





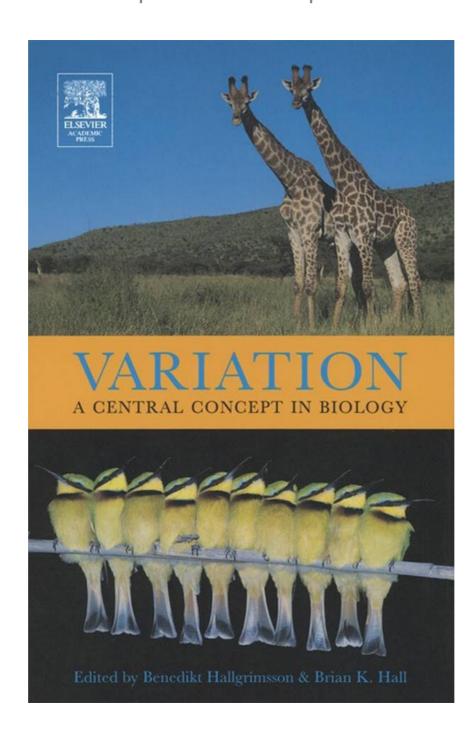
Antoine Fraimout

Evolution de la variation génétique et phénotypique au cours d'une invasion: le cas de *Drosophila suzukii*

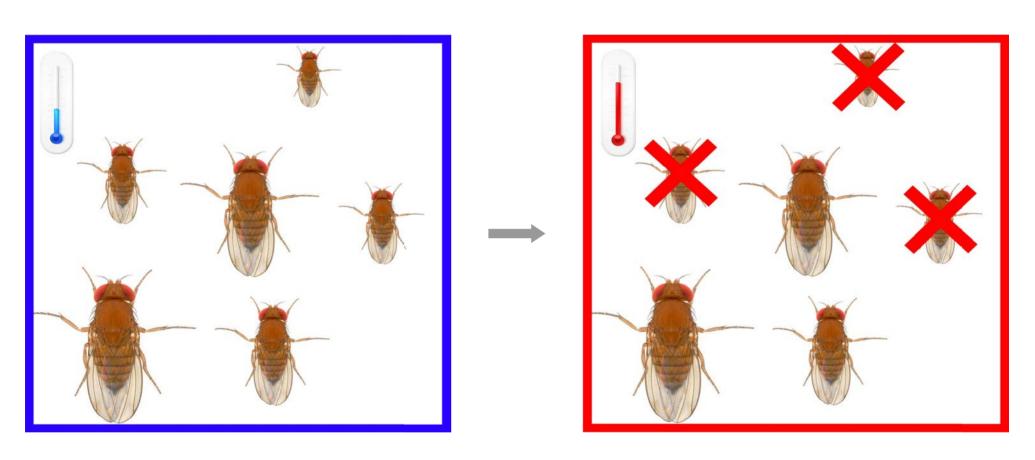








Phenotypic variation is the raw material for evolution by natural selection It determines the capacity of a population to respond to selection

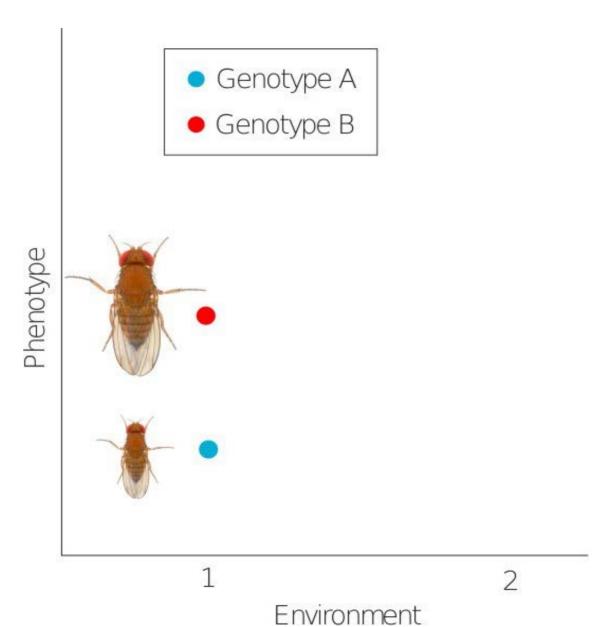


Environmental change

Phenotypic variation has different sources in a population

Phenotypic variation has different sources in a population

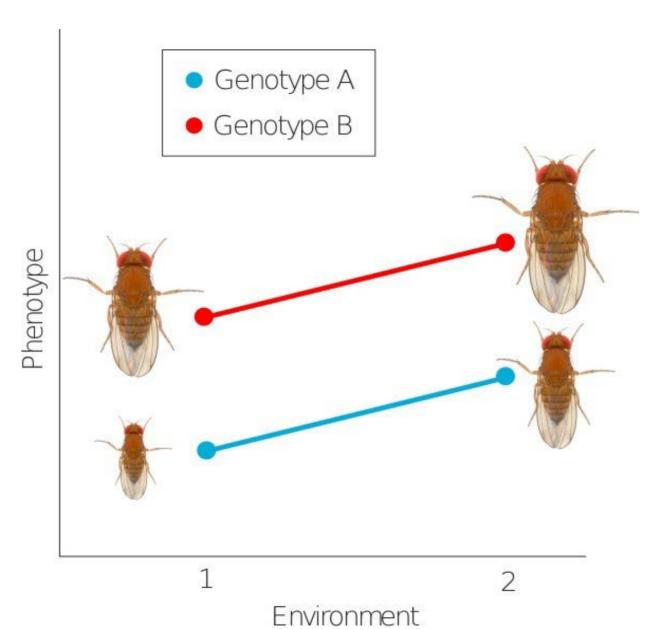
Genetic



 $V_p = V_G$

Phenotypic variation has different sources in a population

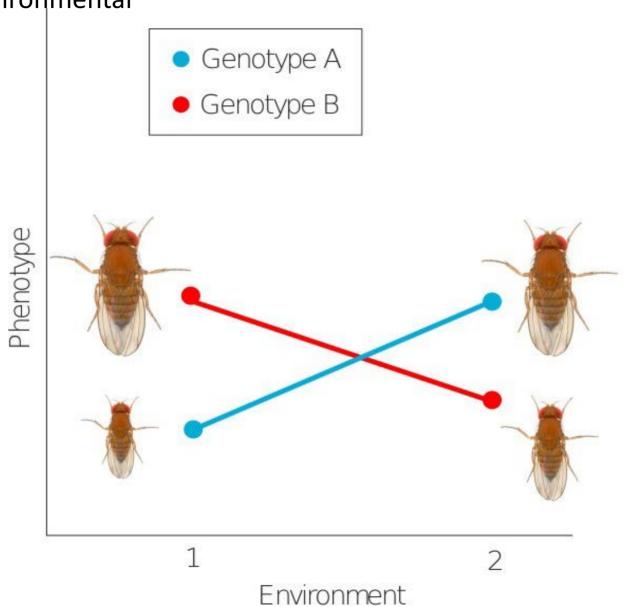
Environmental



 $V_p = V_G + V_F$

Phenotypic variation has different sources in a population

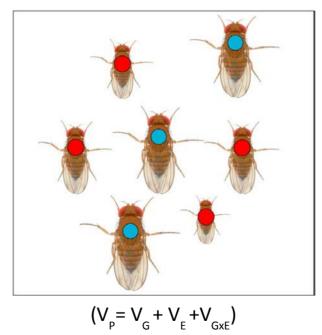
Genetic and environmental

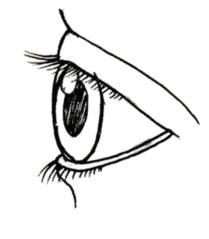


 $V_{p} = V_{c} + V_{c} + V_{c}$

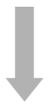
A snapshot in the course of evolution

Observed variation

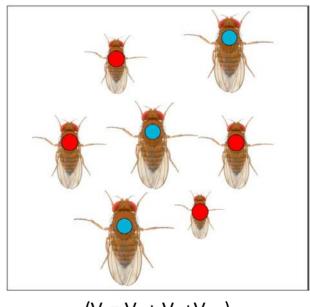




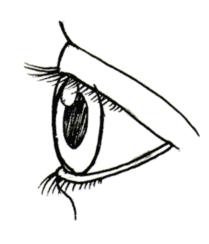
Ancestral variation



Observed variation



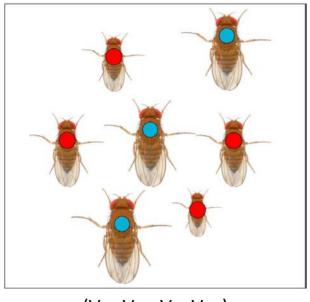




Ancestral variation



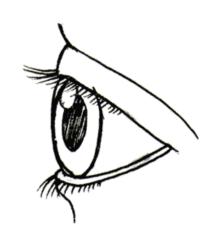
Observed variation







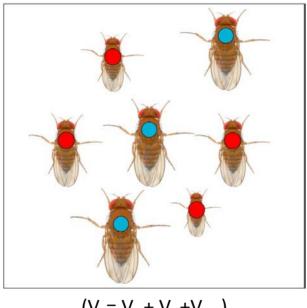
Response to selection



Ancestral variation

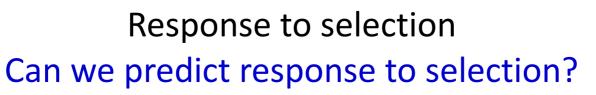


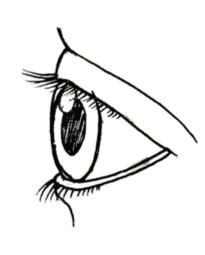
Observed variation



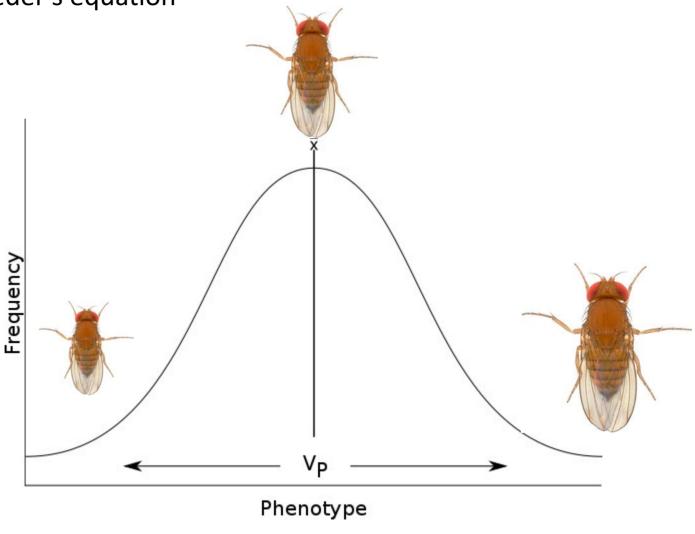








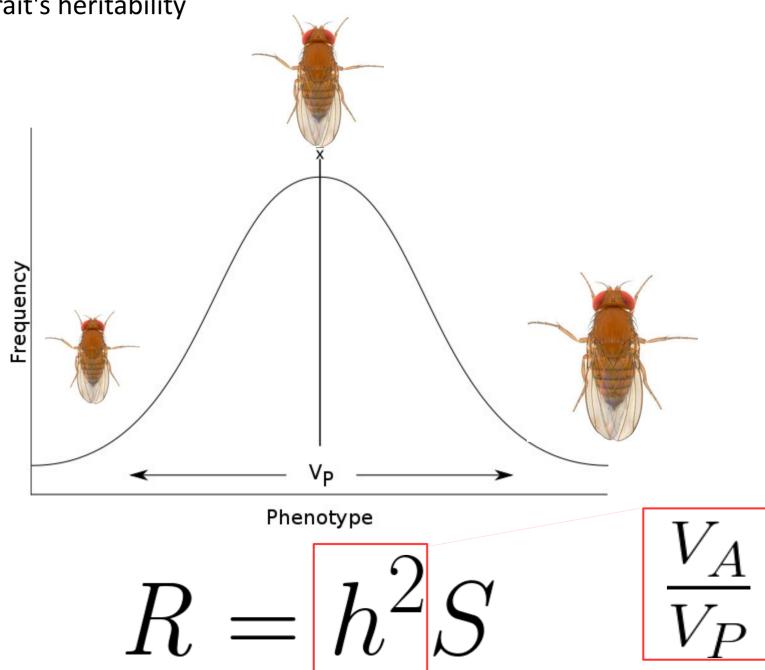
The univariate breeder's equation



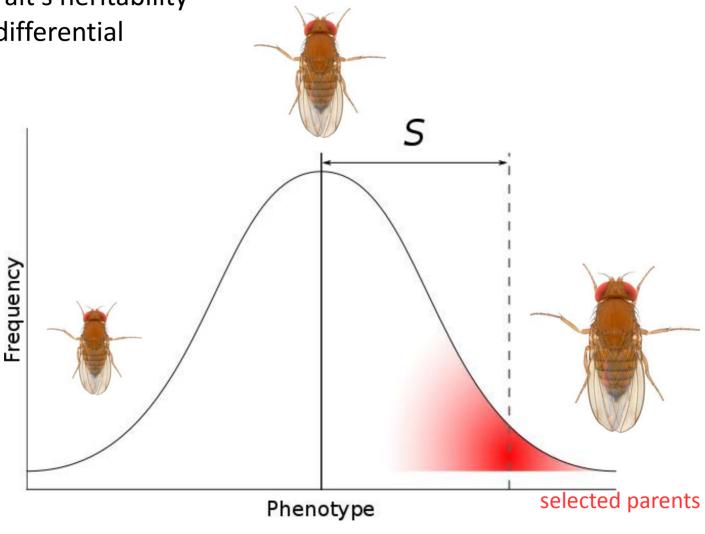
 $R = h^2 S$

Theoretical response to selection

The product of a trait's heritability



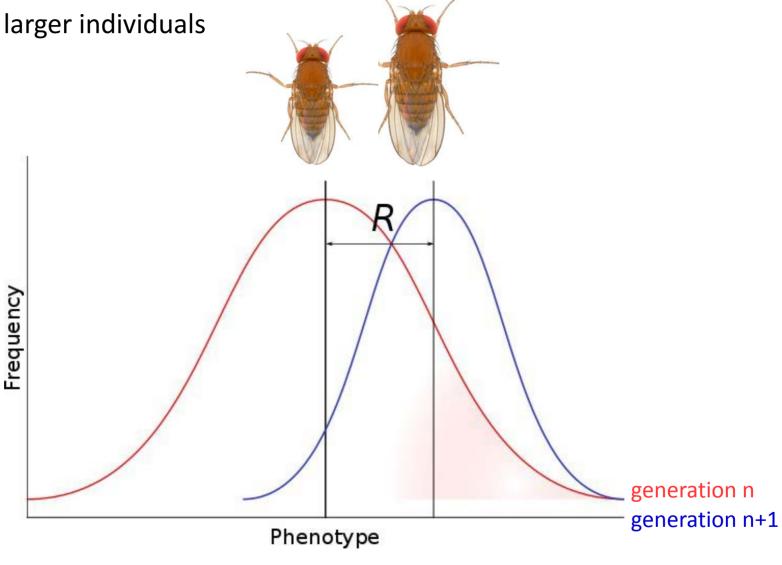
The product of a trait's heritability and the selection differential



$$R = h^2 S$$



Evolution towards larger individuals

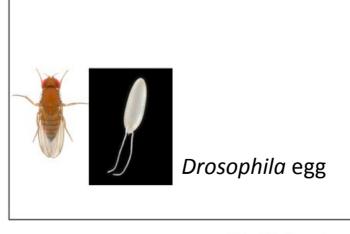


$$R = h^2 S$$

Practical issue

Selection acts on multiple traits

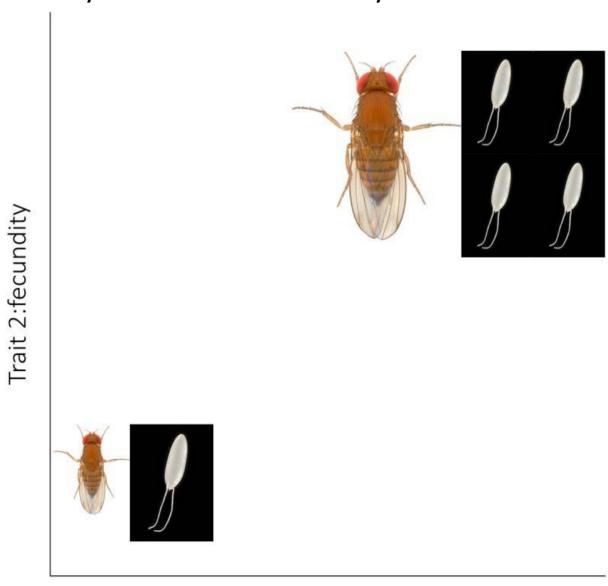
Trait 2:fecundity



Trait 1: size

Practical issue

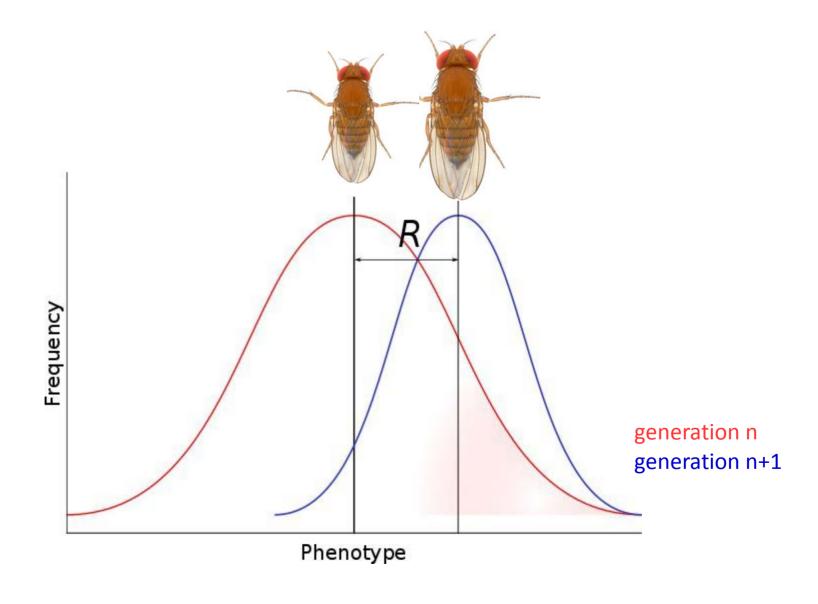
Traits can be genetically correlated and covary



Trait 1: size

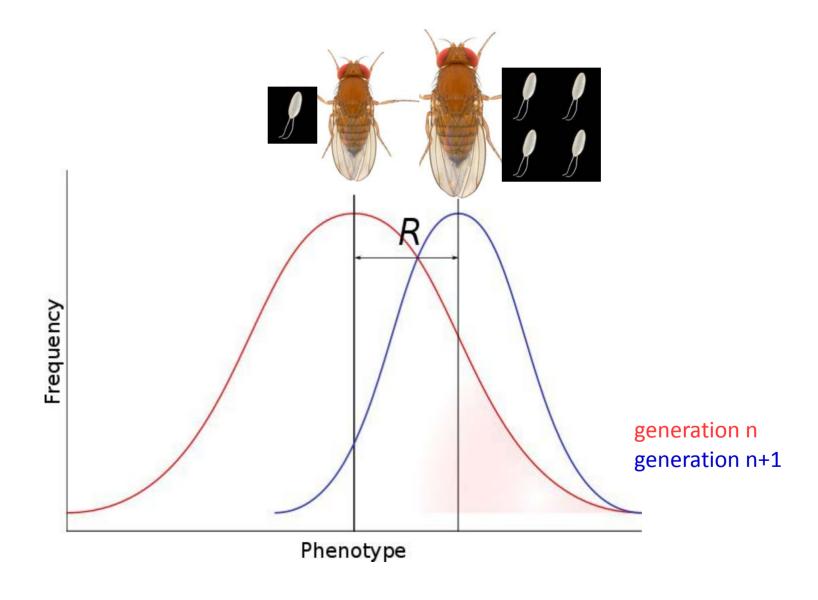
Response to selection

Evolution towards larger individuals



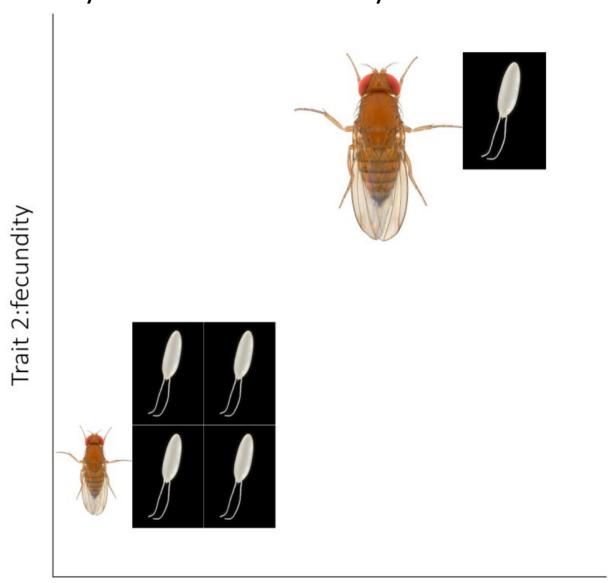
Response to selection

Evolution towards larger and more fecund individuals



Practical issue

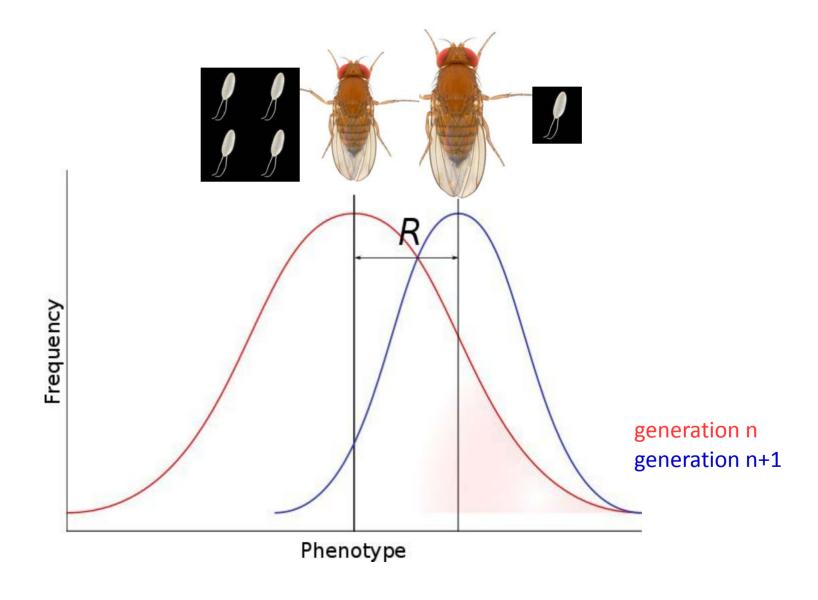
Traits can be genetically correlated and covary



Trait 1: size

Response to selection

Evolution towards larger and LESS fecund individuals



Theoretical response to selection

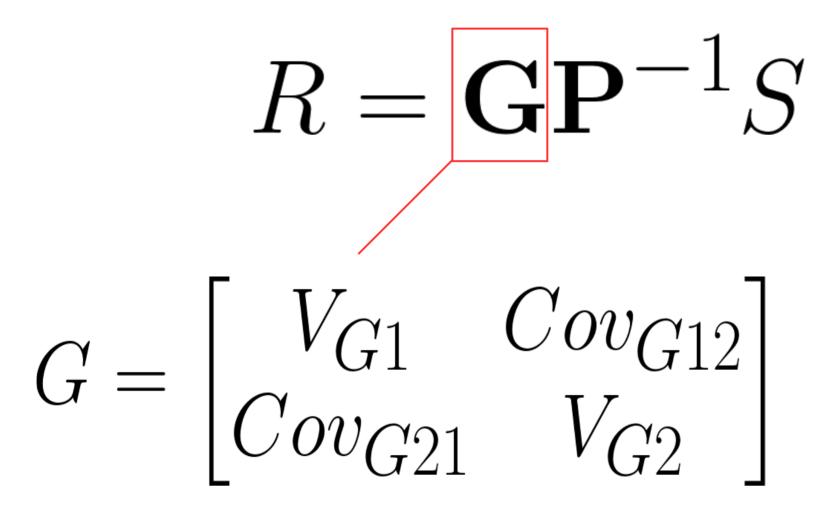
$$R = \mathbf{GP}^{-1}S$$

Theoretical response to selection

Multivariate breeder's equation



Multivariate equivalent of h²



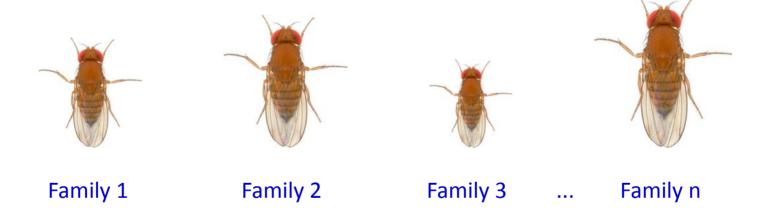
$$R = \mathbf{G}\mathbf{P}^{-1}S$$

$$G = \begin{bmatrix} V_{G1} & Cov_{G12} \\ Cov_{G21} & V_{G2} \end{bmatrix}$$

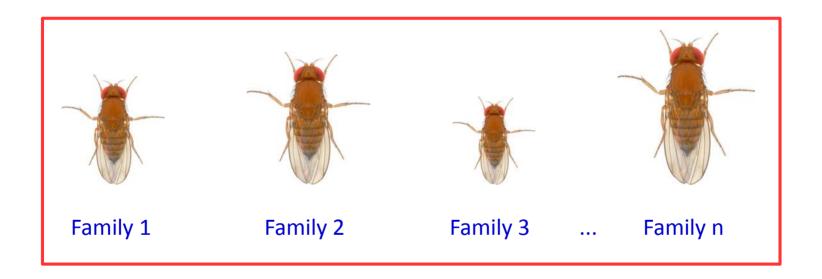
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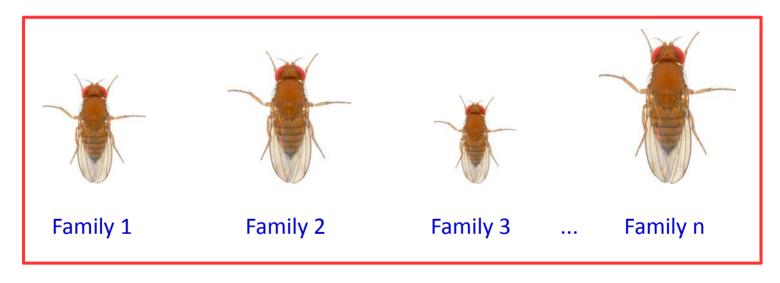
Estimation of quantitative genetic variation



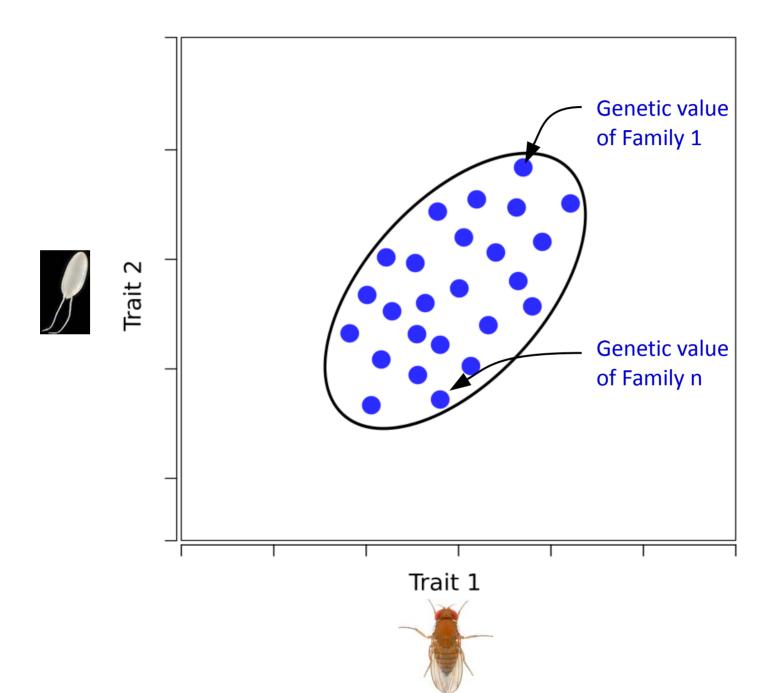
Estimation of quantitative genetic variation Common garden design

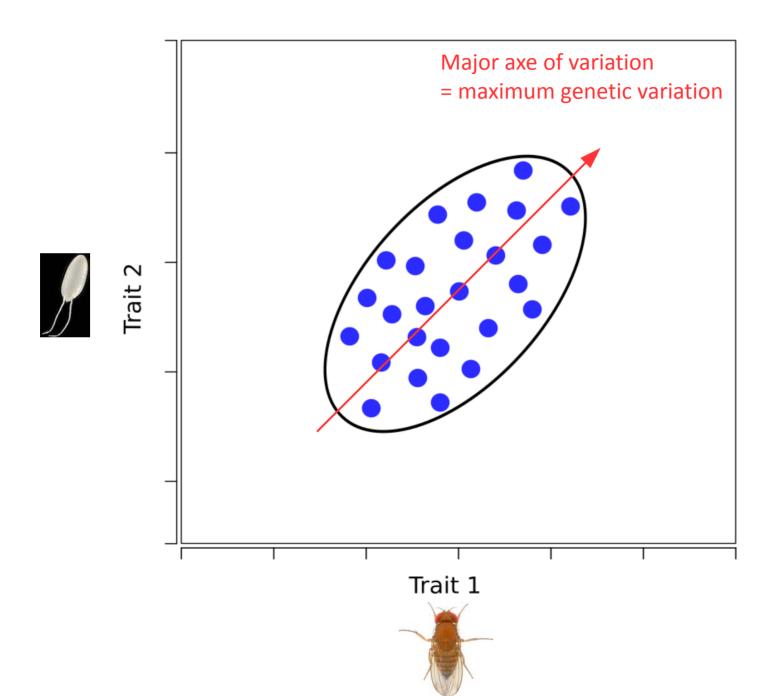


Estimation of quantitative genetic variation Phenotyping individuals within/between families

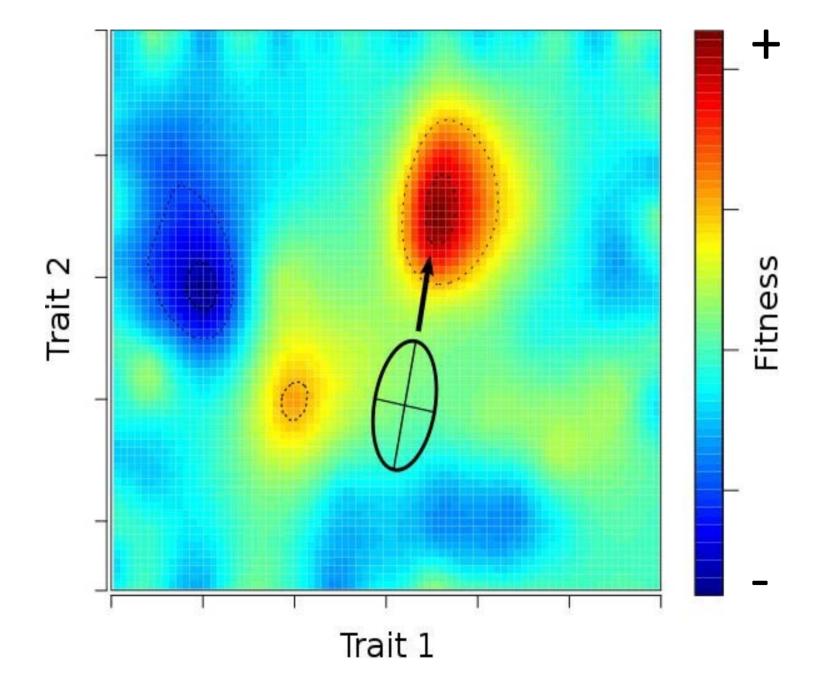


(co)variation between families —

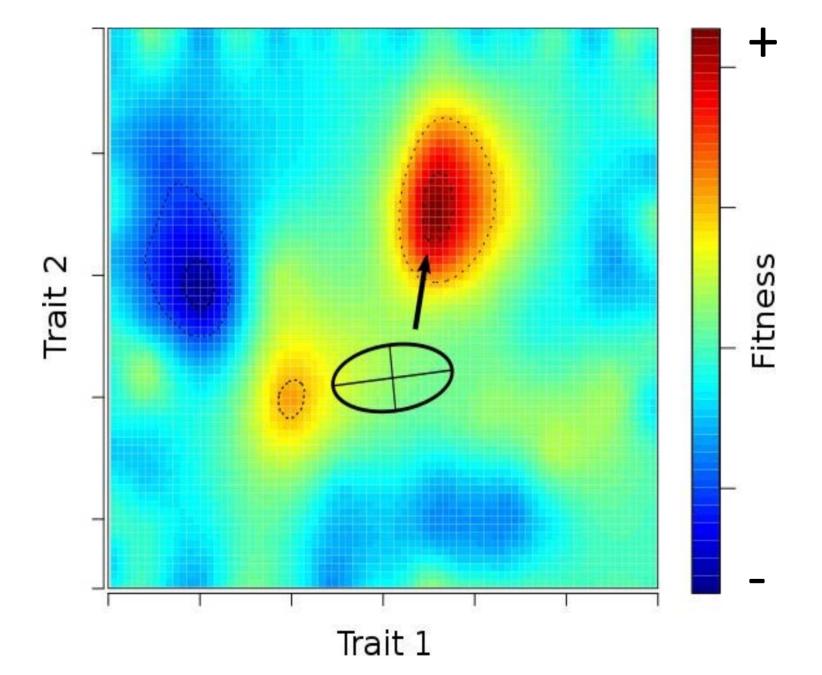




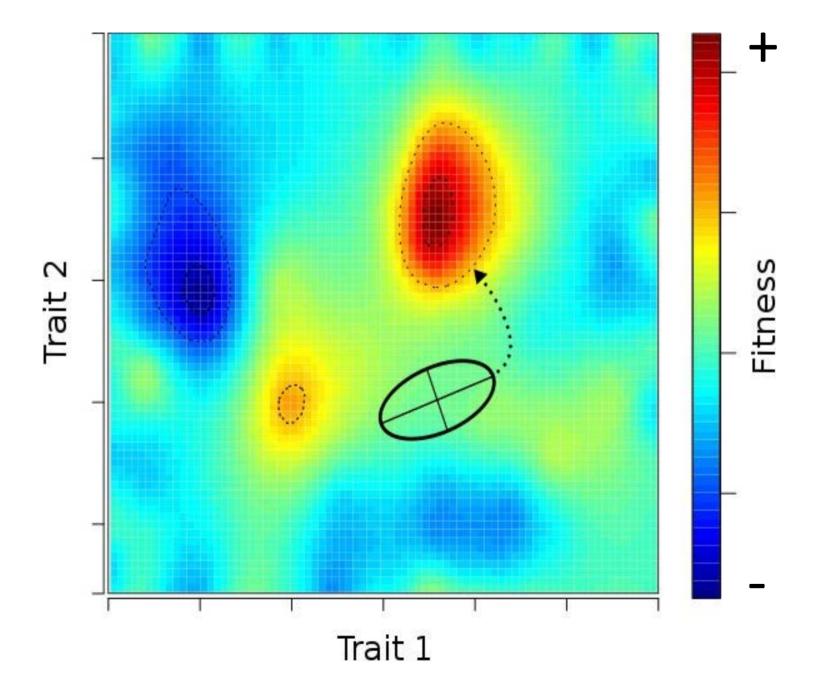
The **G** matrix and the adaptive landscape



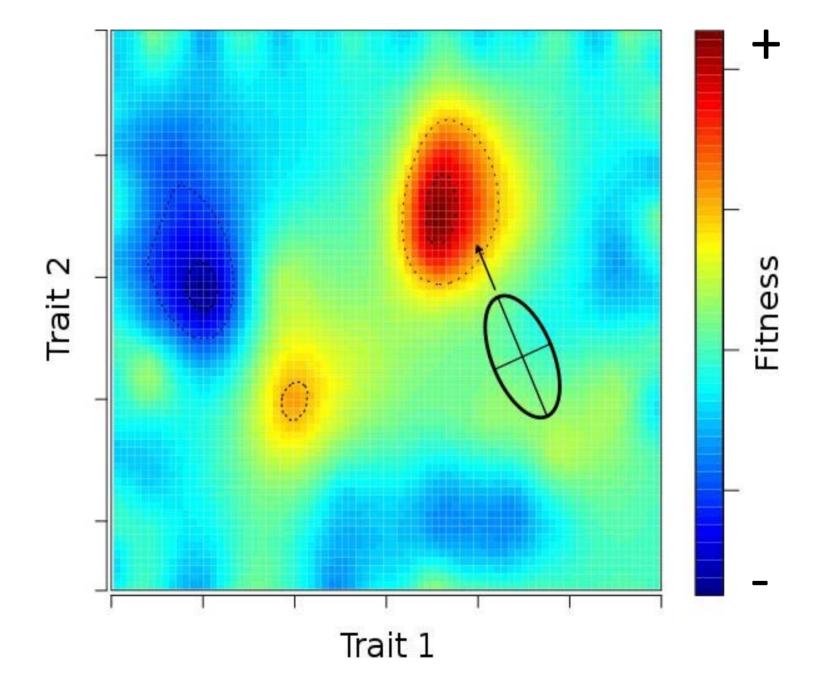
The **G** matrix and the adaptive landscape



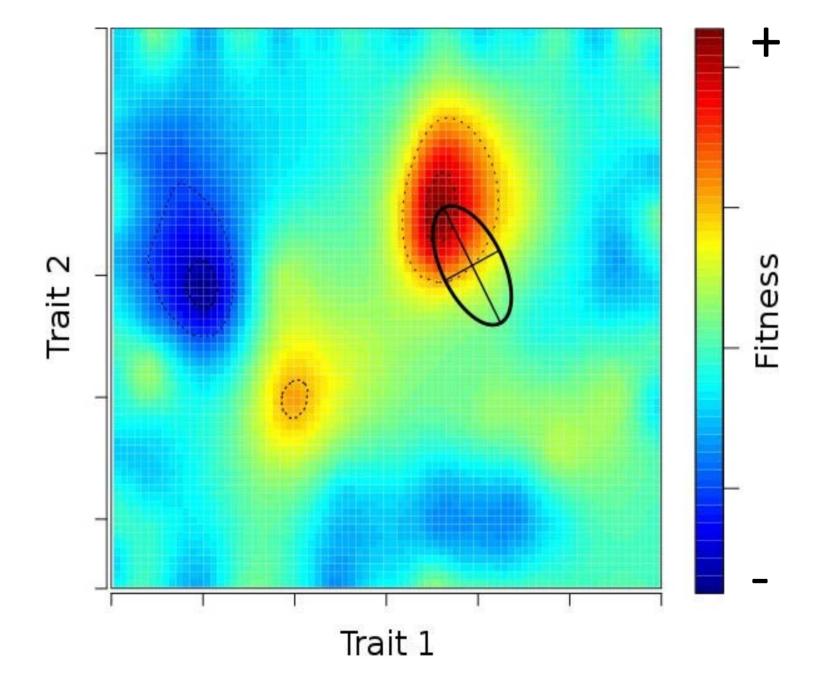
The **G** matrix and the adaptive landscape



The **G** matrix and the adaptive landscape



The **G** matrix and the adaptive landscape



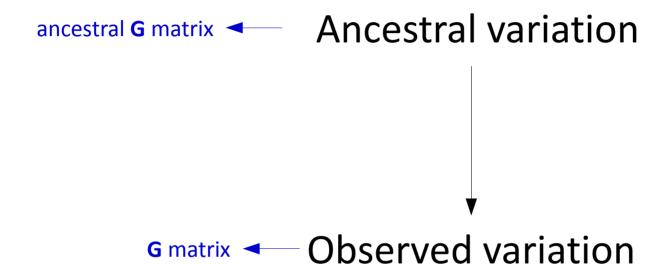
The G matrix: a central object in evolutionary biology

It summarizes genetic variation in population It contains the sign and strength of covariation Used in predictive models of phenotypic evolution Predictive models rely on the stability of the **G** matrix...

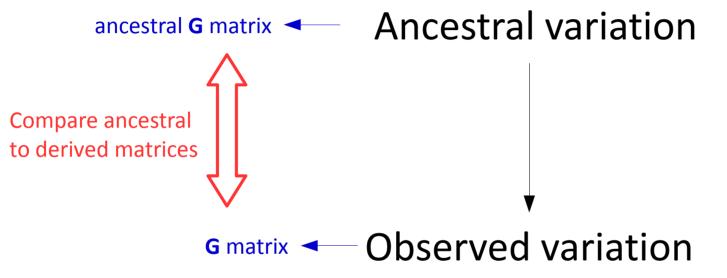
$$R = \mathbf{GP}^{-1}S$$

Main questions

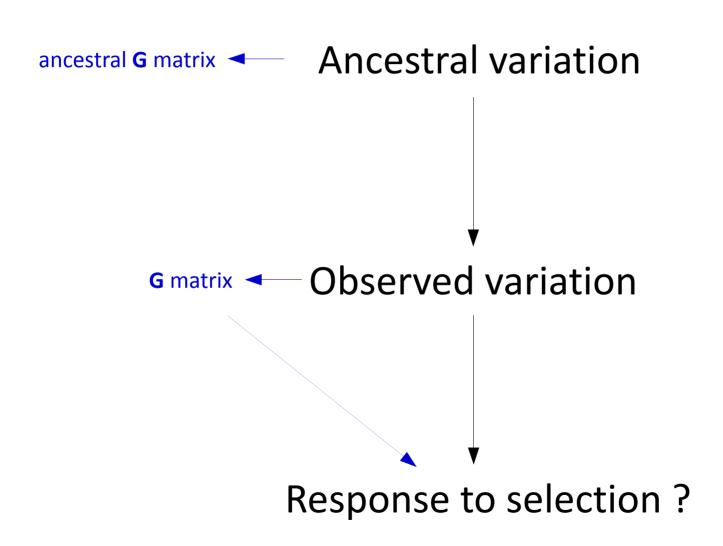
Main questions



Main questions

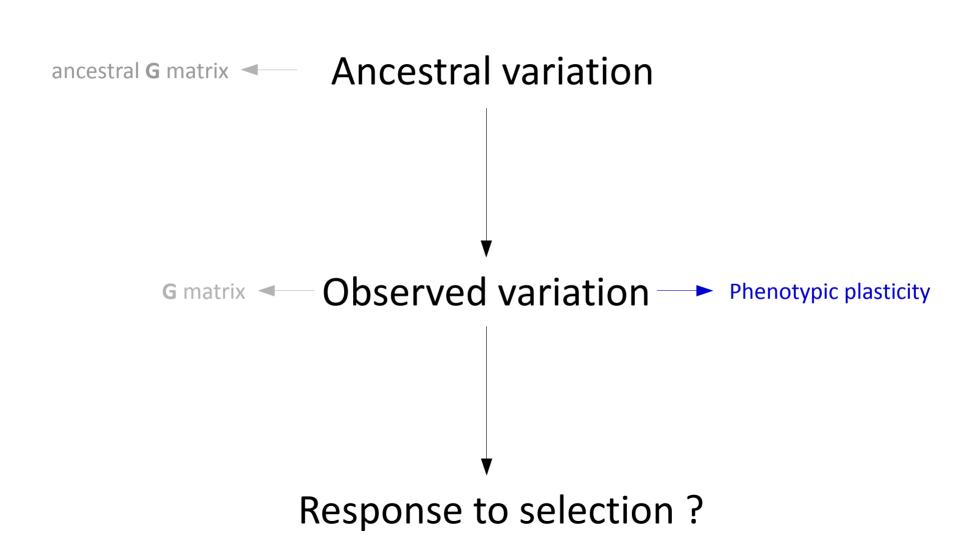


Main questions



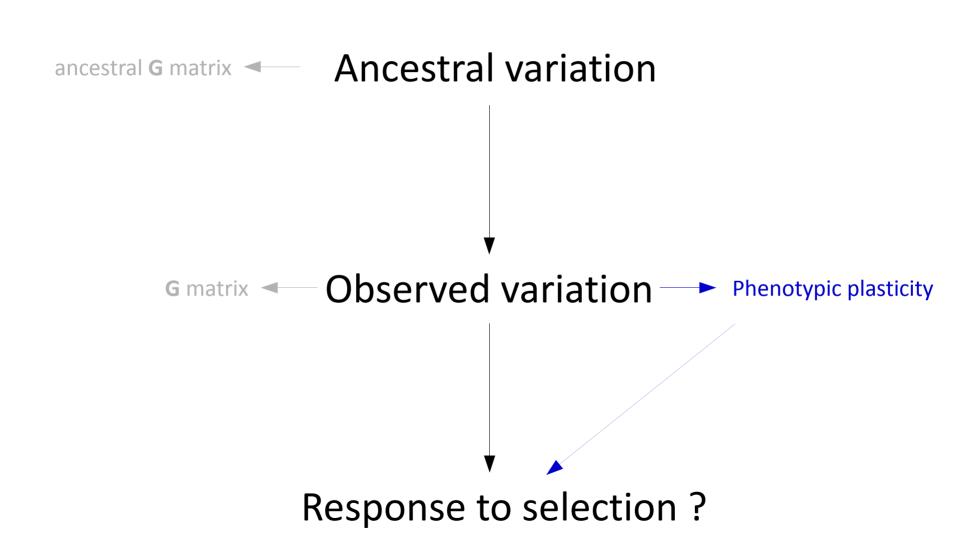
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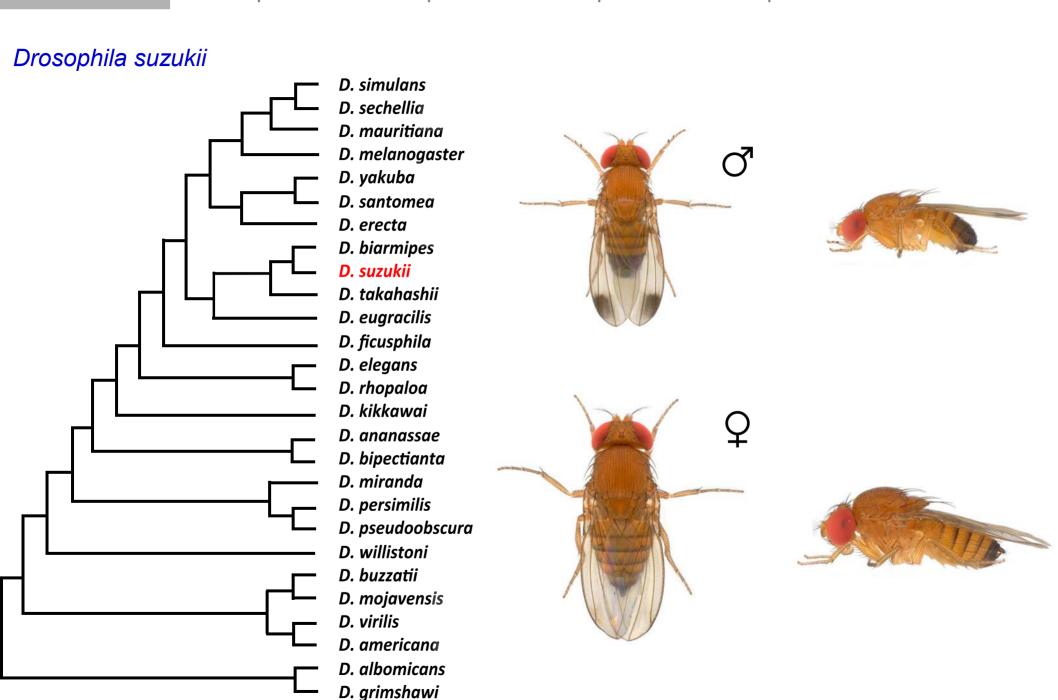
The role of phenotypic plasticity?



Main questions

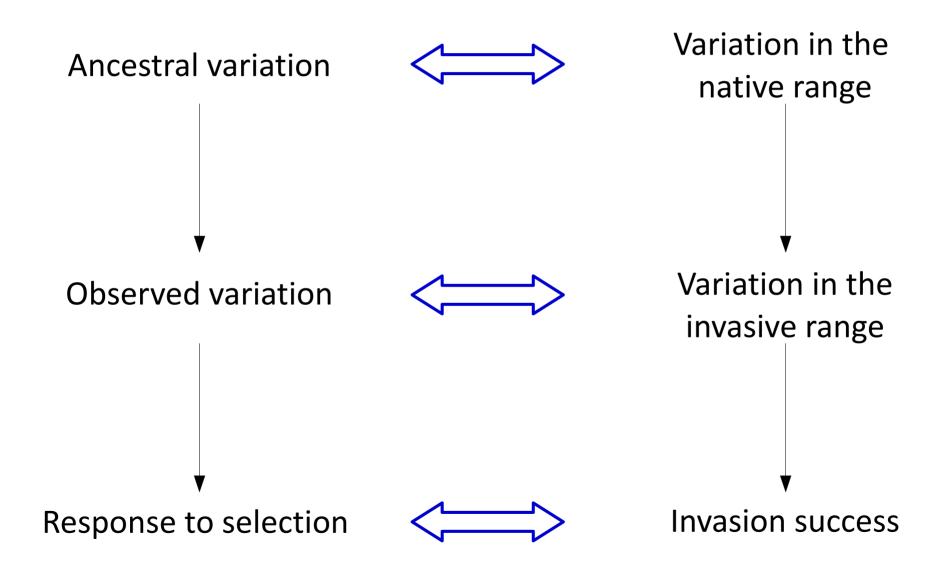
The role of phenotypic plasticity?





Larvae develop inside the fruit causing severe damages and allowing for secondary contaminations

An ideal study model



Variation in the native range

(ancestral variation)

Variation in the invasive range

(observed variation)

Invasion success

(response to selection)

1. Invasion history

Links between populations

Variation in the invasive range (observed variation)

Invasion success

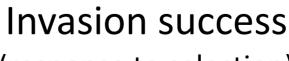
(response to selection)



2. Evolution of G

Did **G** evolved during the invasion?

Variation in the invasive range (observed variation)



(response to selection)

1 . Invasion history
Links between populations

2. Evolution of **G**Did **G** evolved during the invasion?

Variation in the invasive range (observed variation)

3. Phenotypic plasticity

Role in invasive success

Invasion success (response to selection)

1 . Invasion history Links between populations

- 2. Evolution of GDid G evolved during the invasion?
- 3. Phenotypic plasticity Role in invasive success

4. Niche modeling Link evolution to ecology

Variation in the invasive range (observed variation)

Invasion success (response to selection)

Field sampling

native range

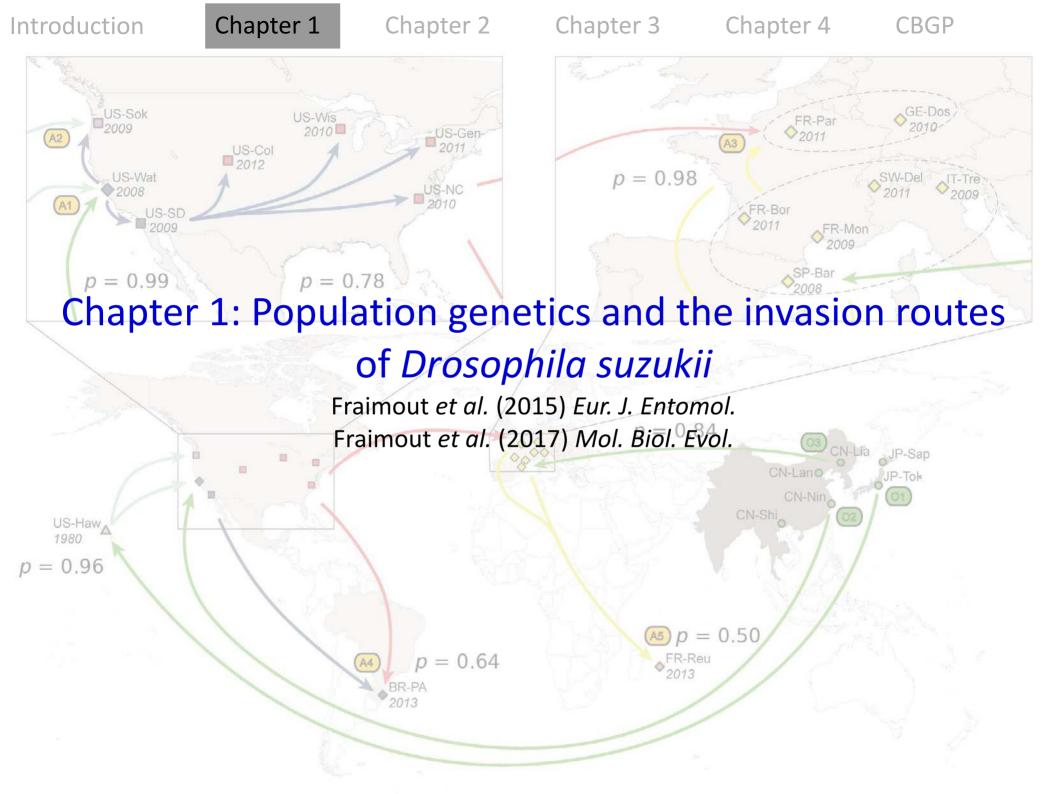


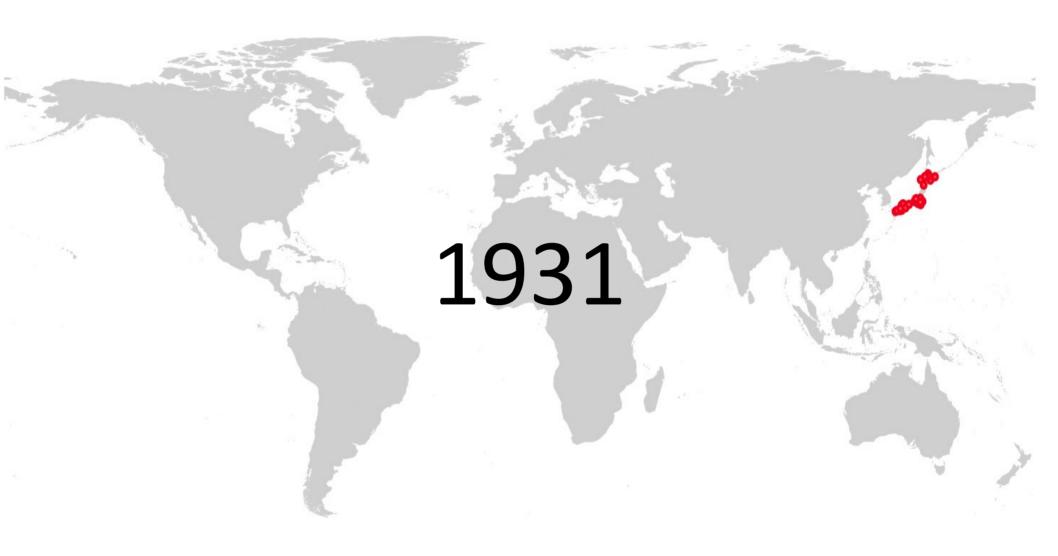


Drosophila model "easy" to rear in controled conditions

Allows for establishment of laboratory stock populations and families



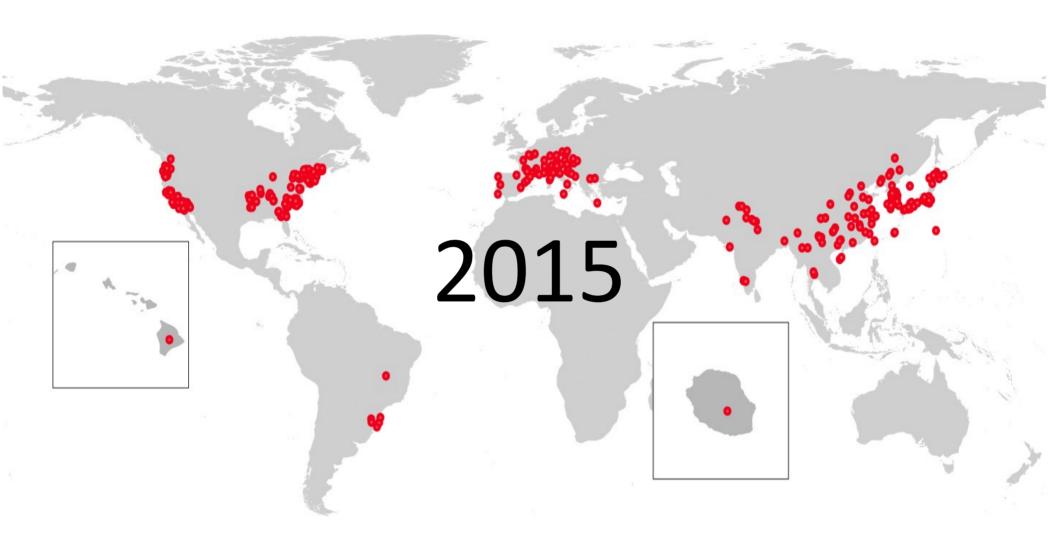












How to reconstruct invasion routes?

From molecular data

1. Sampling & Genotyping

Large sampling scheme in native and invasive ranges

Sampling of *D. suzukii* – 23 populations (6 native, 17 invasive, 684 individuals)



How to reconstruct invasion routes?

From molecular data

1. Sampling & Genotyping

Large sampling scheme in native and invasive ranges

Genotyping at polymorphic loci (Fraimout et al. 2015)

Development of 25 specific microsatellites markers





How to reconstruct invasion routes?

From molecular data

1. Sampling & Genotyping

Large sampling scheme in native and invasive ranges

Genotyping at polymorphic loci (Fraimout et al. 2015)

Development of 25 specific microsatellites markers

Characterizing genetic variation among samples

To group samples in genetic clusters

Genetic clustering – 7 focal groups



Genetic groups of *D. suzukii* estimated with BAPS software (Corander et al. 2003)

How to reconstruct invasion routes?

From molecular data

2. Establish relationship among populations

Testing the origins of each invasive groups with invasion scenarios Using representative samples

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From molecular data

2. Establish relationship among populations

Testing the origins of each invasive groups with invasion scenarios Using representative samples

Simulating datasets under competing invasion scenarios approximate Bayesian computation (DIYABC v.2.0.1, Cornuet et al. 2014)

How to reconstruct invasion routes?

From molecular data

2. Establish relationship among populations

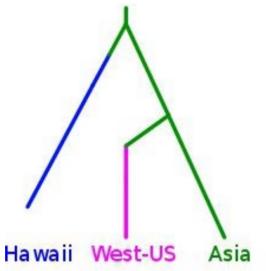
Testing the origins of each invasive groups with invasion scenarios Using representative samples

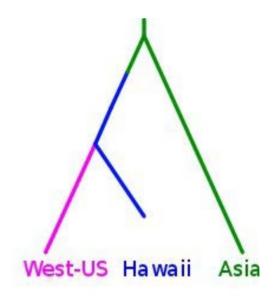
Simulating datasets under competing invasion scenarios approximate Bayesian computation (DIYABC v.2.0.1, Cornuet et al. 2014)

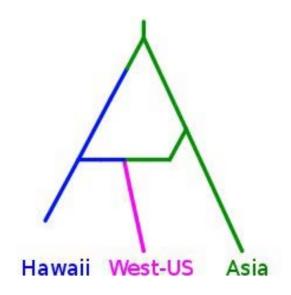
Performing model choice using Random forests ABC-Random Forest (R package, Pudlo *et al.* 2015)

What are the origins of western USA populations?

Simulating datasets

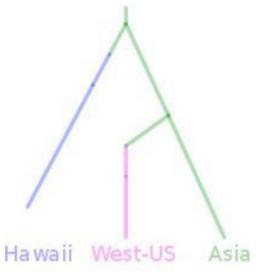


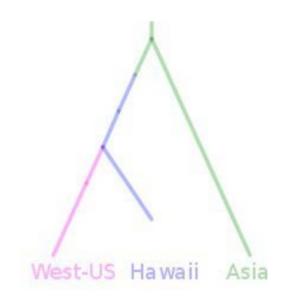




What are the origins of western USA populations?

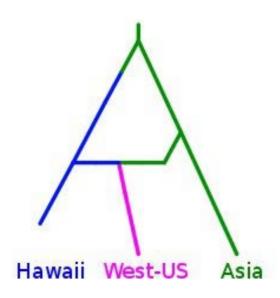
Performing model choice



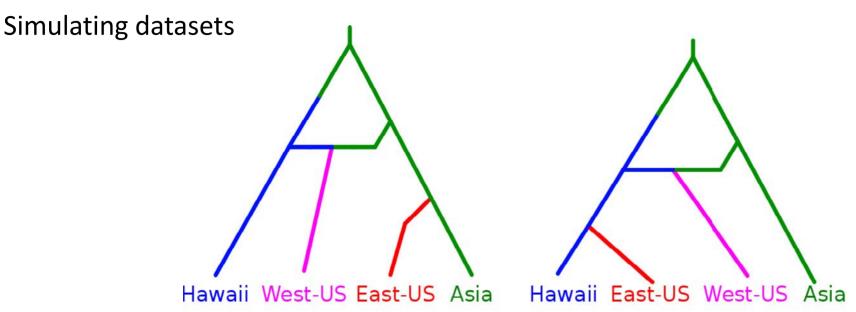


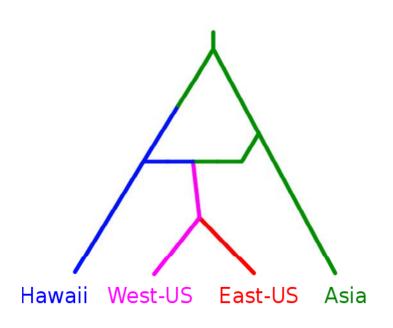
posterior probability of the best model p = 0.99

western USA admixed between Hawaii & Asia

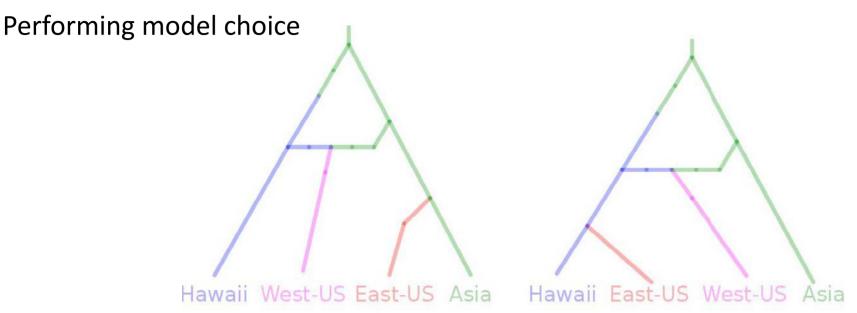


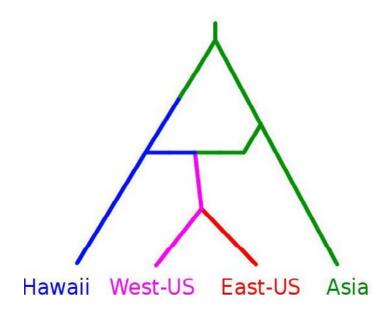
What are the origins of eastern USA populations?





What are the origins of eastern USA populations?





posterior probability of the best model p = 0.78

eastern USA derived from western USA

How to deal with simultaneous introductions?

How to deal with simultaneous introductions?

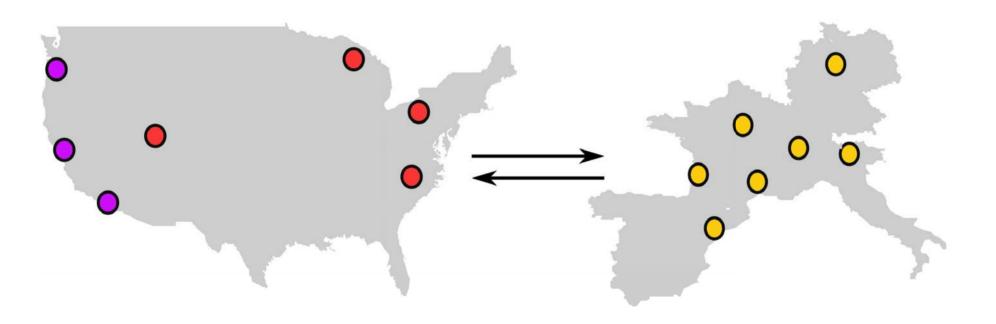
Introduction dates in USA and Europe overlap (2008)

How to deal with simultaneous introductions?

Introduction dates in USA and Europe overlap

Europe as a source for USA?

USA as a source for Europe?

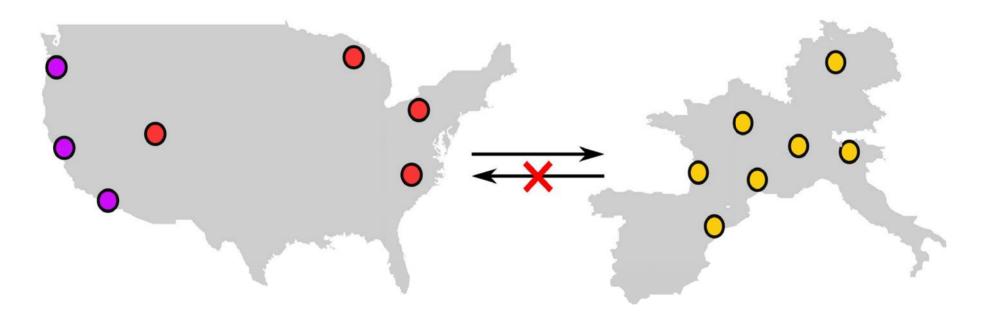


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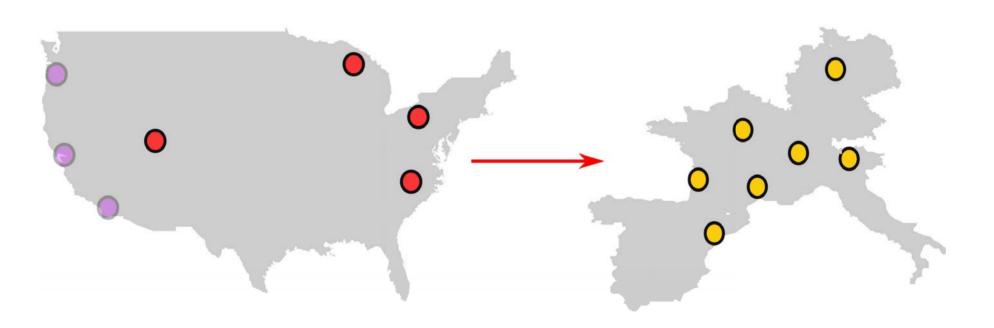


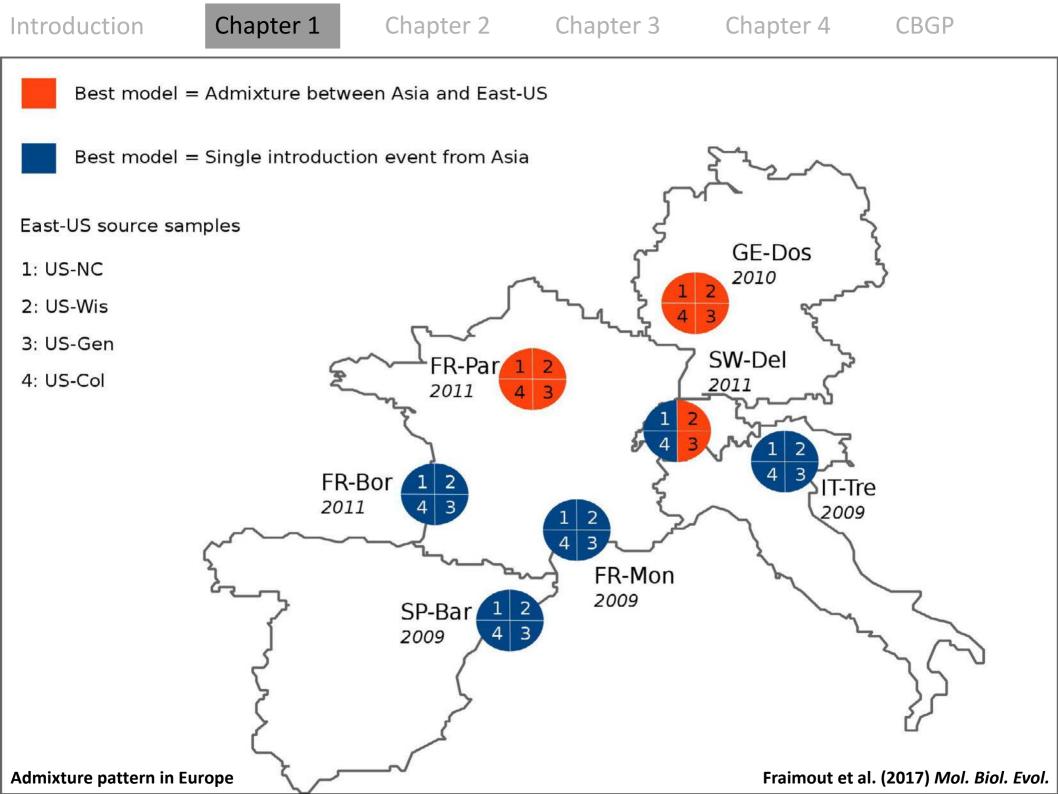
How to deal with simultaneous introductions?

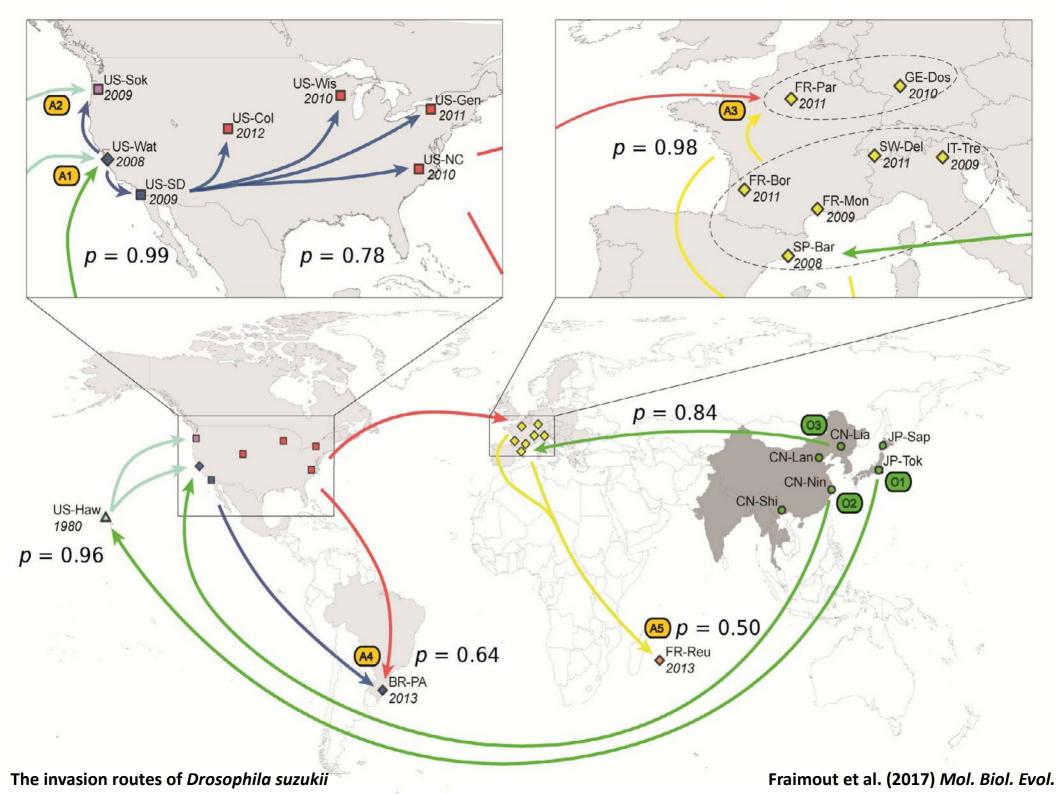
Introduction dates in USA and Europe overlap

Europe as a source for USA?

Eastern USA as a source for Europe!







Conclusions on Chapter 1

A complex invasion history

Multiple introductions event from different sources

Most likely human-mediated on large scales (human migration, fruit-trade)

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A complex invasion history

Multiple introductions event from different sources

Most likely human-mediated on large scales (human migration, fruit-trade)

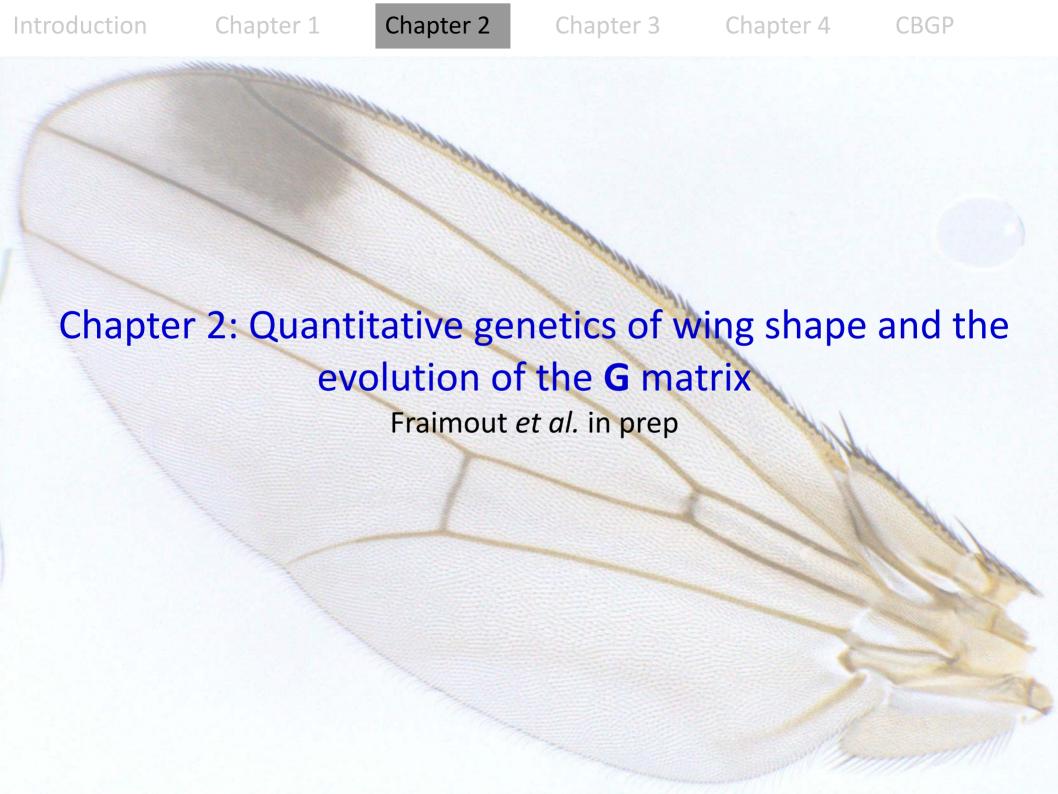
Genetic variation

Overall loss of genetic variation in invasive populations

All invasive populations experienced bottlenecks (with different severity)

Admixture in western USA

From two highly differentiated populations (Hawaii & Asia)



Breeding design: isofemale lines

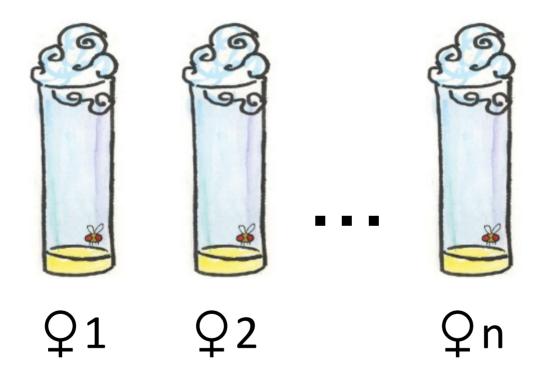
Established from single females caught in the field

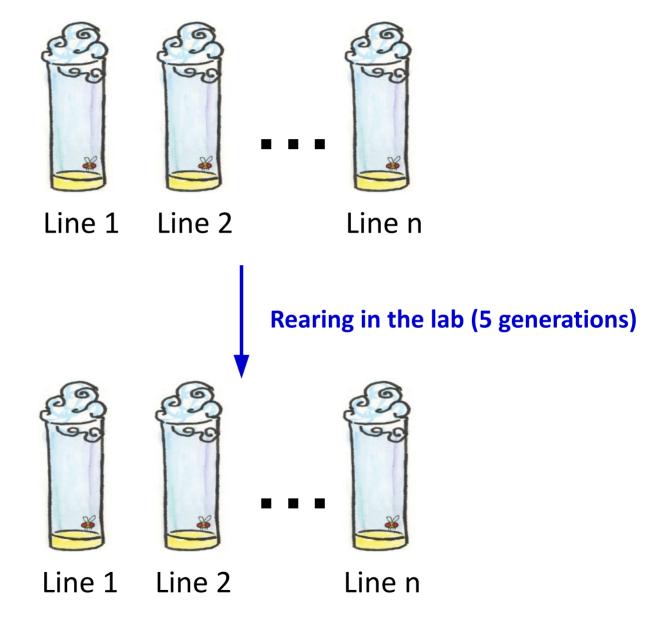


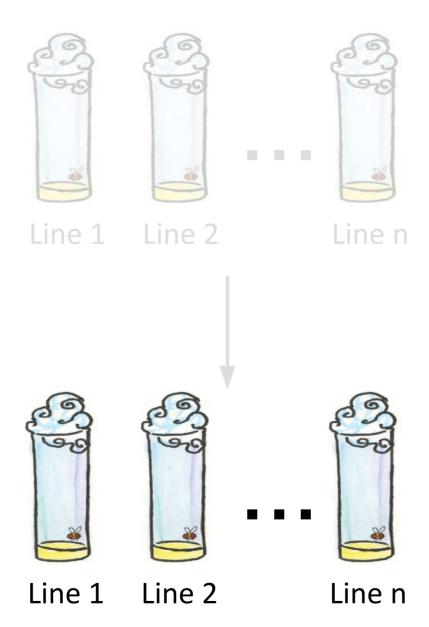
19

Breeding design: isofemale lines

Multiple females caught at each localities







Generation 5 ready for phenotyping

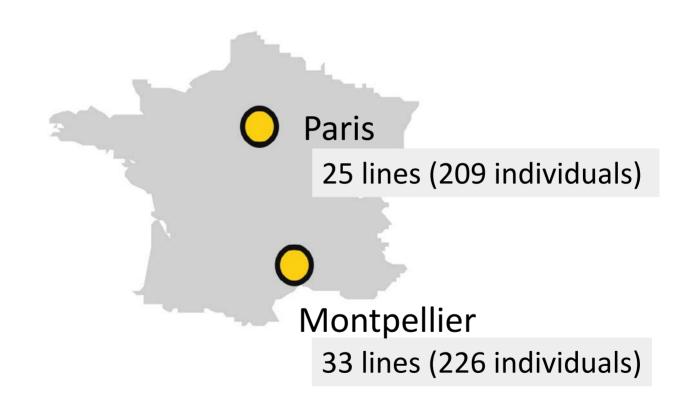
Study populations

Native range, Japan



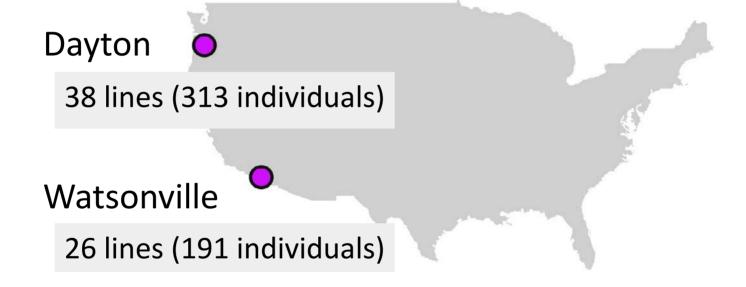
Study populations

Invasive range, France



Study populations

Invasive range, USA



Study populations

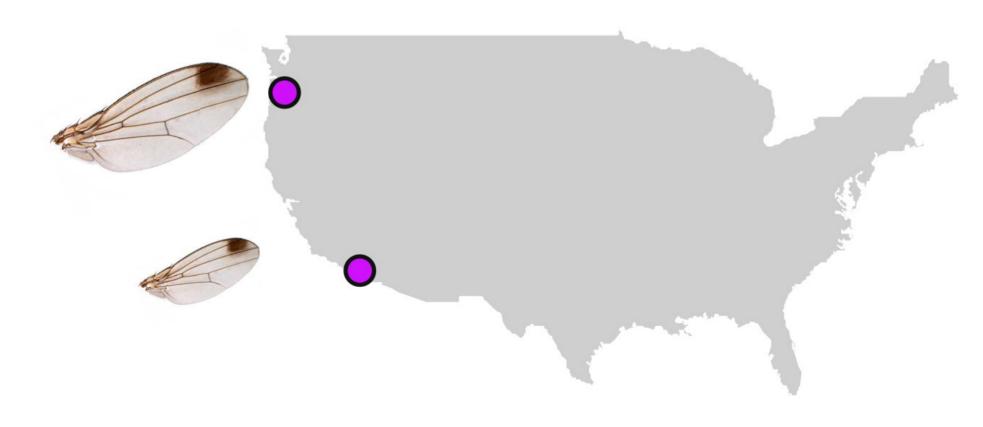
1323 individuals phenotyped

Sampling design: North/South gradient

Allows to test for latitudinal clines in morphology

Observed in other *Drosophila sp.*

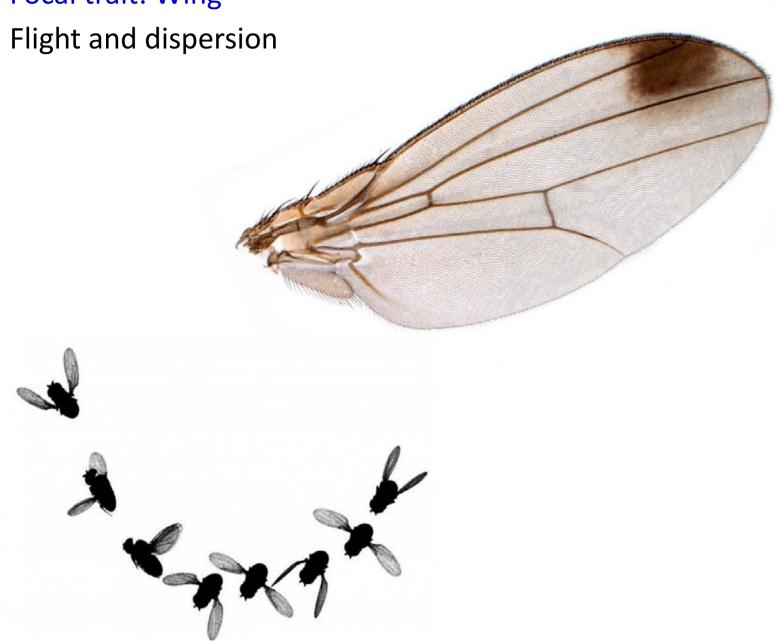
Suggested to be adaptive, related to climate



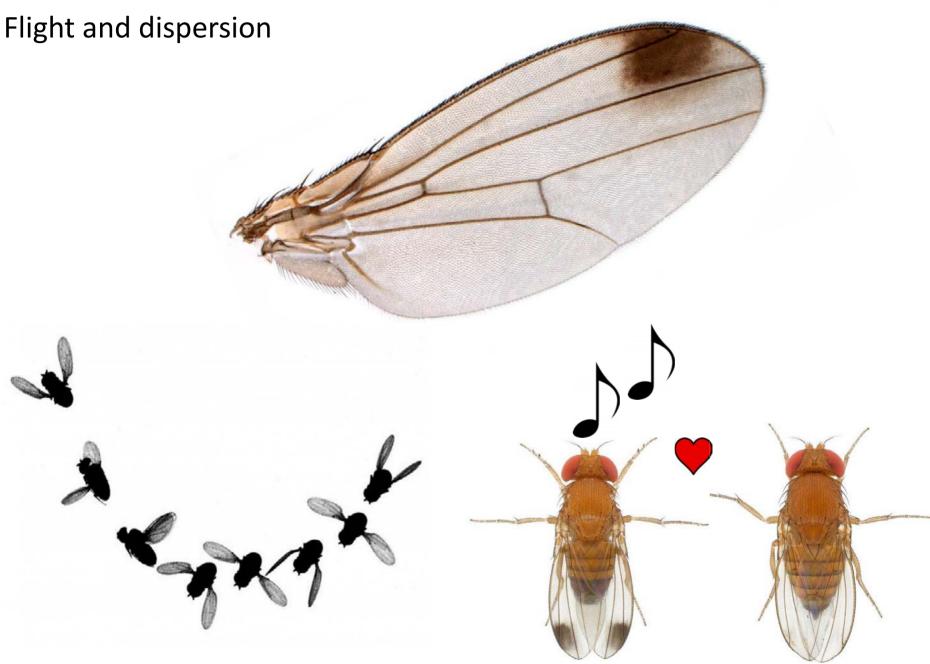
Focal trait: Wing



Focal trait: Wing

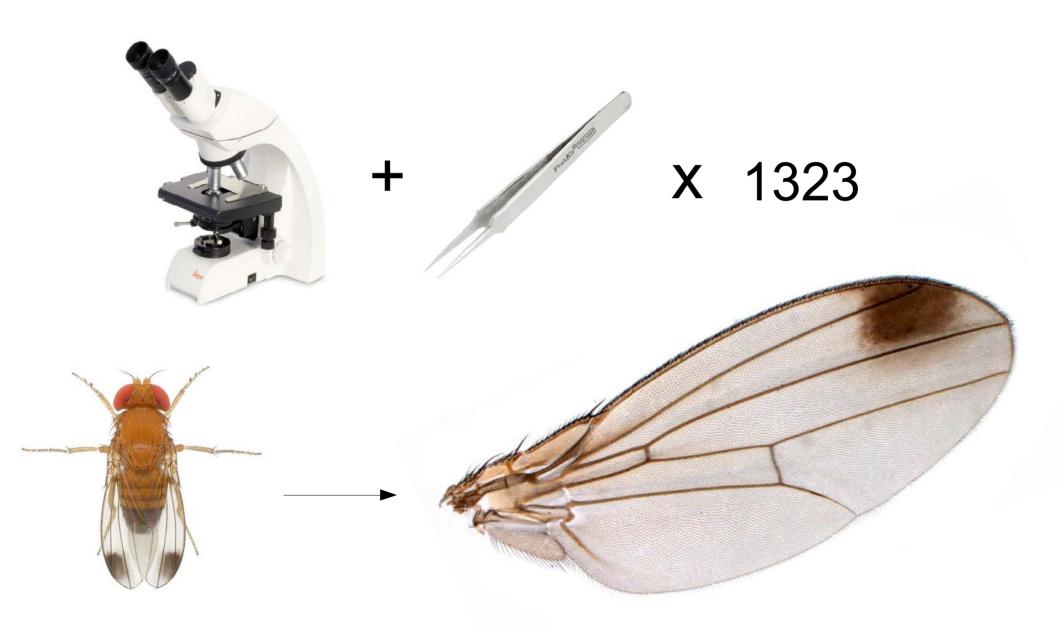


Focal trait: Wing



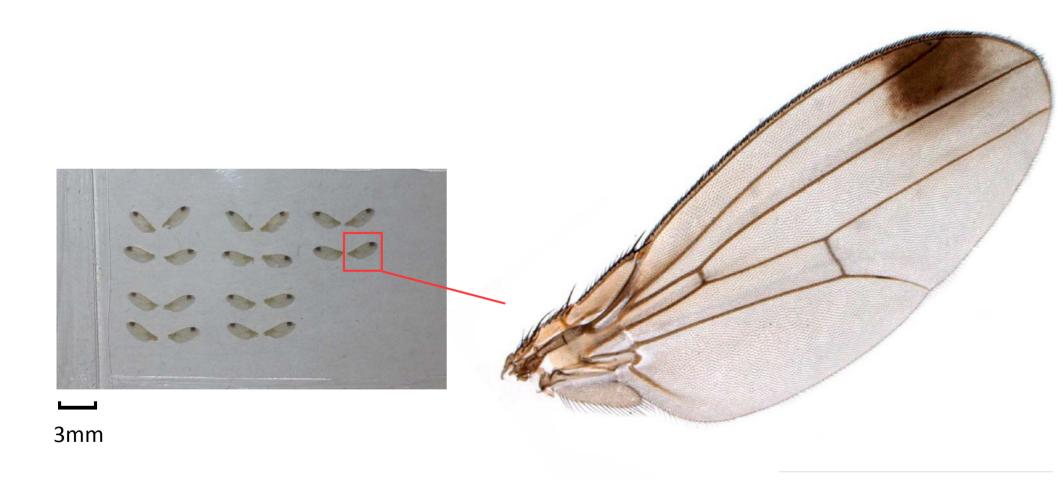
Phenotyping: wing shape

Extracting and mounting wings



Phenotyping: wing shape

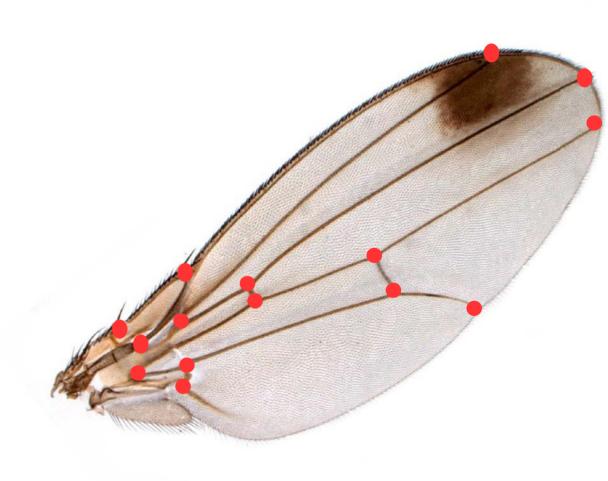
Mounting and digitalizing wings



Phenotyping: wing shape

Geometric morphometrics

15 landmarks placed on the wing

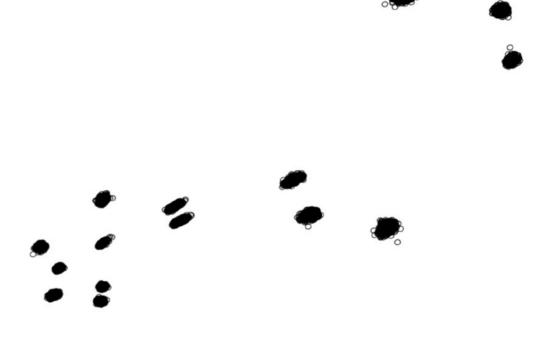


Phenotyping: wing shape

Geometric morphometrics

15 landmarks placed on the wing

Extraction of wing shape subtle variation



Phenotyping: wing shape

Geometric morphometrics

15 landmarks placed on the wing Extraction of wing shape subtle variation

Multivariate data



Comparative analyses

1. Estimating phenotypic divergence among populations

2. Estimating G matrix from wing shape data for each population

3. Comparing G matrices between populations

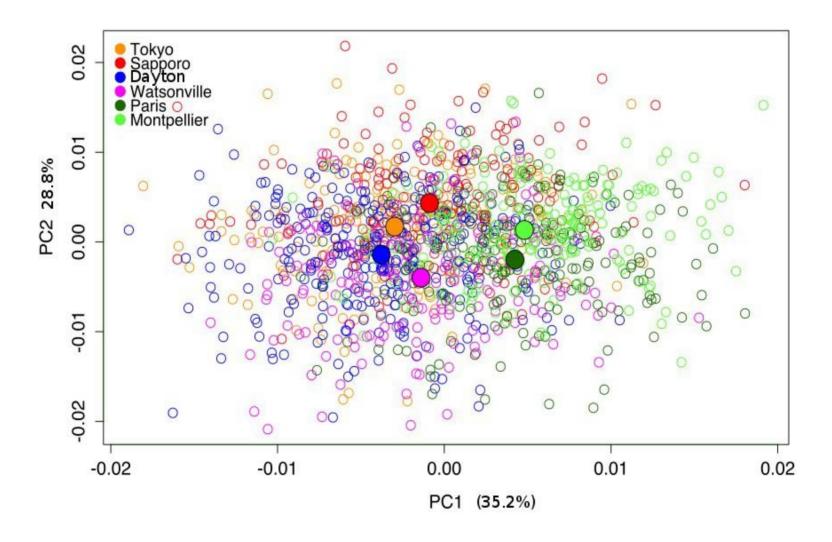
Similarity (correlation between matrices)

Volume (total genetic variance)

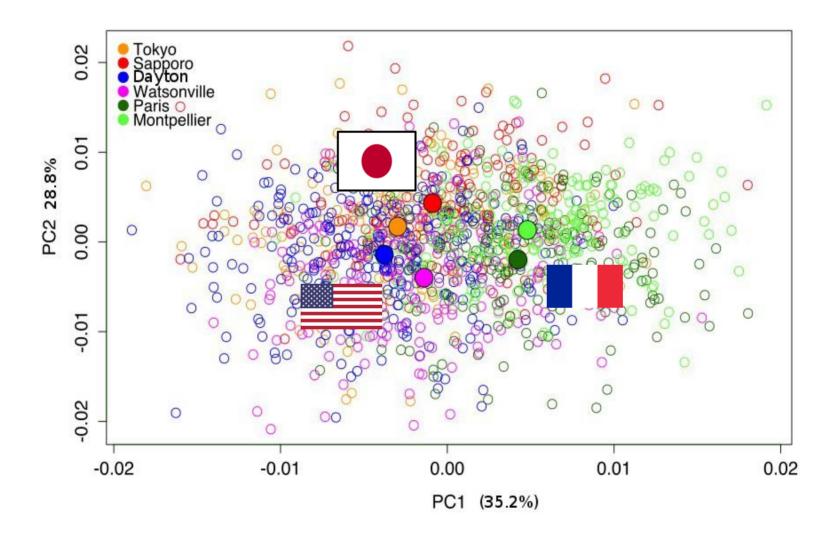
Orientation

Eccentricity (structuration of the variance)

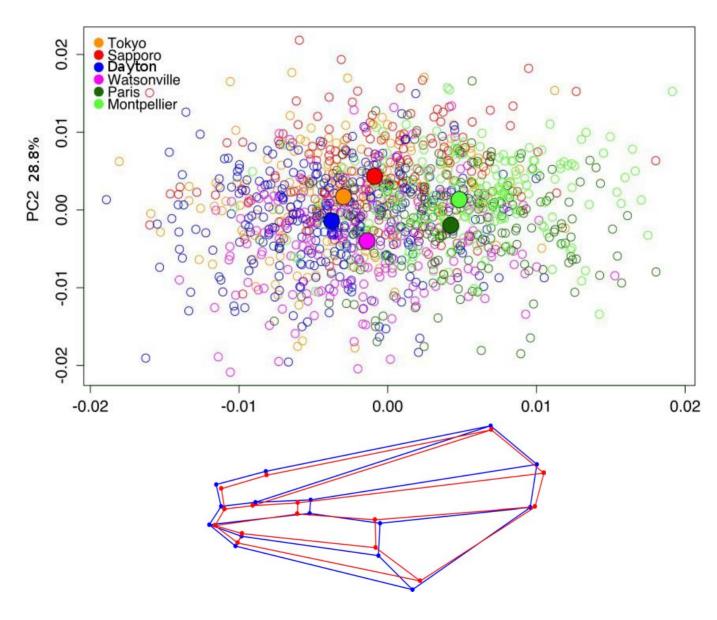
Is there divergence in wing shape among populations?



Is there divergence in wing shape among populations?

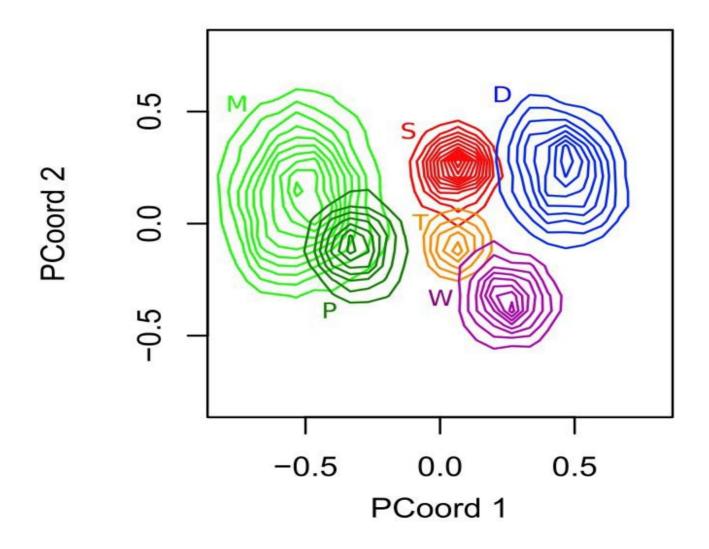


Is there divergence in wing shape among populations?



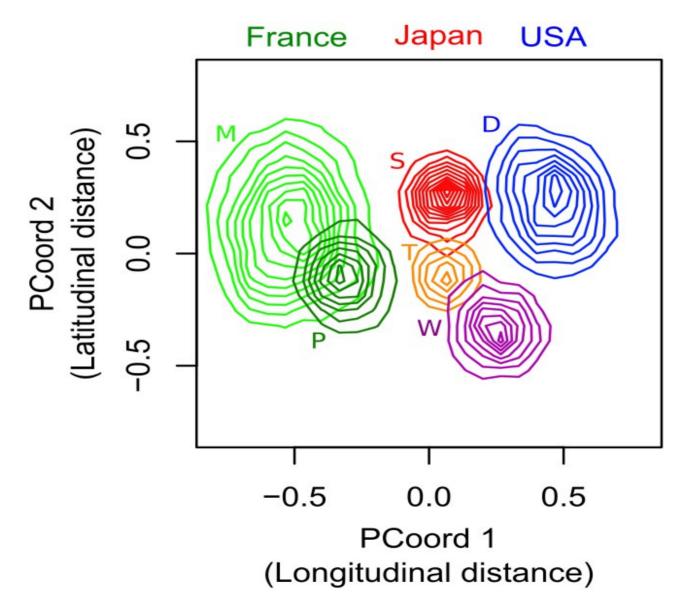
Distance between **G** matrices

Matrices at the center of the confidence interval



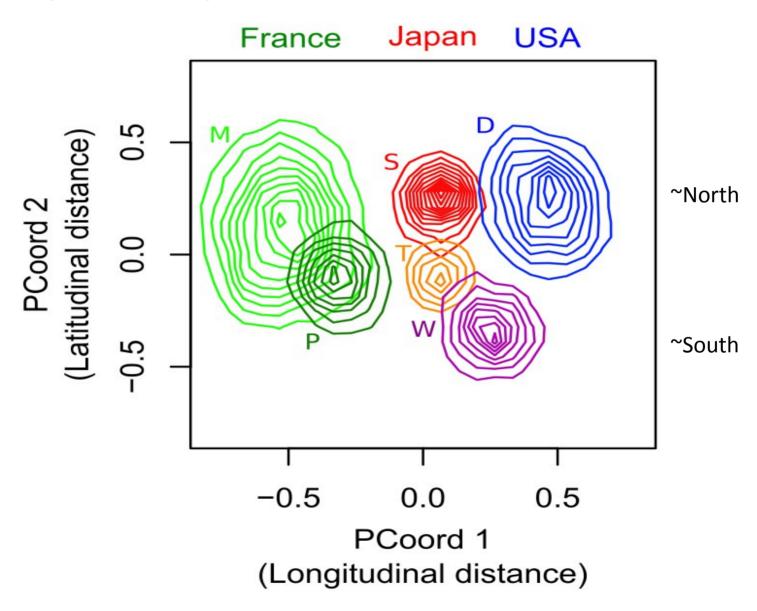
Distance between **G** matrices

Longitudinal signal (between continents)



Distance between **G** matrices

Latitudinal signal (North/South) but not consistent for France



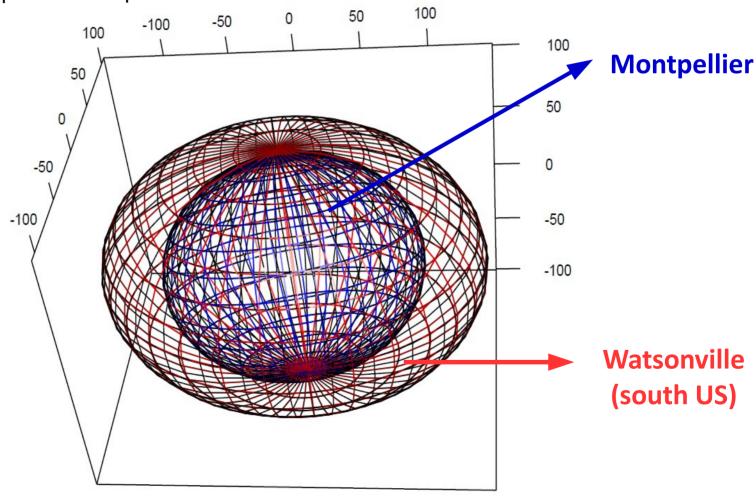
Comparisons of **G** matrices

1. Volume: total genetic variance

Comparisons of **G** matrices

1. Volume: total genetic variance

southern USA population > France, northern USA southern USA population = Japan

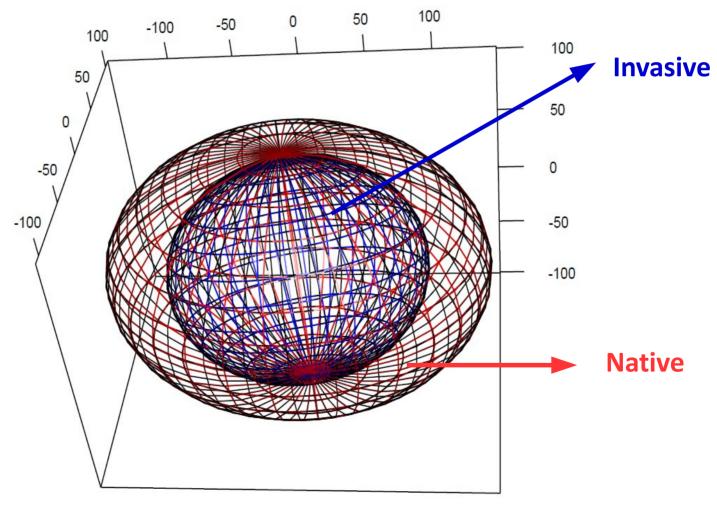


3D representation of matrices' volume differences

Comparisons of **G** matrices

1. Volume: total genetic variance

Trend for Native > Invasive (n.s)

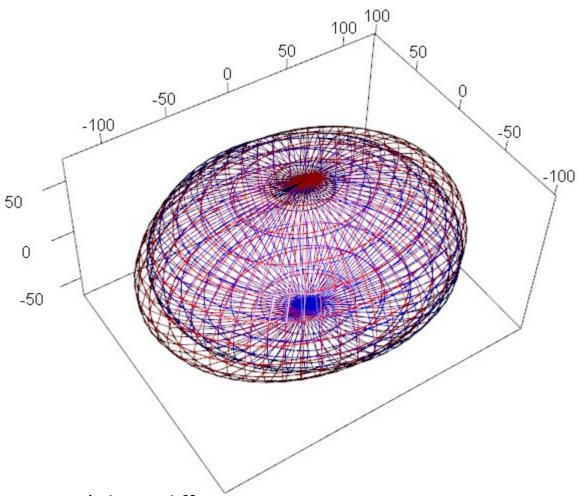


3D representation of matrices' volume differences

Comparisons of **G** matrices

2. Orientation and eccentricity

No significant differences or trend between populations Matrices have the same orientation and the same shape



3D representation of matrices' shape differences

Conclusions on Chapter 2

Phenotypic divergence

Weak but non-random divergence in wing shape: geographic signal

Conclusions on Chapter 2

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Weak but non-random divergence in wing shape: geographic signal

Evolution of G during the invasion

Weak but non-random divergence among matrices: geographic signal

Conclusions on Chapter 2

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Weak but non-random divergence among matrices: geographic signal

Changes in the volume of **G**

Populations experiencing bottleneck tend to have smaller volumes

Admixed southern USA population has greater volume

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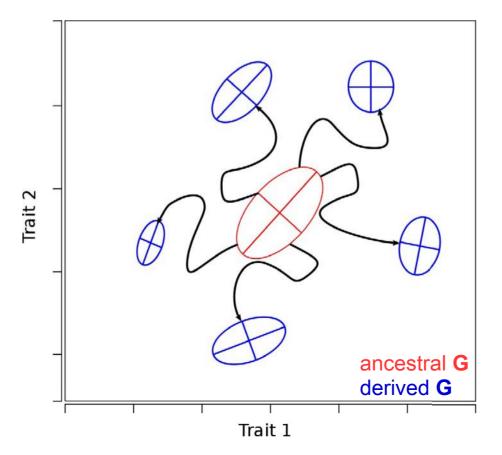
Admixed southern USA population has greater volume

Dominant role of neutral evolution in the divergence?

Conclusions on Chapter 2

Evolution of G during the invasion

Under drift **G** should have diverge randomly

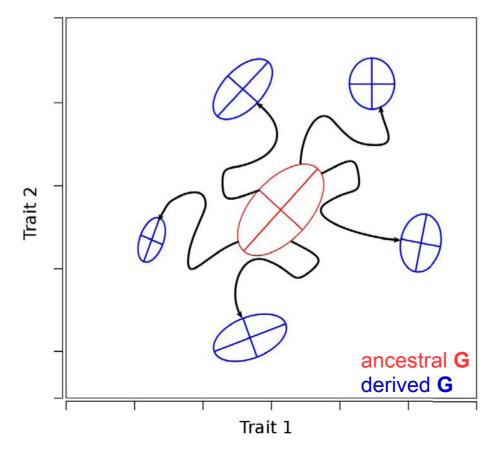


Conclusions on Chapter 2

Evolution of G during the invasion

Under drift **G** should have diverge randomly

Here stability of **G** on several aspects (orientation and shape)



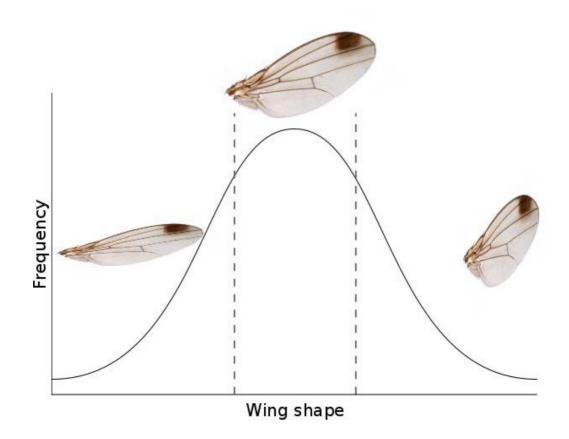
Conclusions on Chapter 2

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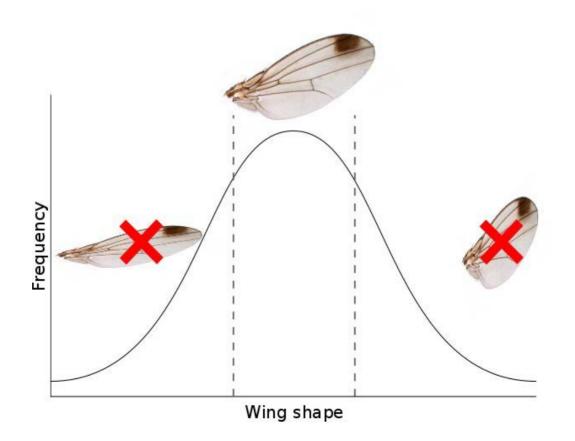
Stabilizing selection on the wing?



Conclusions on Chapter 2

Stabilizing selection on the wing?

Wing shape may be under strong stabilizing selection

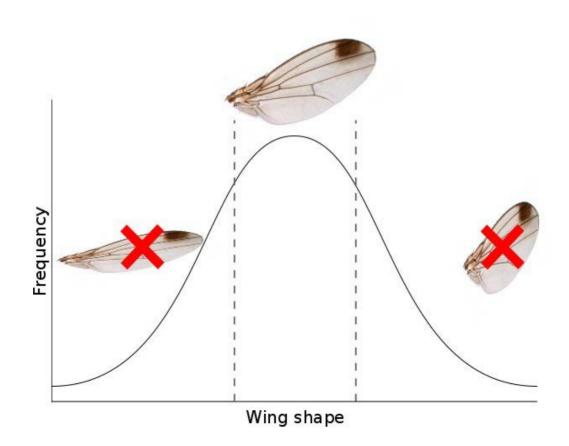


Conclusions on Chapter 2

Stabilizing selection on the wing?

Wing shape may be under strong stabilizing selection

Close to an adaptive peak



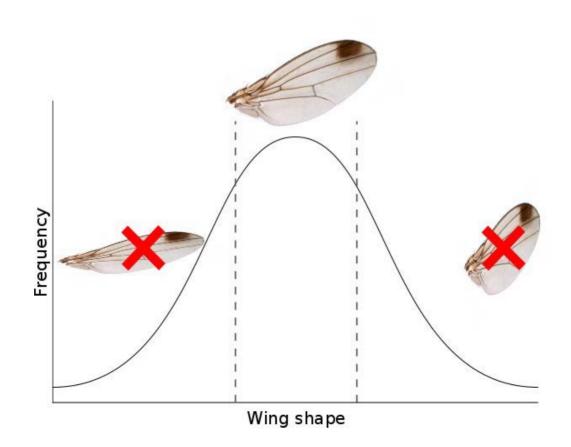
Conclusions on Chapter 2

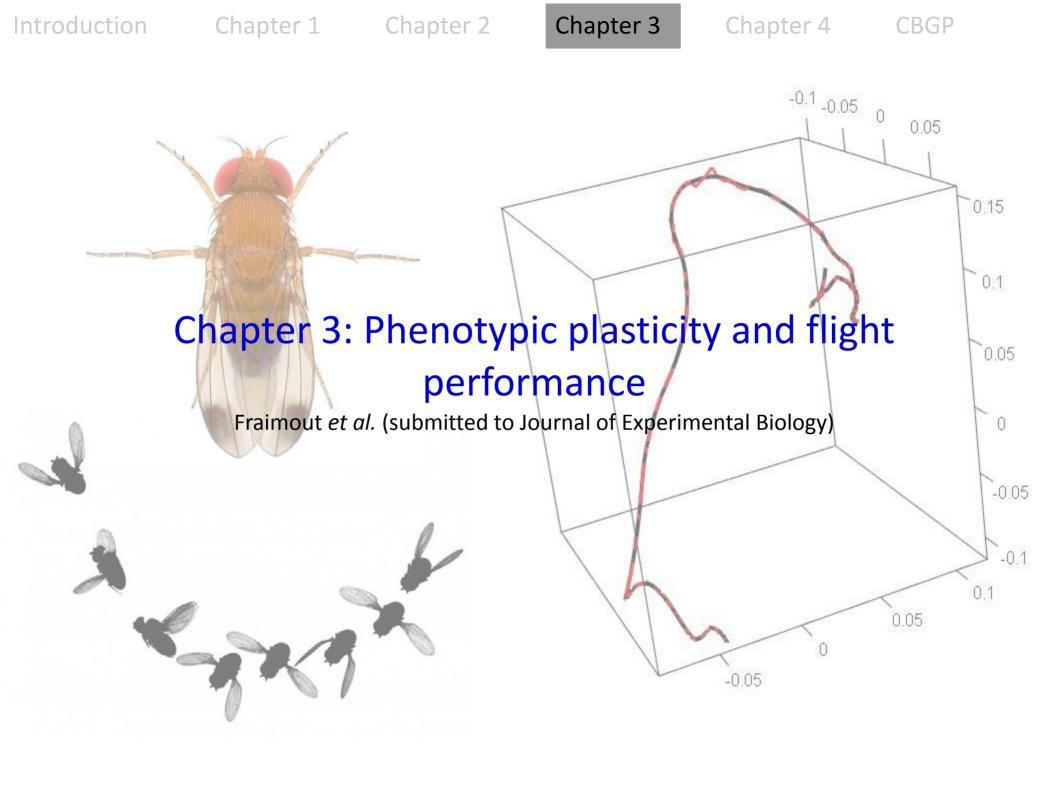
Stabilizing selection on the wing?

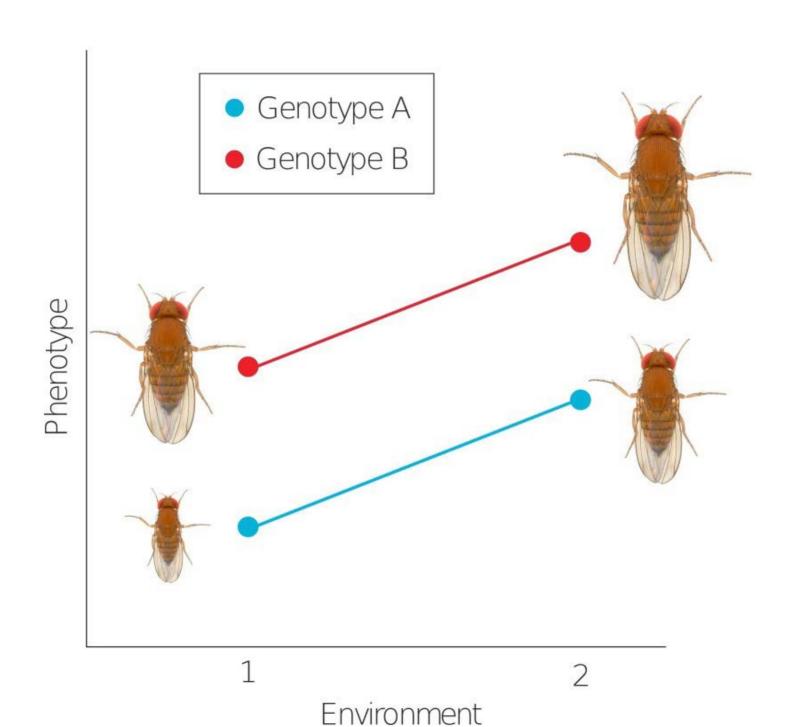
Wing shape may be under strong stabilizing selection

Close to an adaptive peak

Because of its role in flight performance (and foraging, courtship etc.)







The role of phenotypic plasticity in biological invasions

Does phenotypic plasticity facilitate invasion?

Invasive species are thought to be more plastic

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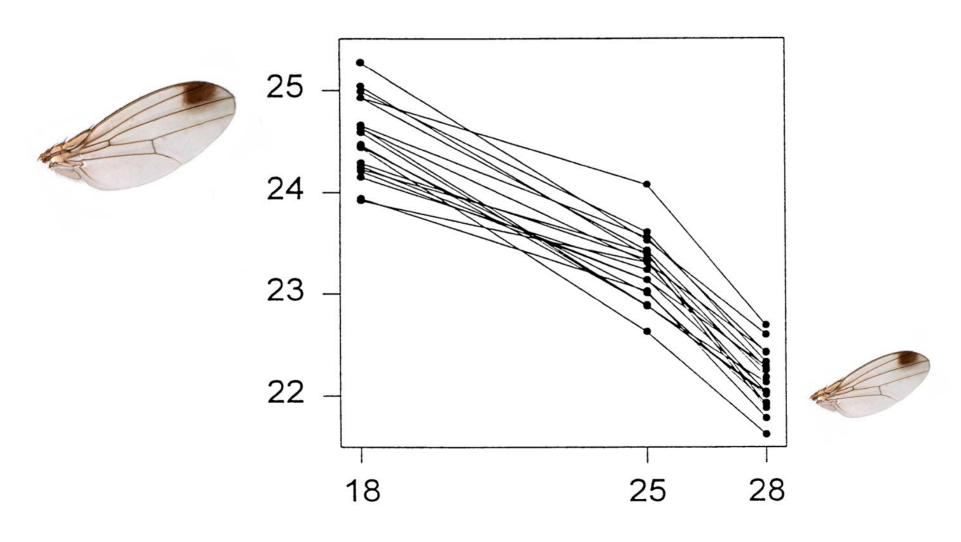
Link between plastic response and performance rarely tested empirically

The role of phenotypic plasticity in *D. suzukii*'s invasion

- 1. Comparing phenotypic plasticity between native and invasive populations
- 2. Estimating effect of plasticity on phenotype's performance
- 3. Comparing performances between native and invasive populations

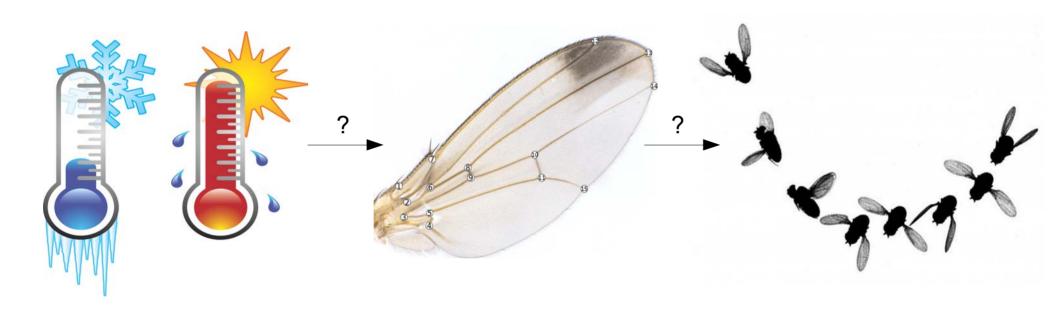
Environmental cue: developmental temperature

Major component of ectotherm's biology
Affects morphology in *Drosophila* (cf. adaptive latitudinal clines)

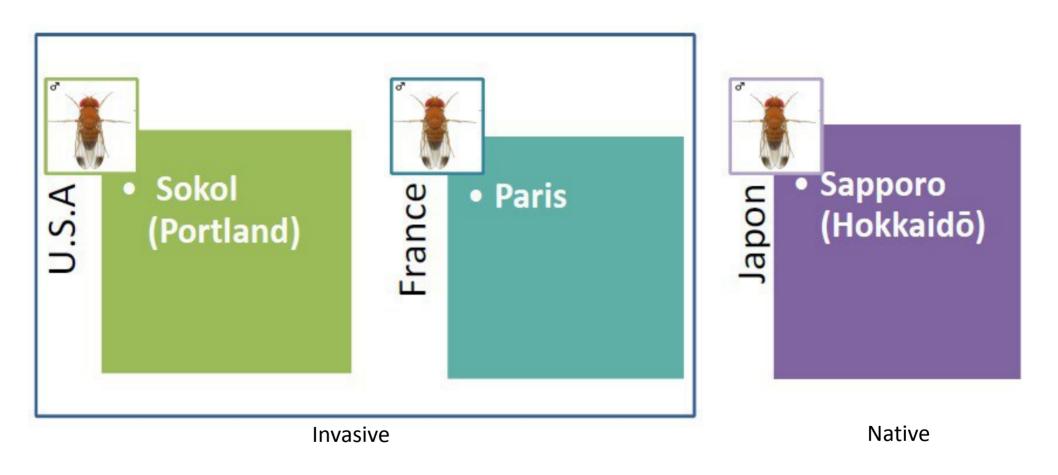


Temperature

Is there a relationship between wing plasticity and flight performance?

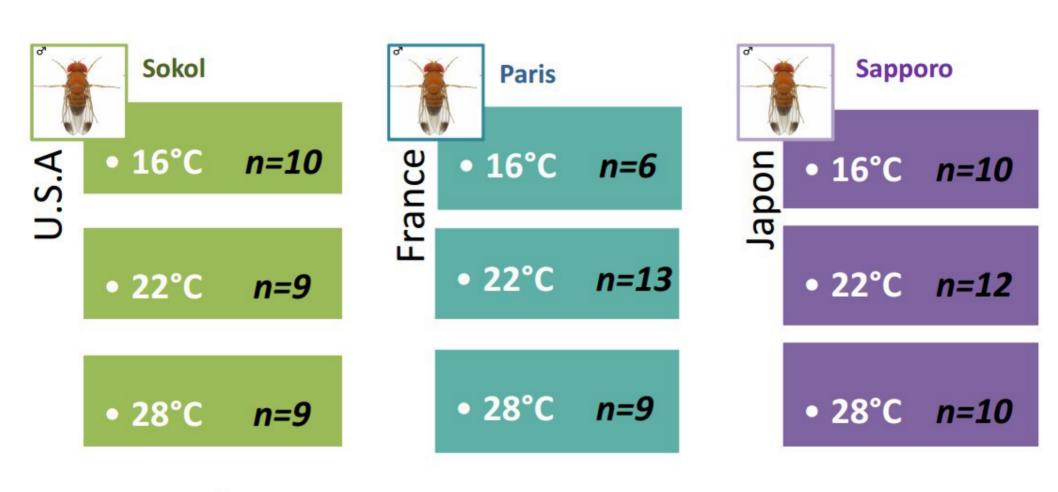


Testing the effect of developmental temperature on 3 populations of *D. suzukii* From northern localities within continents



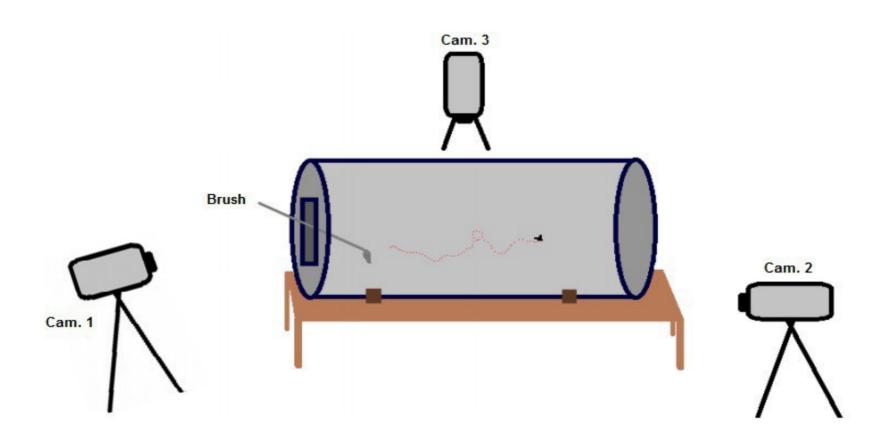
Testing the effect of developmental temperature on 3 populations of *D. suzukii*

3 experimental temperatures per population



Total = 88

Flight acquisition



High speed cameras
Temperature constant but not controlled (~22°C)

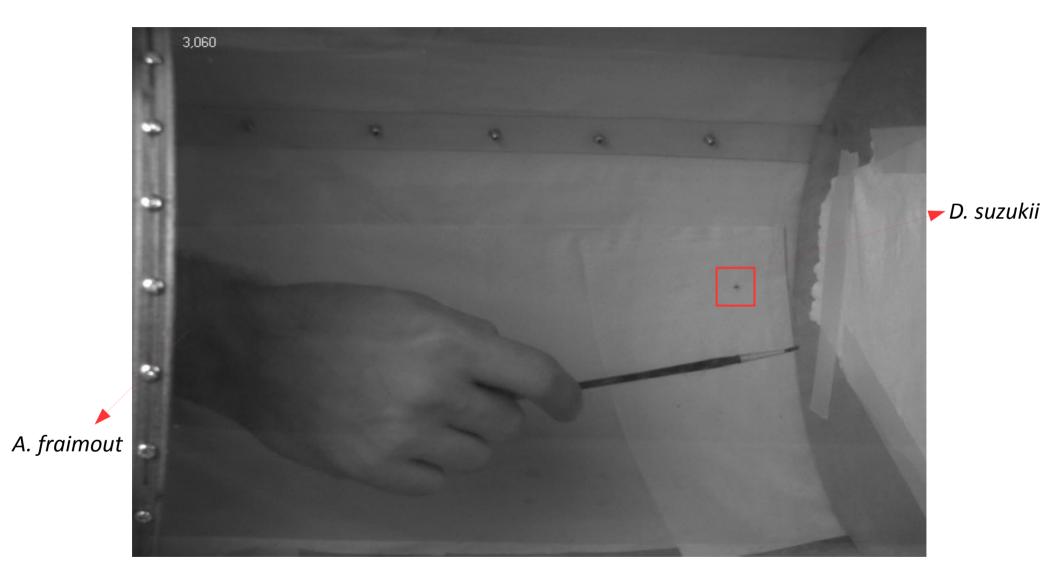
1 male/line

3 flight/male

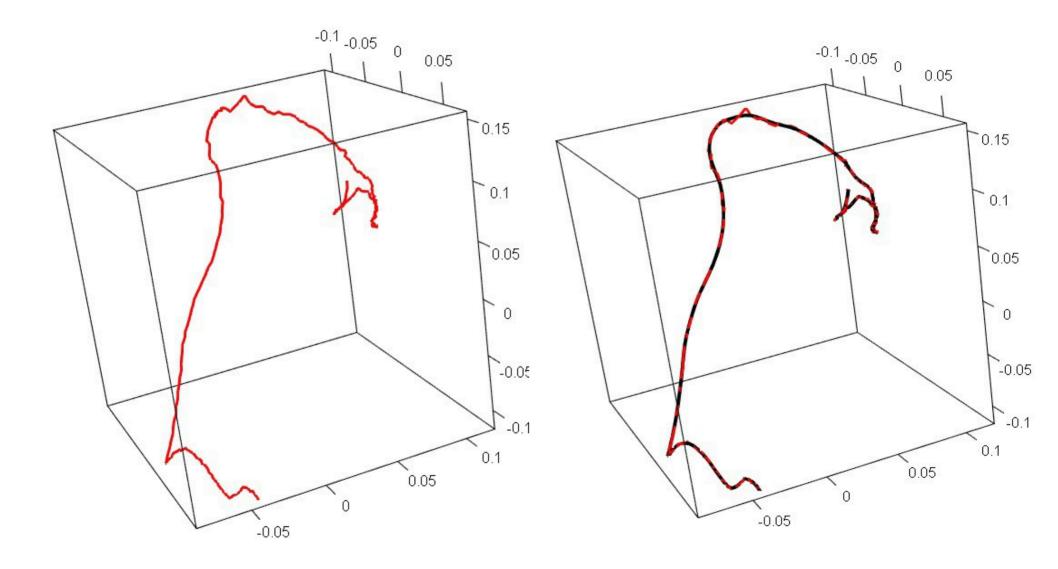
Flight acquisition



Flight acquisition



Estimating 3D trajectories and flight parameters

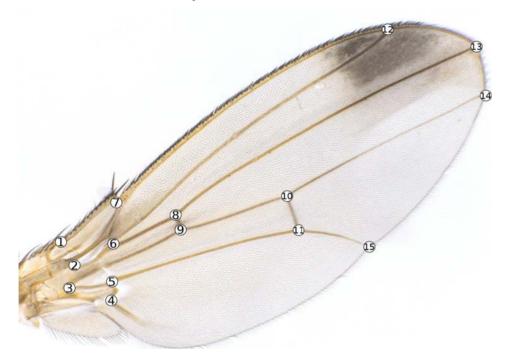


Trajectory smoothing (reducing noise/measurement error)

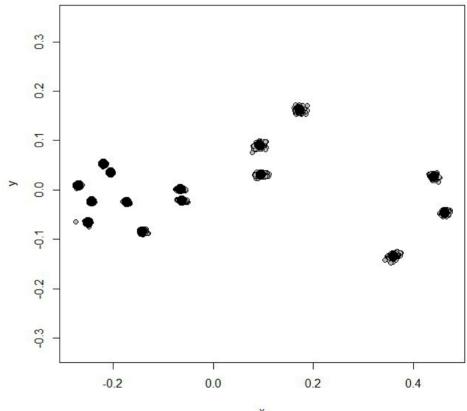
Flight parameters extraction: velocity, acceleration, sinuosity, angular changes and speed

Wing morphology

Geometric morphometrics



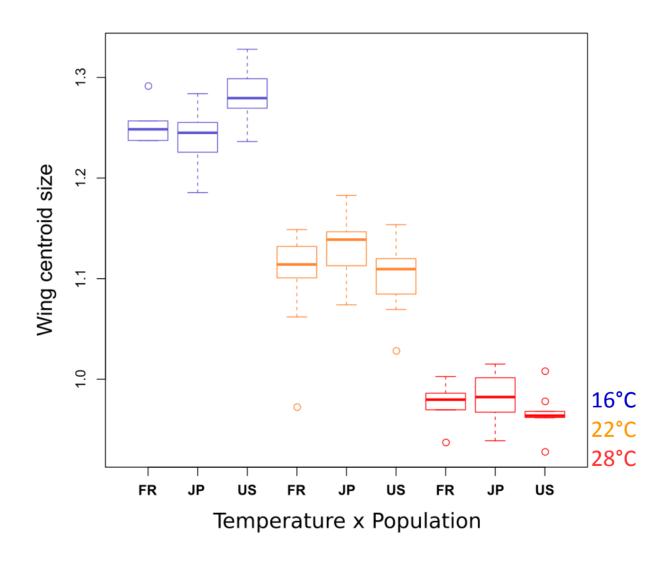
D. suzukii male wing



Procrustes superimposition – from Morpho R package

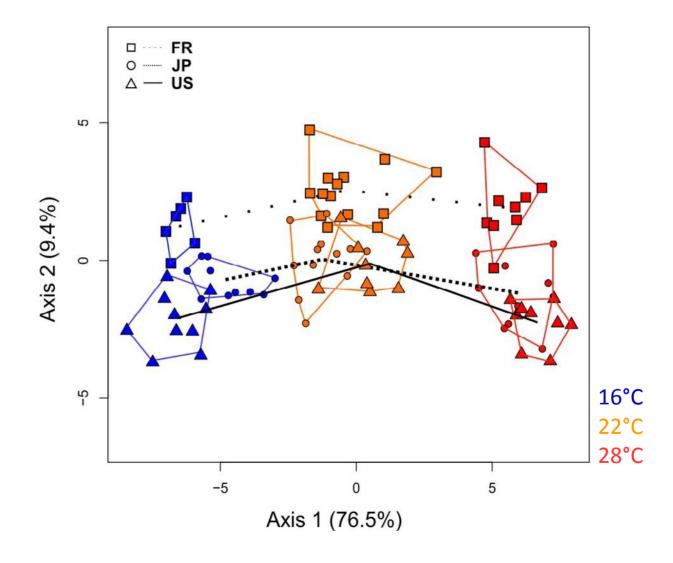
Effect of temperature on wing morphology: wing size

Strong effect of temperature on wing size



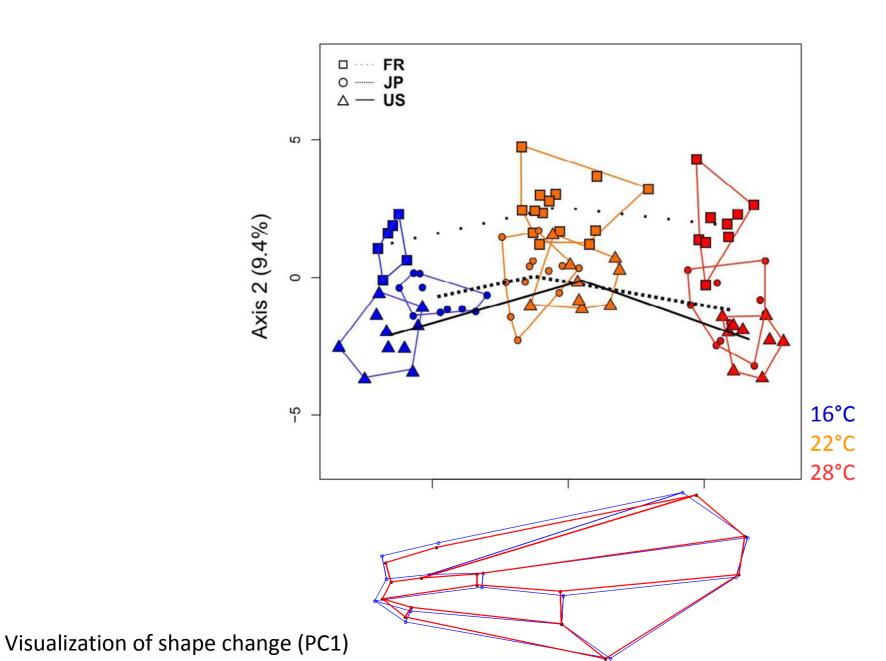
Effect of temperature on wing morphology: wing shape

Strong effect of temperature on wing shape (MANOVA p < 0.001)



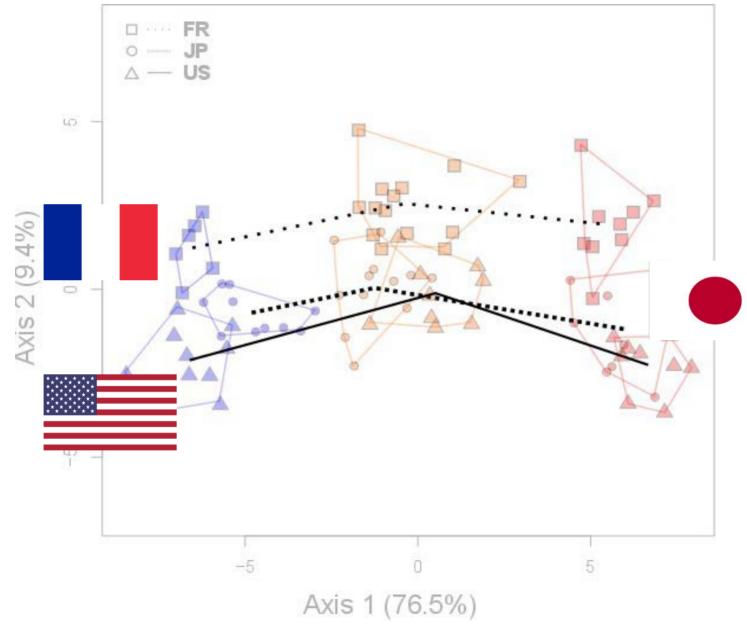
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Effect of temperature on wing morphology: wing shape

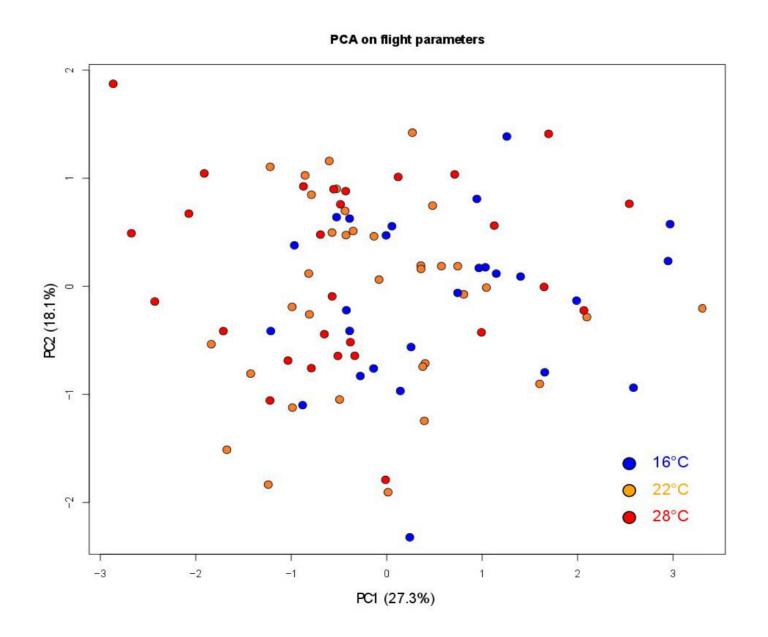
Paralel reaction norms – no difference in phenotypic plasticity

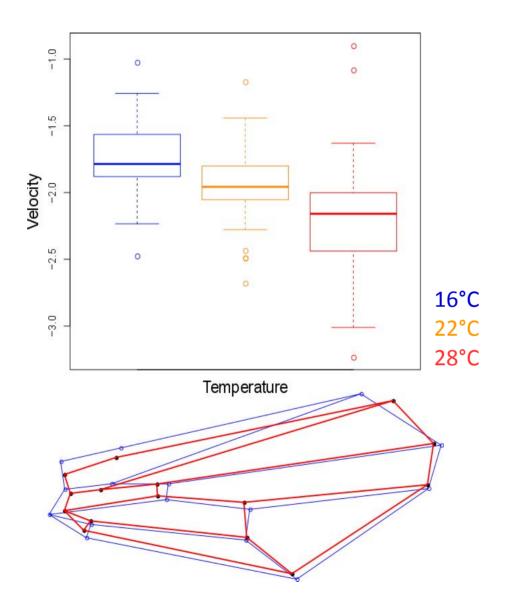


Parallel reaction norm → no difference in plasticity

Effect of temperature on flight

Effect of temperature on global flight (MANOVA p<0.001), but no differences between populations





Effect of temperature on particular flight parameters: velocity and acceleration

Conclusions on Chapter 3

Phenotypic plasticity in *D. suzukii*'s invasion

No difference in wing plasticity between native and invasive Nor in flight performance

Conclusions on Chapter 3

Phenotypic plasticity in D. suzukii's invasion

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Phenotypic plasticity did not seem to facilitate *D. suzukii*'s invasion

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Association between wing morphology and flight

Flies reared at 16°C capable of faster flights

Conclusions on Chapter 3

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Is 16°C an optimal temperature for *D. suzukii*?

Conclusions on Chapter 3

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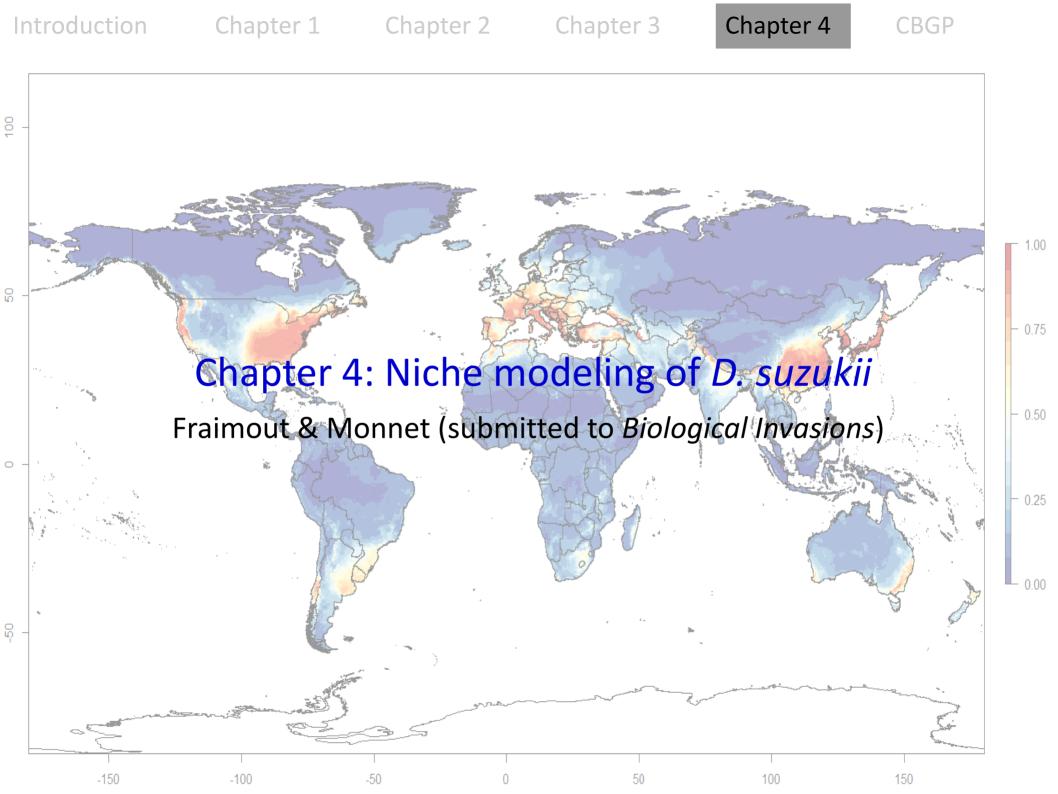
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Adaptive plasticity?

Is 16°C an optimal temperature for *D. suzukii*?

Need to characterize the climatic niche of the species



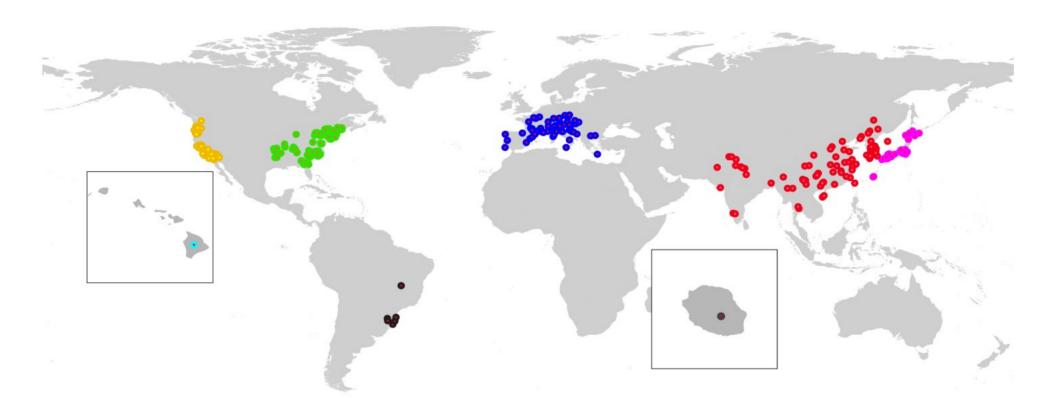
Linking evolution to ecology

Invasive species are thought to experience rapid evolution in response to environmental changes

How much environmental change did *D. suzukii* experience? Can previous result be explained by environmental changes? What is the climatic optimum for *D. suzukii*?

Estimation of the climatic niche of *D. suzukii* from presence data

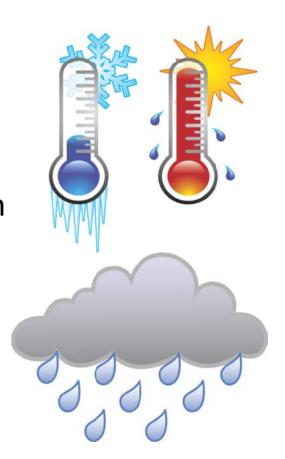
Occurence data worldwide from field, litterature and databases



Estimation of the climatic niche of *D. suzukii* from presence data

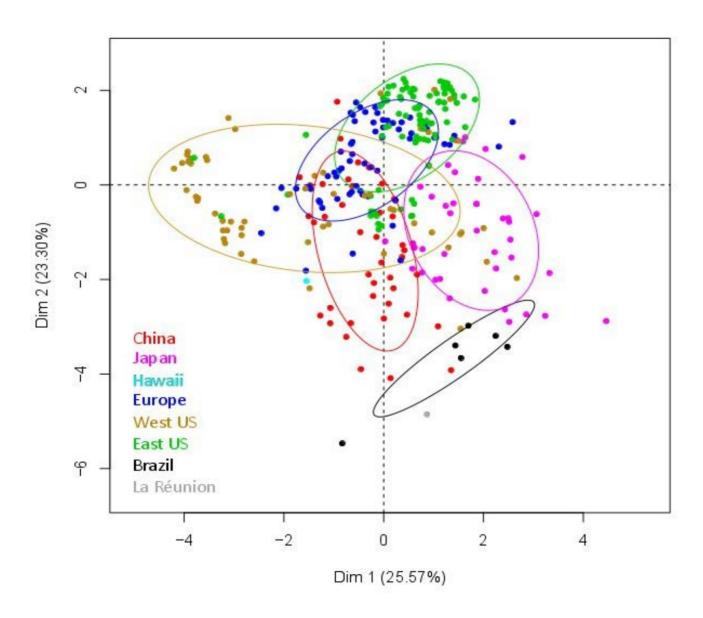
Climatic variables from the worldclim database

Annual mean temperature
Temperature seasonality
Temperature of the coldest month
Temperature of the warmest month
Annual mean precipitation
Precipitation seasonality
Precipitation of the driest month
Precipitation of the wettest month



Estimation of the climatic niche of *D. suzukii* from presence data

Principal component analysis



Quantifying the ancestral niche through species niche modeling (SDM)

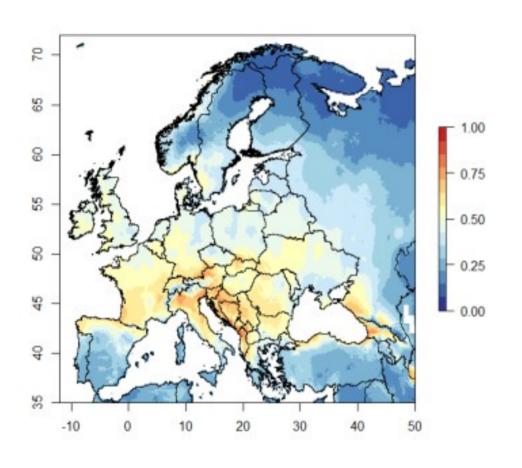


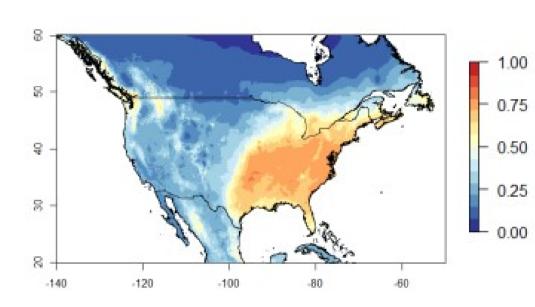
Projection of the ancestral niche in invaded ranges



Projection of the ancestral niche in invaded ranges

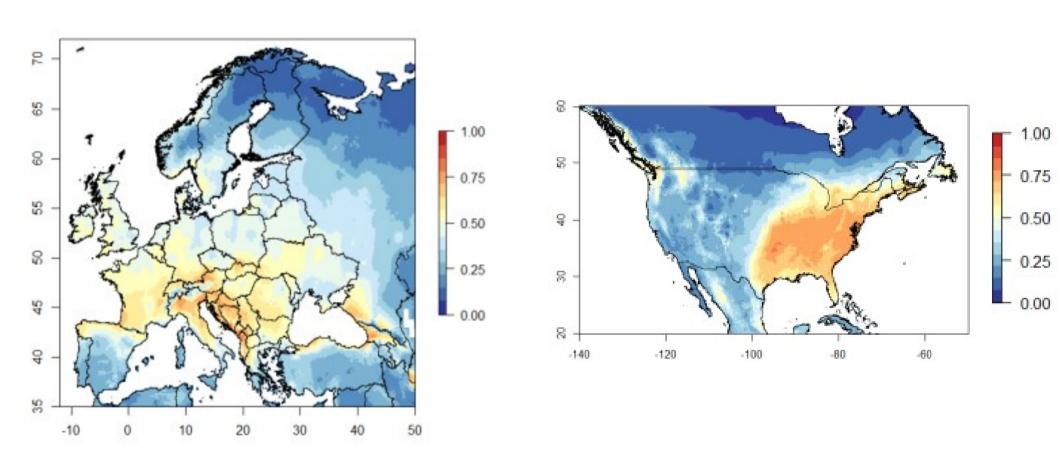
From Asia to Europe and USA



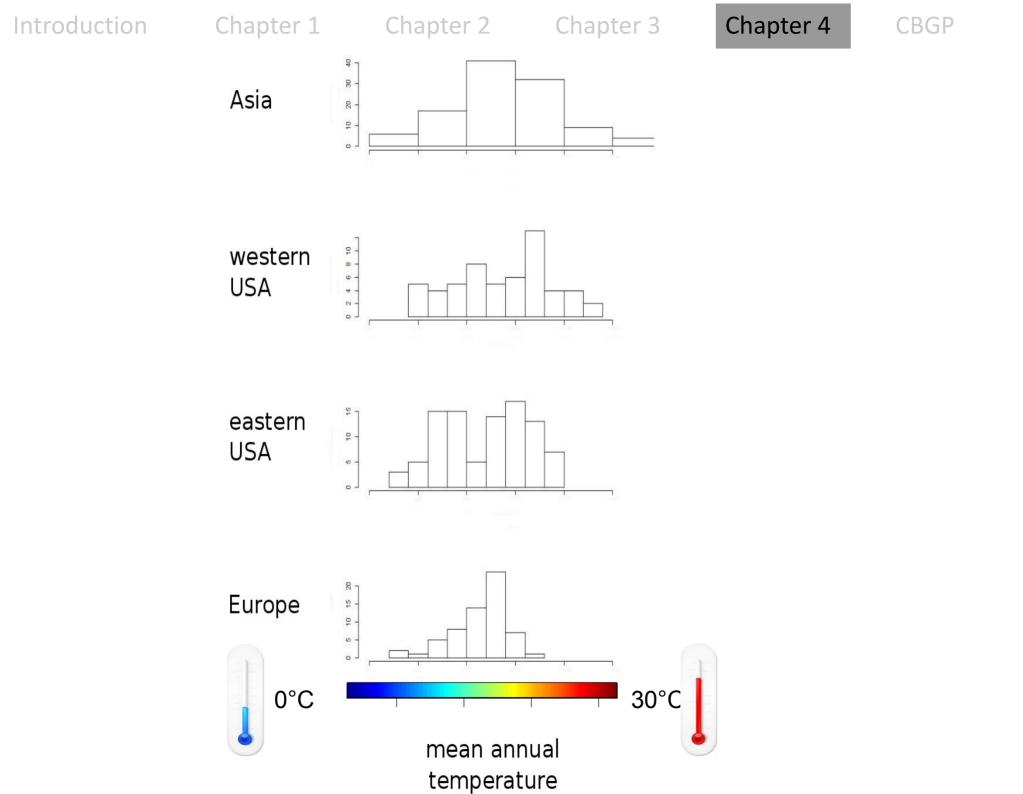


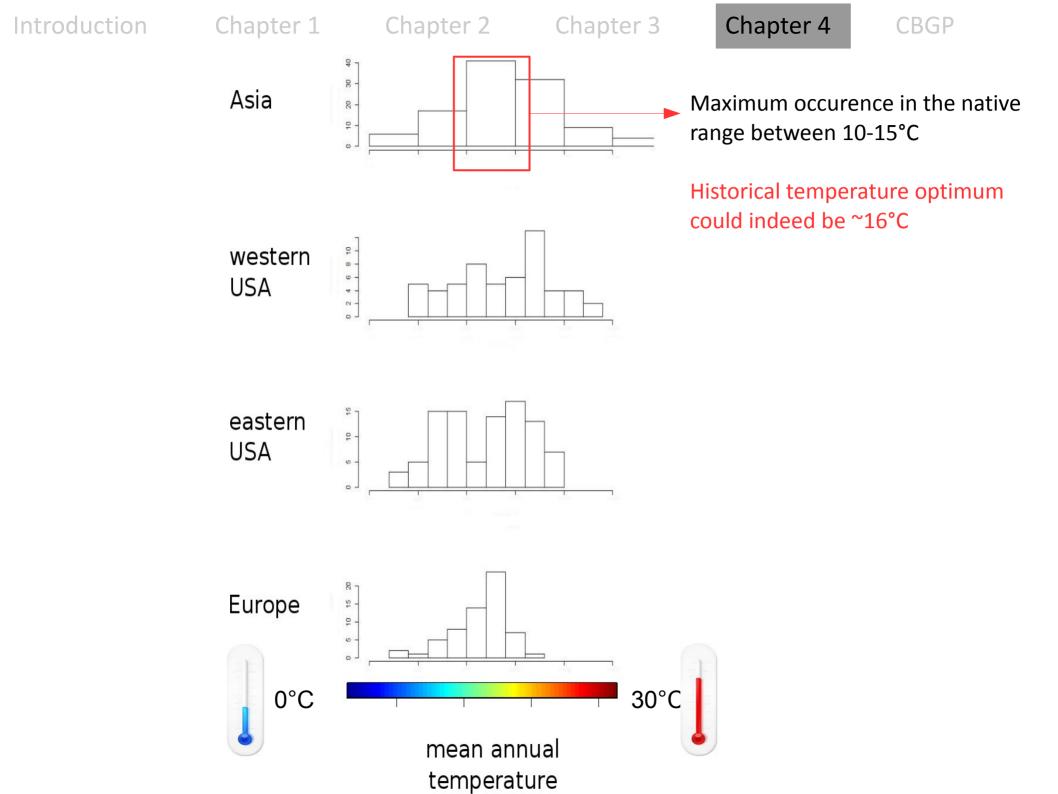
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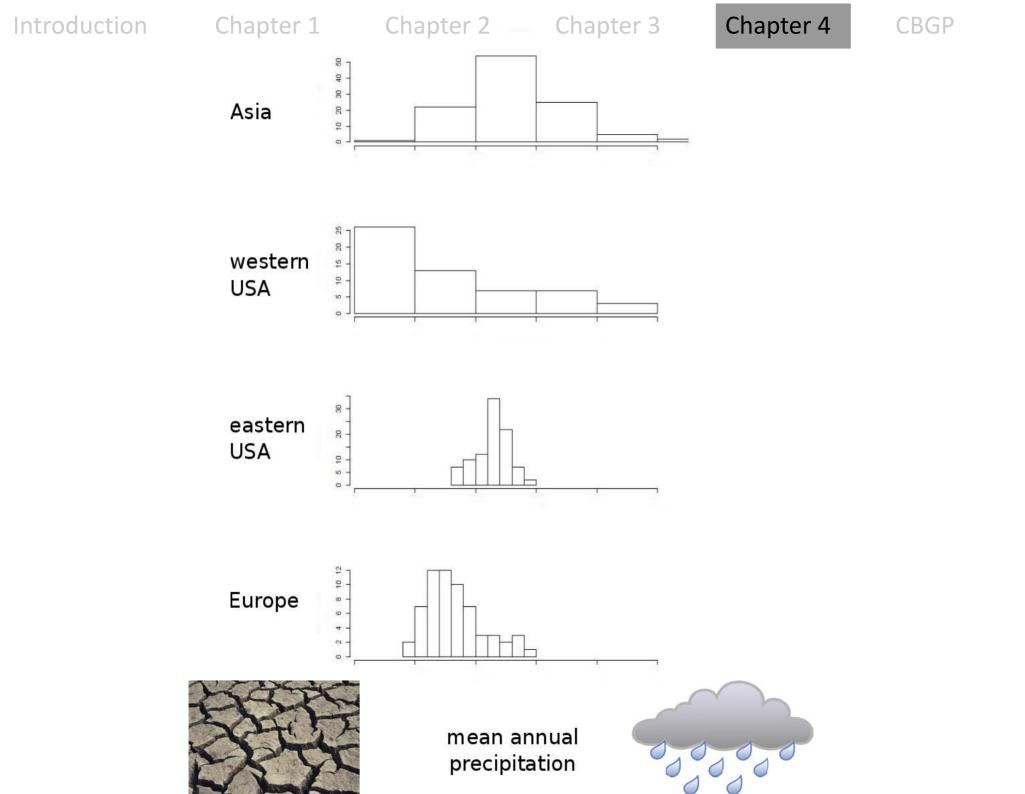
From Asia to Europe and USA

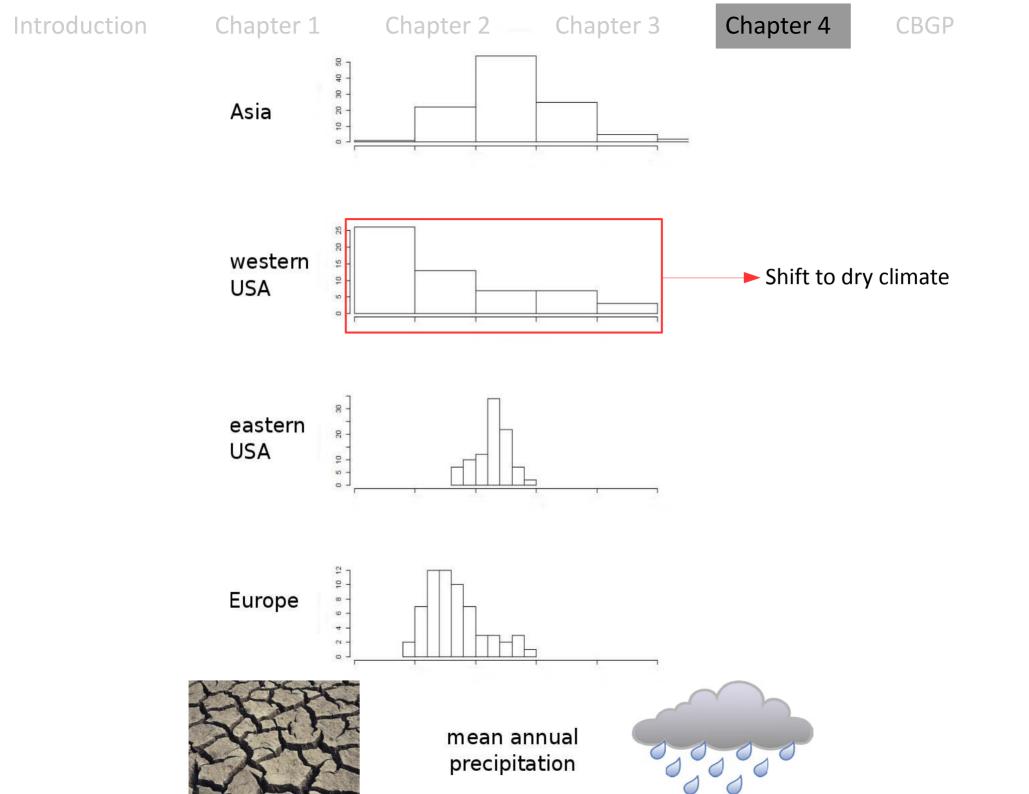


Very low probability of presence in western USA









Conclusions on Chapter 4

Climatic niche

Climate diversity worldwide

Conclusions on Chapter 4

Climatic niche

Climate diversity worldwide

Wide ancestral niche emcompasses invasive climates (eastern USA and Europe)

Conclusions on Chapter 4

Climatic niche

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Optimal climate seems temperate (16°C and not dry)

Conclusions on Chapter 4

Climatic niche

Climate diversity worldwide

Wide ancestral niche emcompasses invasive climates (eastern USA and Europe)

Optimal climate seems temperate (16°C and not dry)

However niche shift to very dry climate in southern USA

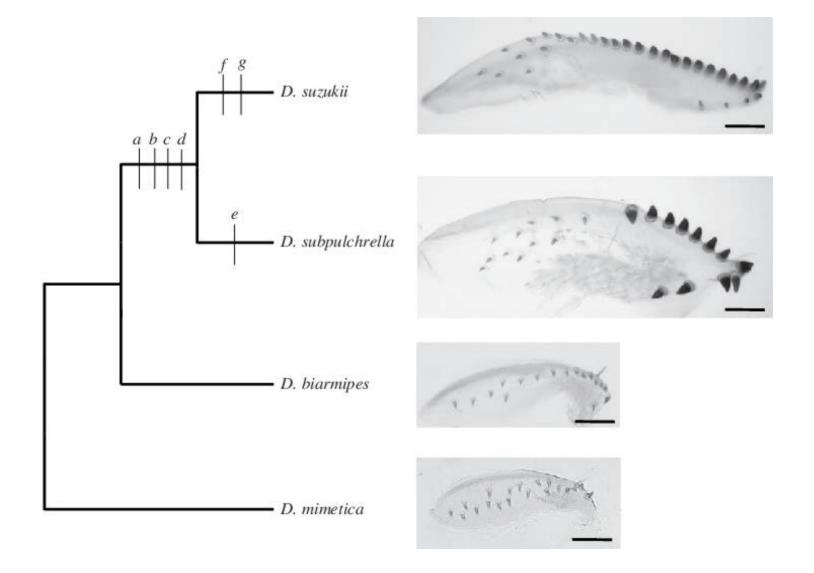
Post-doc CBGP D. suzukii's ovipositor morphometrics

D. suzukii's ovipositor





Introduction



CBGP

How variable is the ovipositor?

Genetic variation?

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Genetic variation?

Between different populations?

How variable is the ovipositor?

Genetic variation?

Between different populations?

Environmental variation (plasticity)?

How variable is the ovipositor?

Genetic variation?

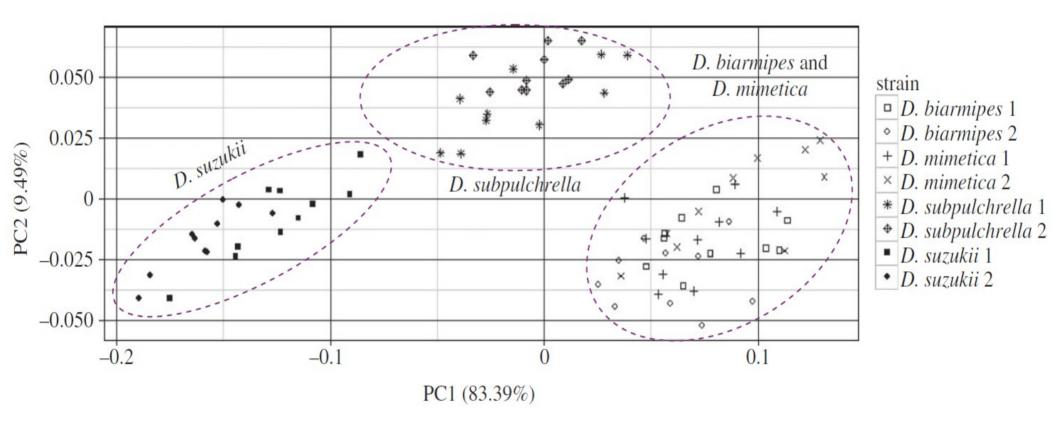
Between different populations?

Environmental variation (plasticity)?

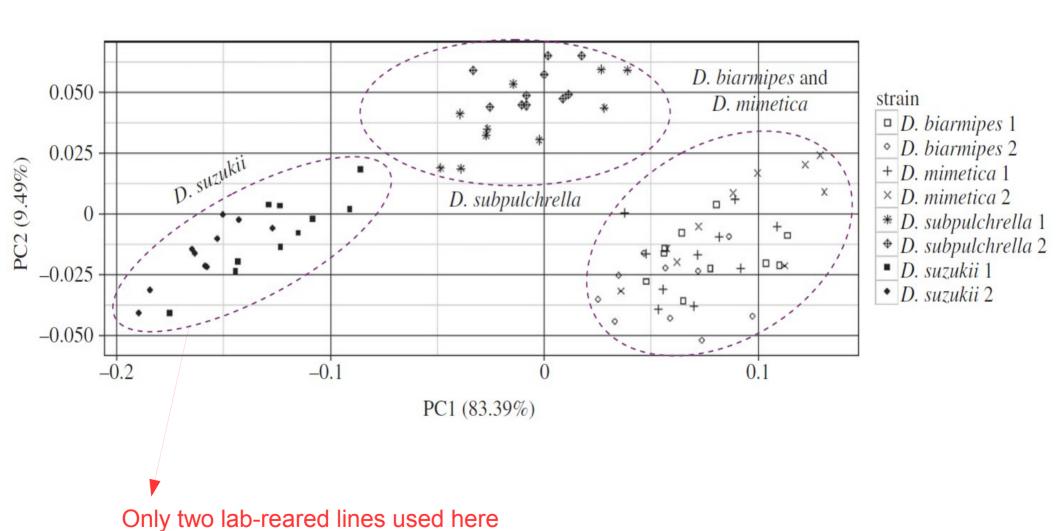
Between different temperatures, substrate etc.

How variable is the ovipositor?

Few information so far

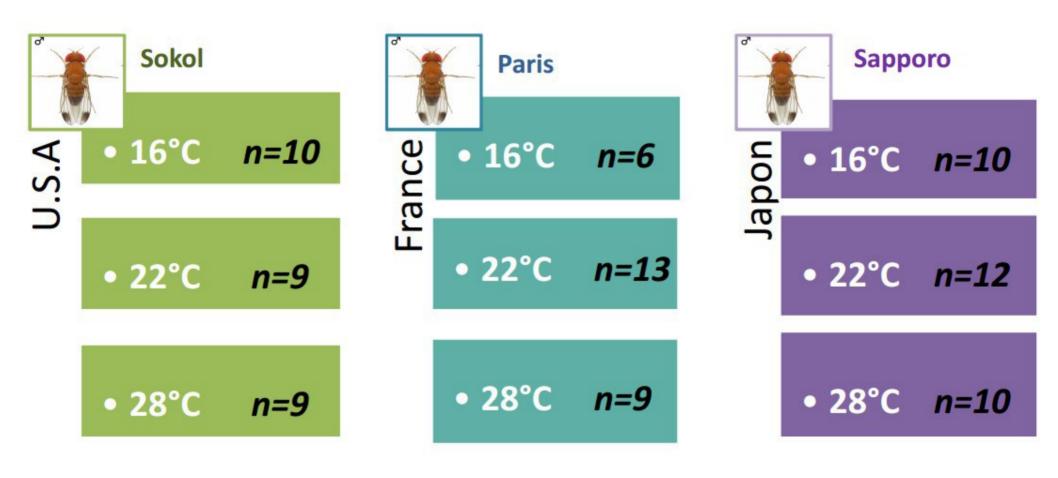


How variable is the ovipositor?



Characterization of ovipositor's morphology

Using multiple lab-reared lines



Total = 88

Within treatment between populations = genetic variation Within population between treatment = plastic variation

Characterization of ovipositor's morphology

Using multiple lab-reared lines + natural populations from

different sources

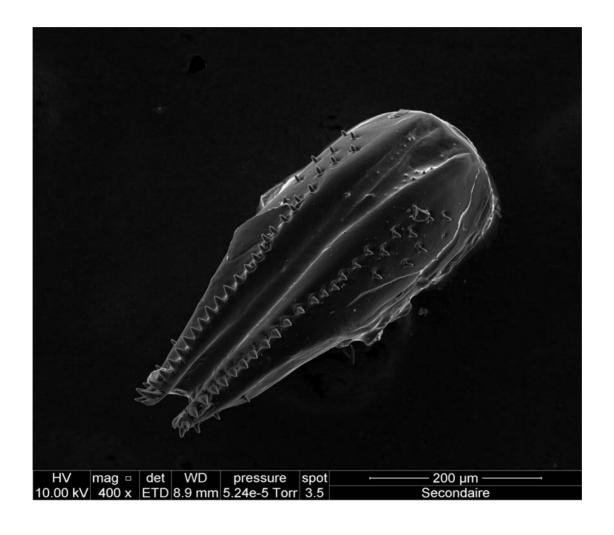






How to quantify the ovipositor?

3D geometric morphometrics from SEM images



How to quantify the ovipositor?

3D geometric morphometrics from SEM images







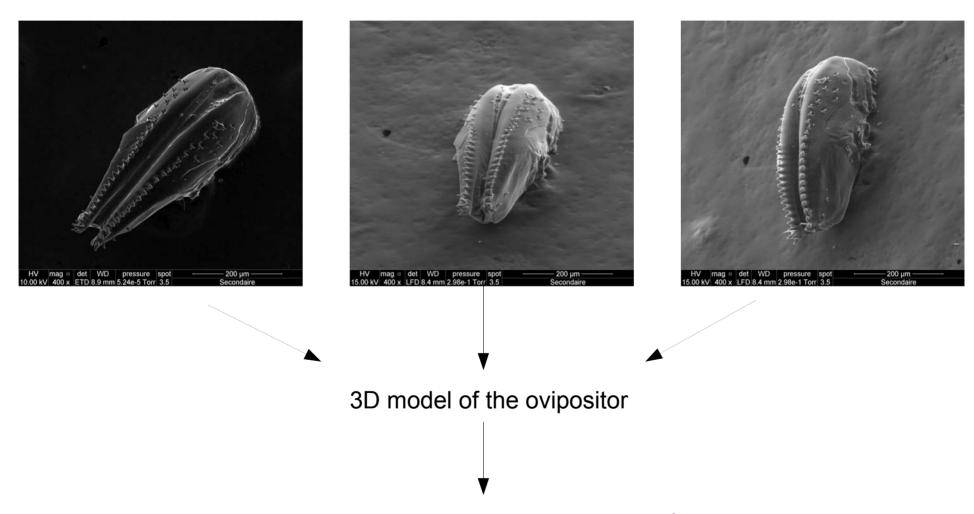
CBGP

3D model of the ovipositor

Quantification of shape differences

How to quantify the ovipositor?

3D geometric morphometrics from SEM images



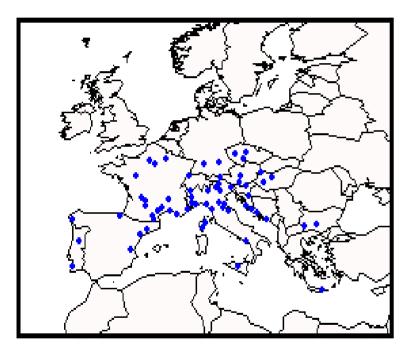
What contribution to ovipositor's variation from genetic and/or environmental components?

CBGP

Merci!

Reciprocal projections in the invaded ranges

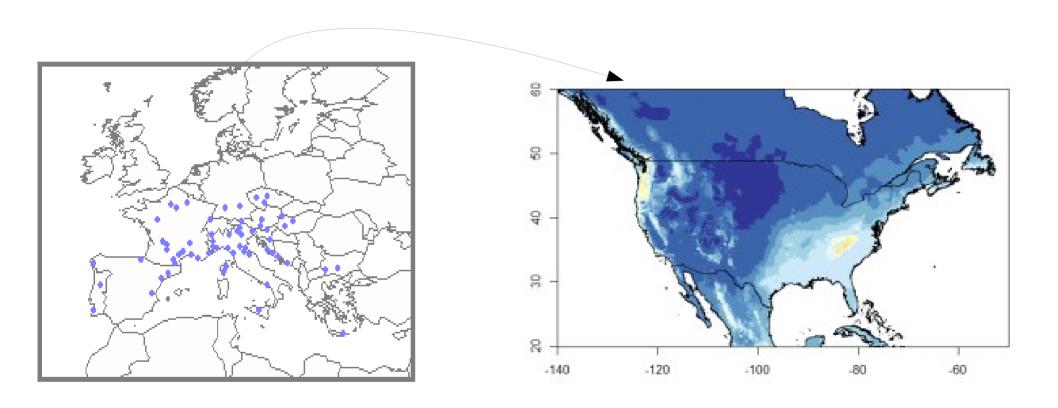
From Europe and USA



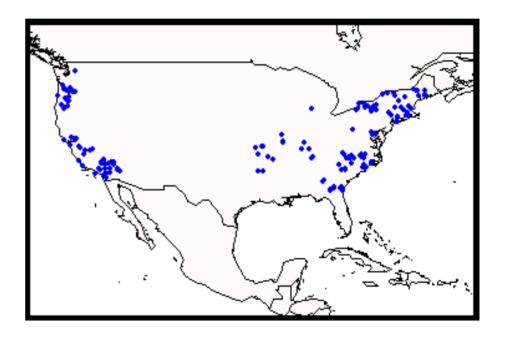
Estimating European niche

Reciprocal projections in the invaded ranges

Model calibrated on European climate poorly predicts presence in USA



Reciprocal projections in the invaded ranges From USA to Europe



Estimating north American niche

Reciprocal projections in the invaded ranges

Model calibrated on north American climate predicts well presence in Europe!

