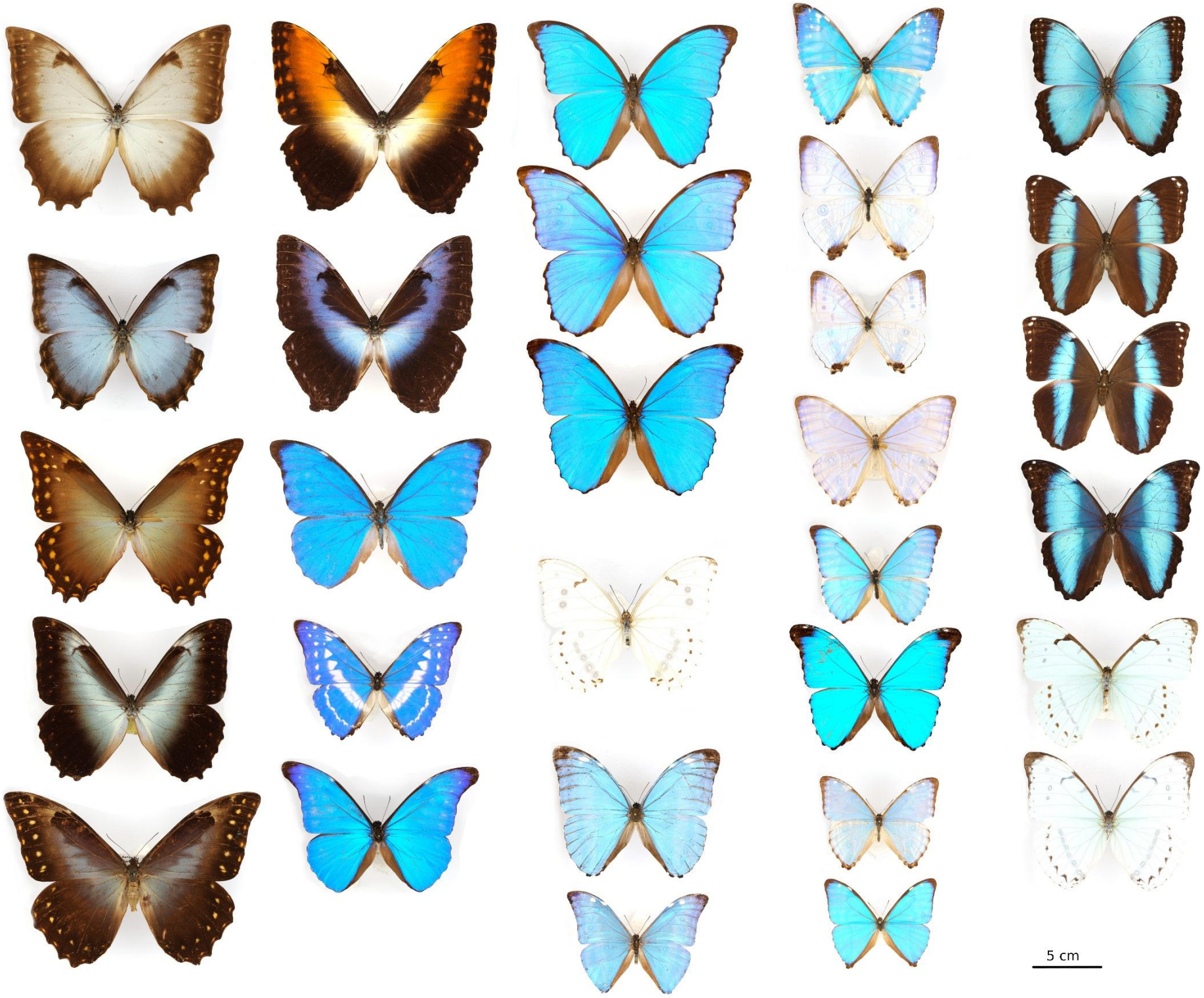
Morphometrics:

Evolution of wing shape and colour in *Morpho* butterflies

Vincent Debat

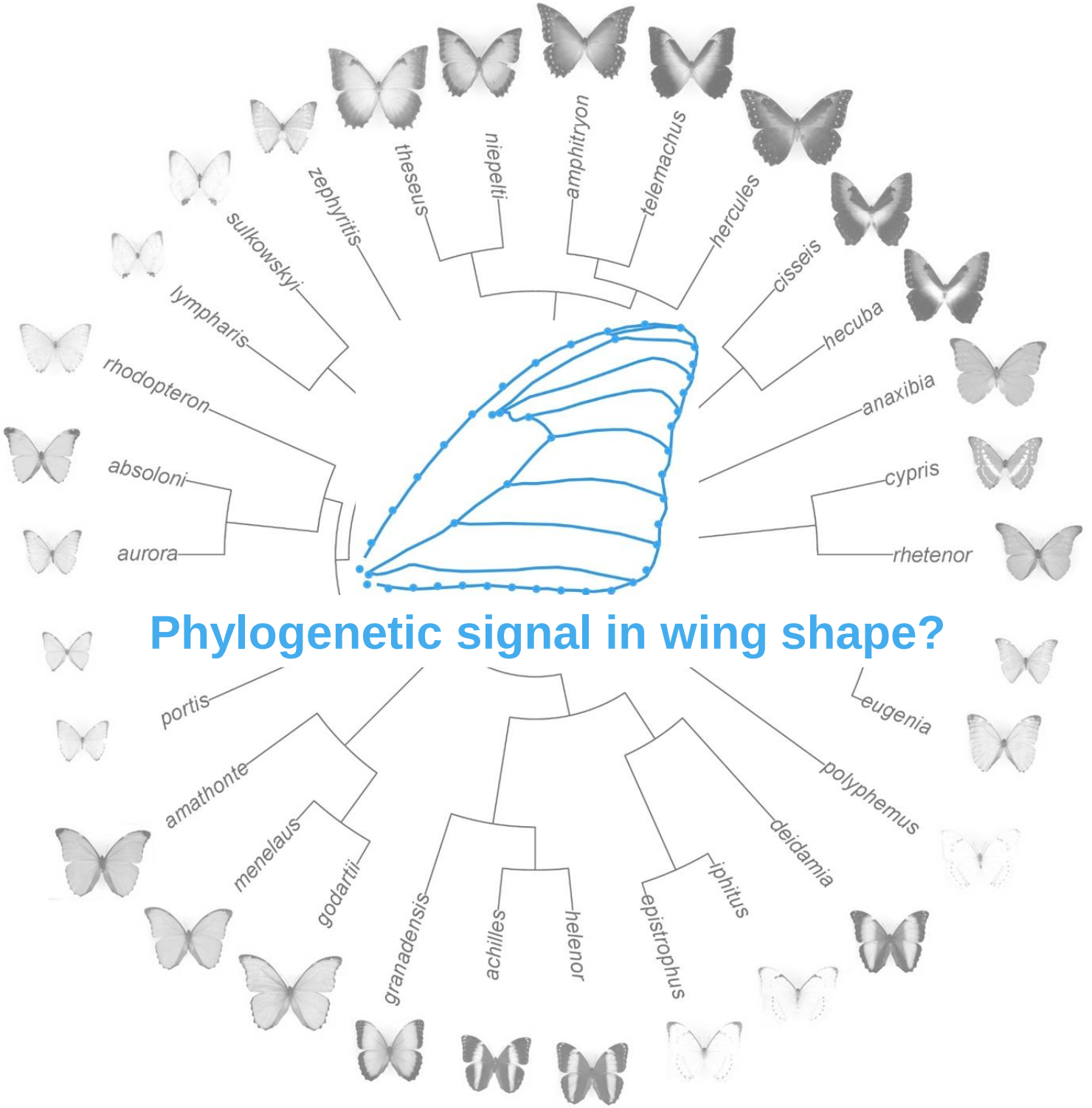
ISYEB, Muséum National d'Histoire Naturelle


5 cm

1. Evolution of wing shape

Chazot *et al. Evolution* 2016
Chazot *et al. J. Evol. Biol.* in revision


theseus
niepelti
amphitryon
telemachus
hercules
cisseis
hecuba
anaxibia
cypris
rhetenor
marcus
eugenia
polyphemus
deidamia
iphitus
epistrophus
helenor
achilles
granadensis
godartii
menelaus
amathonte
portis
aega
aurora
absoloni
rhodopteron
lympharis
sulkowskyi
zephyritis

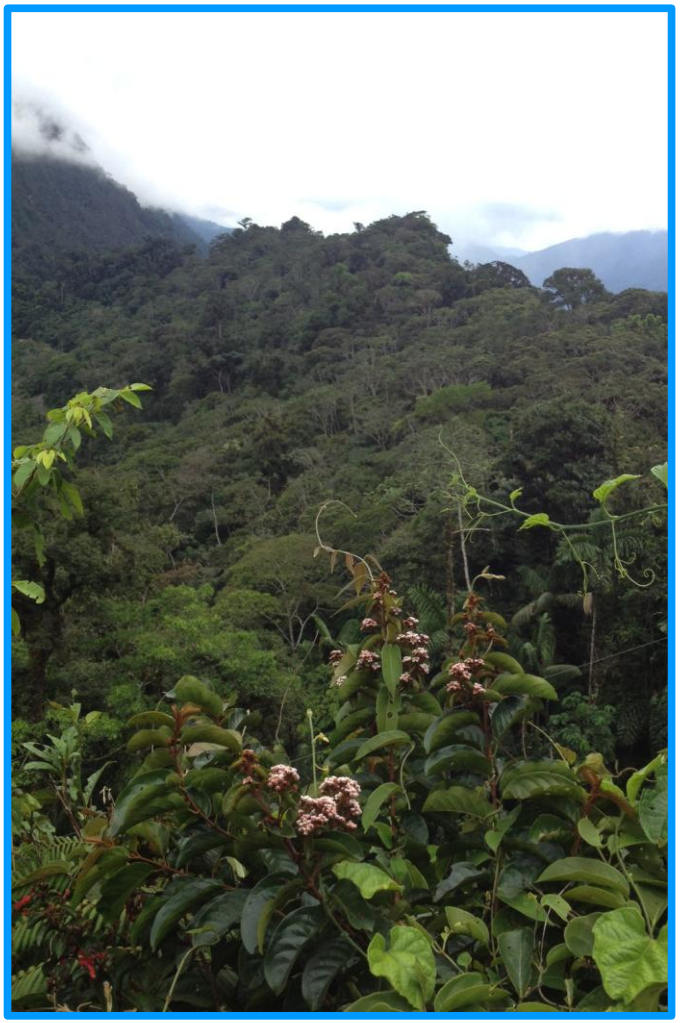


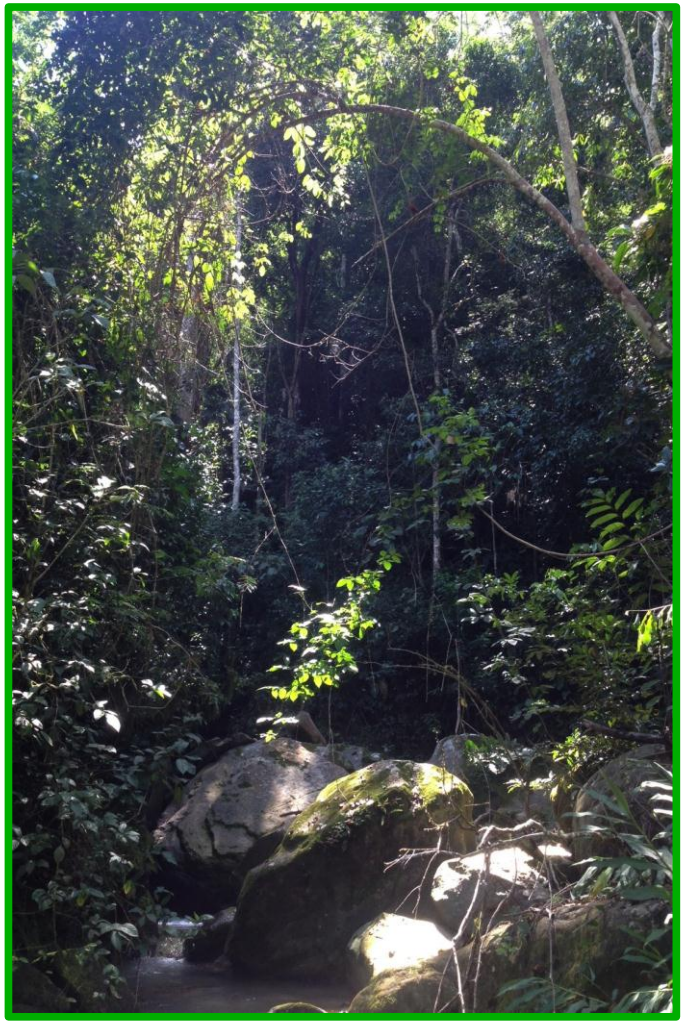
Phylogenetic signal in wing shape?

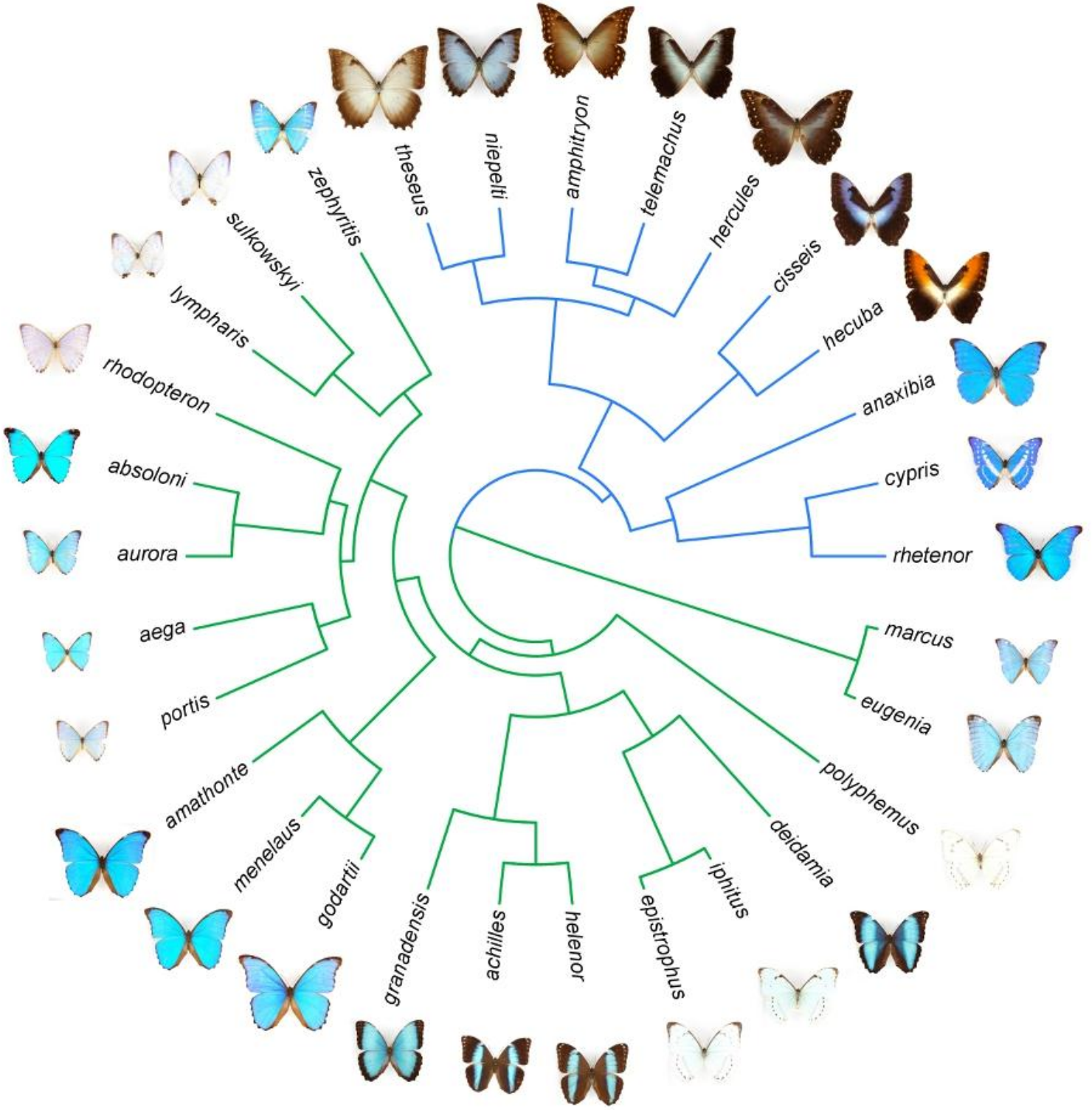
Ecological divergence across microhabitats?

Canopy

Understory

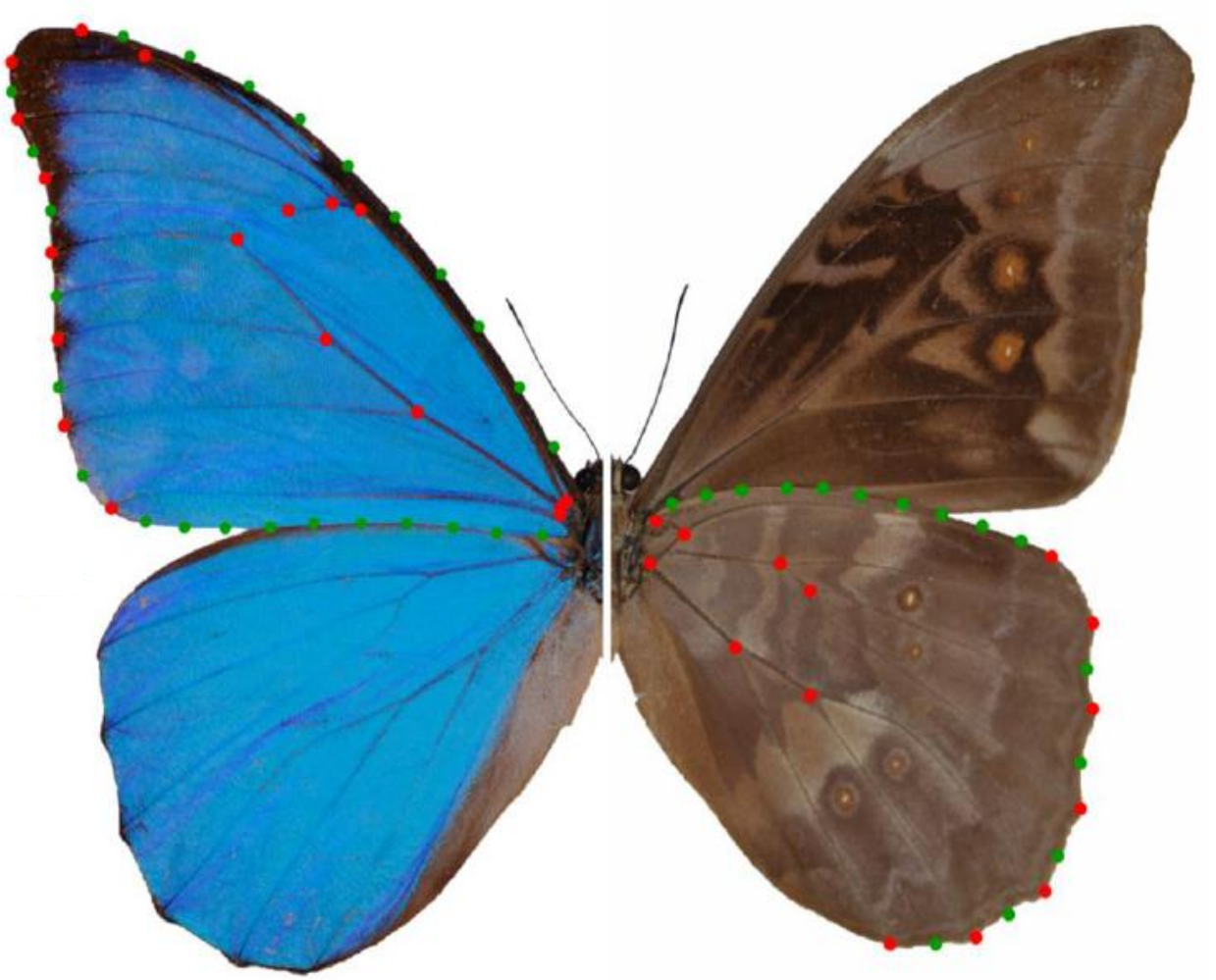





theseus
niepelti
amphitryon
telemachus
hercules
cisseis
hecuba
anaxibia
cypris
rhetenor
marcus
eugenia
polyphemus
deidamia
iphitus
epistrophus
helenor
achilles
granadensis
godartii
menelaus
amathonte
portis
aega
aurora
absoloni
rhodopteron
lympharis
sulkowskyi
zephyritis

Morphometric analysis

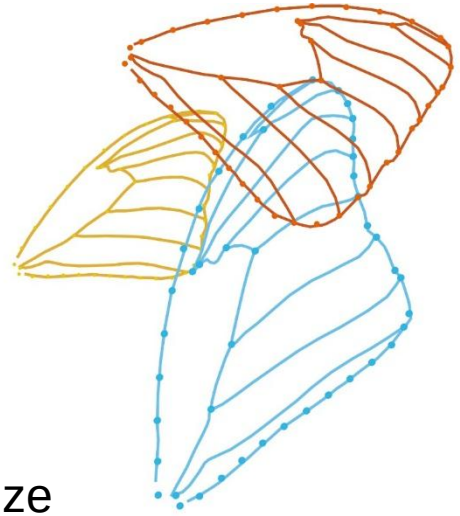
- All 30 species of the genus Morpho
- 911 collection specimens (♂♀), fore- and hind- wings
  - ● Landmarks on veins, ● semi-landmarks on the outline



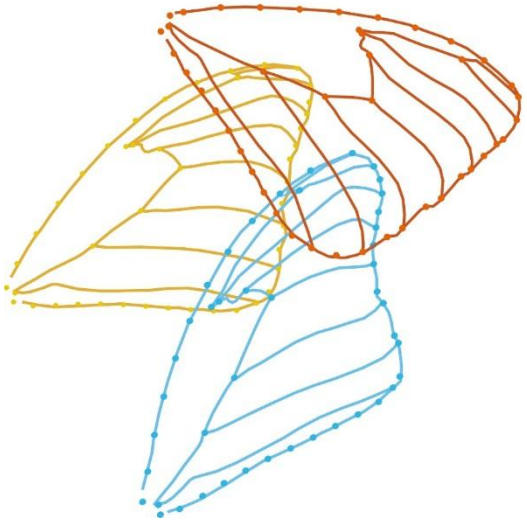
Morphometric analysis

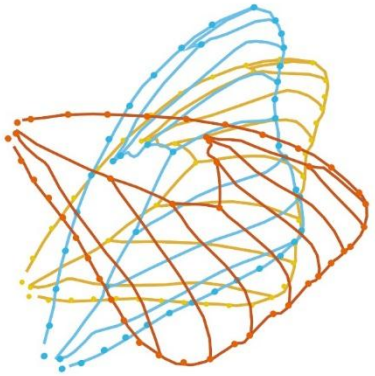
Procrustes superimposition

Raw configurations

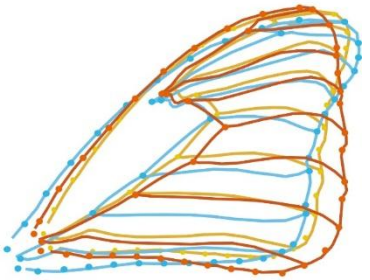


Scaling to unit centroid size



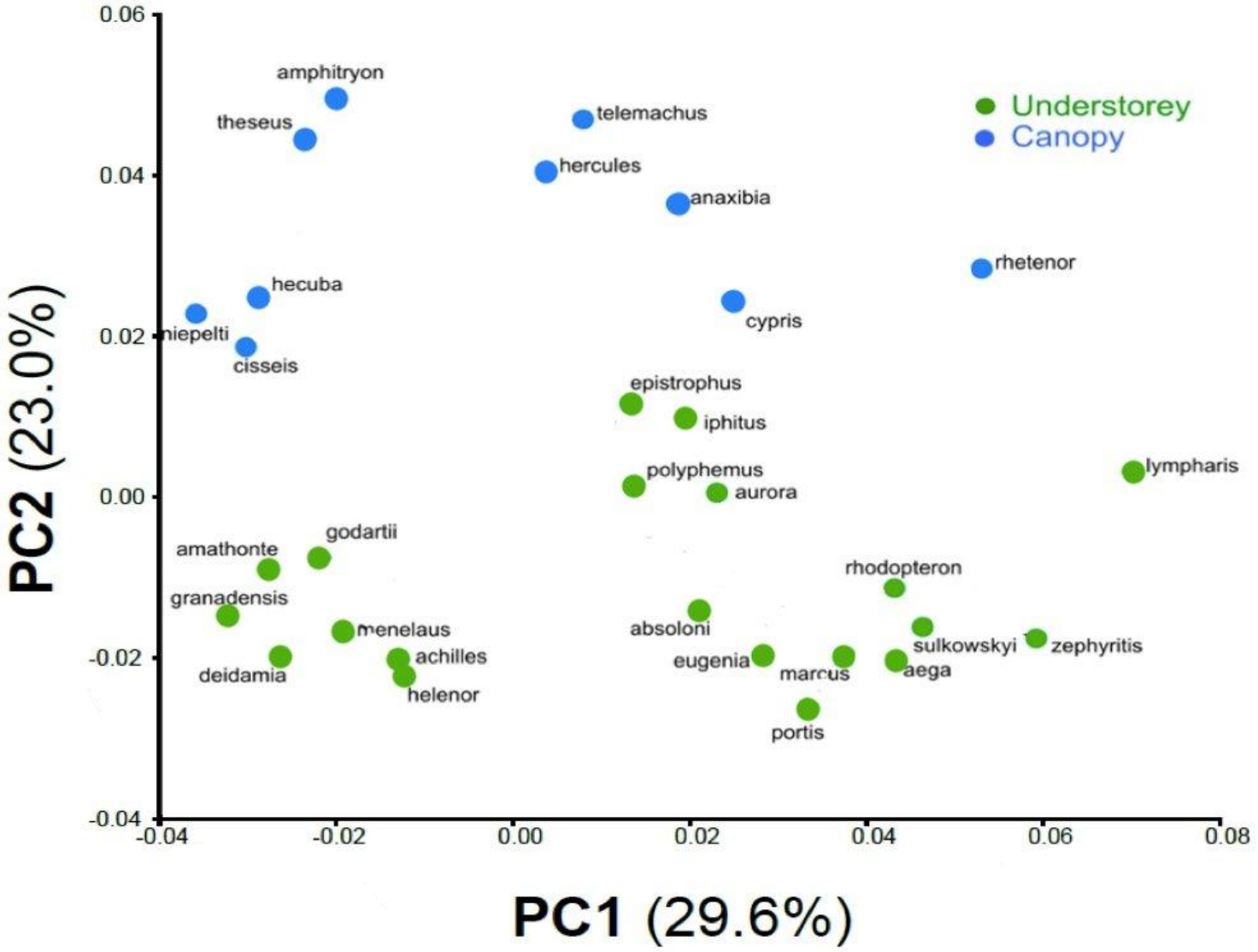


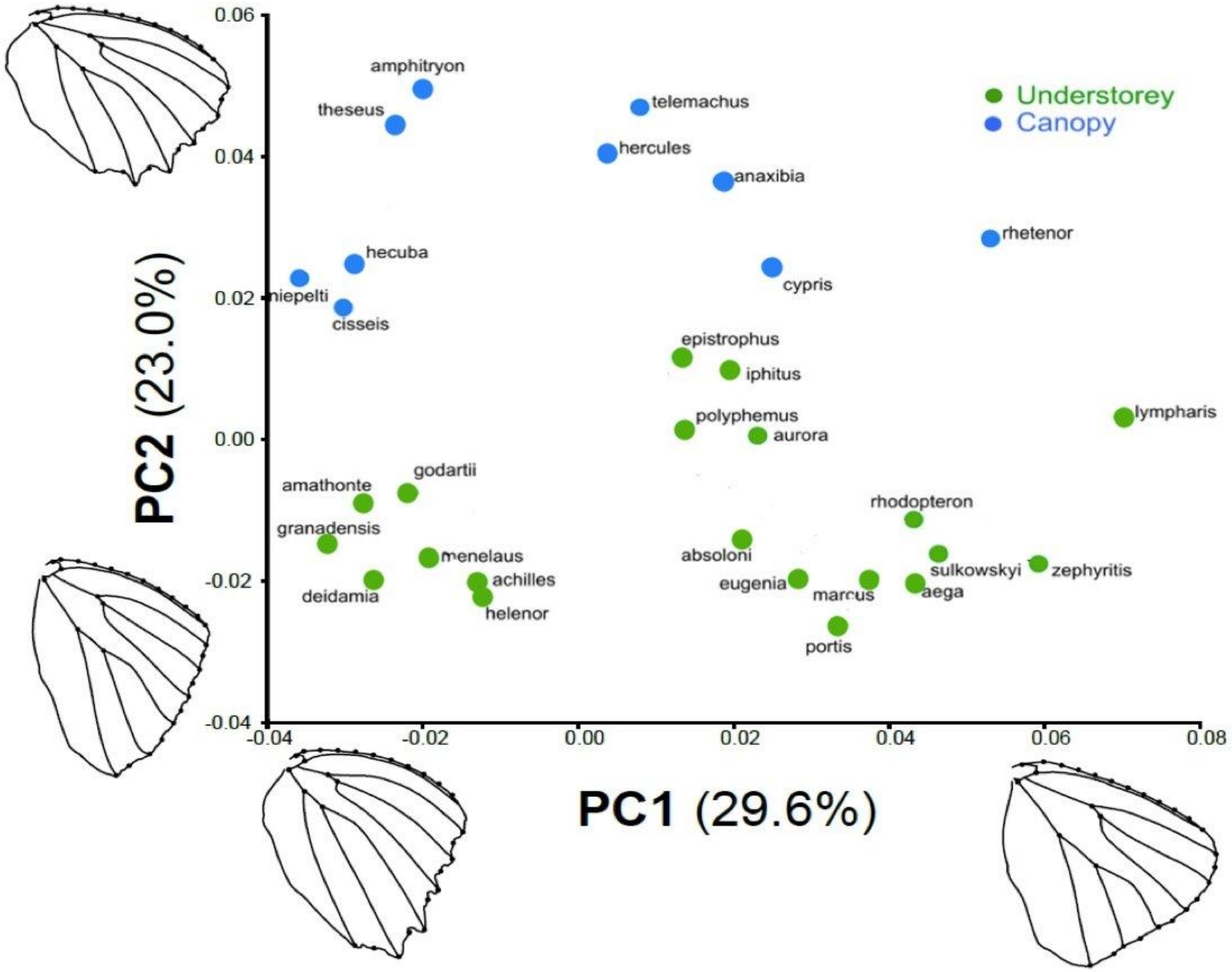
Translation



Rotation

Shape data for multivariate analyses (e.g. PCA)


Understorey
Canopy
amphitryon
theseus
telemachus
hercules
anaxibia
rhetenor
hecuba
cypris
niepelti
cisseis
epistrophus
iphitus
lympharis
polyphemus
aurora
godartii
amathonte
rhodopteron
granadensis
absoloni
menelaus
sulkowskyi
zephyritis
achilles
eugenia
marcus
aega
deidamia
helenor
portis
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08
PC2 (23.0%)
PC1 (29.6%)


Understorey
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polyphemus
aurora
lympharis
godartii
amathonte
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menelaus
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deidamia
helenor
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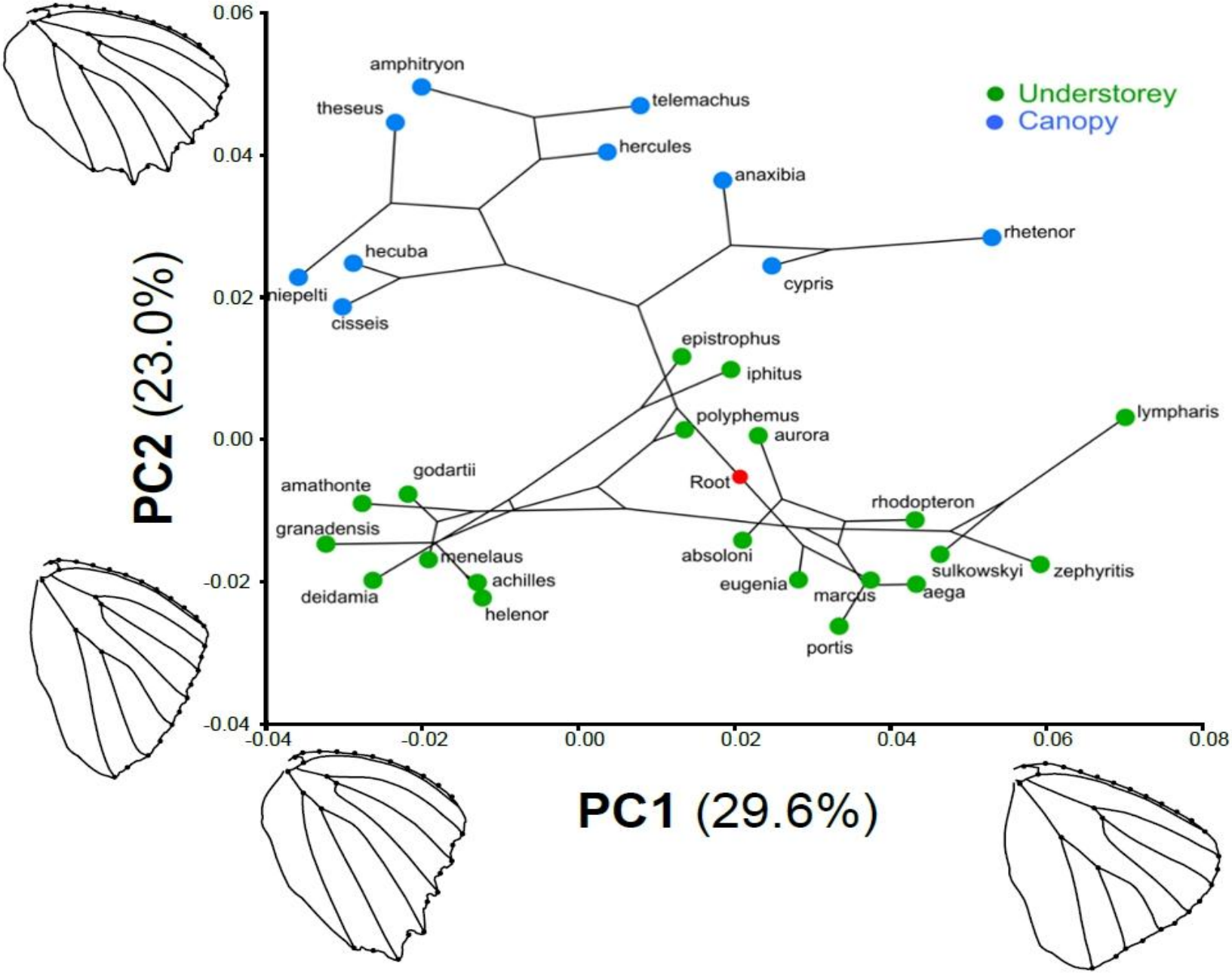
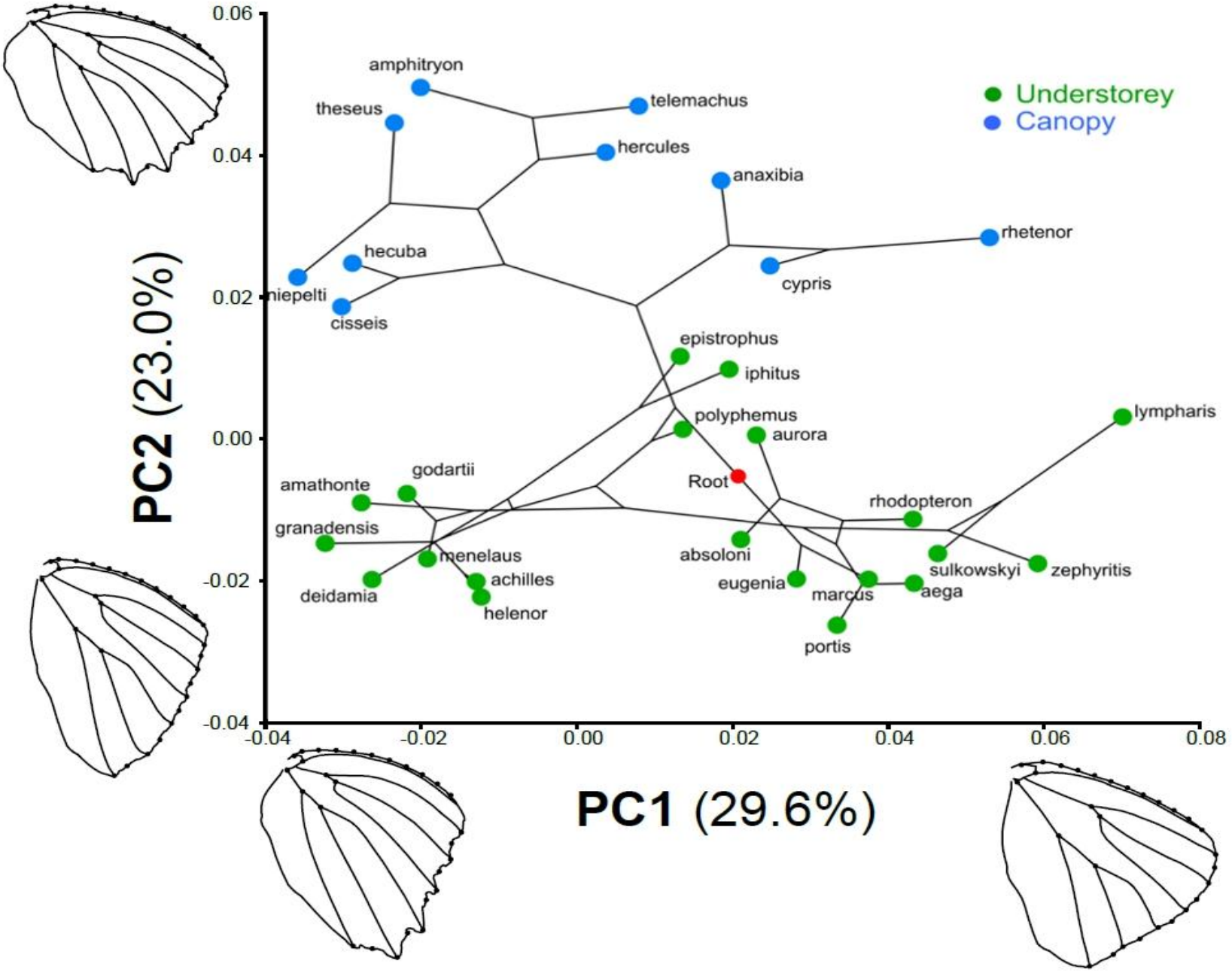
PC2 (23.0%)
PC1 (29.6%)
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08

Strong phylogenetic signal



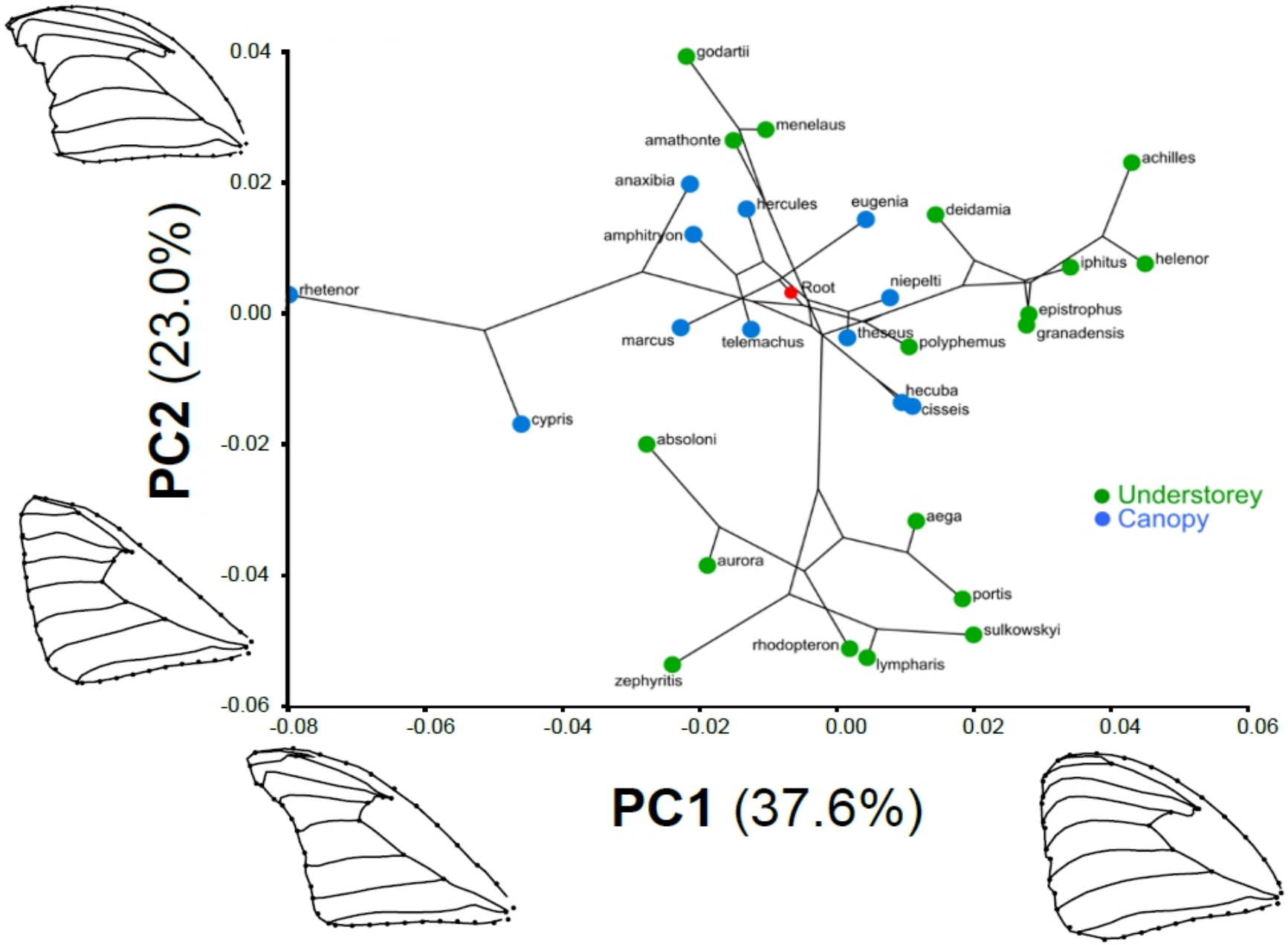
Strong phylogenetic signal

Divergence C/U > expected (PhyloMANOVA***)



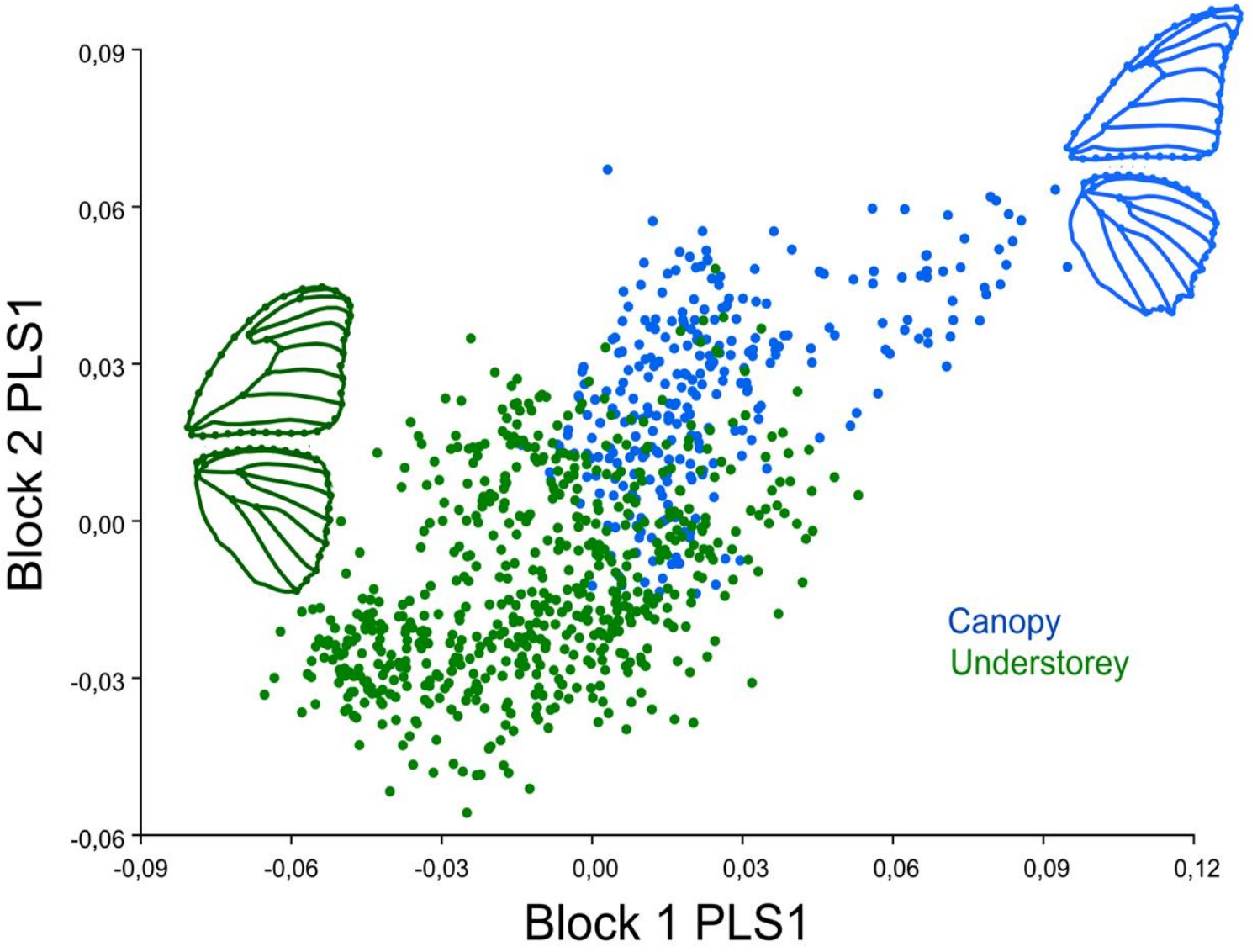
Strong phylogenetic signal

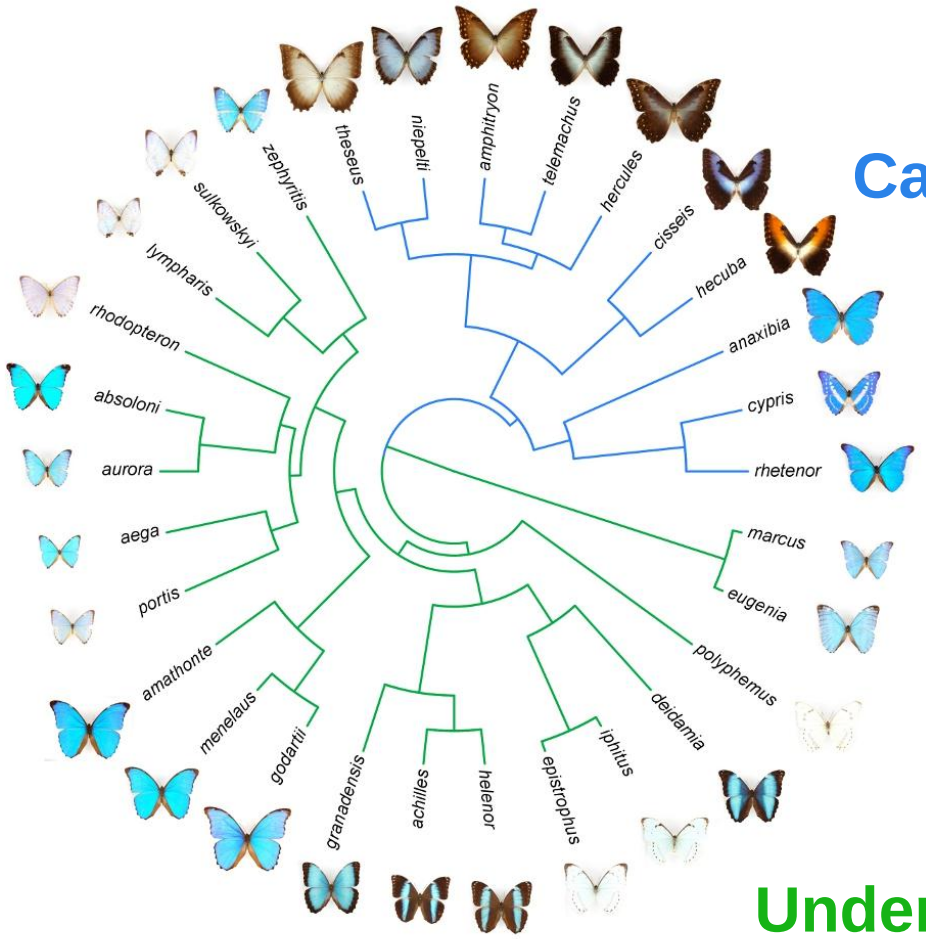
Divergence C/U > expected (PhyloMANOVA***)



Covariation Forewing/Hindwing:

Two-blocks partial least squares regression





Canopy

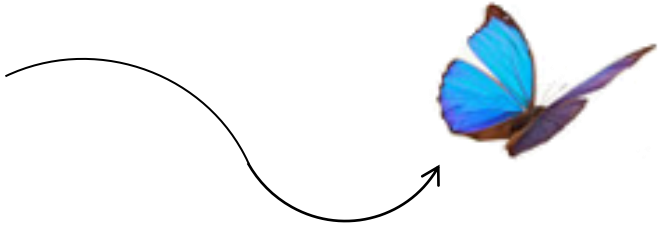
➡ **Efficient gliding flight?**

Understory

➡ **Manoeuvrable flapping flight?**

Evolution of flight behaviour and performance

Camille Le Roy PhD Project



Le Roy *et al J. Exp. Biol.* 2019
Le Roy et al. *Biol. Reviews* 2019
Le Roy et al. In prep

Field sampling, North East Peru

3 canopy species

M. rhetenor

M. theseus

M. cisseis

8 understory species

M. menelaus

M. godartii

M. deidamia

M. helenor

M. achilles

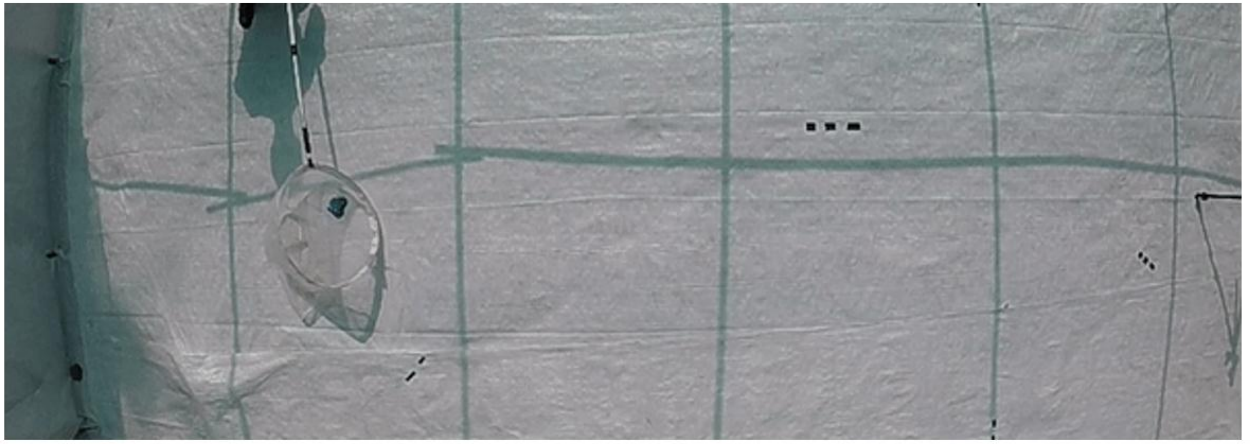
M. marcus

M. sulkowskyi

M. aurora

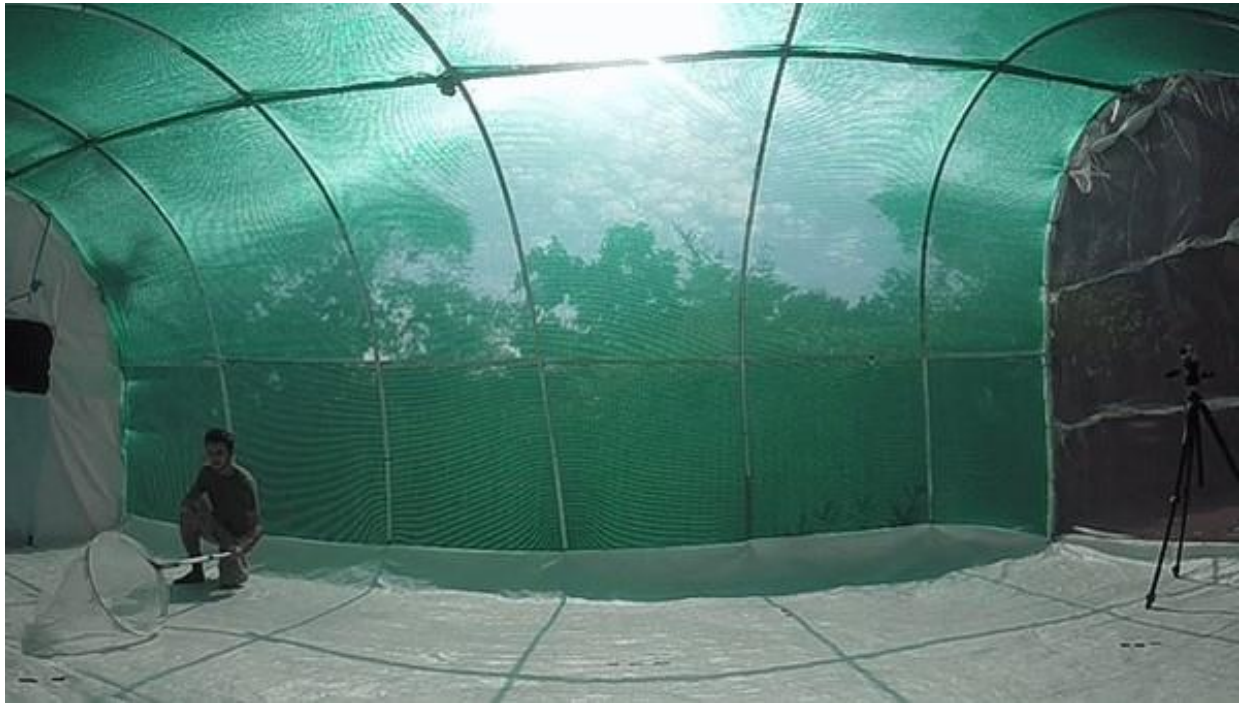
~ 10 individuals per species (males only)

Top view

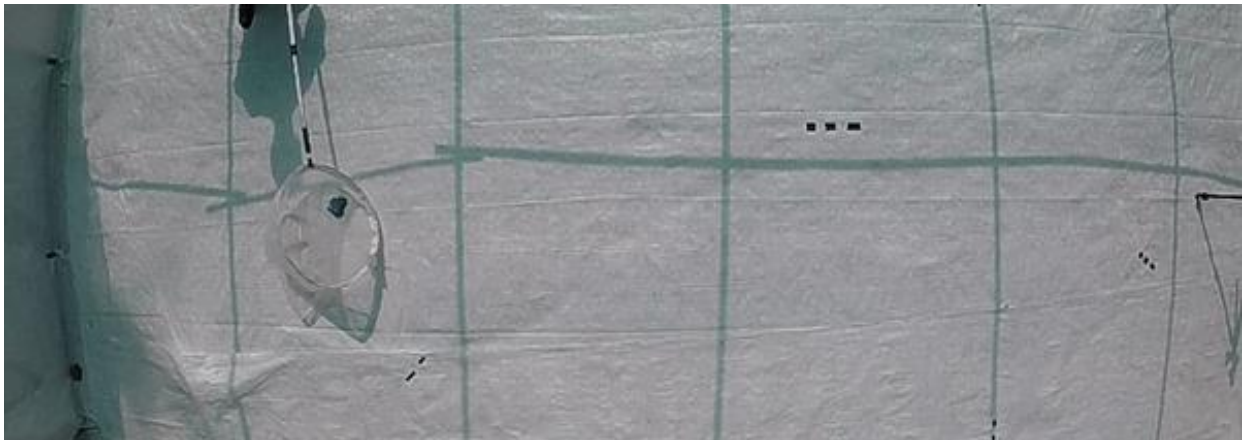


n = 241 flight sequences
(3 flights/individual)

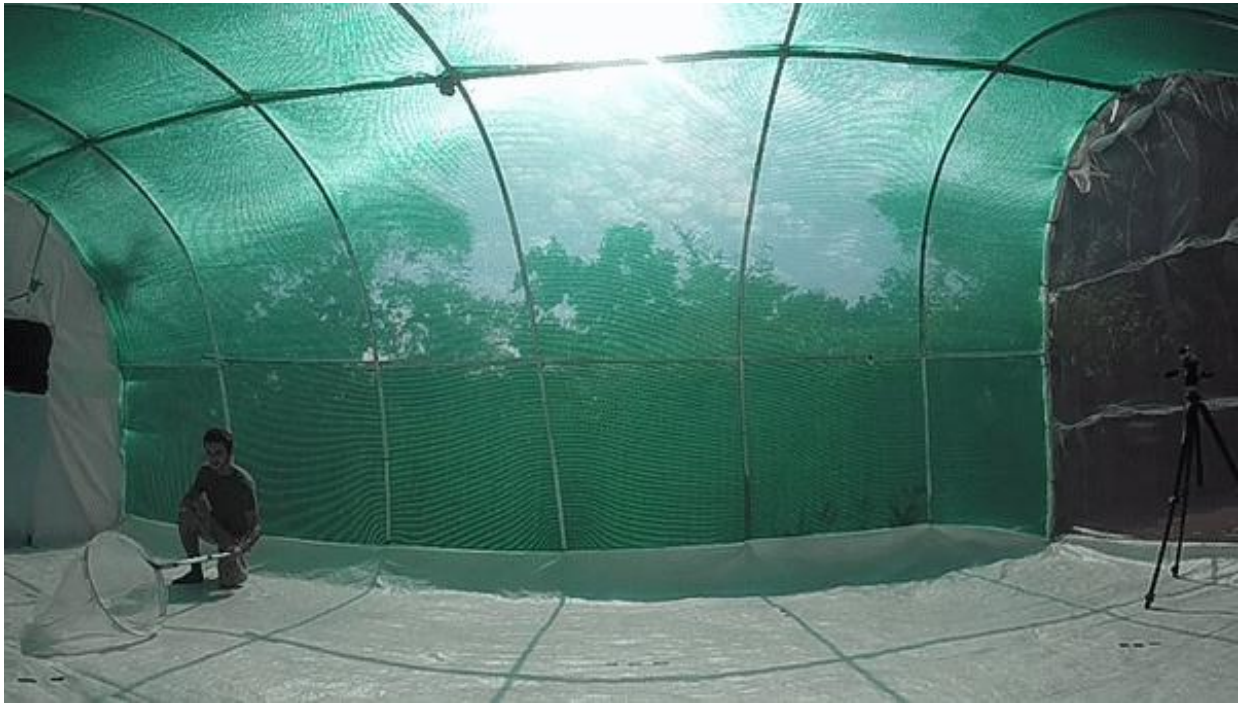
Side view



Top view



n = 241 flight sequences
(3 flights/individual)

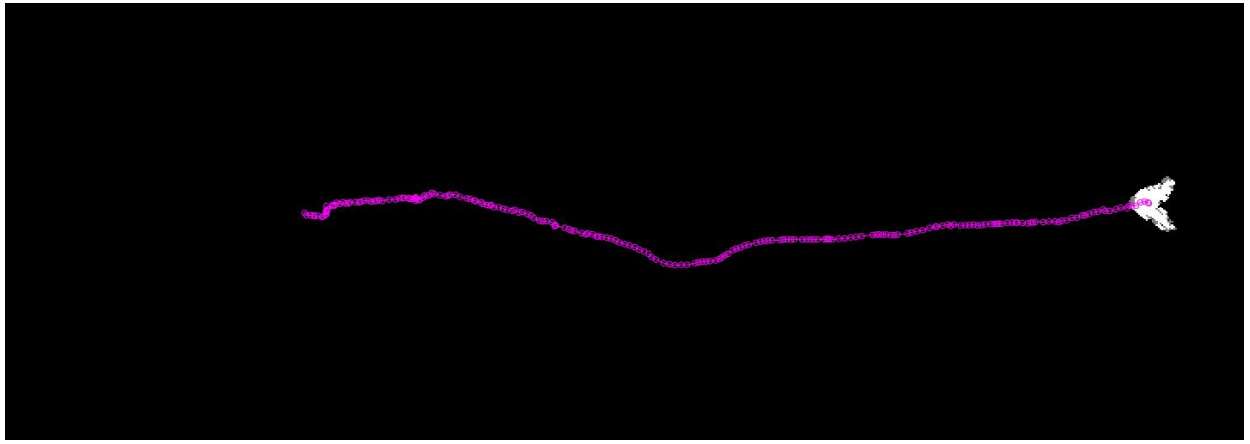


240 frames/s

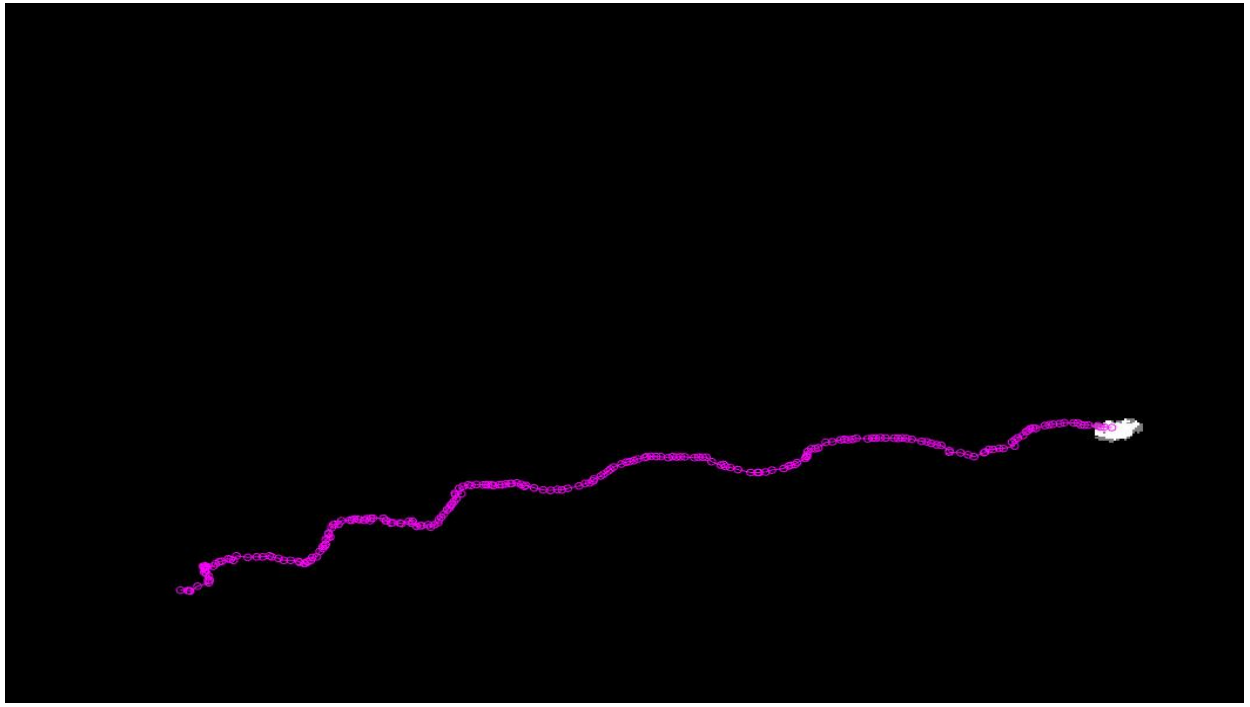
30% of actual speed

Side view

Top view



Side view

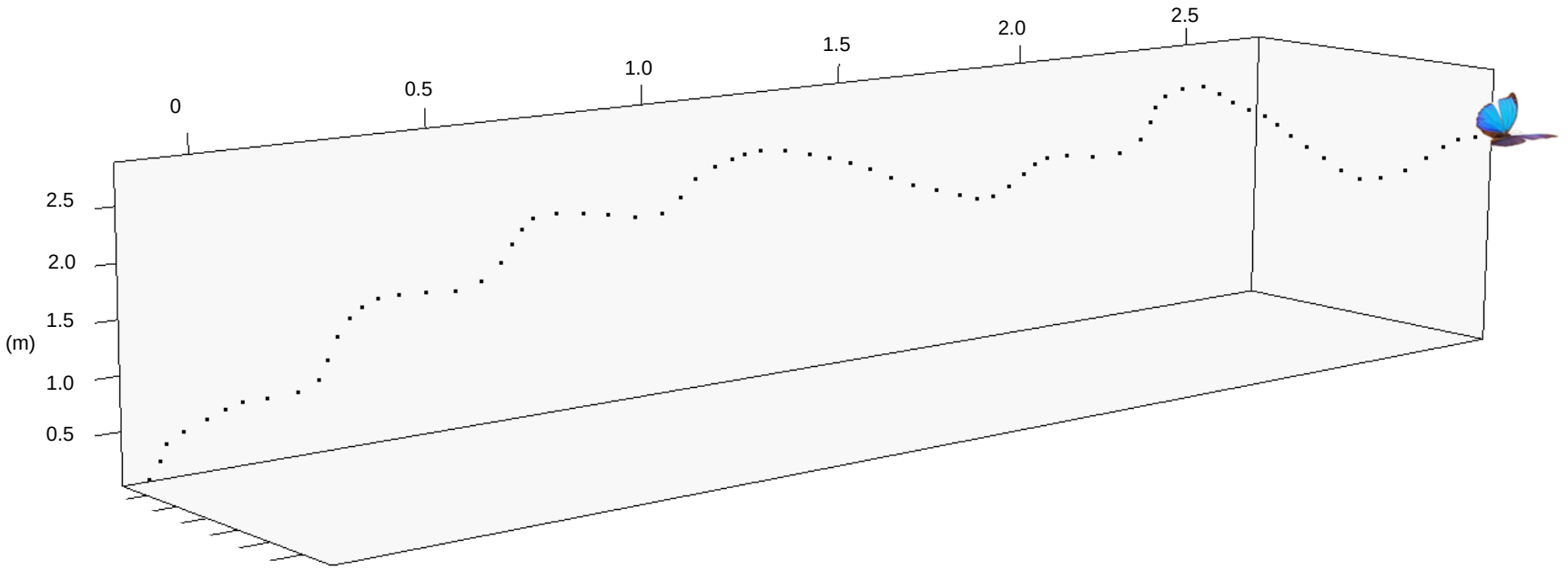


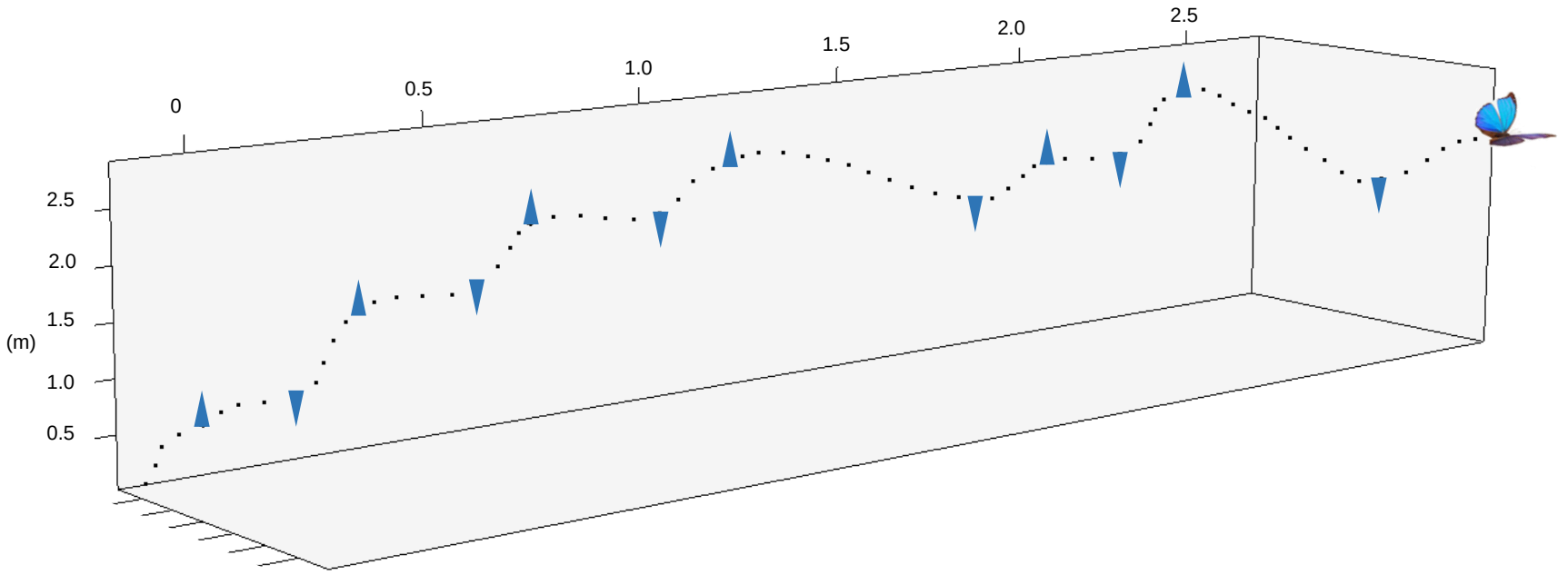
n = 241 flight sequences
(3 flights/individual)

Background subtraction

↓

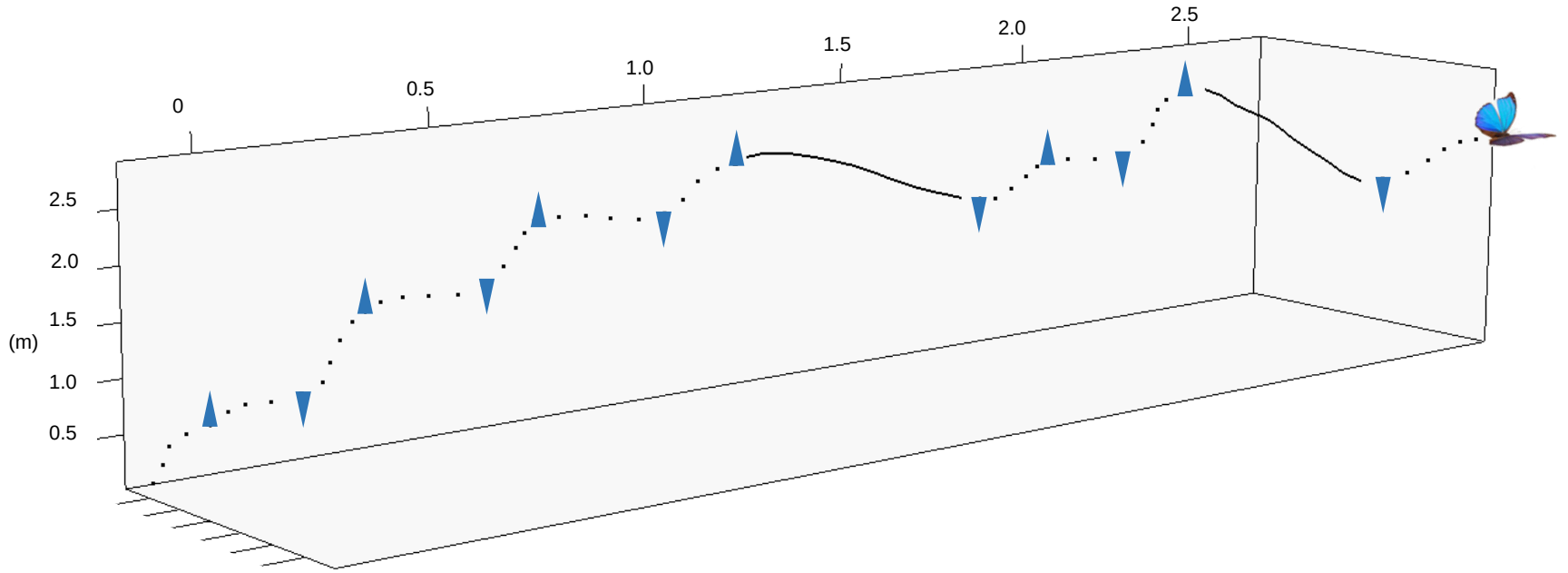
Auto-tracking


0
0.5
1.0
1.5
2.0
2.5
(m)
2.5
2.0
1.5
1.0
0.5



Up-stroke

Down-stroke



Up-stroke

Down-stroke

Gliding phase

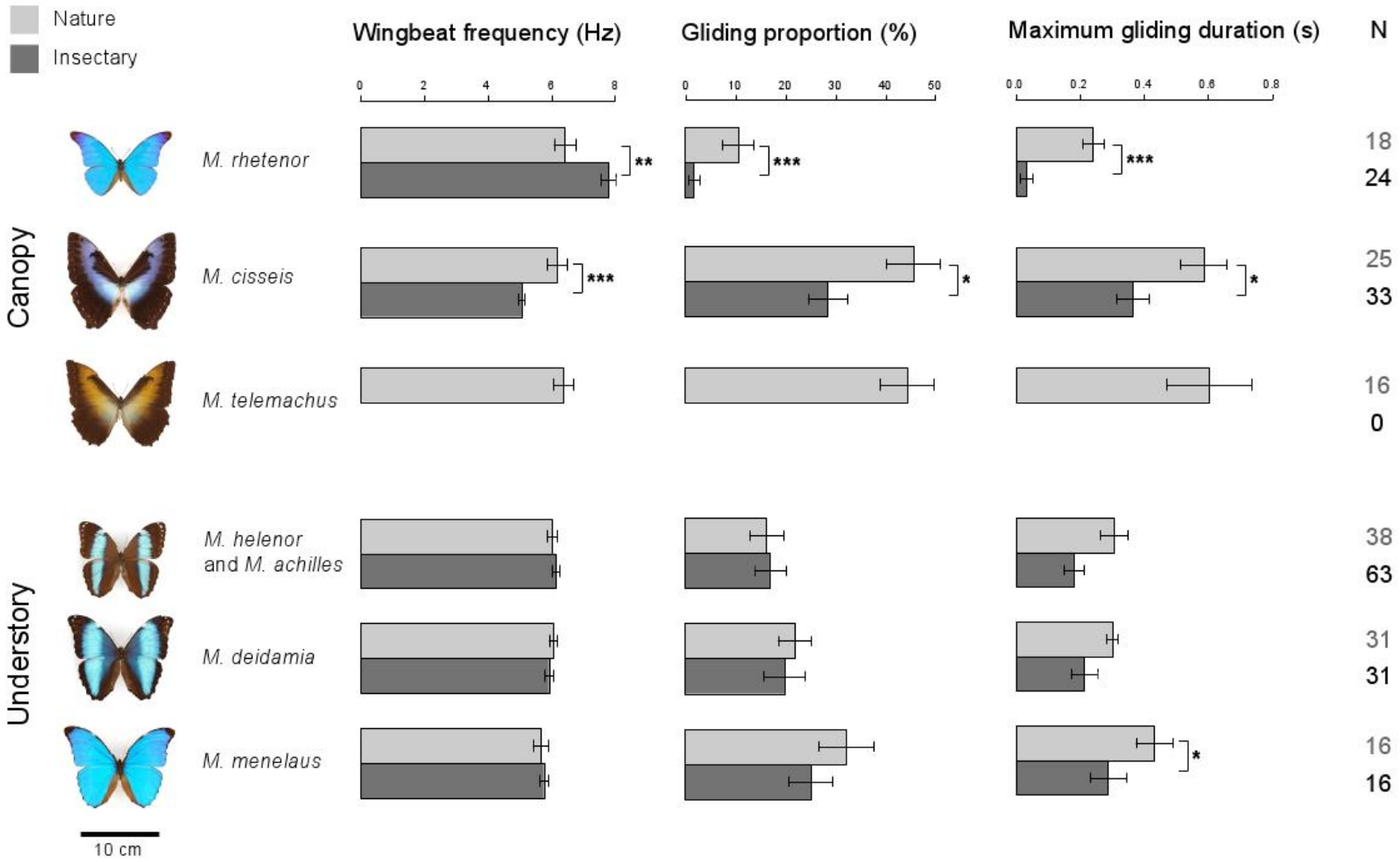
Flapping phase

⇒ **Flight parameters**

Wingbeat frequency, gliding proportion, height, speed, acceleration, sinuosity, advance ratio, etc.

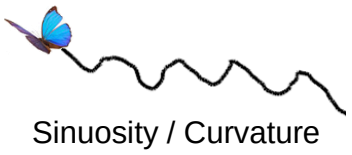
Flight *in natura*

Difference between captivity and nature?

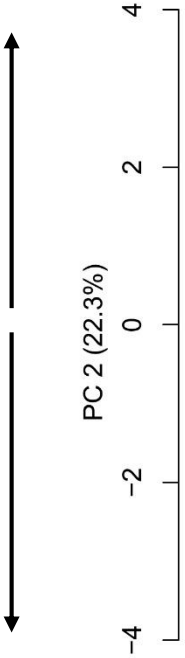


Significant phylogenetic signal

Divergence C/U > expected (PhyloMANOVA***)

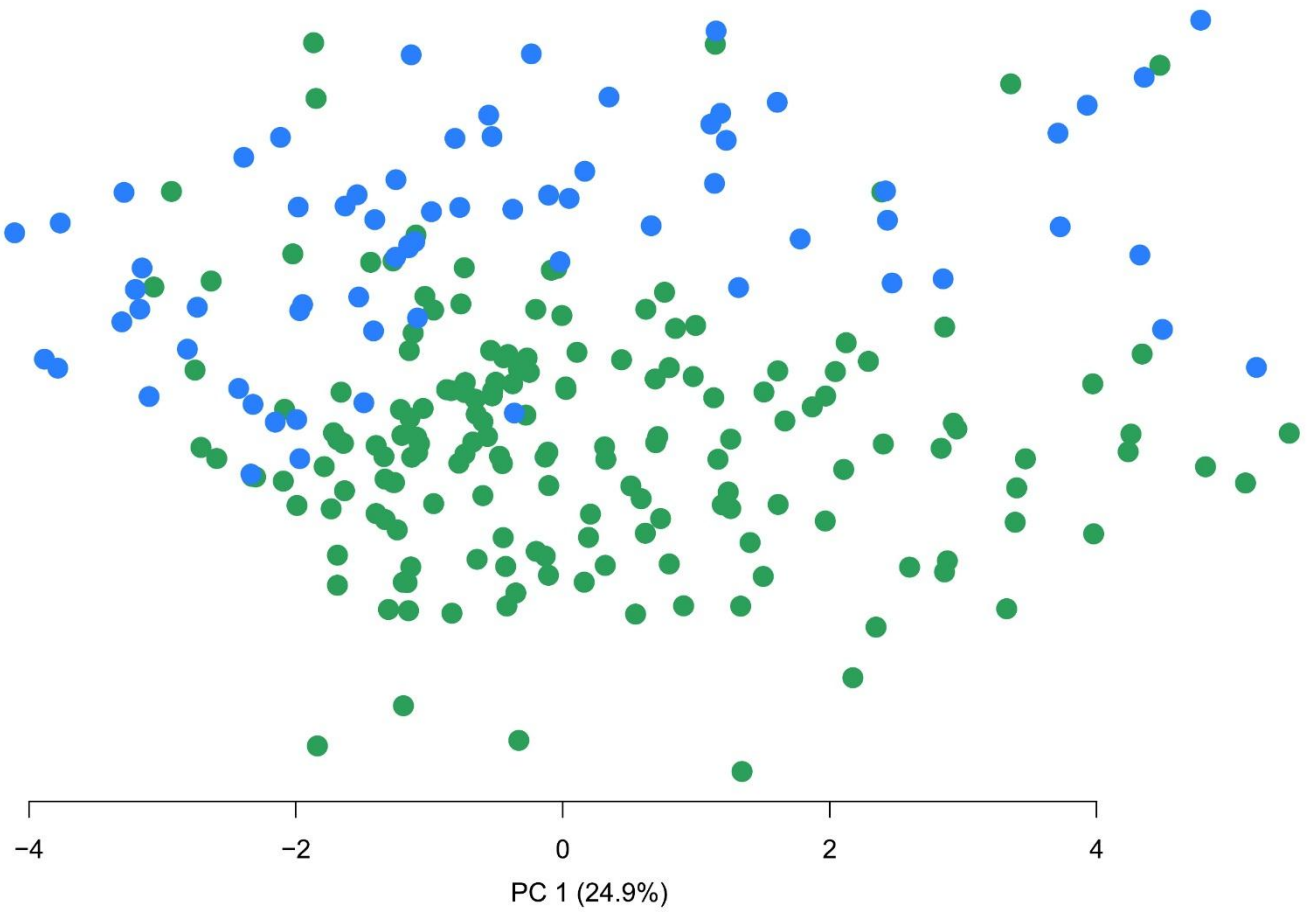


Sinuosity / Curvature



Speed / Acceleration

Advance ratio



Canopy

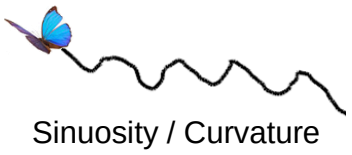
Understory

Wingbeat frequency

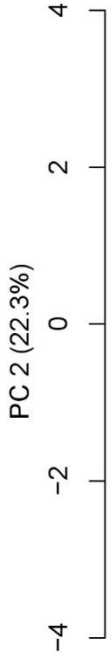
Gliding flight

Significant phylogenetic signal

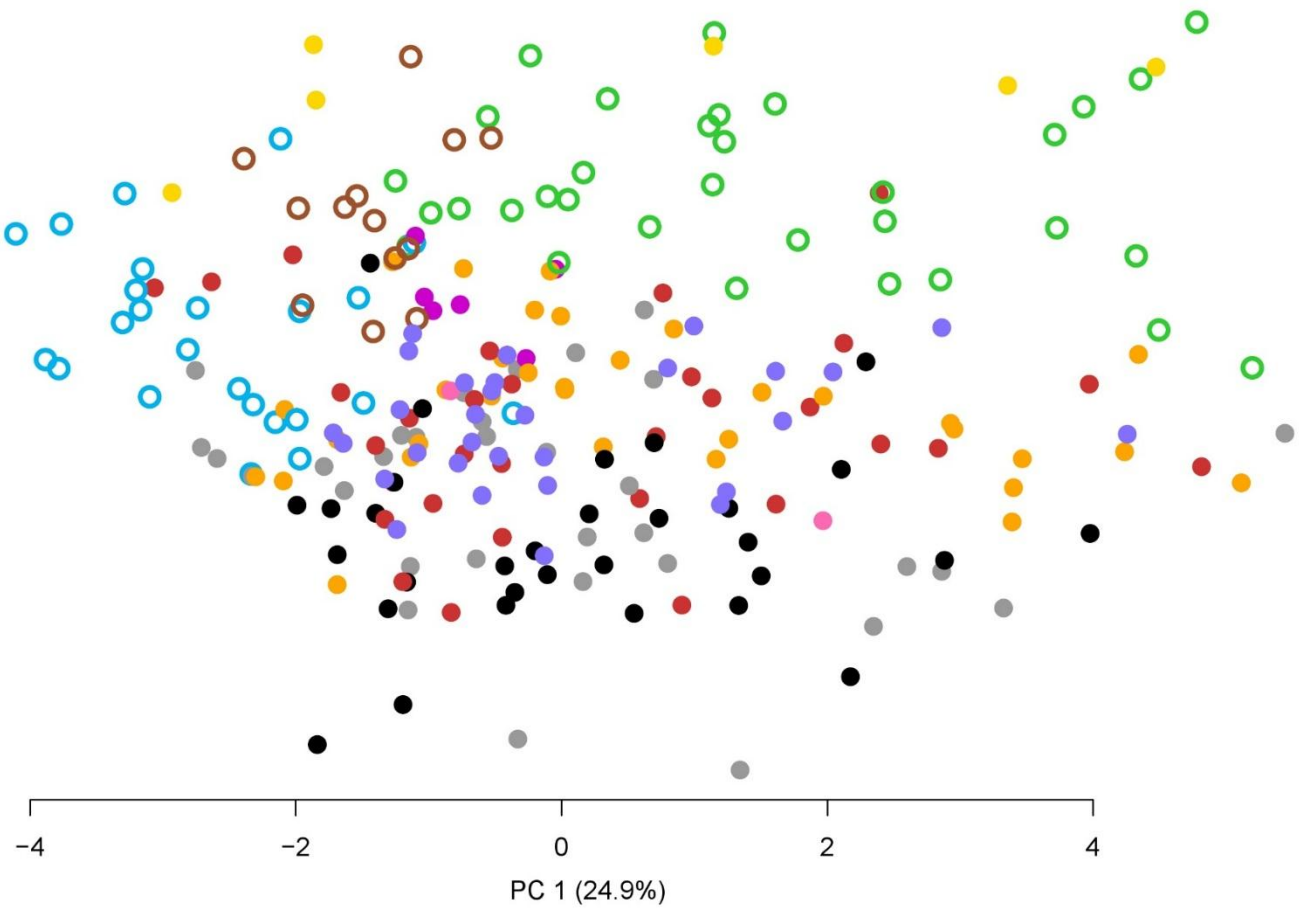
Divergence C/U > expected (PhyloMANOVA***)



Sinuosity / Curvature



Speed / Acceleration
Advance ratio



Canopy

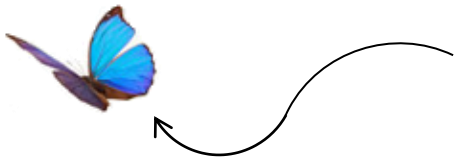
- *rhetenor*
- *cisseis*
- *theseus*

Understory

- *sulkowzskyi*
- *aurora*
- *menelaus*
- *godartii*
- *achilles*
- *helenor*
- *deidamia*
- *marcus*

Wingbeat frequency

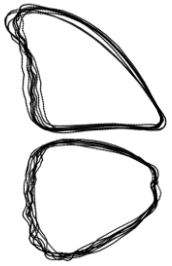
Gliding flight



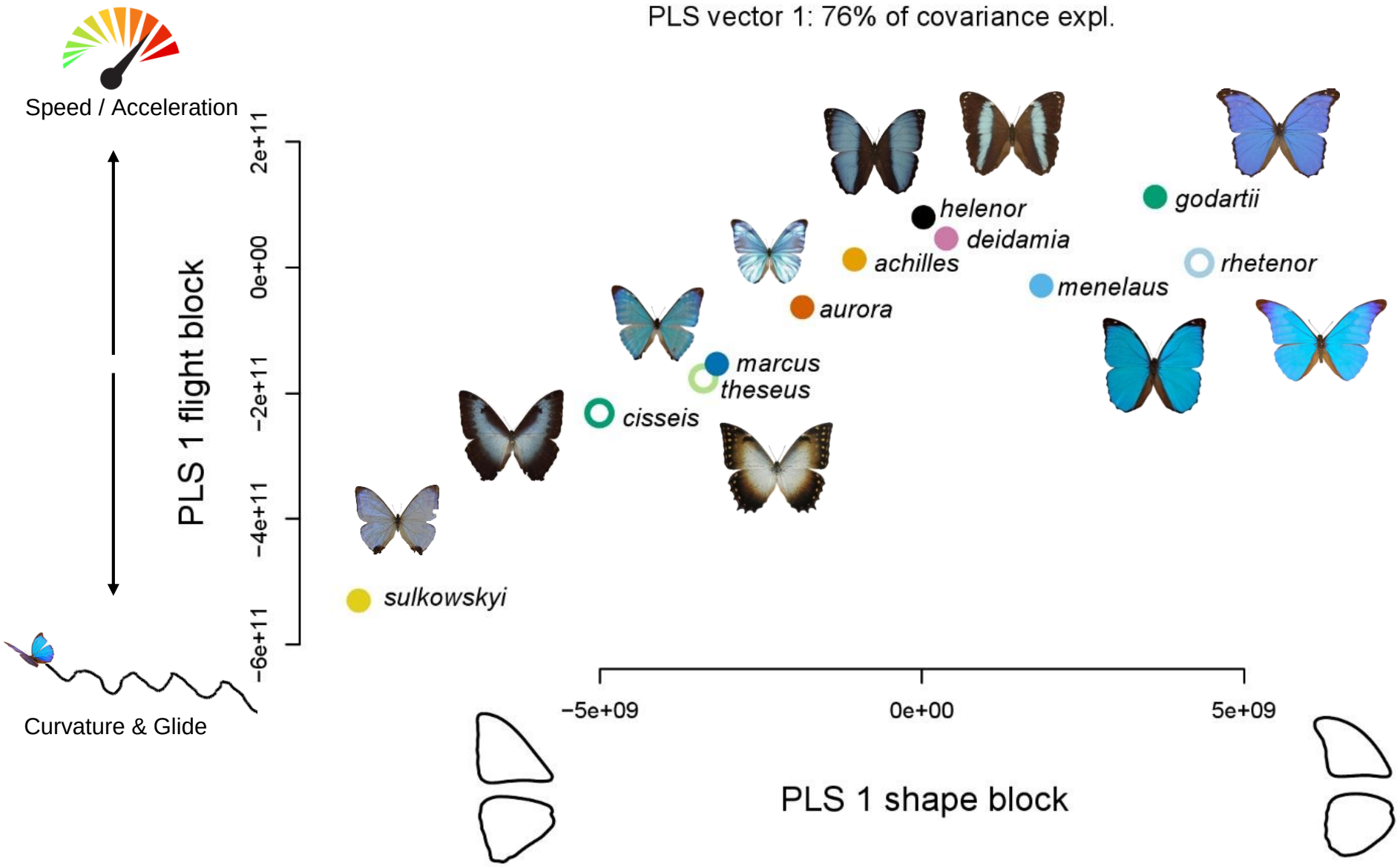
Flight

Covariation?

(two-blocks Partial Least Square analysis)



Wing shape


PLS vector 1: 76% of covariance expl.
Speed / Acceleration
PLS 1 flight block
2e+11
0e+00
−2e+11
−4e+11
−6e+11
Curvature & Glide
helenor
deidamia
godartii
achilles
rhetenor
menelaus
aurora
marcus
theseus
cisseis
sulkowskyi
−5e+09
0e+00
5e+09
PLS 1 shape block

Slow sinuous flight
some long glides

Powerful flight
frequent short glide

Fast upward flight
high wingbeat frequency
very few glides

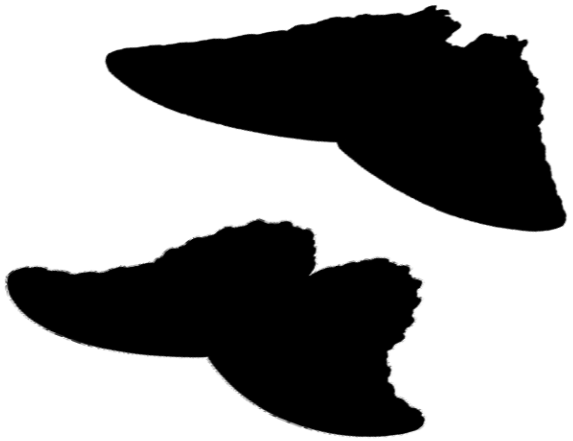
Conclusions

Adaptive divergence of flight behaviour?

Relationship Shape/Flight behaviour:
more than the canopy/understory opposition

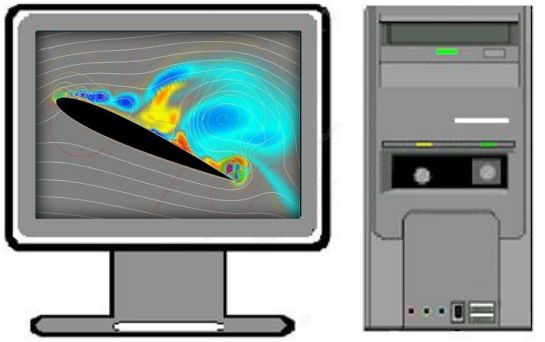
Flight performance (aerodynamics) ?

Aerodynamics of gliding flight



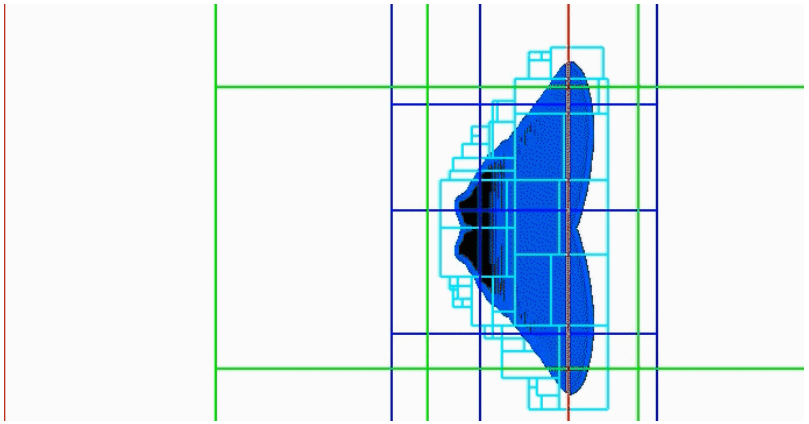
angle of attack
flight speed
dehidral angle

CFD simulation

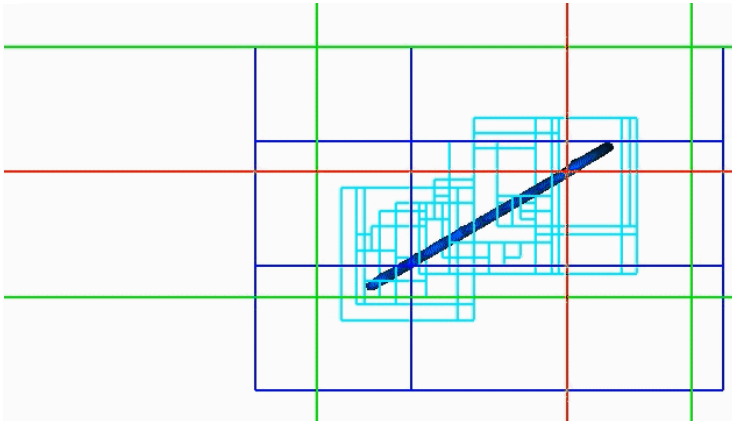


Lift-to-drag ratio

Aerodynamics of gliding flight

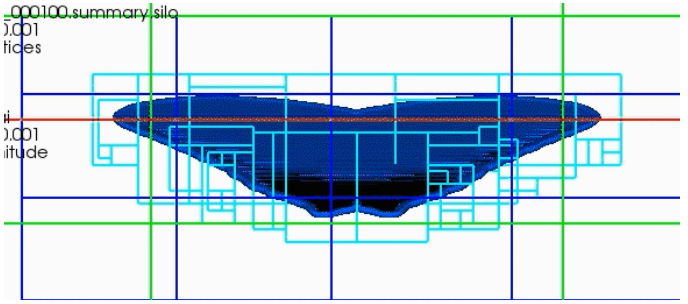


Top view



Side view

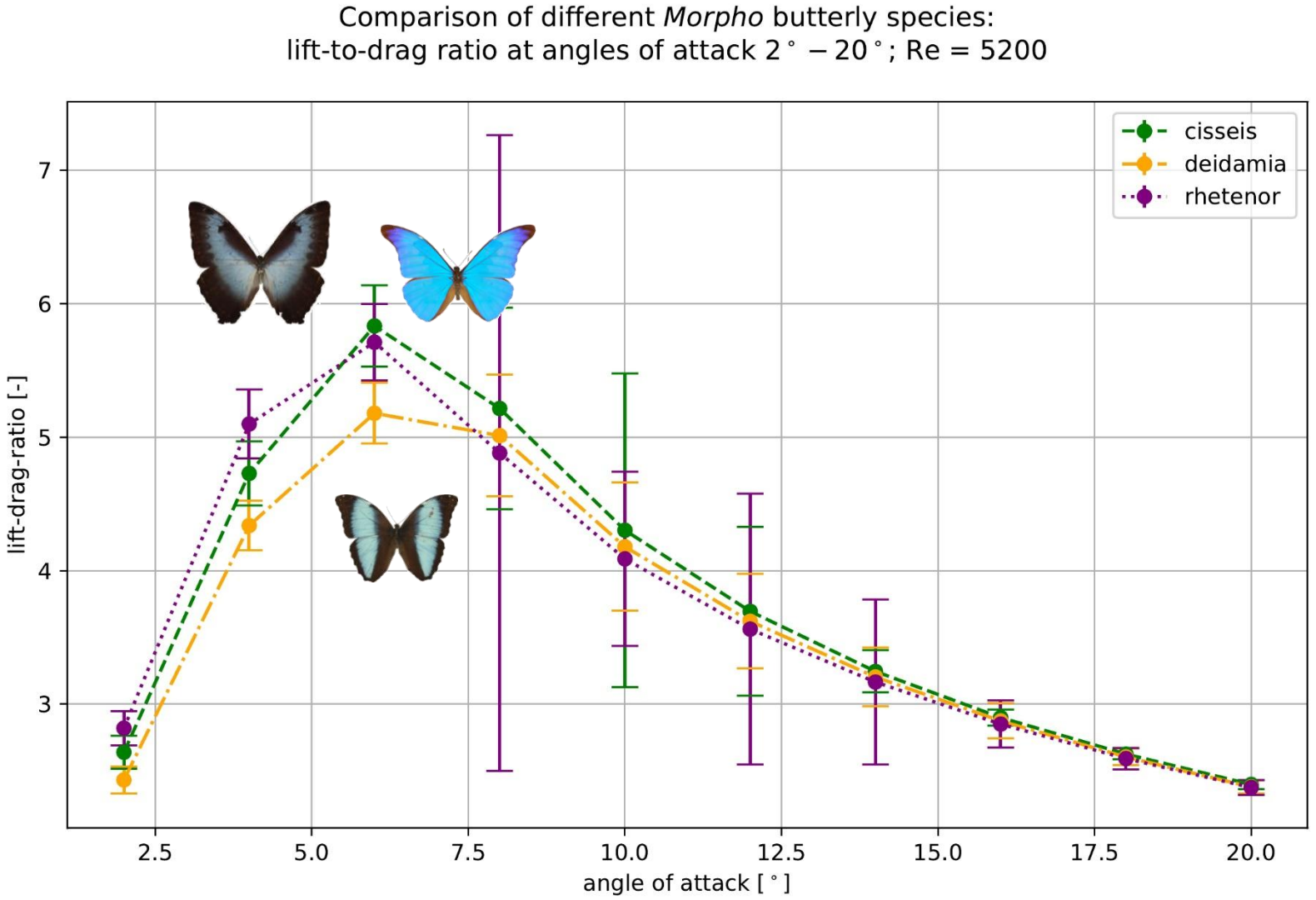
Computational Fluid Dynamics



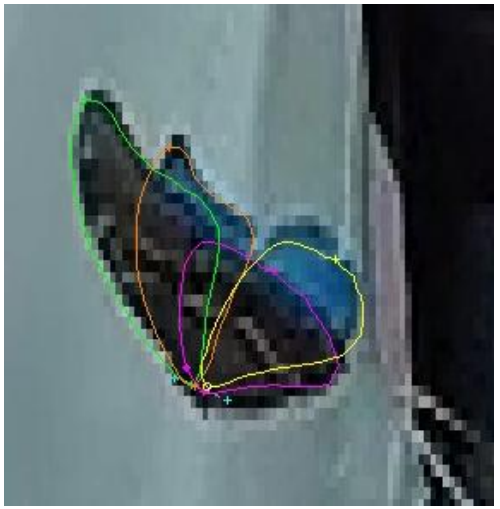
Rear view

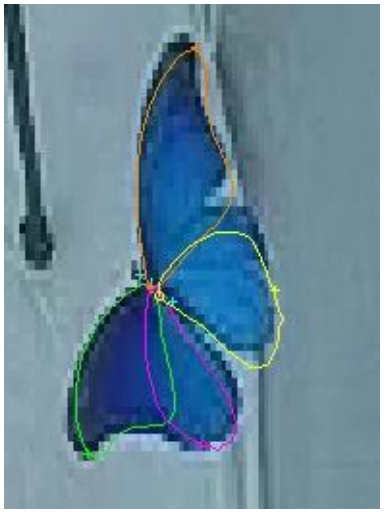
angle of attack: 30°
speed: 1.5 m/s

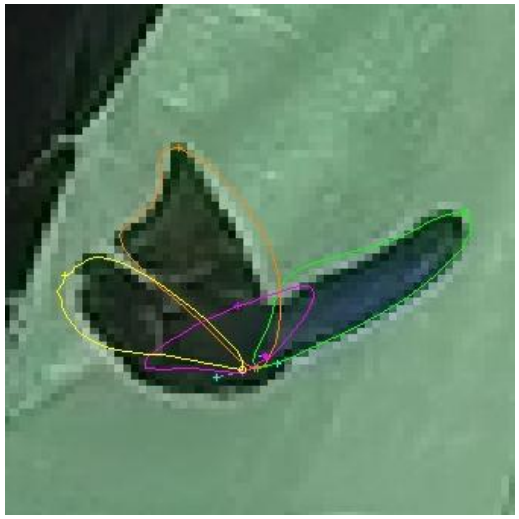
Aerodynamics of gliding flight



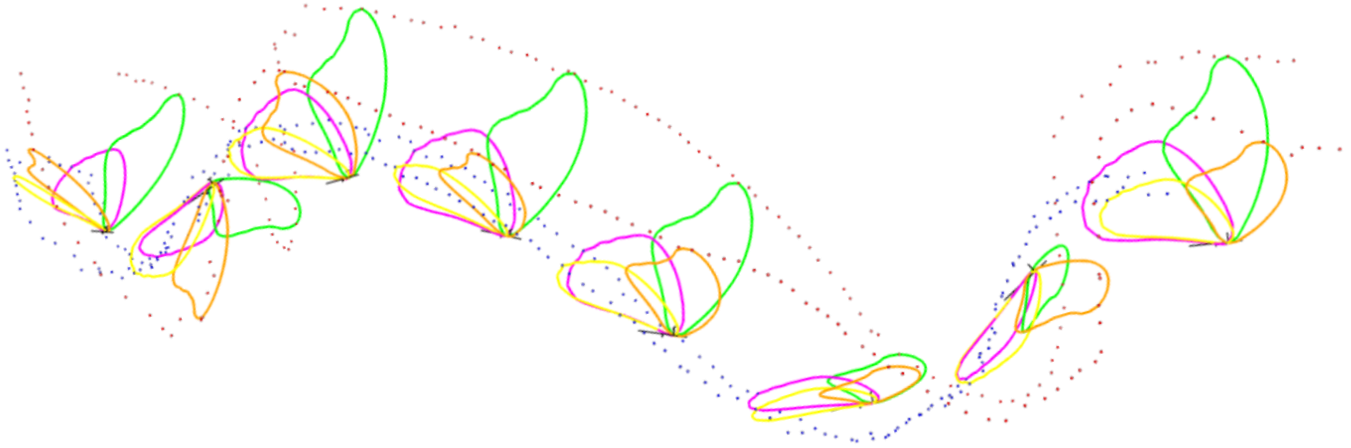
Aerodynamics of flapping flight





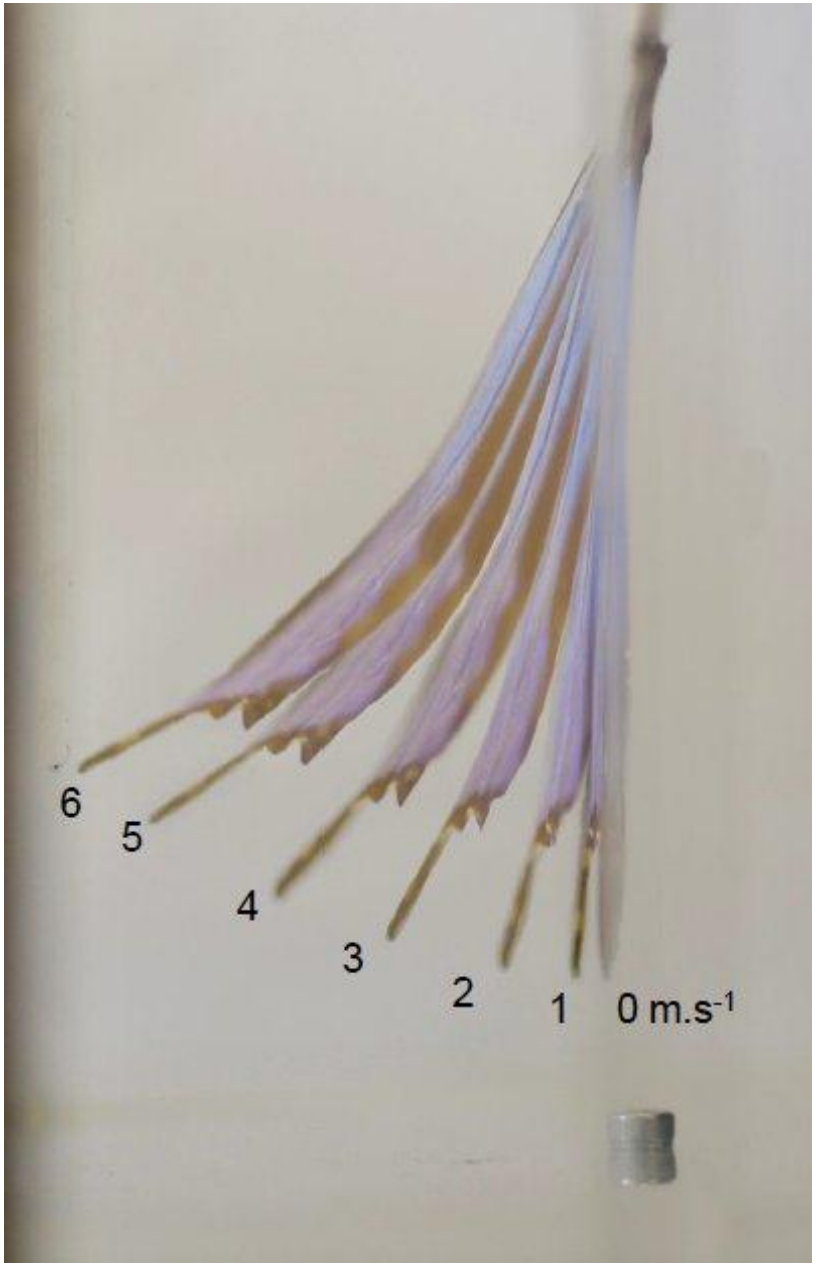


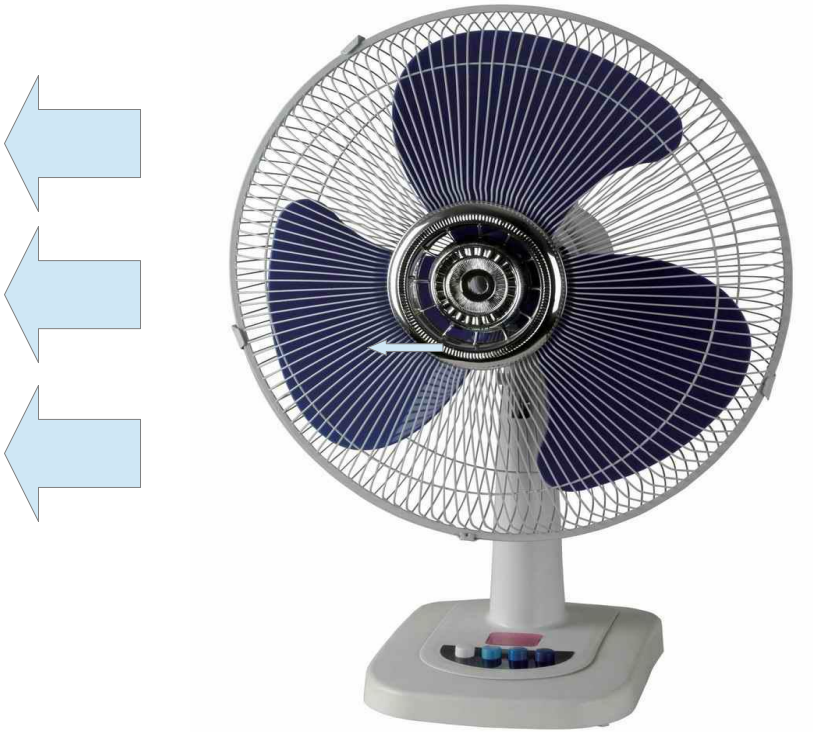
Wingbeat kinematics



CFD

Aerodynamics of flapping flight

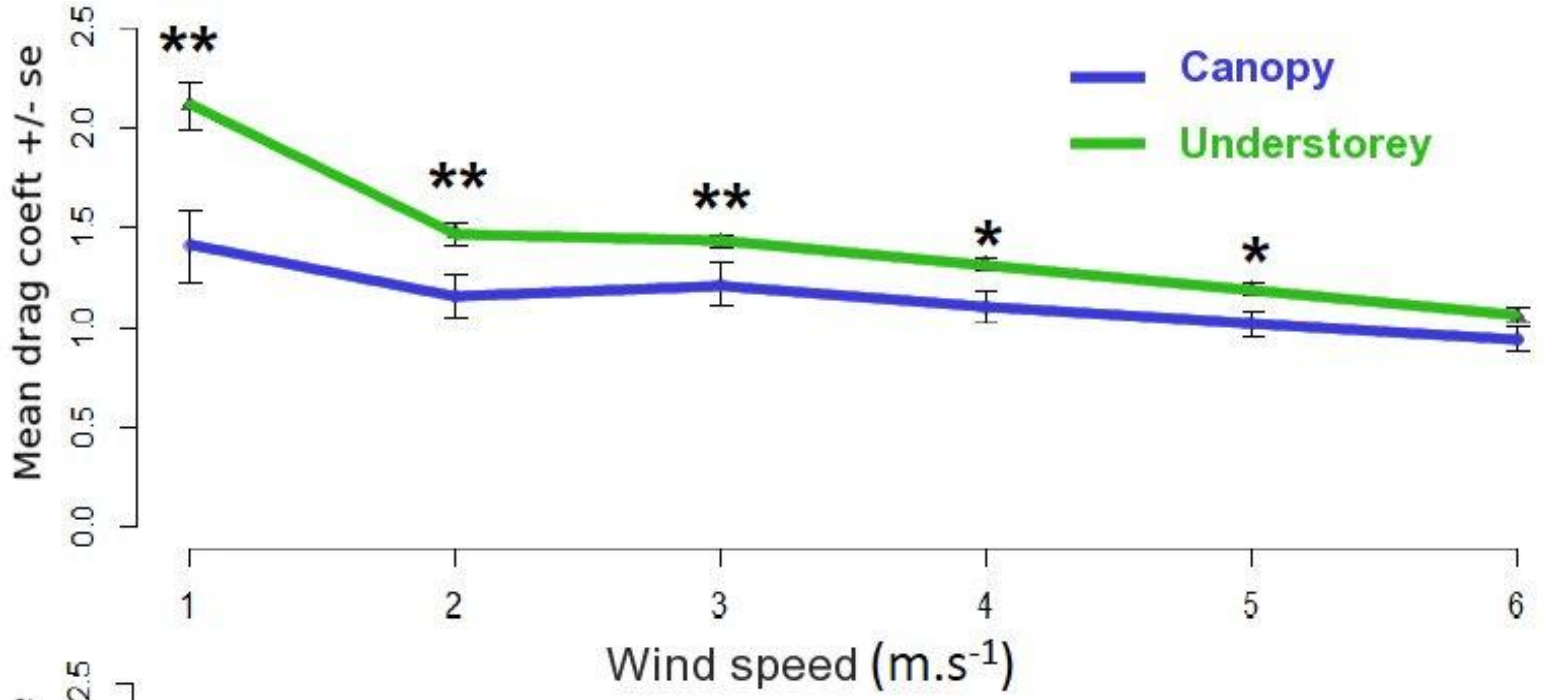




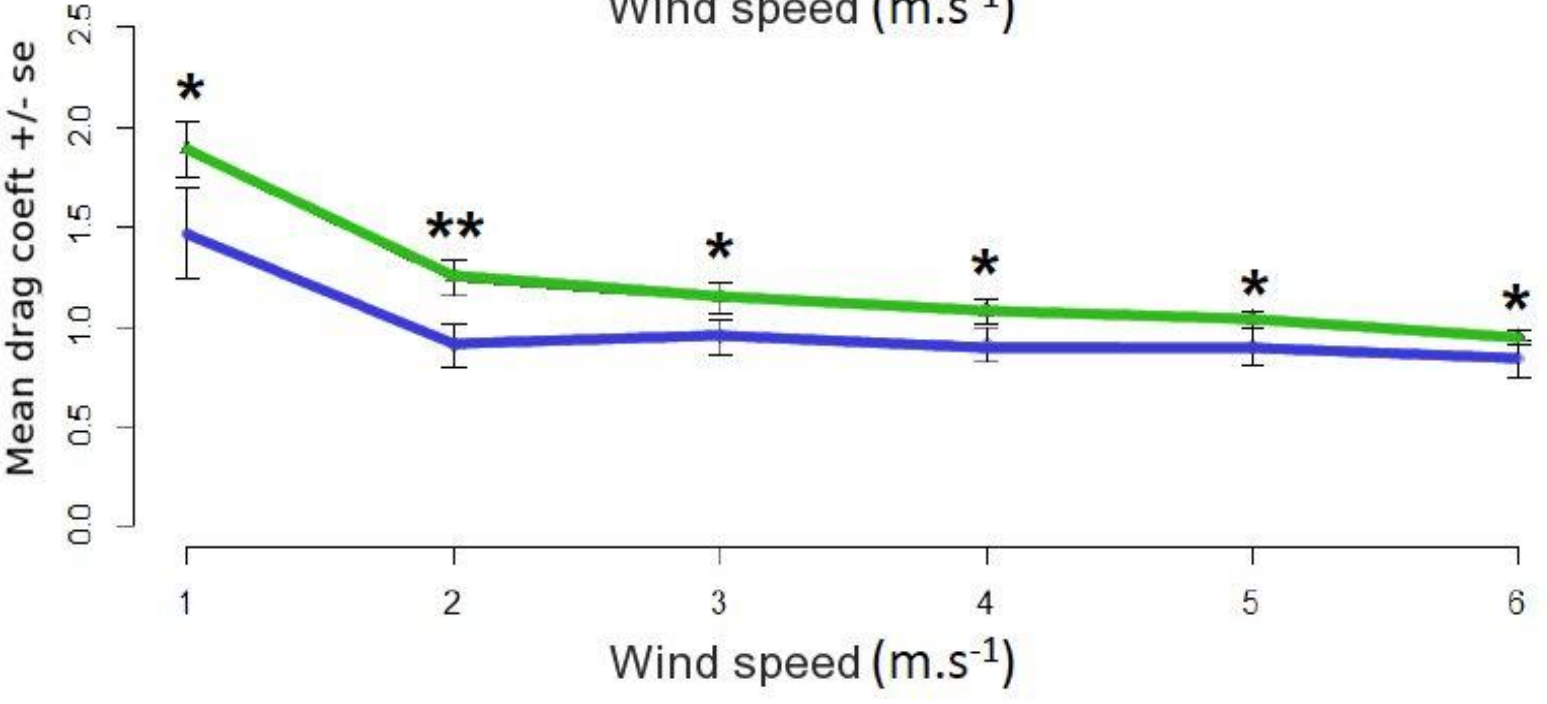
Deformation
Force
Drag

Aerodynamics of flapping flight

Fore-wing



Hind-wing



Conclusions

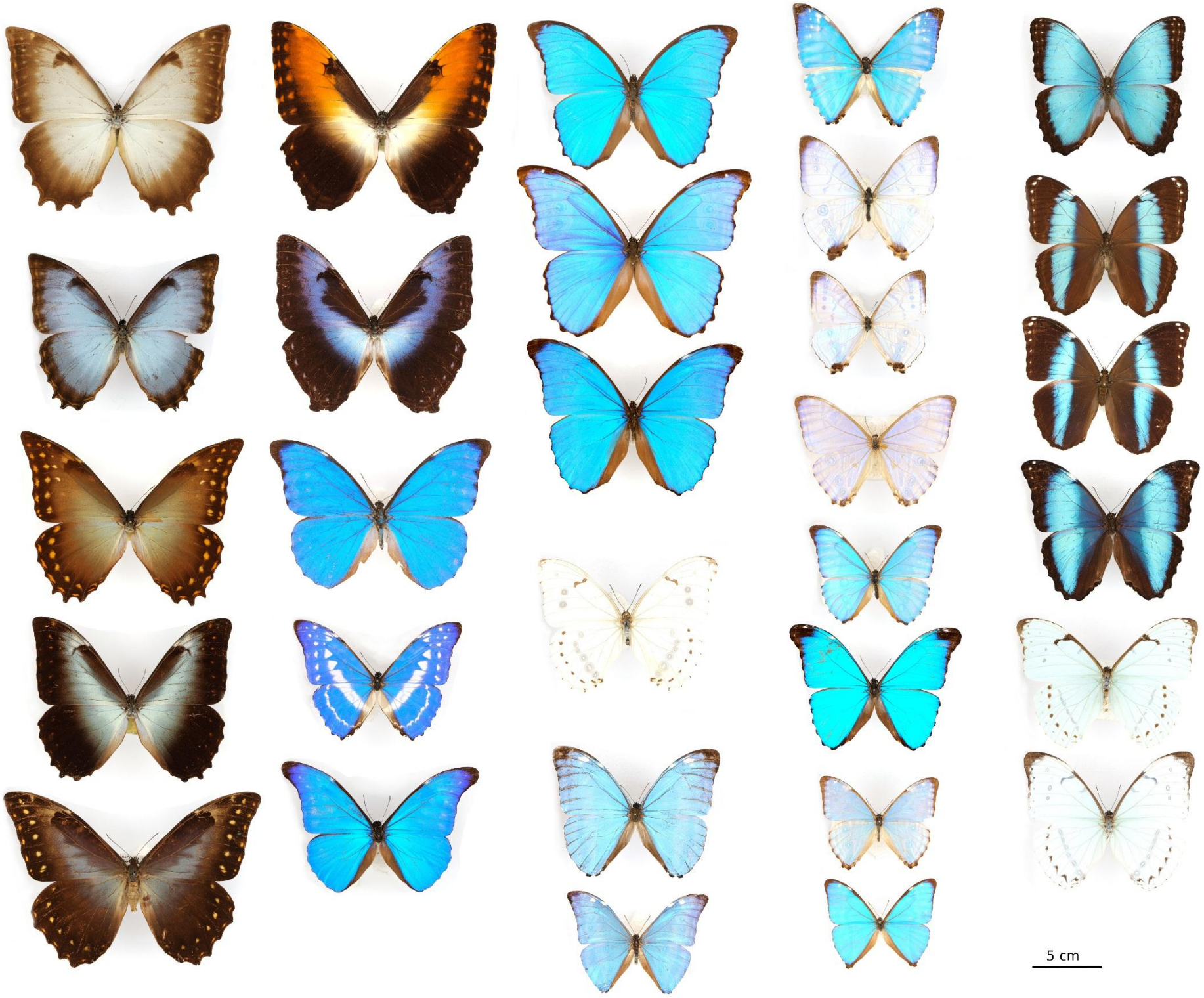
Adaptive divergence of flight behaviour?

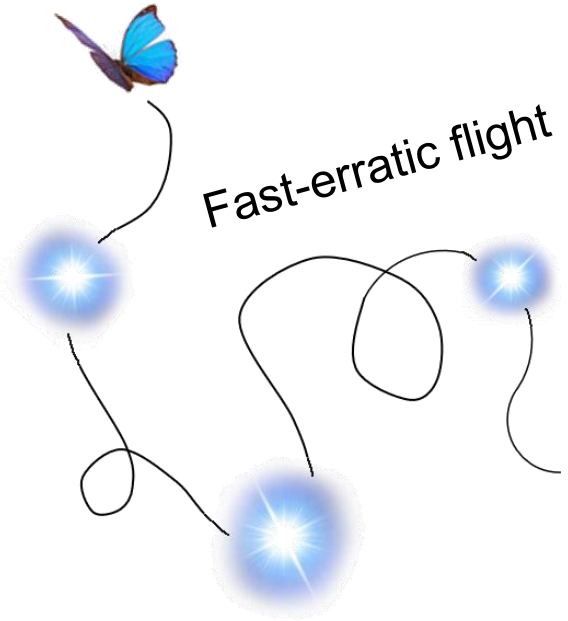
Relationship Shape/Flight behaviour:
more than the canopy/understory opposition

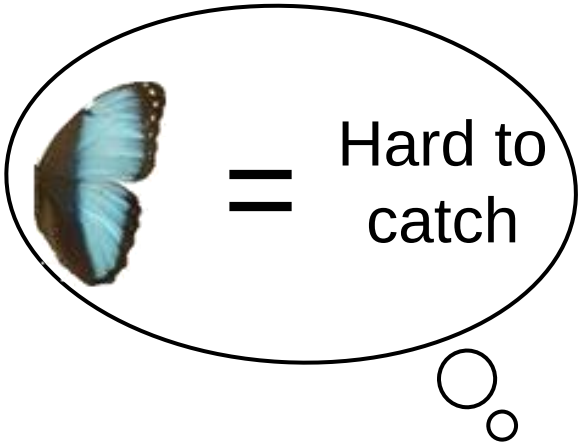
Flight performance (aerodynamics):
=> First results support an adaptive divergence

2. Evolution of wing colour patterns

Debat et al. In: *Evolution & Biodiversity* 2018
Debat et al *Frontiers Ecol. Evol.* 2020
Llaurens et al submitted


5 cm


Fast-erratic flight


=
Hard to
catch

Escape mimicry?

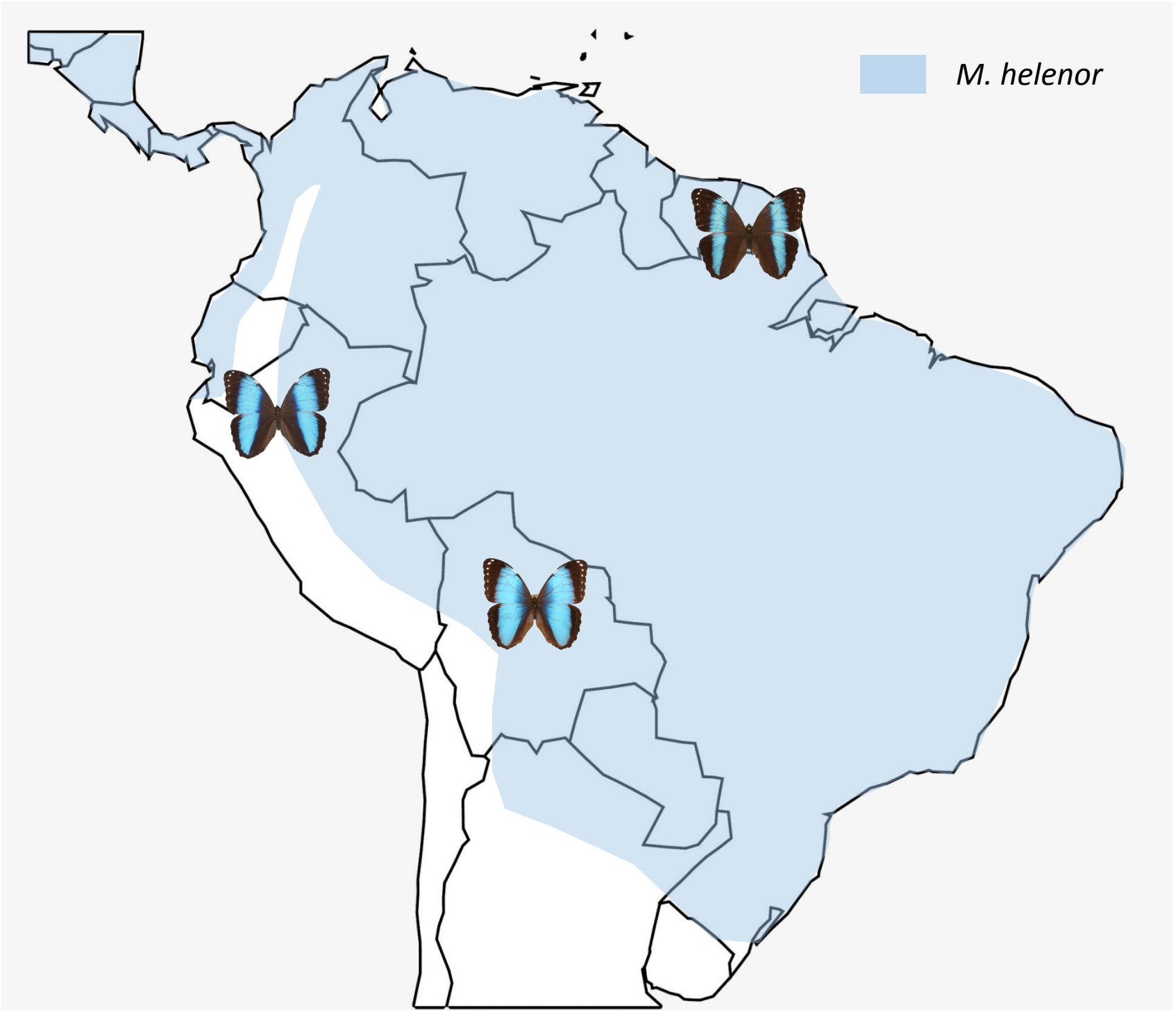
Parallel evolution in three *Morpho* species

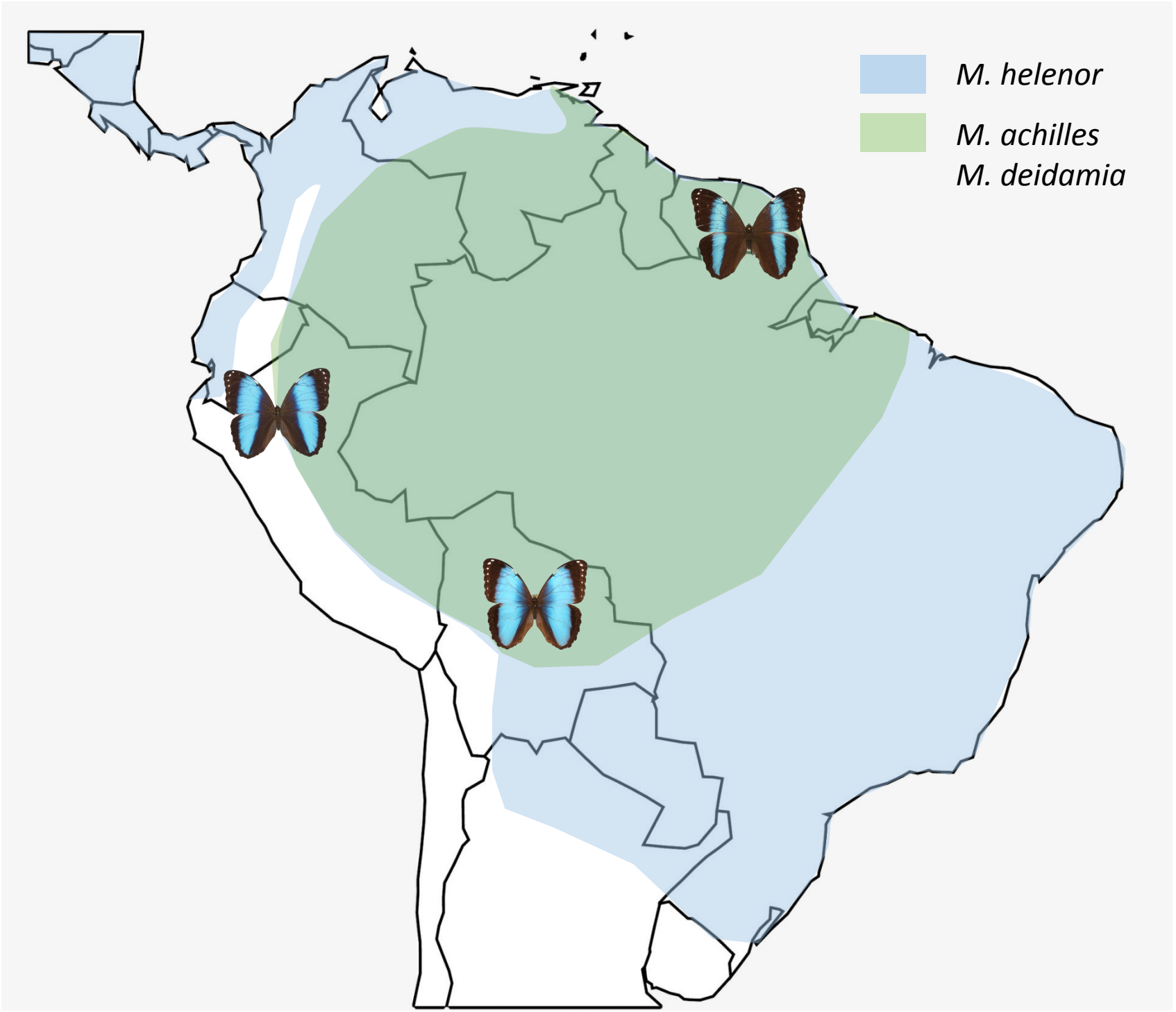
M. deidamia

M. helenor

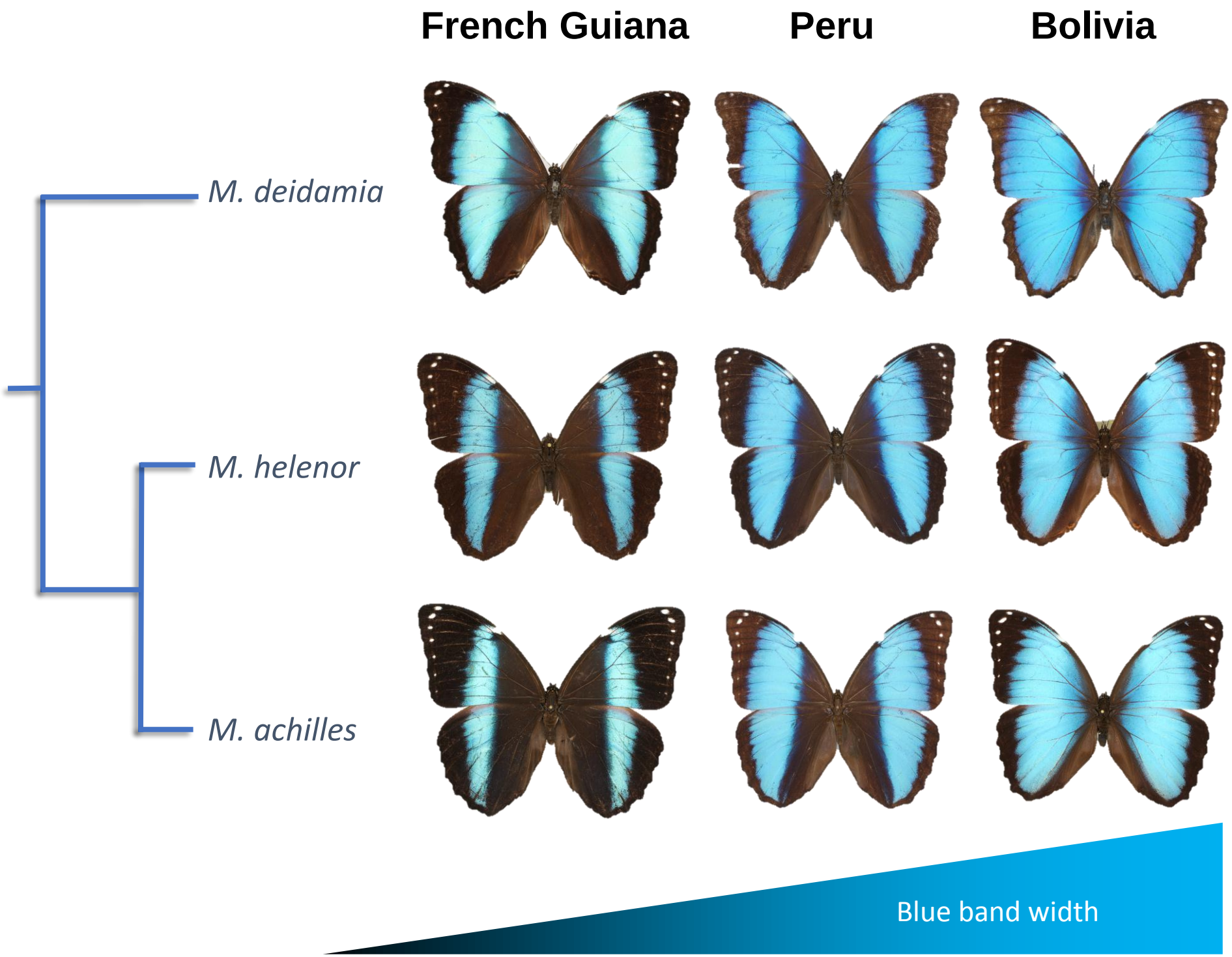
M. achilles

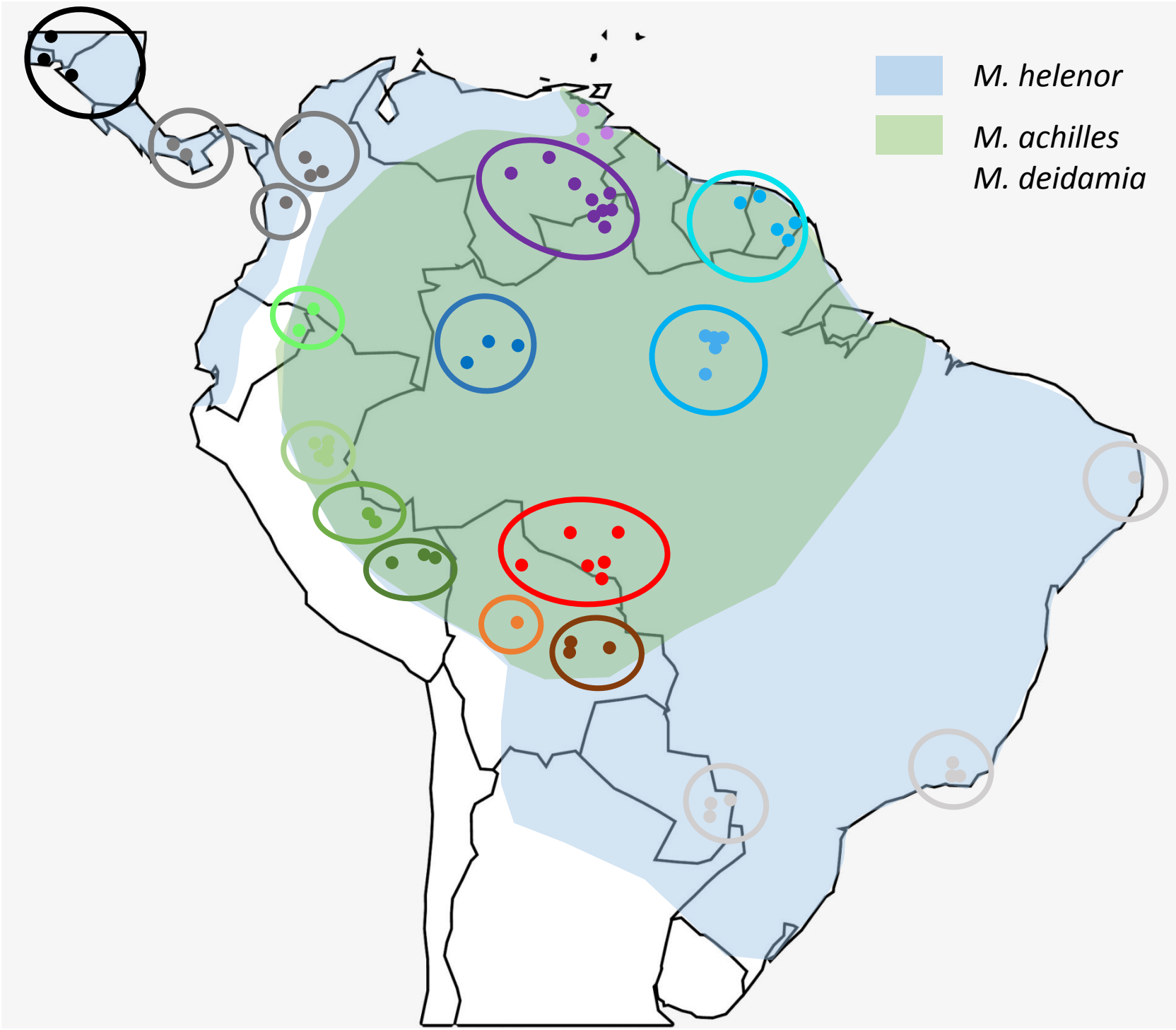

M. helenor


M. helenor


M. helenor
M. achilles
M. deidamia

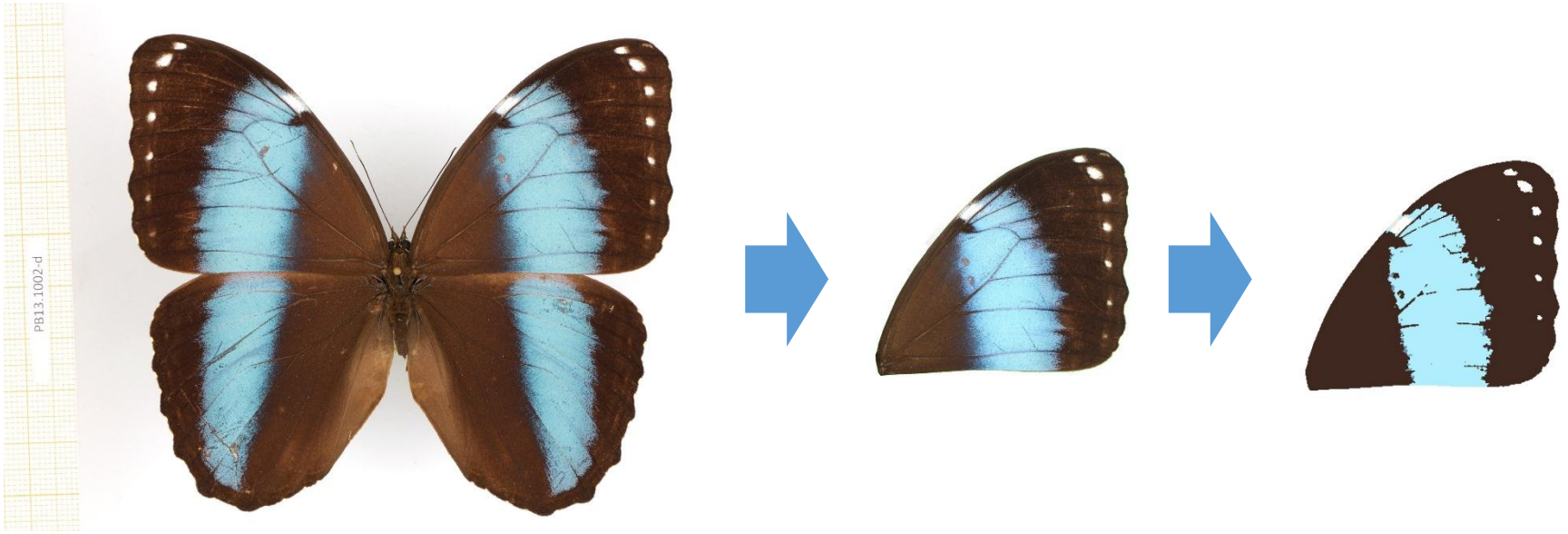

M. helenor
M. achilles
M. deidamia


French Guiana
Peru
Bolivia
M. deidamia
M. helenor
M. achilles
Blue band width


M. helenor
M. achilles
M. deidamia

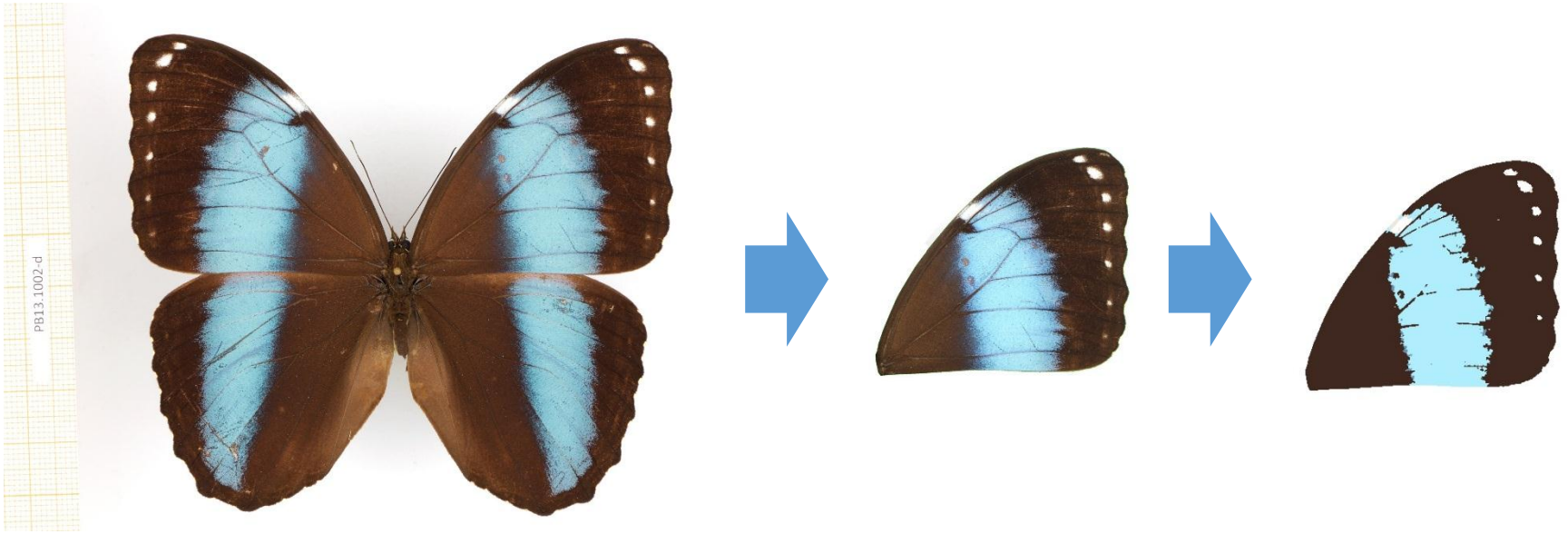
Colour Pattern Modelling

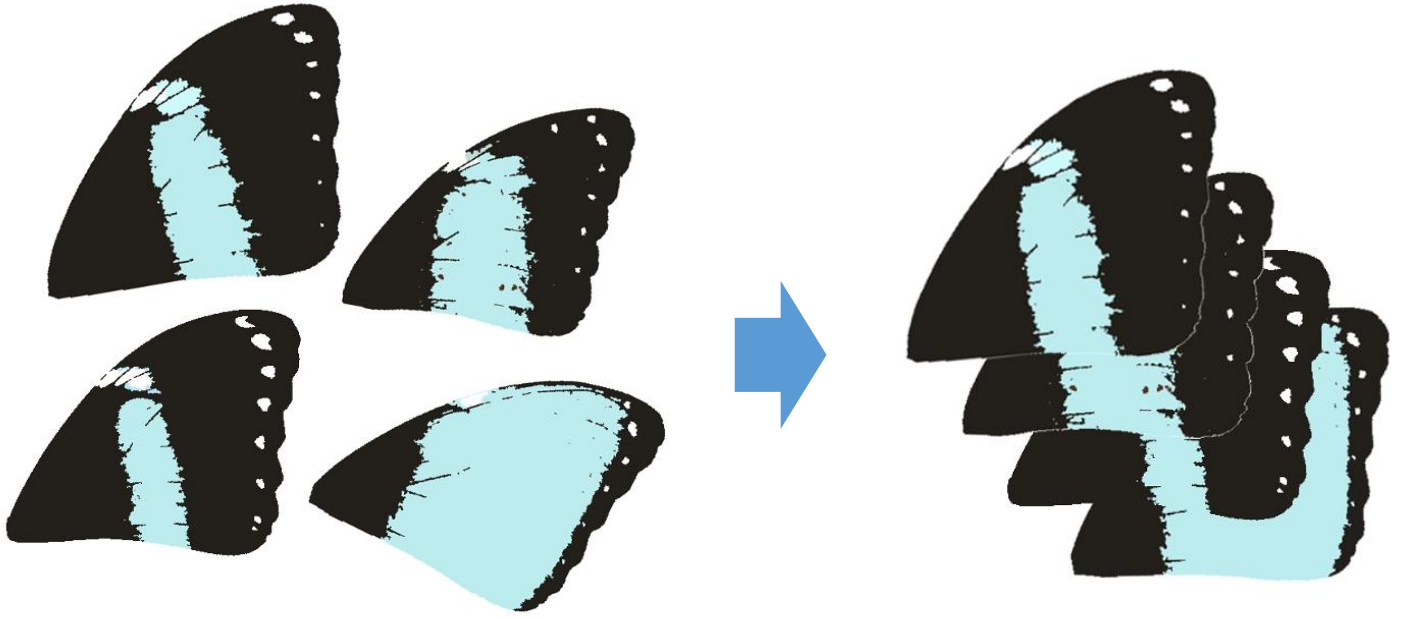
(Le Poul et al 2014 *Nature Communications*)



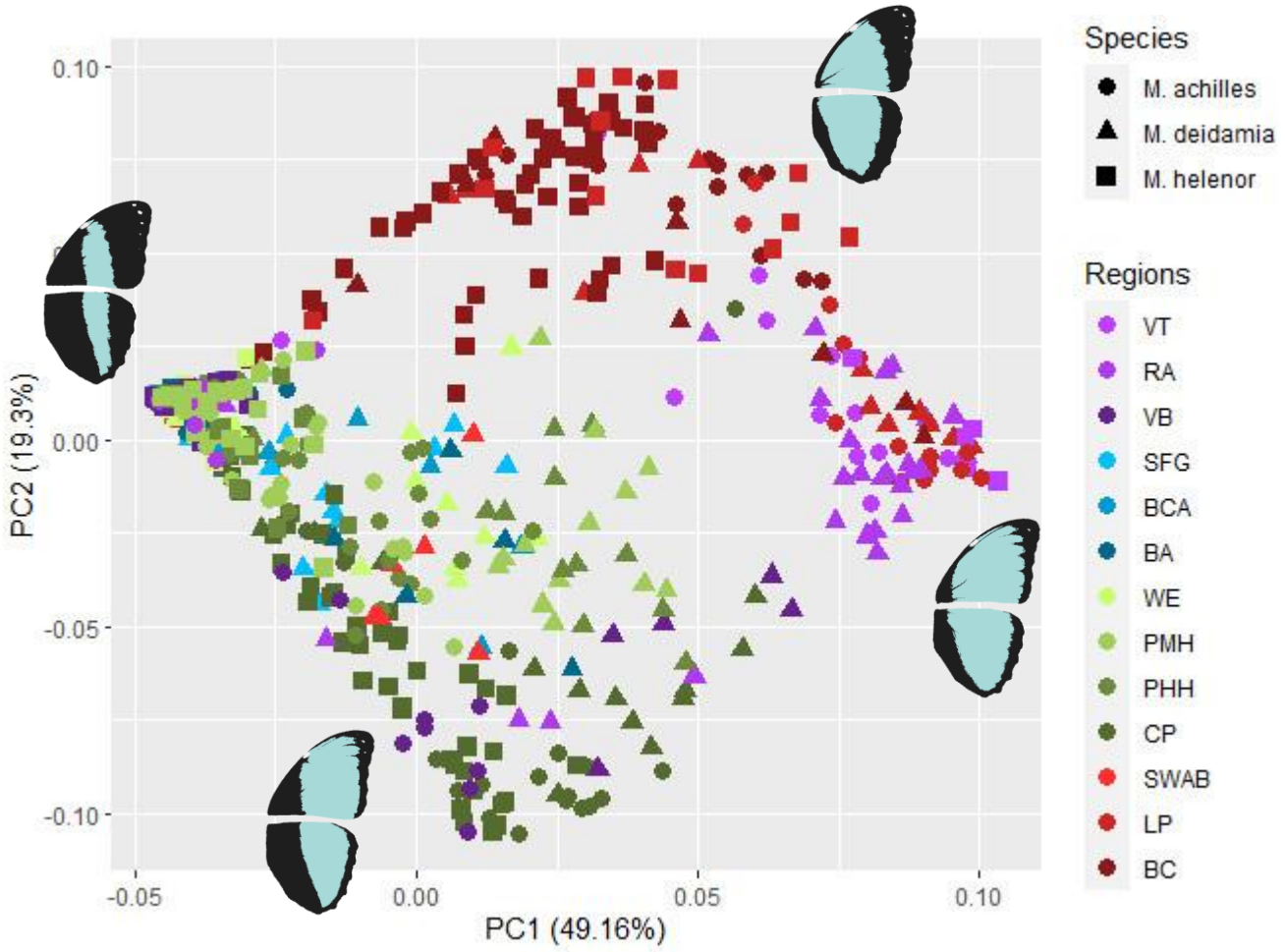
Colour Pattern Modelling

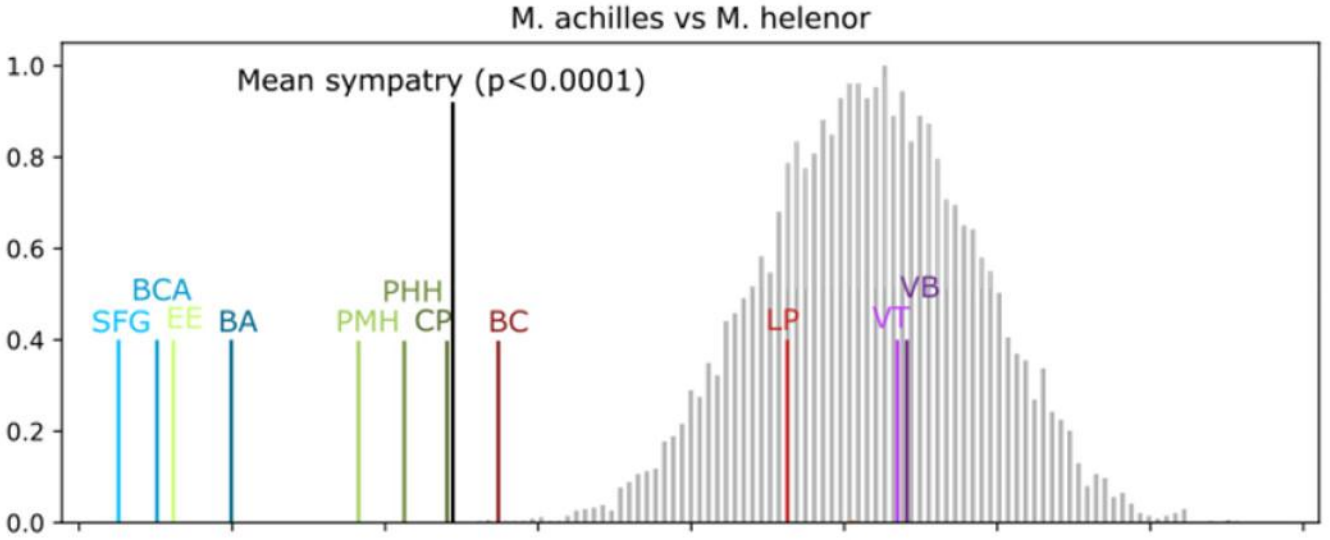
(Le Poul et al 2014 *Nature Communications*)





Homologous pixels colours in PCA


Species
M. achilles
M. deidamia
M. helenor
Regions
VT
RA
VB
SFG
BCA
BA
WE
PMH
PHH
CP
SWAB
LP
BC
PC2 (19.3%)
PC1 (49.16%)
0.10
0.00
-0.05
-0.10
-0.05
0.00
0.05
0.10


M. achilles vs M. helenor
Mean sympatry (p<0.0001)
1.0
0.8
0.6
0.4
0.2
0.0
BCA
SFG
EE
BA
PHH
PMH
CP
BC
LP
VB
VT

Conclusions

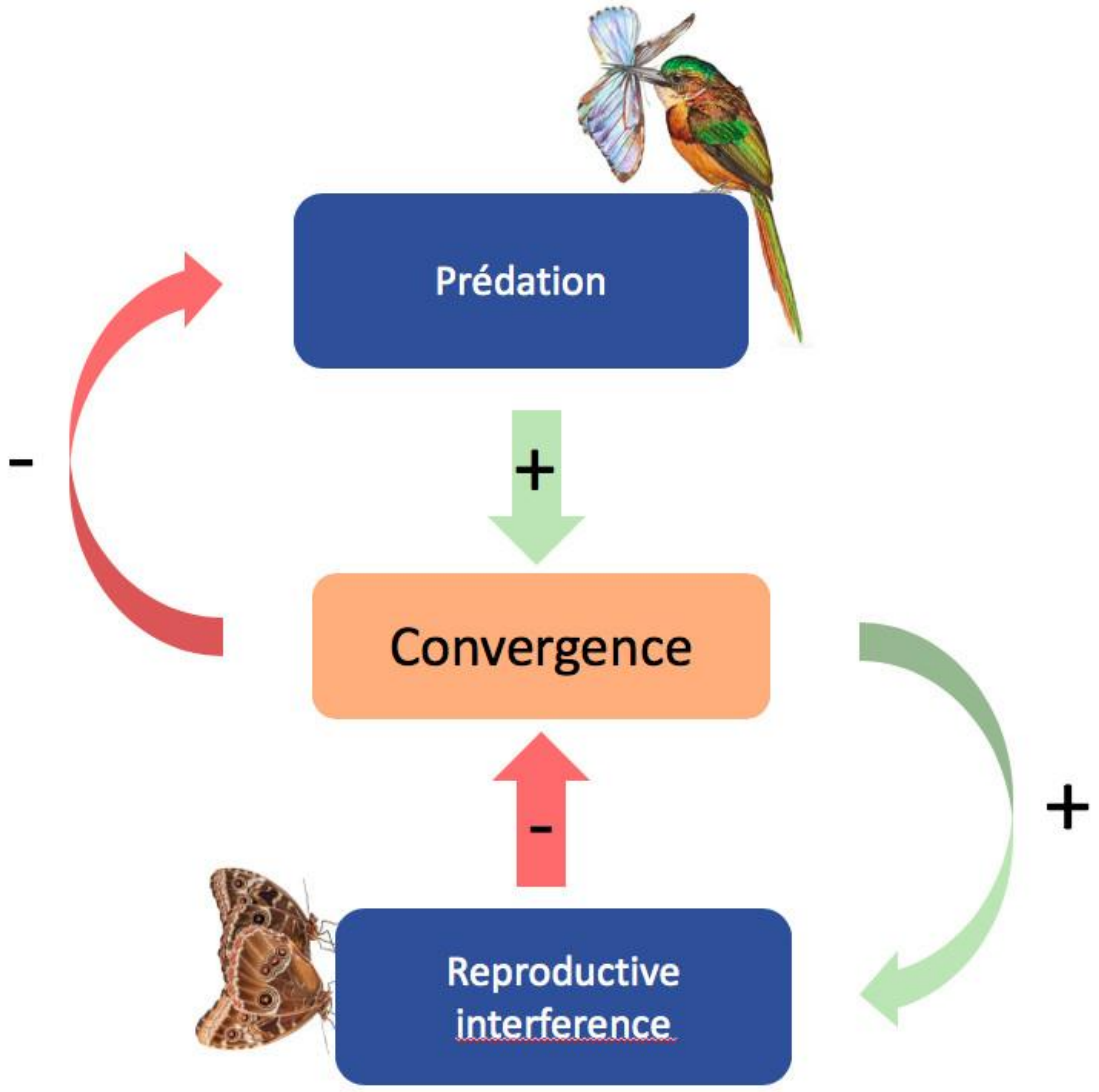
Parallel geographic variation

Local convergence

$\Rightarrow$ Similar selective pressure on the three species?
$\Rightarrow$ Neutral divergence and escape mimicry?

Reproductive interference?

Reproductive interference?

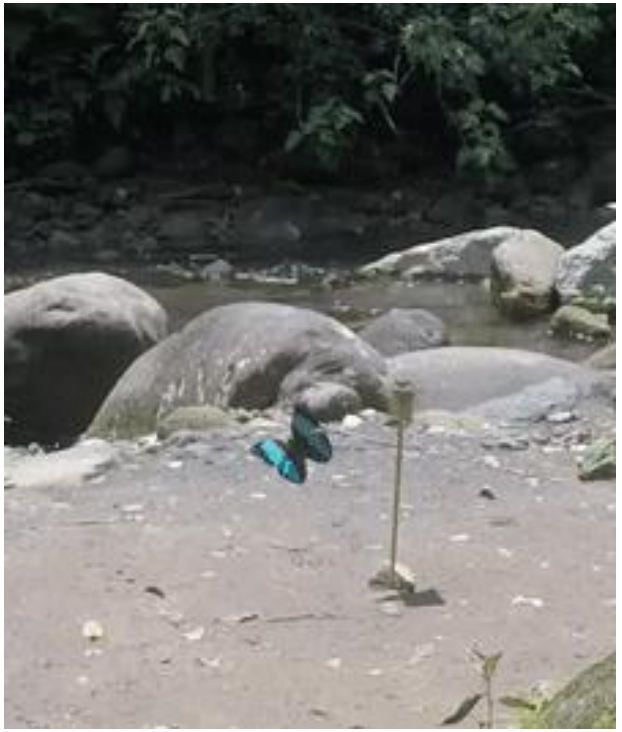


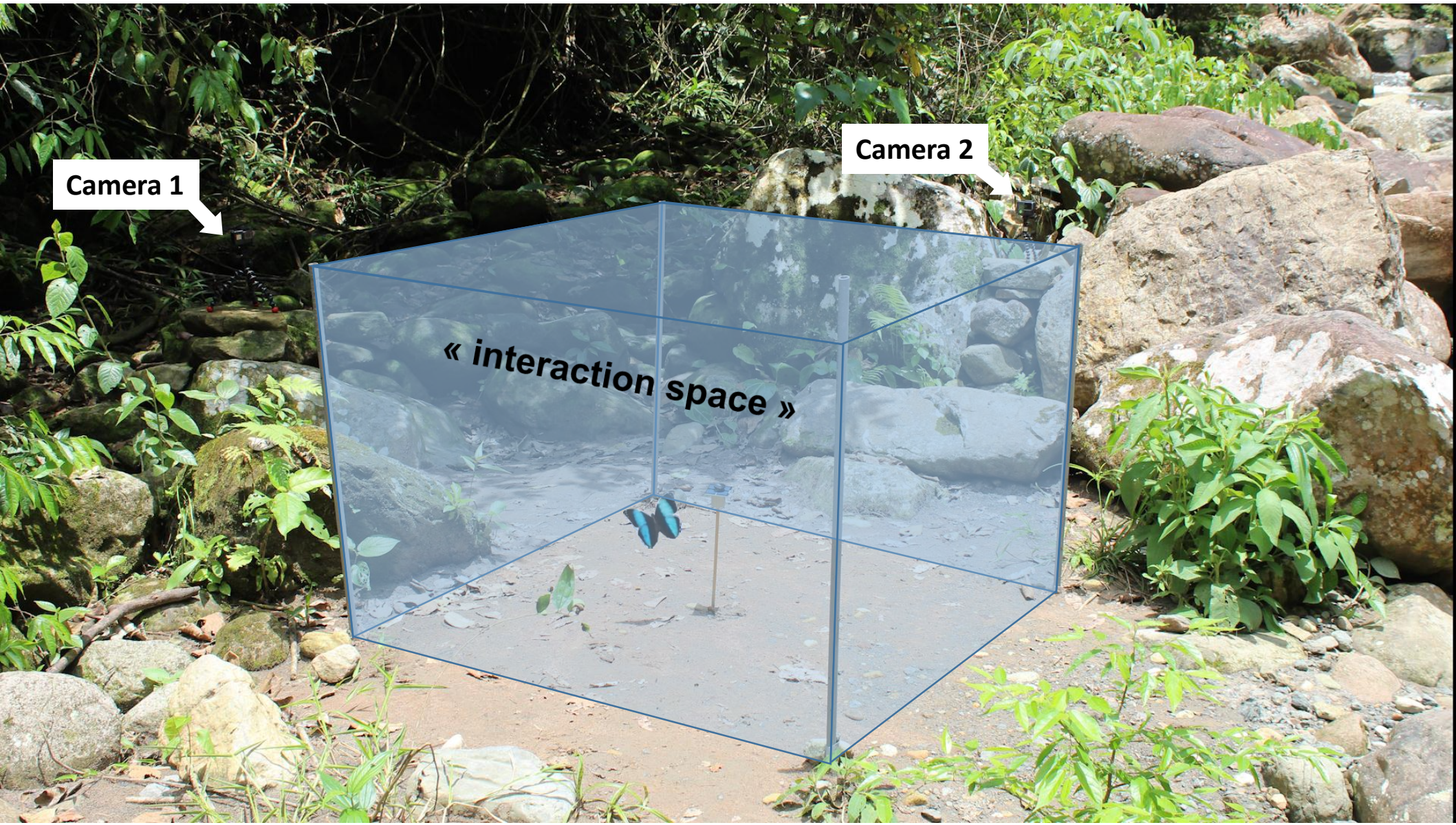
Assessing the visual impact of colour patterns

Solar-powered device

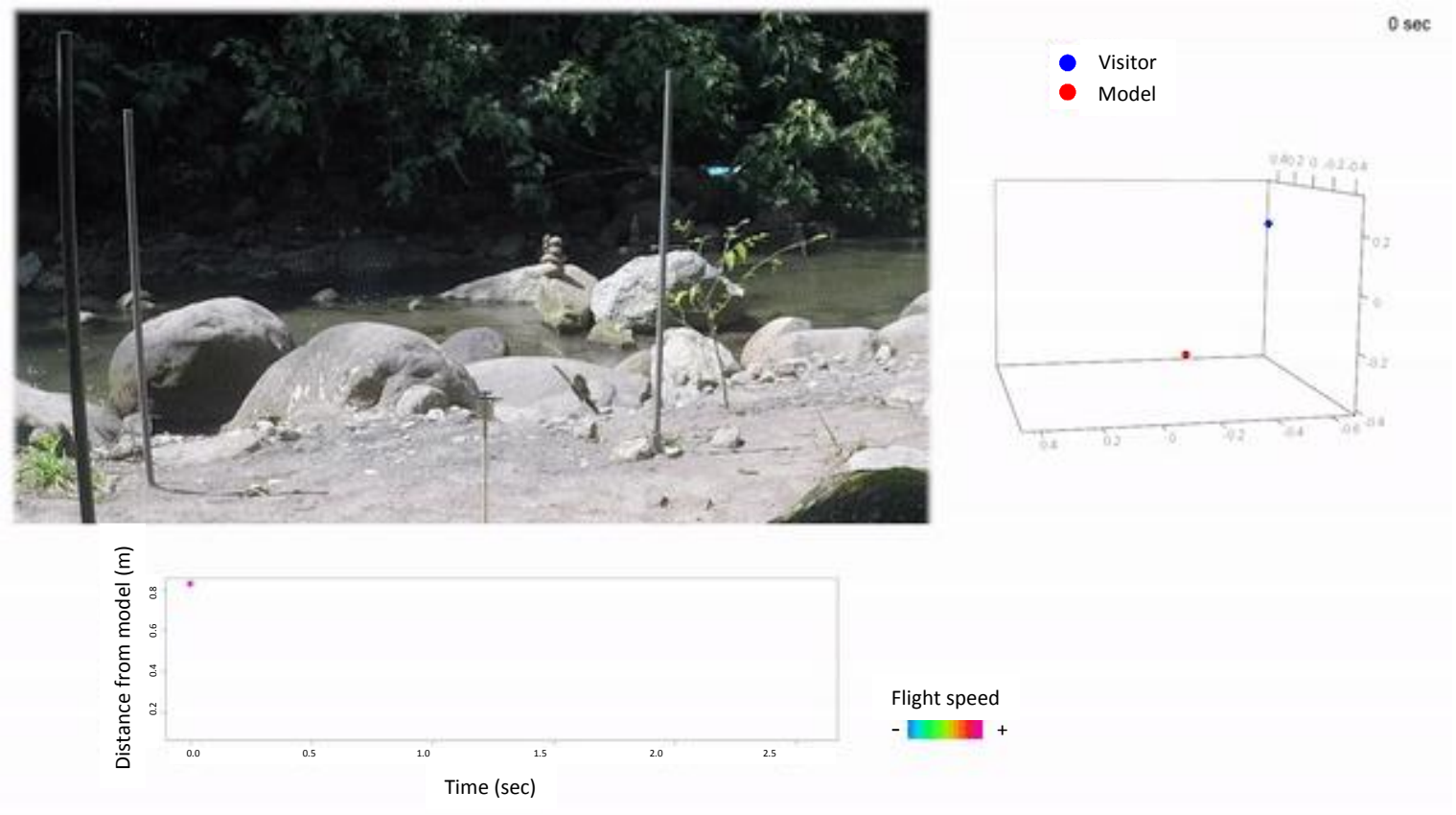
Fake model (real wings)

Wings washed with Hexane




Camera 1
Camera 2
« interaction space »

3D kinematics to characterize interacting behaviour



3D kinematics to characterize interacting behaviour

Perspectives

Integrating shape, flight and colour

Population genomics

Color vision in *Morpho* and predators

Ecology

Many thanks to

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