

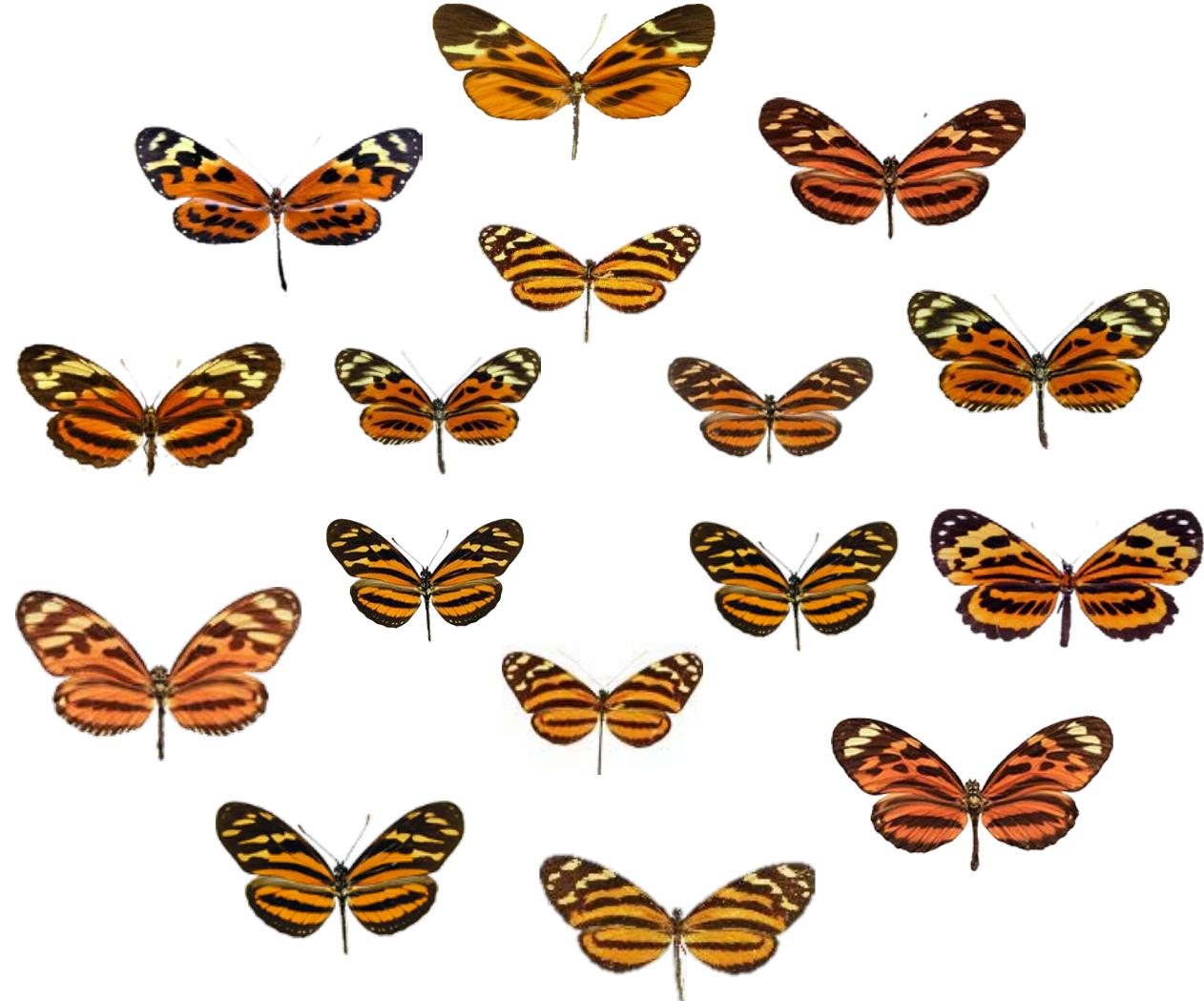
Müllerian mimicry in neotropical butterflies

*“One ring to bring them all,
and in the jungle bind them”*

Maël Doré

Eddie Perochon, Keith Willmott, Sébastien
Lavergne, Nicolas Chazot, André VL Freitas,
Colin Fontaine, Krzysztof Kozak, Neil Rosser,
Marianne Elias

GTOE 2023



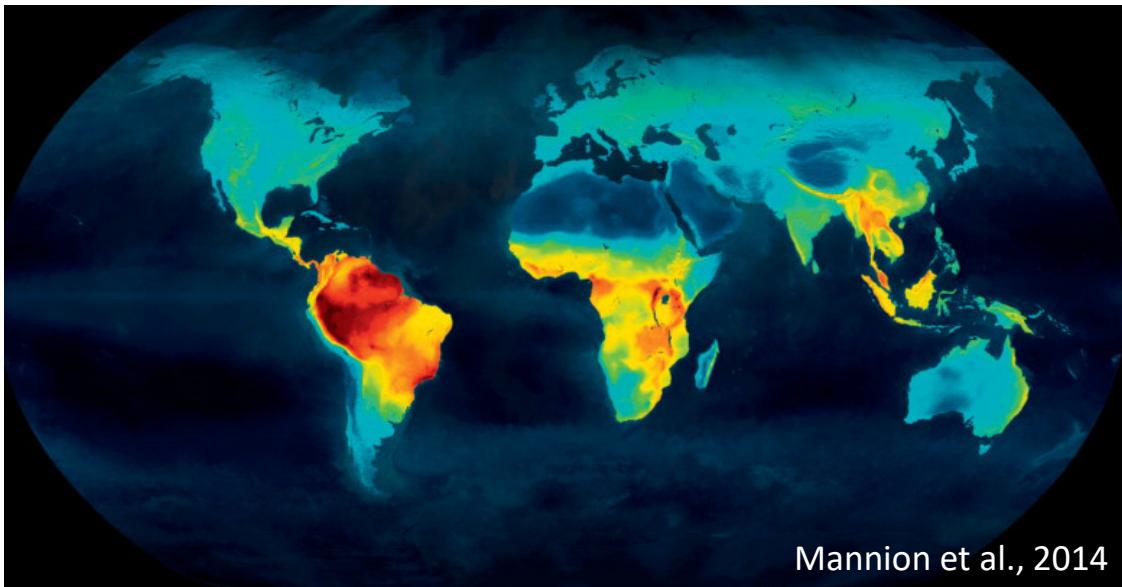
Credit photos: C. Jiggins



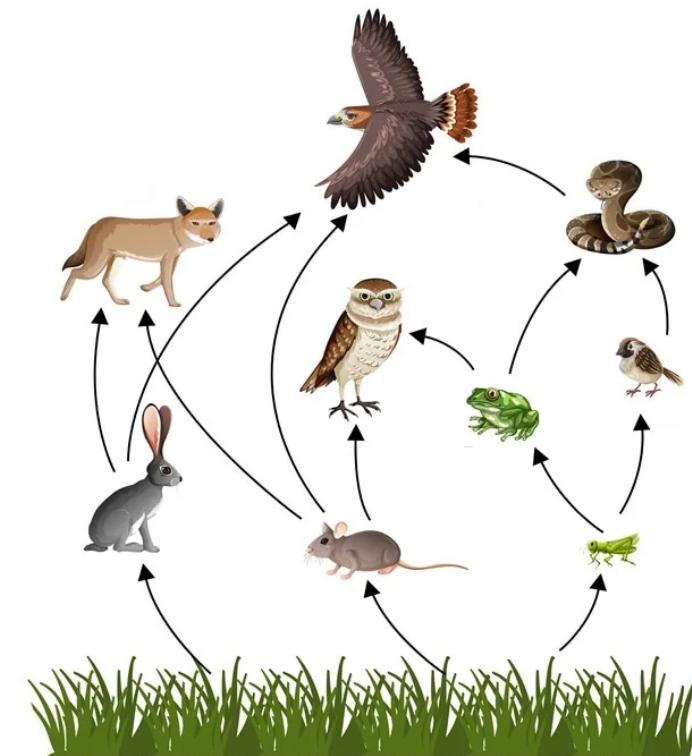
Context

Biodiversity

Biological units



Interactions



Credit: Shutterstock.com

Context

Credits: Thomas Kline



Mutualistic interactions: 

- Cooperative hunting
- Plant facilitation
- Müllerian mimicry

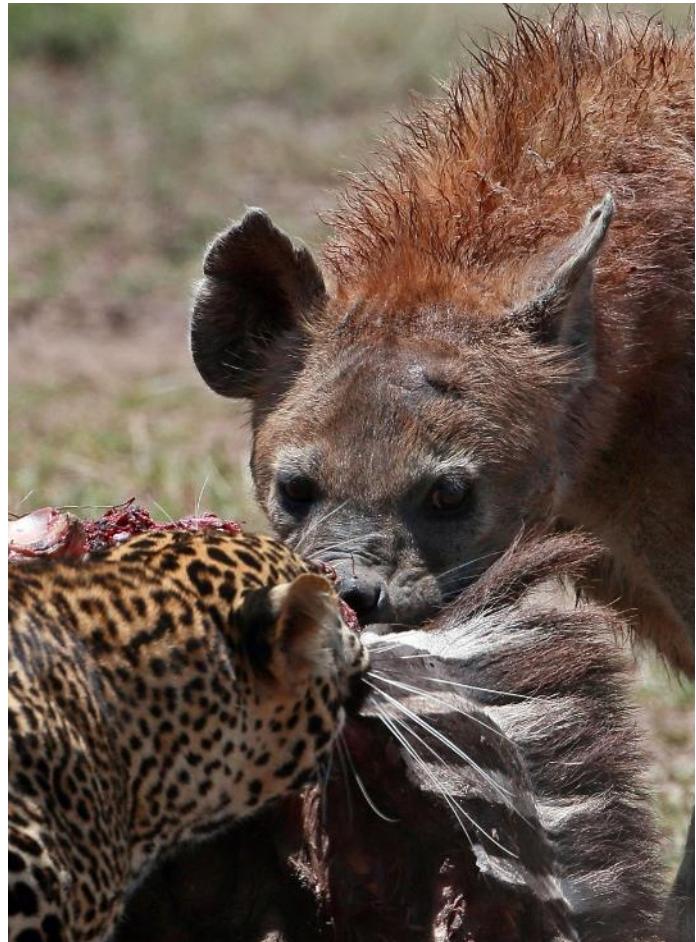


Credits: Amanda R. Liczner



Credits: Jason L. Brown

Context



Credit: Caters News Agency



Credit: Campillo Rafael



Credits: Anytka Olkova & Larry Myers

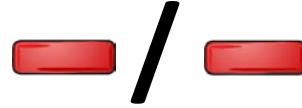
Exploitative competition:

- for local resources
- for habitats
- for space

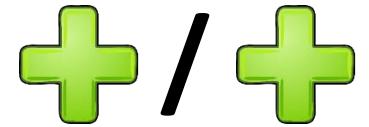


Context

Competition

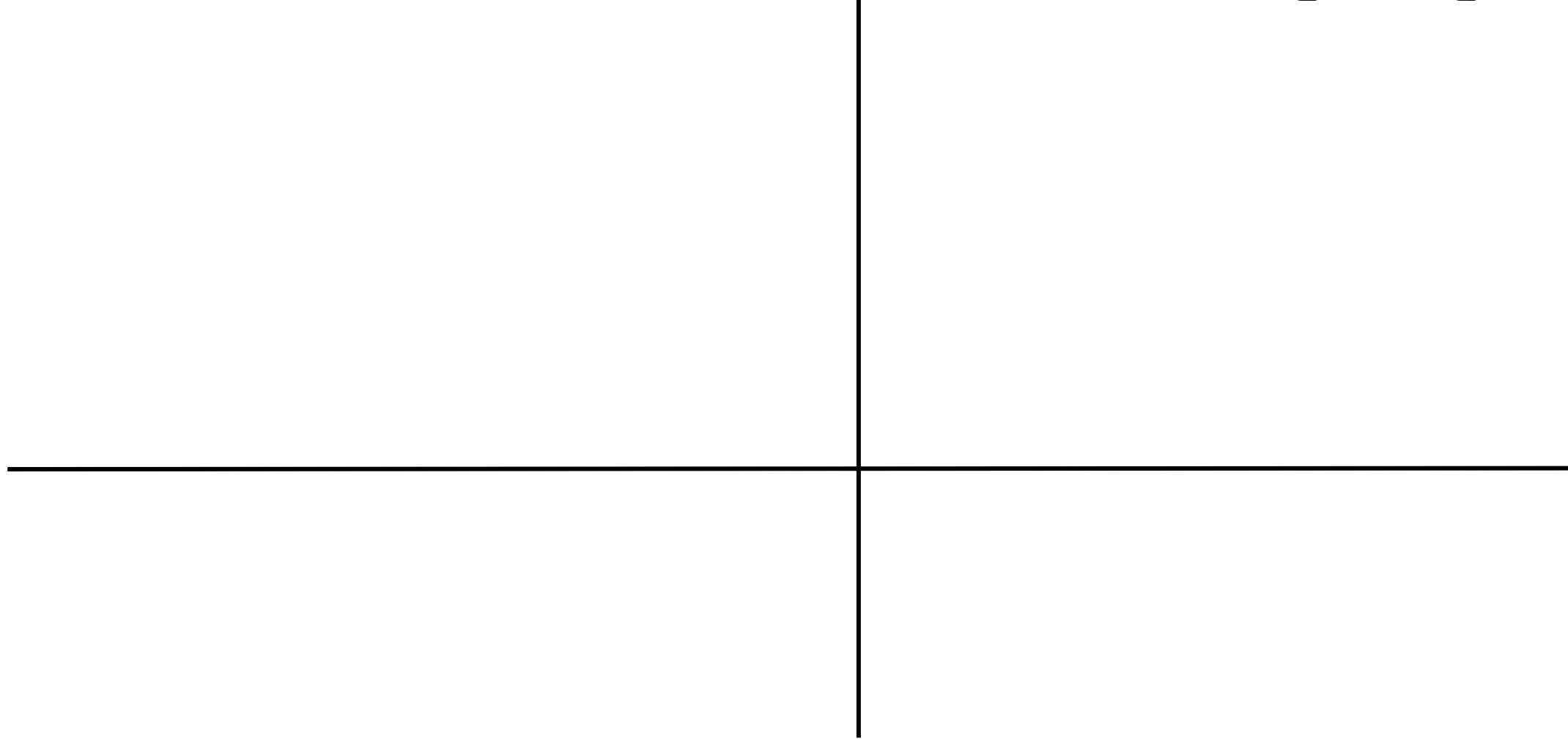


Mutualism

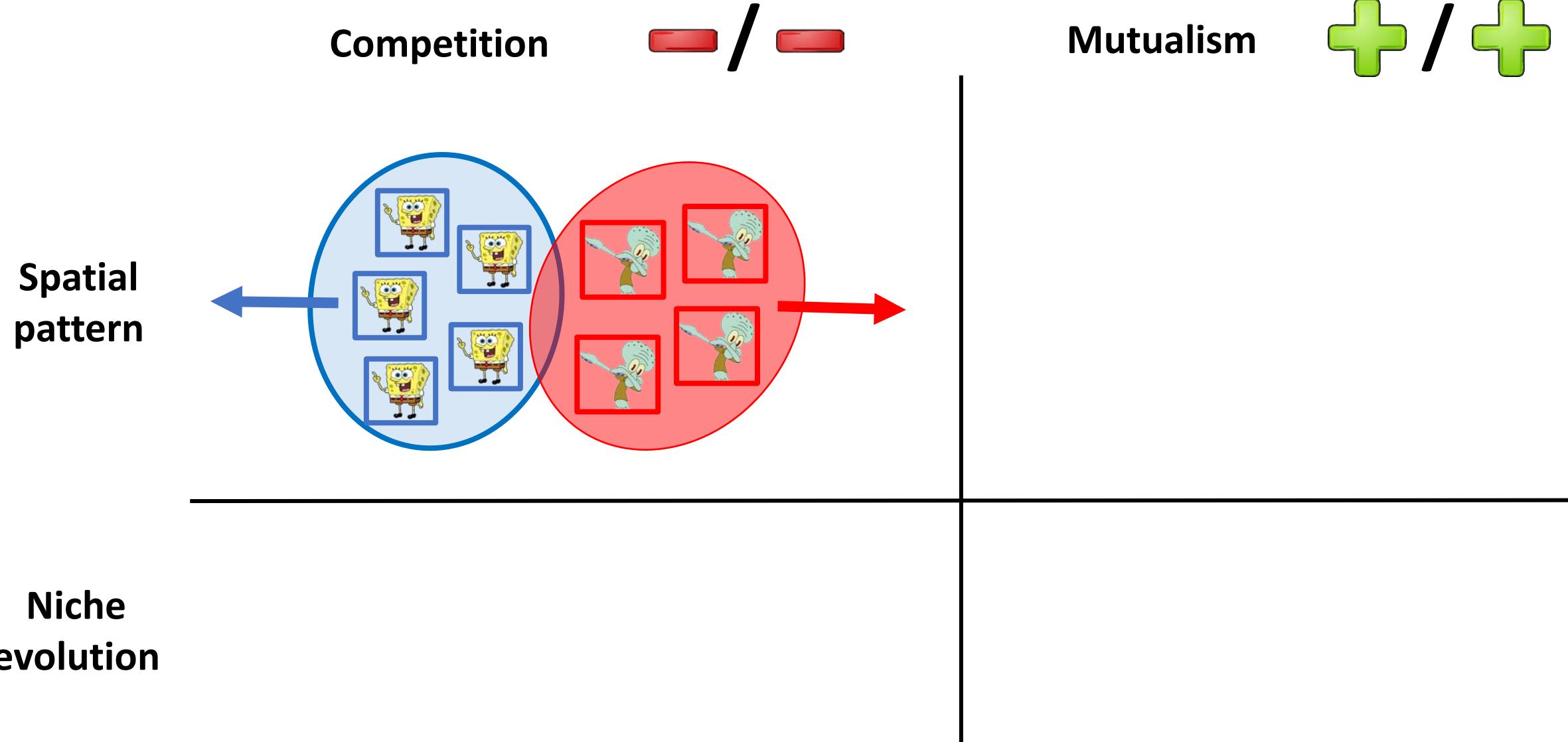


Spatial
pattern

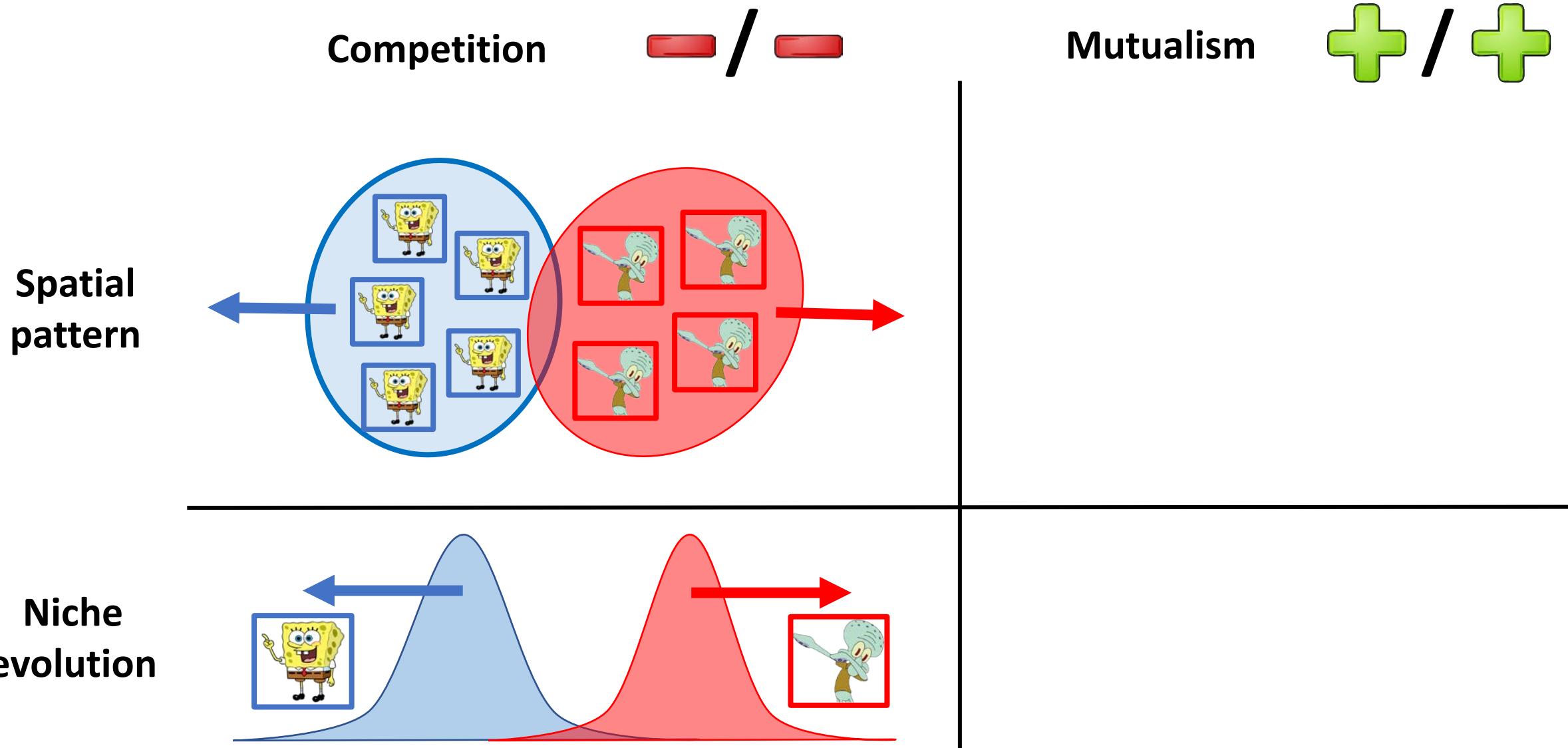
Niche
evolution



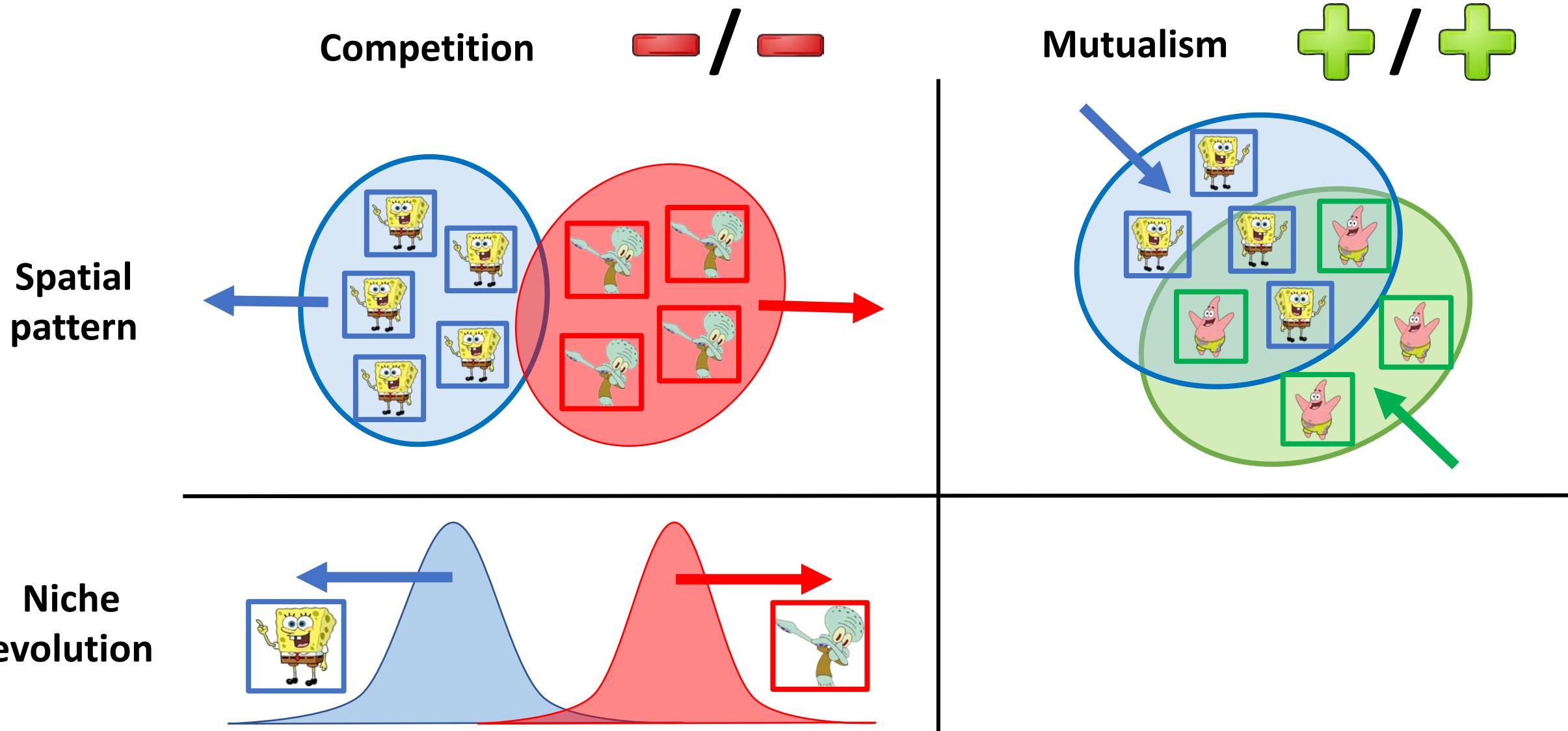
Context



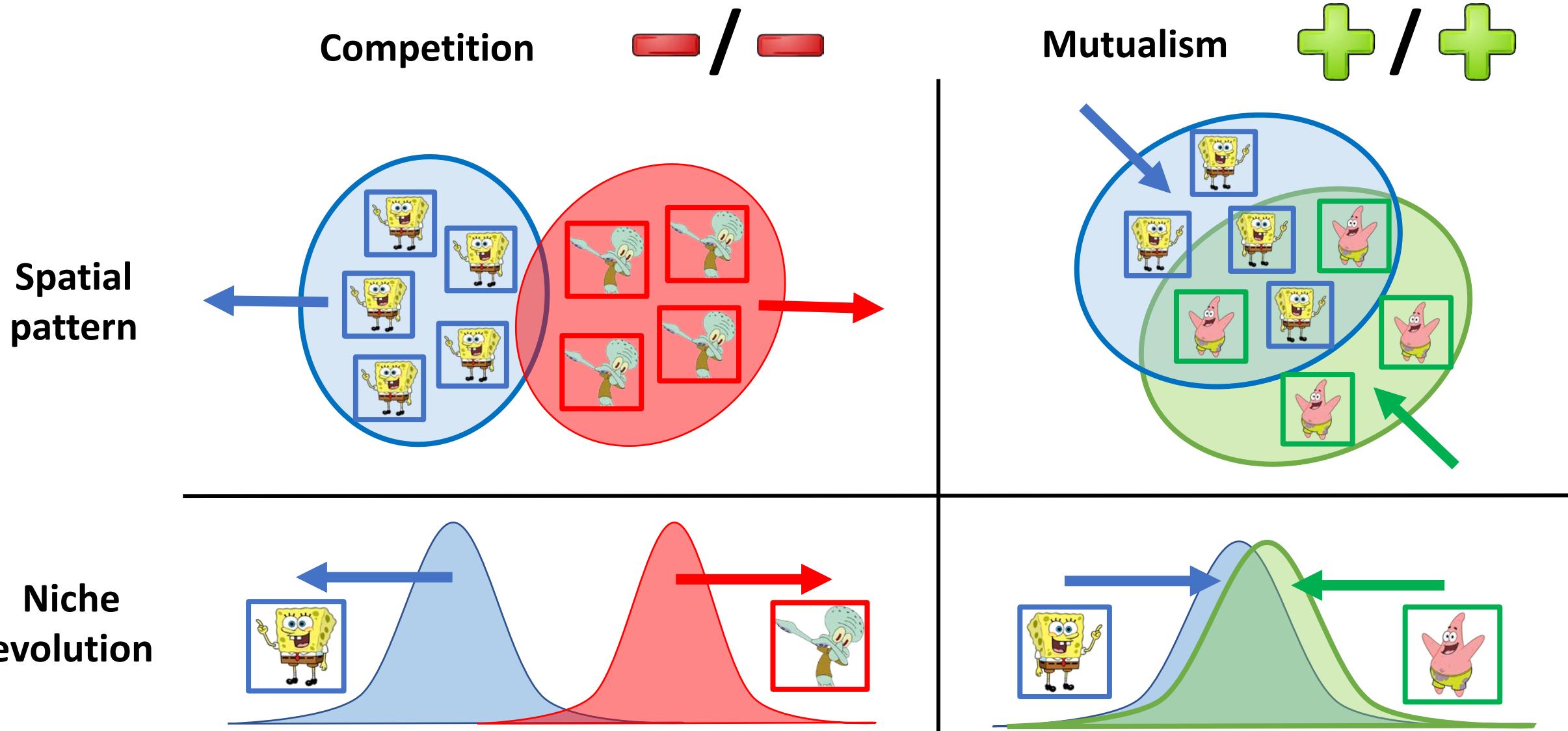
Context



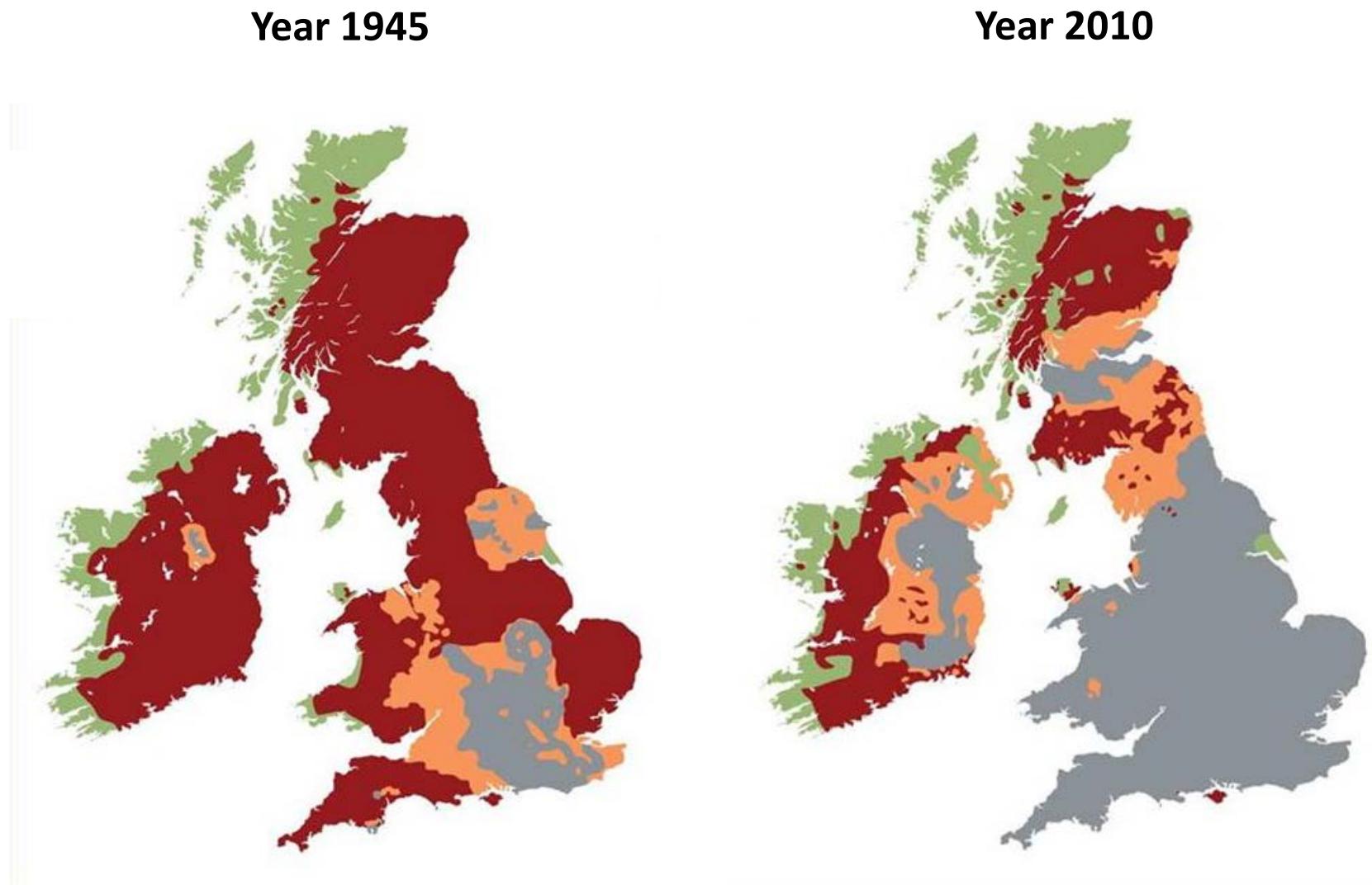
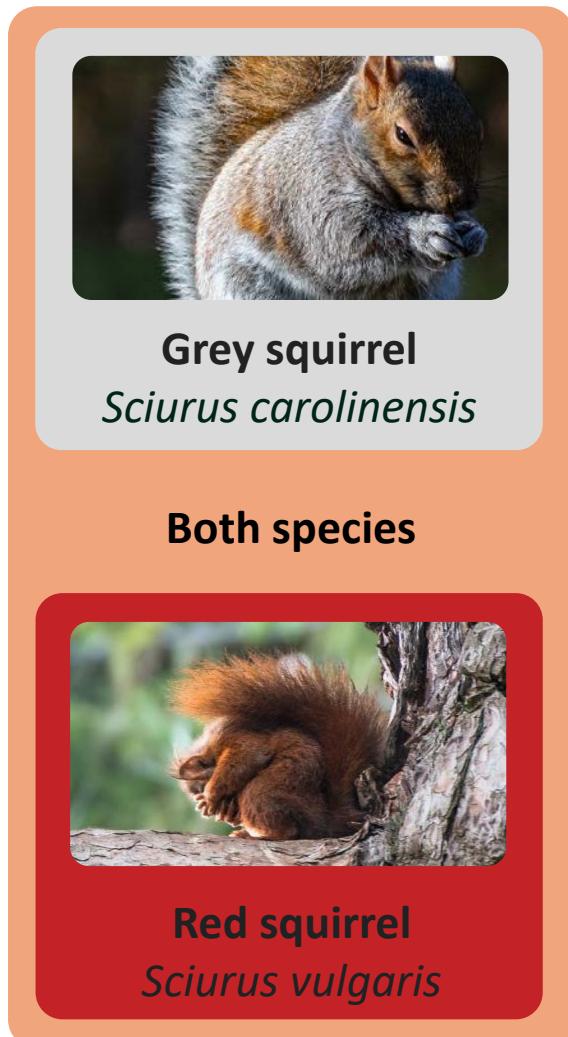
Context



Context



Context



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

Niche evolution

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

Question & Hypotheses

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

**Spatial
pattern**

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

**Niche
evolution**

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

Question & Hypotheses

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

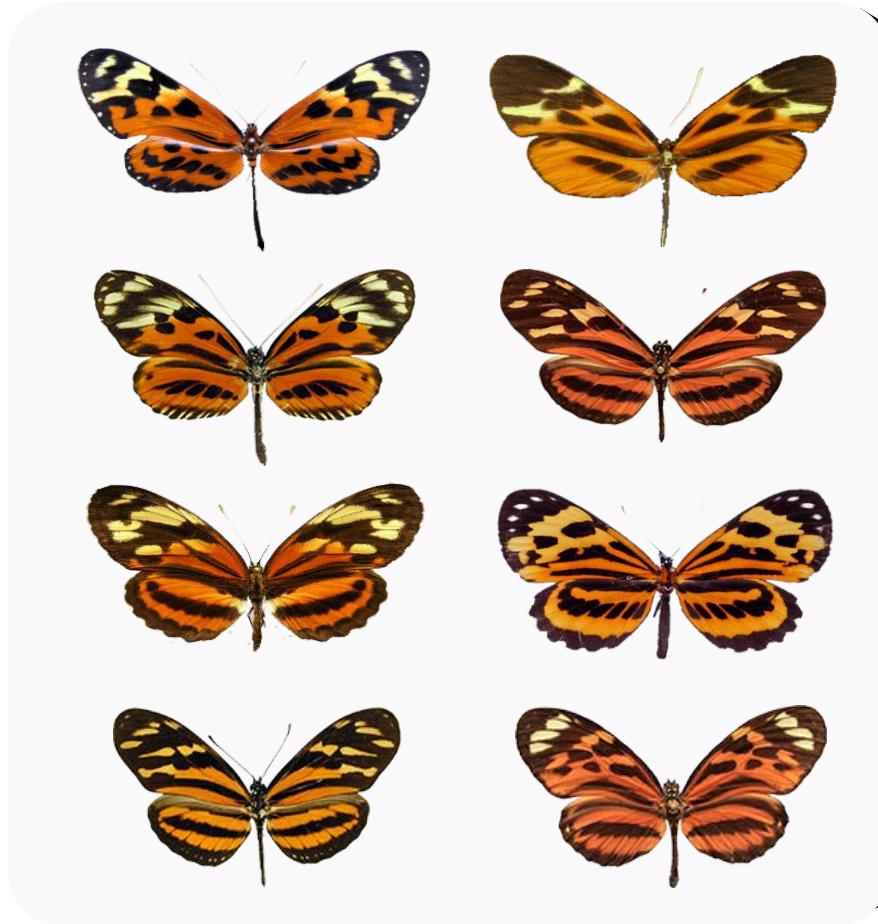
**Spatial
pattern**

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

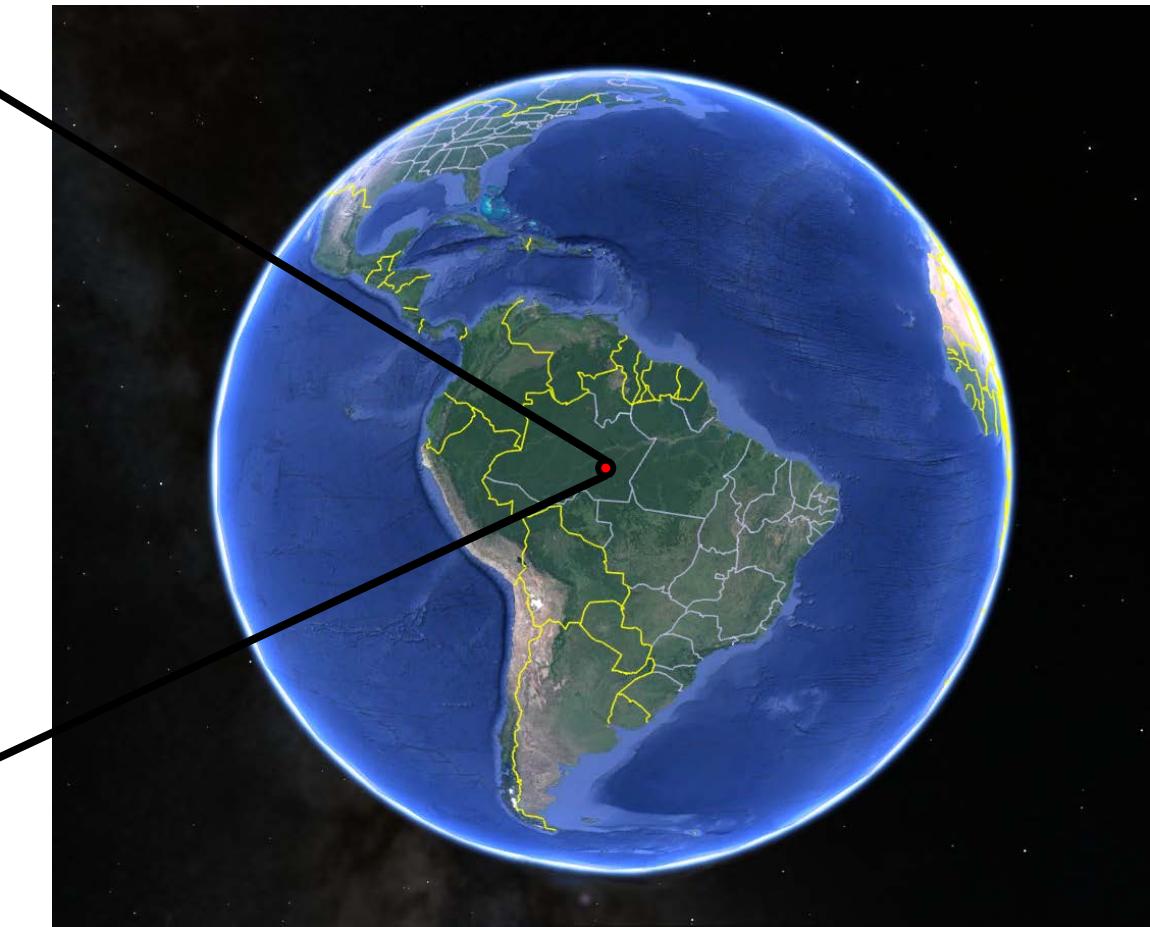
**Niche
evolution**

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

Study system: Müllerian mimicry

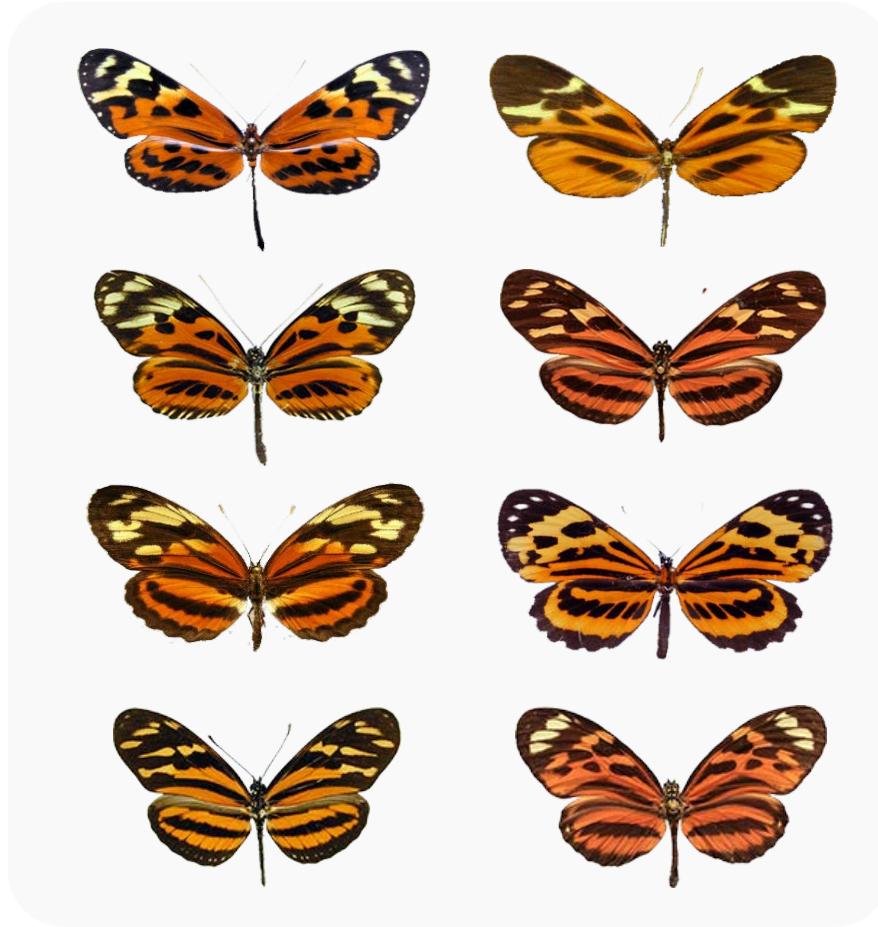


A mimicry ring

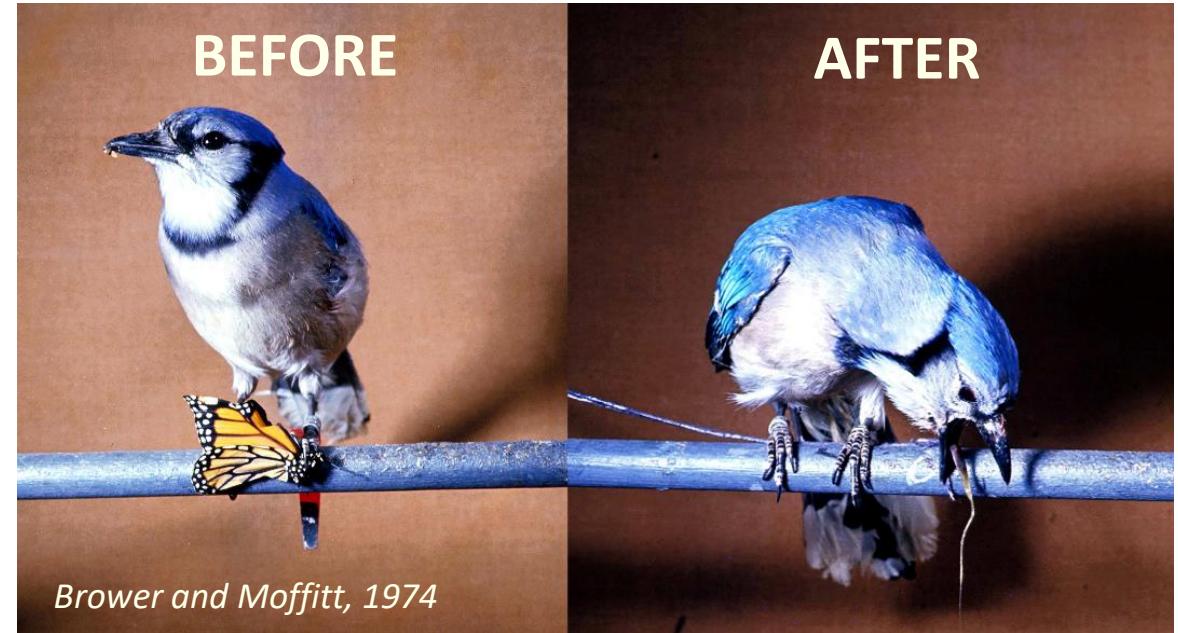


Credits: Google Earth

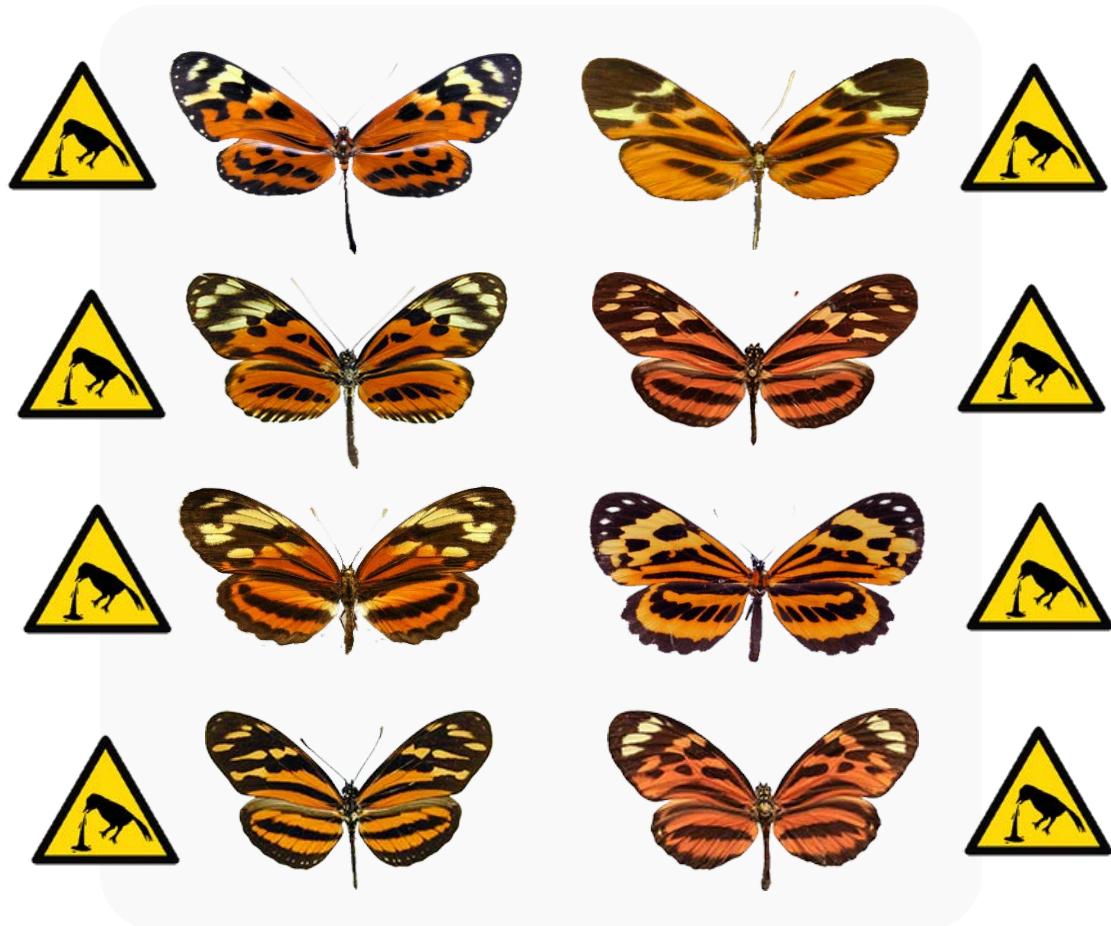
Study system: Müllerian mimicry



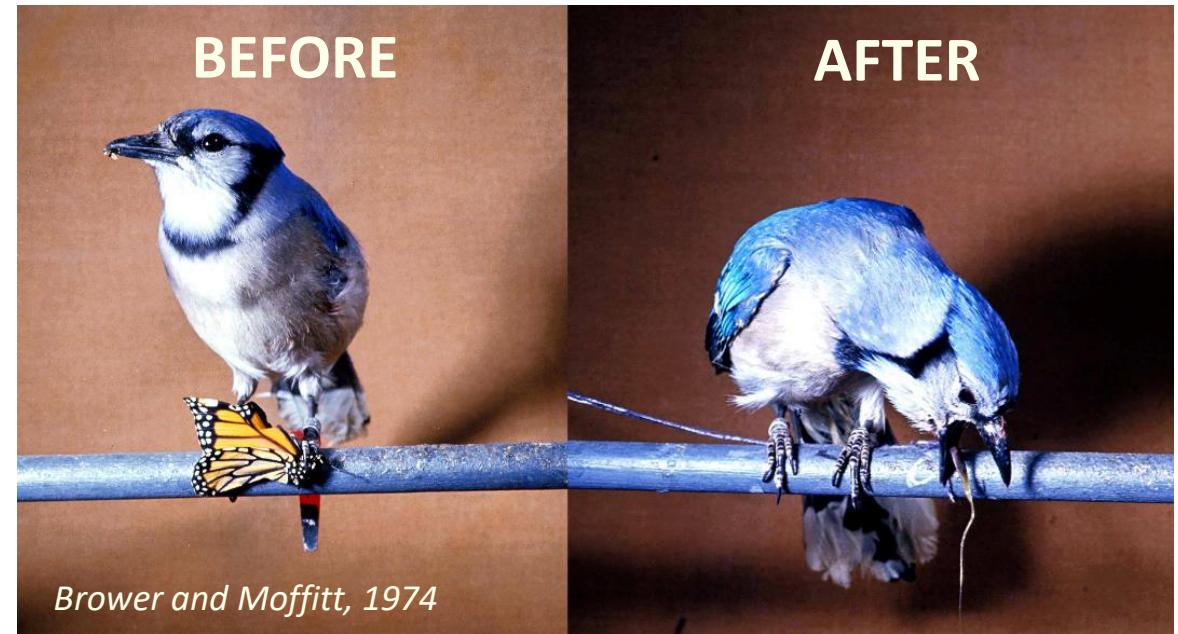
A mimicry ring



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, $1_1 : 1_2 = a_2^2 : a_1^2$.

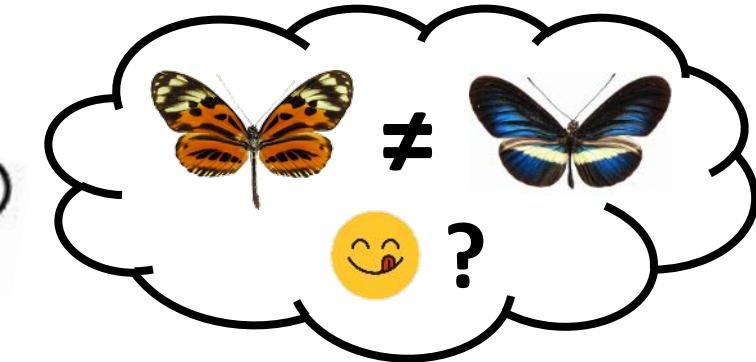
Müller, 1879



Fritz Müller
(1821 – 1897)

Study system: Müllerian mimicry

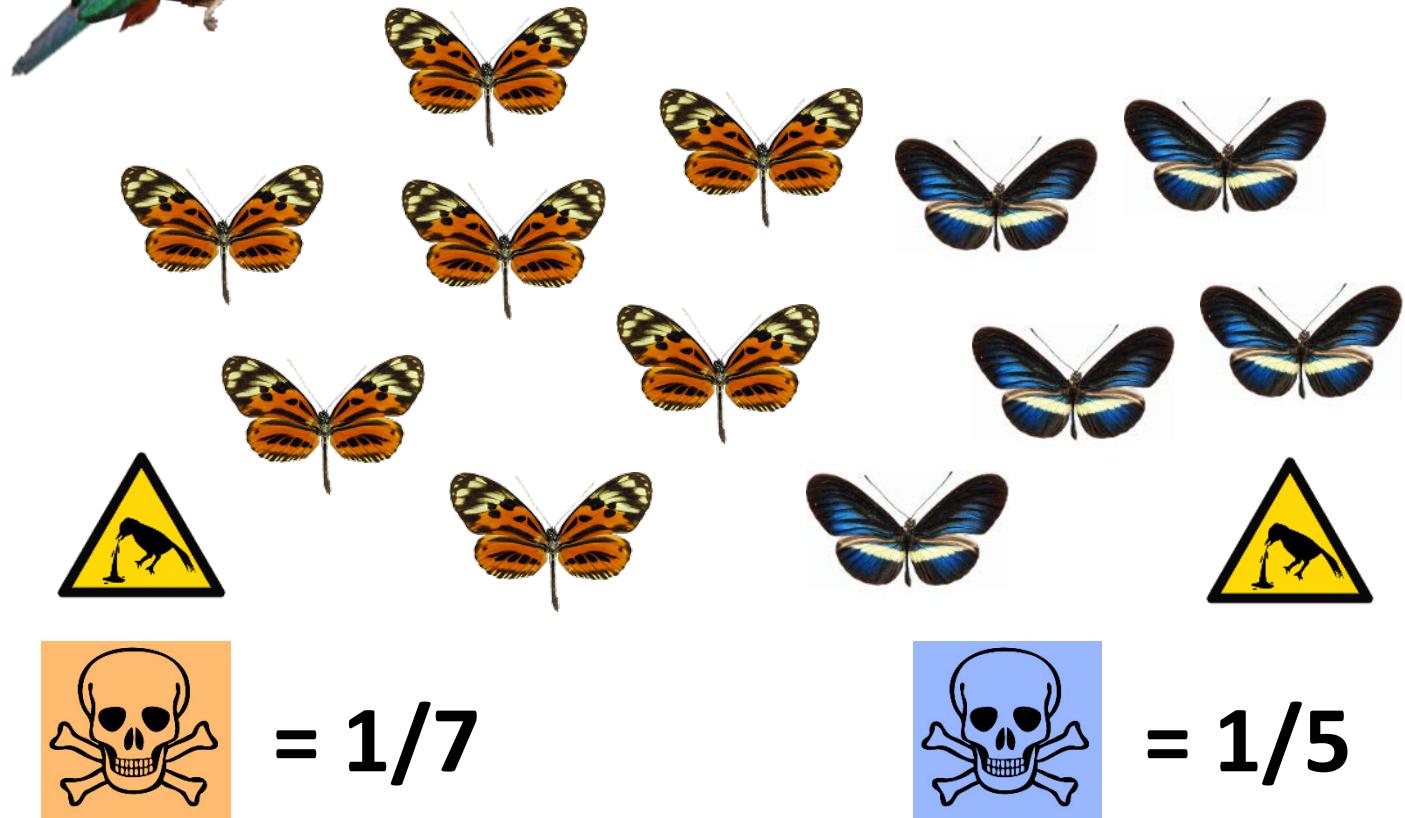
1/ Positive frequency-dependent selection



2/ Advantage for similarity

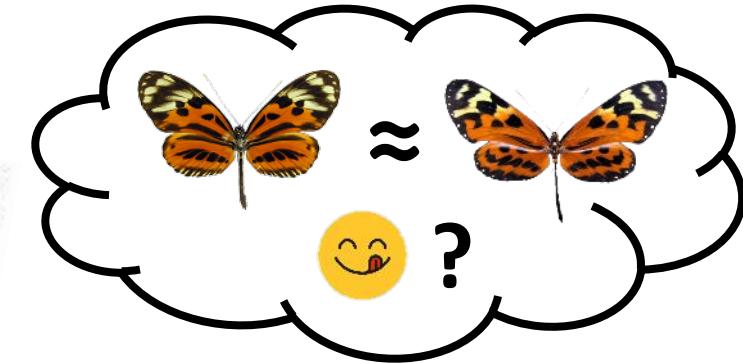
Consequences:

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



Study system: Müllerian mimicry

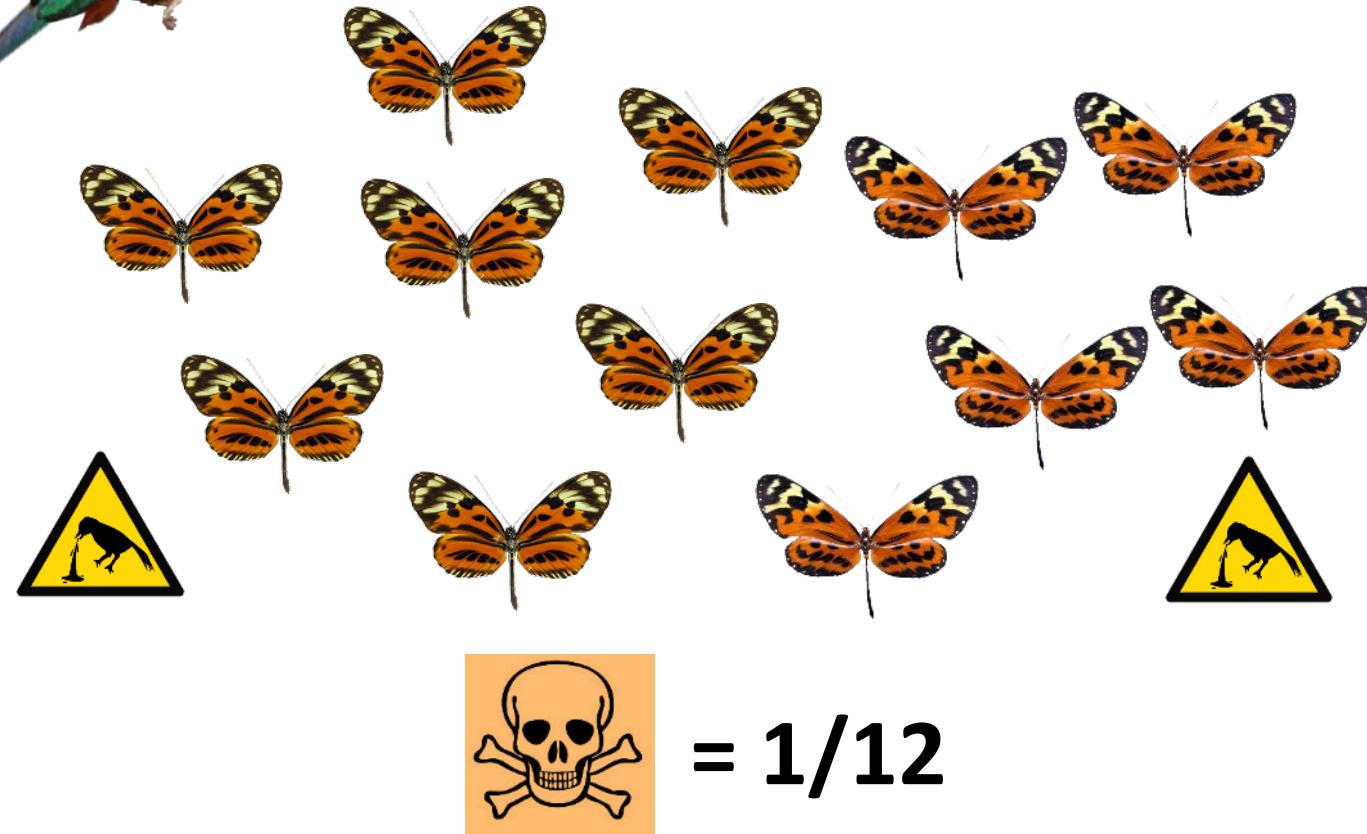
1/ Positive frequency-dependent selection



2/ Advantage for similarity

Consequences:

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



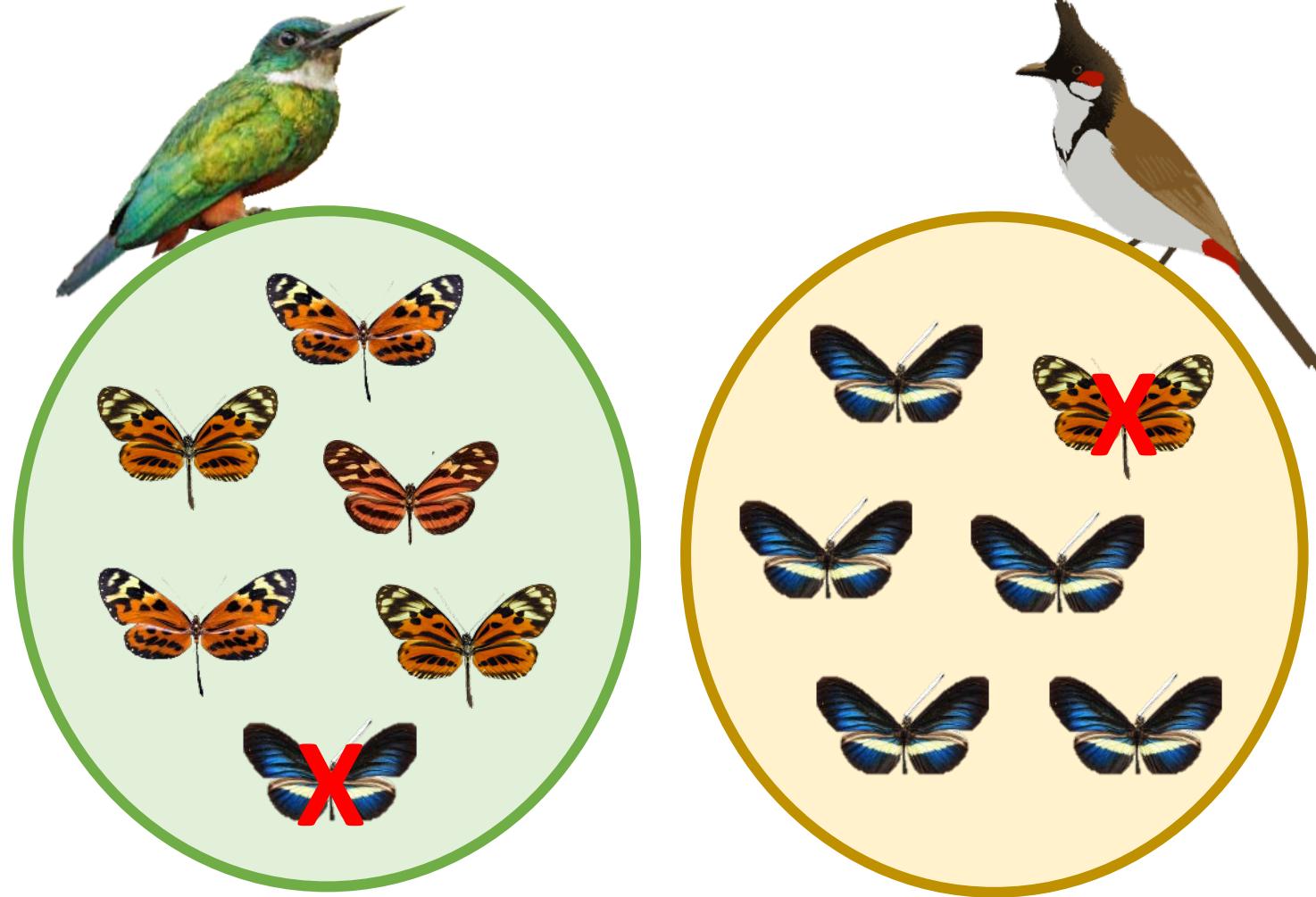
Study system: Müllerian mimicry

1/ Positive frequency-dependent selection

2/ Advantage for similarity

Consequences:

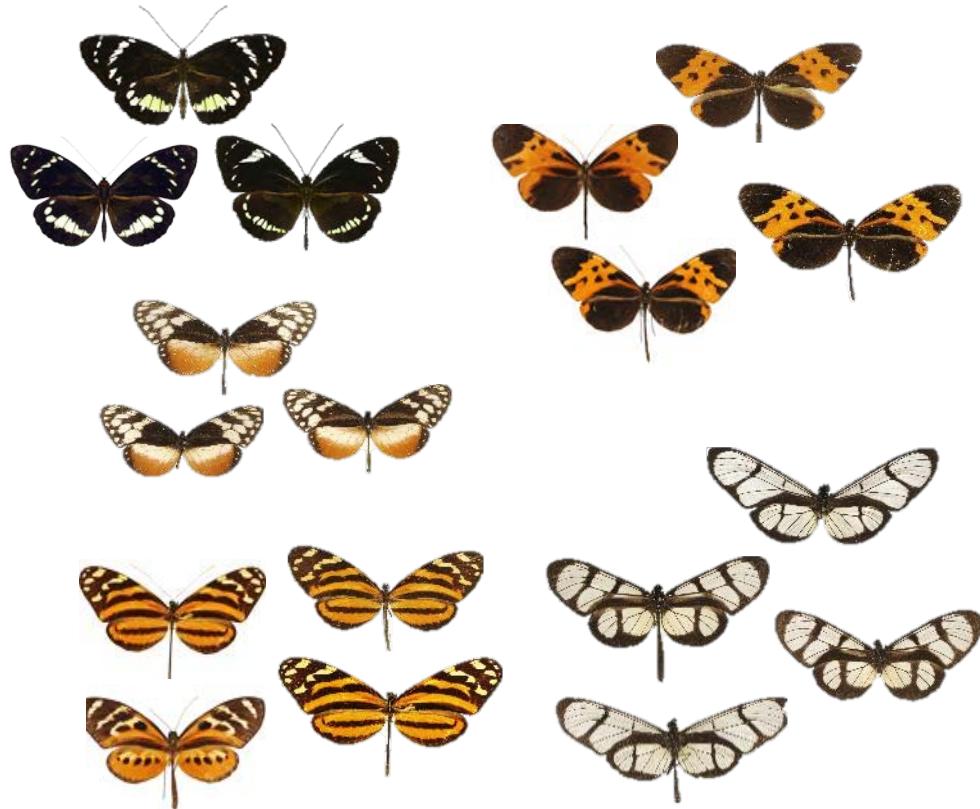
- Local pattern **convergence**
=> **mimicry rings**
- Mutual benefit from cooccurrence
=> **mutualistic interactions**



Study system: Neotropical butterflies

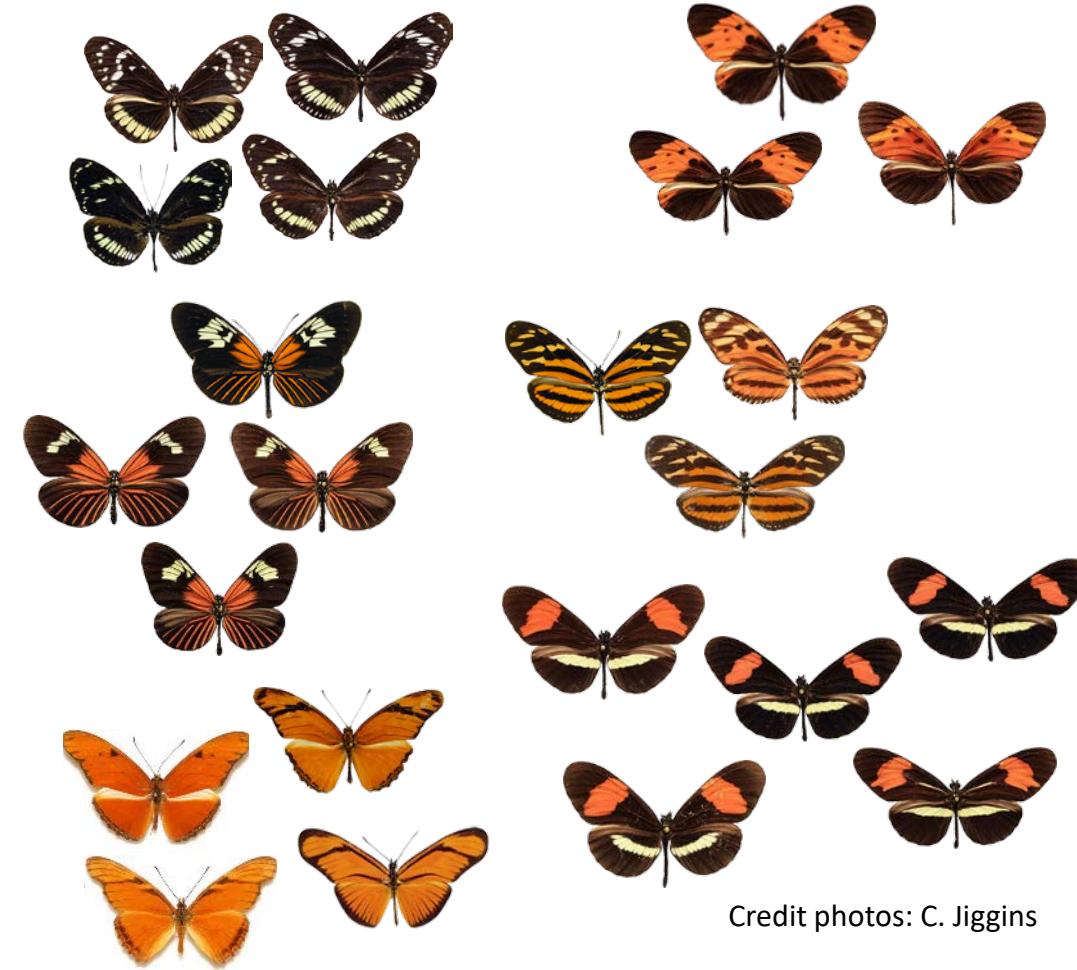
Mimicry

Ithomiini tribe



Phylogeny

Heliconiini tribe

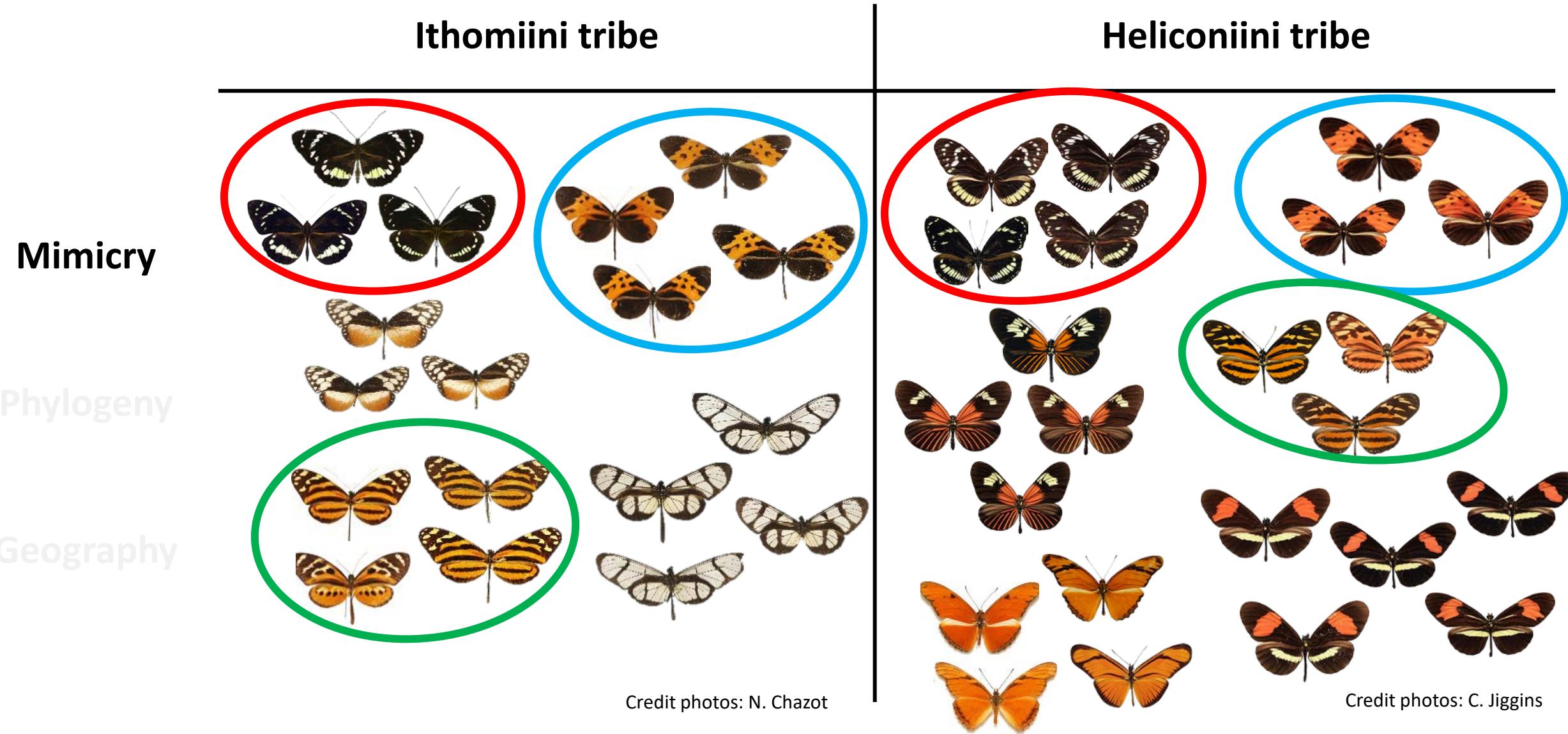


Geography

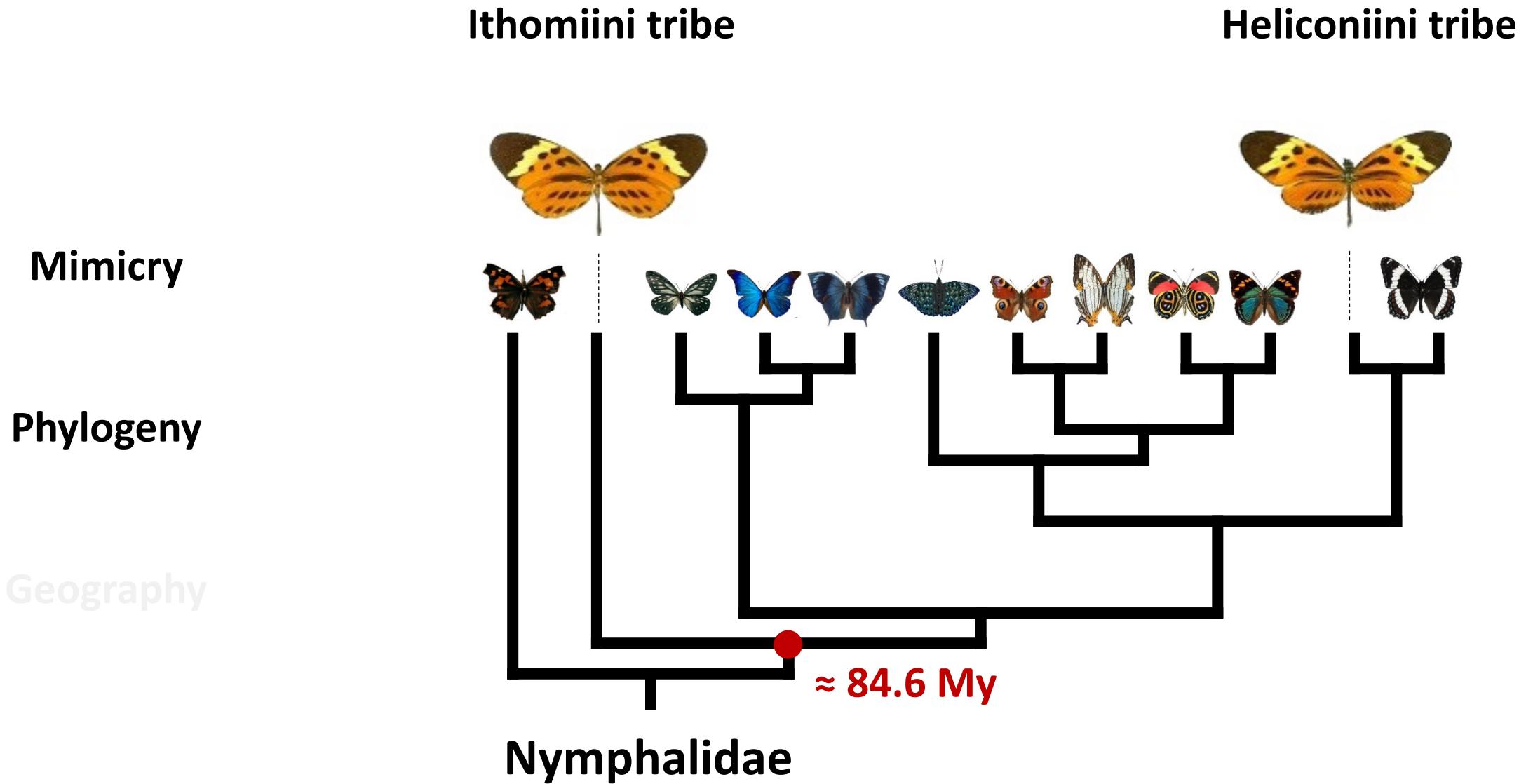
Credit photos: N. Chazot

Credit photos: C. Jiggins

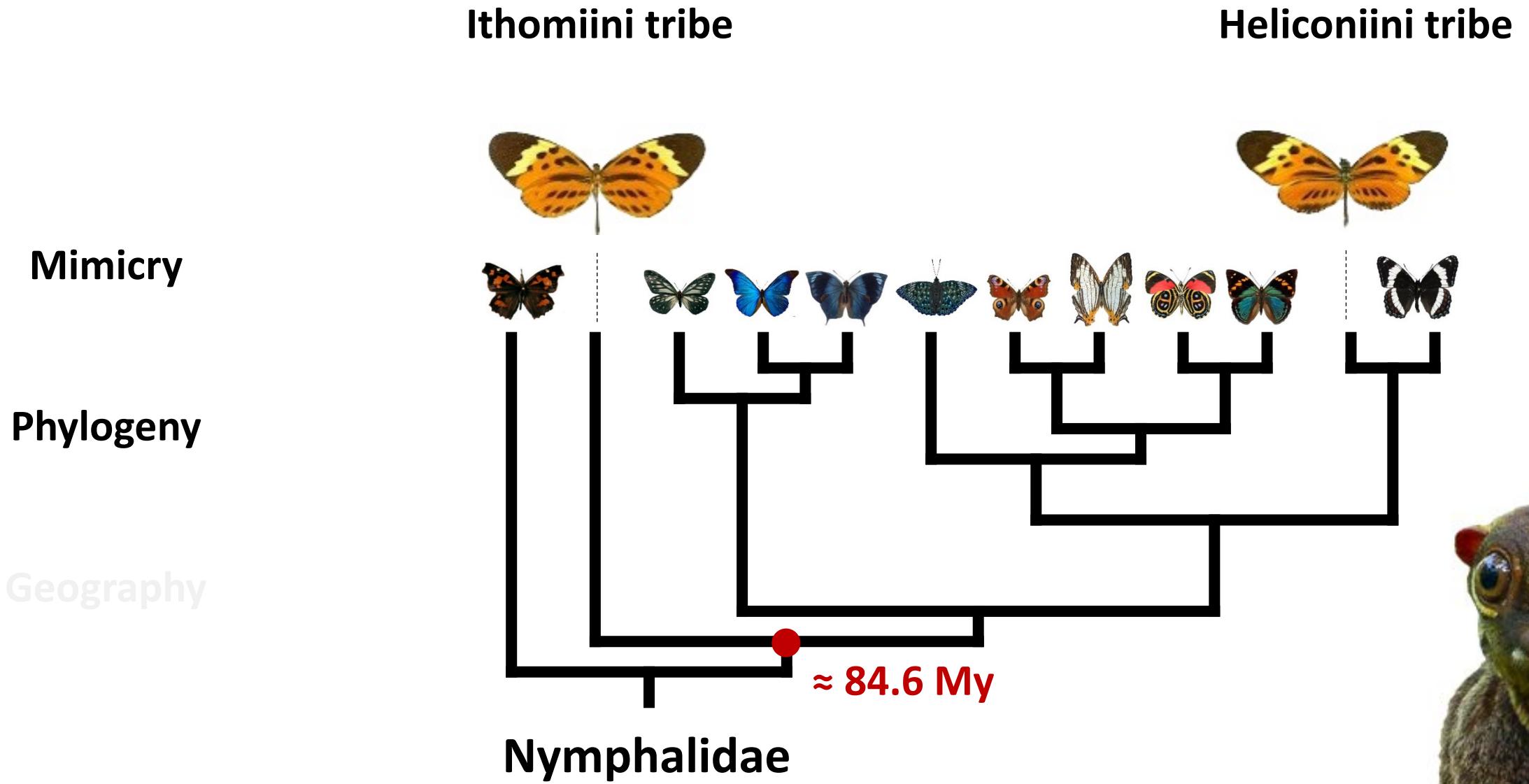
Study system: Neotropical butterflies



Study system: Neotropical butterflies



Study system: Neotropical butterflies



Study system: Neotropical butterflies

Mimicry

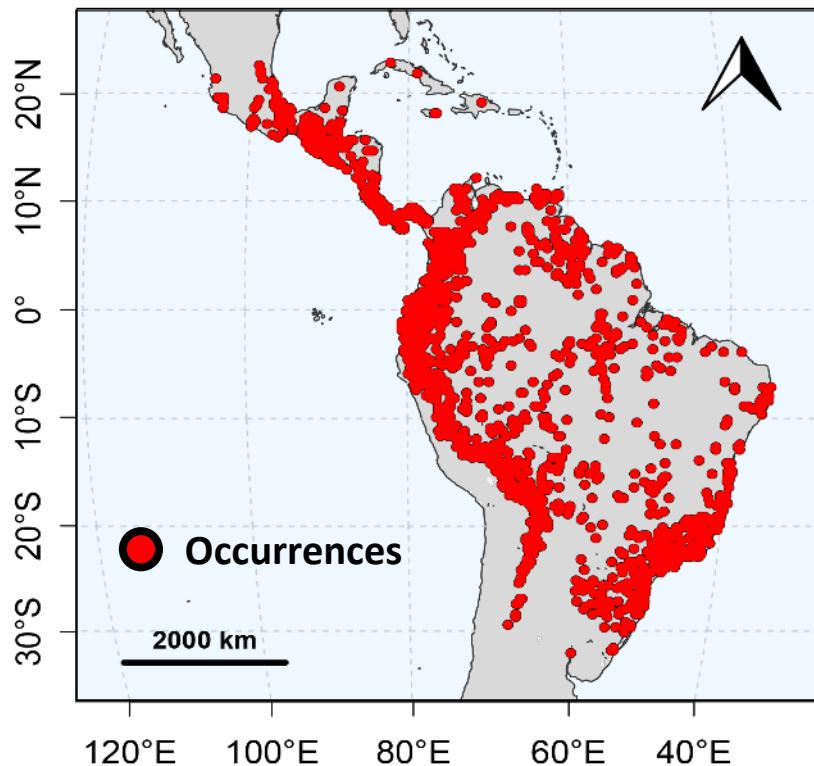
Phylogeny

Geography

Ithomiini tribe

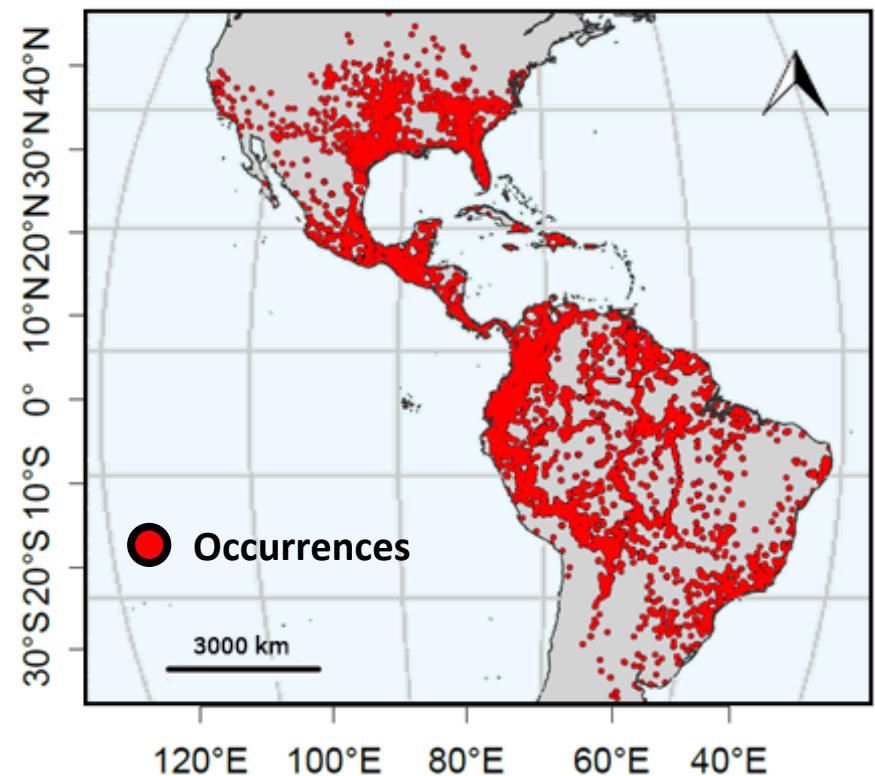
Heliconiini tribe

Occurrence map



Doré et al., 2022

Occurrence map



Perochon et al., in prep

Study system: Neotropical butterflies

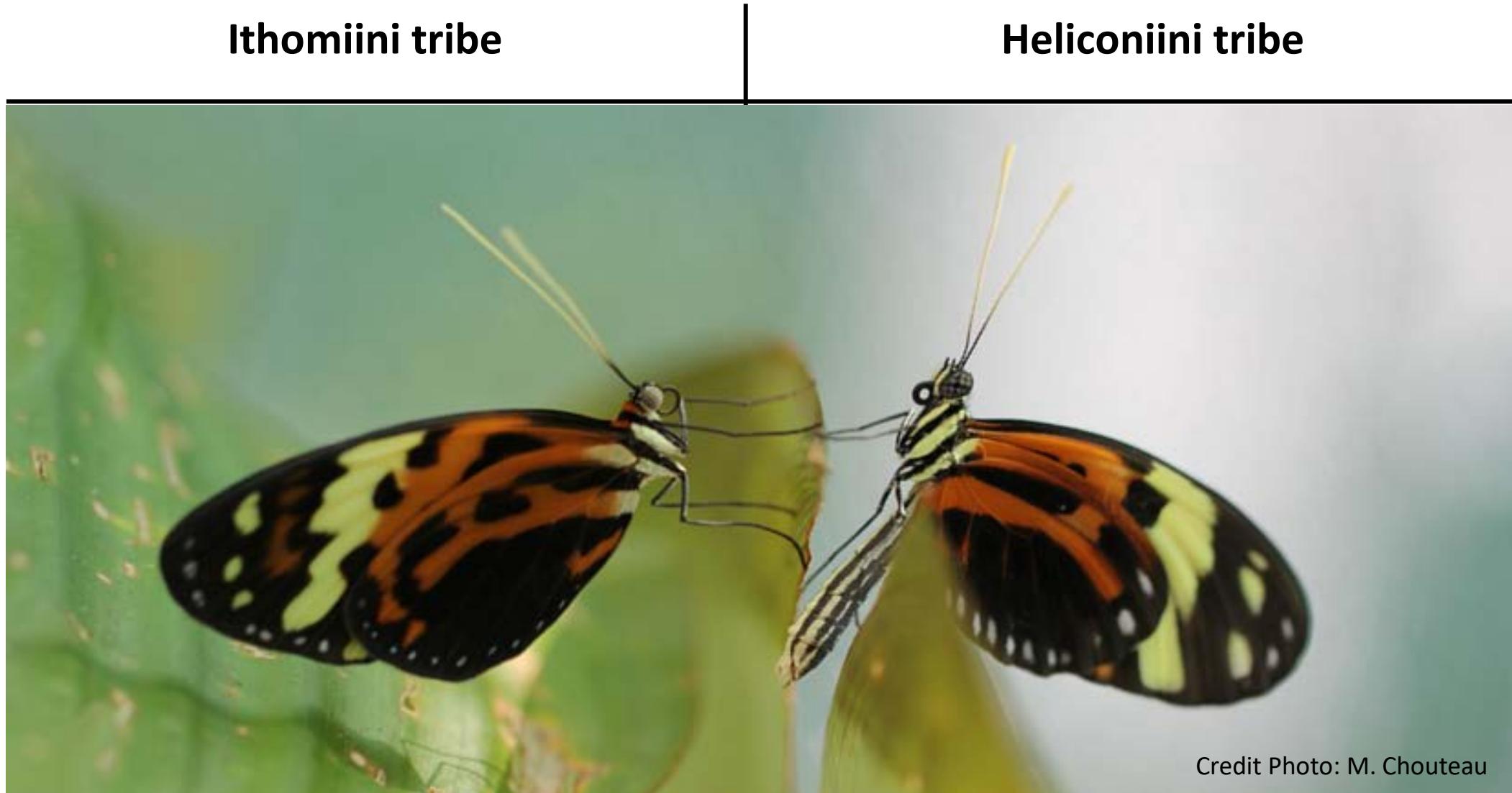
Ithomiini tribe

Mimicry

Phylogeny

Geography

Heliconiini tribe



Credit Photo: M. Chouteau

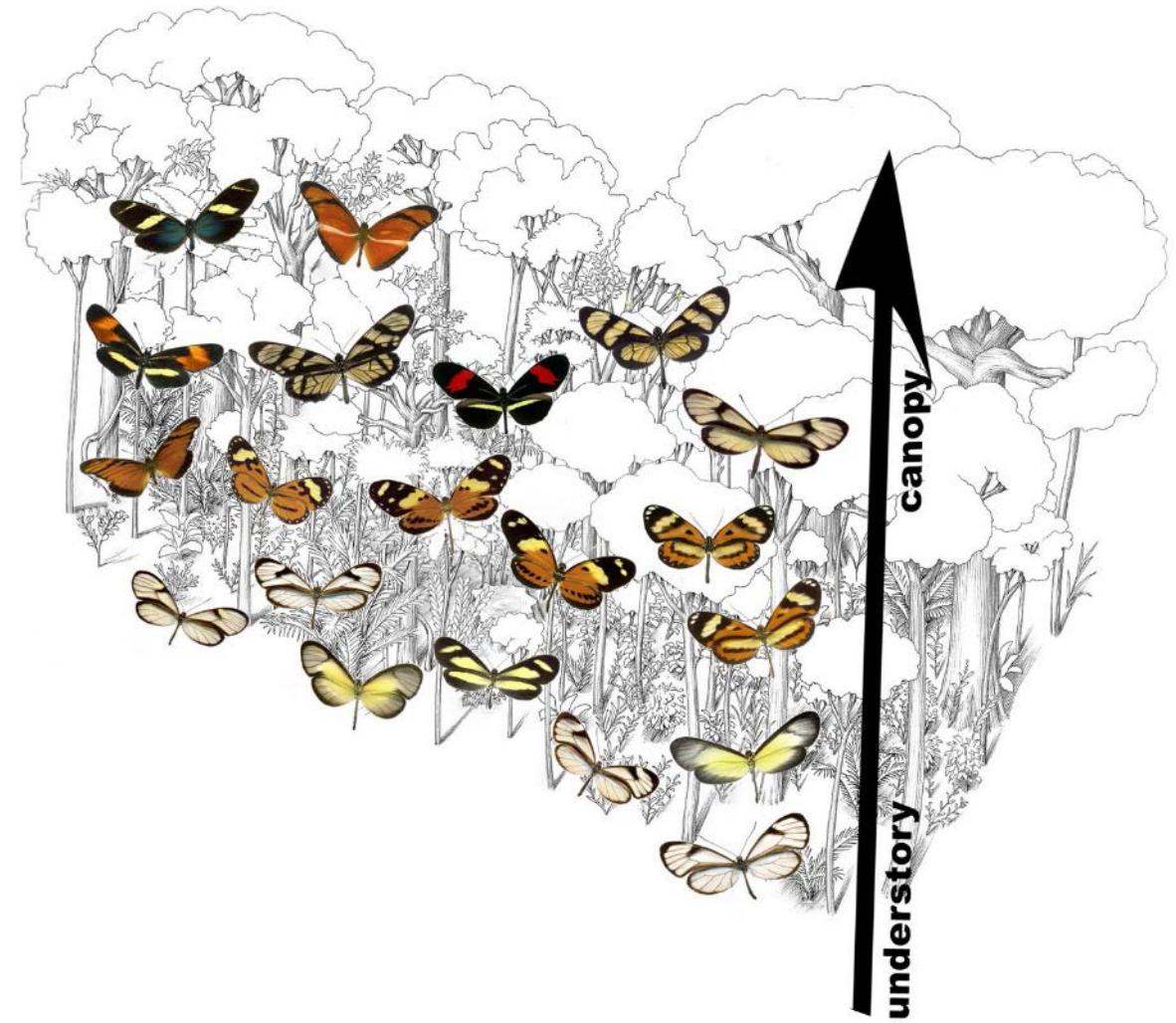
State-of-the-art

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

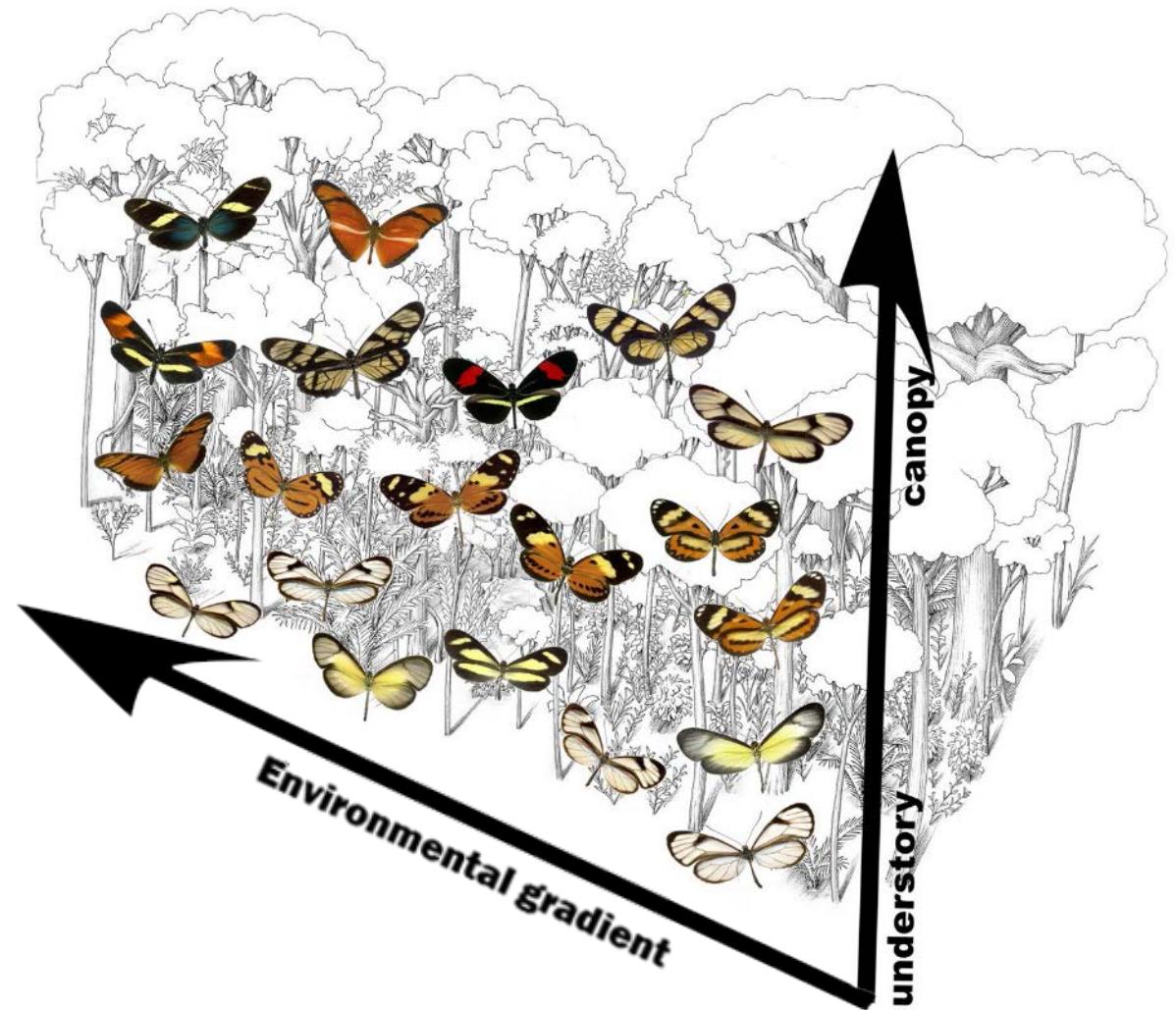
State-of-the-art

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

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



Credits: Arthur Anker

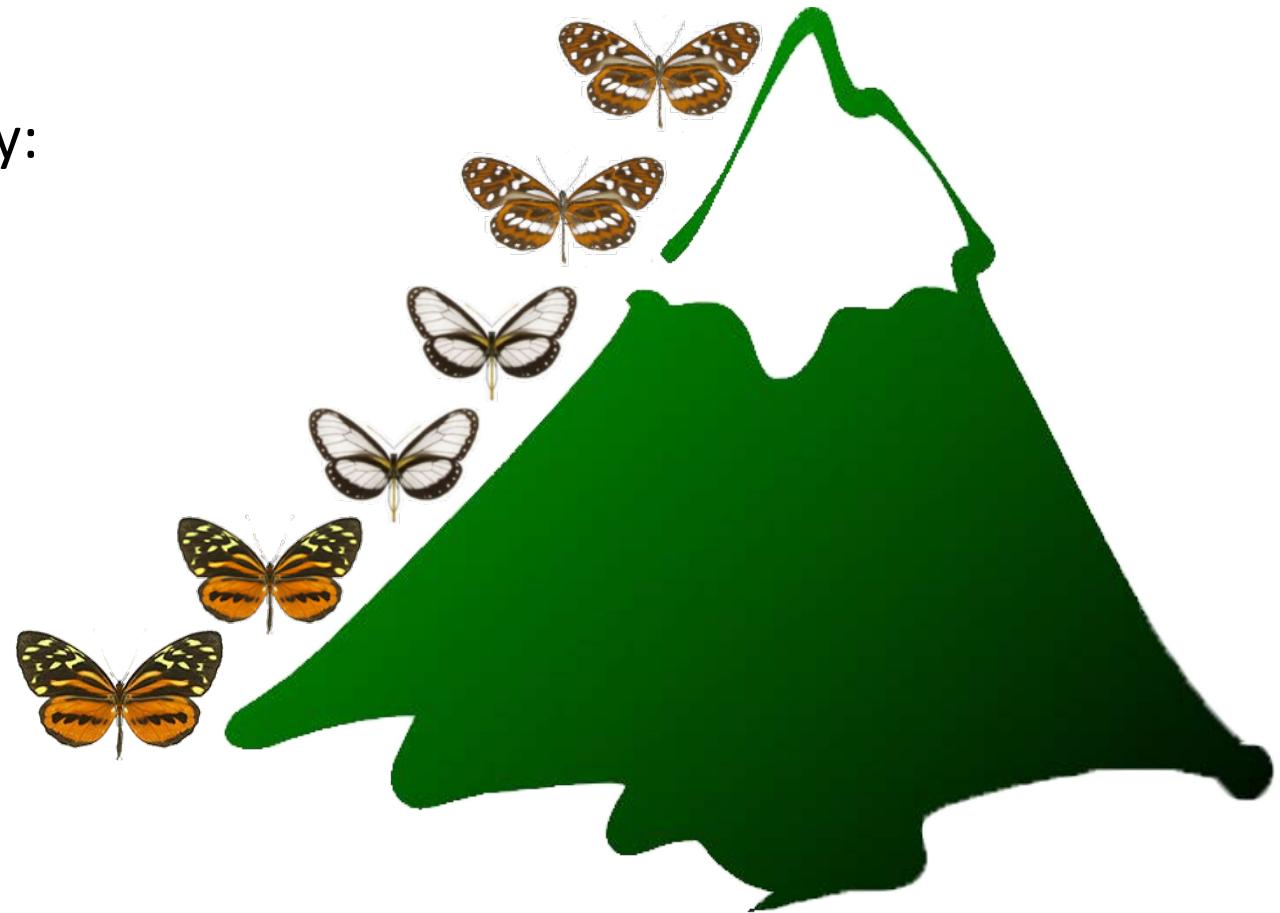
State-of-the-art

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



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

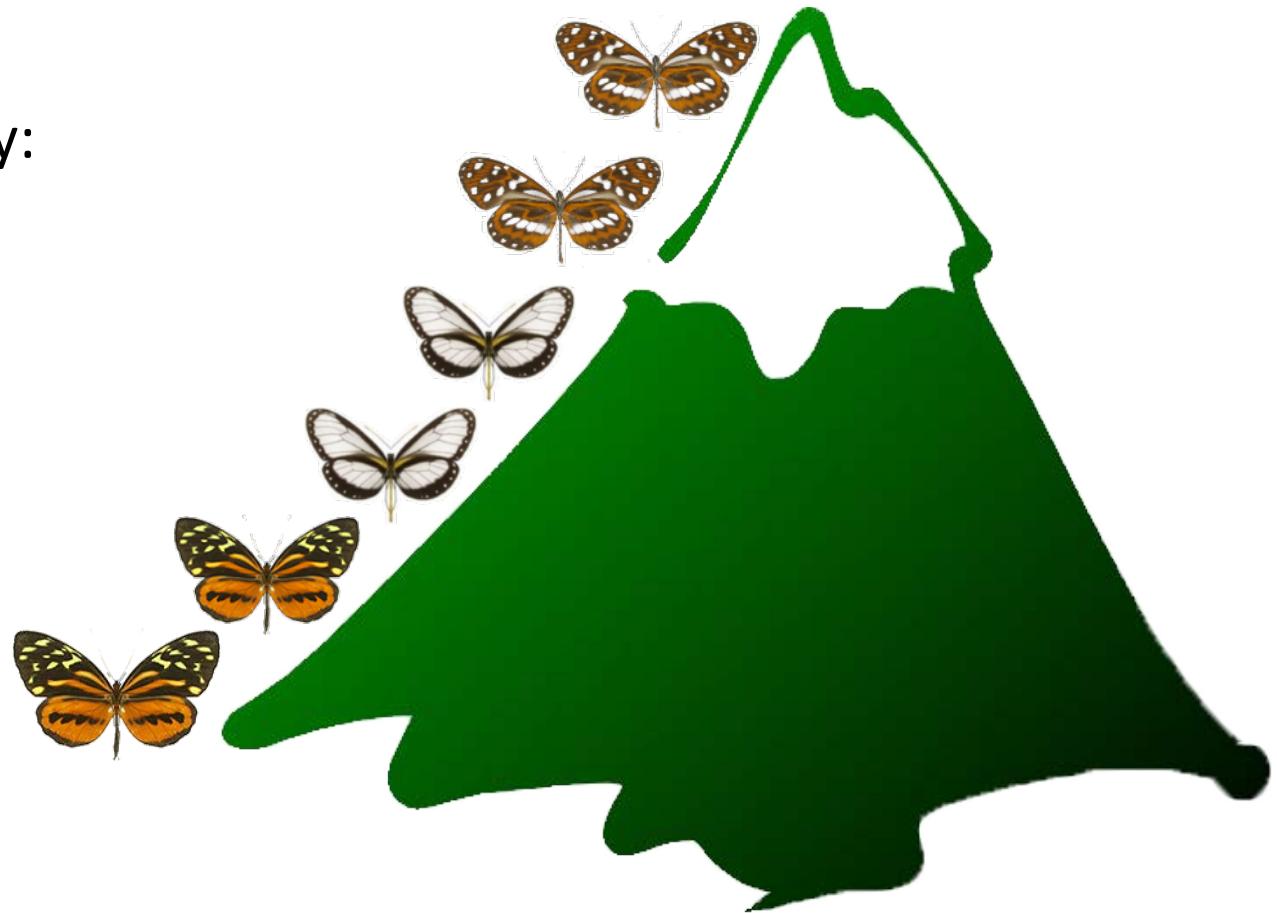
State-of-the-art

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



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

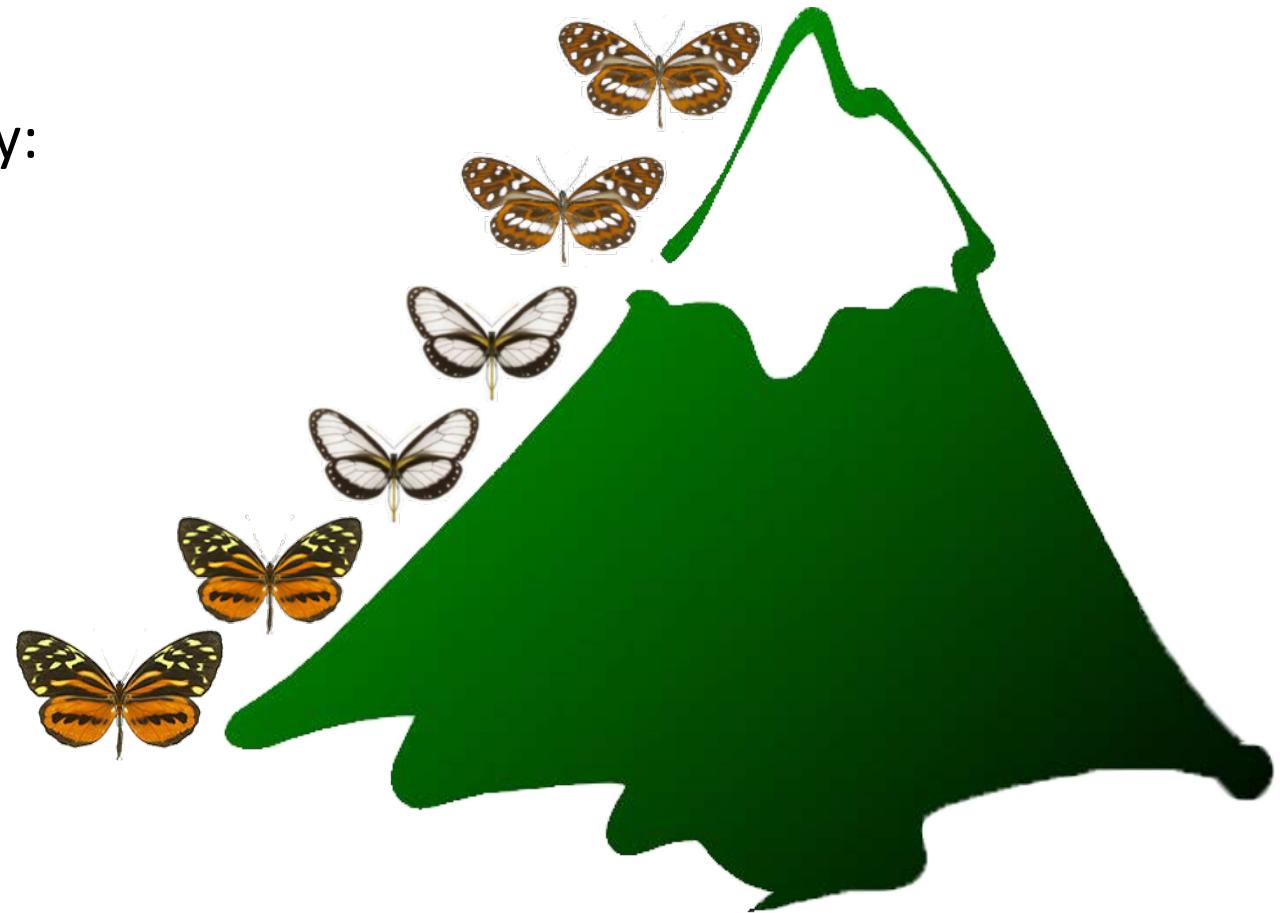
State-of-the-art

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



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**?



Biodiversity patterns: Are large-scale **biodiversity patterns** different between tribes?



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



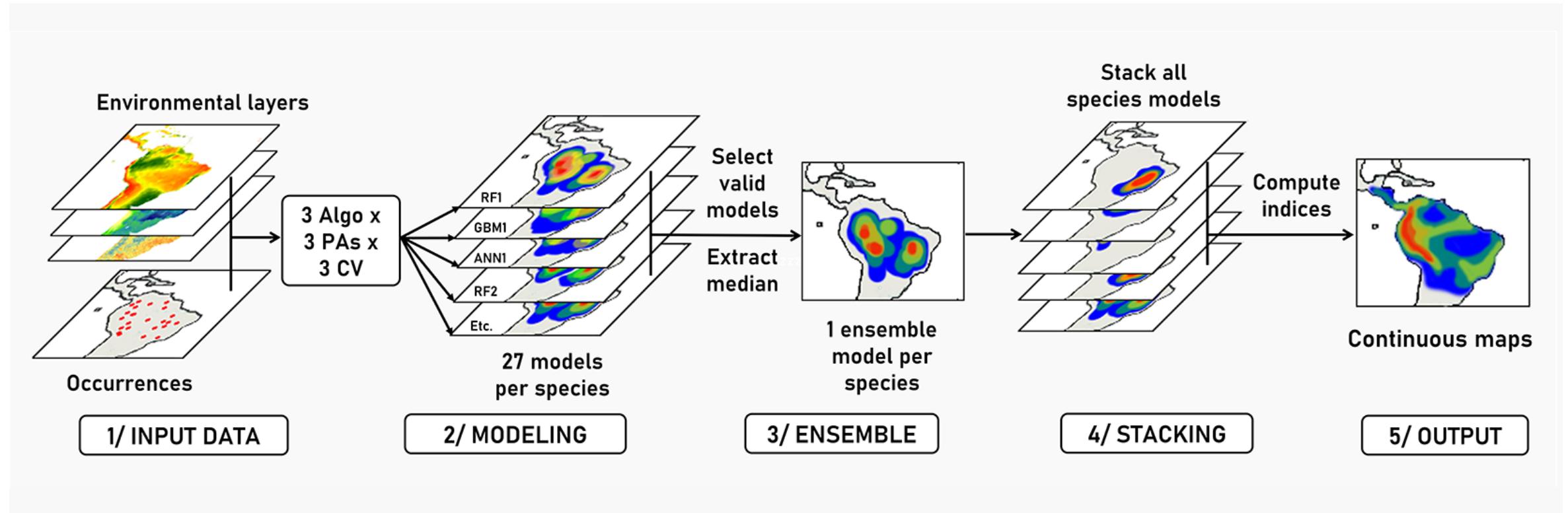
Niche similarity: Do phenotypically similar species have similar climatic niche?



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



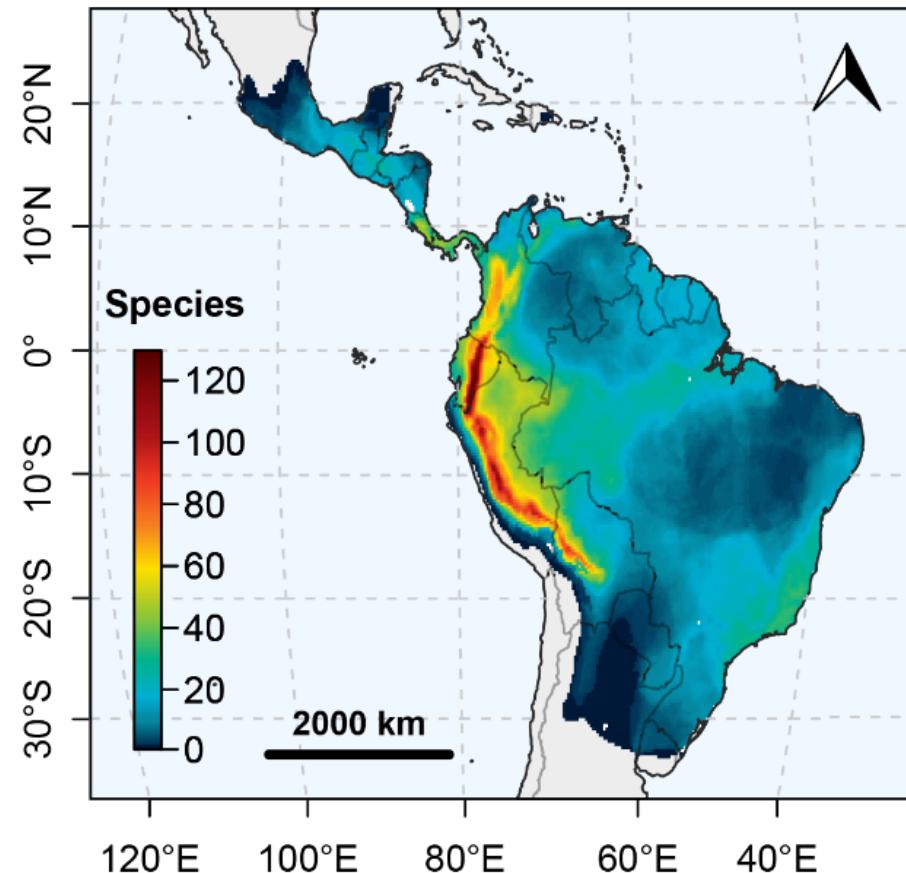
Species Distribution Modeling (SDM)



SDM → Species distribution maps → Diversity indices

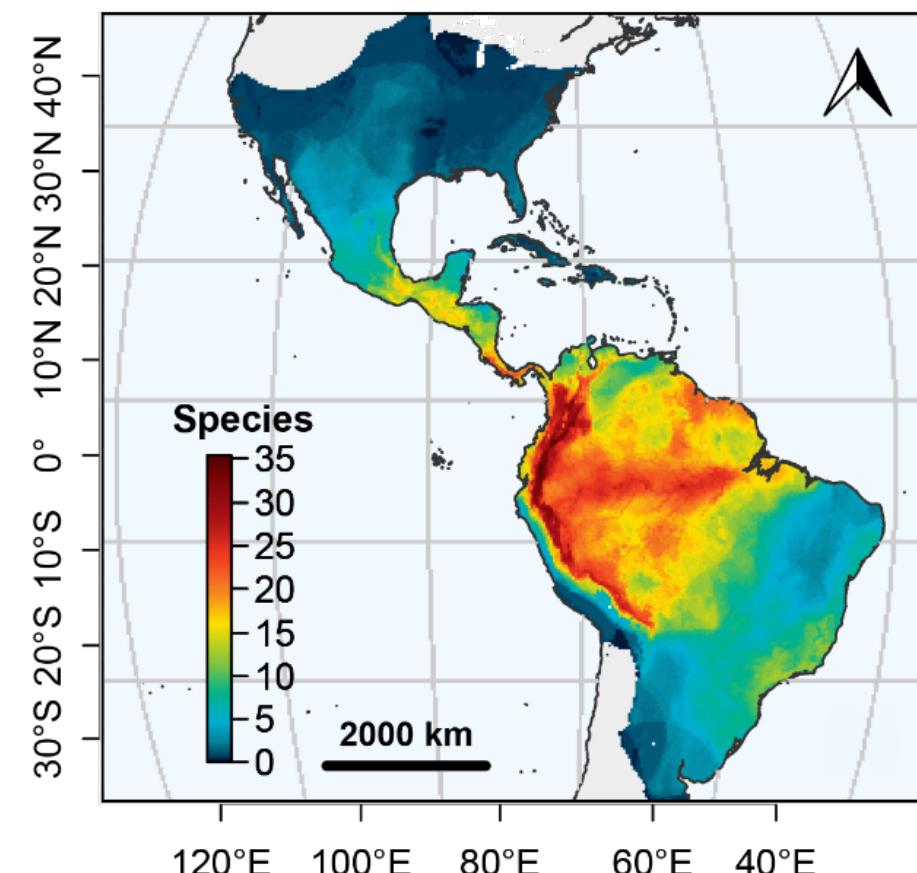
Biodiversity patterns

Ithomiini
(396 species)



Species richness

Heliconiini
(77 species)

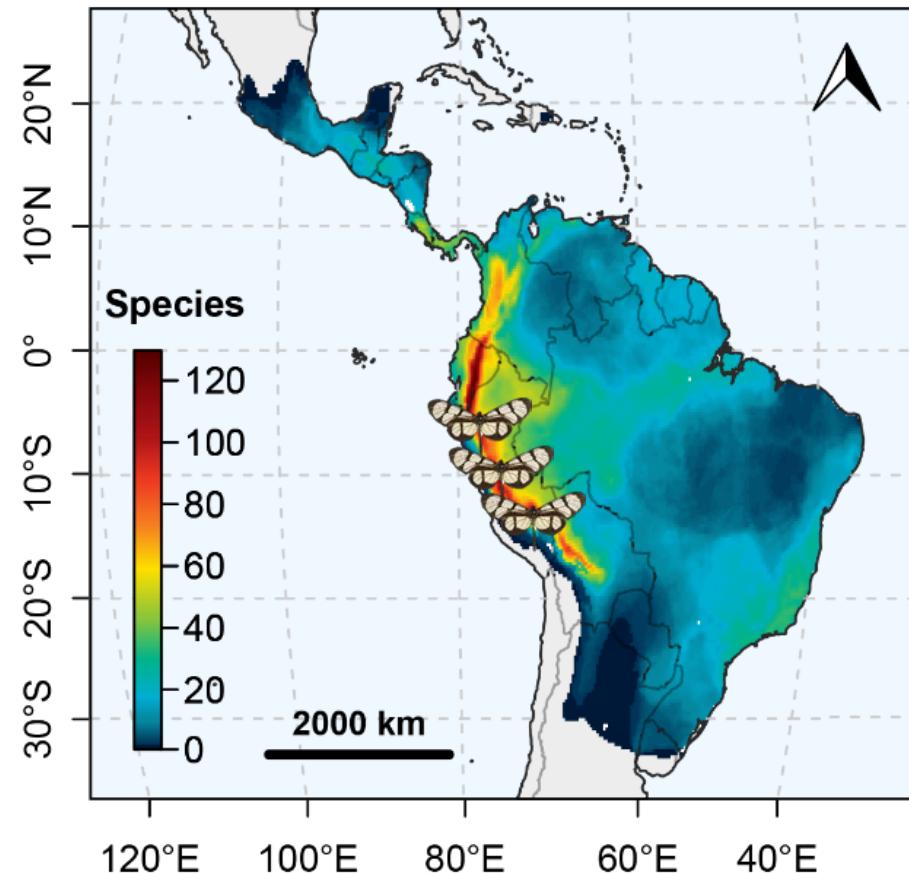


Doré et al., 2022

Pérochon et al., in prep

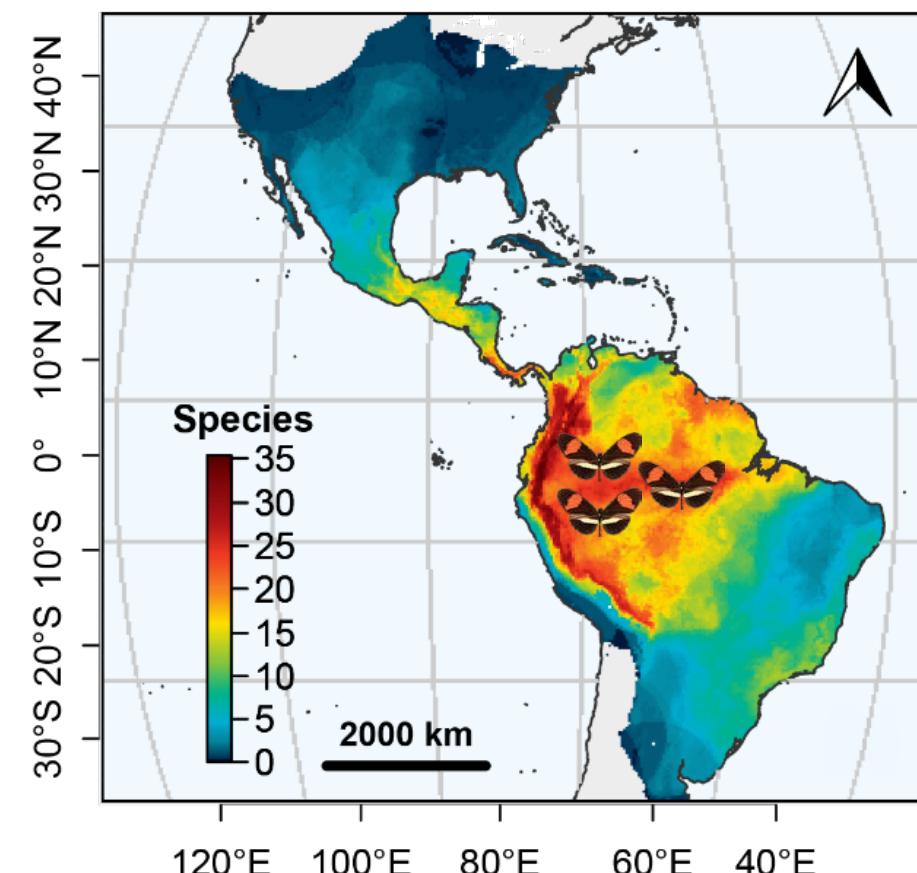
Biodiversity patterns

Ithomiini
(396 species)



Species richness

Heliconiini
(77 species)

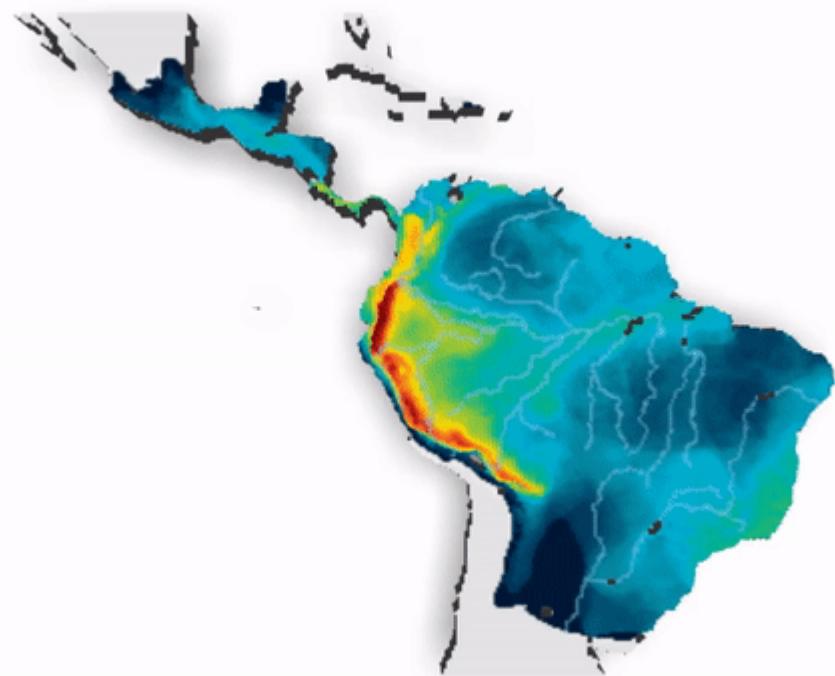


Doré et al., 2022

Pérochon et al., in prep

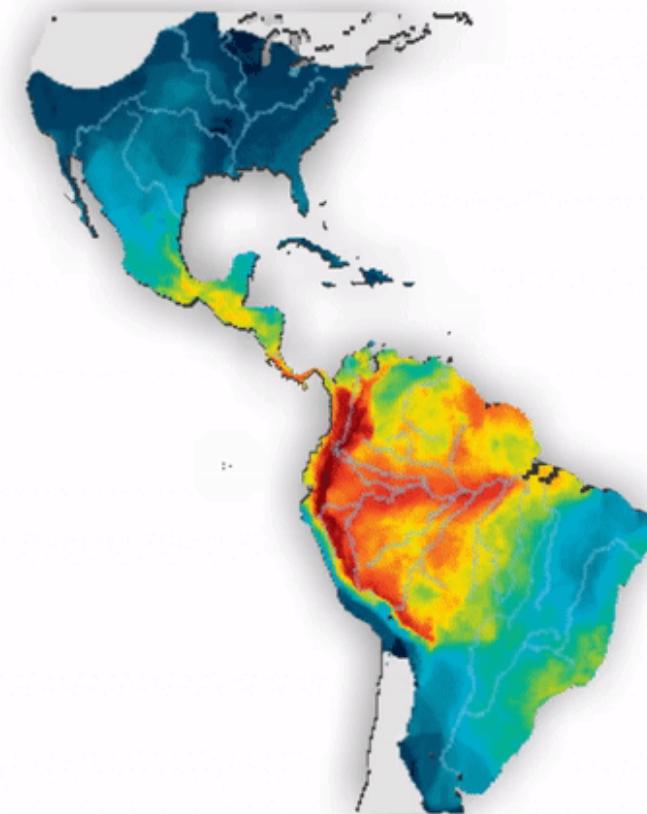
Biodiversity patterns

Ithomiini
(396 species)



Species richness

Heliconiini
(77 species)



Objectives

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



1

Biodiversity patterns: Are large-scale **biodiversity patterns** different between tribes?



2

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



3

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



4

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



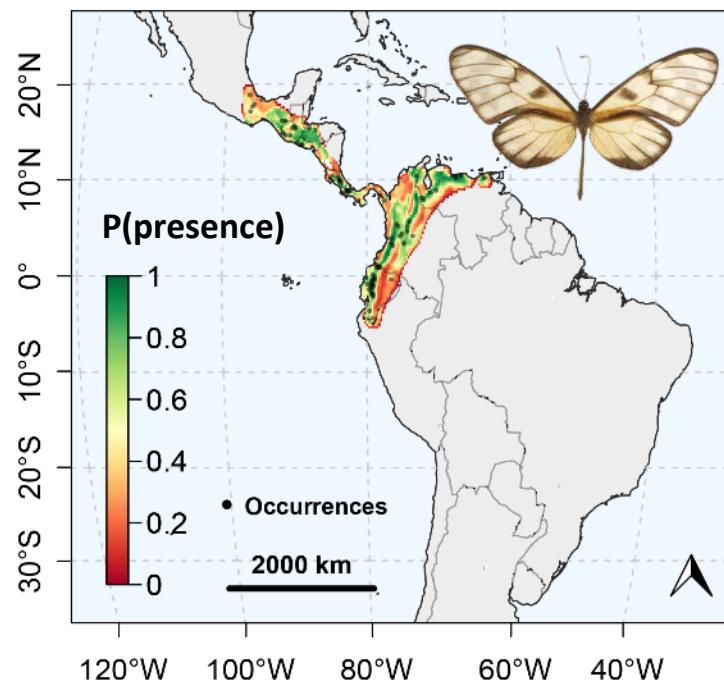
Spatial congruence

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

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

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

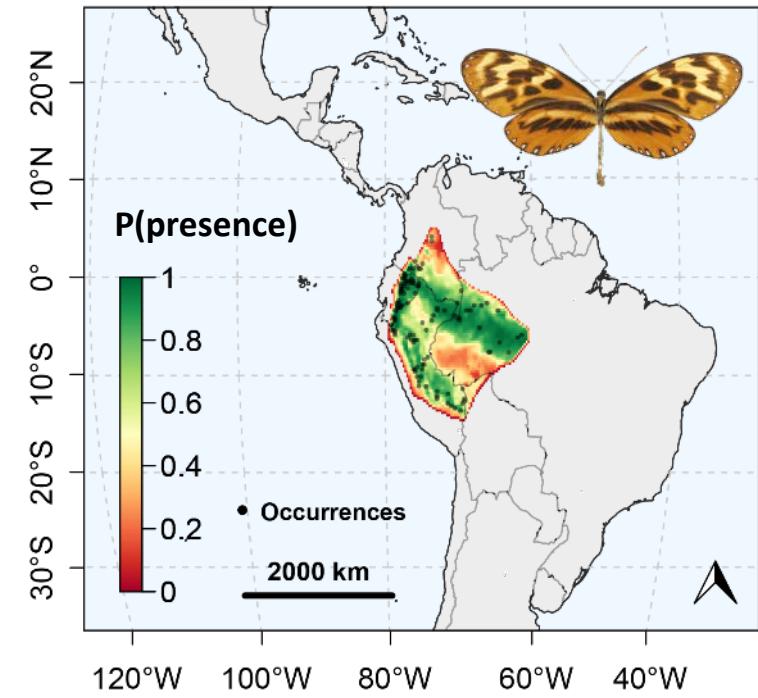
Dircenna jemina (DILUCIDA)



No mimicry

BC = 0.9

Mechanitis mazaeus (MAELUS)



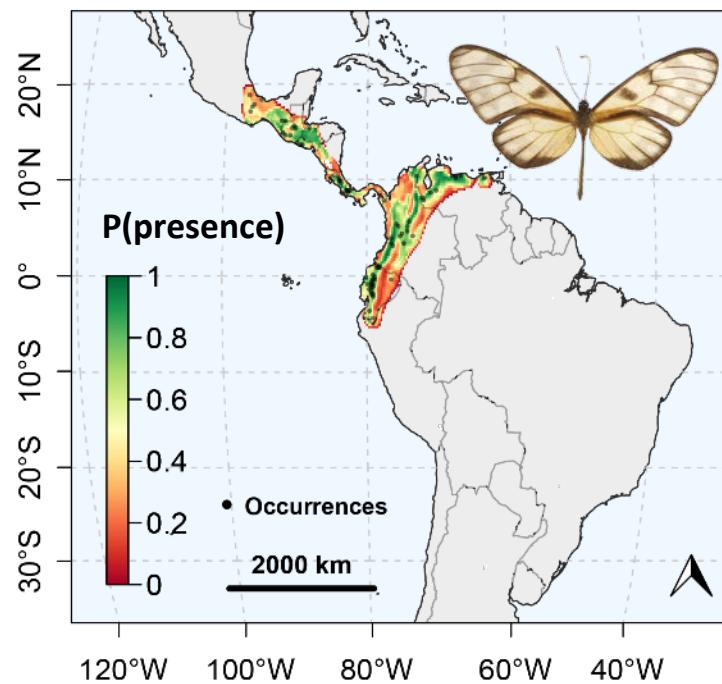
Spatial congruence

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

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

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

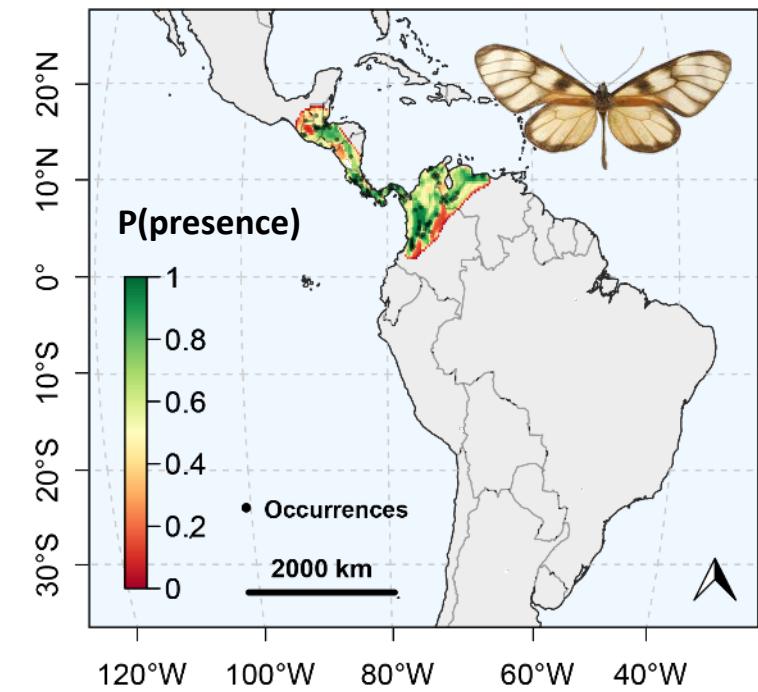
Dircenna jemina (DILUCIDA)



Mimicry

BC = 0.2

Dircenna dero (DILUCIDA)



Spatial congruence

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

Global: Mean $BC_{obs} << \text{Mean } BC_{perm}$

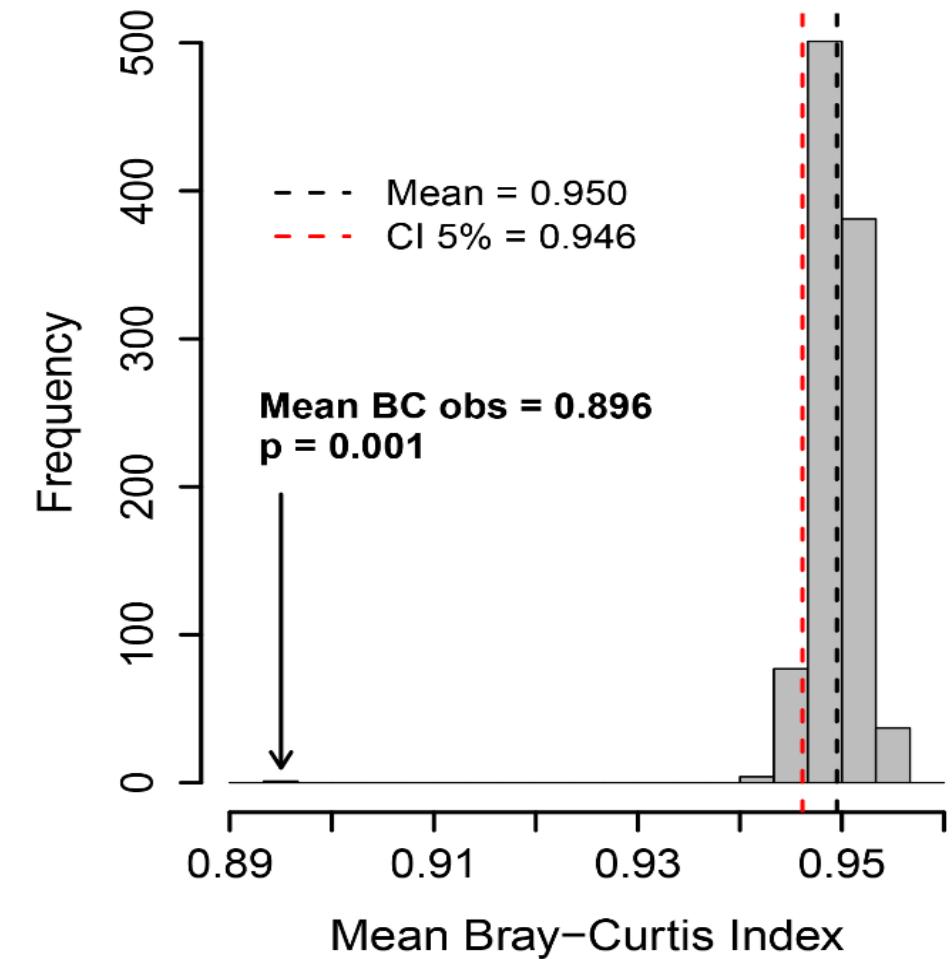


Per phenotypic group: 85% of putative rings

- 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

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

Global: Mean $BC_{obs} << \text{Mean } BC_{perm}$

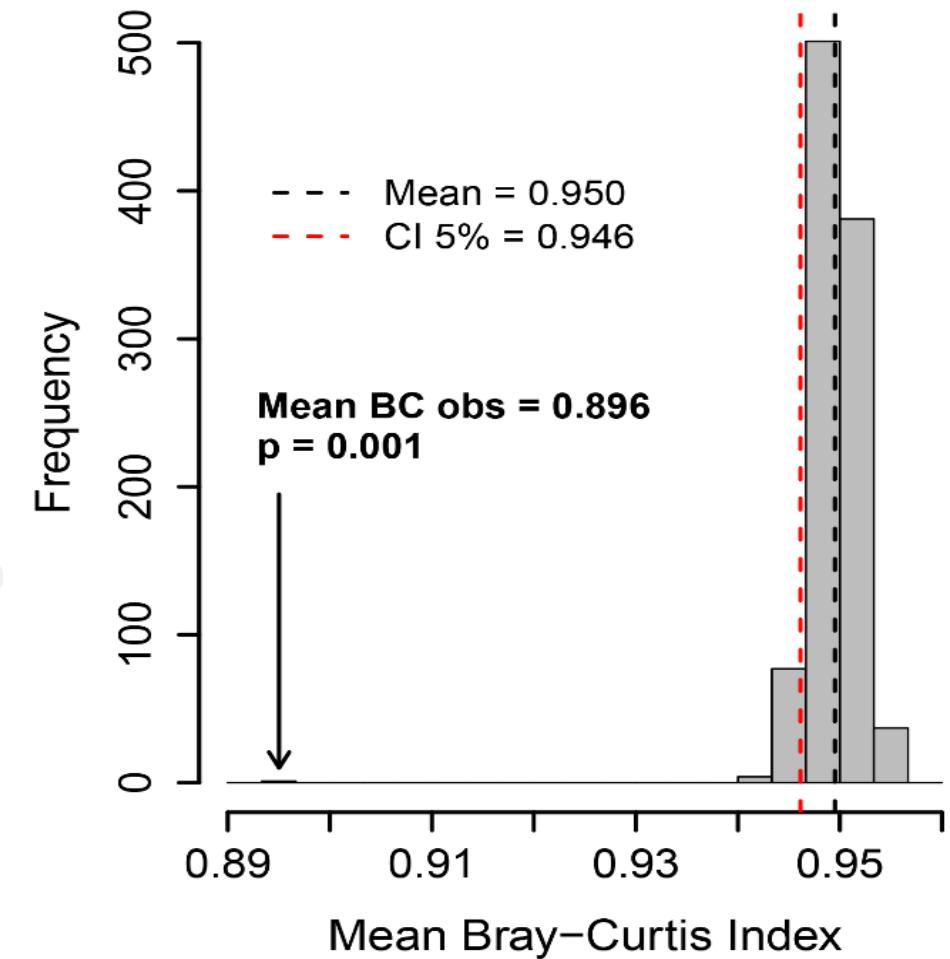


Per phenotypic group: 85% of putative rings

- 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

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

Global: Mean $BC_{obs} << \text{Mean } BC_{perm}$

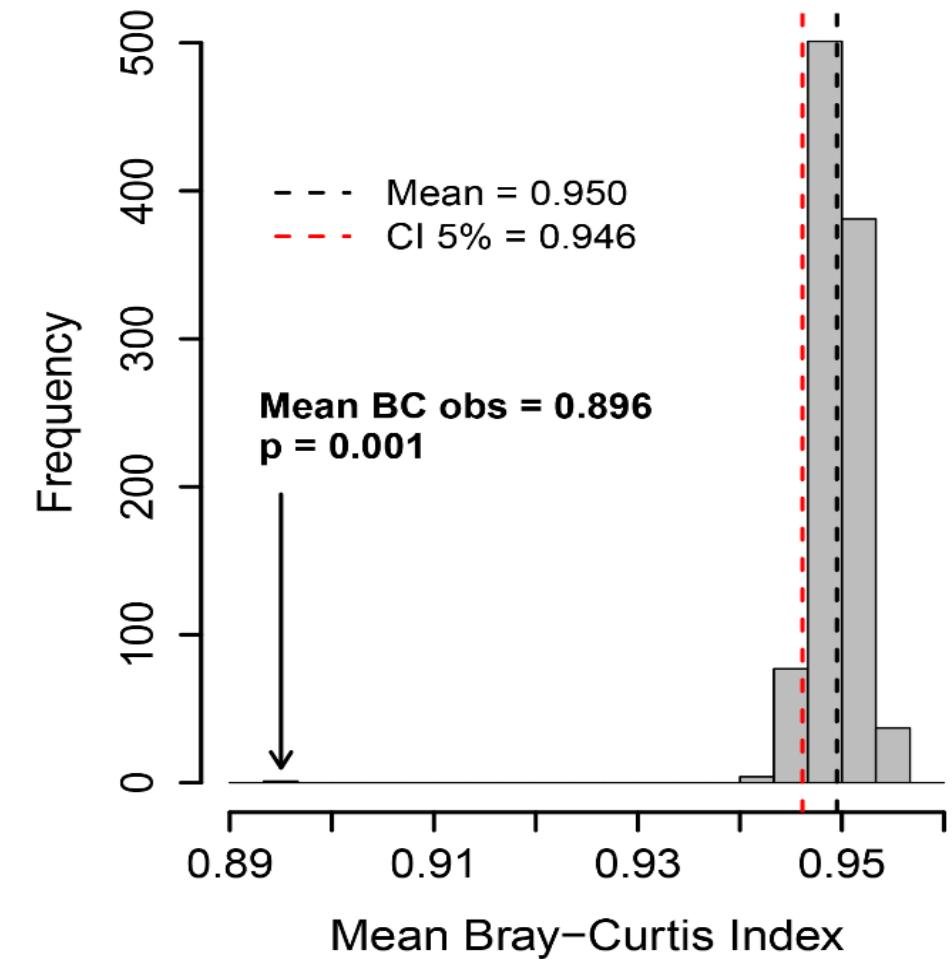


Per phenotypic group: 85% of putative rings

- Non-significant rings = low N

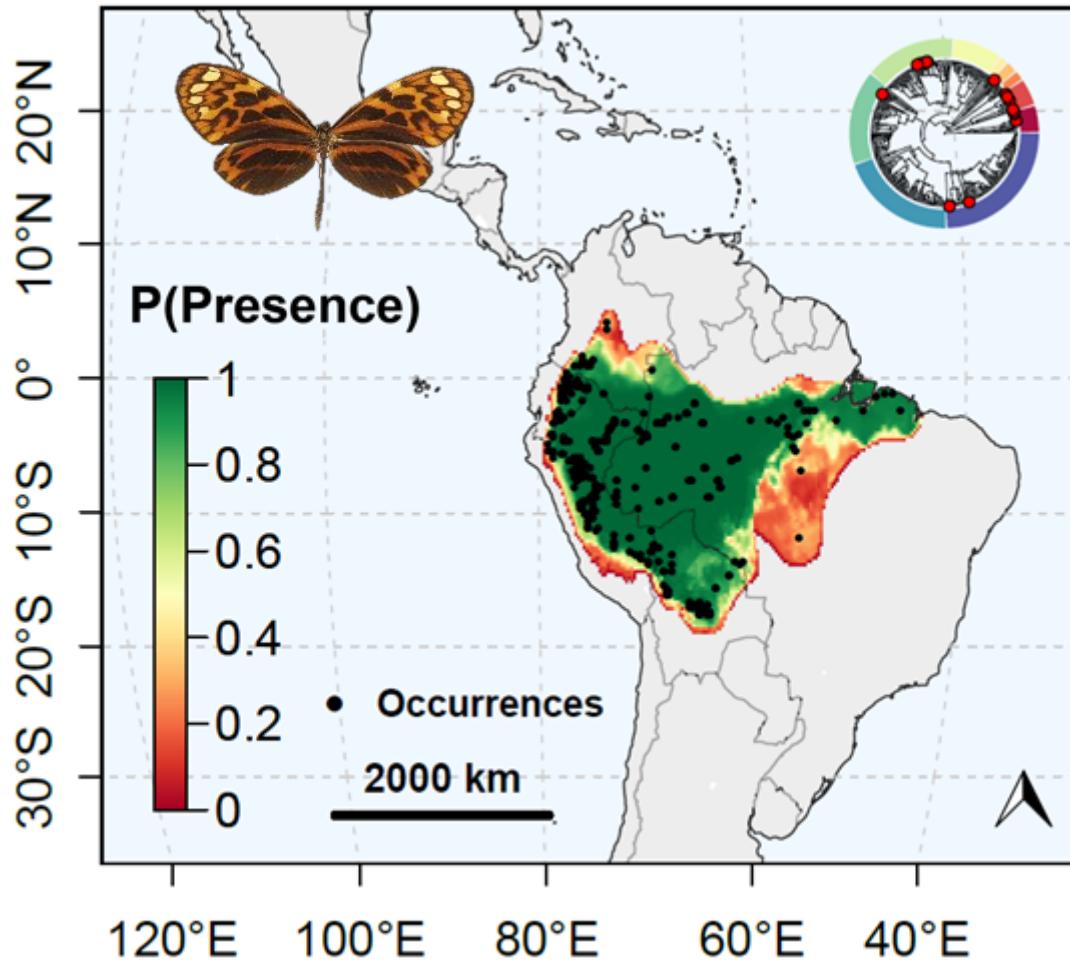
Results: Mimicry promotes the **spatial congruence** of phenotypically similar species at **large-scale**

Next: What happens between tribes?

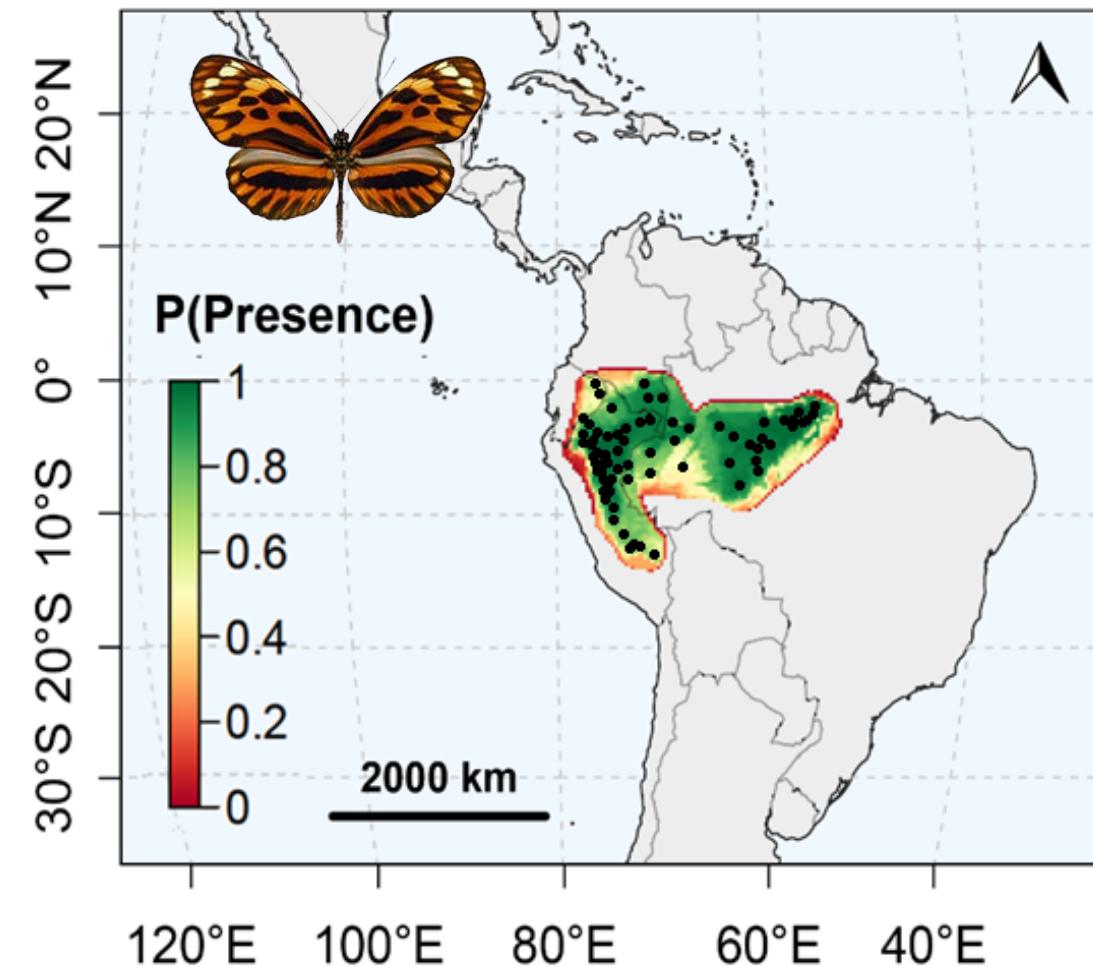


Spatial congruence

Ithomiini: pattern MAELUS
(16 species)

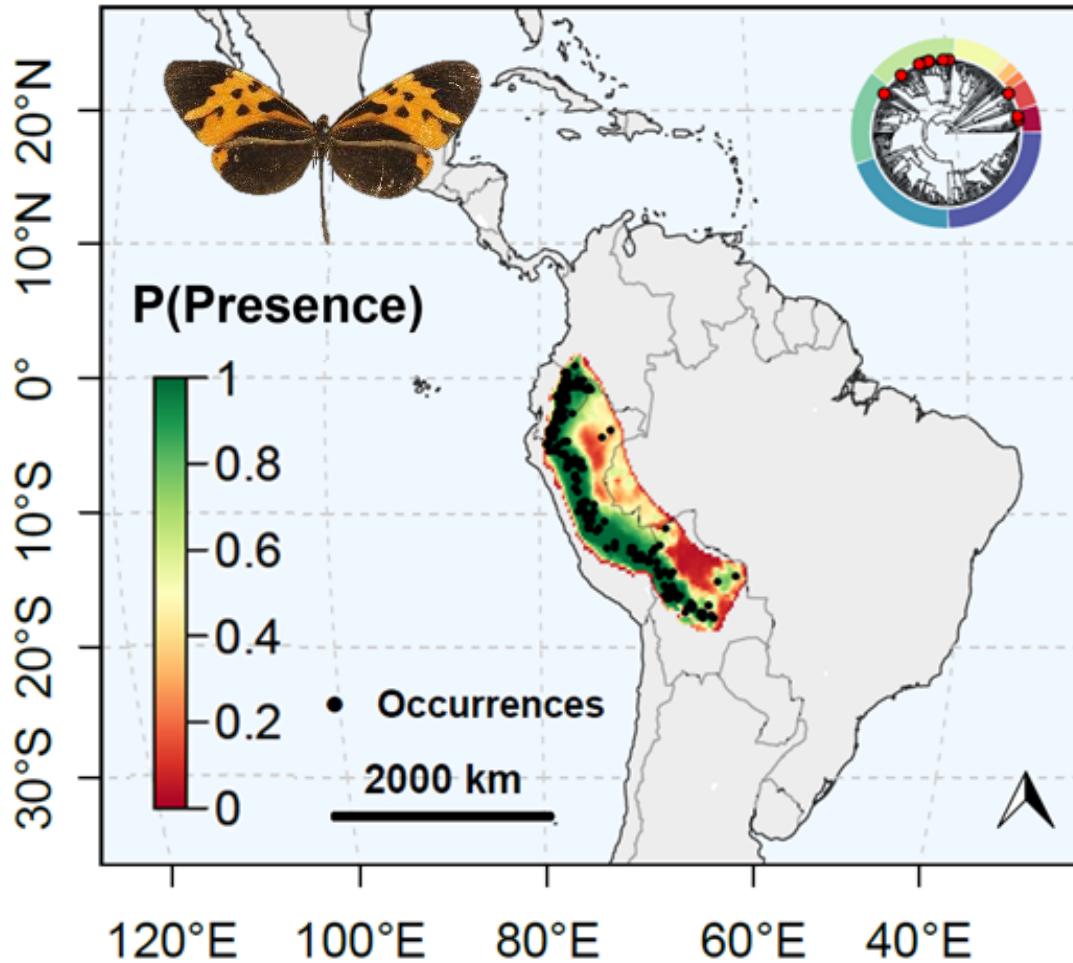


Heliconiini: pattern MAELUS
(5 species)

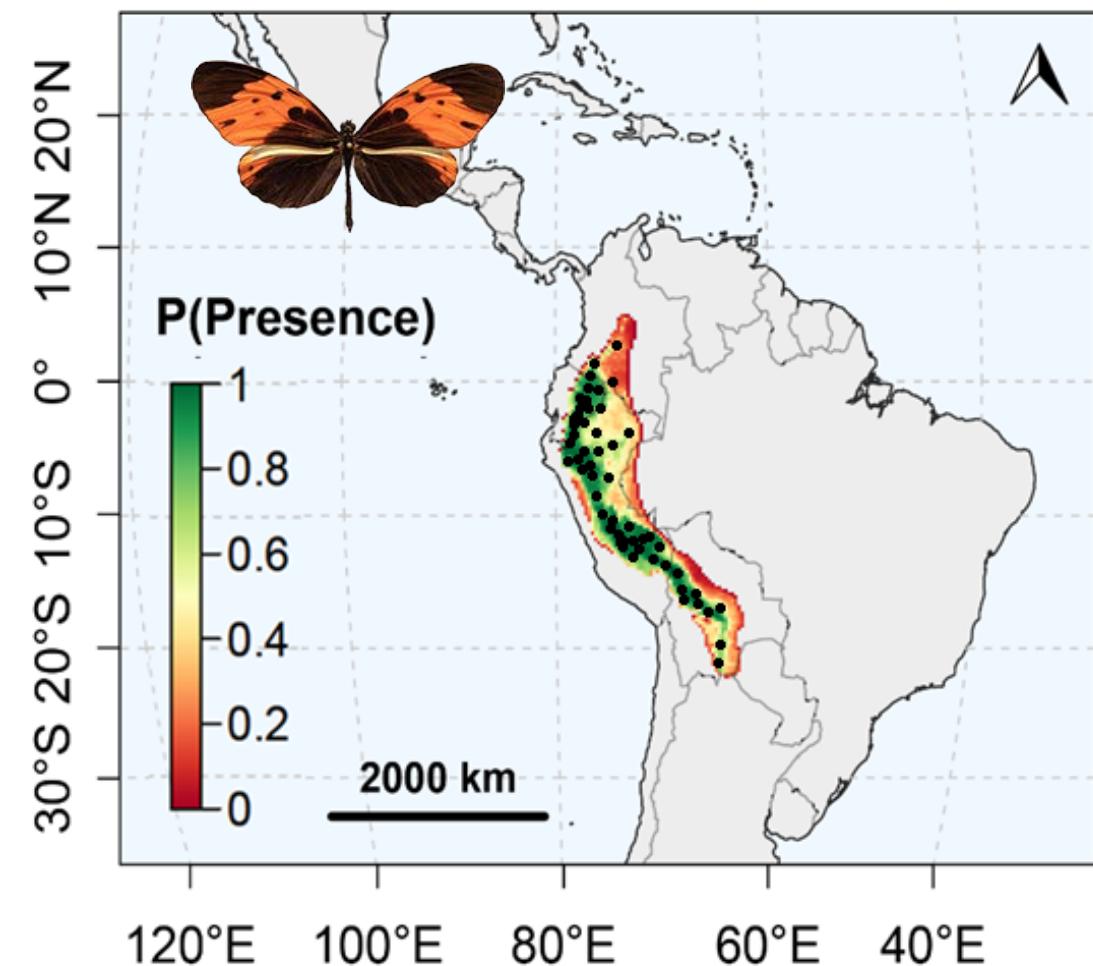


Spatial congruence

Ithomiini: pattern MOTHONE
(14 species)

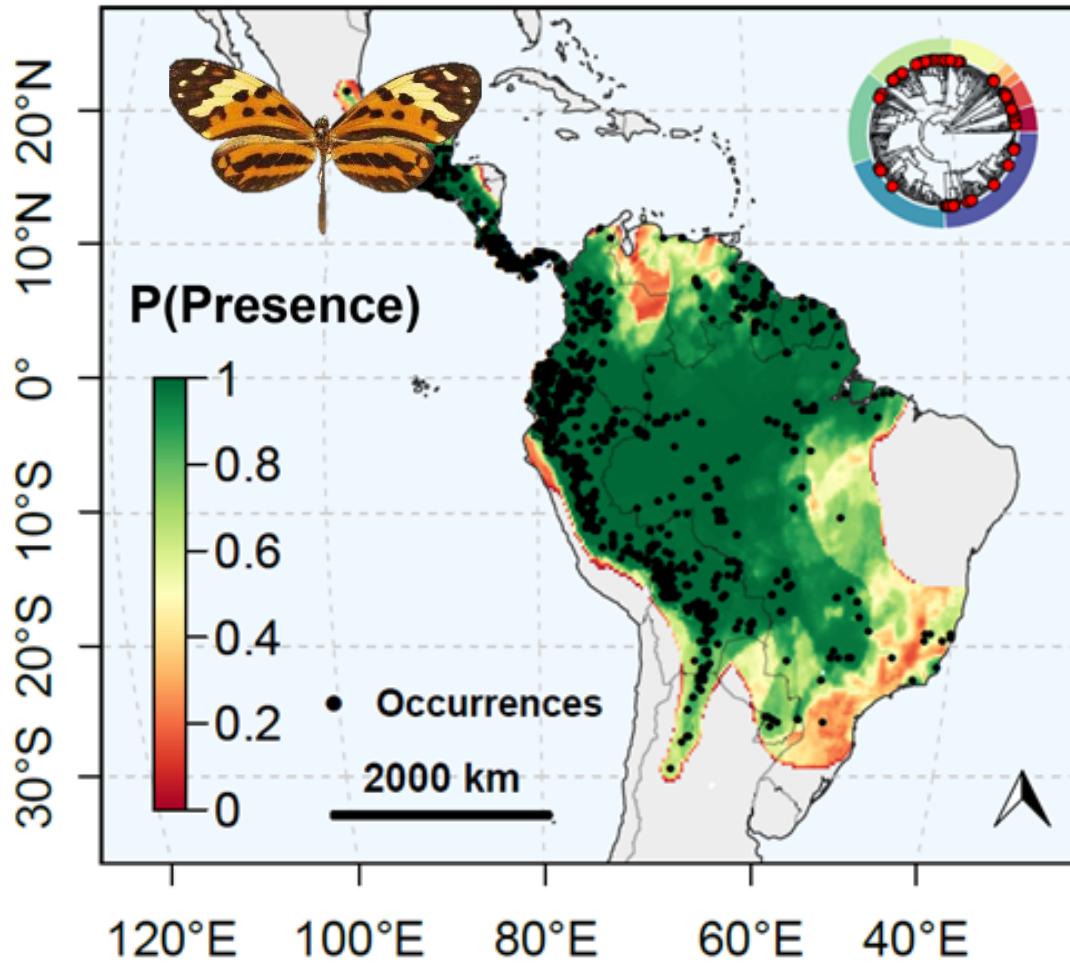


Heliconiini: pattern MOTHONE
(3 species)

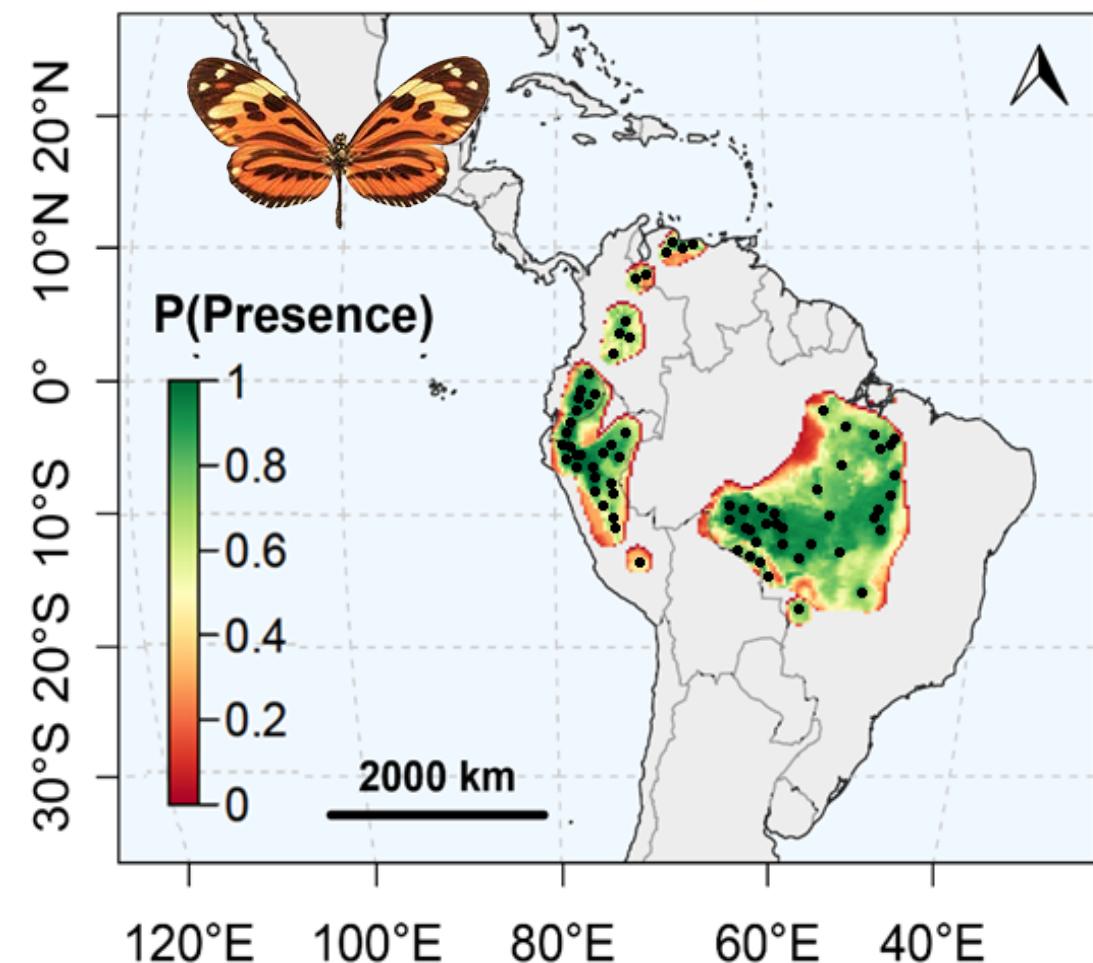


Spatial congruence

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**?



Biodiversity patterns: Are large-scale **biodiversity patterns** different between tribes?



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



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



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?

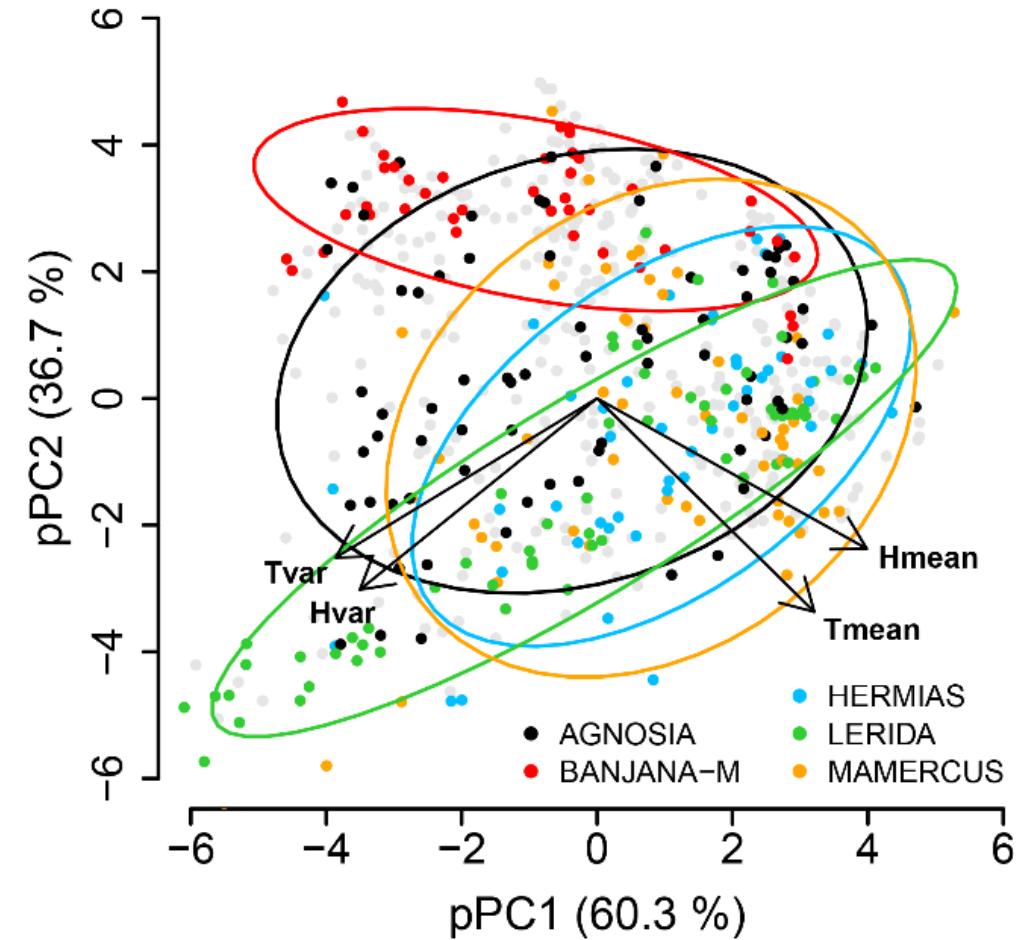
Global: perMANOVA, $R^2 = 0.41$, $p = 0.001$



Per phenotypic group:

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

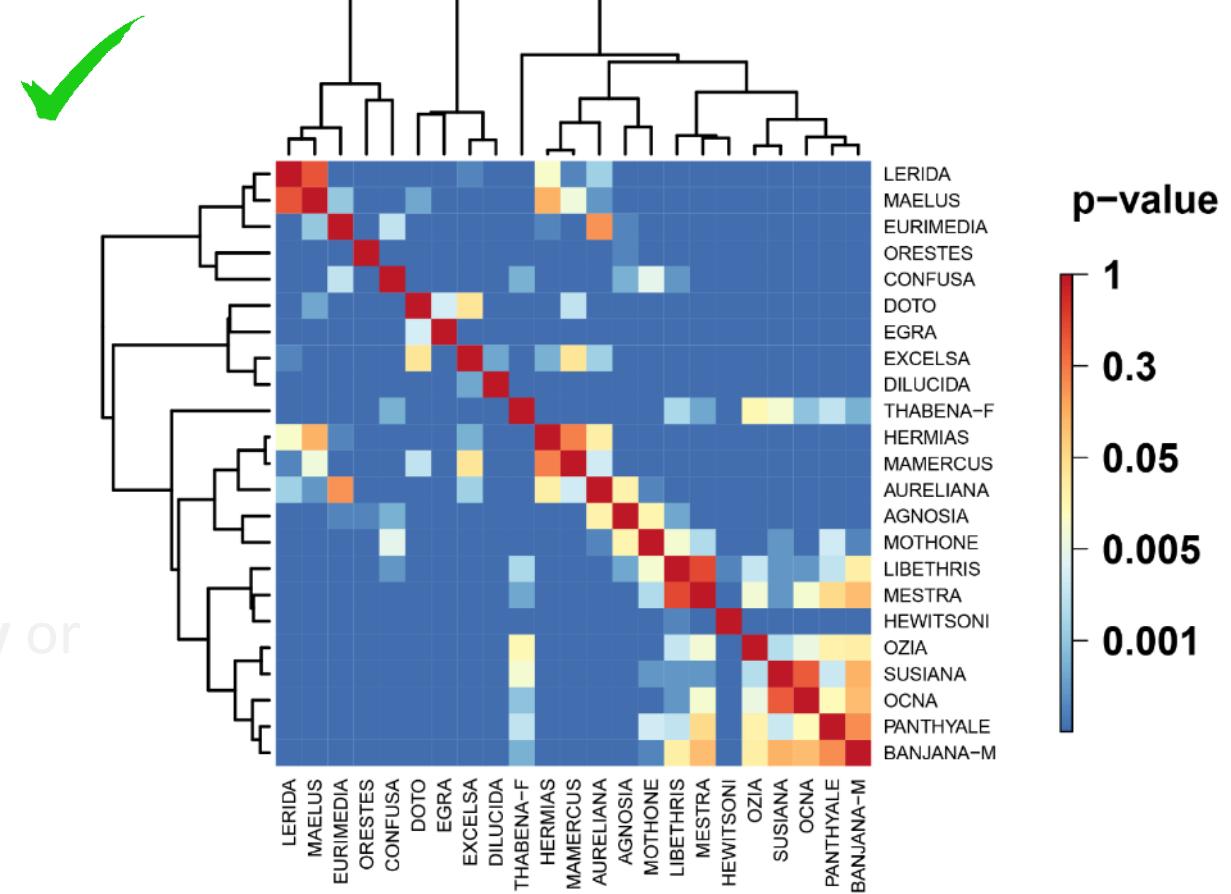
Next: Is this pattern due to shared ancestry or evolutionary convergence?



Climatic niche similarity

Question: Do phenotypic groups occupy different climatic niche?

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



Per phenotypic group:

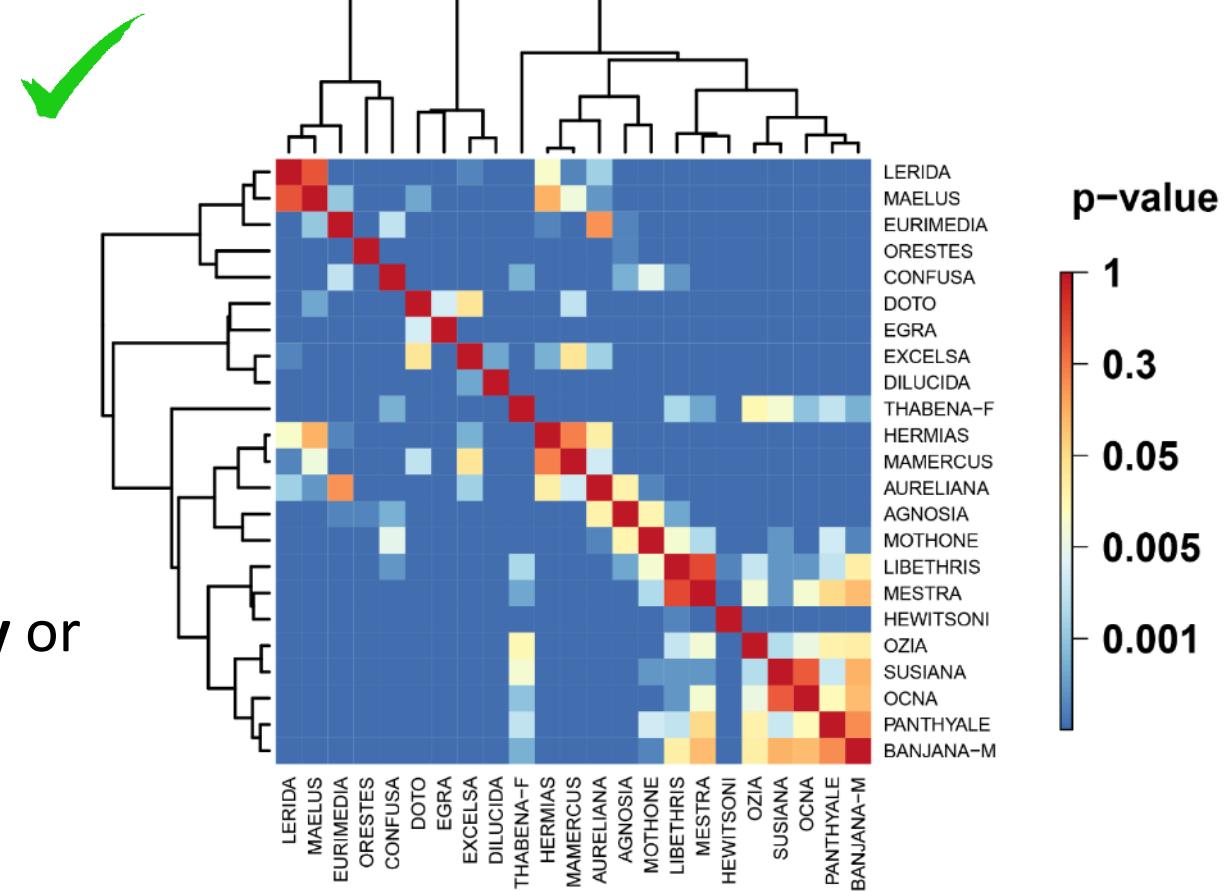
- 81.0% pairs with $p < 0.05$
- 66.4% pairs with $p < 0.001$

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

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?

Objectives

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



1

Biodiversity patterns: Are large-scale **biodiversity patterns** different between tribes?



2

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



3

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



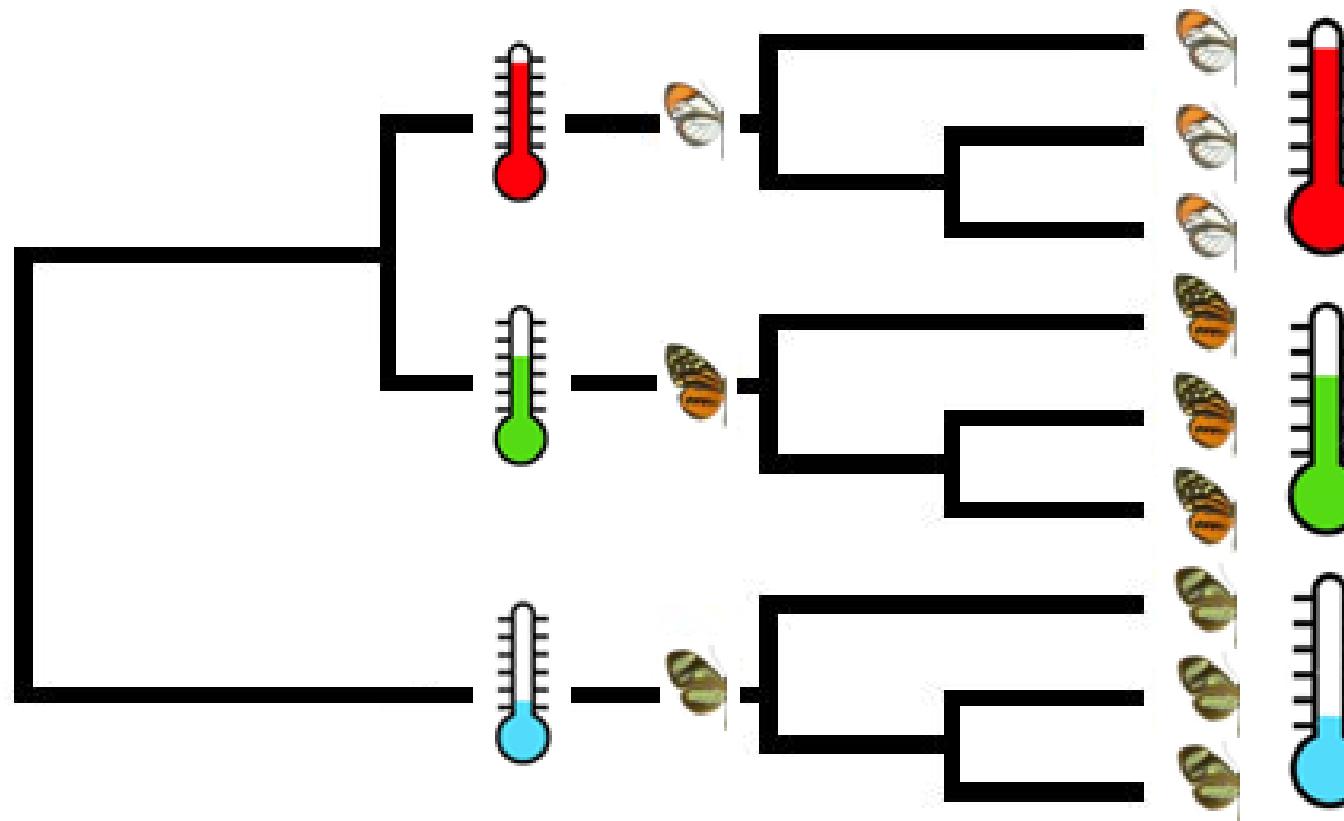
4

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



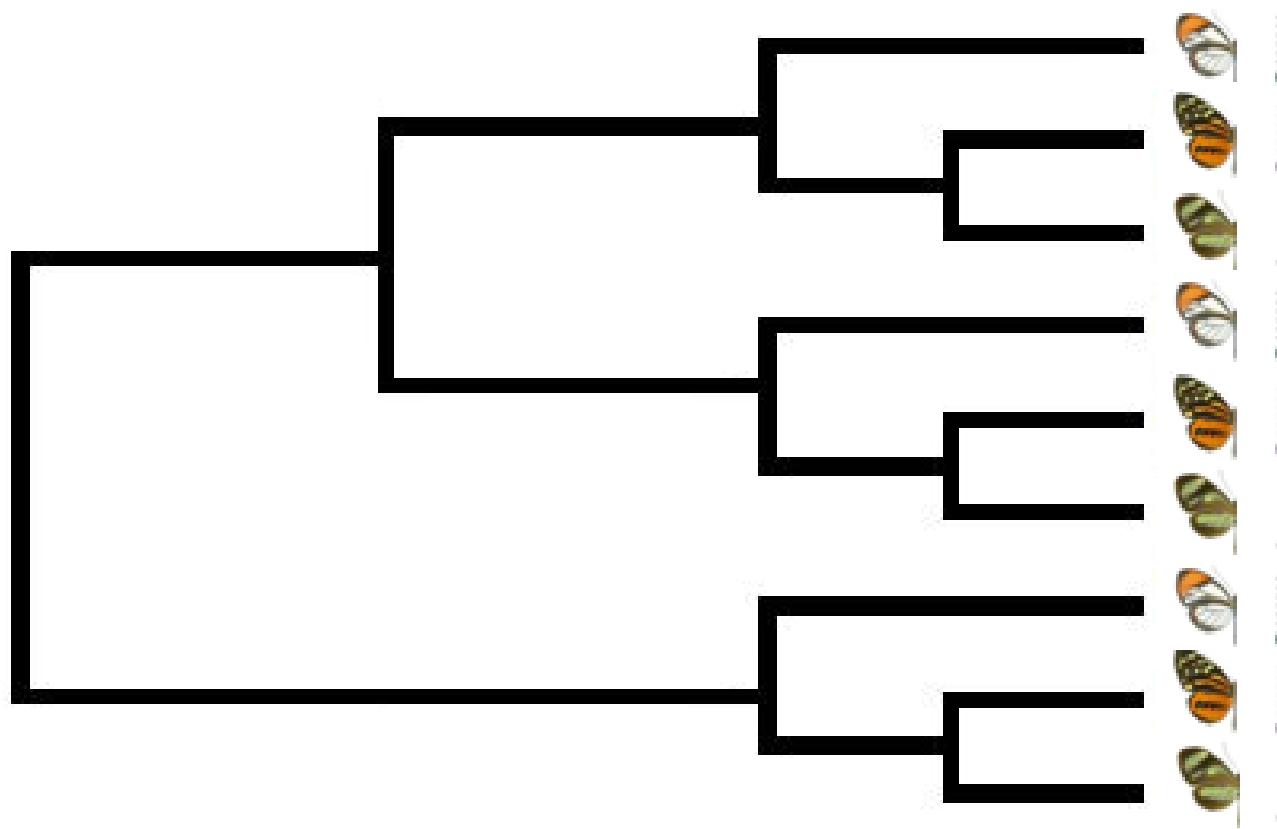
Climatic niche evolution

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



Climatic niche evolution

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



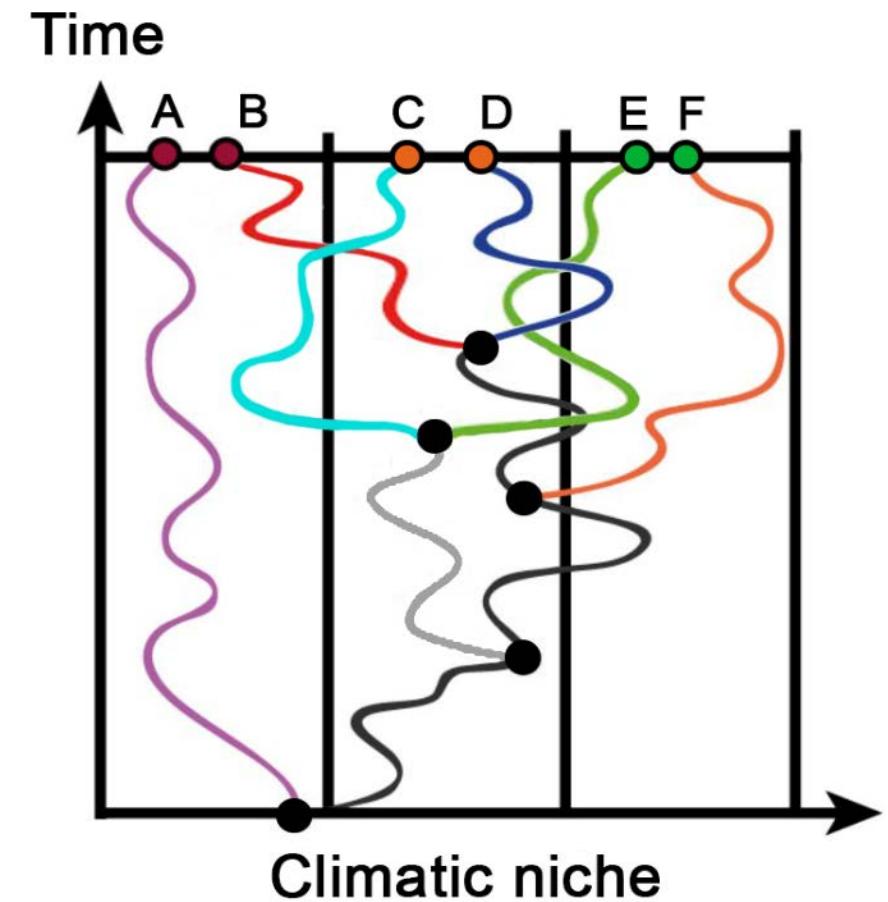
Climatic niche evolution

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

Results: Evolutionary association between climatic niche and color patterns



Climatic niche evolution

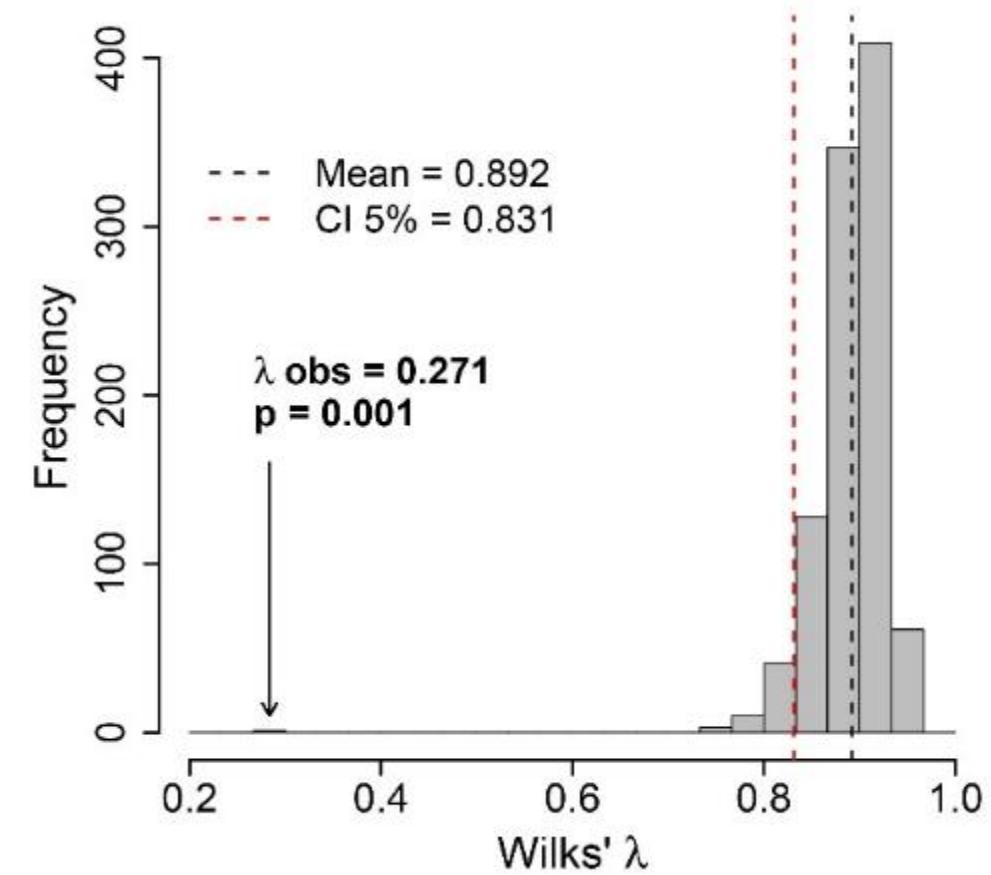
Question: Is the **climatic niche** of phenotypically similar species more similar than expected from the **phylogeny**?

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

phyloMANOVA: $\lambda_{\text{obs}} \ll \lambda_{\text{simul}}$



Results: Evolutionary association between climatic niche and color patterns



Climatic niche evolution

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

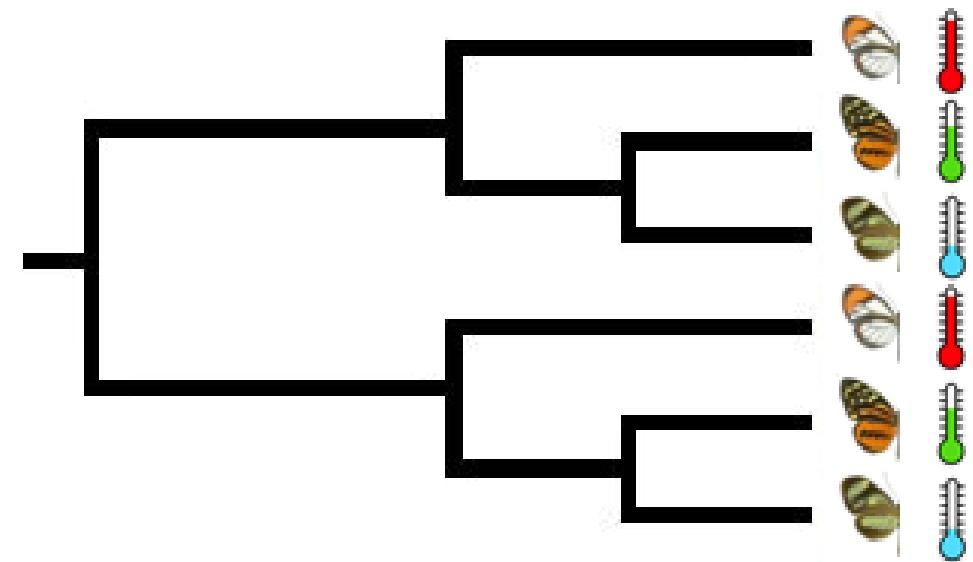
Simulate the evolution of climatic niche under
multivariate **neutral evolutionary model**

phyloMANOVA: $\lambda_{\text{obs}} \ll \lambda_{\text{simul}}$



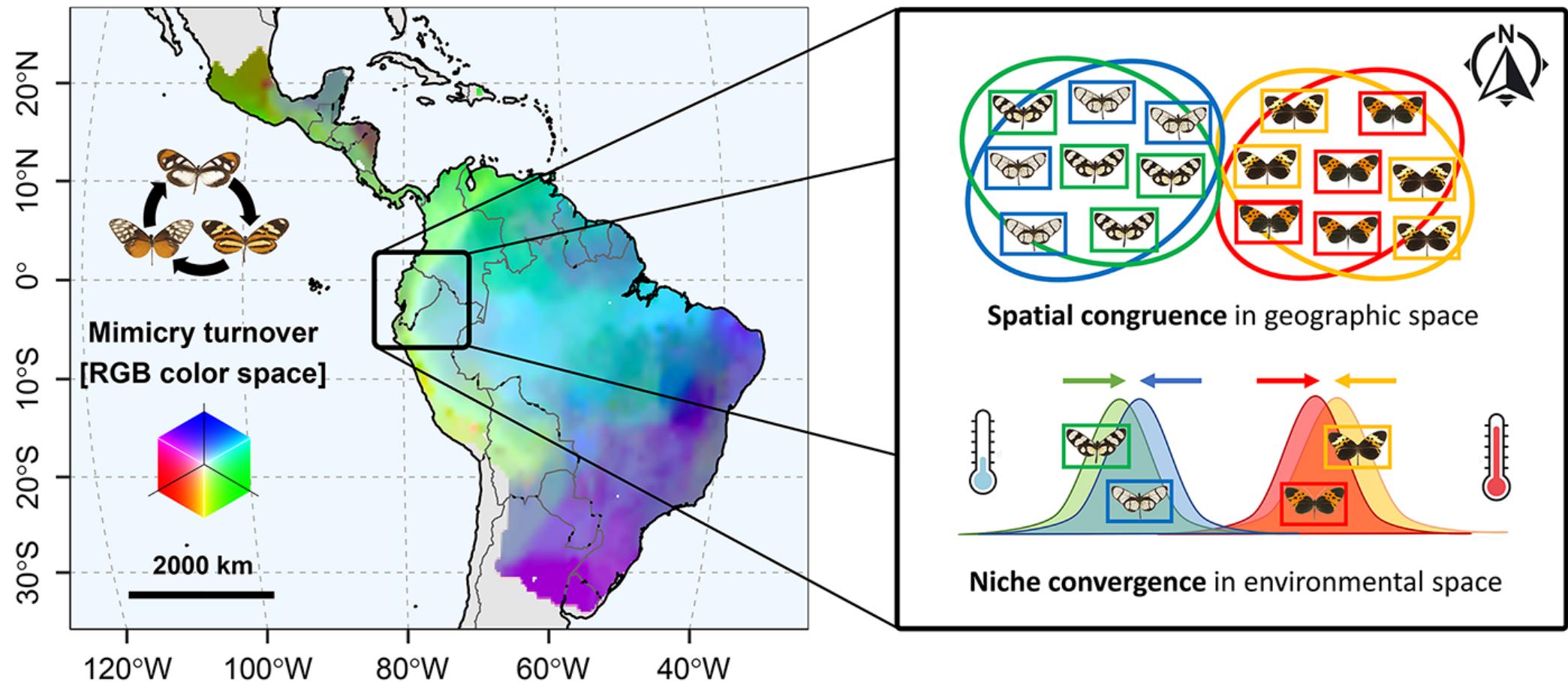
Results: **Evolutionary convergence** between
climatic niche and **color patterns**

Evolutionary convergence



Conclusion

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



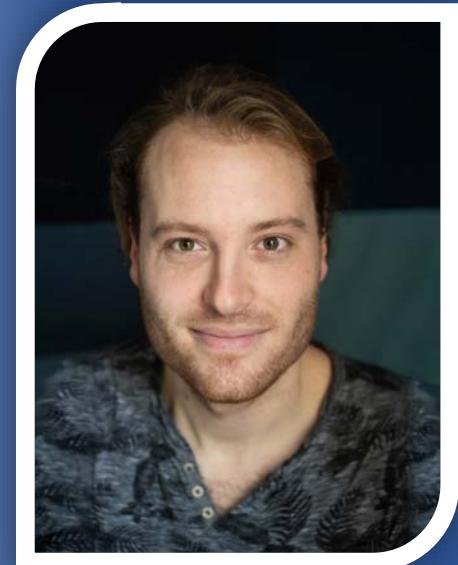
Research team

Advisors: Marianne Elias (ISYEB) & Colin Fontaine (CESCO)

Funding: PhD Grant (French MESR) & Marianne Elias (HFSP Grant)

Main collaborators:

- Eddie Pérochon, Université de Lausanne, Switzerland
- Keith Willmott, Florida University, USA
- Andre Freitas, Campinas State University, Brazil
- Nicolas Chazot, SUAS, Sweden
- Sébastien Lavergne, LECA, France
- Neil Rosser, Harvard University, USA
- Krzysztof Kozak, STRI, Panama



SCAN ME



Thanks for your
attention

References

- Beccaloni, G.W. (1997). Vertical stratification of ithomiine butterfly (Nymphalidae: Ithomiinae) mimicry complexes: The relationship between adult flight height and larval host-plant height. *Biol. J. Linn. Soc.*, 62, 313–341.
- Birskis-Barros, I., Freitas, A. V., & Guimarães Jr, P. R. (2021). Habitat generalist species constrain the diversity of mimicry rings in heterogeneous habitats. *Scientific Reports*, 11(1), 5072.
- Chazot, N., Willmott, K.R., Santacruz Endara, P.G., Toporov, A., Hill, R.I., Jiggins, C.D., et al. (2014). Mutualistic Mimicry and Filtering by Altitude Shape the Structure of Andean Butterfly Communities. *Am. Nat.*, 183, 26–39.
- Doré, M., Willmott, K., Leroy, B., Chazot, N., Mallet, J., Freitas, A.V.L., et al. (2022). Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. *Divers. Distrib.*, 28, 2912–2930.
- Elias, M., Gompert, Z., Jiggins, C. & Willmott, K. (2008). Mutualistic interactions drive ecological niche convergence in a diverse butterfly community. *PLoS Biol.*, 6.
- Müller, F. (1879). Ituna and Thyridia; a remarkable case of mimicry in butterflies. *Trans. Entomol. Soc. Lond.*, xx–xxix.
- Pérochon, E., Rosser, N., Kozak, K. M., Willmott, K., Elias, M. & Doré M. Müllerian mimicry as a driver for congruence of geographic distribution drivers in two distant Neotropical butterfly tribes. *in prep.*
- Willmott, K.R. & Mallet, J. (2004). Correlations between adult mimicry and larval host plants in ithomiine butterflies. *Proc. R. Soc. B Biol. Sci.*, 271, S266–S269.