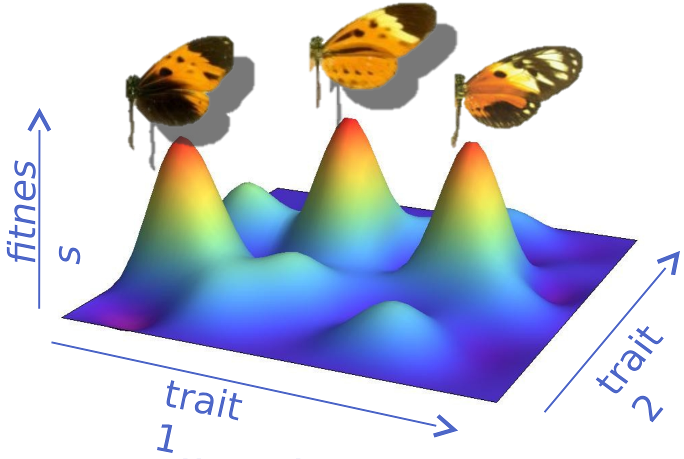
Violaine Llaurens

with M Arias, S Billiard, M Chouteau, F Prunier & M Joron



Heliconius numata

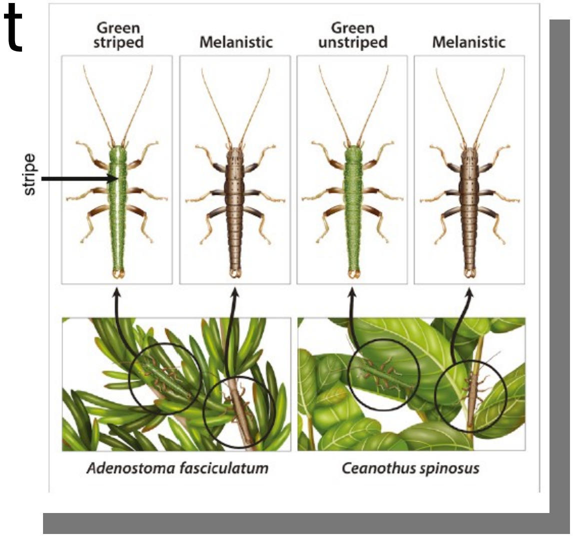
Polymorphism within a mimetic butterfly species: causes & consequences of balancing selection

Aussois, May 14th 2018

Adaptive variations

- Example of adaptive variat

Antirhinum majus
striatum
pseudomajus



Timema christinae

Dendrobates variabilis

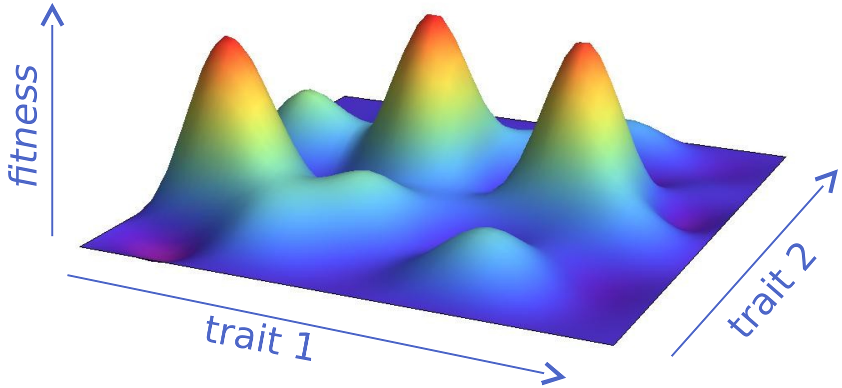
Dendrobates fantasticus

Dendrobates ventrimaculatus

- Comeault et al. 2015, Whibley et al. 2006, Symula *et al.* 2001

Adaptive variations

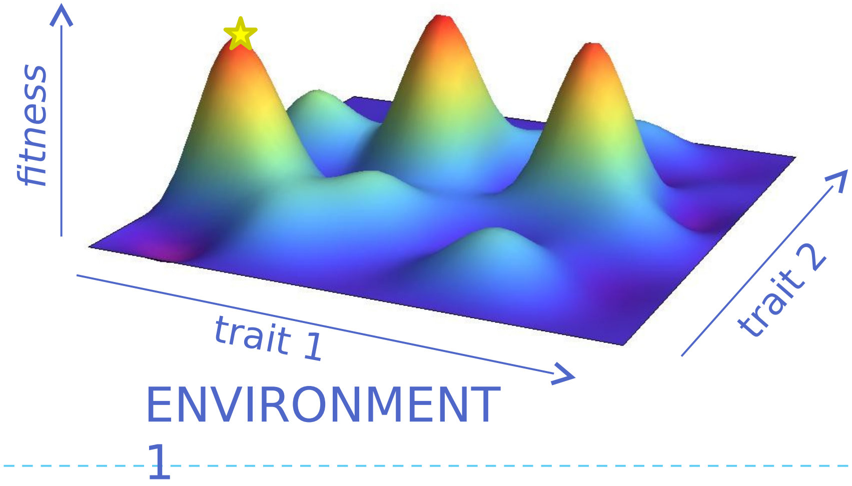
- Example of adaptive variations
- And create multidimensional adaptive landscapes



see Svensson & Calsbeek book for a review

Origin of variations

- Mutations:
  - Generally neutral or deleterious
  - Often not sufficient to generate new adaptive phenotype



Origin of variations

- Mutations:
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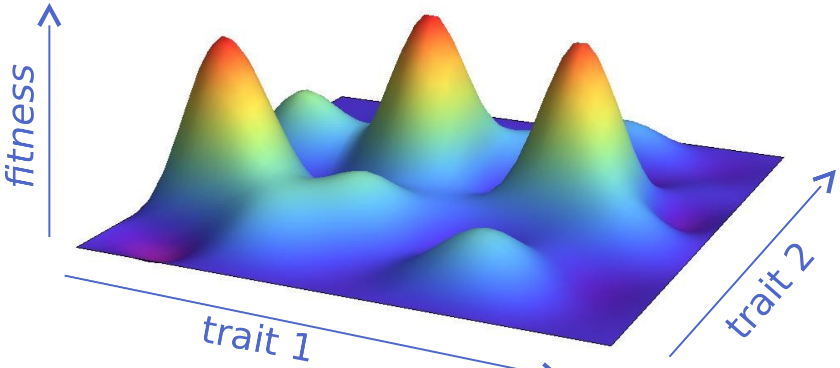
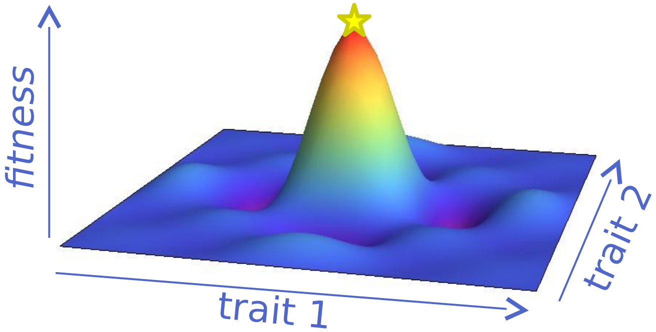
  - Often not sufficient to generate new adaptive phenotype
- Migration often associated with locally maladapted variants



ENVIRONMENT 1



ENVIRONMENT 2

Origin of variations

- Mutations:
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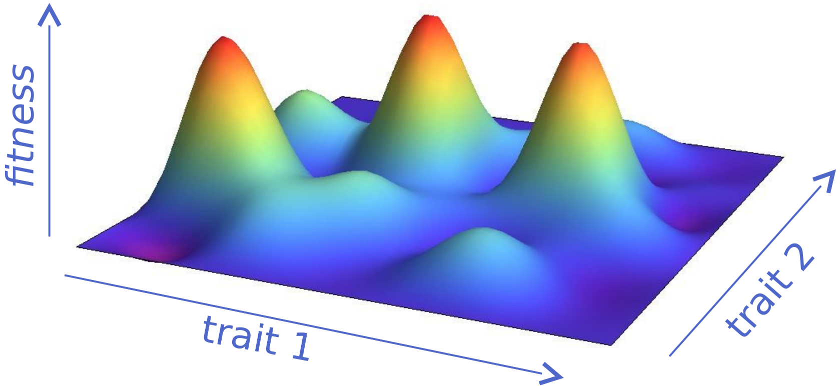
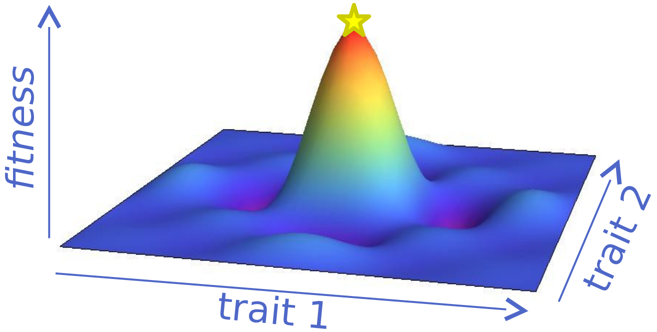
  - Often not sufficient to generate new adaptive phenotype
- Migration often associated with locally maladapted variants



ENVIRONMENT 1



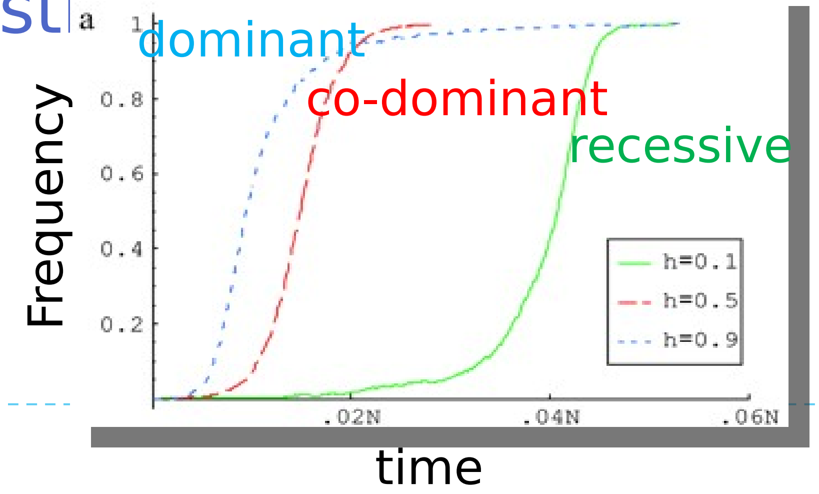
ENVIRONMENT 2

Origin of variations

- Mutations:
  - Generally neutral or deleterious
  - Often not sufficient to generate new adaptive phenotype
- Migration often associated with locally maladapted variants
- New variants appear at heterozygous state

□ Dominance over ancest

invasion probability



Teshima & Przeworki 2006 Genetics

Balancing selection as a tool

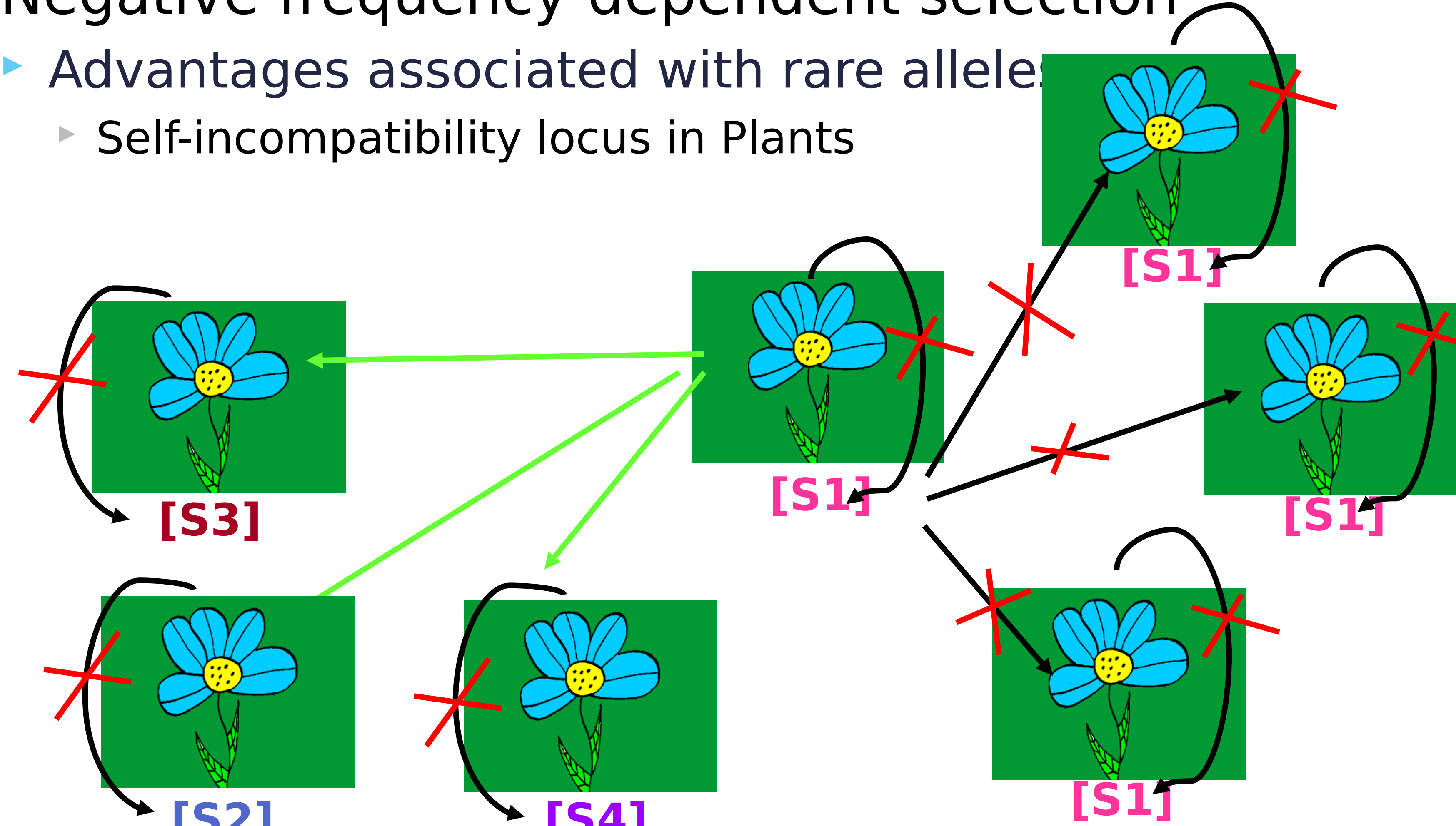
- Balancing selection : maintained several alleles at balanced frequencies
  - Typically maintaining several adaptive peaks in sympatry
  - Either stable or transient

- Unique opportunity to compare several adaptive variants in a common genetic background

- Investigate the influence of dominance in adaptation

Mechanims of balancing selection

- Negative frequency-dependent selection
  - Advantages associated with rare alleles
    - Self-incompatibility locus in Plants



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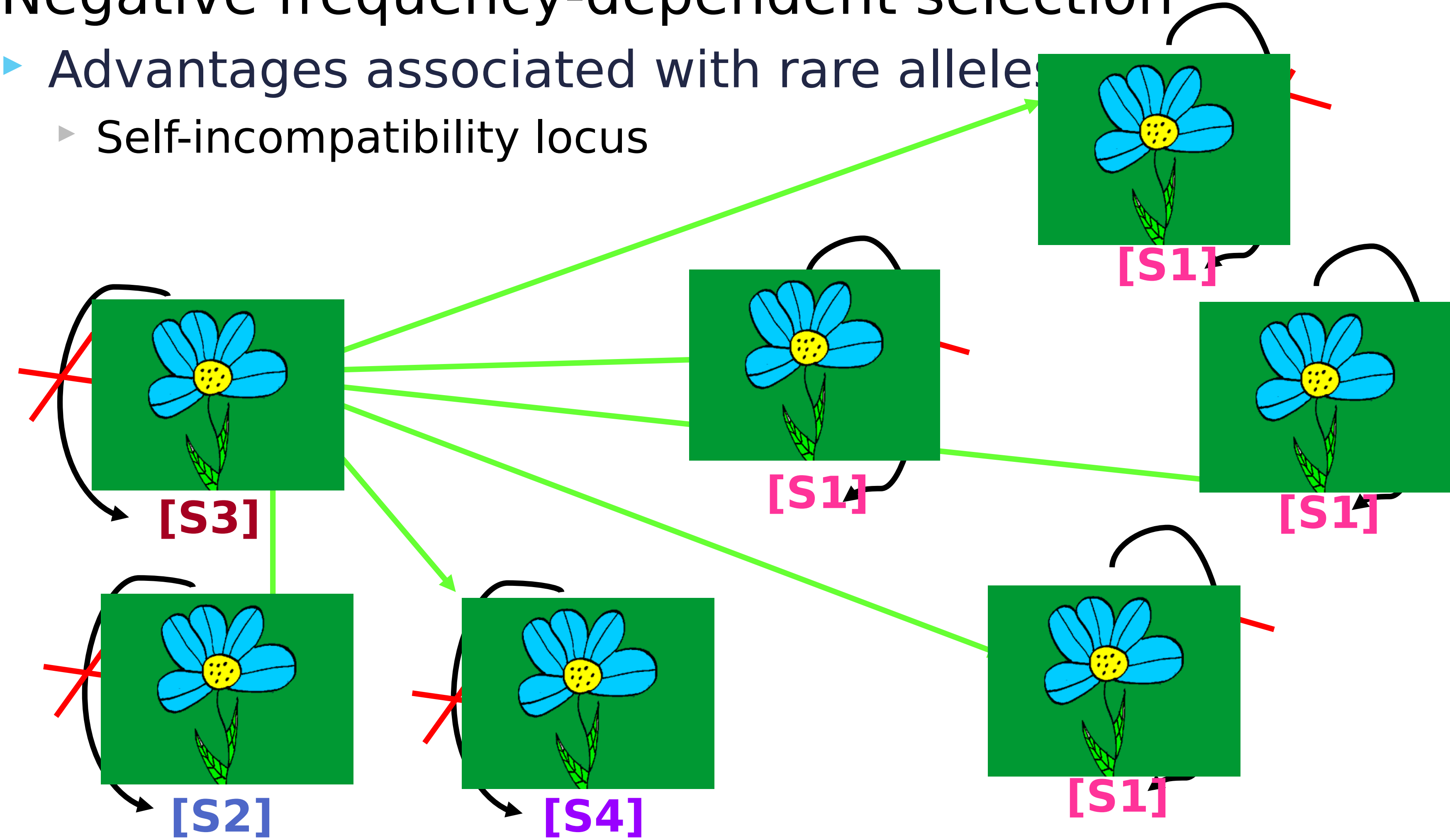
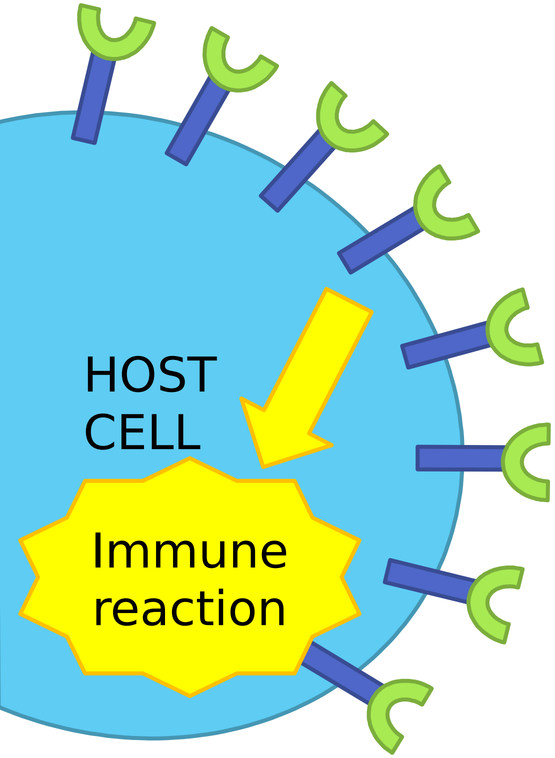


Mechanims of balancing selection

- Negative frequency-dependent selection
  - Advantages associated with rare alleles
    - Self-incompatibility locus
    - Manual preference in Humans

Mechanisms of balancing selection

- Negative frequency-dependent selection
- Heterozygote advantage
  - MHC in guppies



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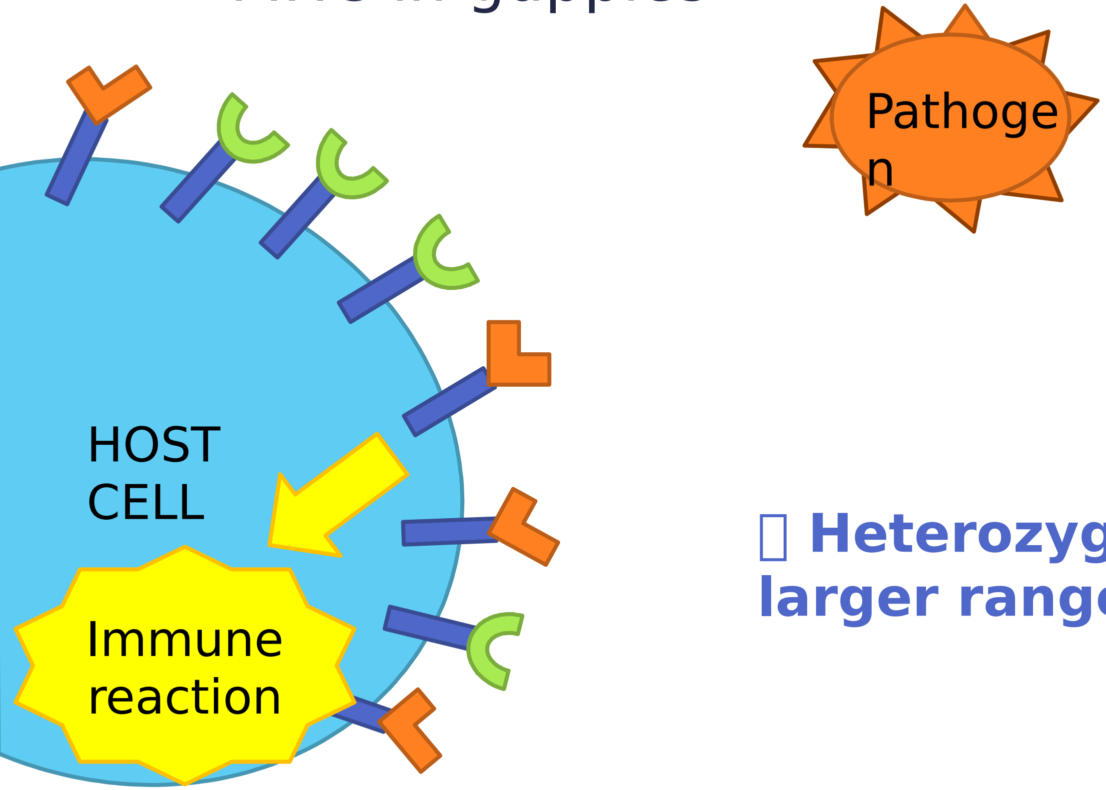
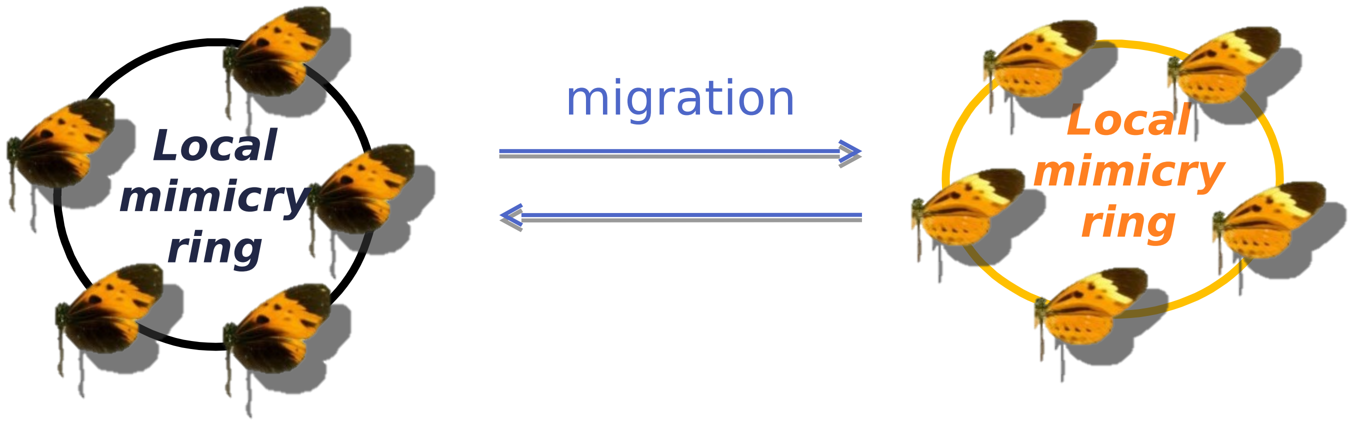


** Heterozygotes resisting to a larger range of parasites**

Mechanisms of balancing selection

- Negative frequency-dependent selection
- Heterozygote advantage
- Selection/migration equilibrium



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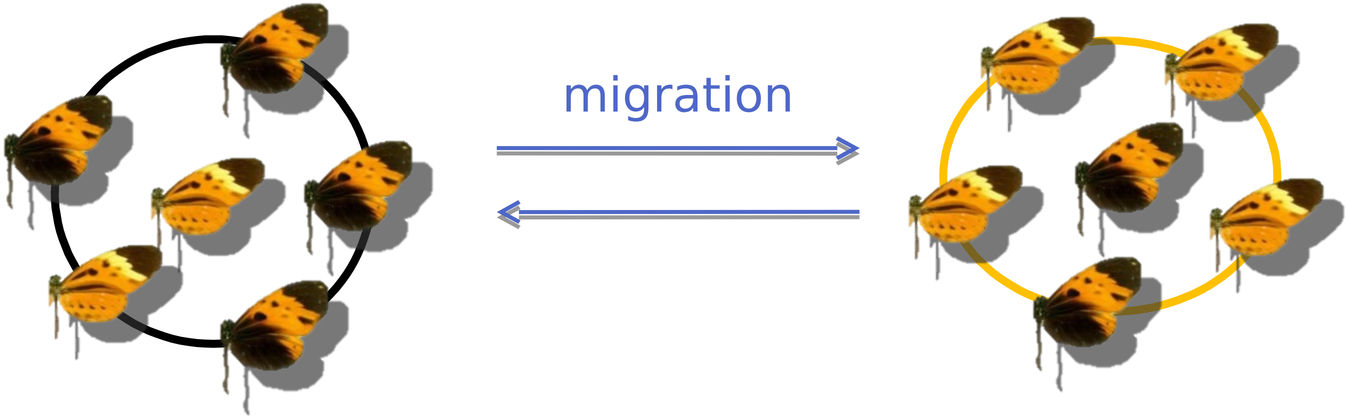

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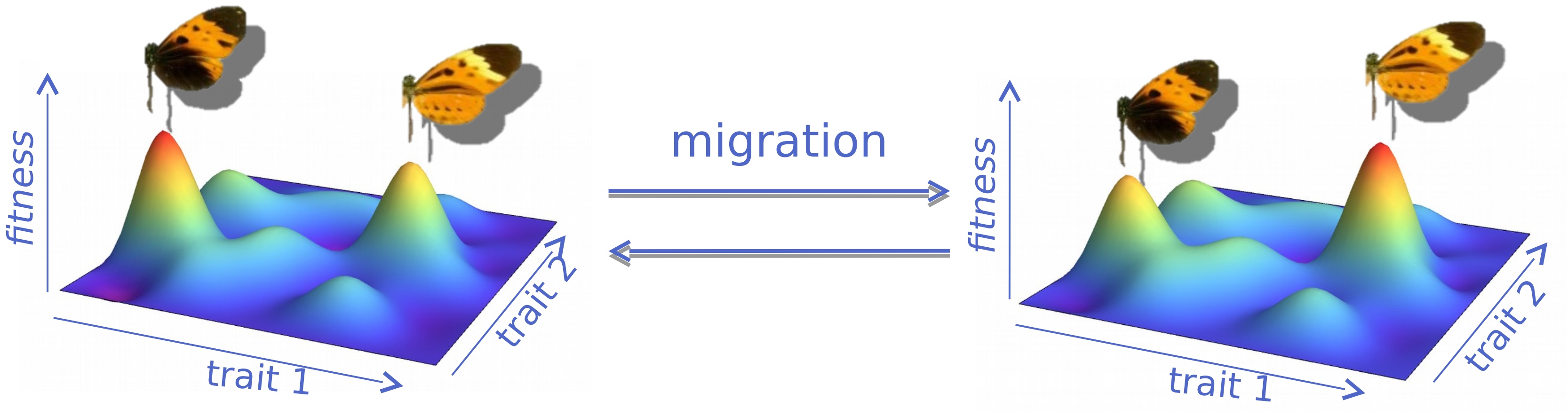
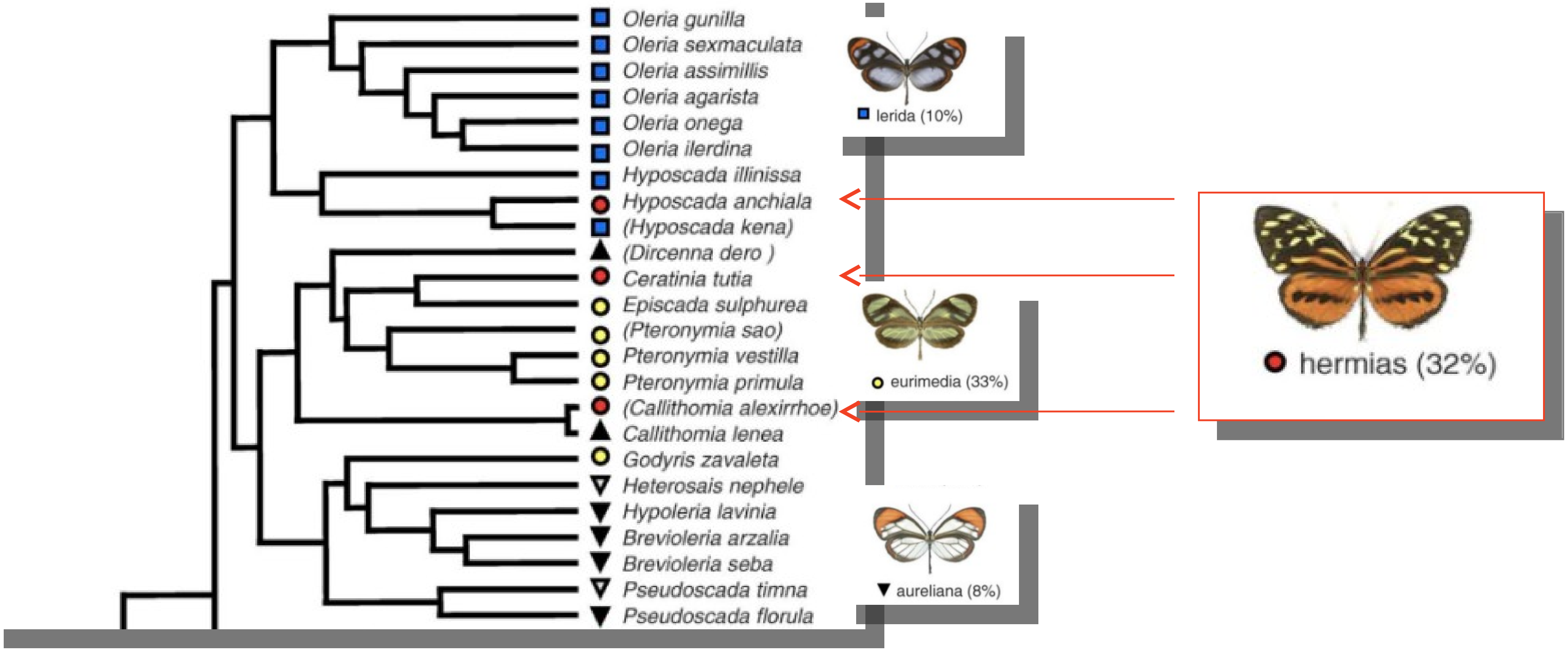


ENVIRONMENT 1

ENVIRONMENT 2

Polymorphic mimicry as a case-study

- Müllerian mimicry: evolutionary convergence among toxic species towards similar color patterns

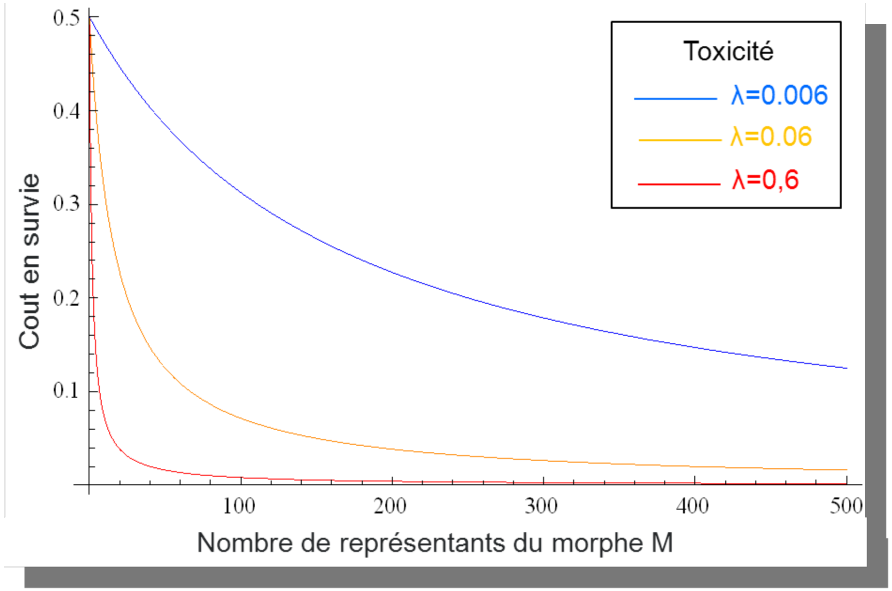


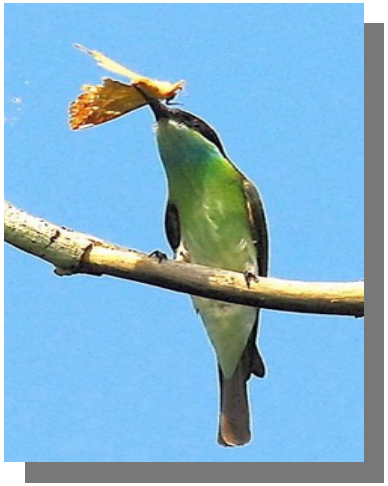
Elias et al. 2008

Polymorphic mimicry as a case-study

- Müllerian mimicry: evolutionary convergence among toxic species towards similar color patterns

- Strong positive number dependent selection by predators at local scale





Polymorphic mimicry as a case-study

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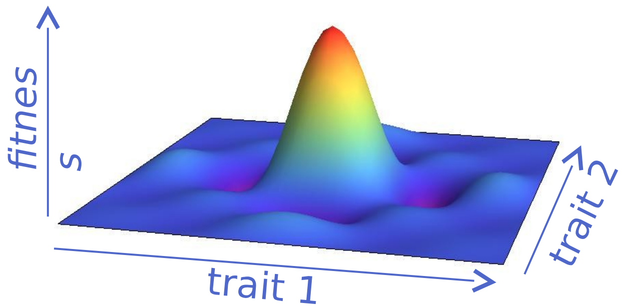
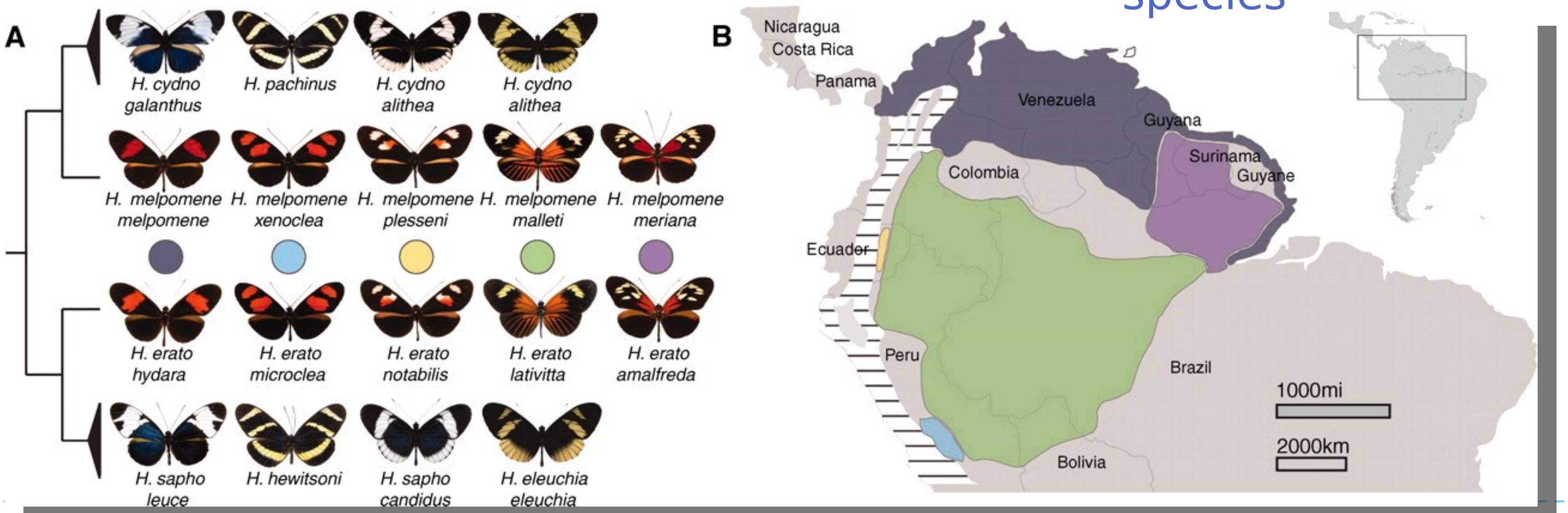
Geographic races of mimetic species



Most *Heliconius* species



Reed et al. 2011

Polymorphic mimicry as a case-study

- Müllerian mimicry: evolutionary convergence among toxic species towards similar color patterns

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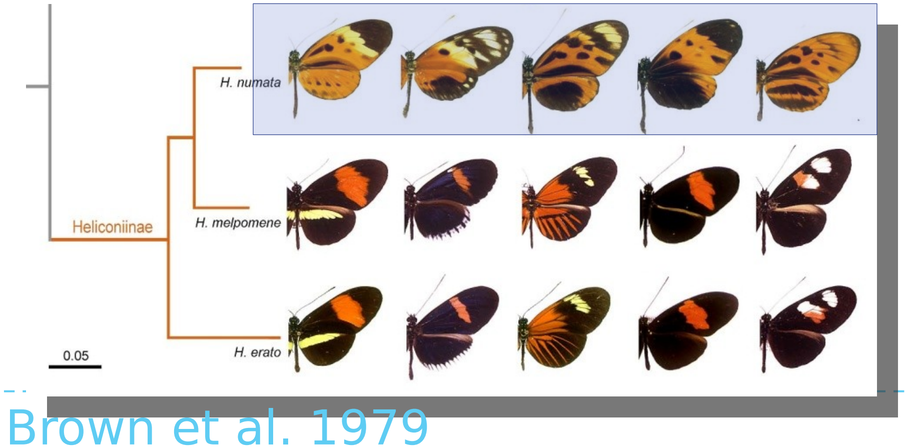
Geographic races of mimetic species

- Few cases of polymorphic mimicry

Heliconius numata



Brown et al. 1979

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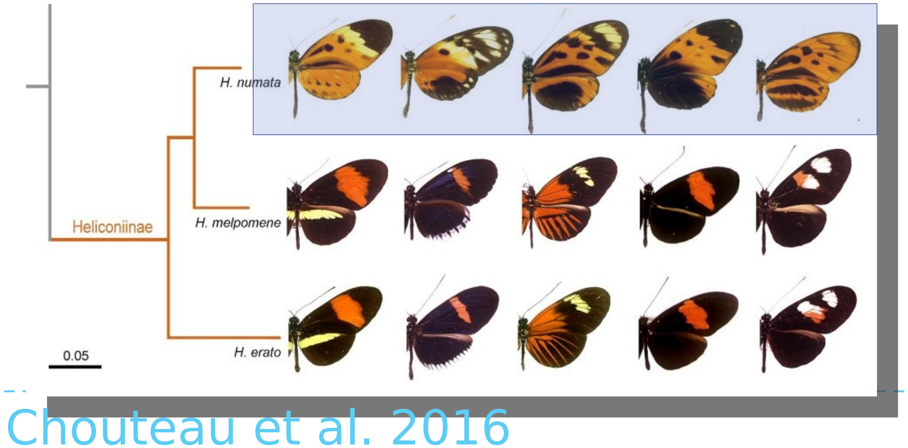
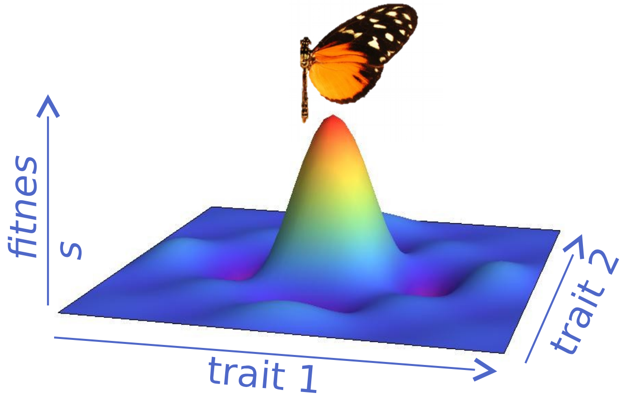
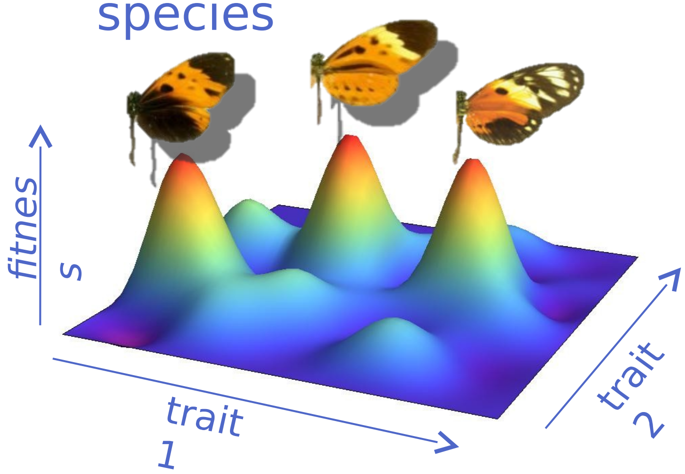
Heliconius numata





Most *Heliconius* species

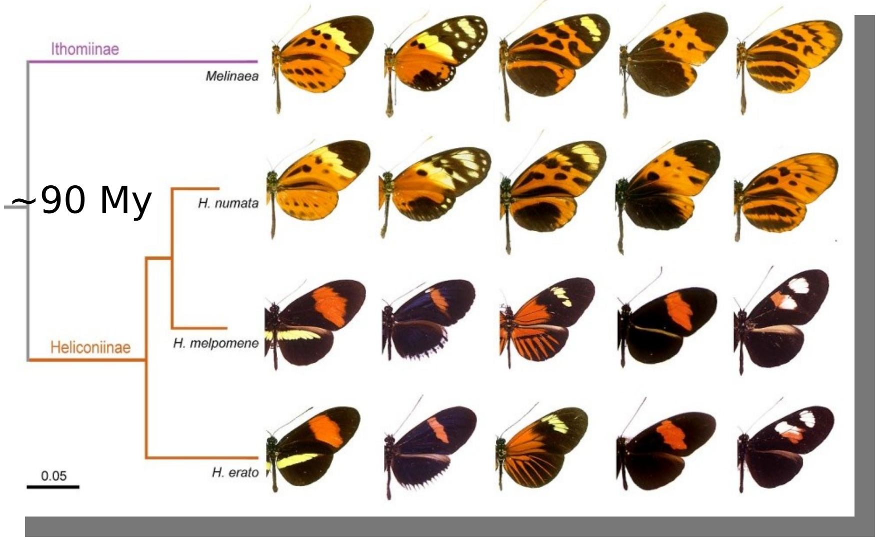


Heliconius numata

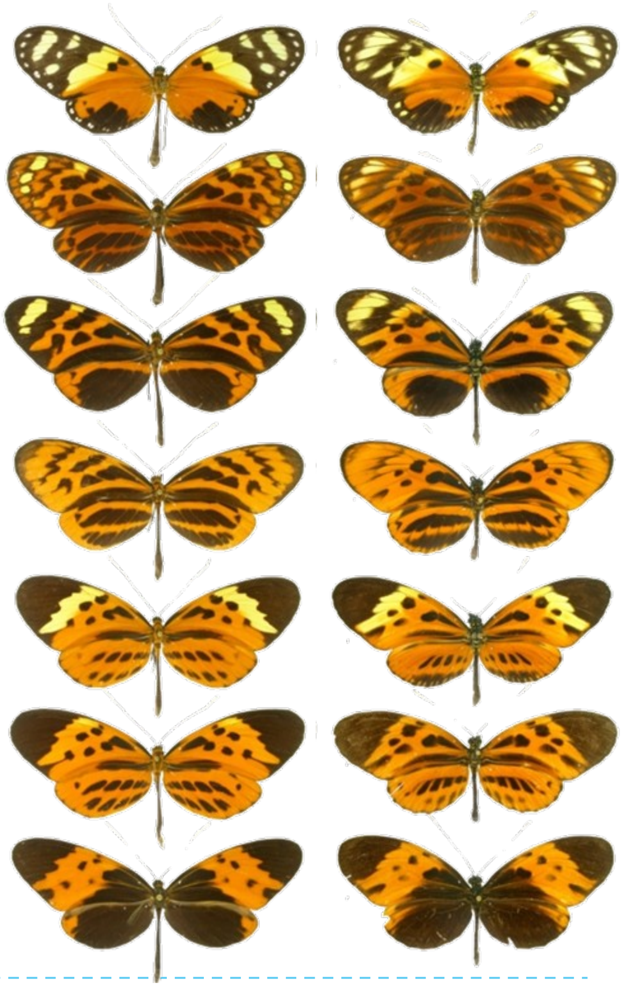
Chouteau et al. 2016

Heliconius numata as a model

- *H. numata :* striking resemblance with several species from the distantly related genus Melinaea (~90 My divergence)



~90 My

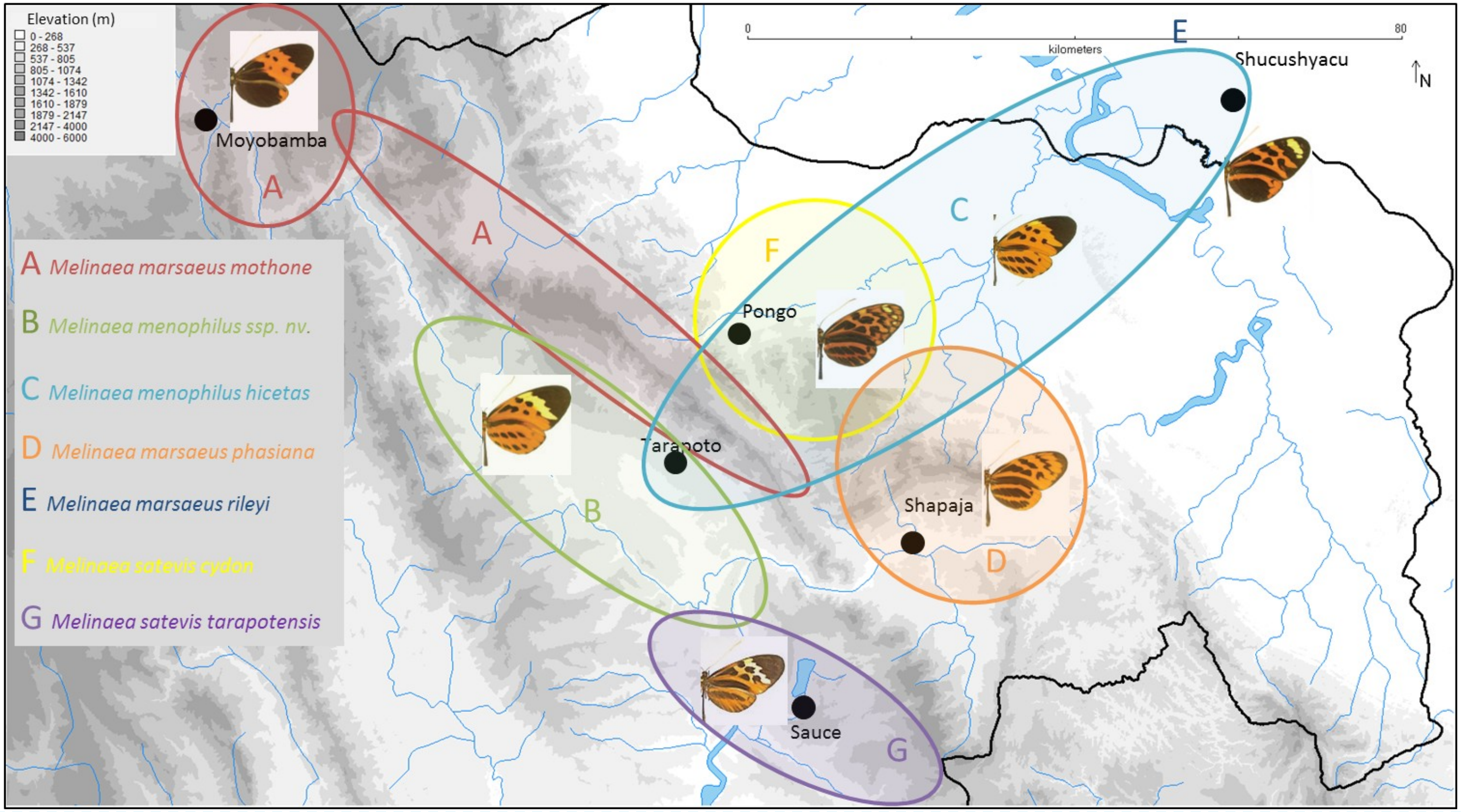


7 Melinaea sp.

H. numata

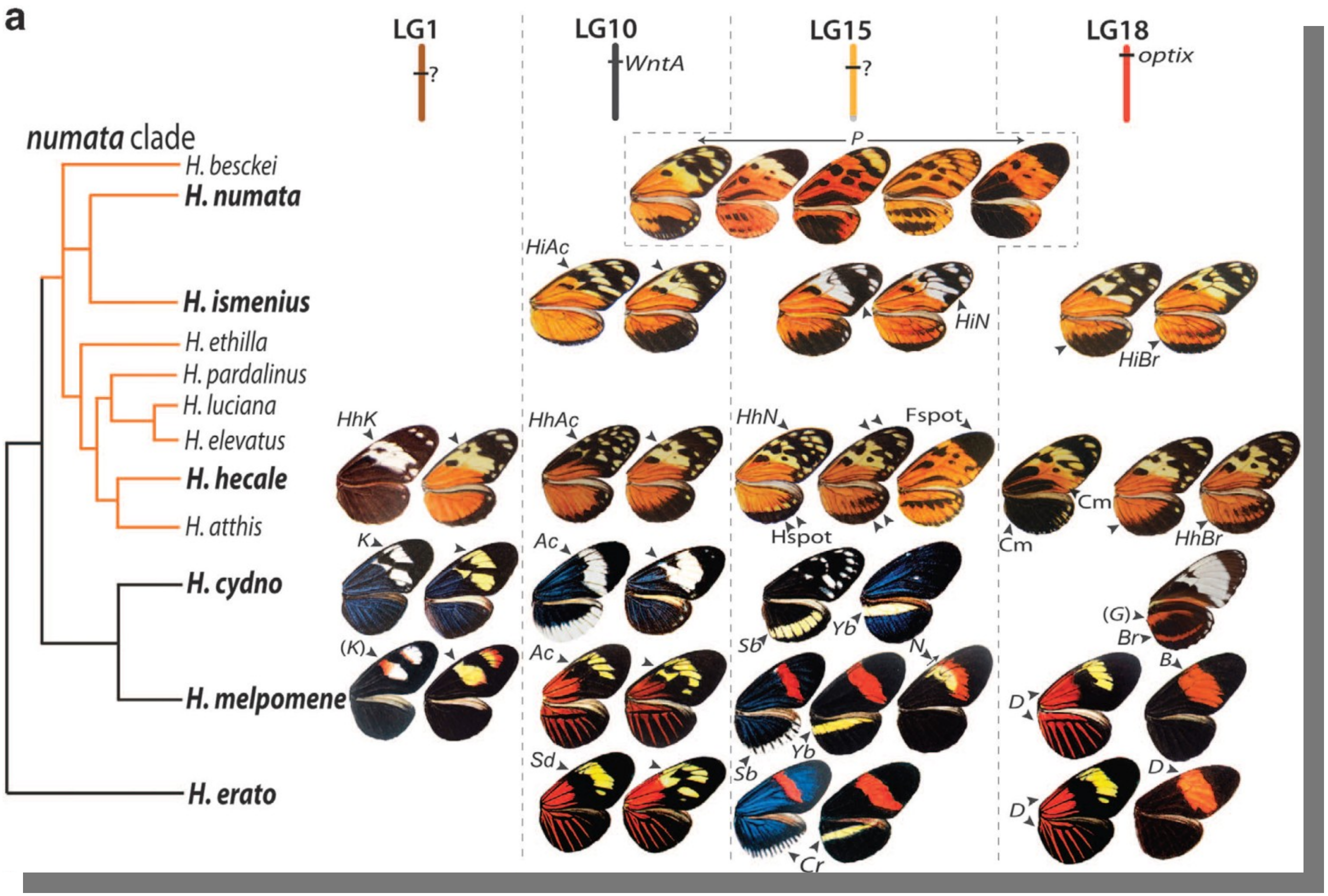
Origin of polymorphism *in Heliconius numata*

- Polymorphism driven by selection-migration equilibrium



Distribution of *Melinaea ssp* (San Martin Department – PERU) – from Mélanie McClure

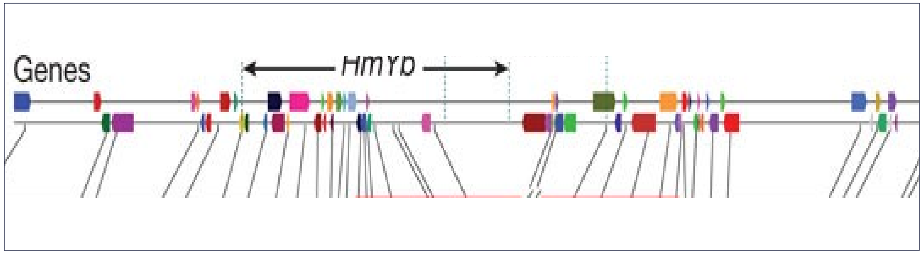
Genetic architecture of mimetic colour pattern in the *Heliconius* genus



- Huber et al. 2015

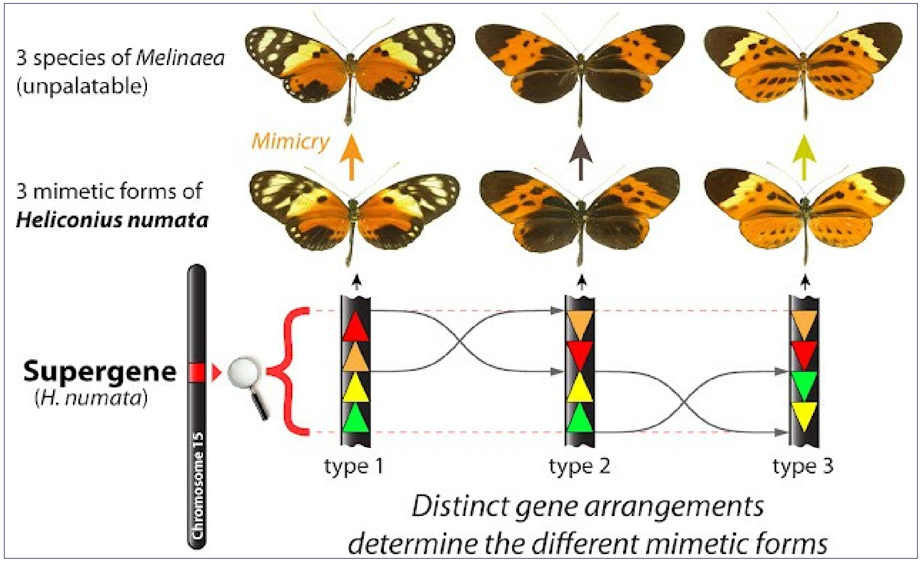
Genetic architecture of polymorphic mimicry in *H. numata*

- Supergene encoding for color pattern variations



- Polymorphic gene order corresponding to different mimetic alleles
- Limited recombination

 GENETIC ARCHITECTURE FAVOURING POLYMORPHISM

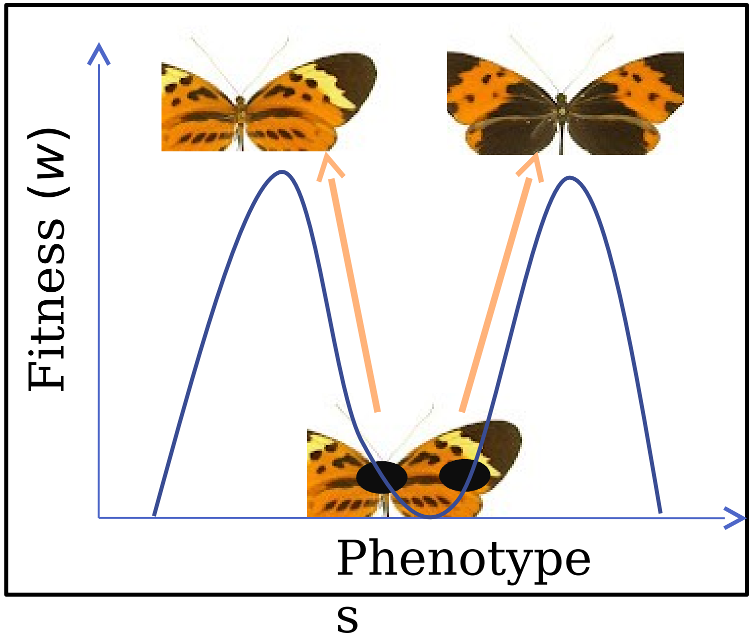


- Joron et al. 2011

Genetic architecture of polymorphic mimicry

- Polymorphic mimicry

 High frequency of heterozygotes



- Selection on intermediate phenotype by predators

➔ Selection on dominance in natural populations ?

- Persistence of polymorphism ?

 Role of mating system ?

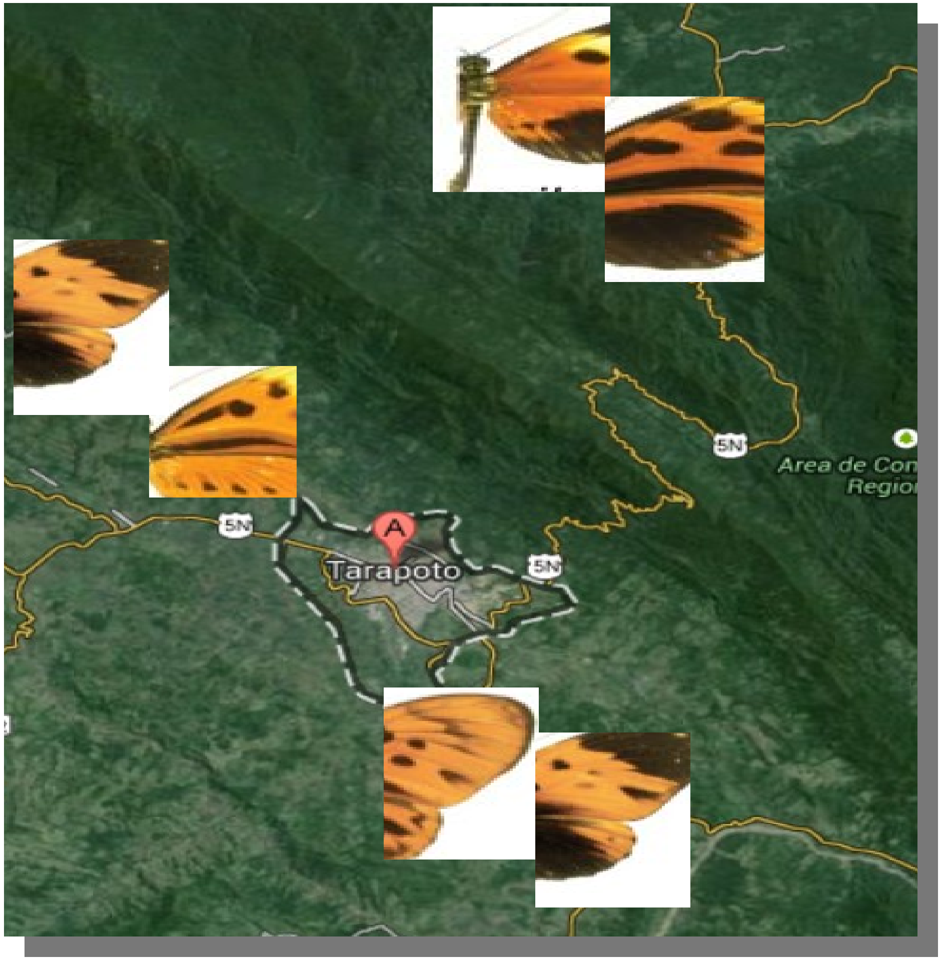
Selection on intermediates within natural populations

- Test in natural populations (Perù) using artificial butterf

Monica Arias
Labex Phd

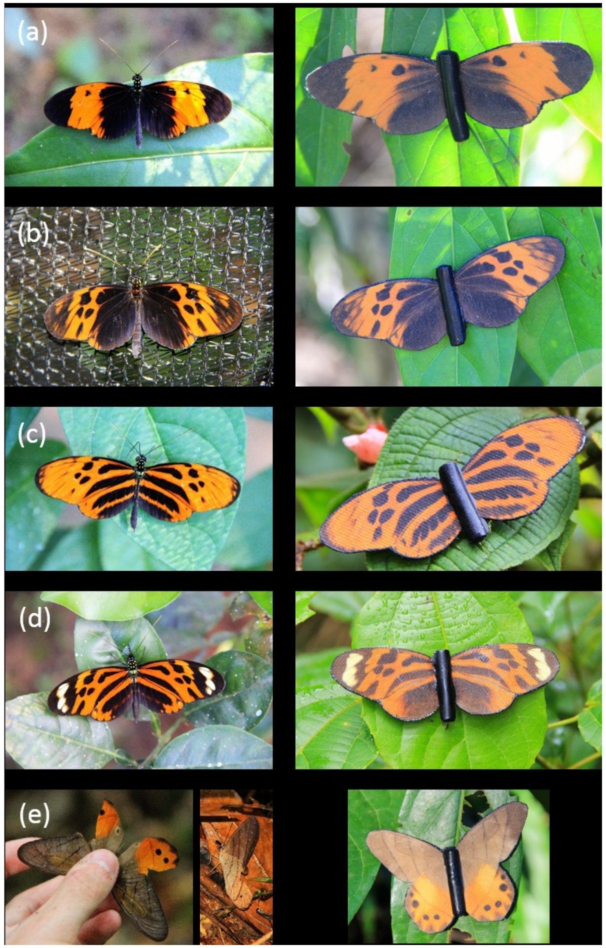
Arias et al. 2016

Selection on intermediates within natural populations – study sites



- Arias et al. 2016

Selection on dominance within natural populations- experimental design



Local (*bicoloratus*)

Intermediate (*bic/arc*)

Local (*arcuella*)

Exotic but aposematic

Local but cryptic and palatab

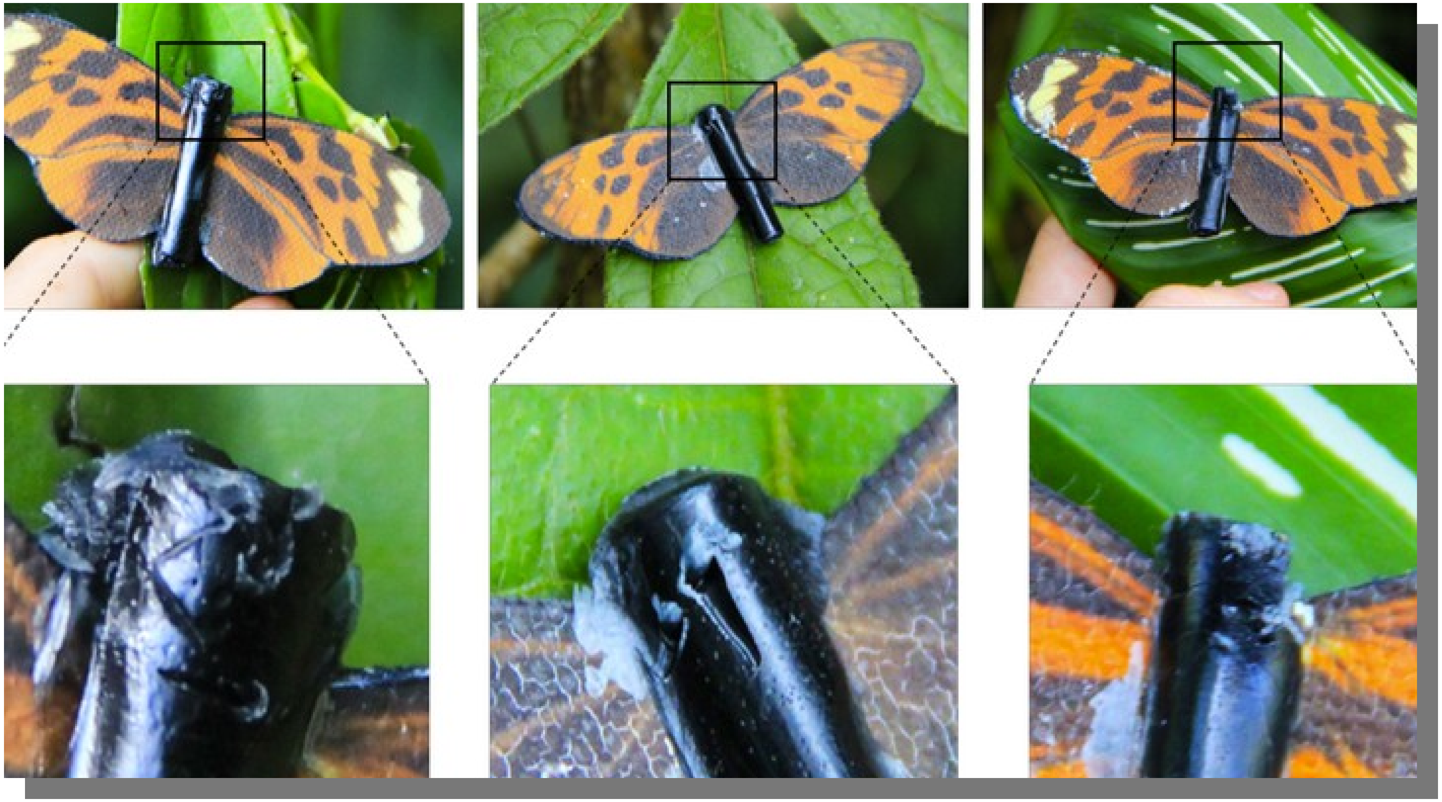
- Arias et al. 2016

Selection on intermediates within natural populations- experimental design

- Experimental sites
  - Light gap on a transect: 150 per trial
- Five colour patterns per gap
- Left 72 hours before checking

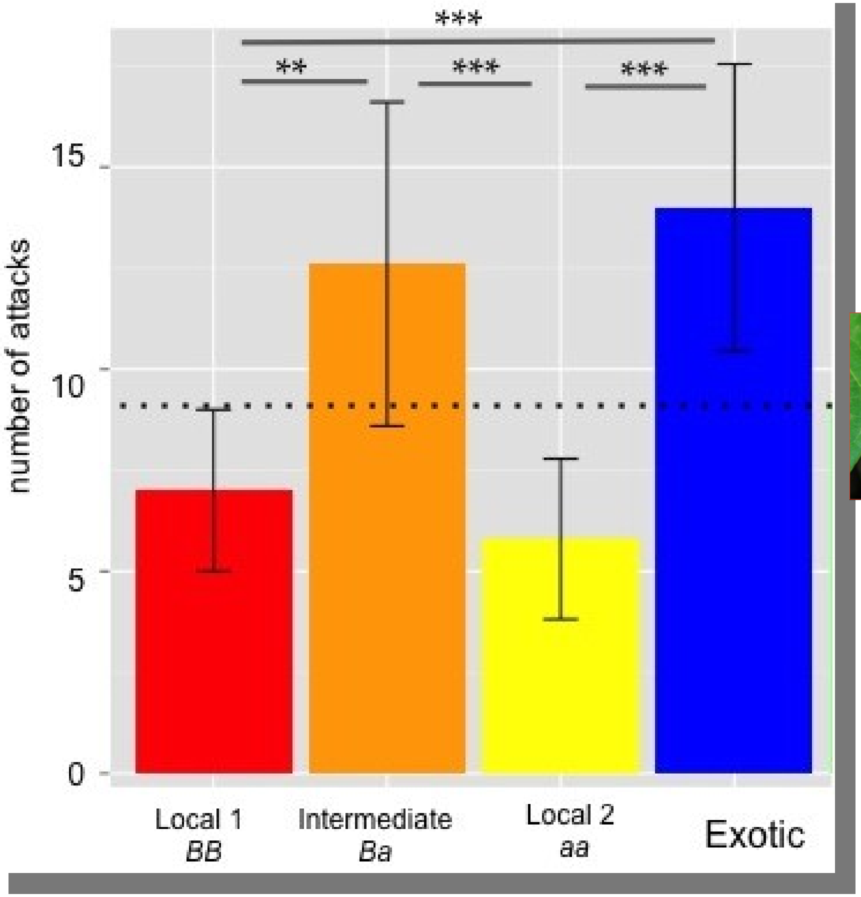
Arias et al. 2016

Selection on dominance within natural populations- attacks



- Arias et al. 2016

Selection on intermediates within natural populations



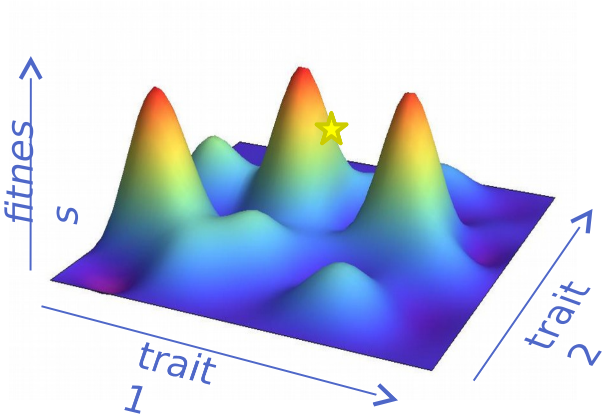
- Significantly higher attacks:
  - On exotic morphs
  - On heterozygotes exhibiting an intermediate phenotype

➔ Overall, significant selection against co-dominance in heterozygotes carrying sympatric alleles.

Arias et al. 2016

Selection on dominance within natural populations

- Selection againt intermediate detected within natural population
  - Selection acting on slightly deviating heterozygotes
- Impact on polymorphism ?

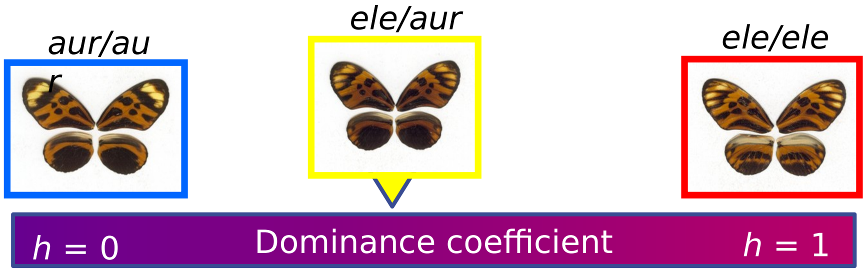


Arias et al. 2016

Modeling the impact of dominance

- Modelling dominance

$$h = \frac{T_{aur/ele} - T_{aur/aur}}{T_{ele/ele} - T_{aur/aur}}$$



Llaurens et al. 2013

Modeling impact of dominance

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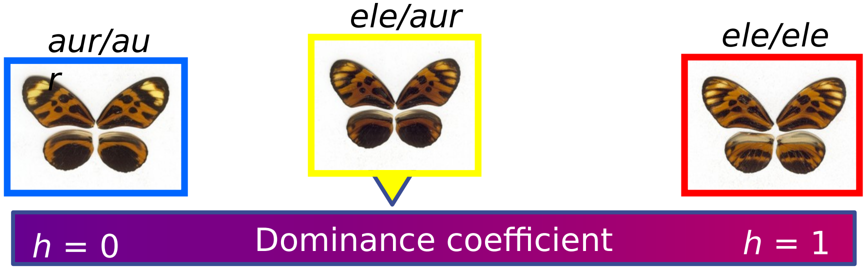


- Modelling predator behavior

- Modelling predator behavior
  - Generalisation function

  - Generalisation function

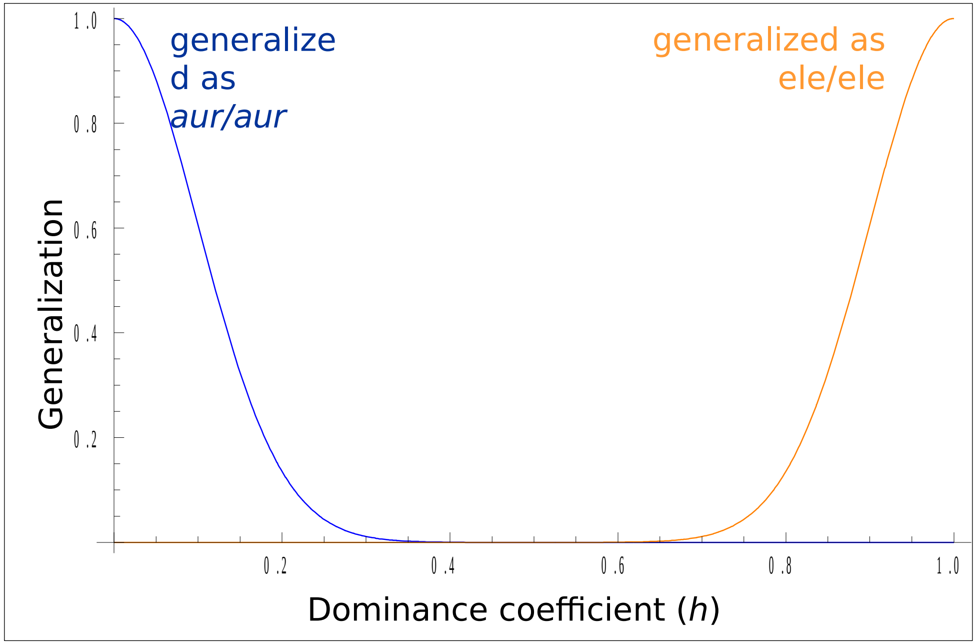
$$g(h) = e^{-(h-1)^2/2\gamma^2}$$

With h : *dominance coefficient*

And width of predators generalisation capacities.

With h : *dominance coefficient*

And width of predators generalisation capacities.



Llaurens et al. 2013

Modeling the impact of dominance

- Two mimicry rings:
  - Local rings (no migration)
  - Same abundance in each locality

Predation rate *d*

Spatial heterogeneity σ

- One mimetic species:
  - Two populations

Migration *m*

  - Frequency dependent selection

Toxicity of the polymorphic species λ

Number of individual sharing the same phenotype

- Two mimicry rings:
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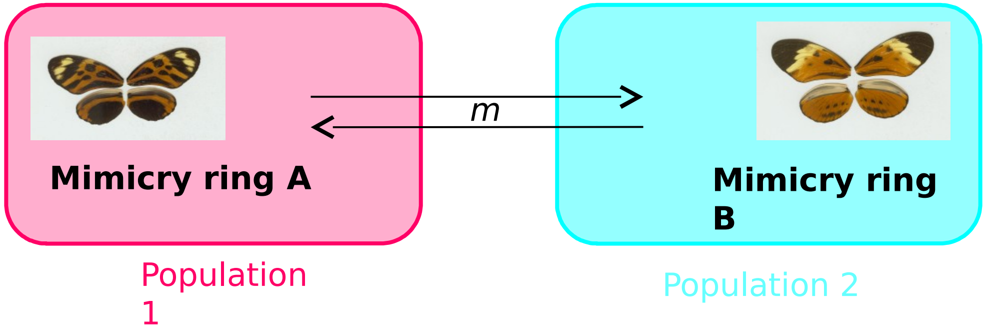


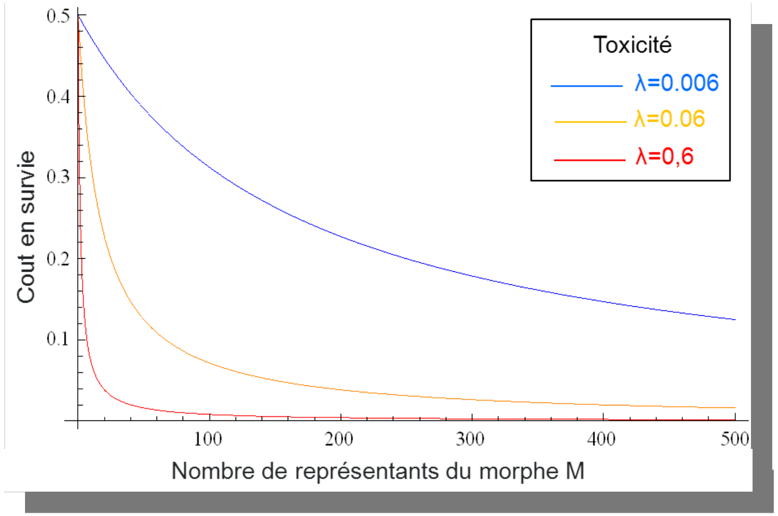
Mimicry ring A

m

Mimicry ring B

Population 1

Population 2



Llaurens et al. 2013

Modeling the impact of dominance

$$Naa_1(t+1) =$$

$$\left.\frac{-d(1-\sigma)}{1+\lambda(Naa_1(t)+g(h)Nab_1(t))}Naa_1(t)\right\}\text{Predation}$$

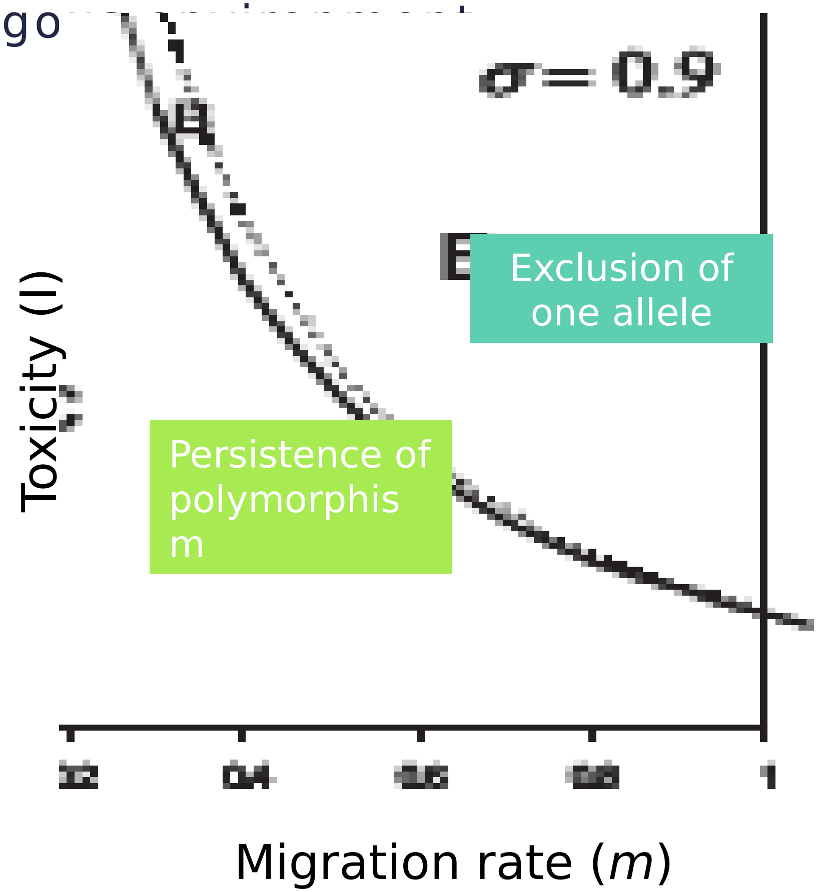
$$\left.+m\left(Naa_2(t)-Naa_1(t)\right)\right\}\text{Migration}$$

$$\left.+\frac{r}{2}(\frac{(Nab_1(t)+2Naa_1(t))^2}{4Ntot_1}(1-\frac{Ntot_1(t)}{K})\right\}\text{Reproduction}$$

Llaurens et al. 2013

Persistence of polymorphism

- Persistence of polymorphism due to migration/selection balance, in heterozygo
- In haploid model :



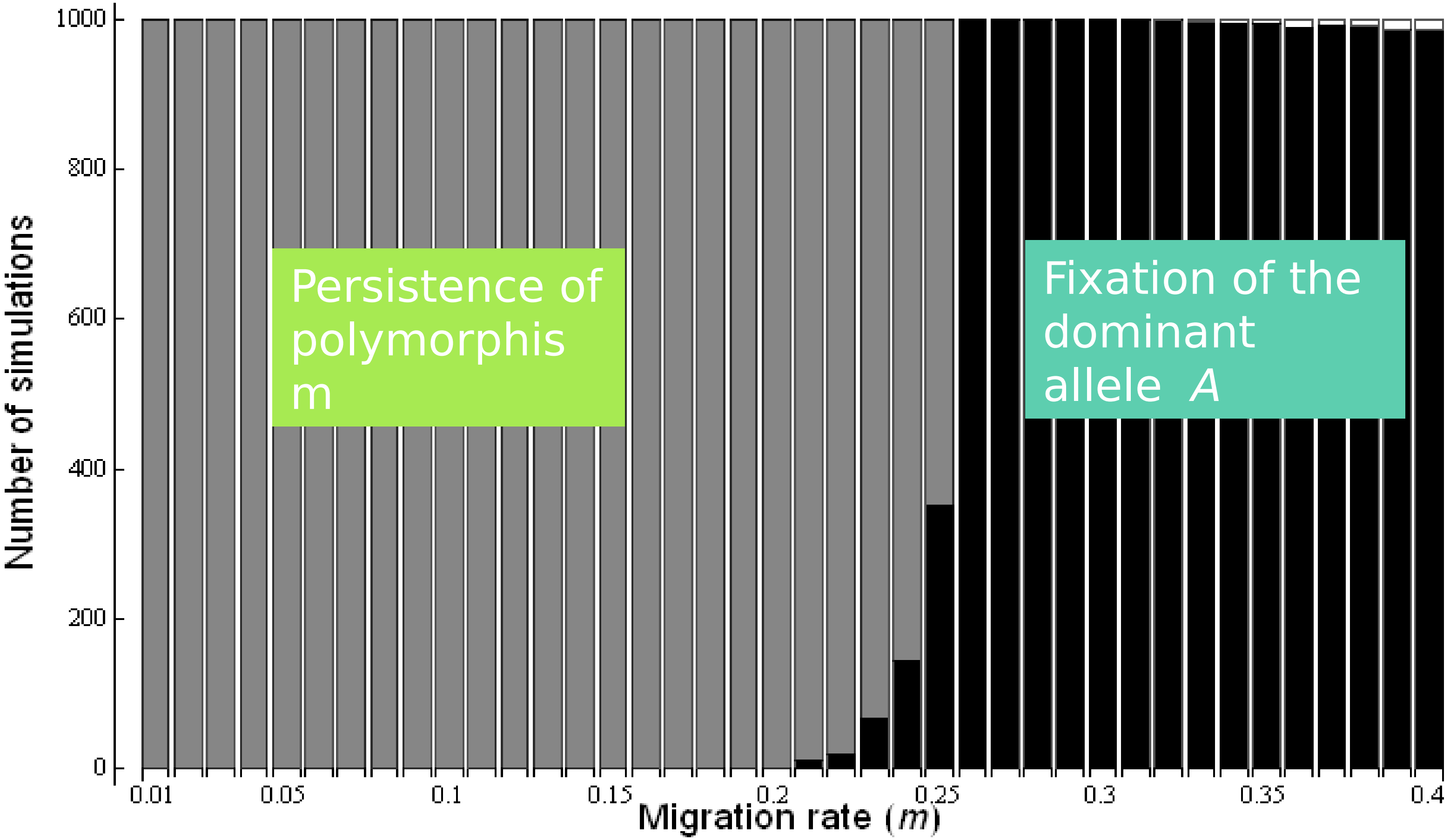
Exclusion of one allele

Persistence of polymorphism

Joron & Iwasa 2005

Persistence of polymorphism

- Strict dominance ($h = 1$) & $d = 0.5$, $\lambda = 0.025$



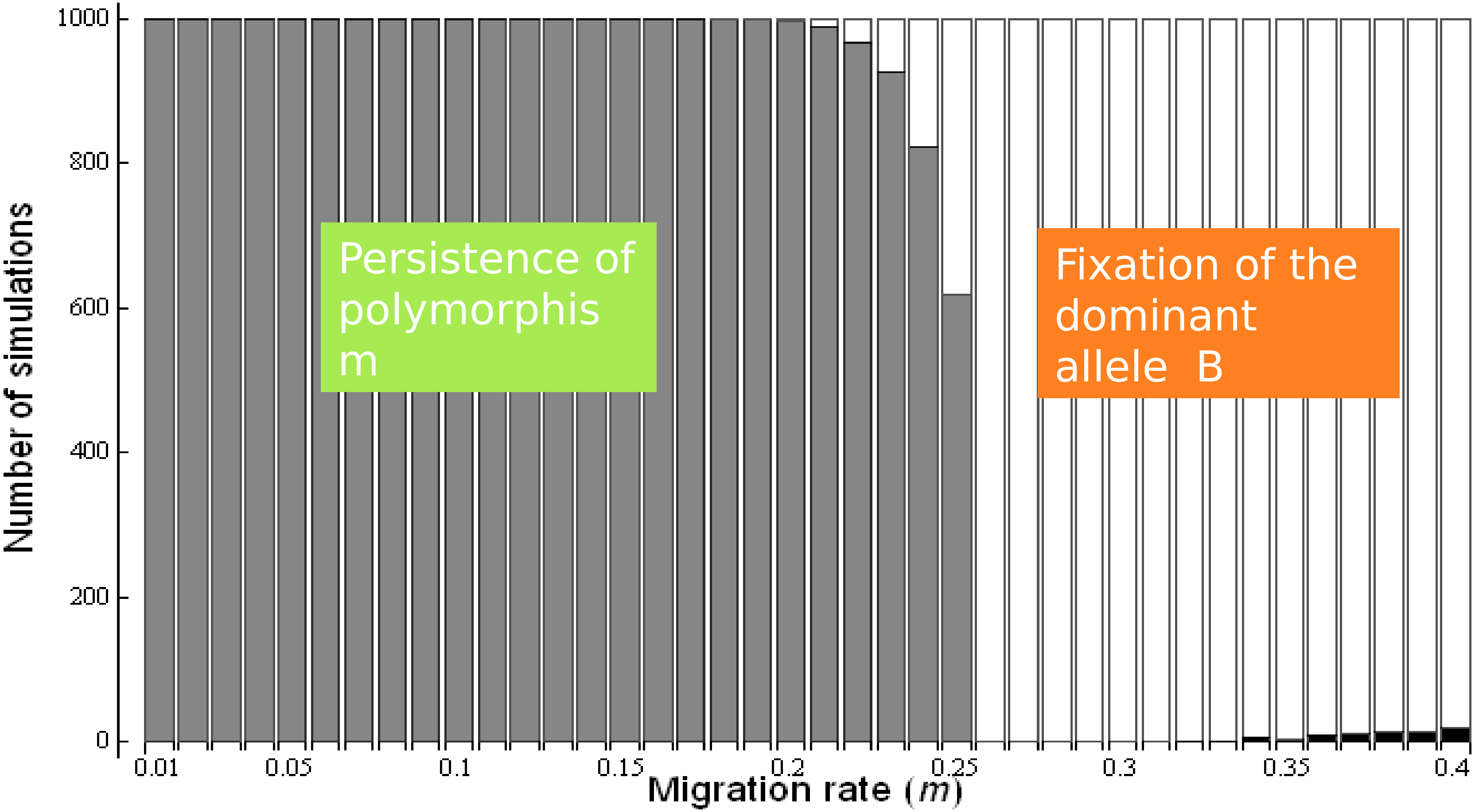
Persistence of polymorphis m

Fixation of the dominant allele *A*

Llaurens et al. 2013

Persistence of polymorphism

- Strict dominance *(h=1):* B > A



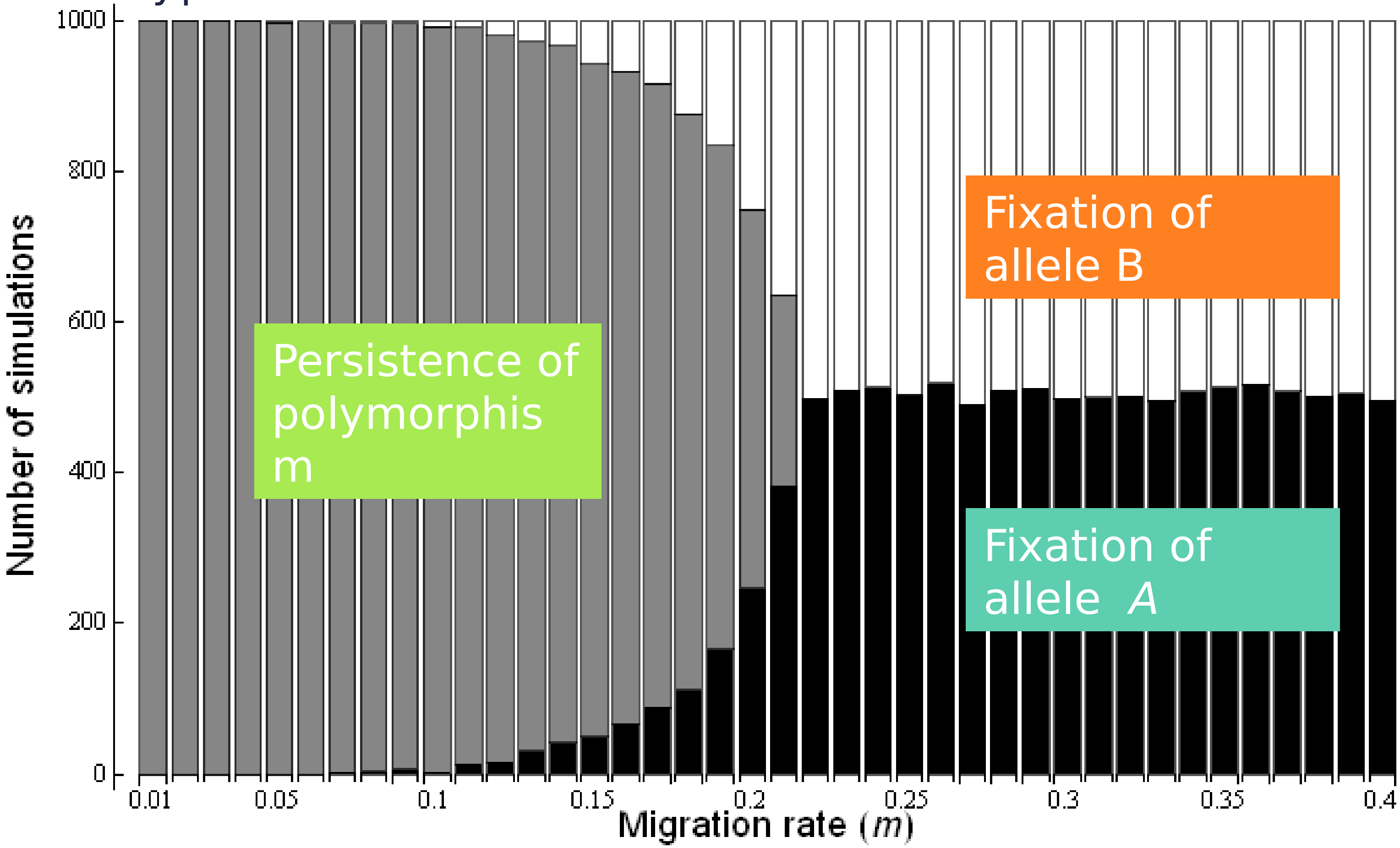
Persistence of polymorphism

Fixation of the dominant allele B

Llaurens et al. 2013

Persistence of polymorphism

- Co-dominance *(h=0.5):* heterozygote AB with intermediate phenotype



Llaurens et al. 2013

Persistence of polymorphism

- Co-dominance *(h=0.5):* heterozygote AB with intermediate phenotype

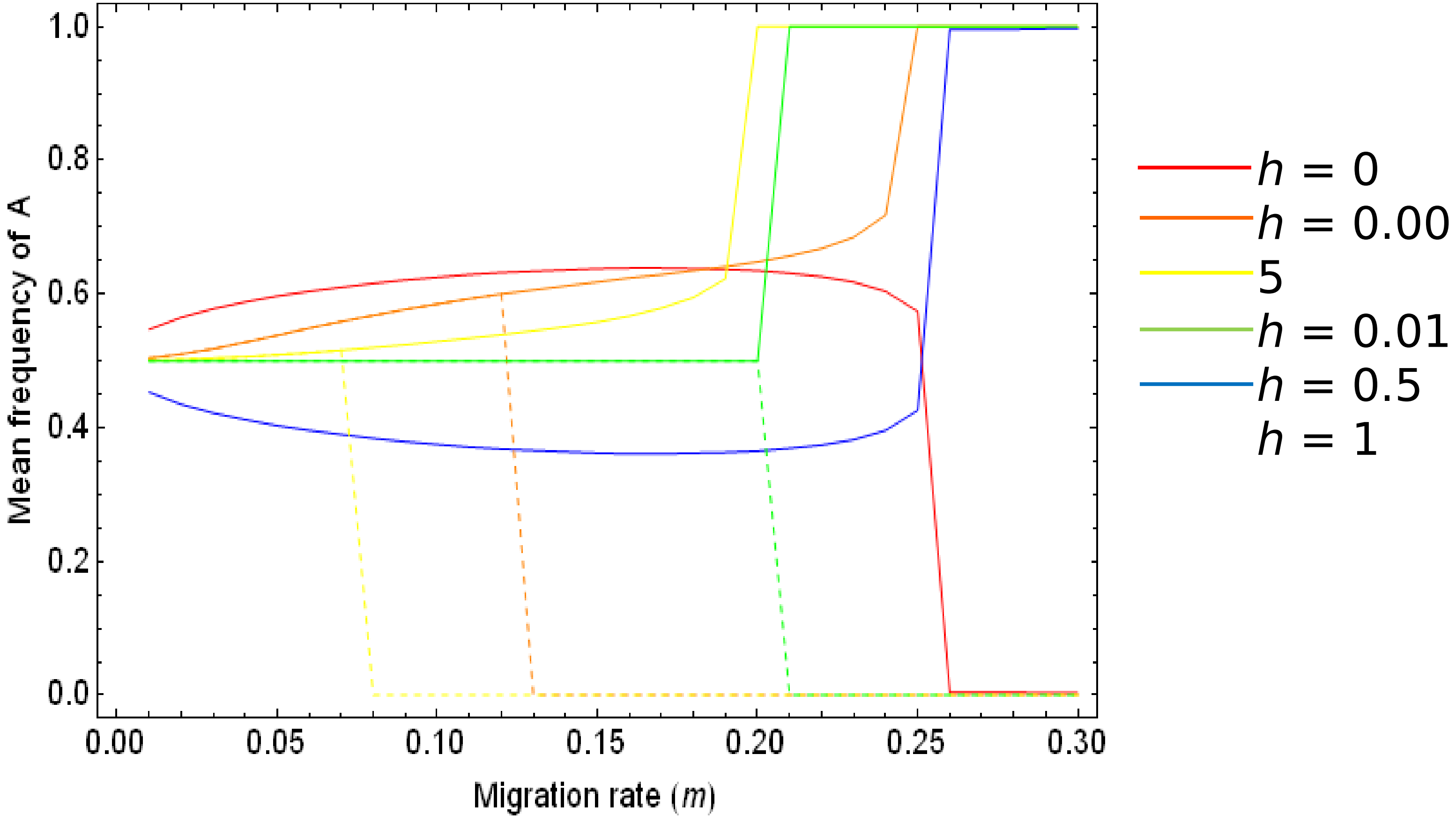
➔ ***Loss of polymorphism for lower values of m***

➔ ***Migration load higher when heterozygotes are intermediate***

Llaurens et al. 2013

Allelic frequencies in the metapopulation

- Fixation and frequencies depend on dominance



Llaurens et al. 2013

Persistence of polymorphism

- Selection /migration balance
- Modulates by heterozygote behaviour
- Dominant alleles tend to be fixed when migration increases

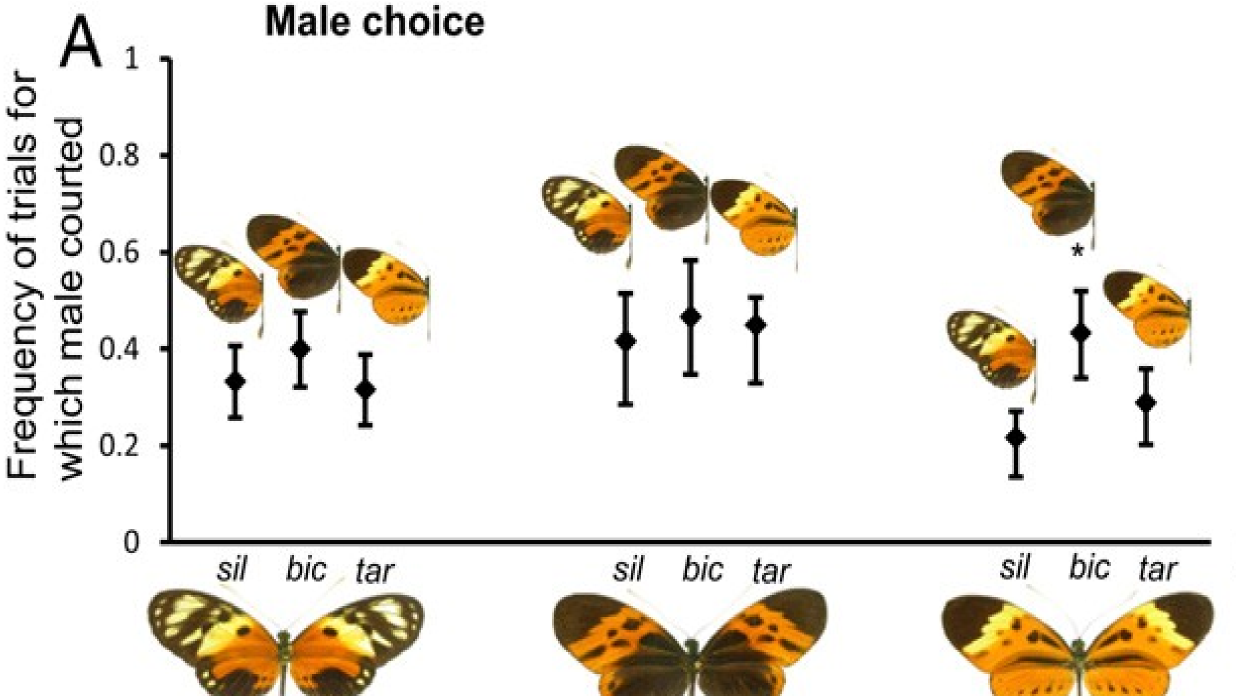
➔Nevertheless polymorphism is stable throughout

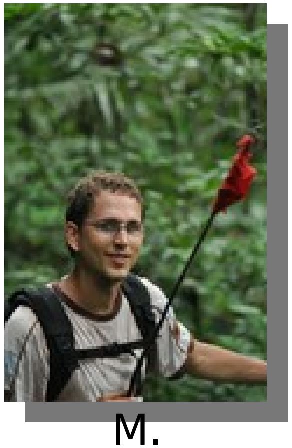
***H. numata* range**

Llaurens et al. 2013

Mate preferences for wing colour patterns

- Male & female preferences for wing colour patterns.





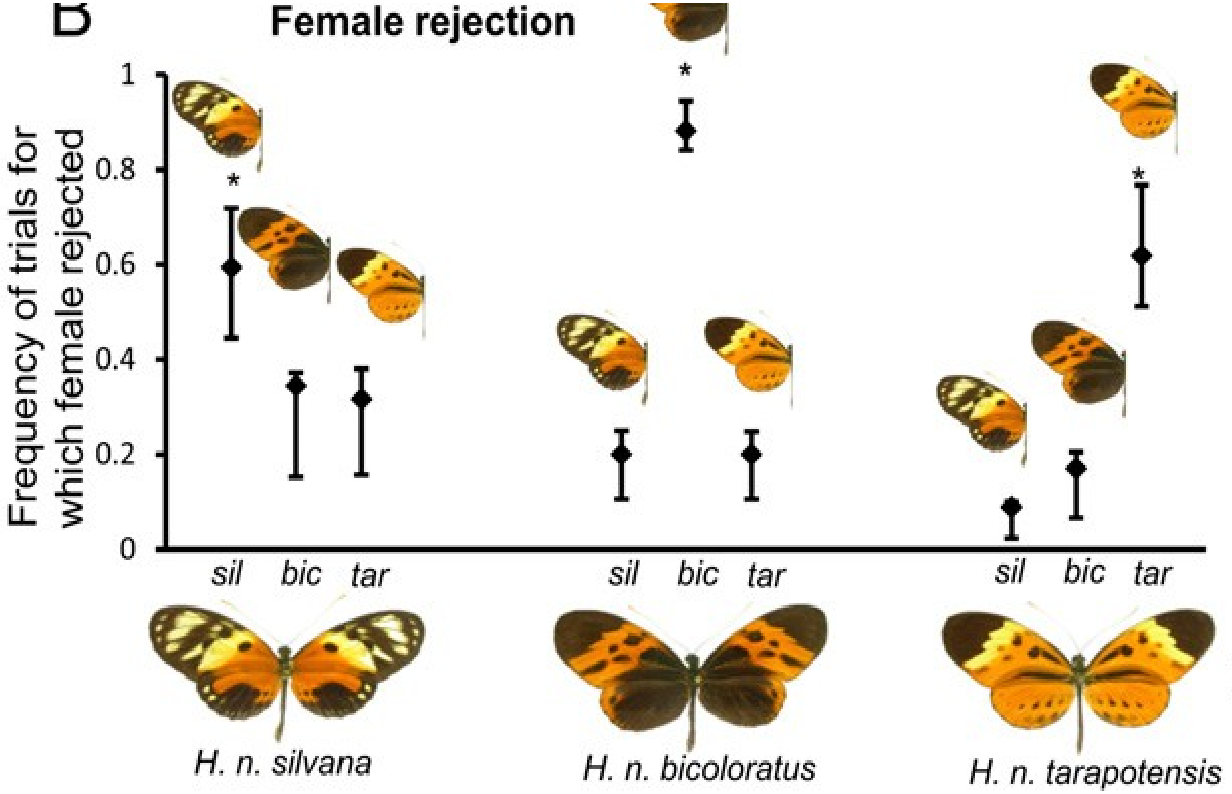
M. Chouteau
Marie Curie
postdoc

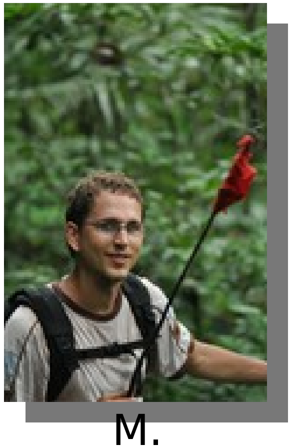
 NO PREFERENCE DETECTED IN MALES

- Chouteau et al. 2017

Mate preferences for wing colour patterns

- Male & female preferences for wing colour patt





M. Chouteau
Marie Curie postdoc

 STRONG COLOUR PATTERN-BASED DISASSORTATIVE PREFERENCES IN FEMALES

- Chouteau et al. 2017

Mate preferences for wing colour patterns

- Realized mating:
  - Tetrad experiments with 2 males and 2 females with different morphs
  - Mating events recorded

▯ STRONG COLOUR PATTERN-BASED DISASSORTATIVE MATING

Number of matings in tetrad		
	Male	
Female		
	10	13
	30*	7*
	 Male	
Female 		
	15	14
	24* 	7* 
	Male	
Female 		
	6*	28*

- Chouteau et al. 2017

Dominance and disassortative mating

- Consequences on polymorphism within populations ?

- From the previous model
  - Mate preference parameter, which depends on resemblance
    - Mate=0 ▯ Strict assortative mating
    - Mate=0,5 ▯Random Mating
    - Mate=1 ▯ Strict disassortative mating

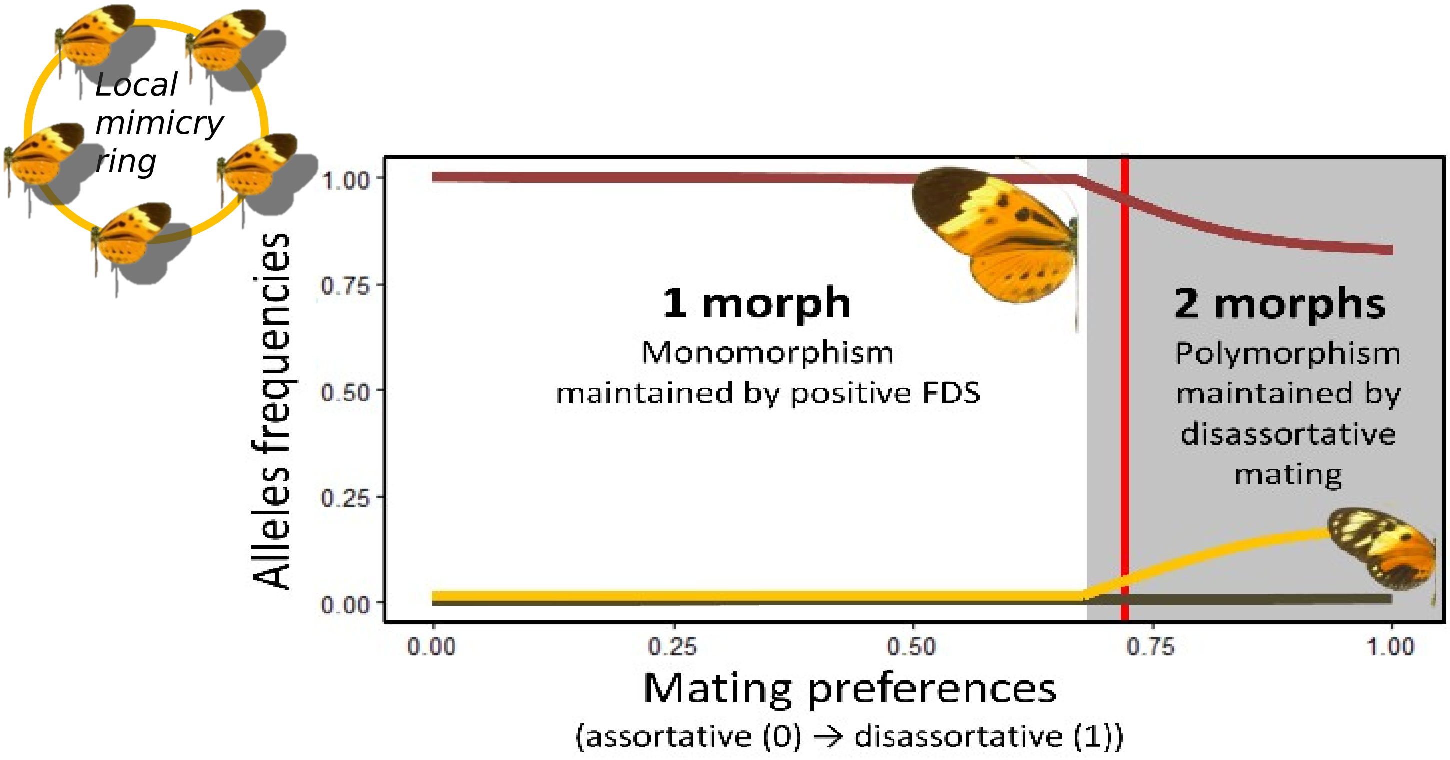
$$Pref_{[i][j]} = mate(1 - Res_{[i][j]}) + (1 - mate)Res_{[i][j]}$$

  - Three mimetic alleles with:

Chouteau et al. submited

Effect of disasssortative mating - within a single population

- Disassortative mating **within a single** population, assuming:



Chouteau et al. submited

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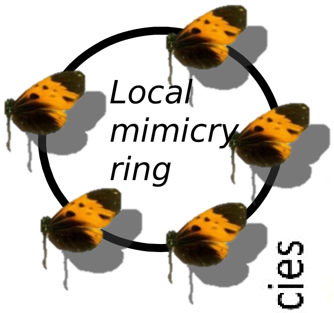

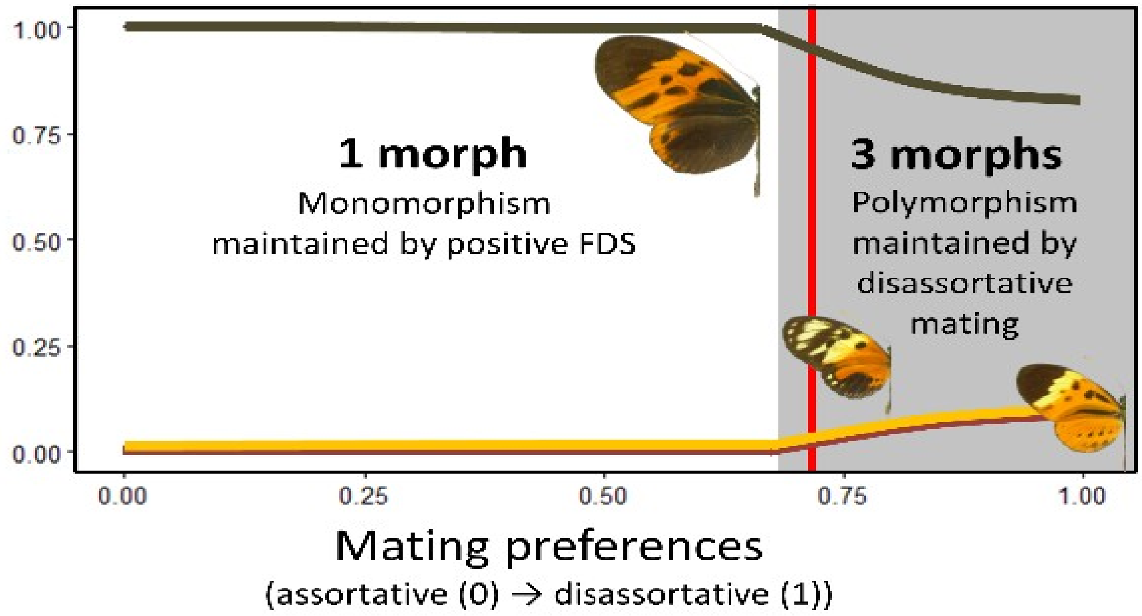

Chouteau et al. submited

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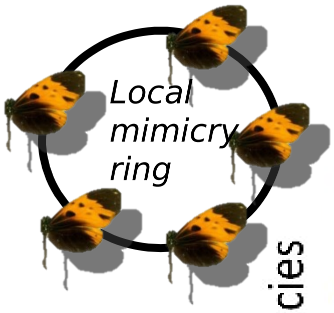
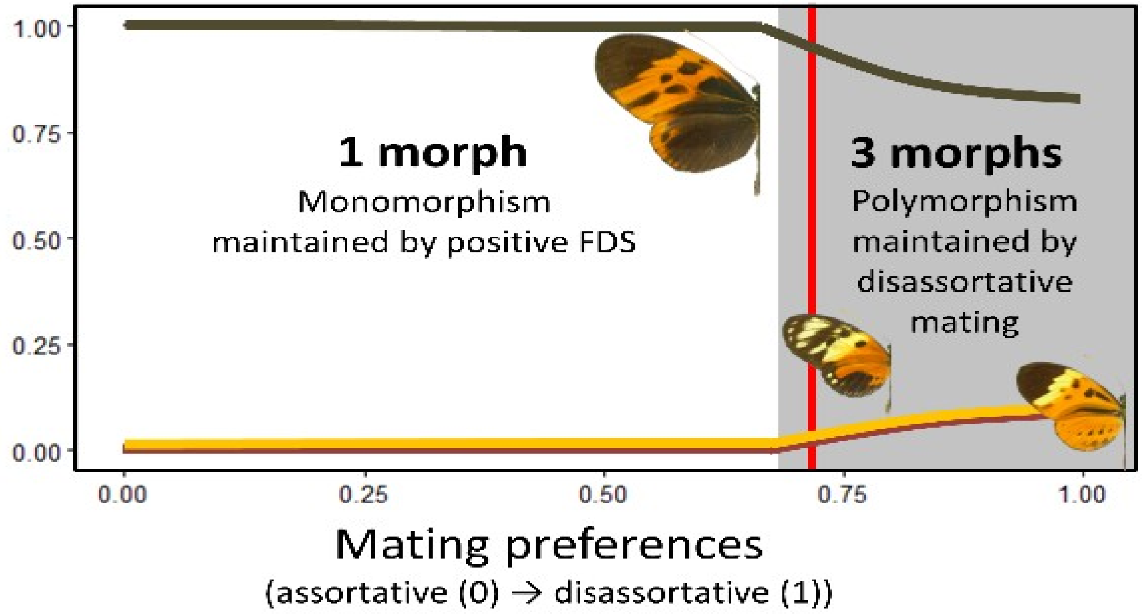


Observed level of disassortative preference



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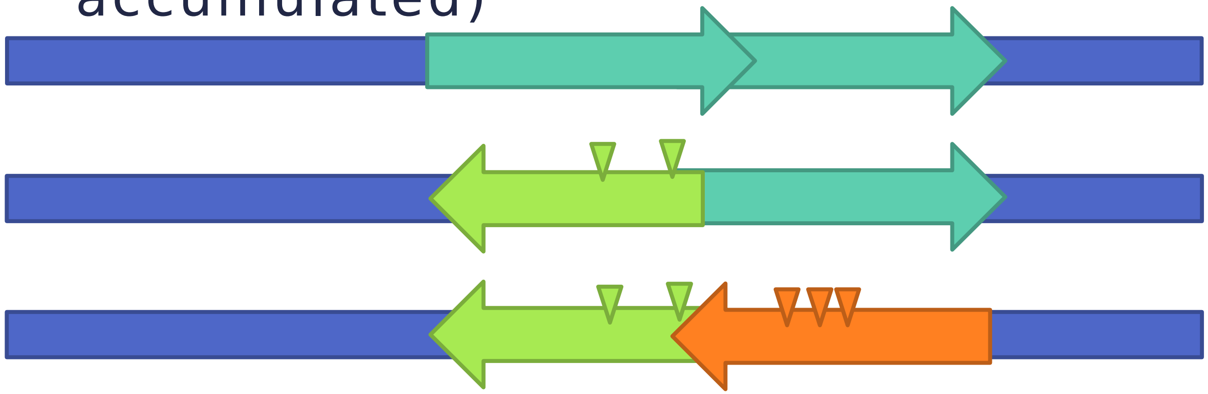
Origin of disasssortative mating ?

- Inversions: linked deleterious mutations (captured or accumulated)



Ancestral allele (recessive)

Derived allele 1

Derived allele II (dominant)

- Disassortative mating:
  - Purge of deleterious mutations in recessive alleles (frequently occurring at homozygous state)
  - Accumulation of deleterious mutations associated with dominant allele
  - Increase of heterozygote advantage
  - Promote disassortative mating

Chouteau et al. submited

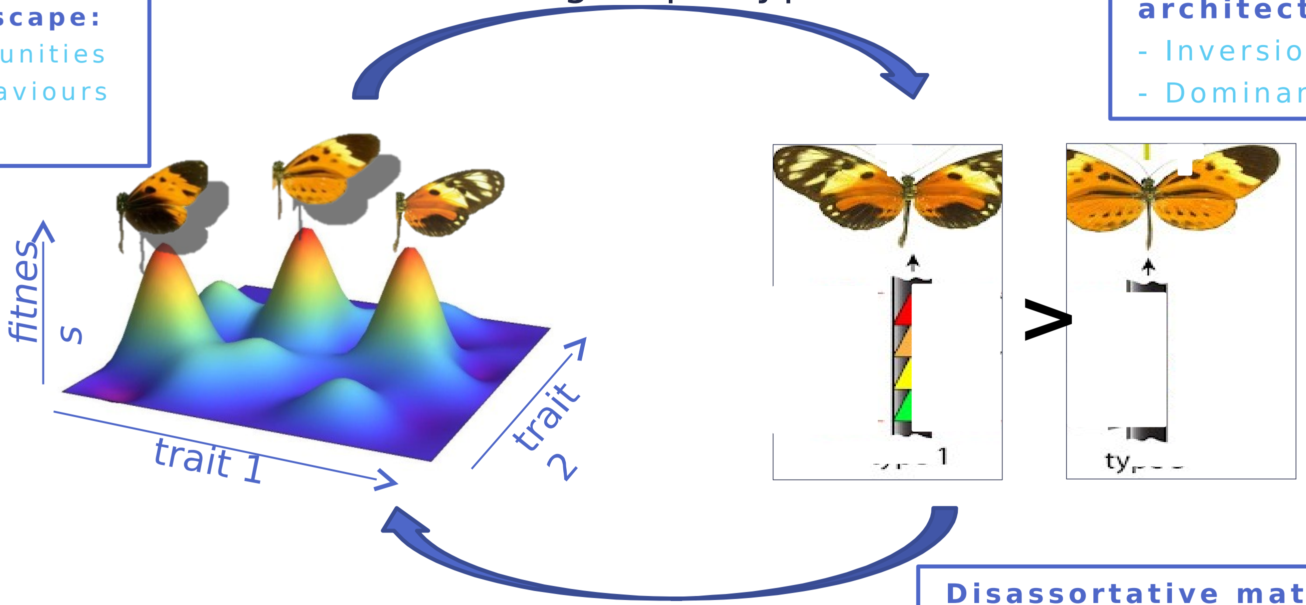
Genetic architecture associated with polymorphism

- Dominance influences
  - Polymorphism in sympatry
  - Gene flow among populations

- Origin of disassortative mating ?
  - Linked to genetic load associated with inversions ?
  - Linked to dominance among haplotypes ?

Adaptive landscape:
- Mimetic communities
- Predators behaviours

Genetic architecture:
- Inversions
- Dominance



Disassortative mating:
- Linked preference locus ?
- Linked genetic load ?

Thank you for your attention

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