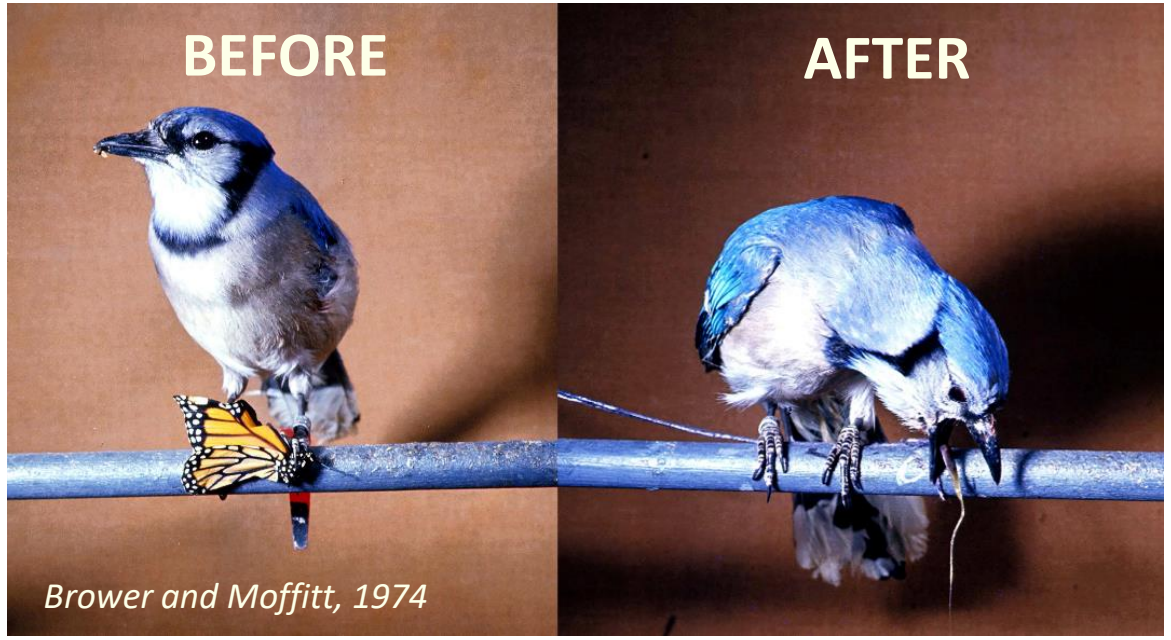


Credits: Google Earth

Study system: Müllerian mimicry



A mimicry ring



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)

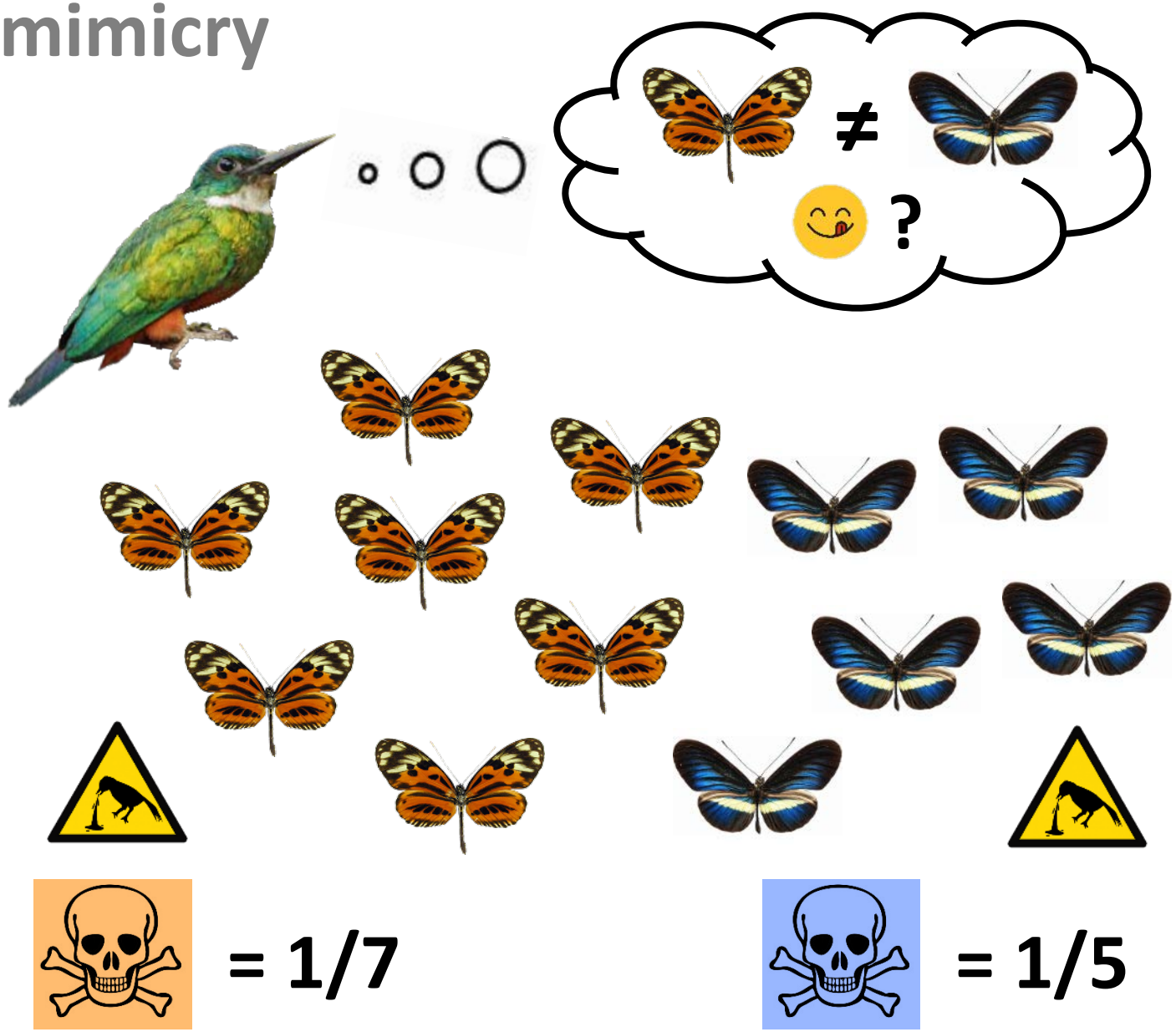
Study system: Müllerian mimicry

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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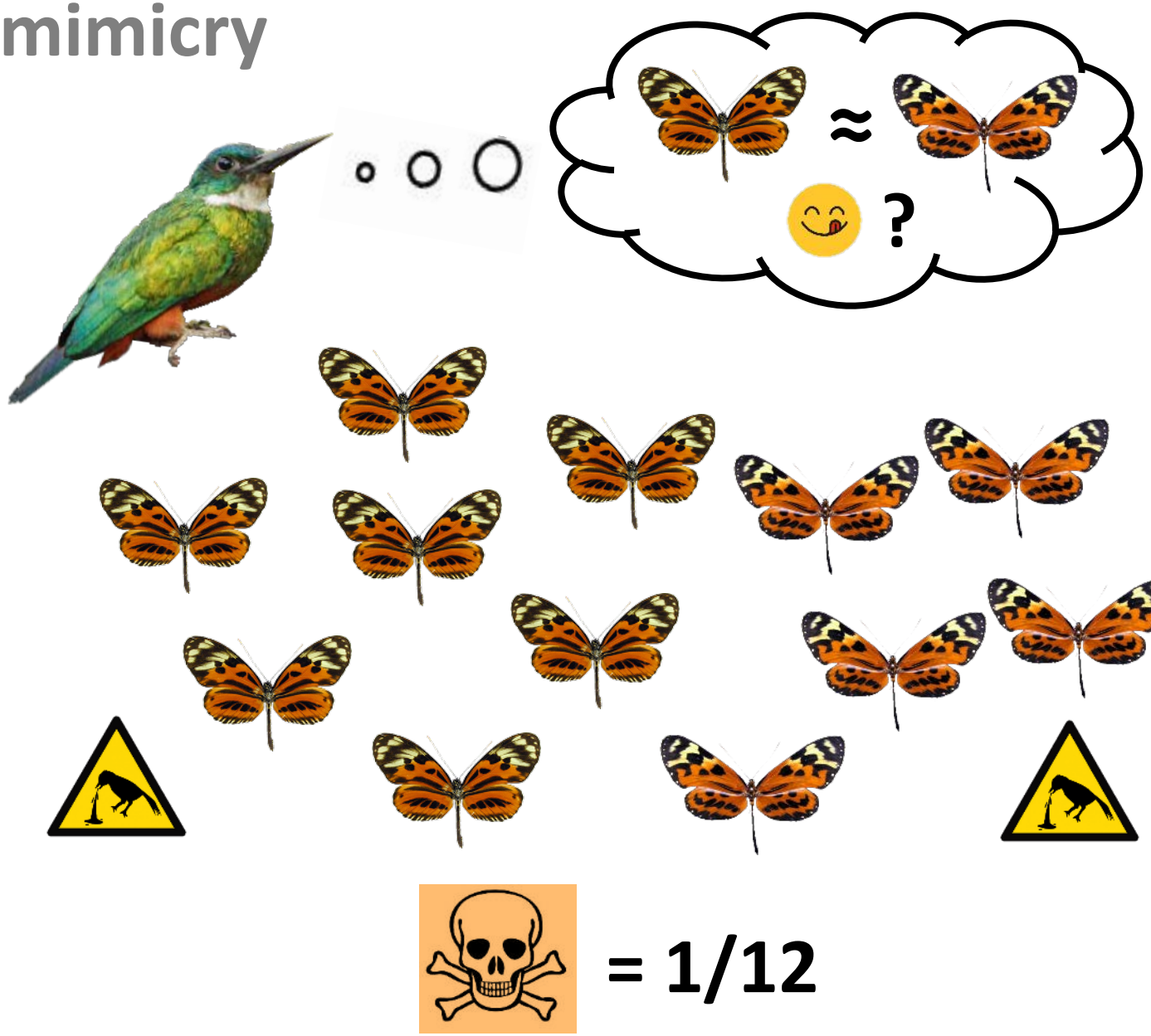

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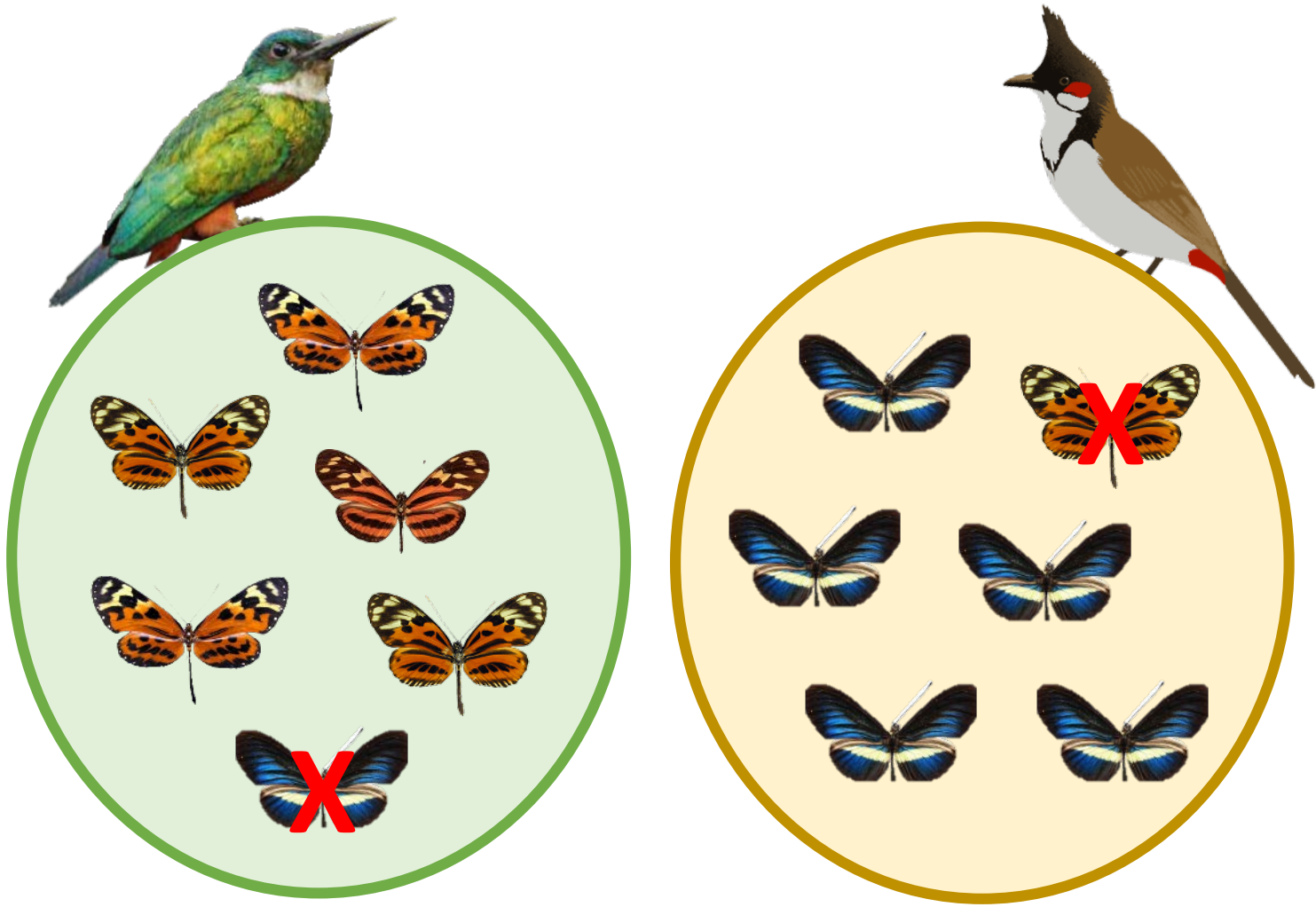


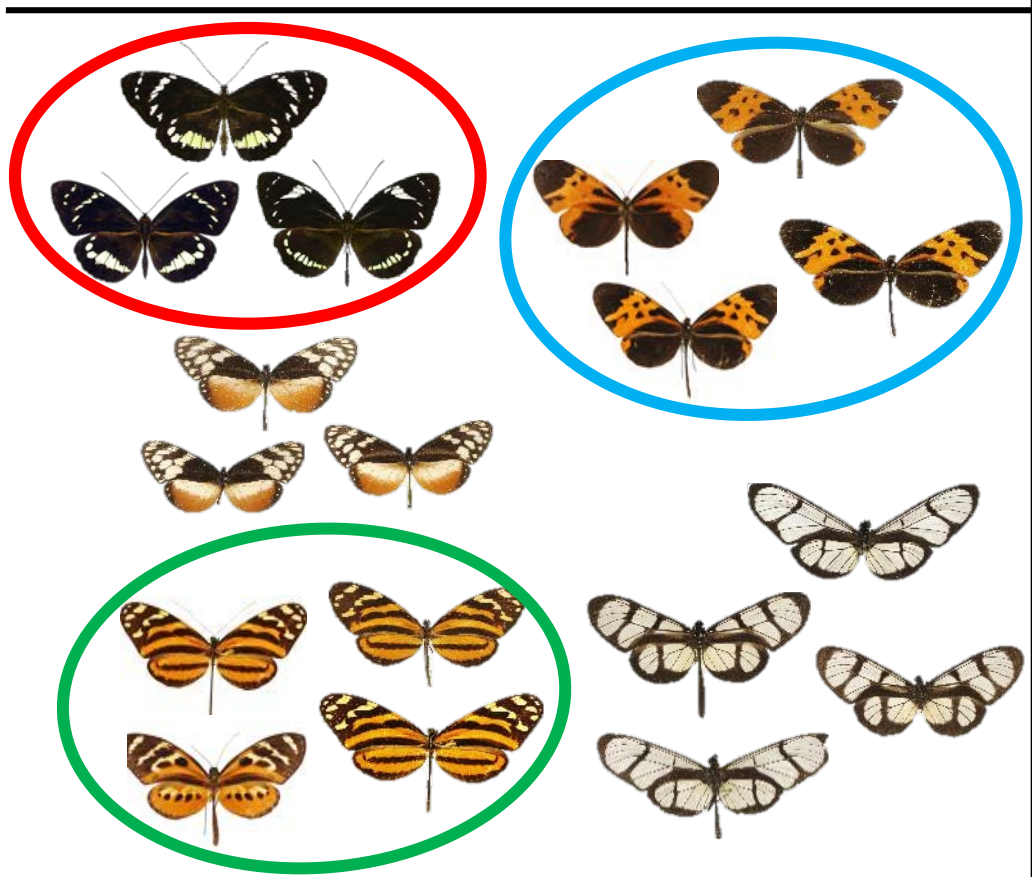
Study system: Neotropical butterflies

Ithomiini tribe | **Heliconiini tribe**

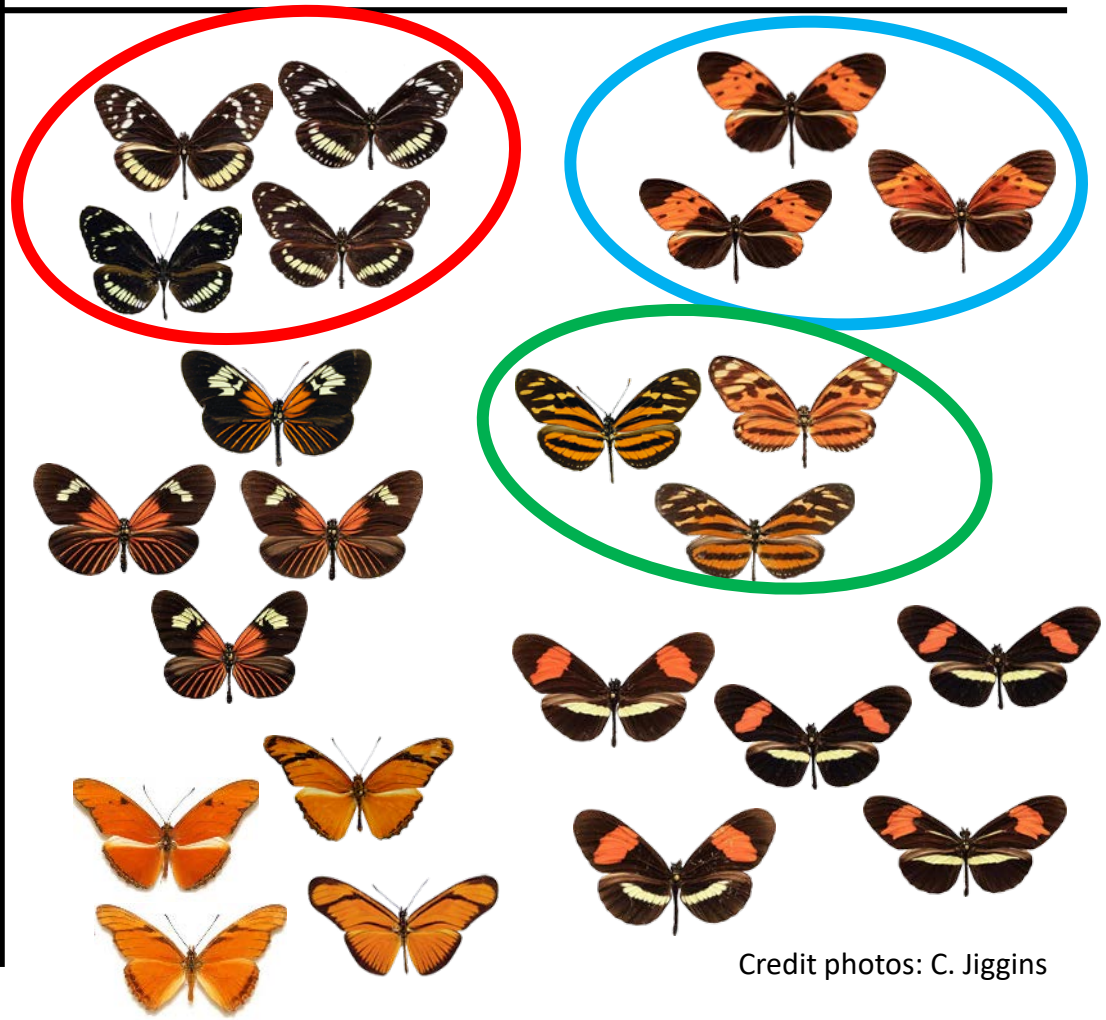
Mimicry

Phylogeny

Geography



Credit photos: N. Chazot



Credit photos: C. Jiggins

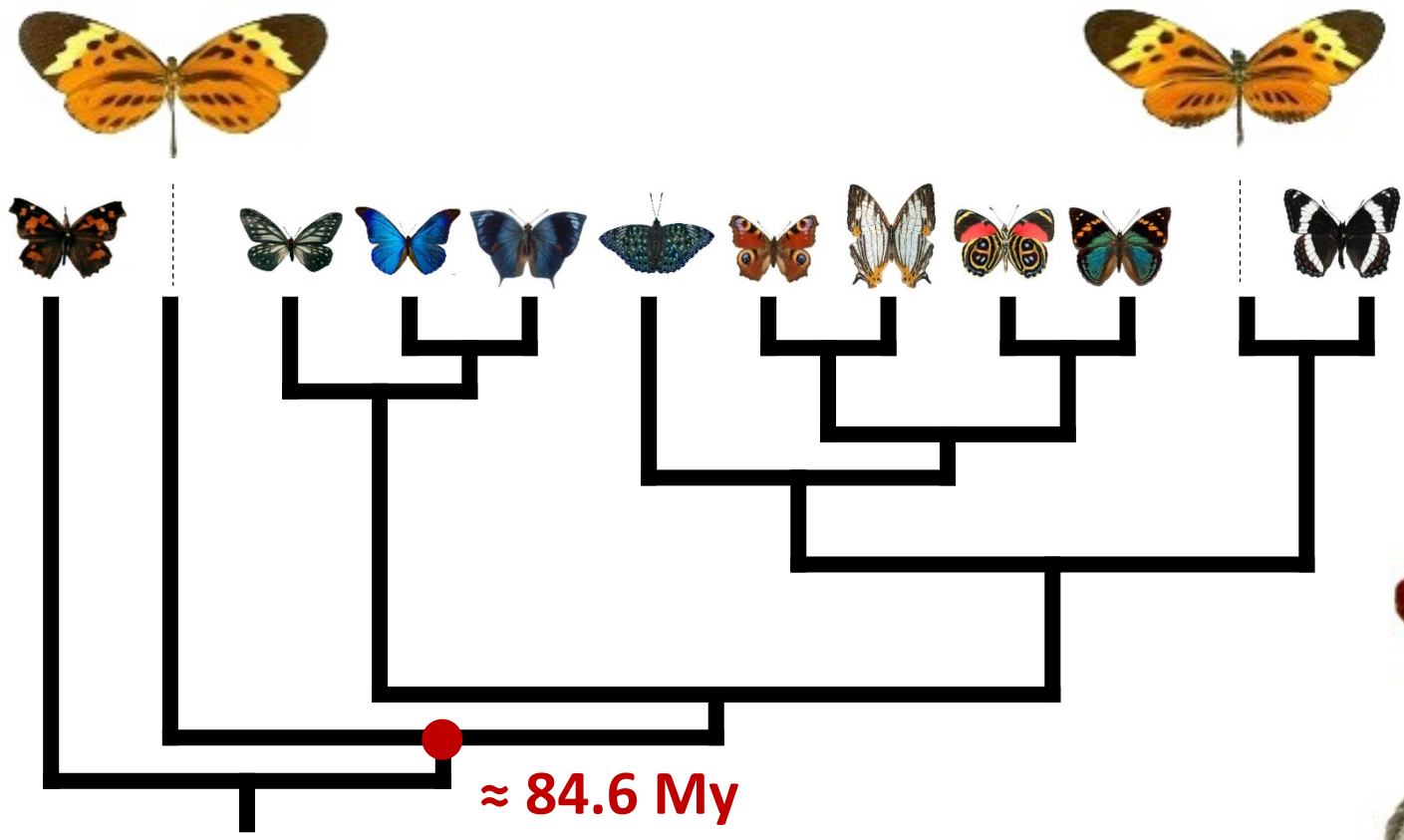
Study system: Neotropical butterflies

Ithomiini tribe **Heliconiini tribe**

Mimicry

Phylogeny

Geography



Study system: Neotropical butterflies

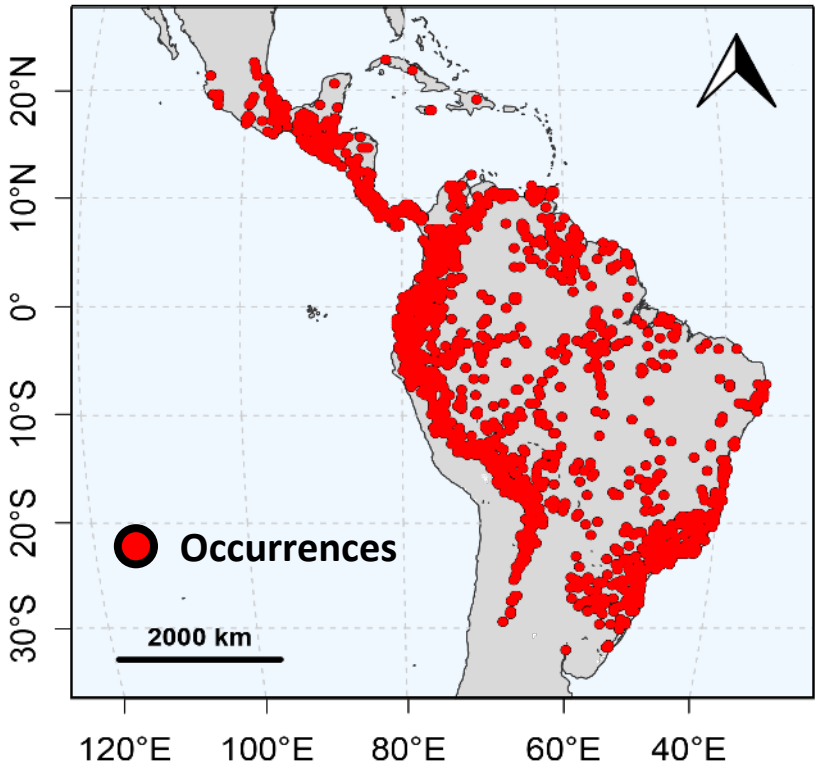
Mimicry

Phylogeny

Geography

Ithomiini tribe

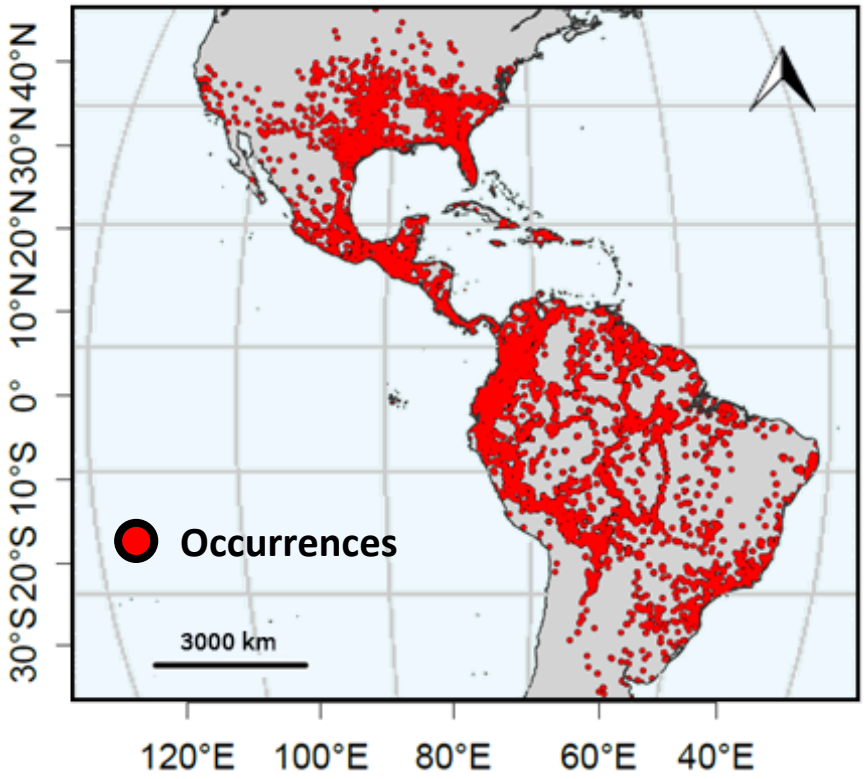
Occurrence map



Doré et al., 2022

Heliconiini tribe

Occurrence map



Perochon et al., in prep

Study system: Neotropical butterflies

Ithomiini tribe | **Heliconiini tribe**

Mimicry

Phylogeny

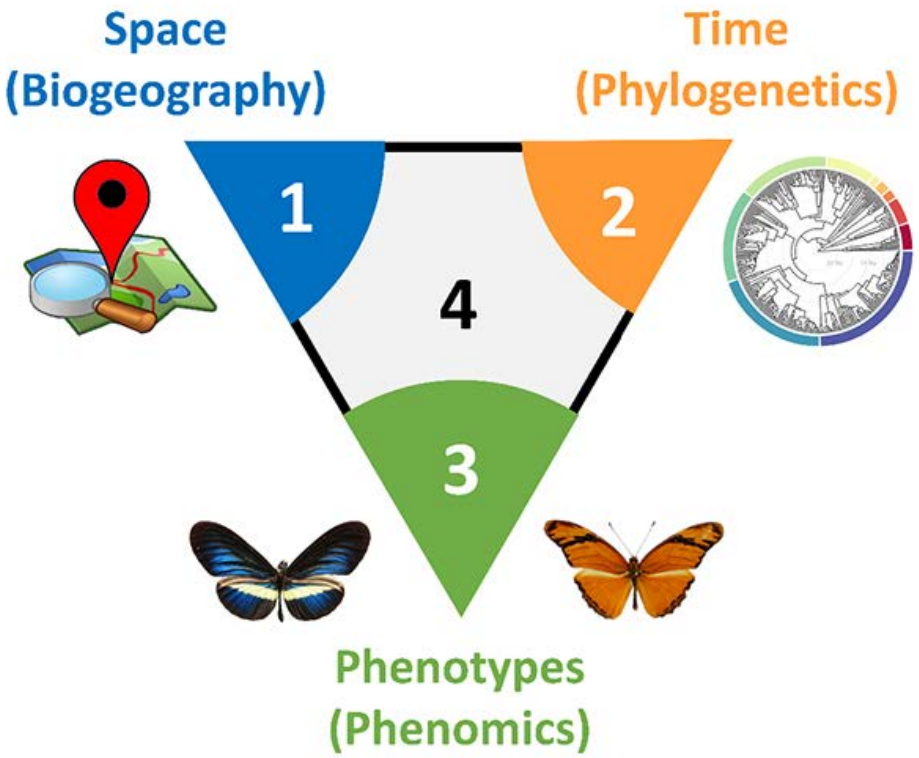
Geography

Credit Photo: M. Chouteau

Outlines and objectives

CHAPTER 1

Map **biodiversity patterns**



CHAPTER 2

Resolve **deep evolutionary relationships**

CHAPTER 3

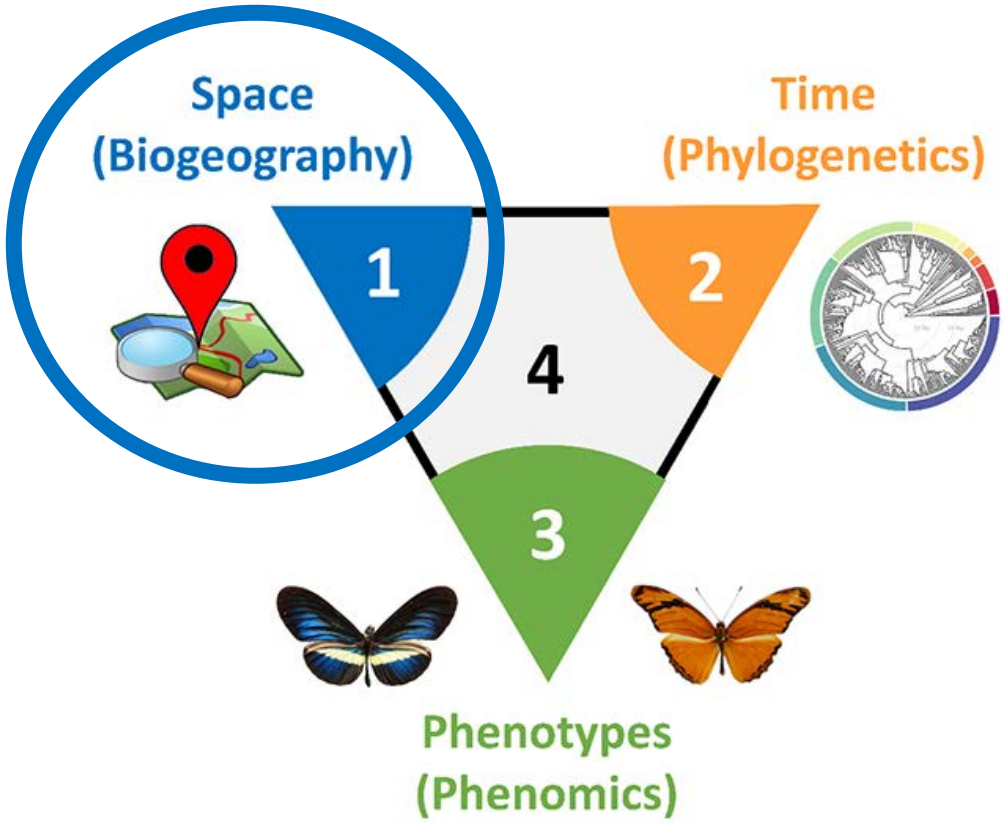
Quantify **phenotypic similarity** in wing patterns

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

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

CHAPTER 1

Map **biodiversity patterns**



Stage M2: Heliconiini

Eddie Pérochon

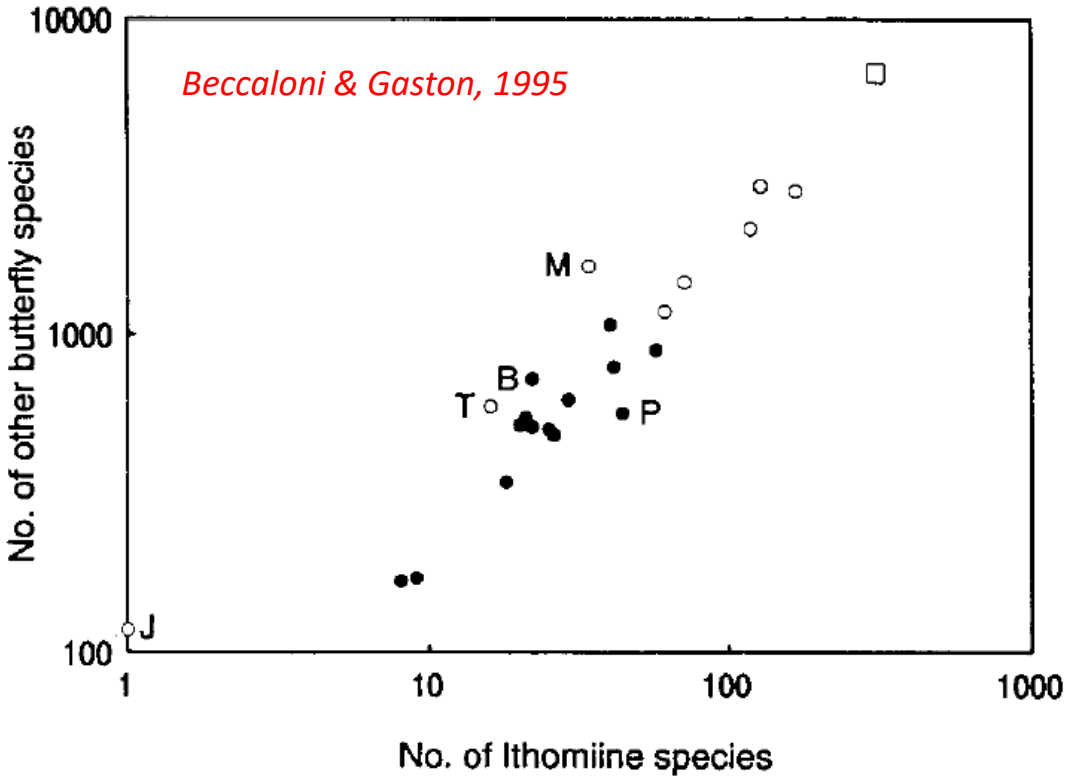
Reference:

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

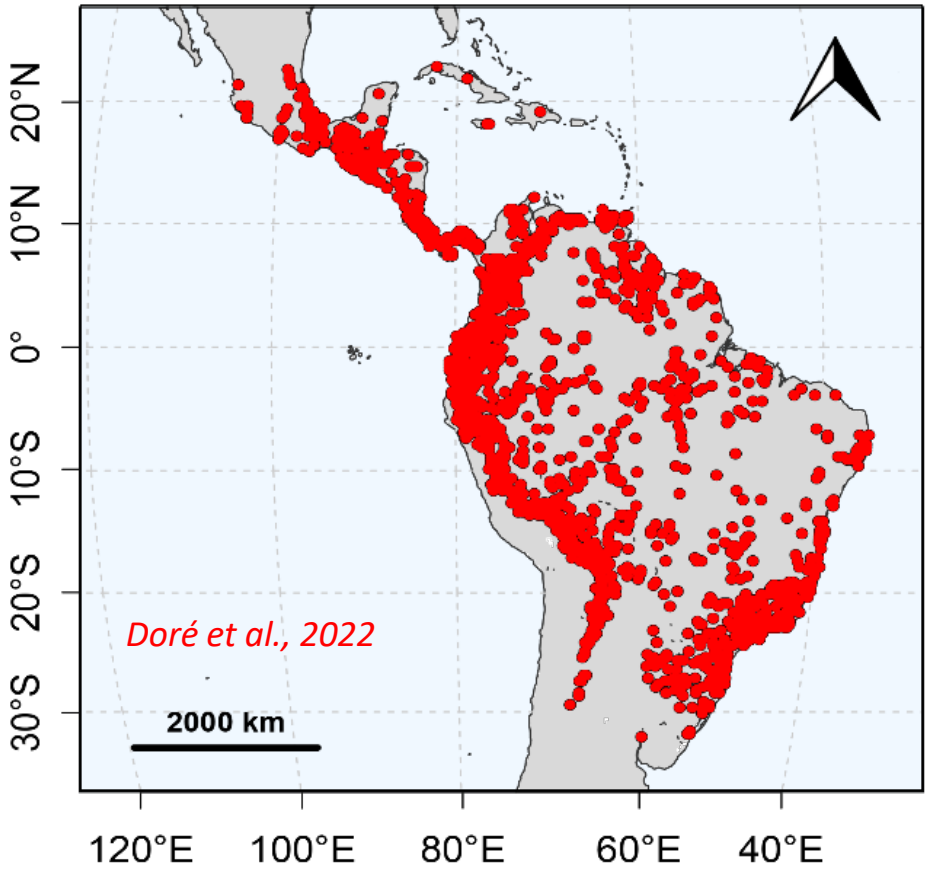
1/ Map **species distributions**

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

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

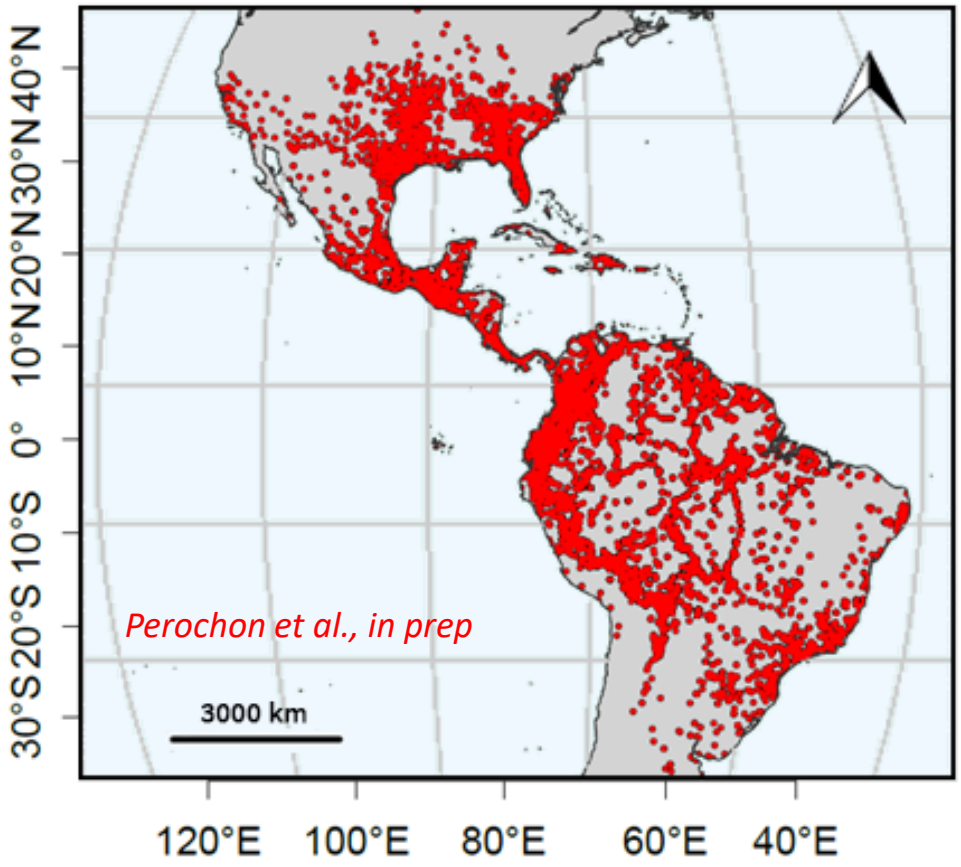
Available data

Ithomiini tribe (396 species)



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

Heliconiini tribe (77 species)



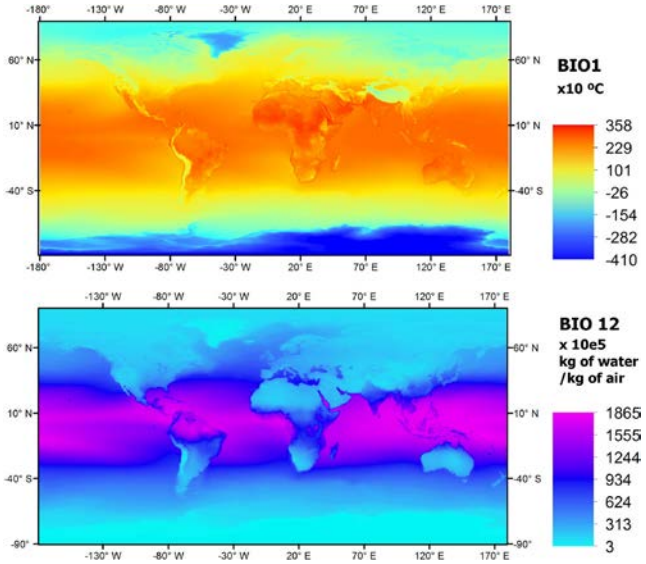
77,577 occurrences across **4,168 sites**

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

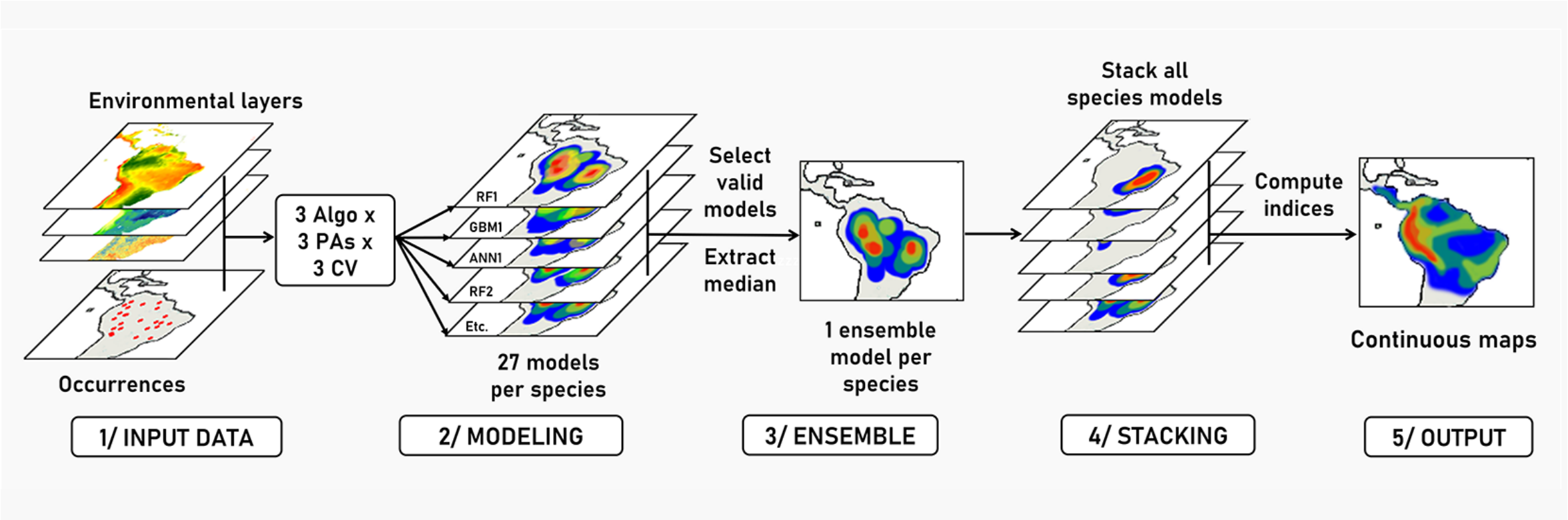
Farr et al., 2007

Vegetation cover

GFCC v.3.0

Sexton et al., 2013

Species Distribution Modeling (SDM)

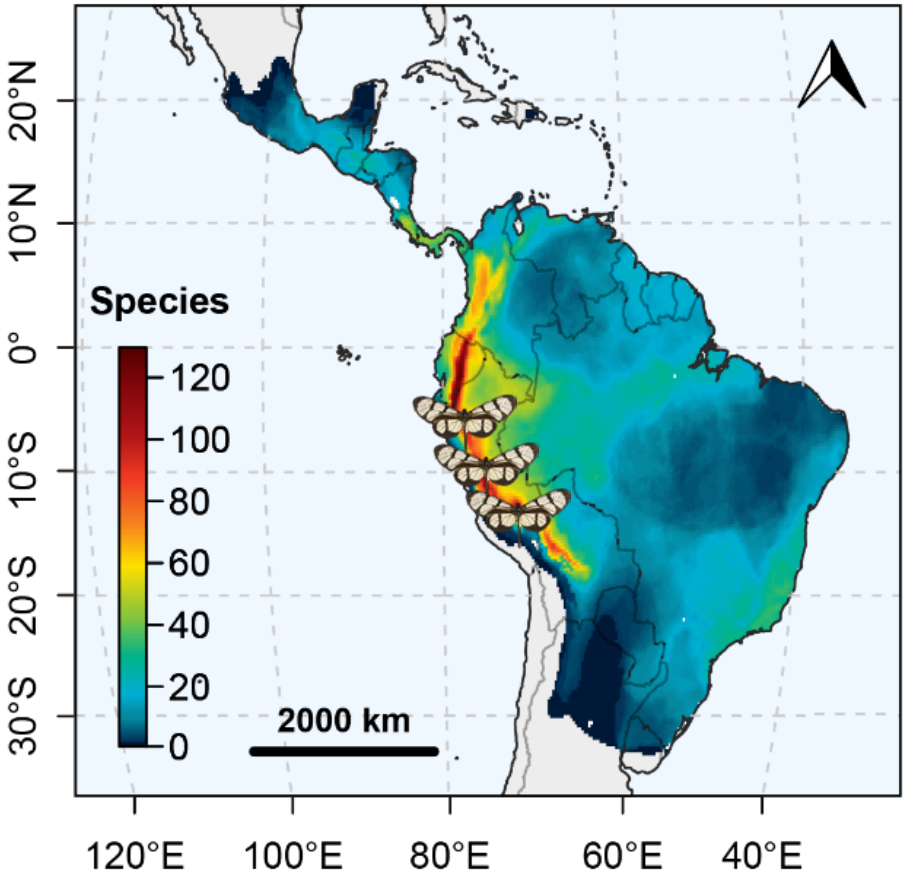


SDM → Species distribution maps → Diversity indices

Biodiversity patterns

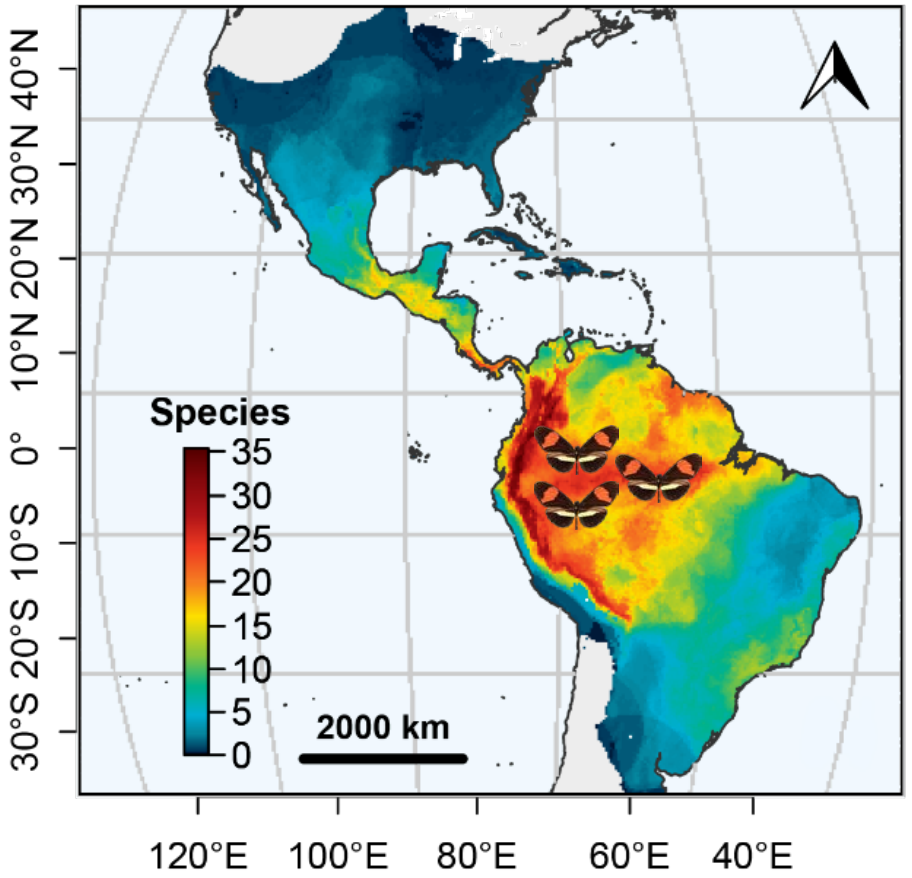
Species richness

Ithomiini
(396 species)



Doré et al., 2022

Heliconiini
(77 species)



Pérochon et al., in prep

Anthropogenic threats

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

Current anthropogenic threats
≈
Human Footprint

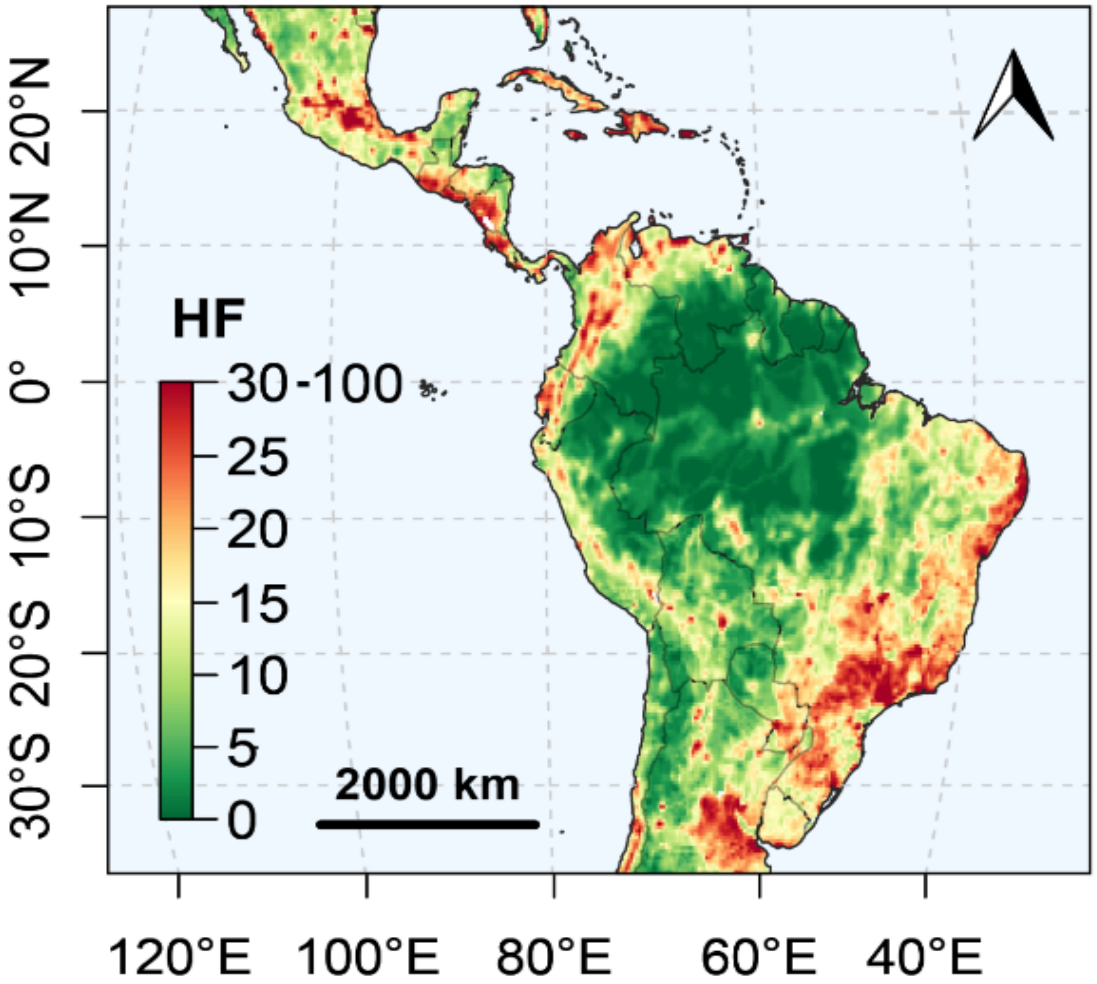
(1) Human population density

(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**

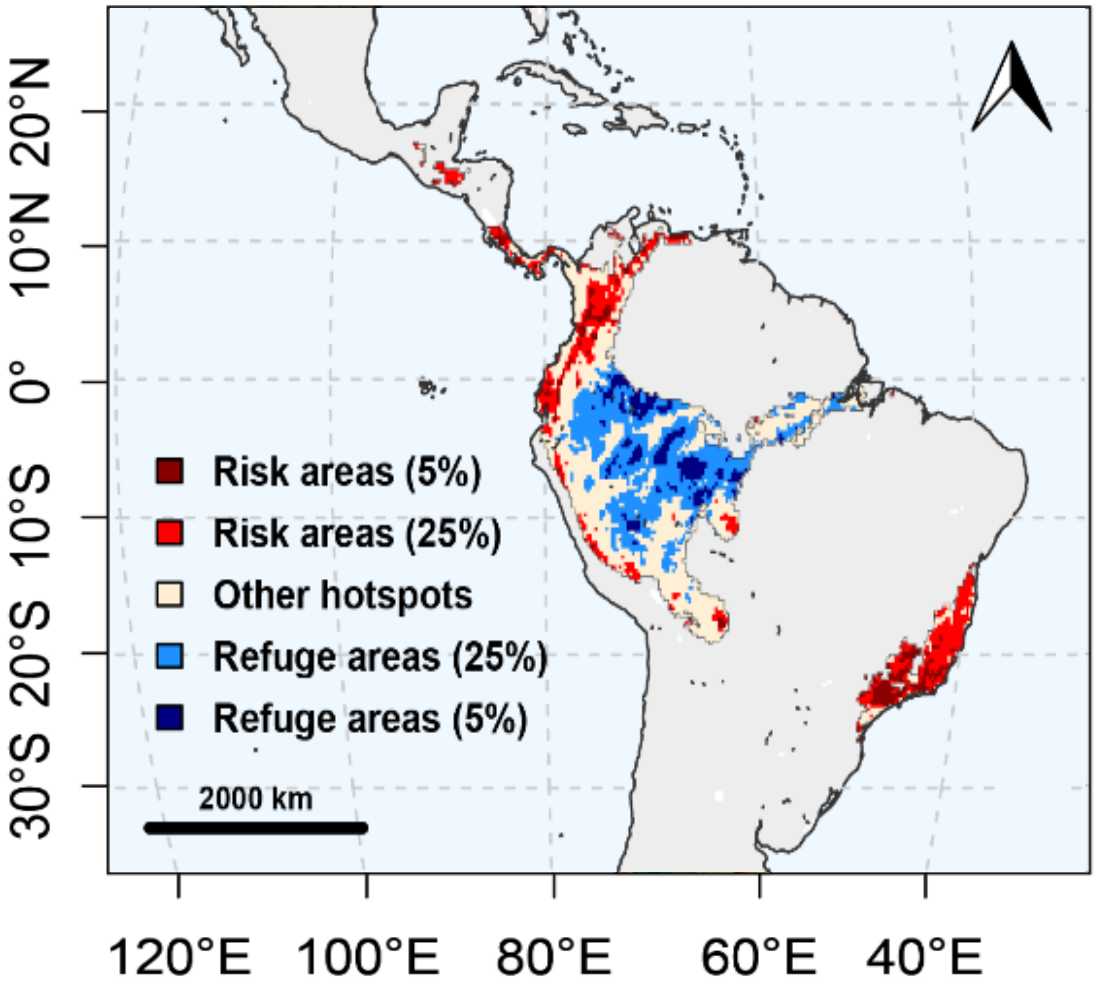
Current anthropogenic threats
≈
Human Footprint

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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Current anthropogenic threats
≈
Human Footprint

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

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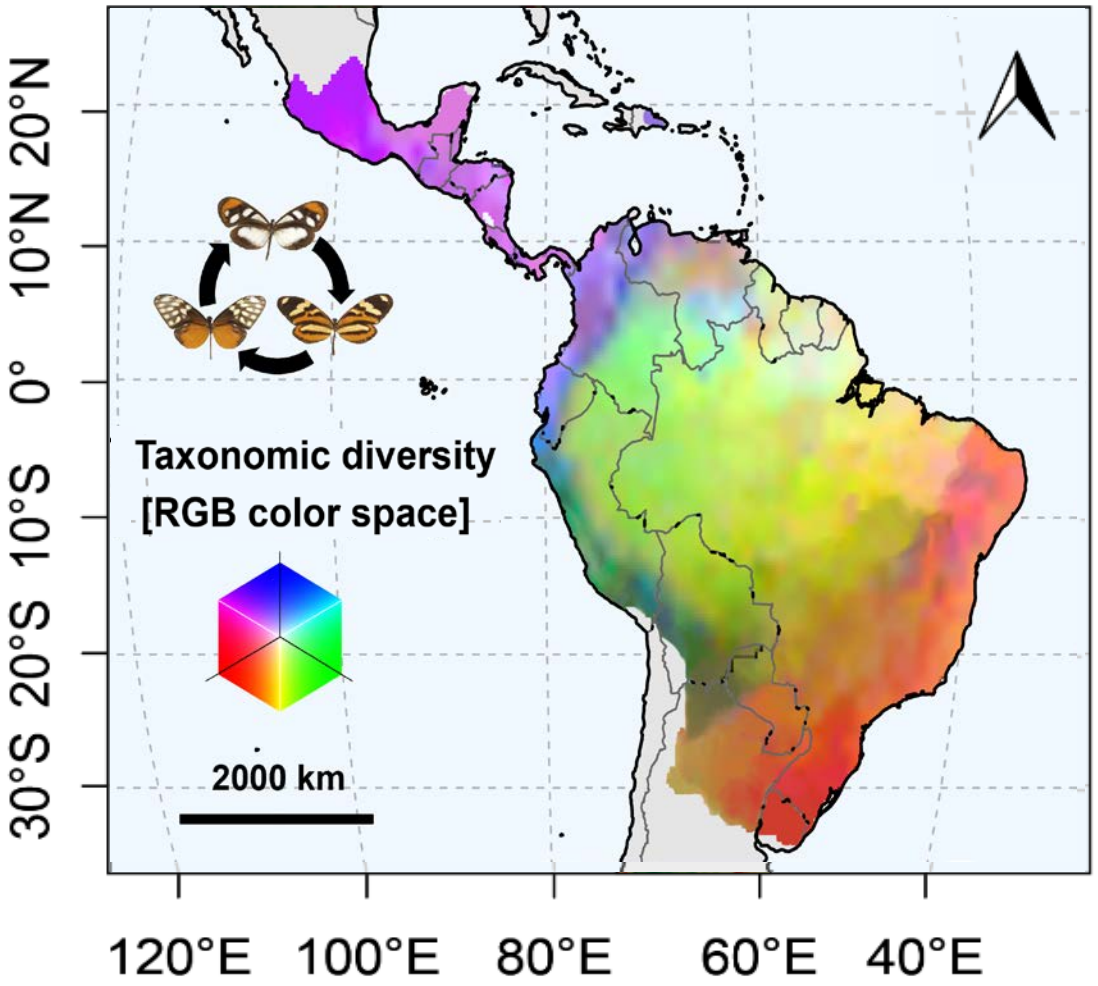
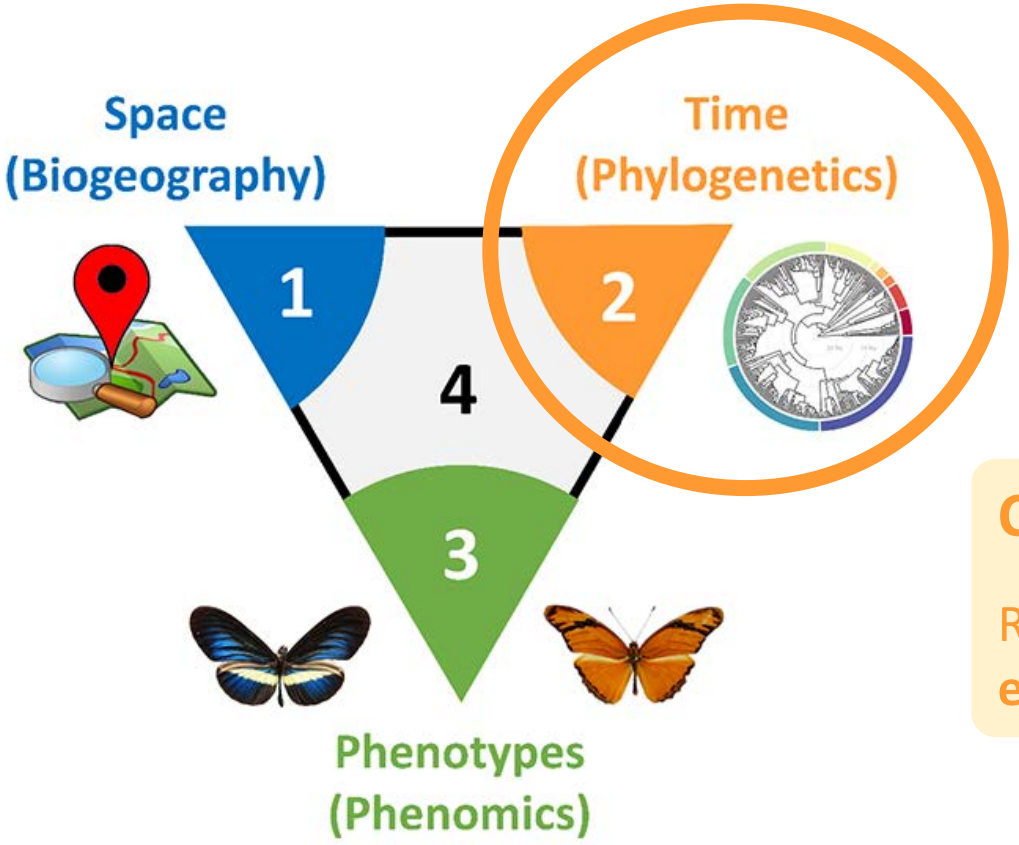
Limits: **Low redundancy** with other areas
Climate change and **deforestation**

Taxonomic β-Diversity



CHAPTER 2: Phylogenomics resolve deep evolutionary relationships in clearwing butterflies



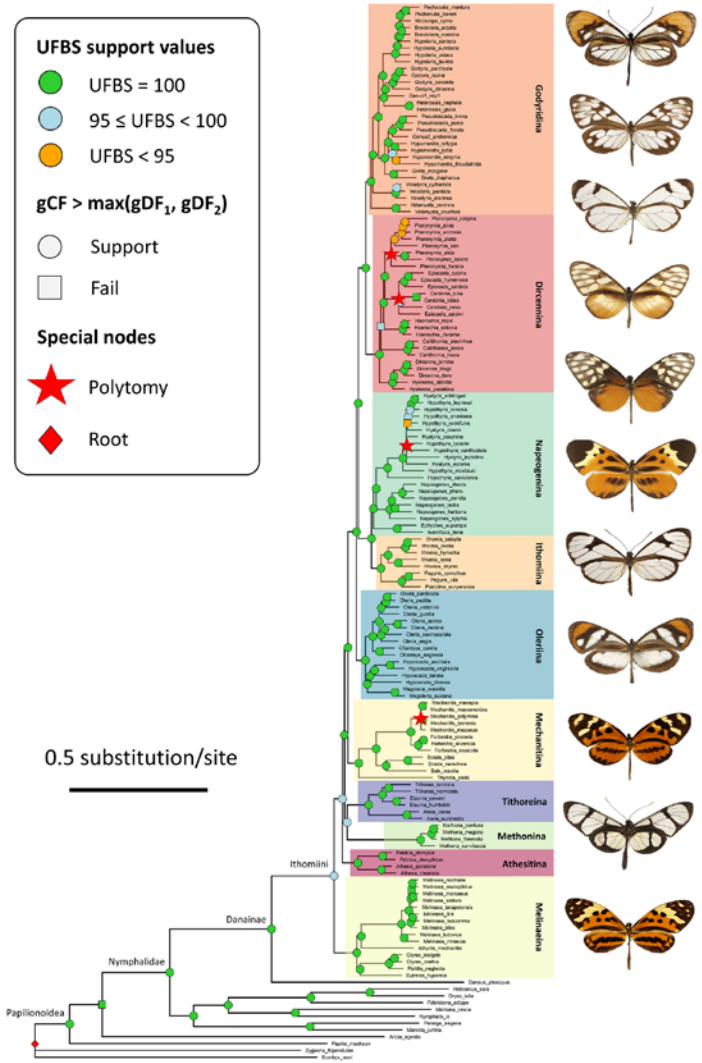
CHAPTER 2

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

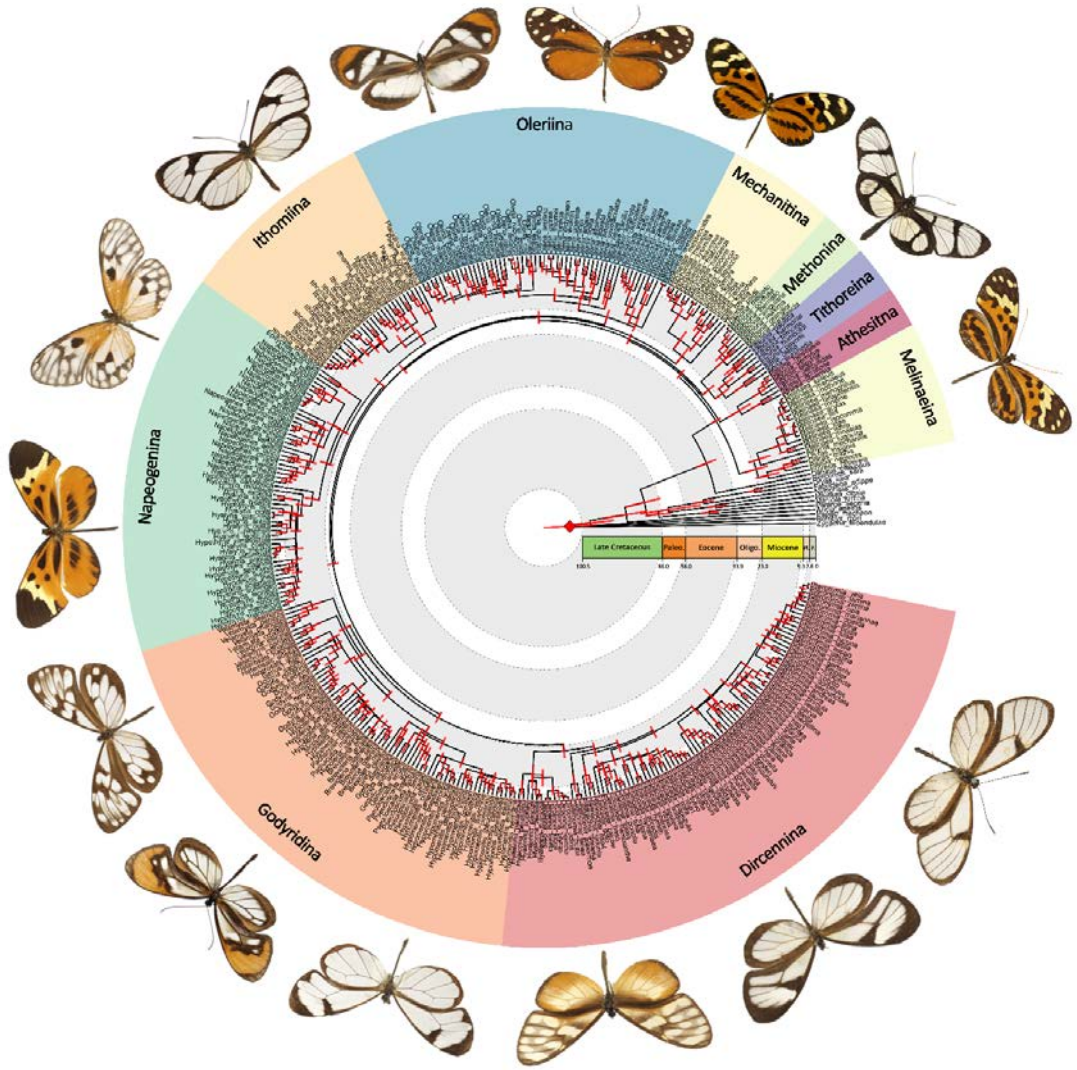
90 % of extent **species**

100% of extent **genera**

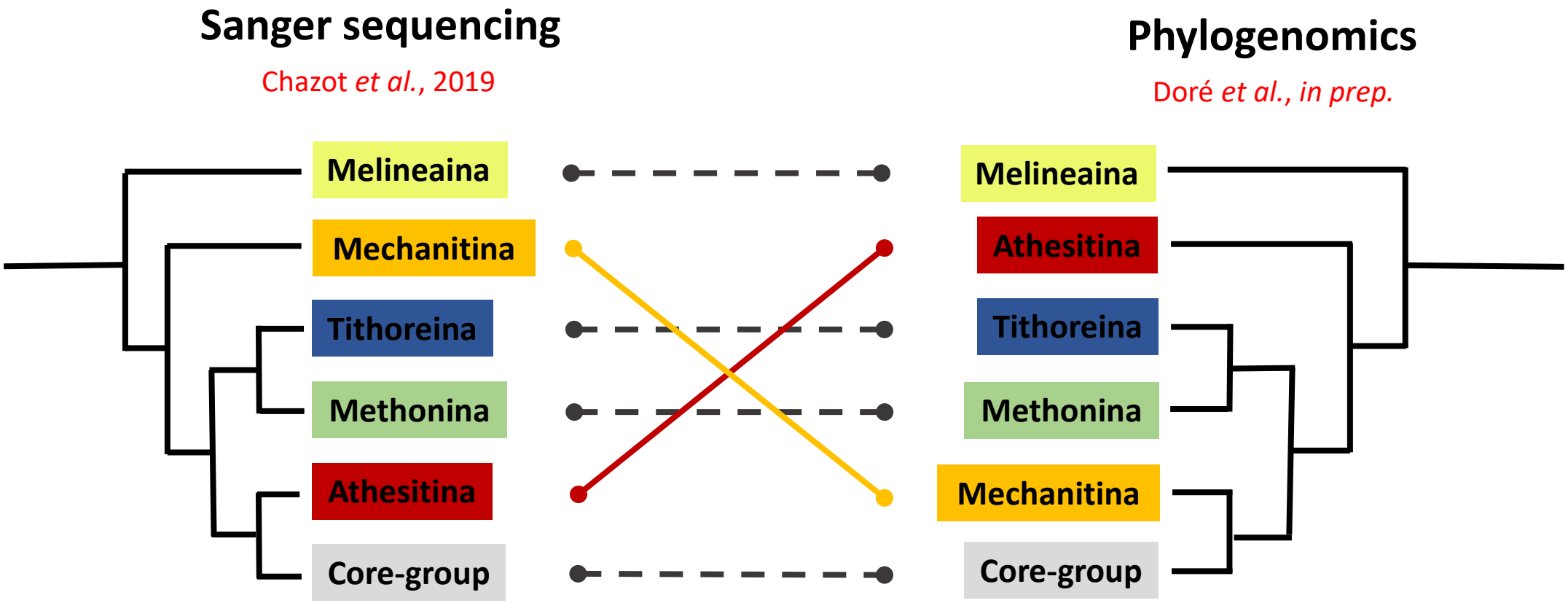
9,930 sites across **8 genes**

Fixed backbone from WGS phylogeny

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



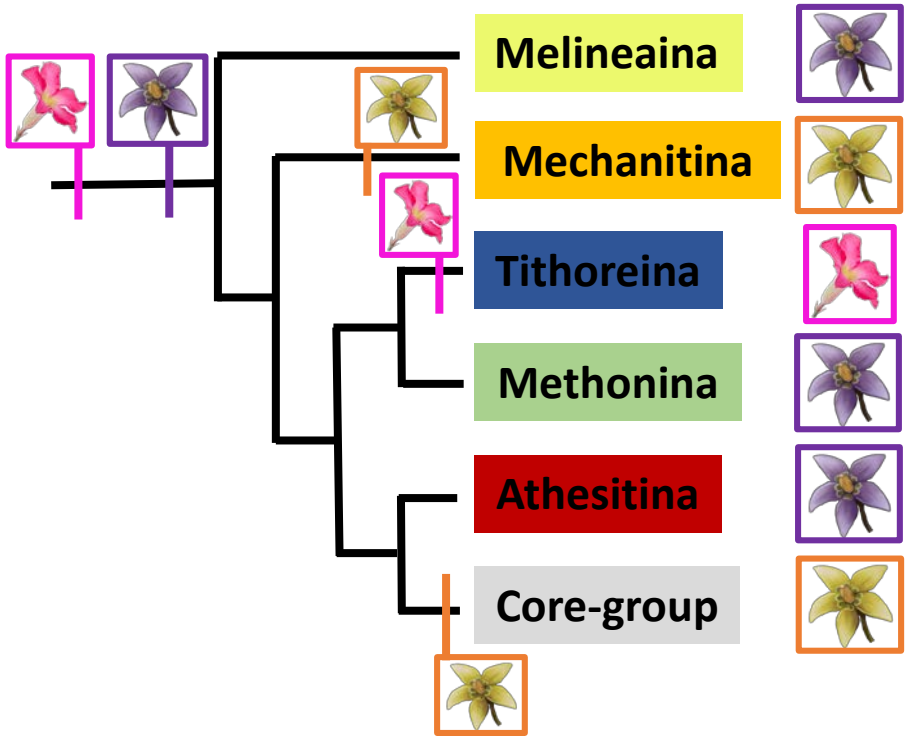
Phylogenomics resolving conflicts



Phylogenomics resolving conflicts

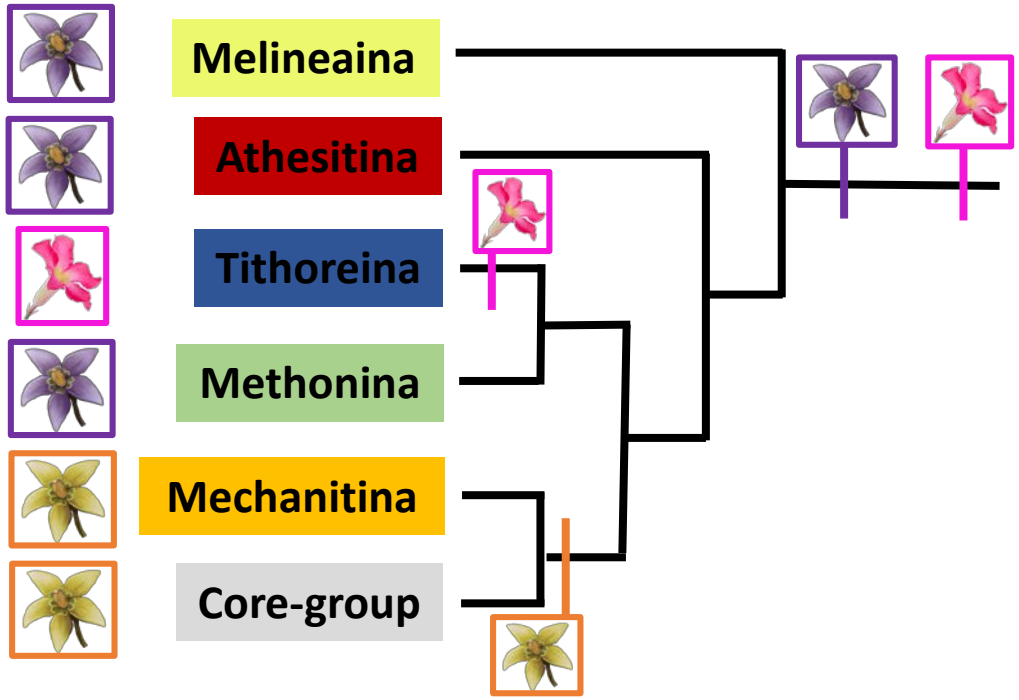
Sanger sequencing

Chazot *et al.*, 2019



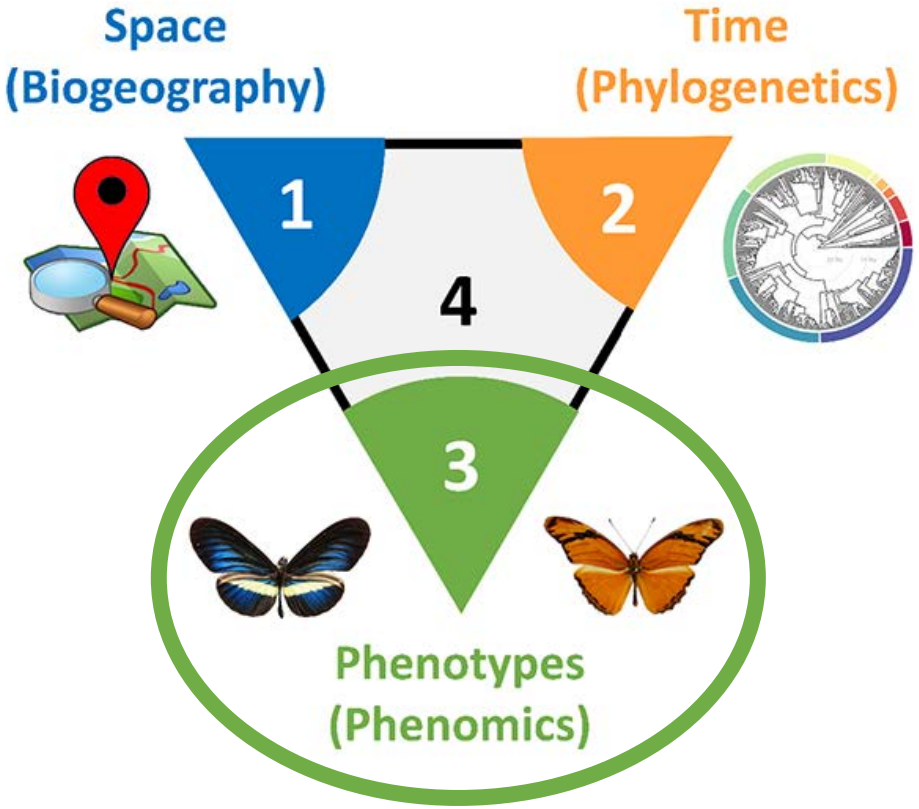
Phylogenomics

Doré *et al.*, *in prep.*



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

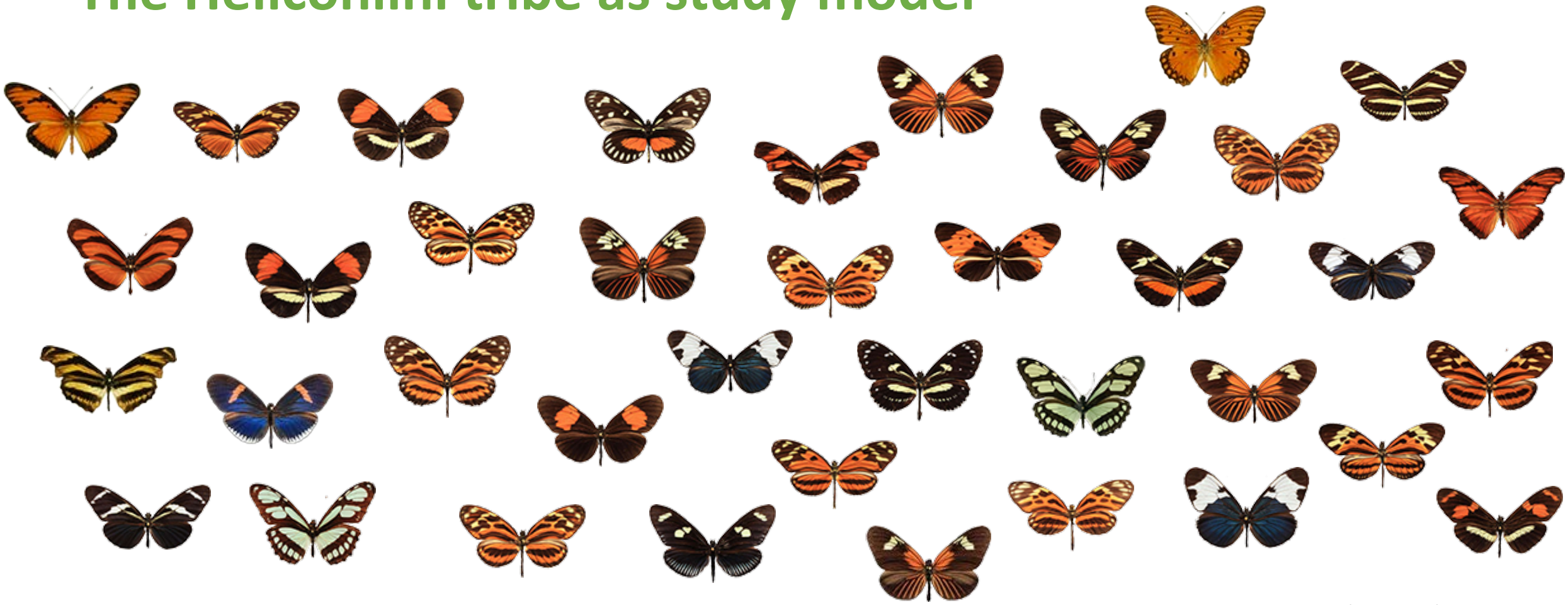


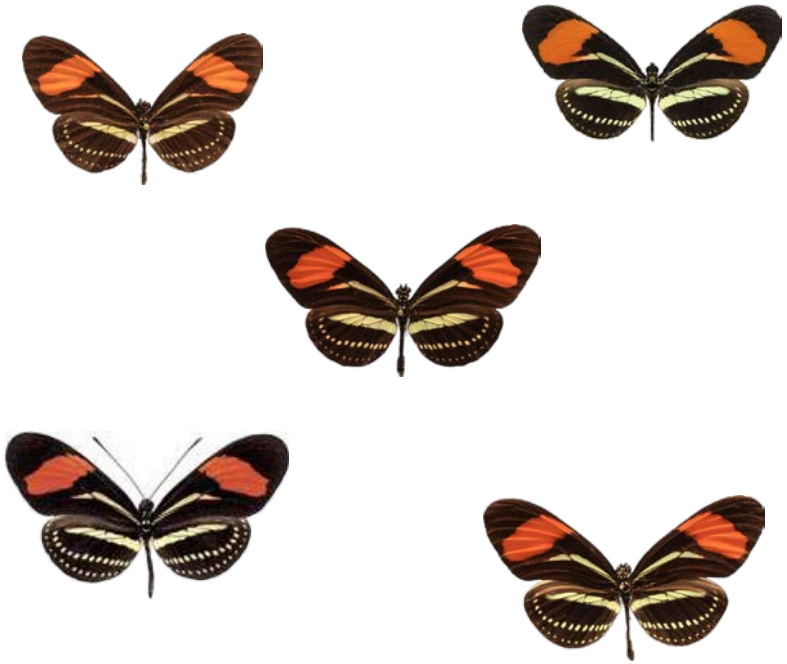
Photo credits: C. Jiggins

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

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

How to delineate mimicry rings?

POSTMAN ring



RED BAND ring

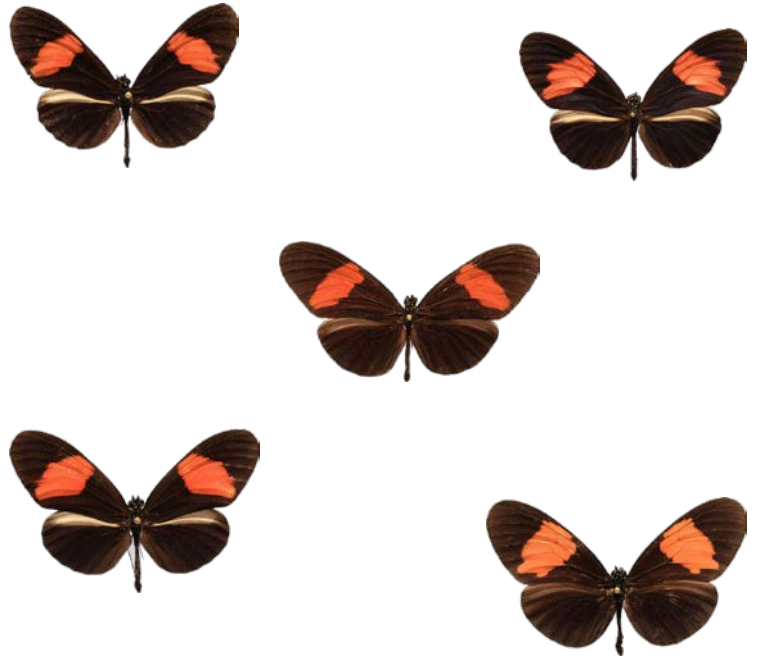
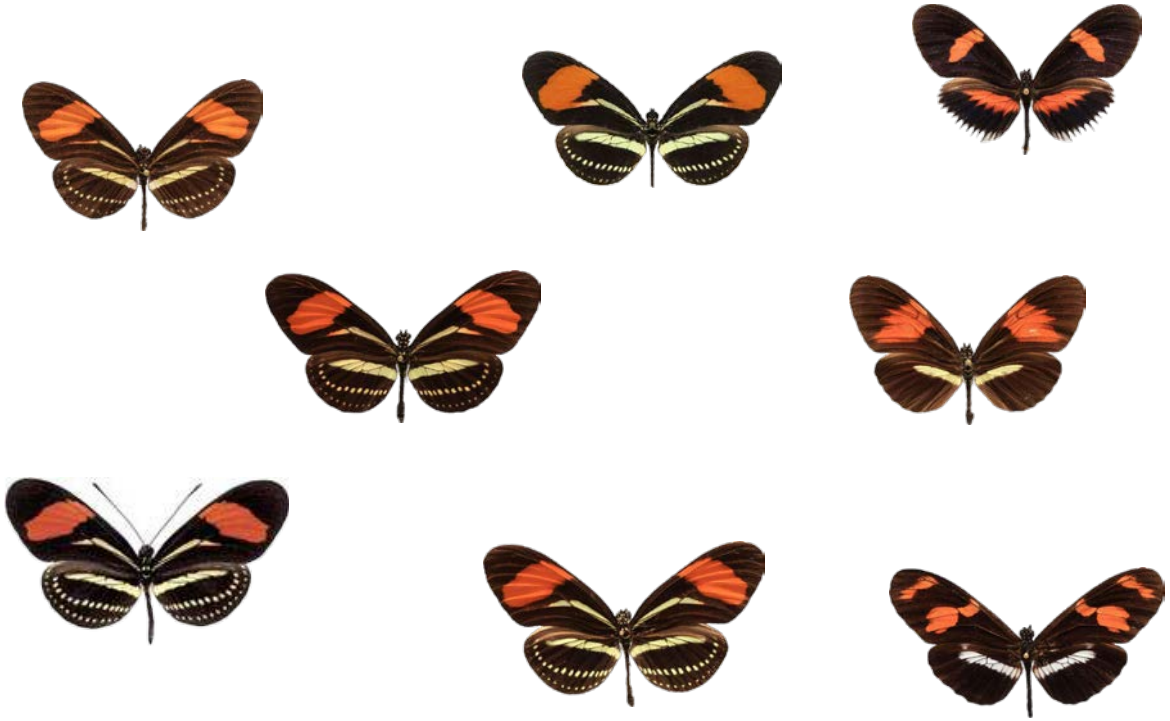


Photo credits: C. Jiggins

How to delineate mimicry rings?

POSTMAN ring



RED BAND ring

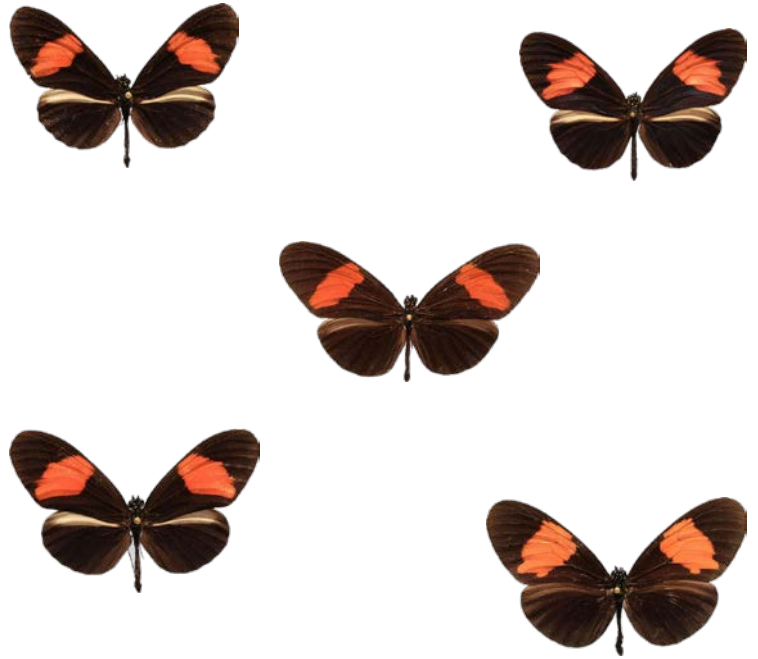


Photo credits: C. Jiggins

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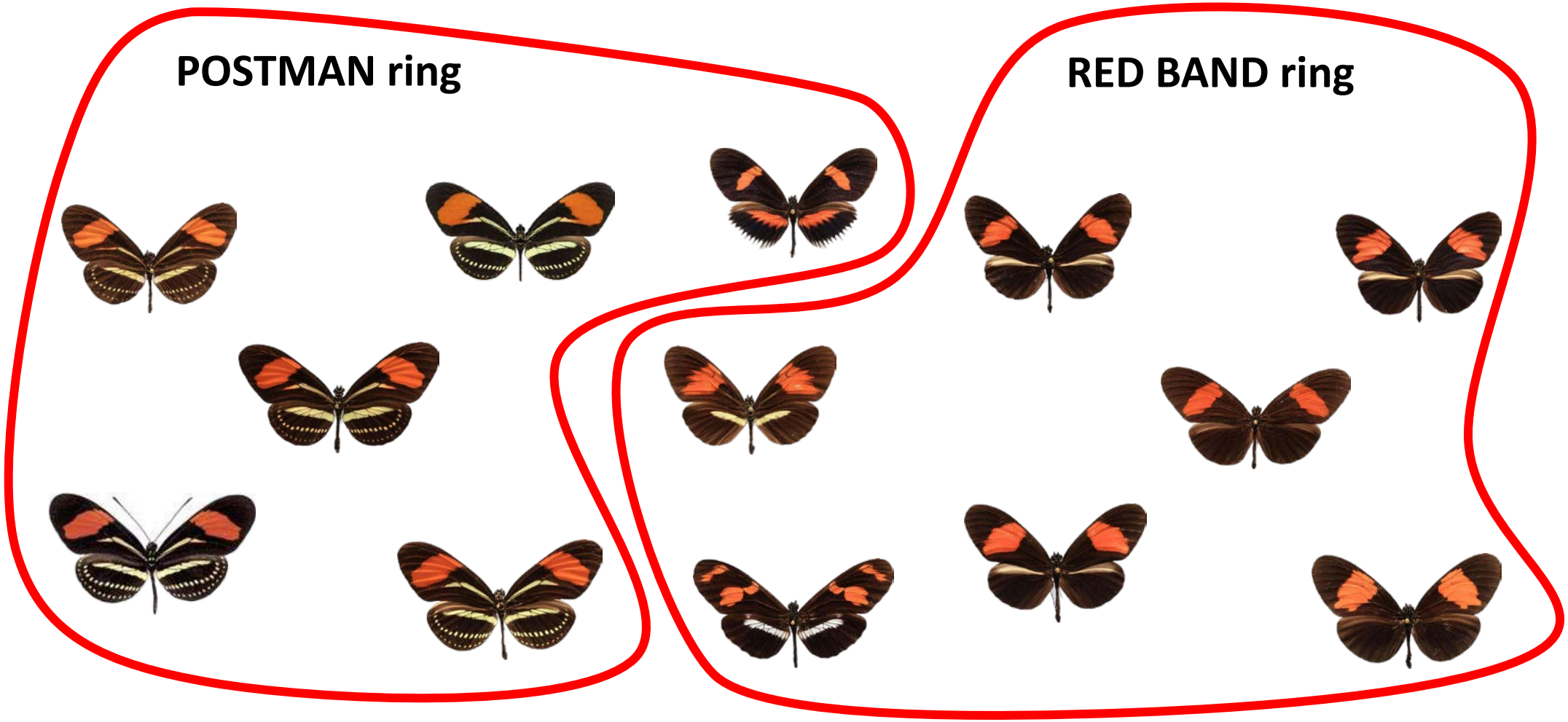
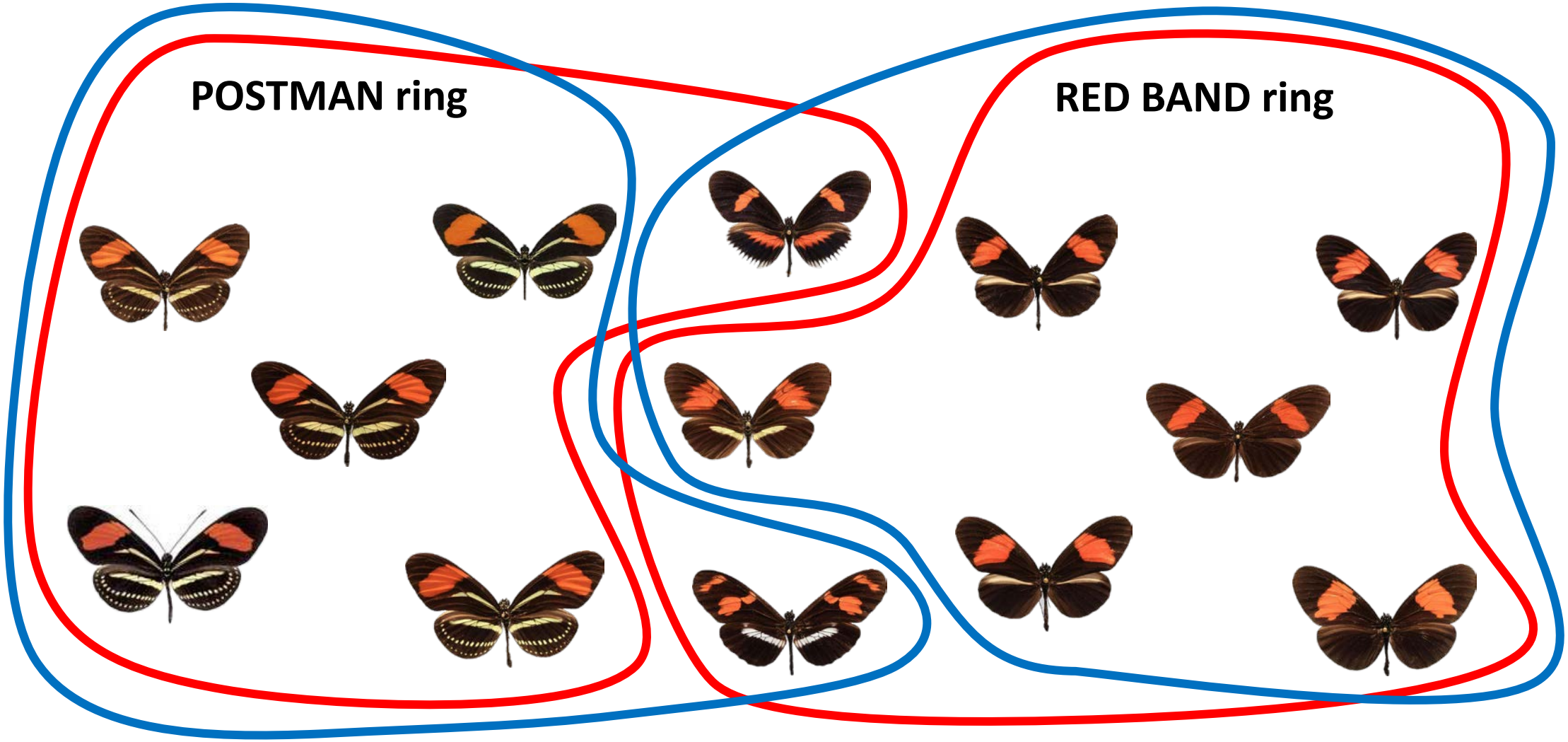


Article A

Photo credits: C. Jiggins

How to delineate mimicry rings?

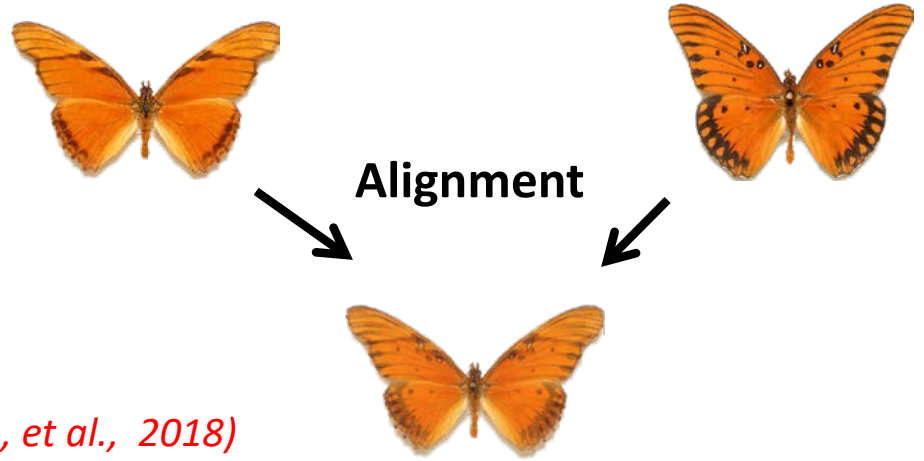


Article A

Article B

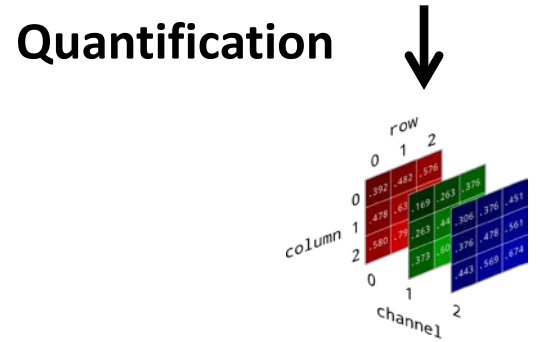
Photo credits: C. Jiggins

How to delineate mimicry rings?

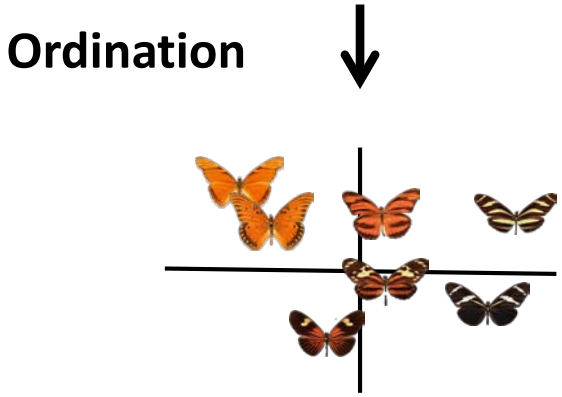


Quantitative approach:

- 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



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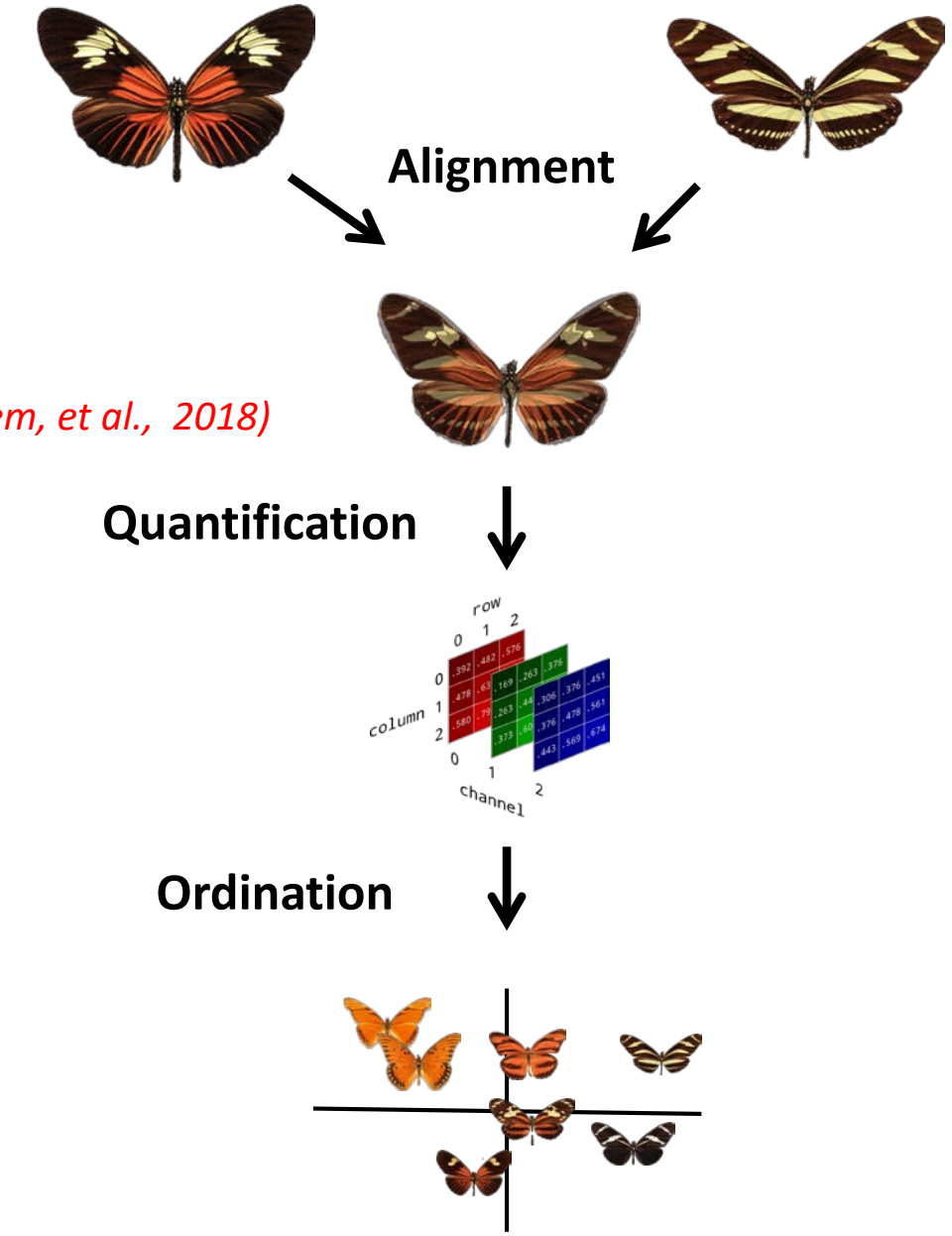

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How to delineate mimicry rings?

Quantitative approach:

- Quantify **visual signal** => ***patternize***
- Issues : **alignment** of pattern and outlines in case of high diversity

Photonic signal ≠ **Perception** of this signal

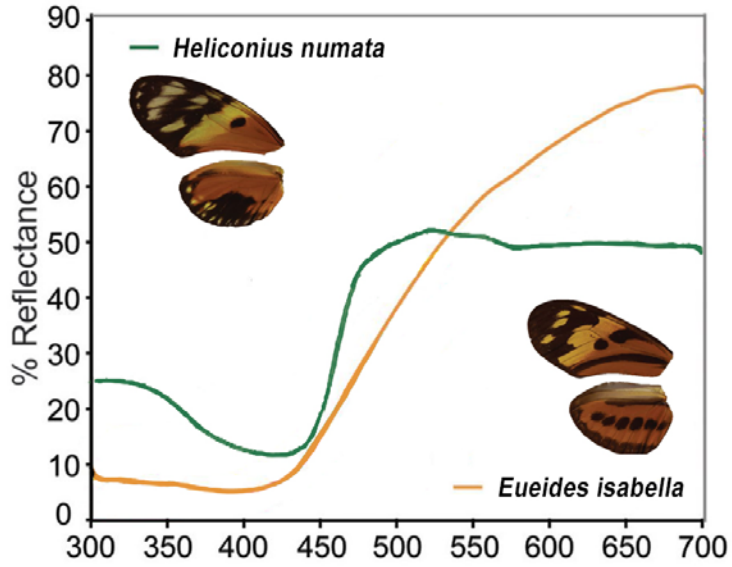
Photo credits: C. Jiggins

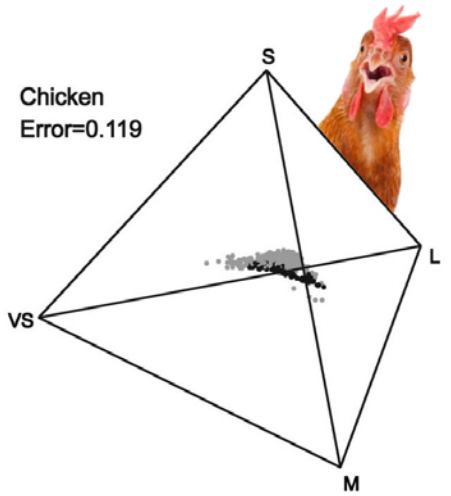
How to delineate mimicry rings?

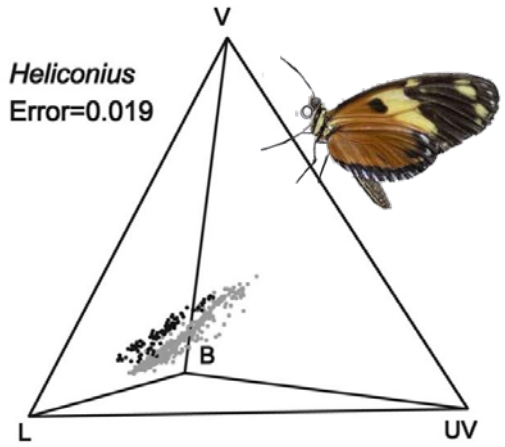
Quantitative approach:

- Quantify **visual signal** => ***patternize***
- Issues : **alignment** of pattern and outlines in case of high diversity

Photonic signal **≠ Perception** of this signal







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 ( , ) )

.

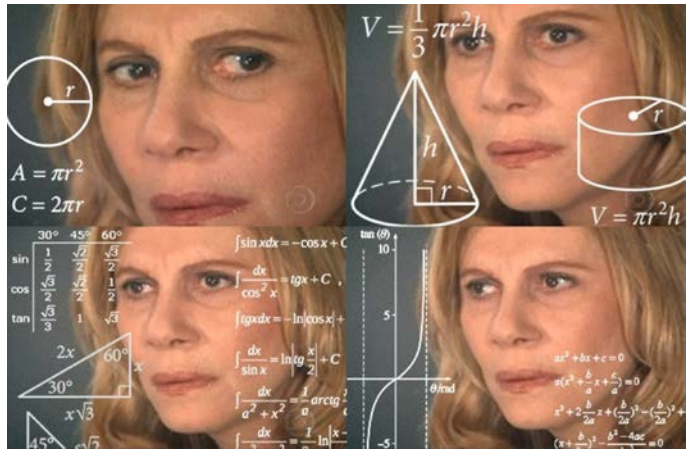
.

.

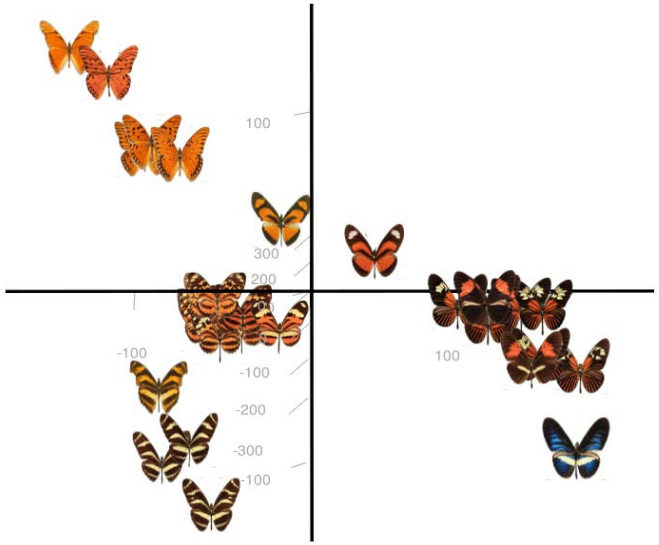
75,240 ( , ) )

Embedding method:
Machine learning algorithm
(t-STE)

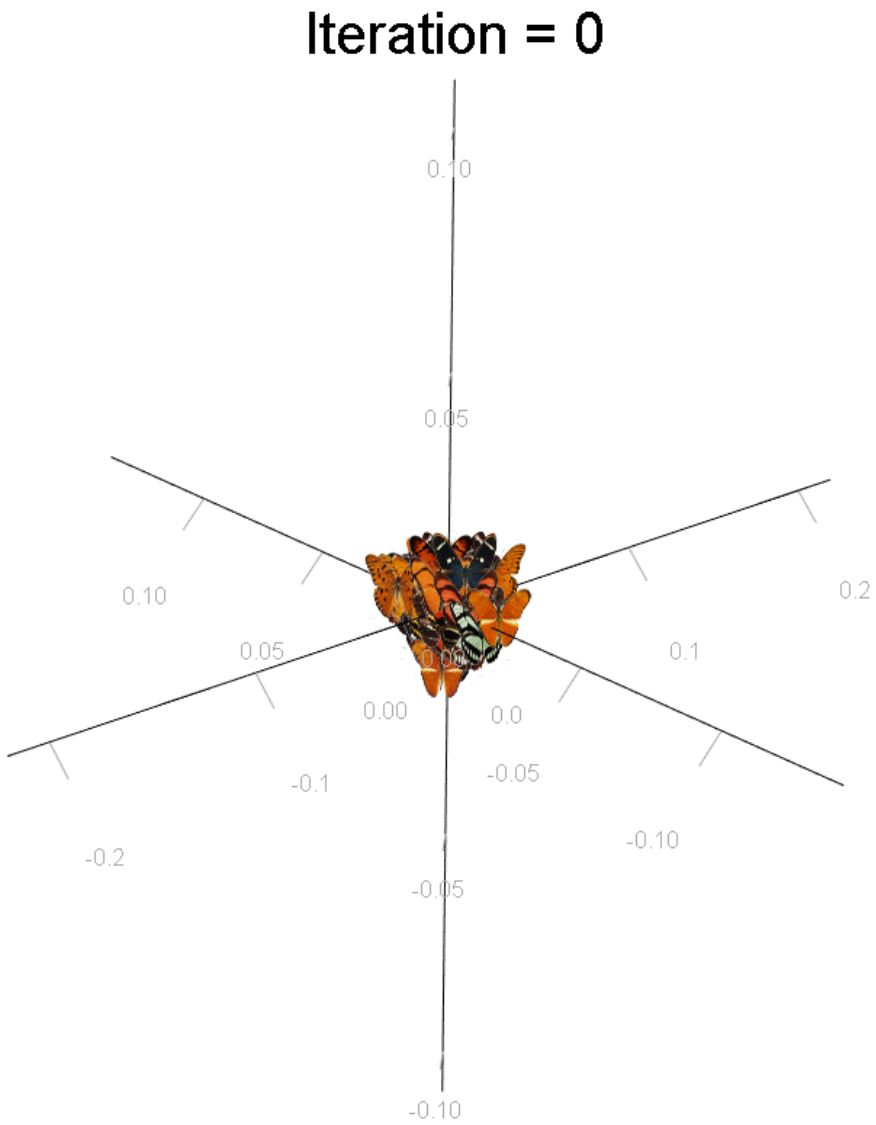
(van der Maaten & Weinberger, 2012)

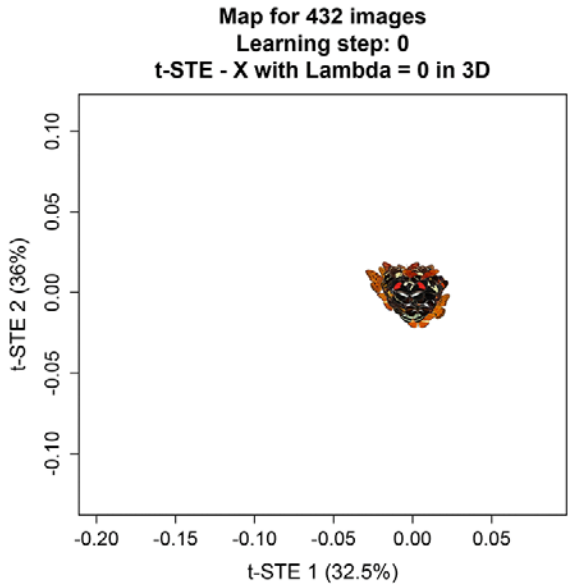


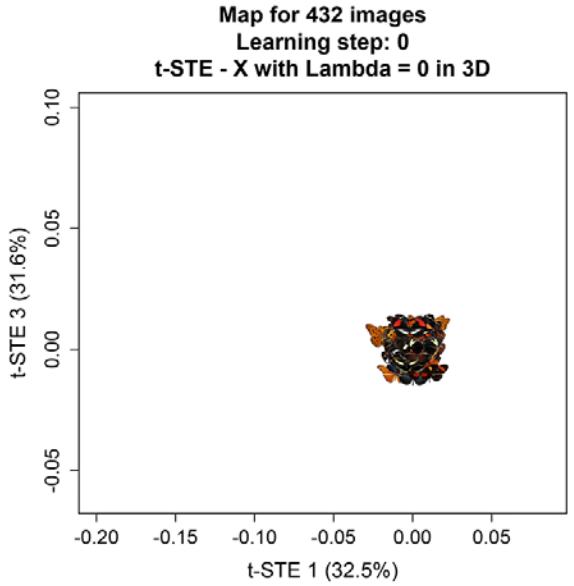
Output = **coordinates** in space of reduced dimensionality
=
Perceptual map

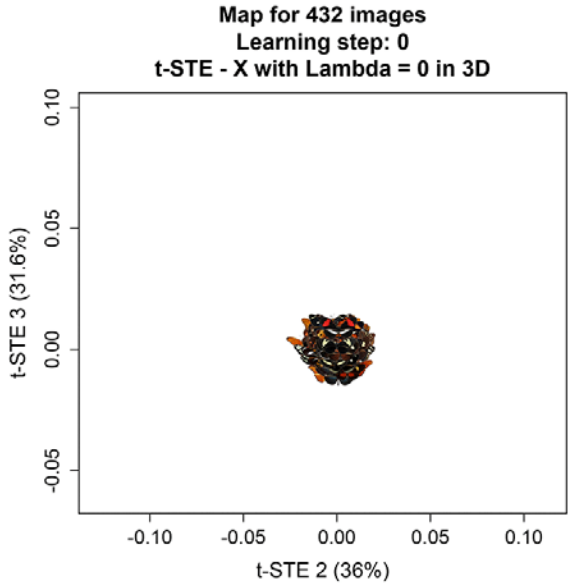


Embedding method: t-STE









Perceptual space

75,240 triplets for **432** images

The spatial scale of mimicry rings

Why do we have a **continuum**?

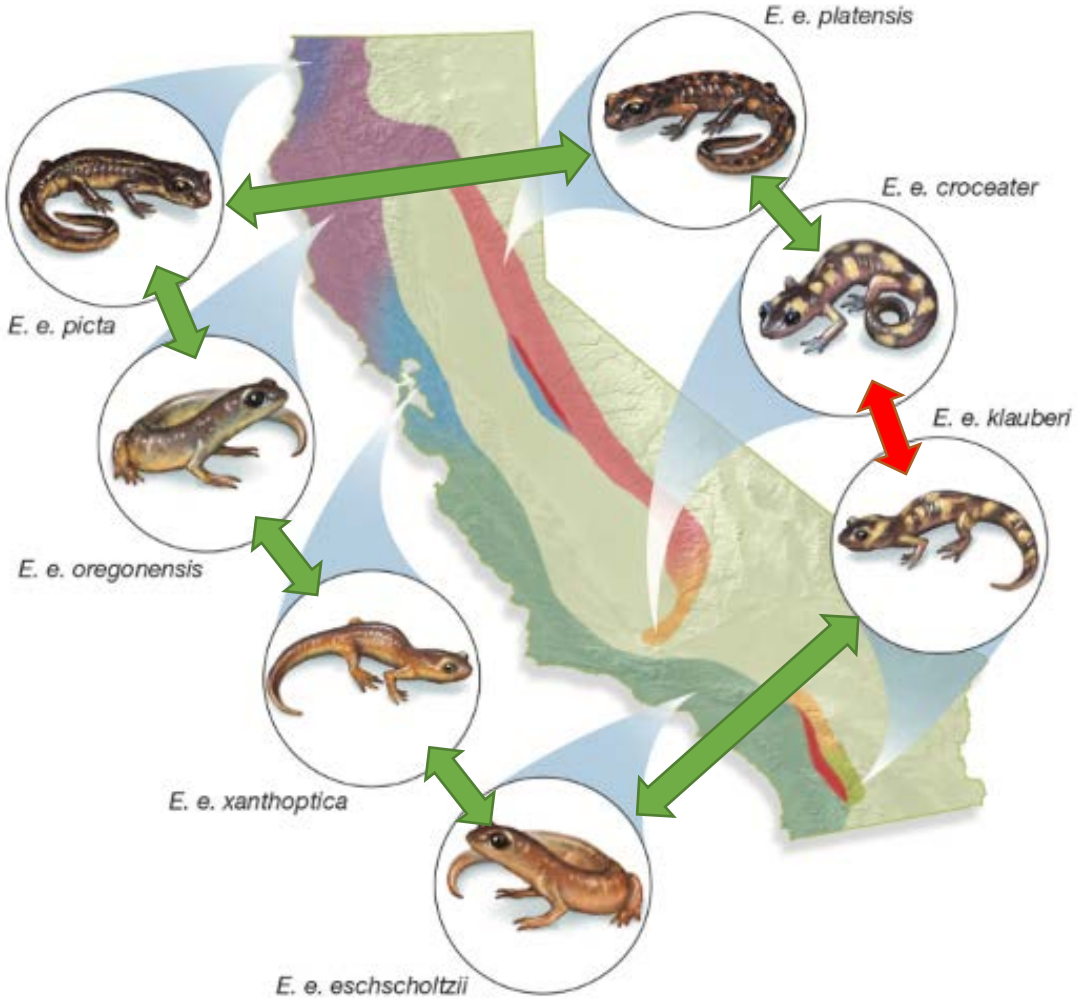
Analogy with **ring species**

- **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**?

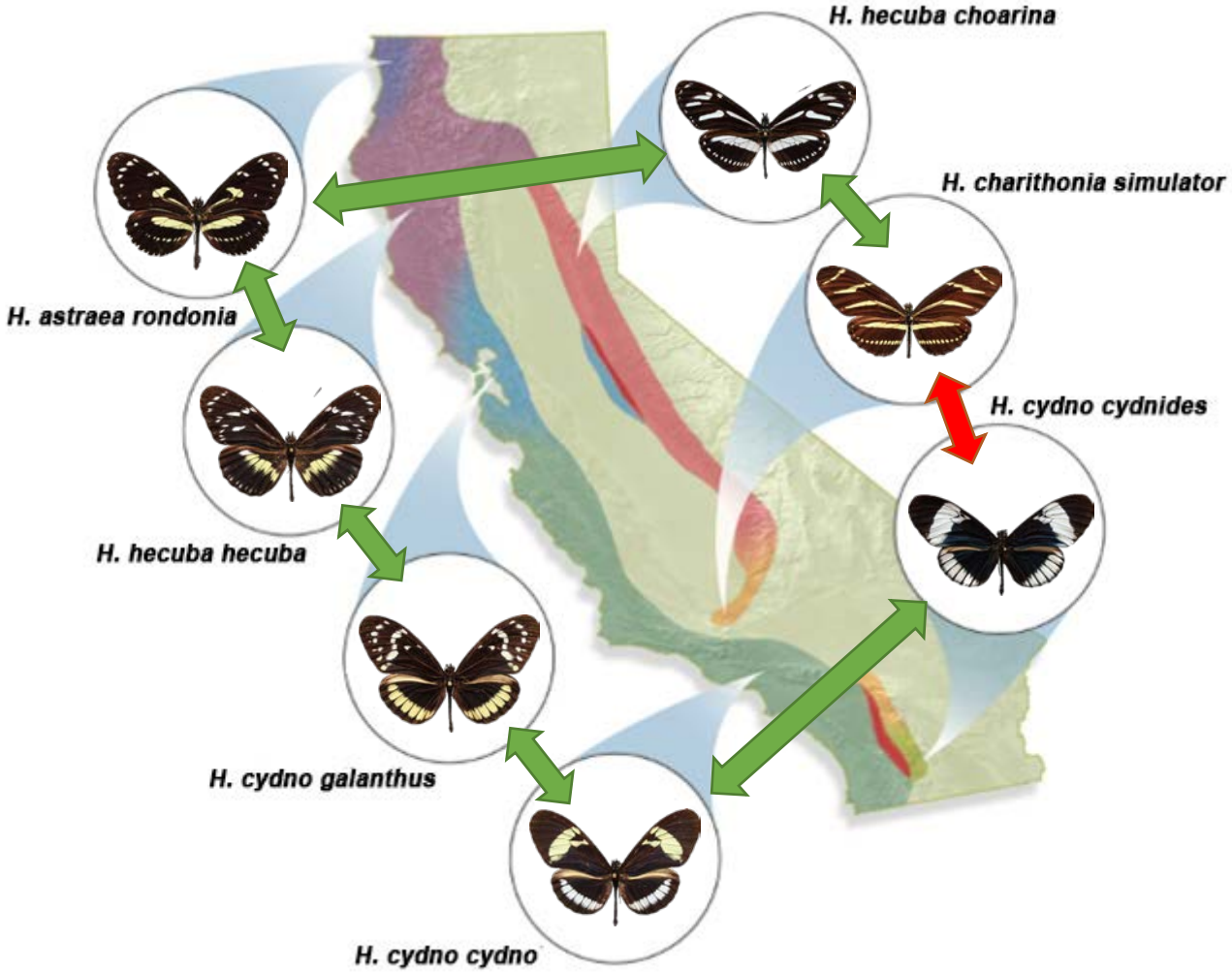
Analogy with **ring species**

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

Conclusion:

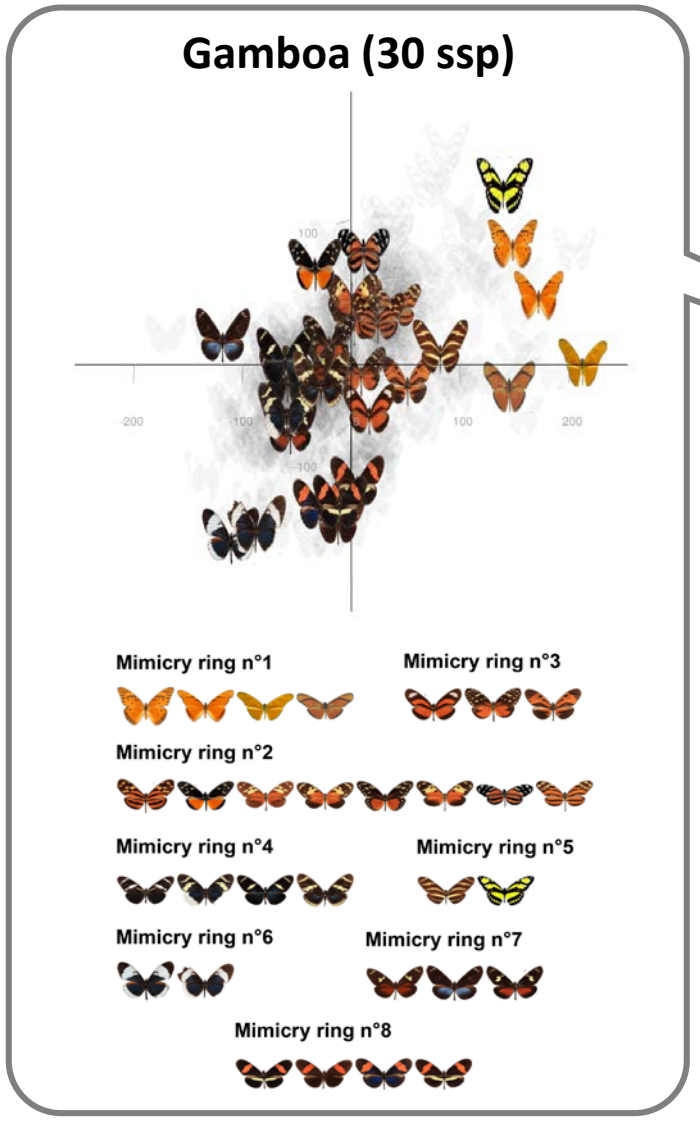
- Expected to find a **continuum** at the **global scale**
- Mimicry rings should be defined at **community-level?**

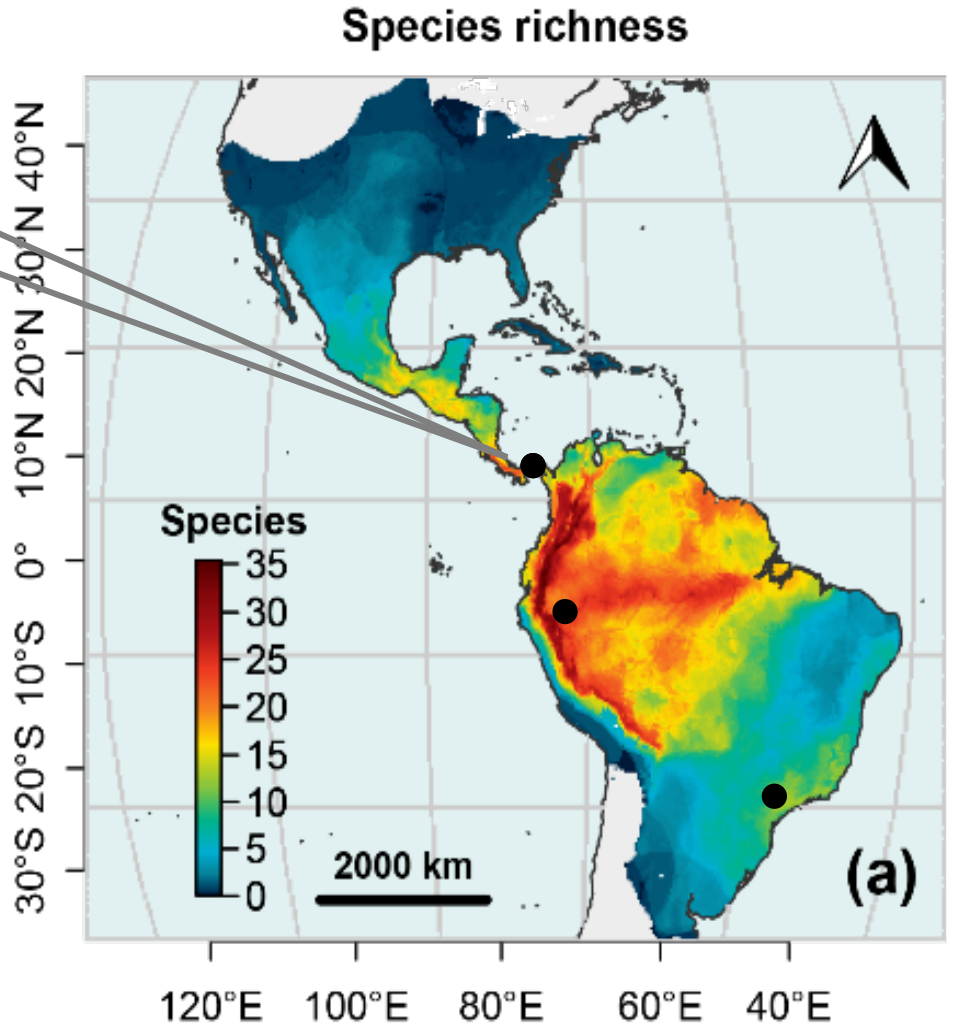
Next step: Apply the perceptual map approach at **community-level**



Source: Chegg.com

Interactive map of Müllerian mimicry communities





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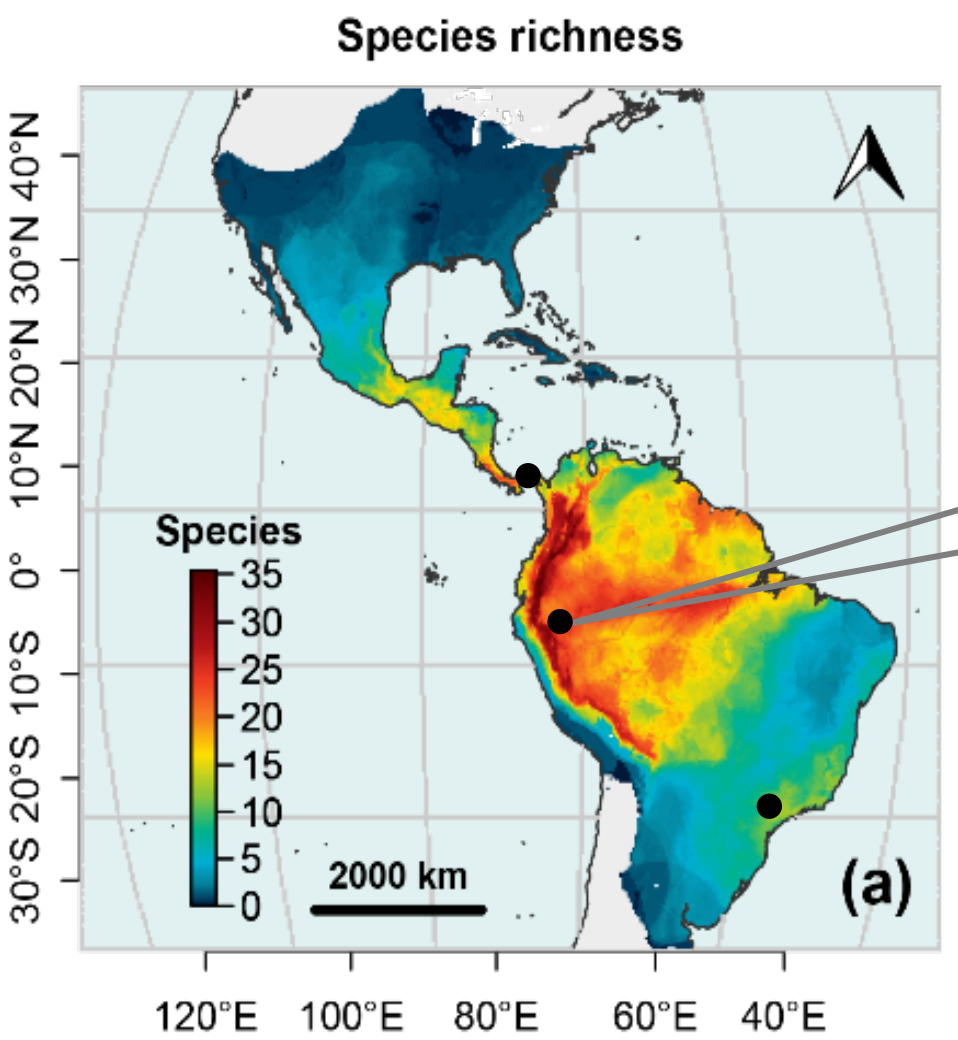
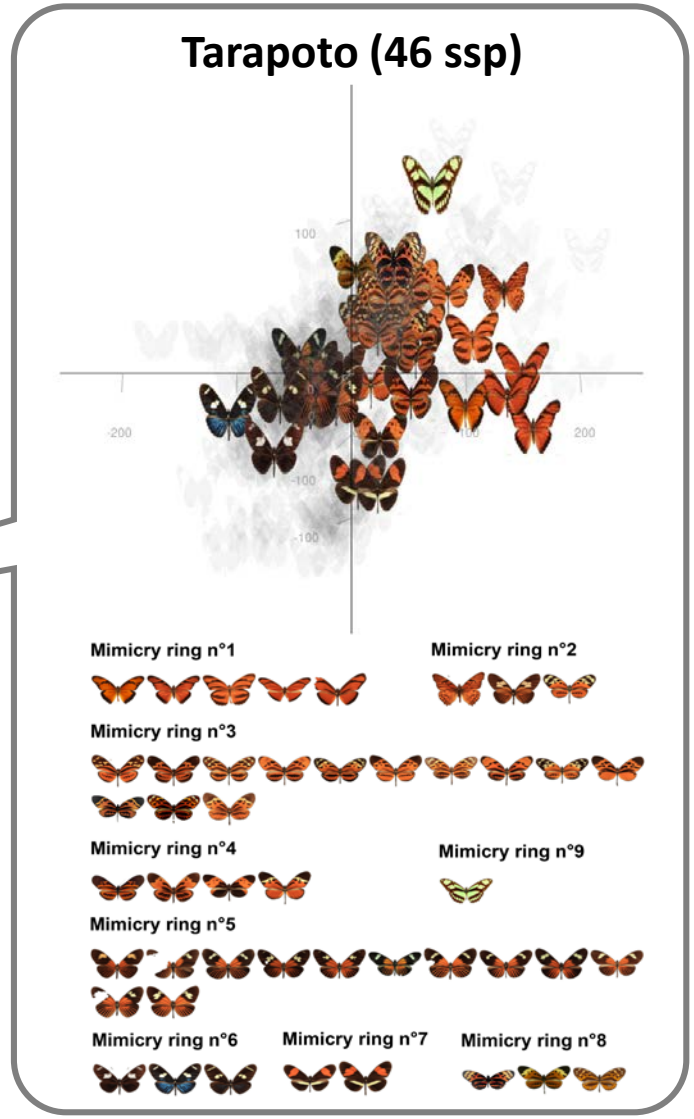
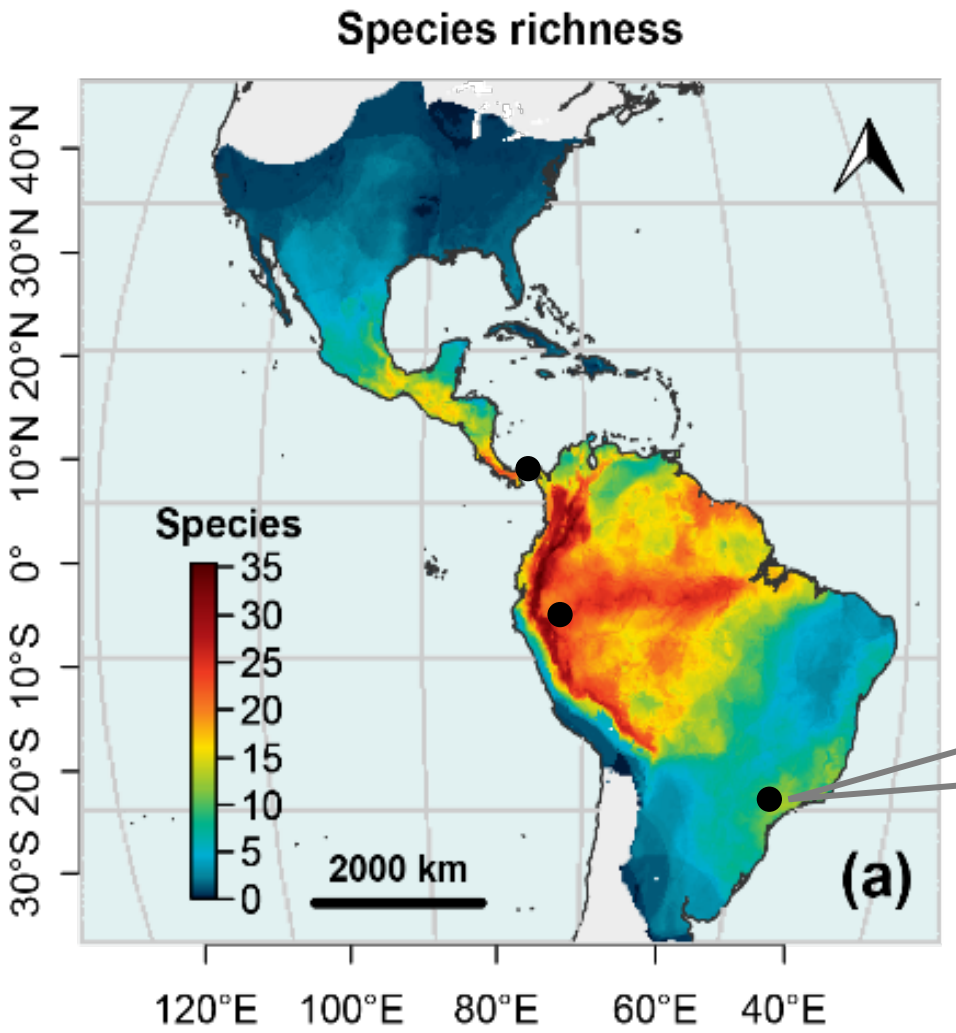
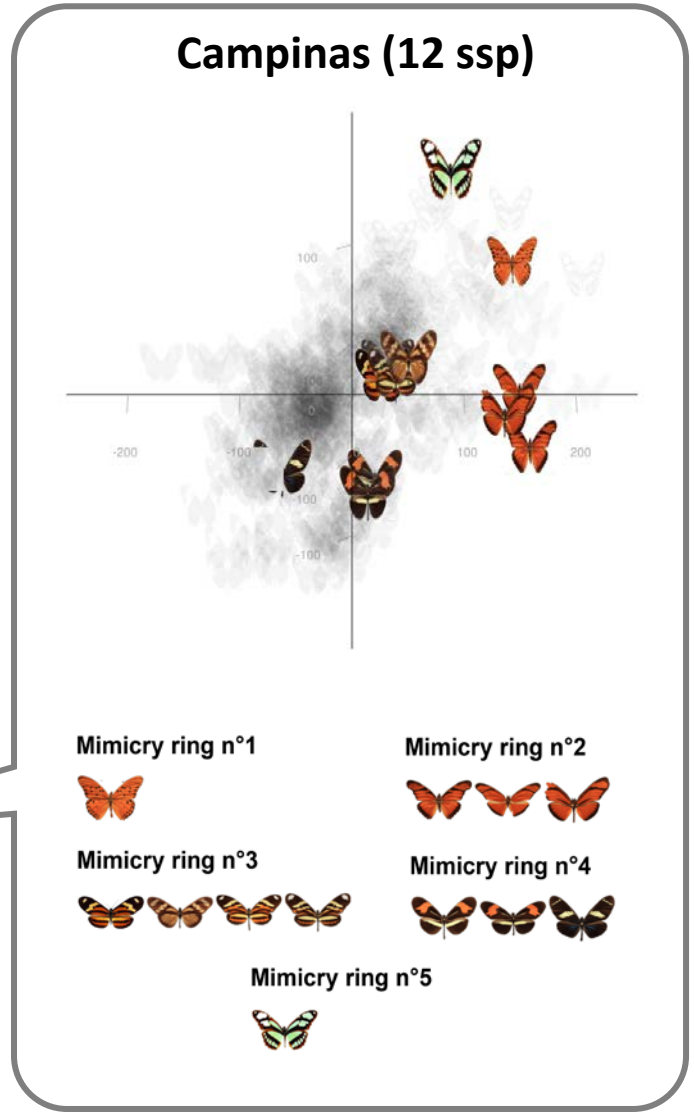




Interactive map of Müllerian mimicry communities

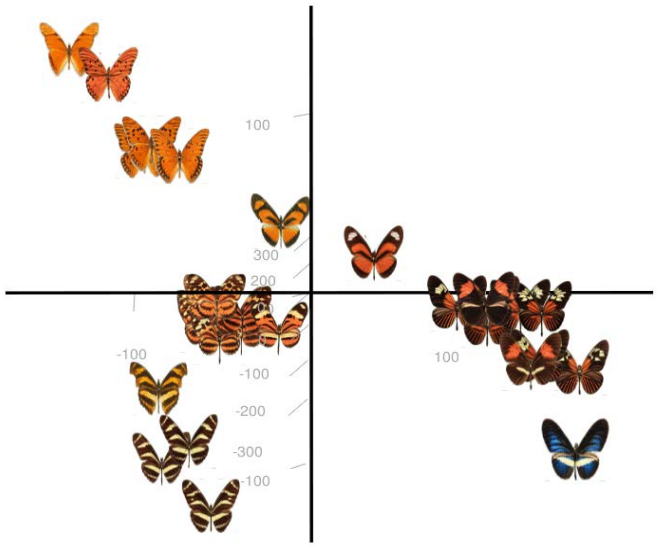




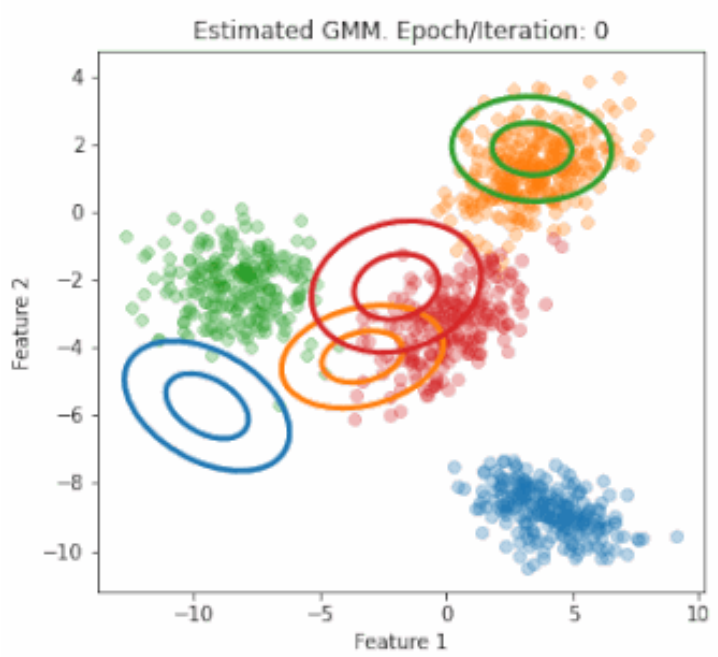
Clustering method

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

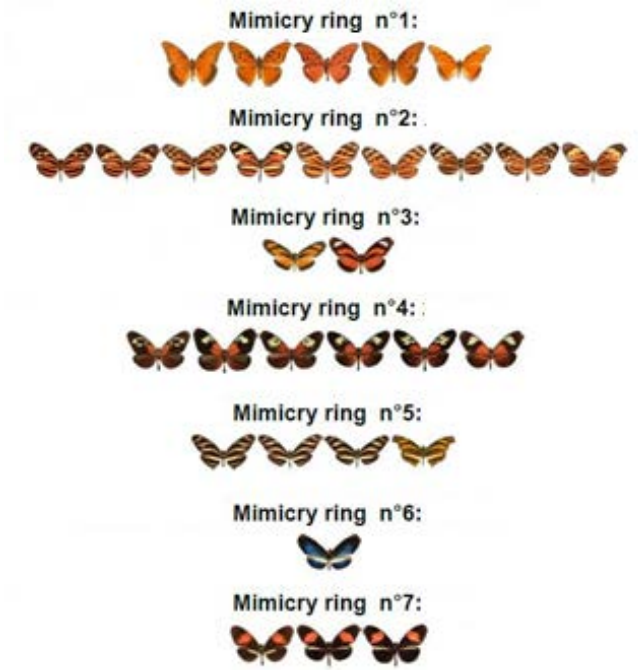
Input = **coordinates**
on the perceptual map



Clustering method:
Gaussian Mixture Models
(GMM)



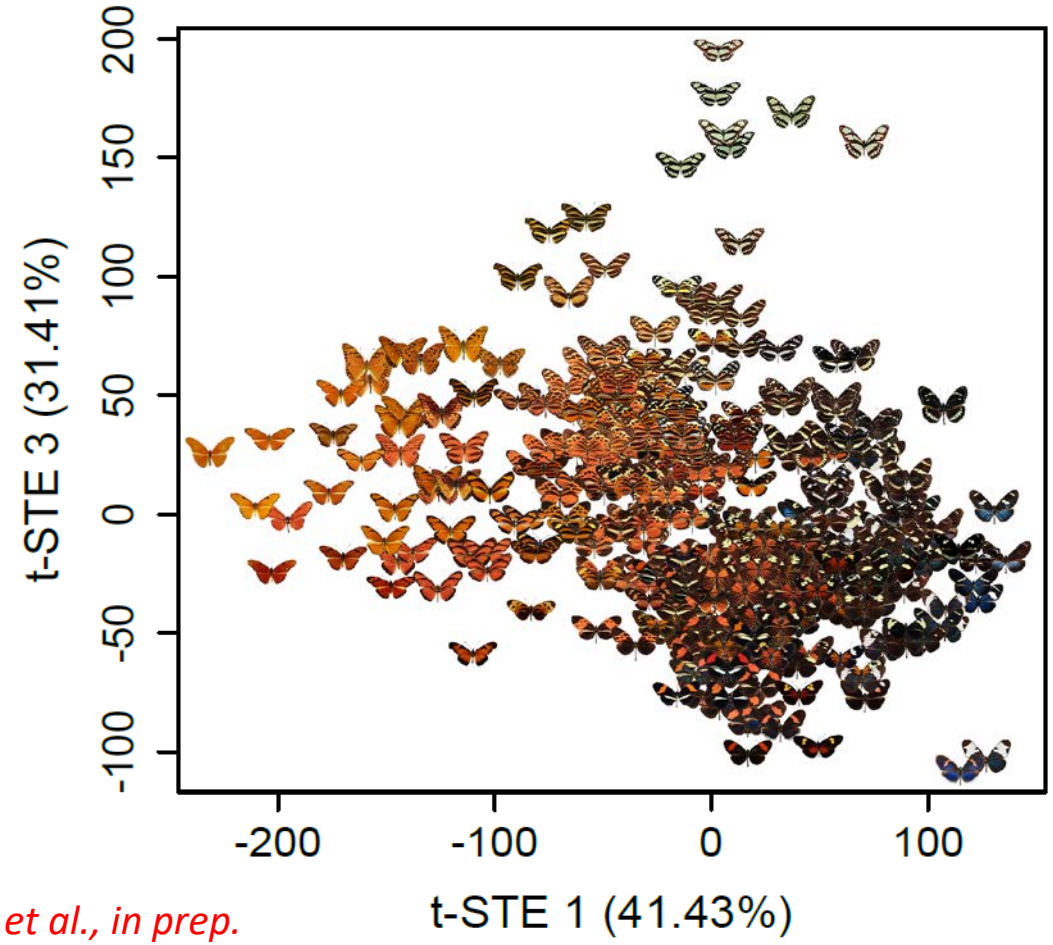
Output = **clusters**
of wing patterns
=
Mimicry rings



Credits: J. Zhang

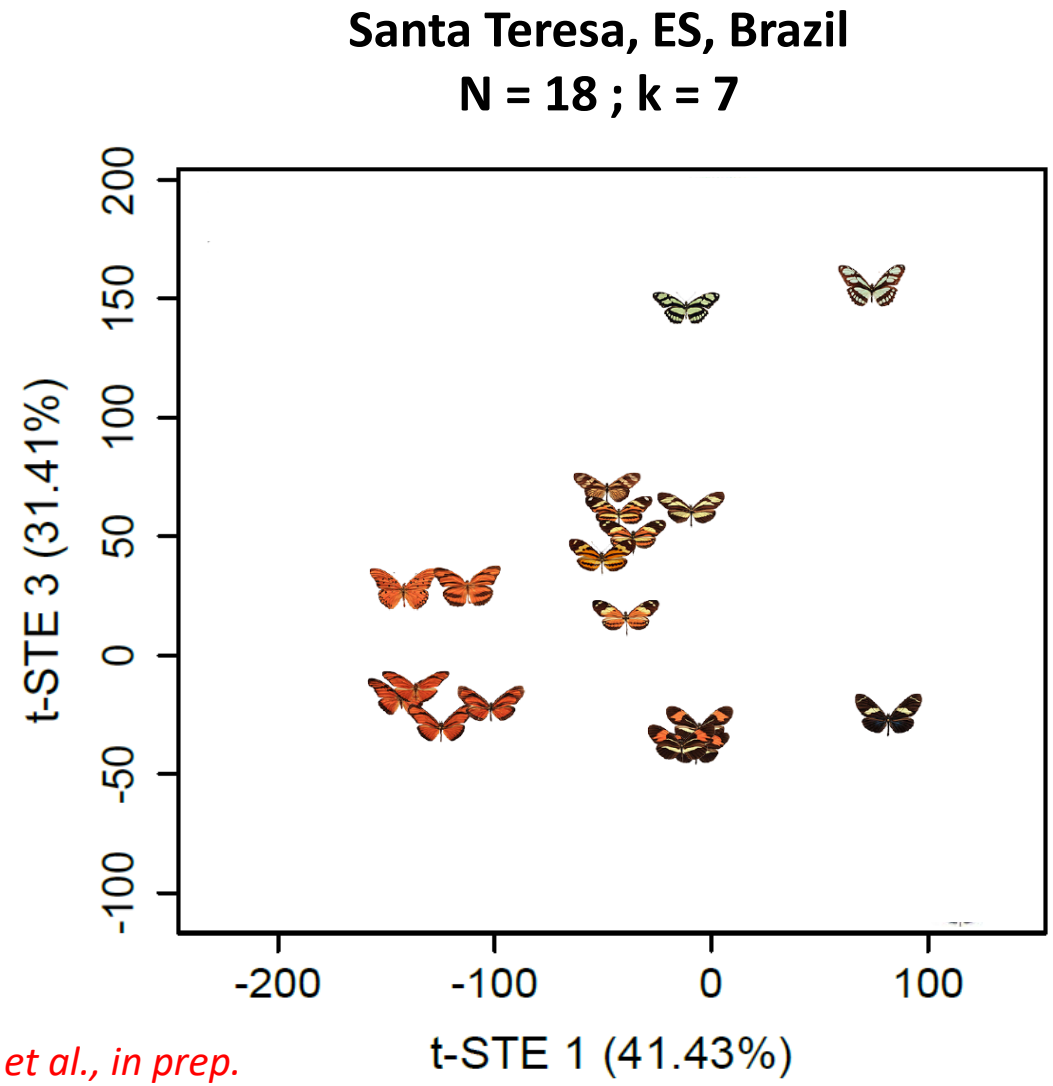
Local perceptual maps

All subspecies
N = 432



Doré et al., in prep.

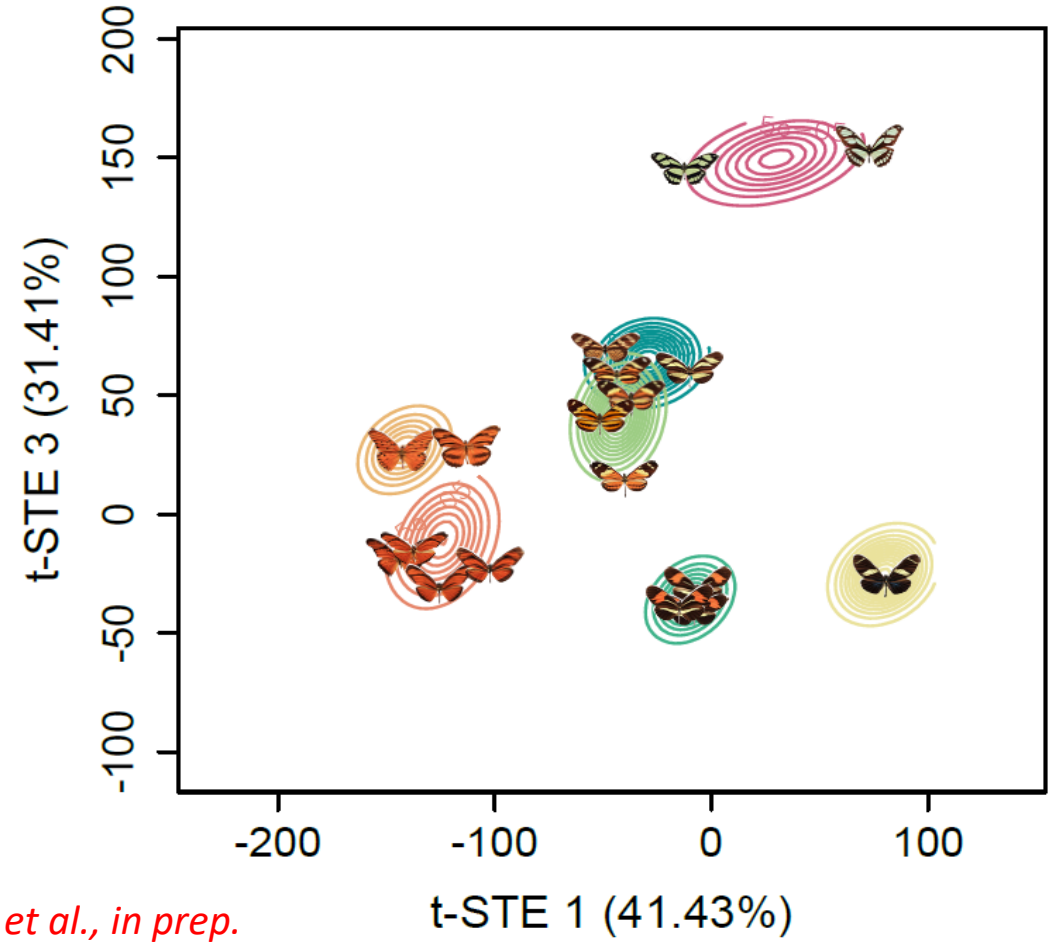
Local perceptual maps



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

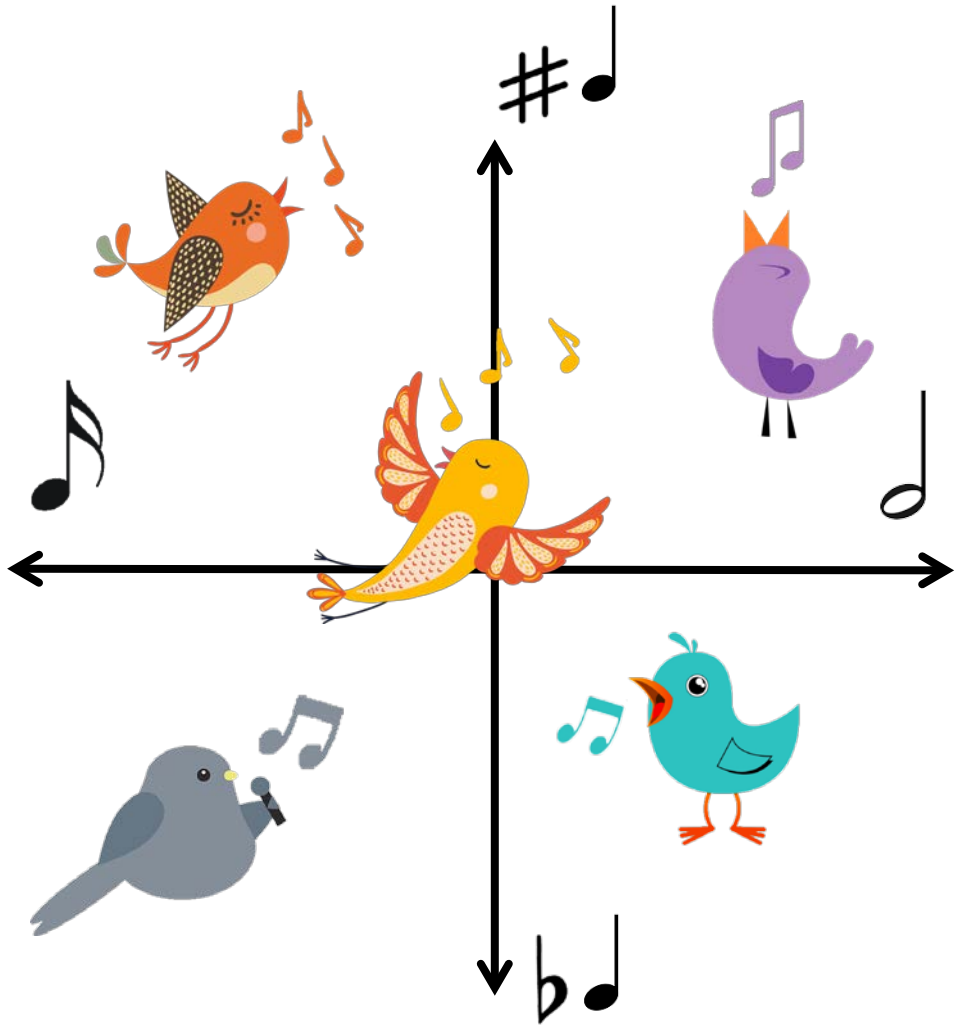
Mimicry ring n°6

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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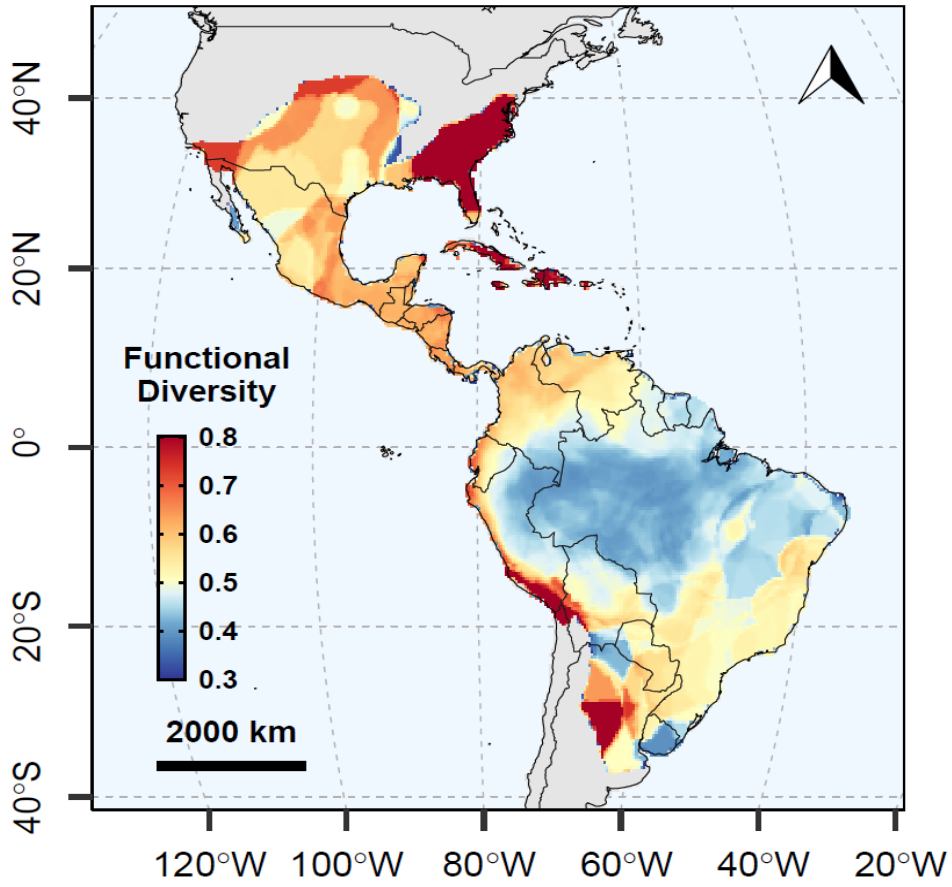

Doré et al., in prep.

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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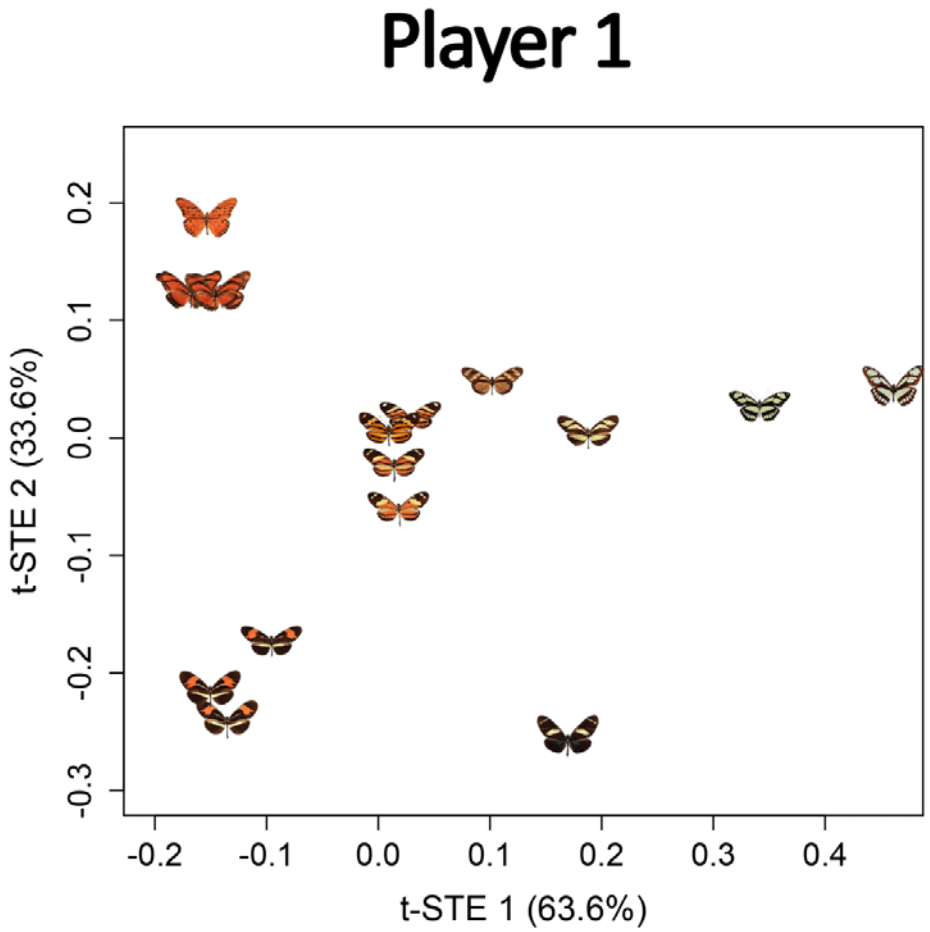


Comparison of indivudal perceptual maps

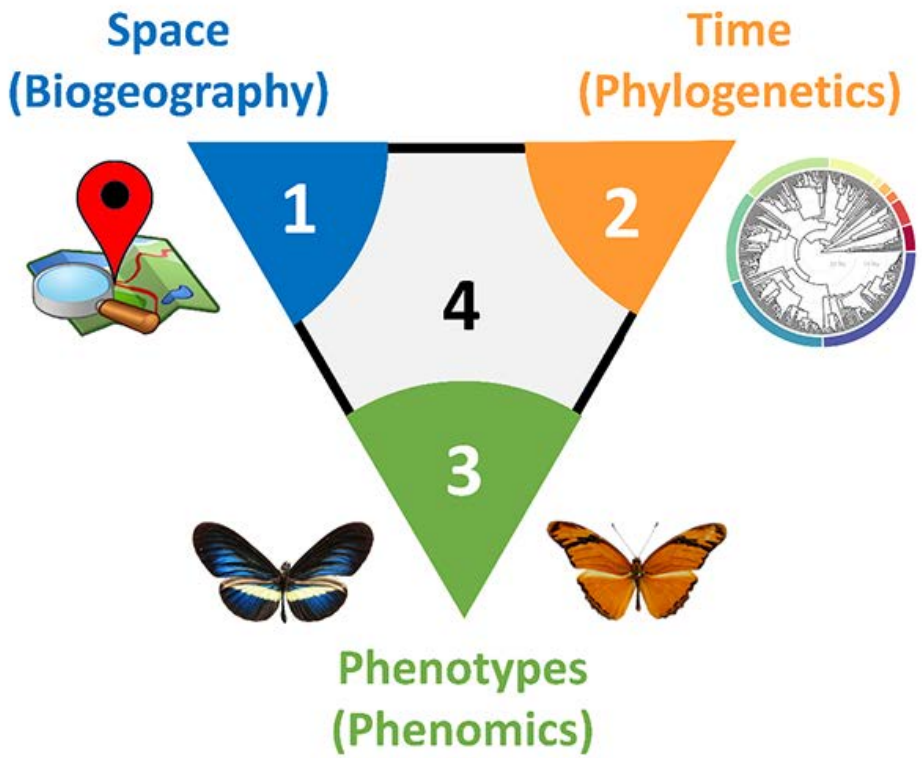
Outlines and objectives

CHAPTER 1

Map **biodiversity patterns**

CHAPTER 3

Quantify **phenotypic similarity** in wing patterns

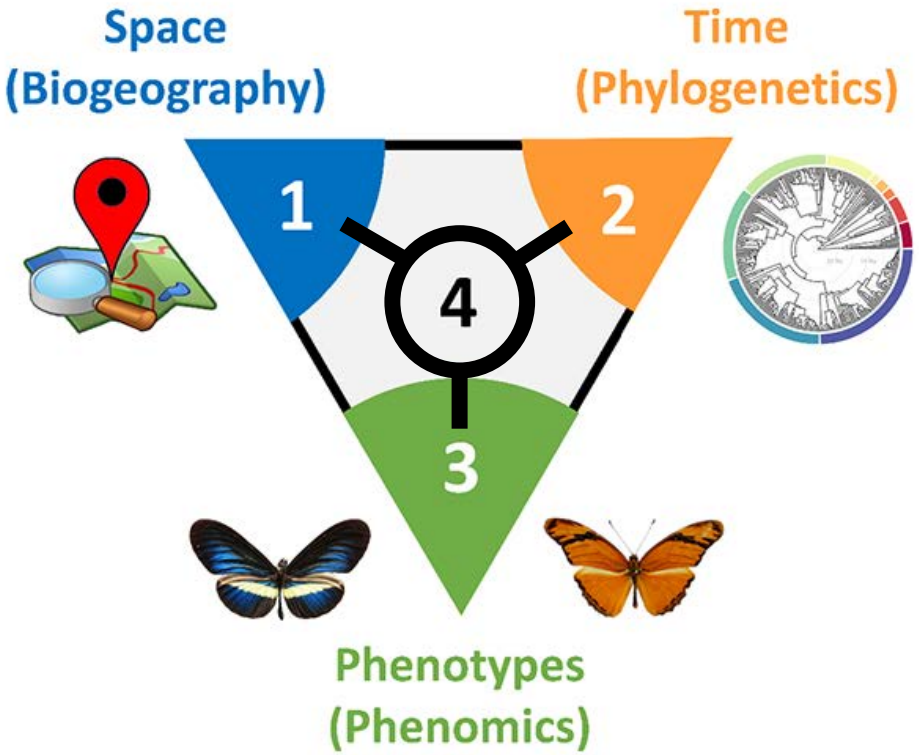


CHAPTER 2

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 phenotypic groups / putative mimicry rings

39 phenotypic groups / putative mimicry rings

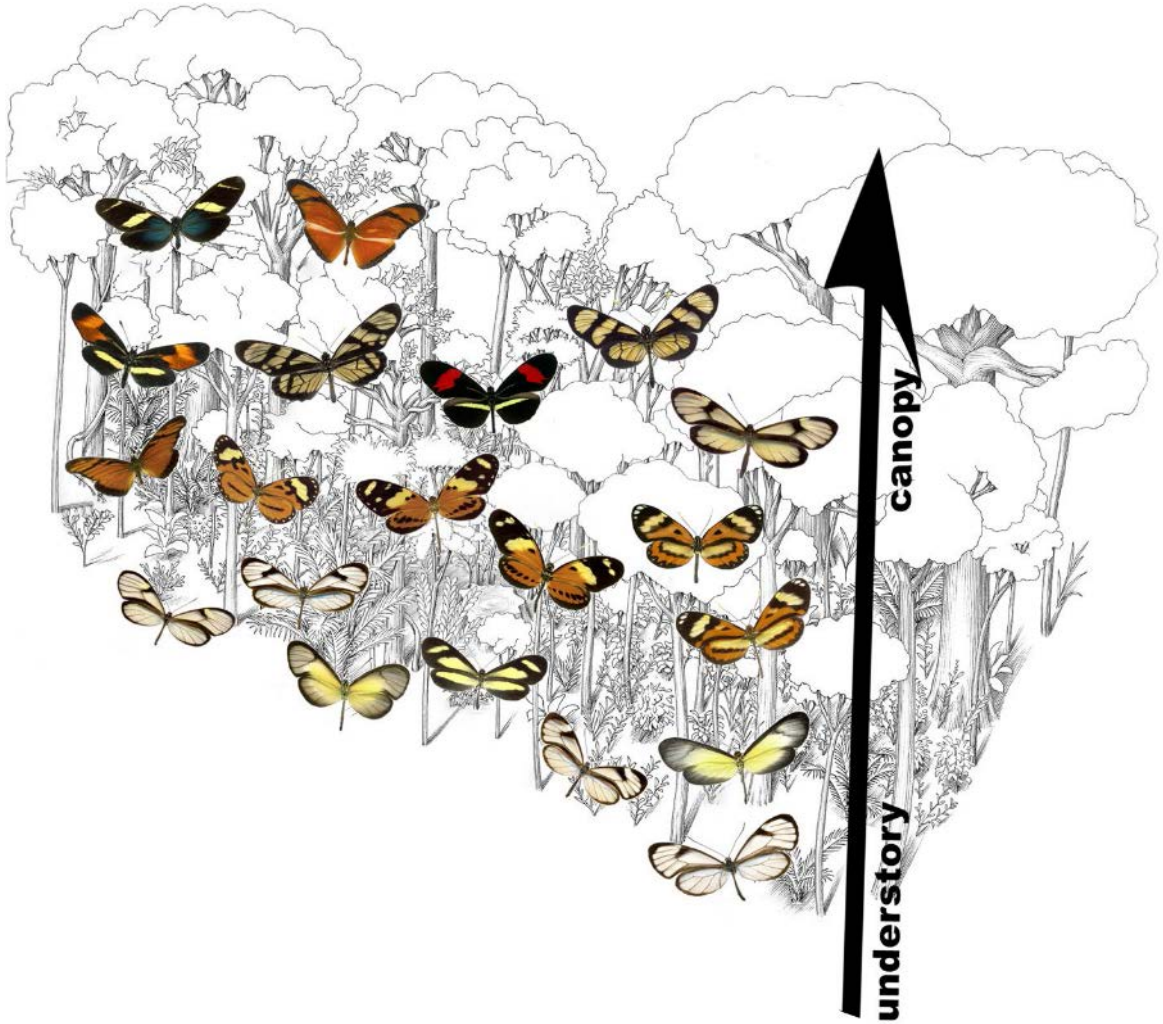
State-of-the-art

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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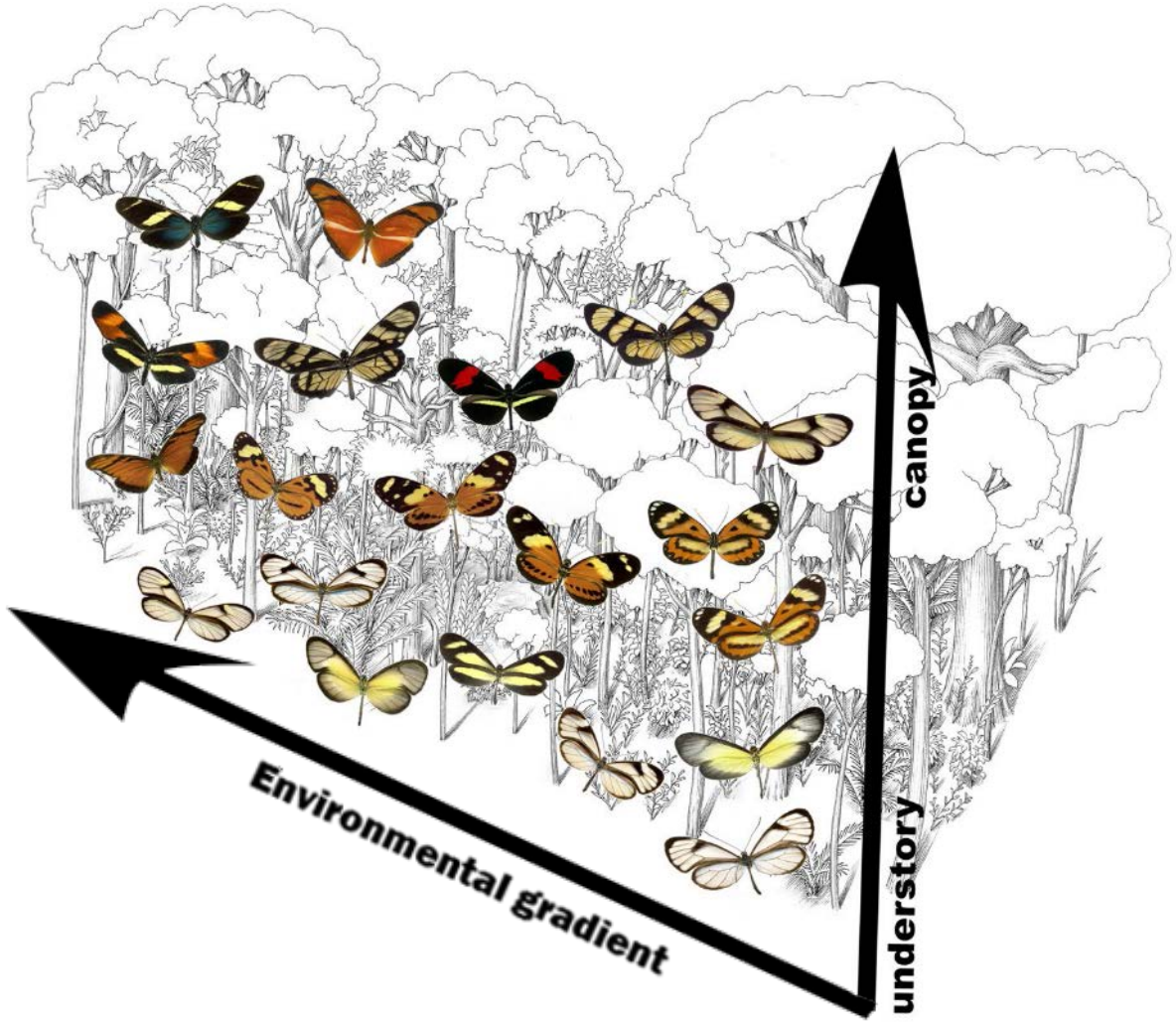

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Credits: Arthur Anker

State-of-the-art

Structuration of mimetic communities by:

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- **altitude** *(Chazot et al., 2014)*

Limits :

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

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

Objectives

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

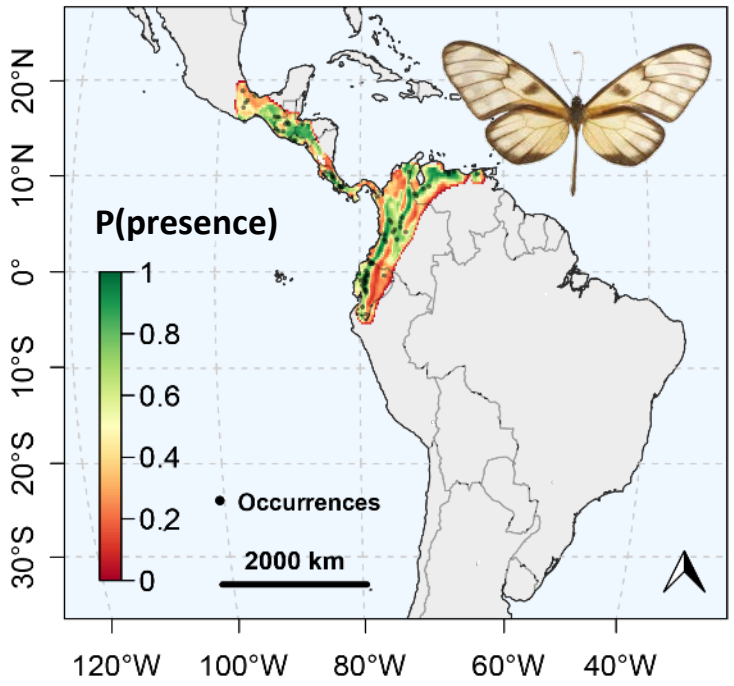
Spatial congruence

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

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

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

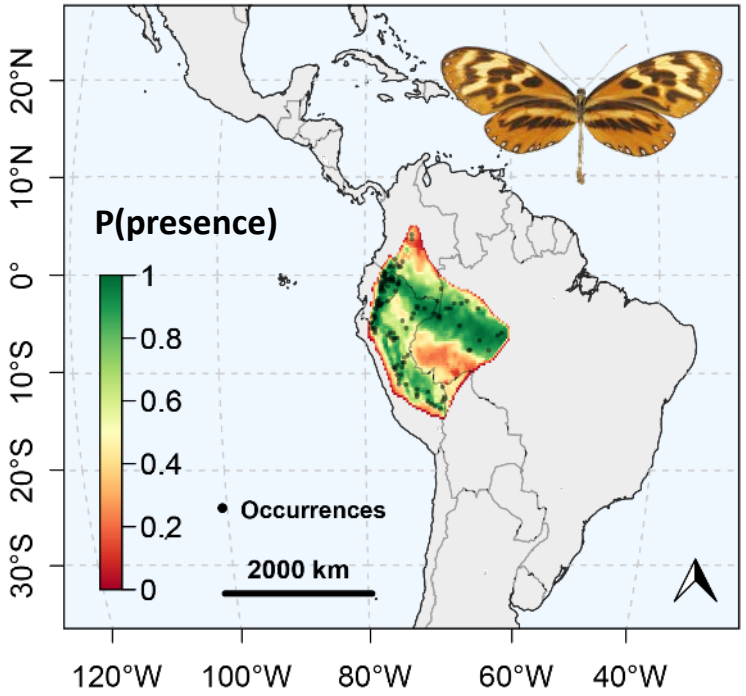
Dircenna jemina **(DILUCIDA)**



No mimicry

BC = 0.9

Mechanitis mazaeus **(MAELUS)**



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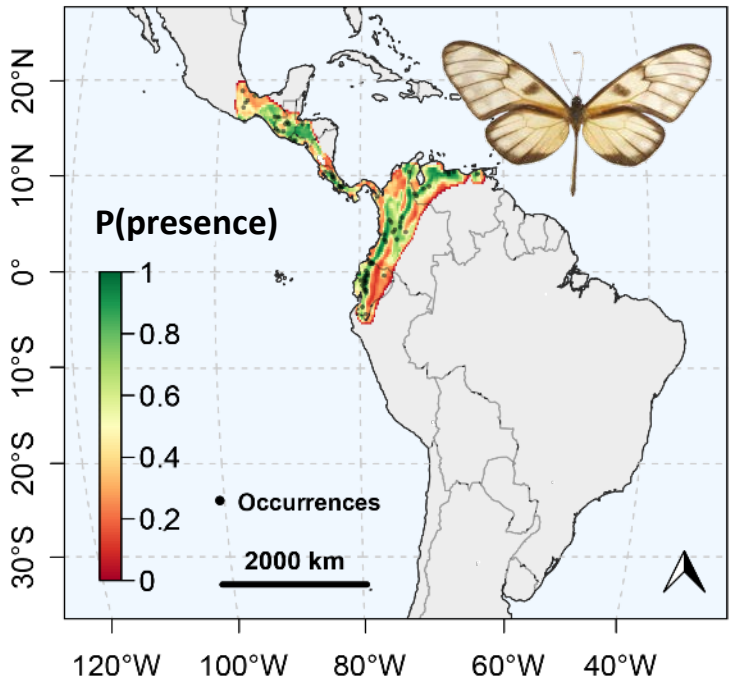
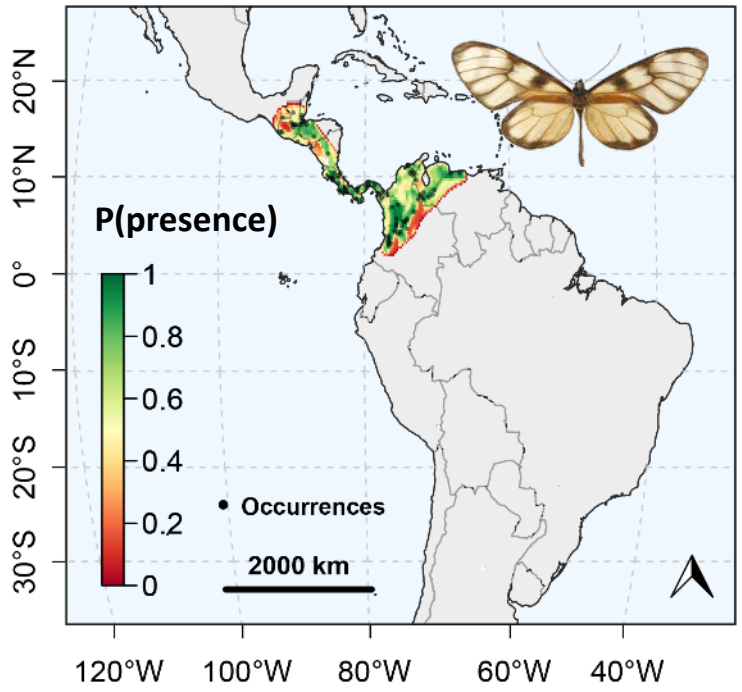


Mimicry

BC = 0.2

Dircenna dero **(DILUCIDA)**



Spatial congruence

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

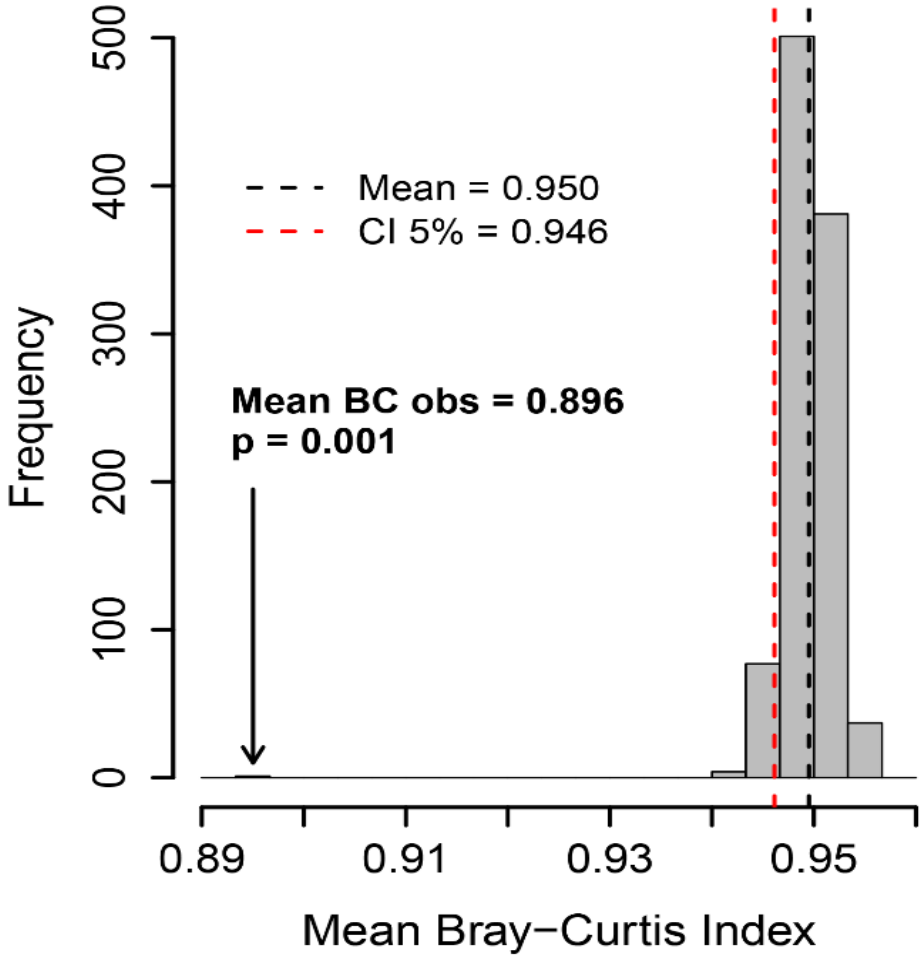
Global: Mean BC_{obs} << Mean BC_{perm} ✓

Per ring: Significant for 85% of **putative** rings

- Non-significant rings = low N

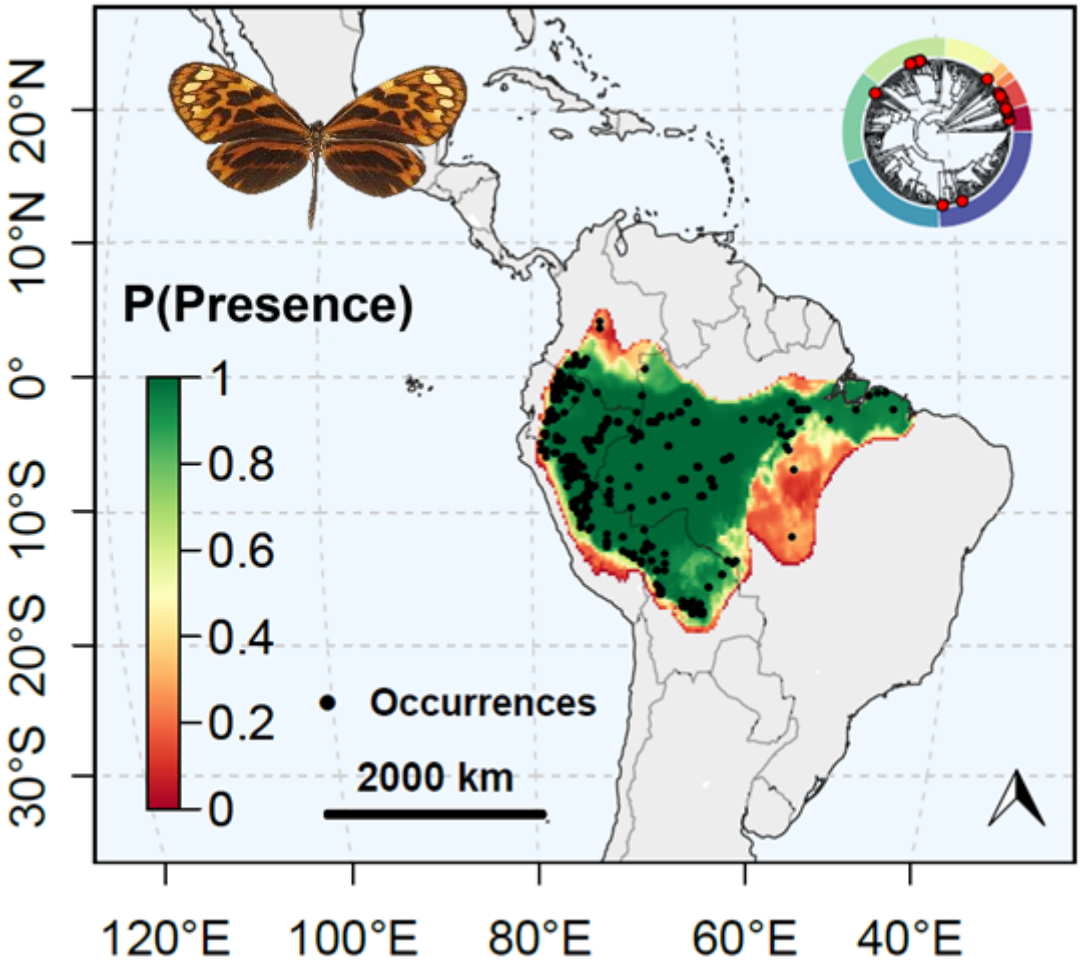
Results: Mimicry promotes the **spatial congruence** of phenotypically similar species at **large-scale**

Next: What happens between tribes?

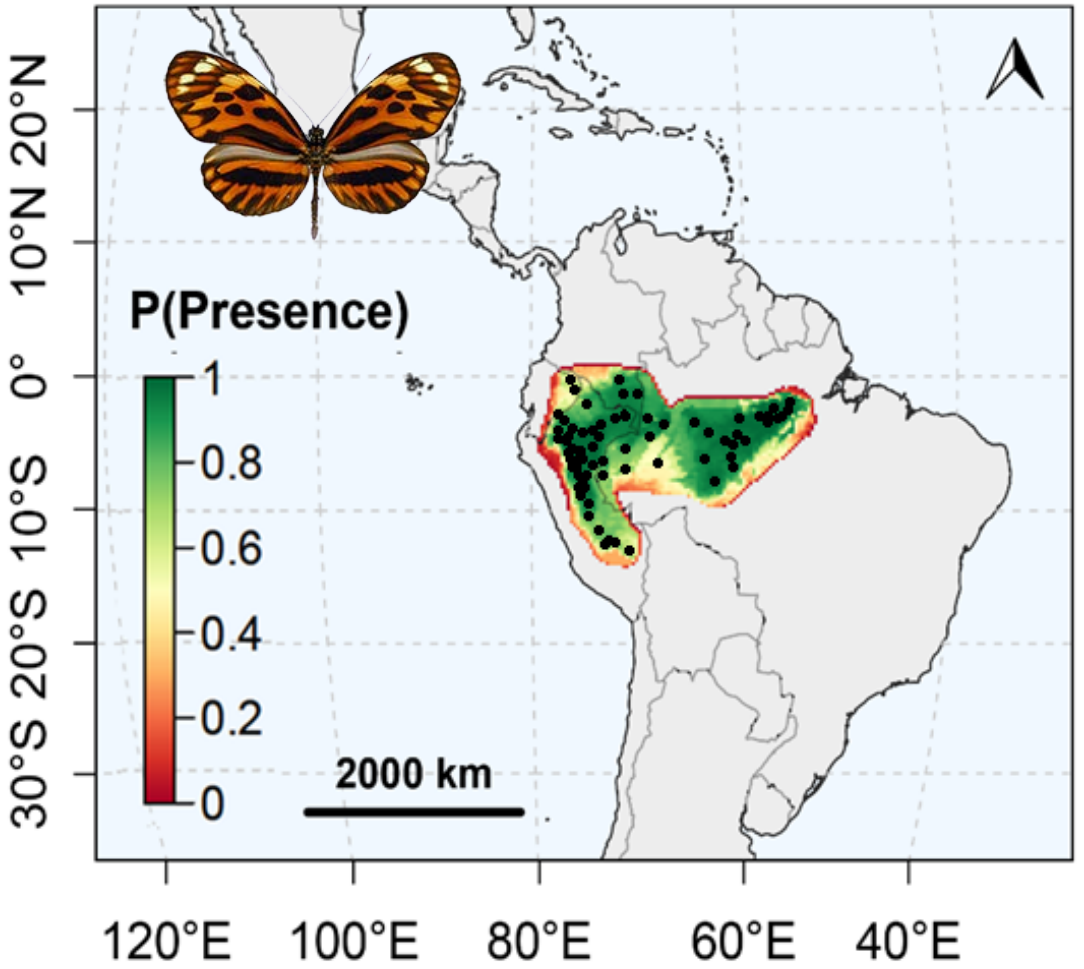


Spatial congruence

Ithomiini: pattern MAELUS
(16 species)

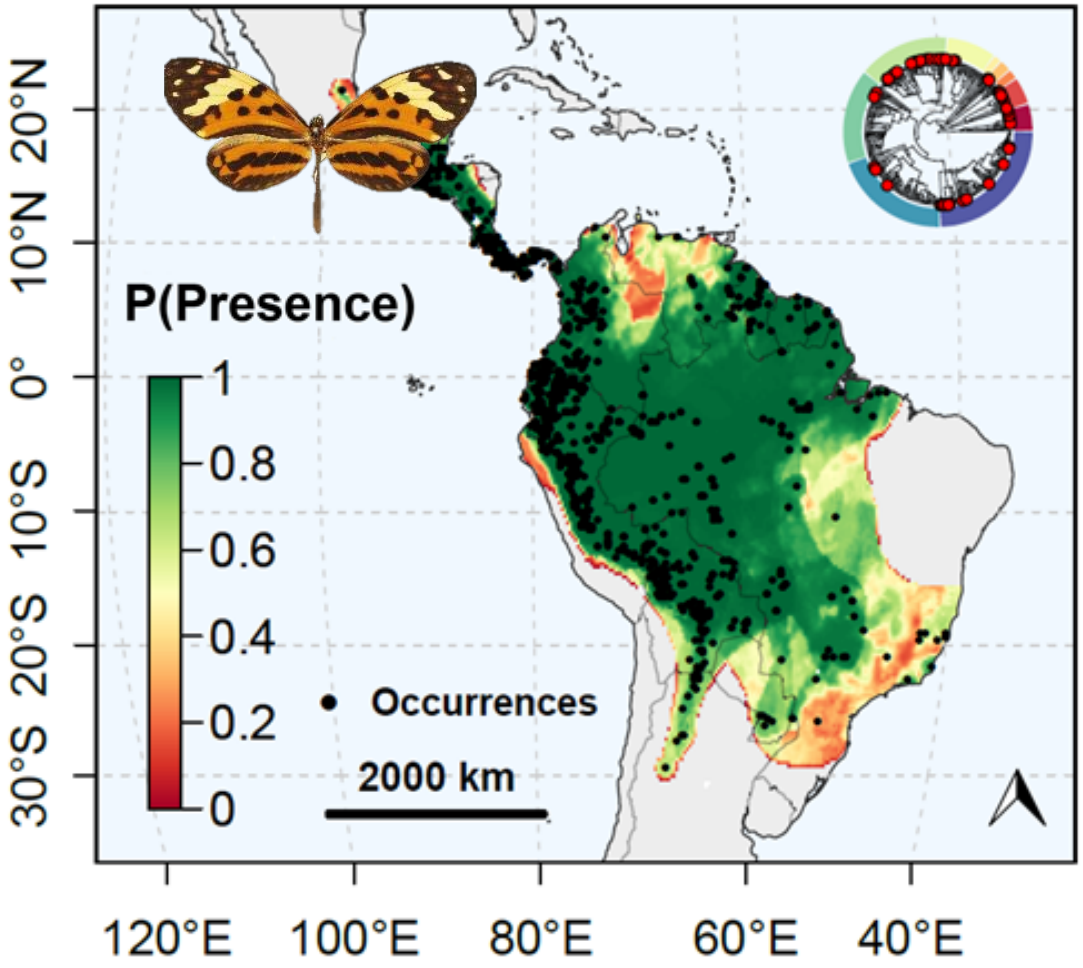


Heliconiini: pattern MAELUS
(5 species)

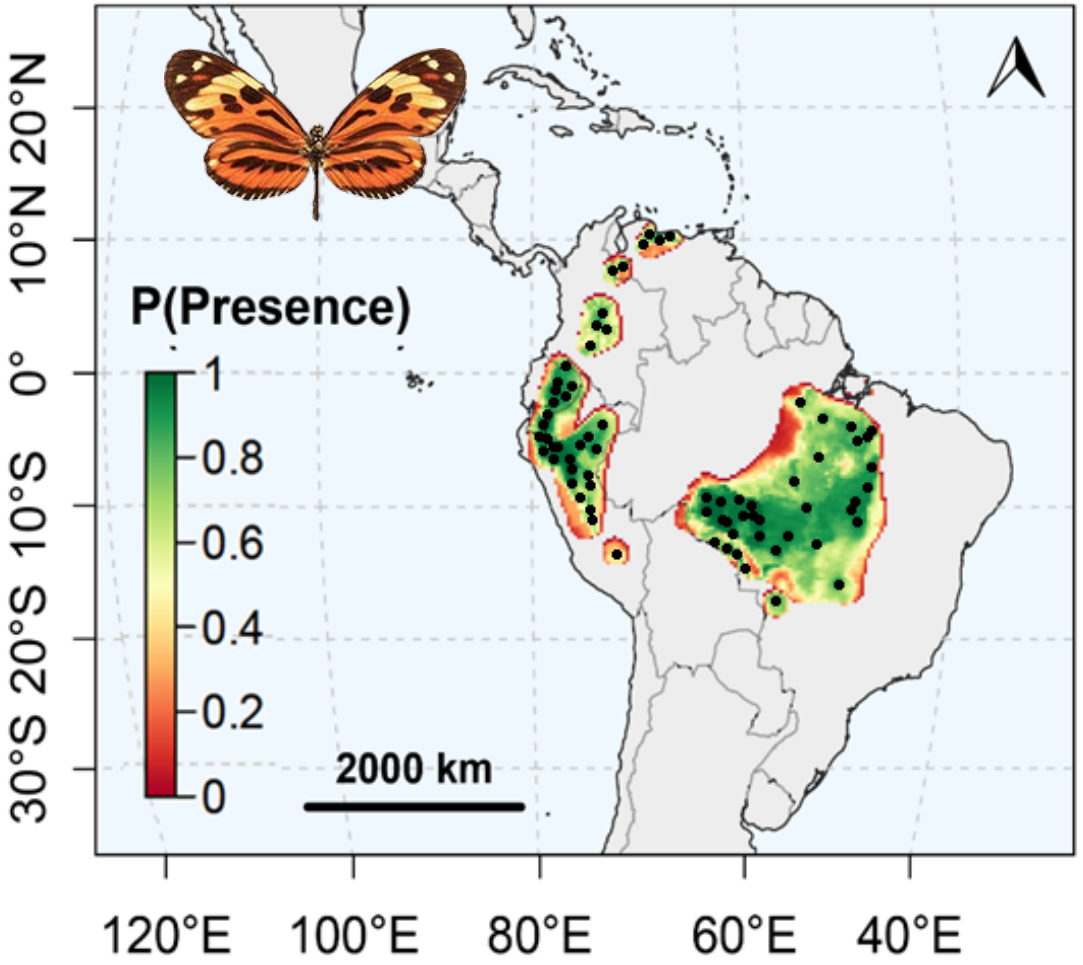


Spatial congruence

Ithomiini: pattern MAMERCUS (64 species)



Heliconiini: pattern MAMERCUS (10 species)



Objectives

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

Climatic niche similarity

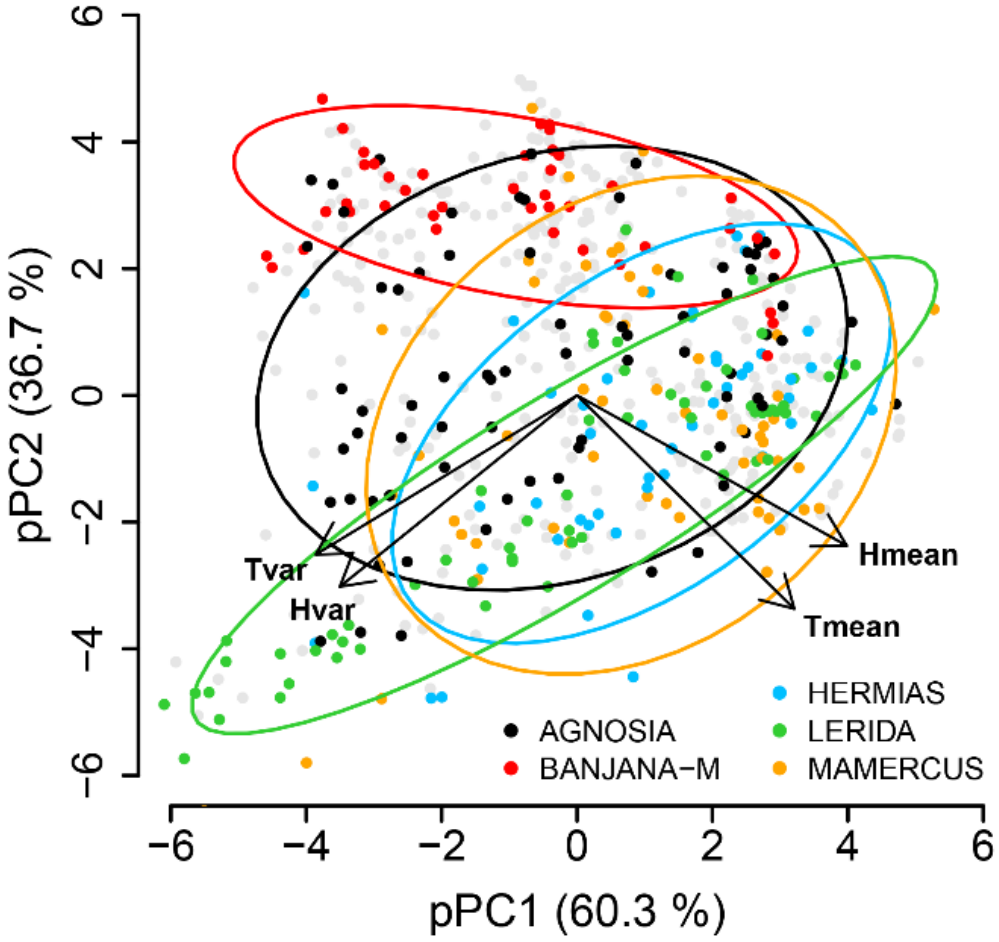
Question: Do **phenotypic groups** occupy different **climatic niche**?

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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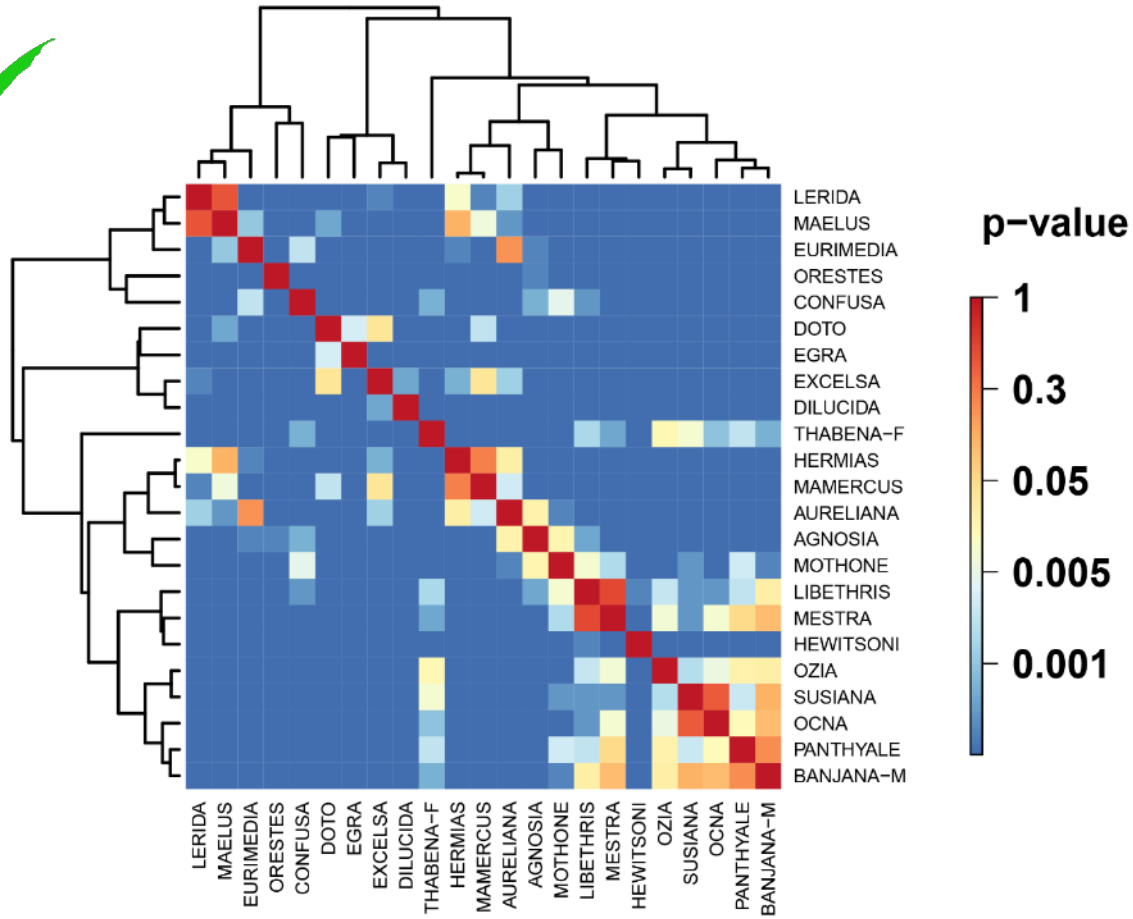

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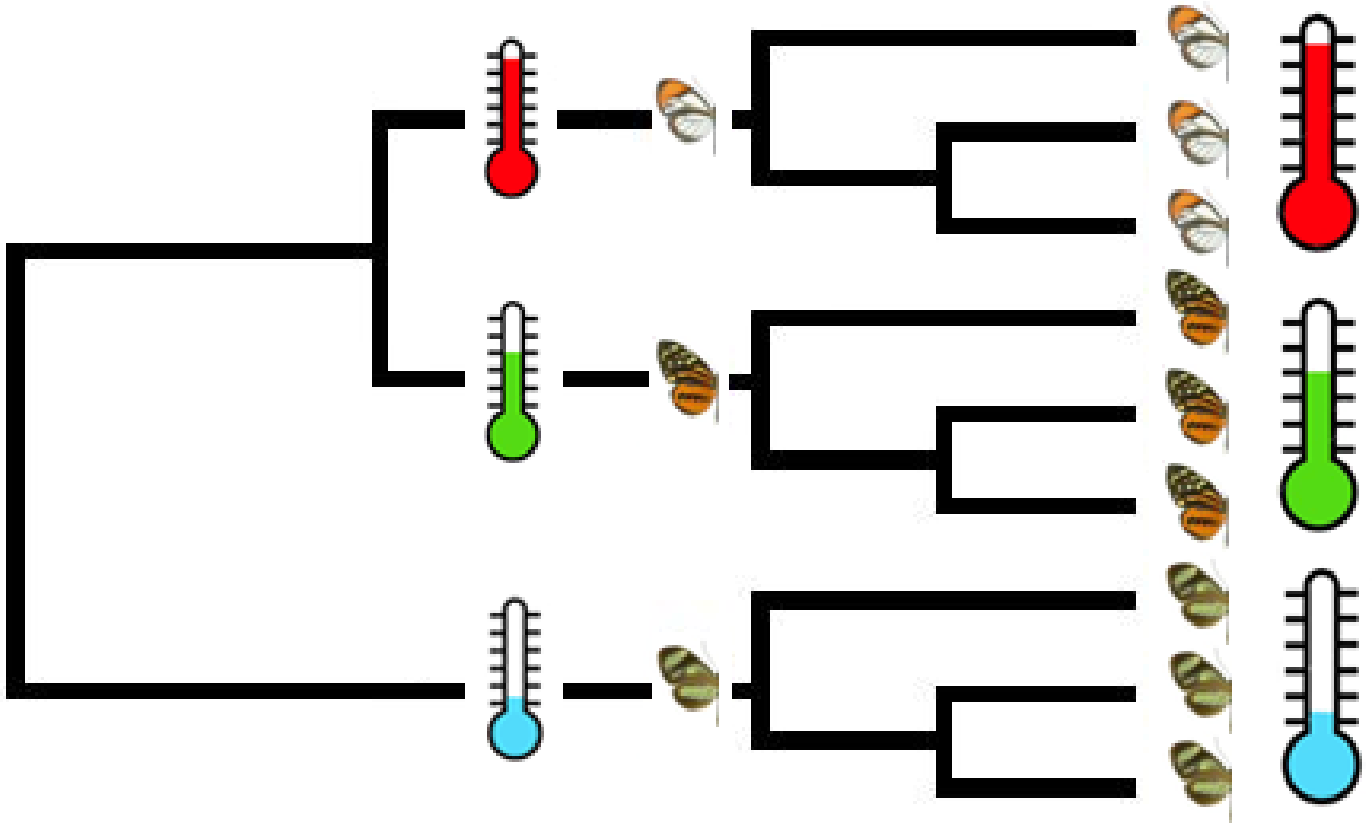
Climatic niche evolution

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



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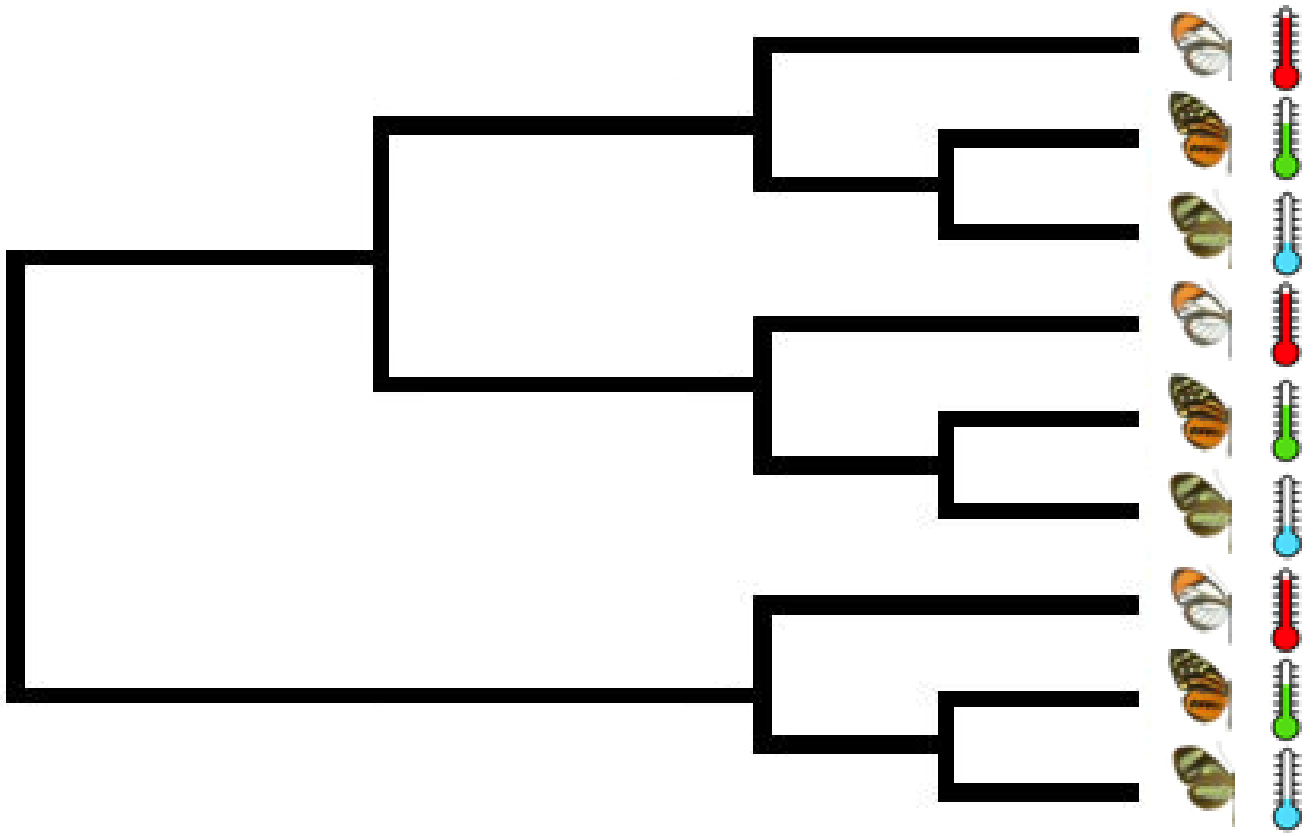


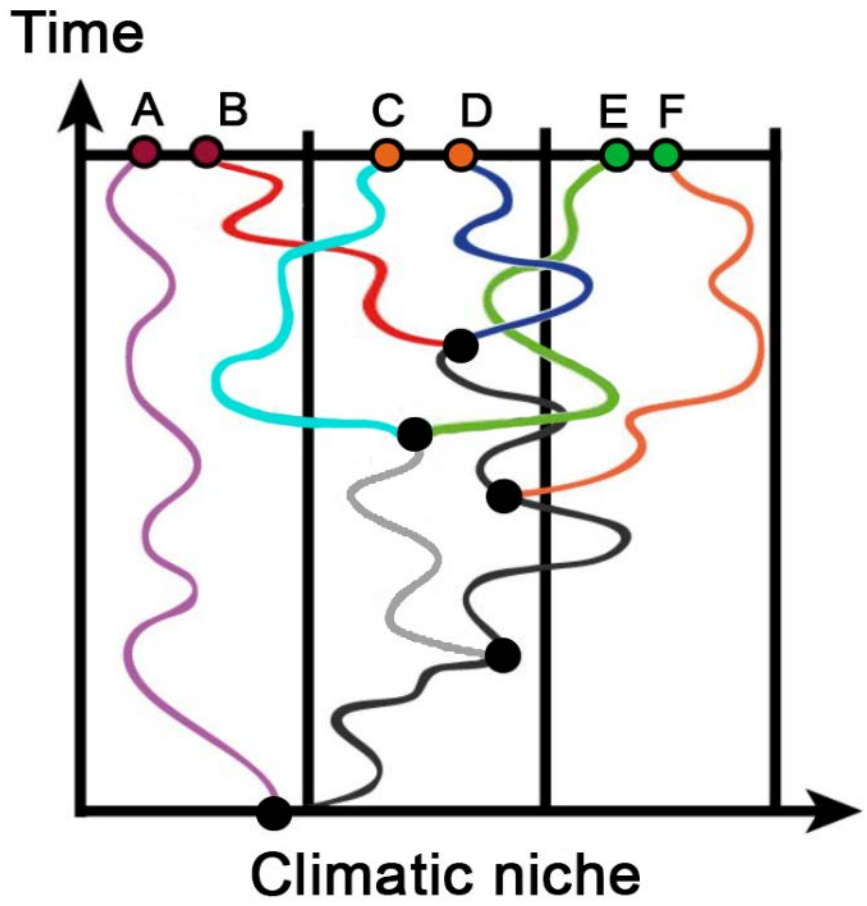
Climatic niche evolution

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 **color patterns**



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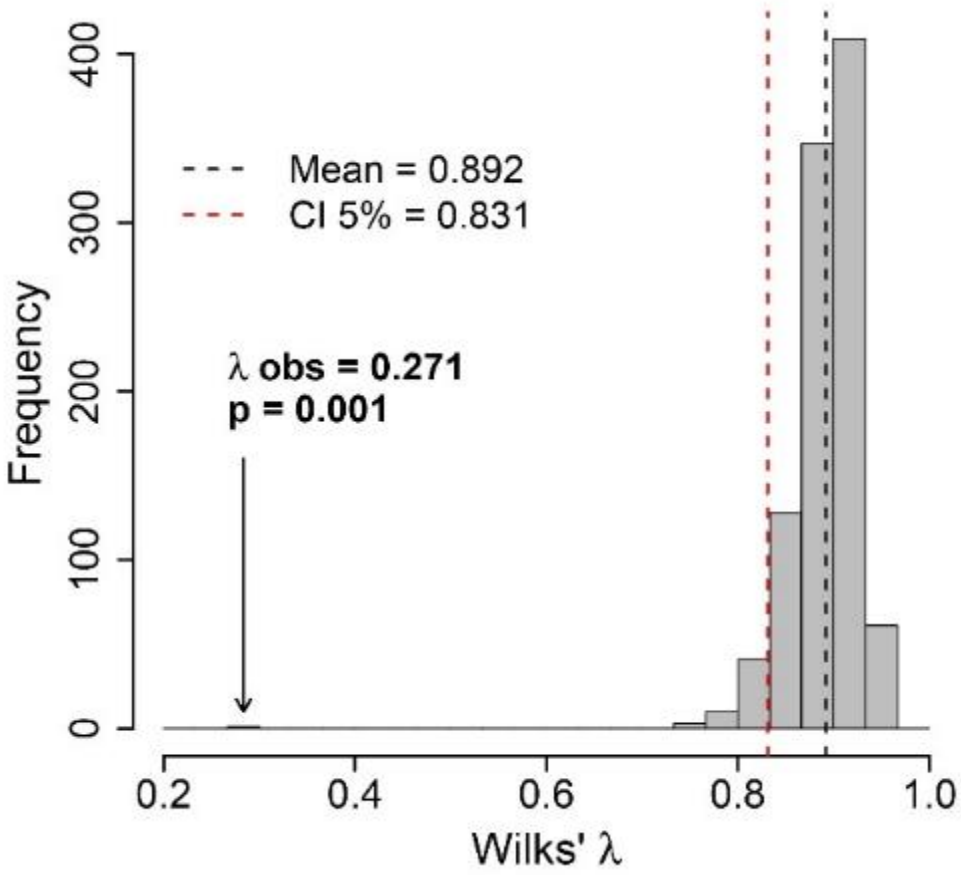

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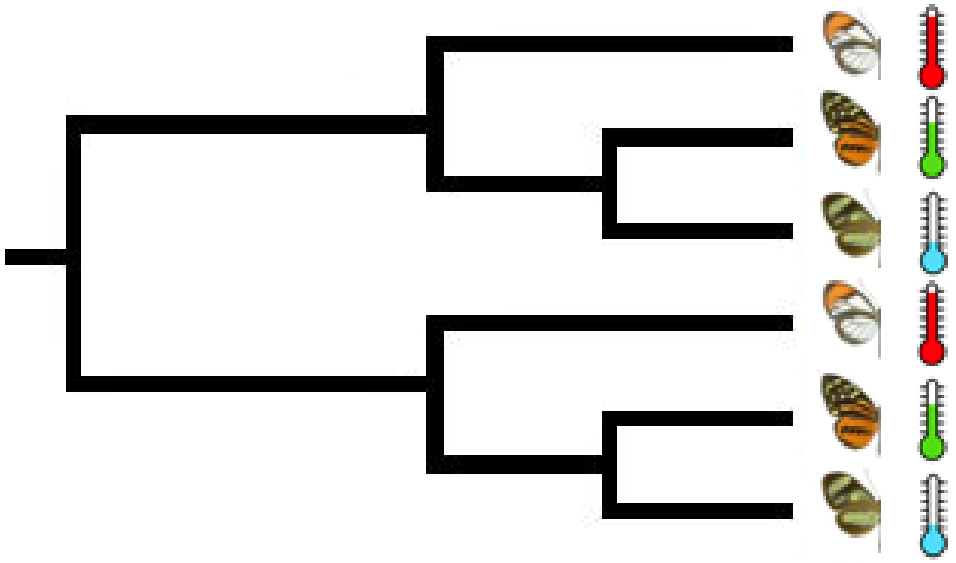
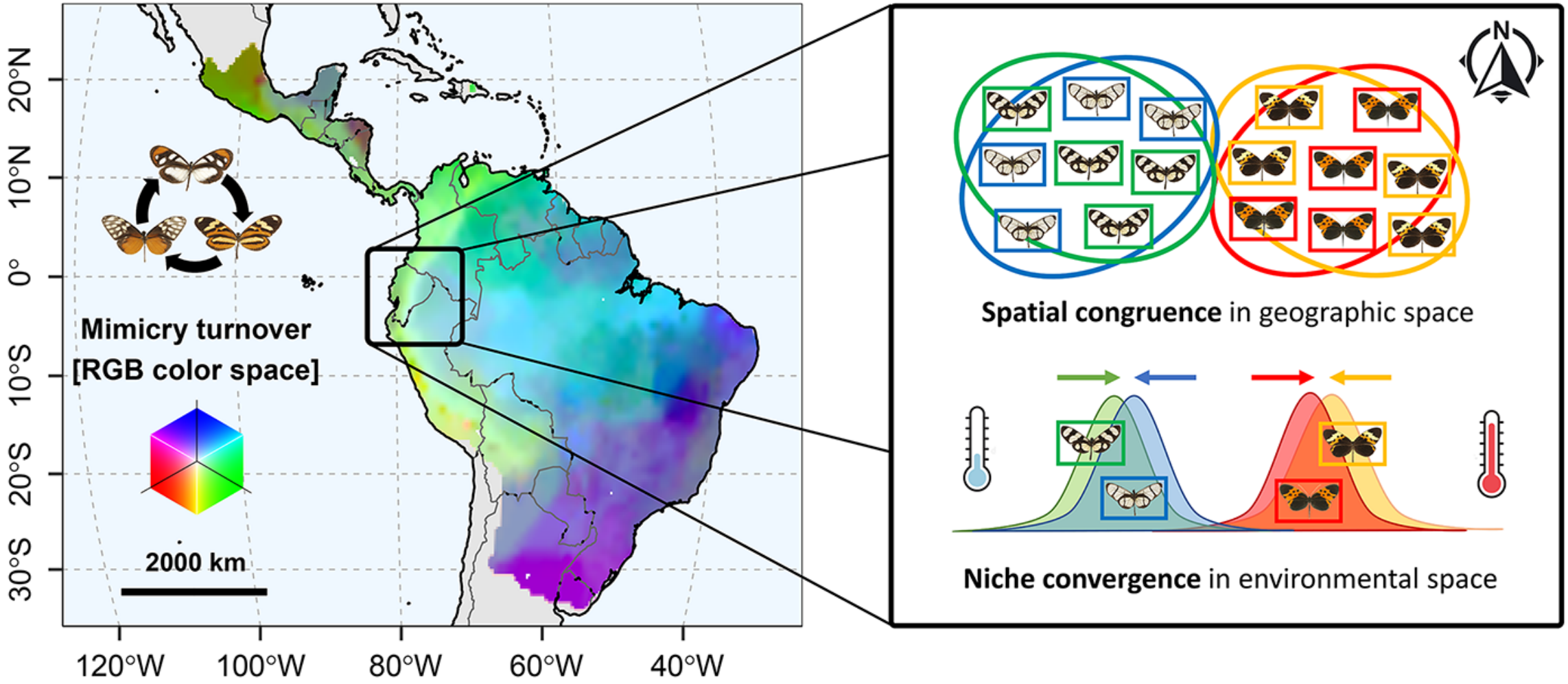
Results: **Evolutionary convergence** between **climatic niche** and **color patterns**

Evolutionary convergence



Conclusion


20°N
10°N
0°
10°S
20°S
30°S
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

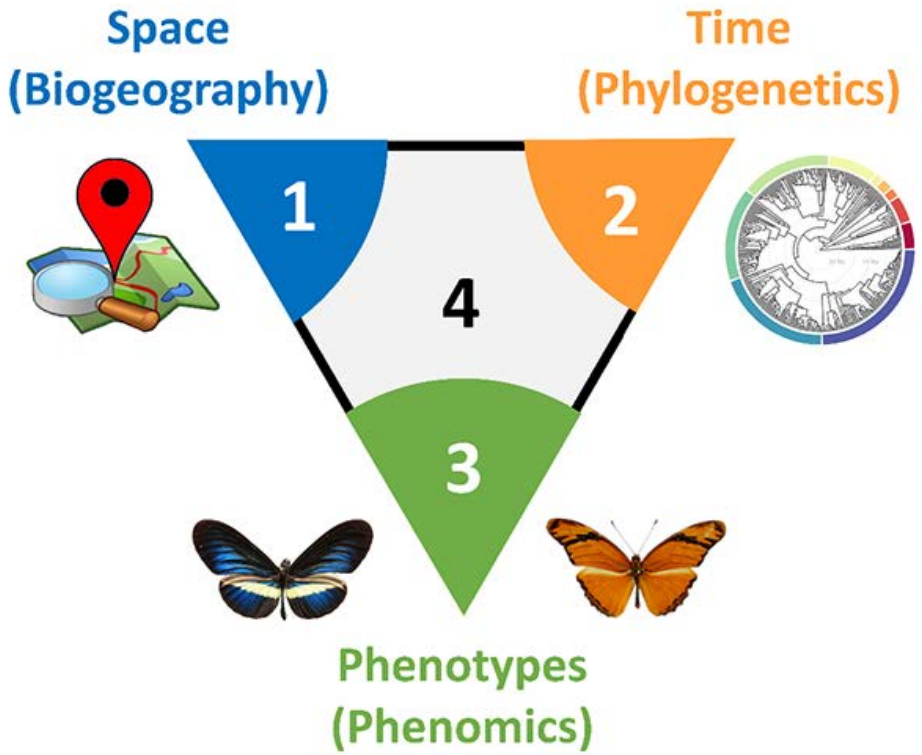
SUMMARY AND PERSPECTIVES

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

Address the **Wallacean shortfall**

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

Enable **multi-scale** analyses



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 **mutualistic interactions** in shaping **species distributions** and **niche evolution**

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

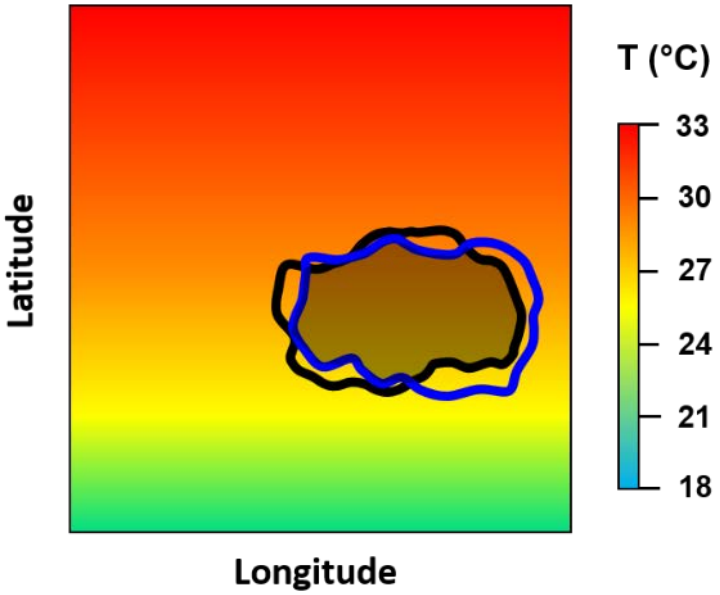
Neotropical mimetic butterflies facing climate changes

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

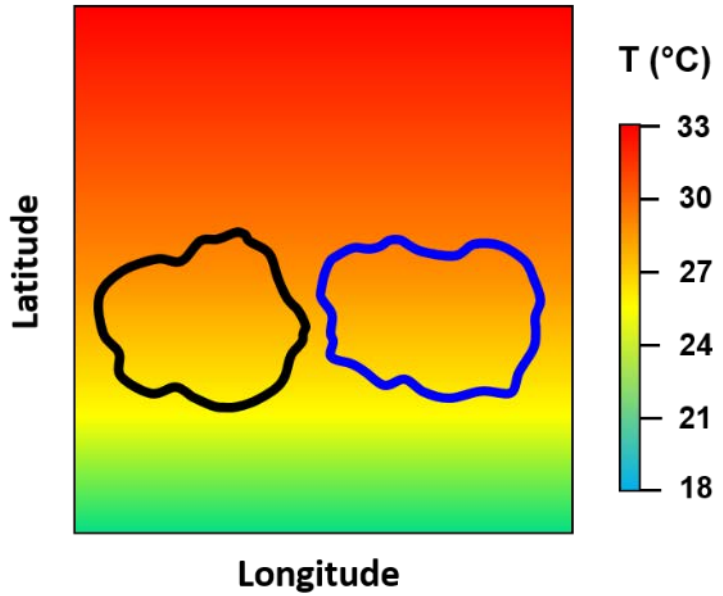
- Sensitivity to interaction disruption and **cascade of extinctions**

Which response to **climate change**?

Cohesion?

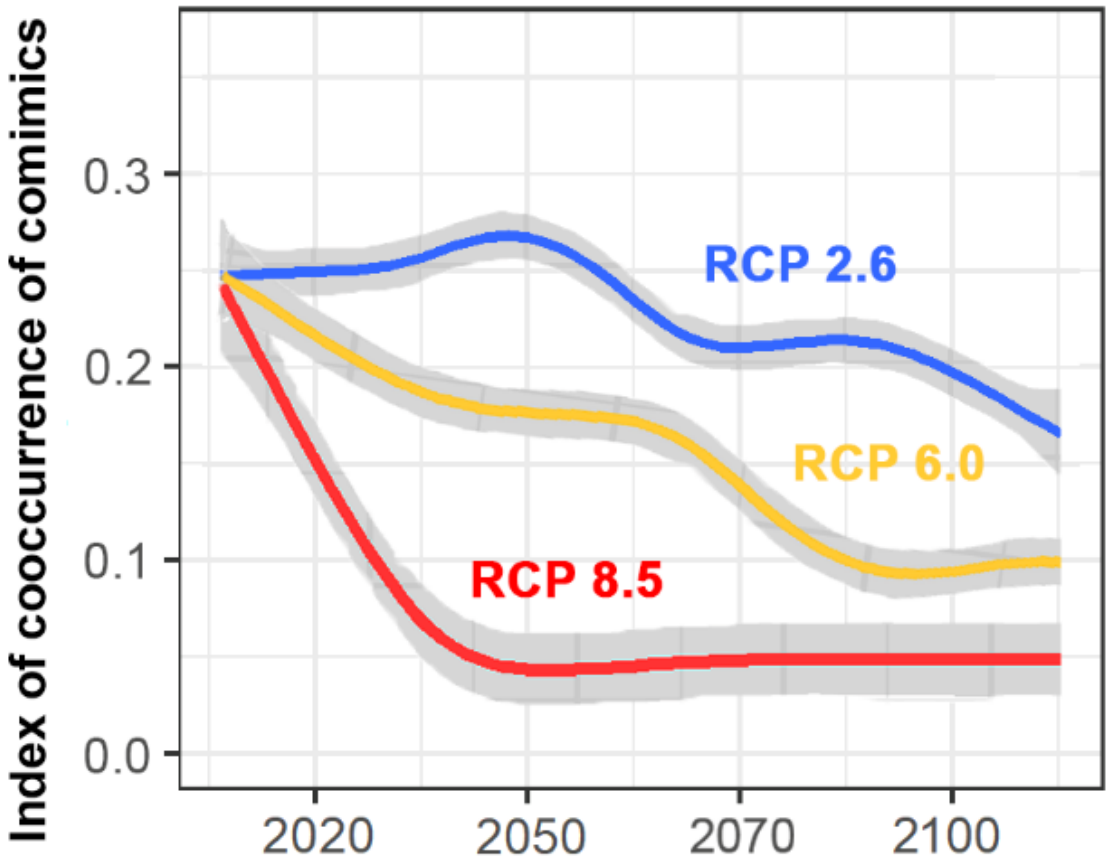


Disassembly?



Neotropical mimetic butterflies facing climate changes

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



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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

Thanks for your attention

Hypomenitis enigma (Ithomiini). Credits: M. Elias

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