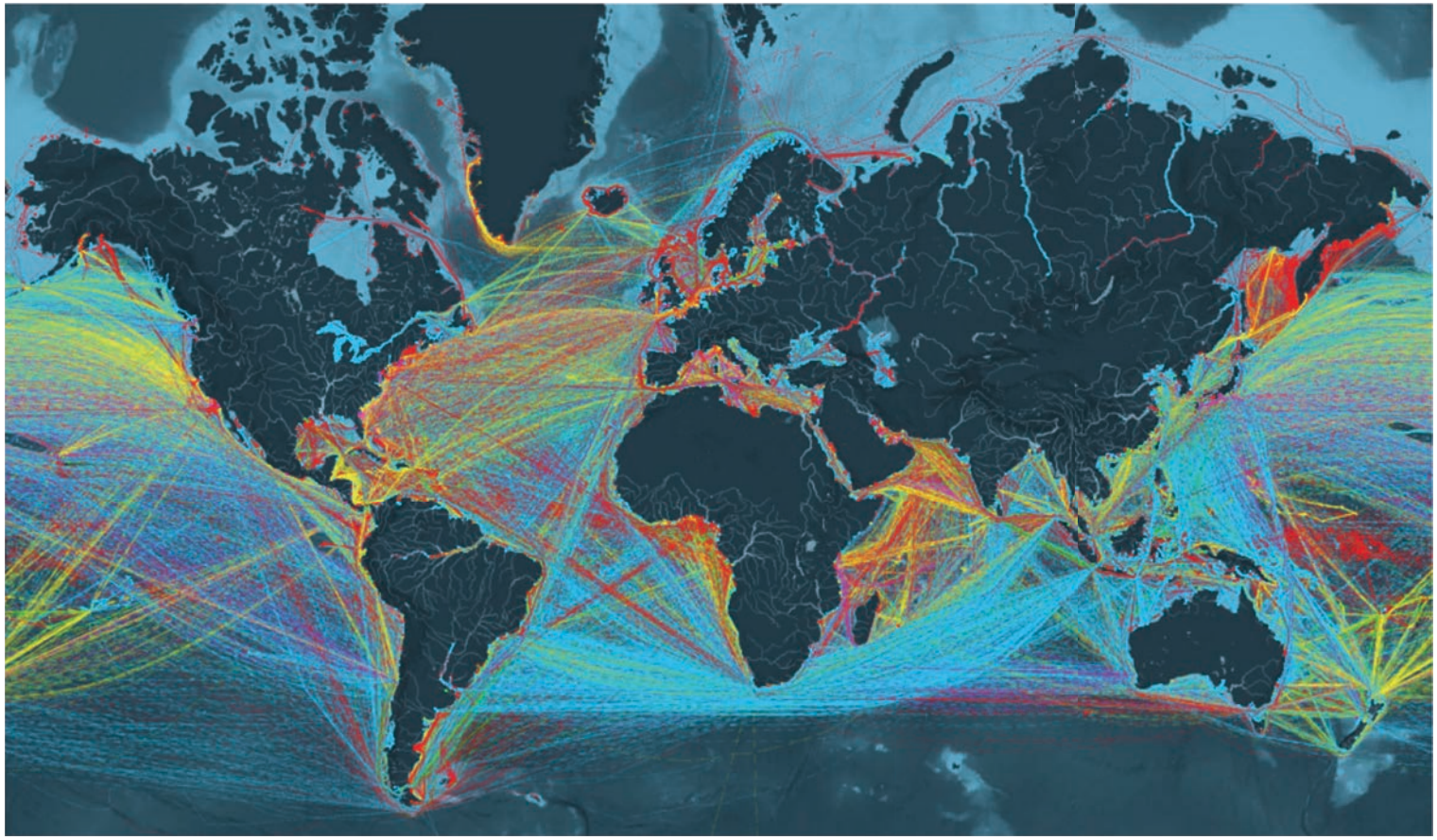
Adaptive responses of *Drosophila suzukii*, a generalist invasive species

Laure Olazcuaga

13 December 2019

Supervision: Arnaud Estoup and Mathieu Gautier

Biological invasions



Shipping routes (2012)

Impacts of biological invasions

Local biodiversity

Harlequin ladybird

Crop pest

Fall armyworm

Human health

Annual ragweed

What factors promote invasion success?

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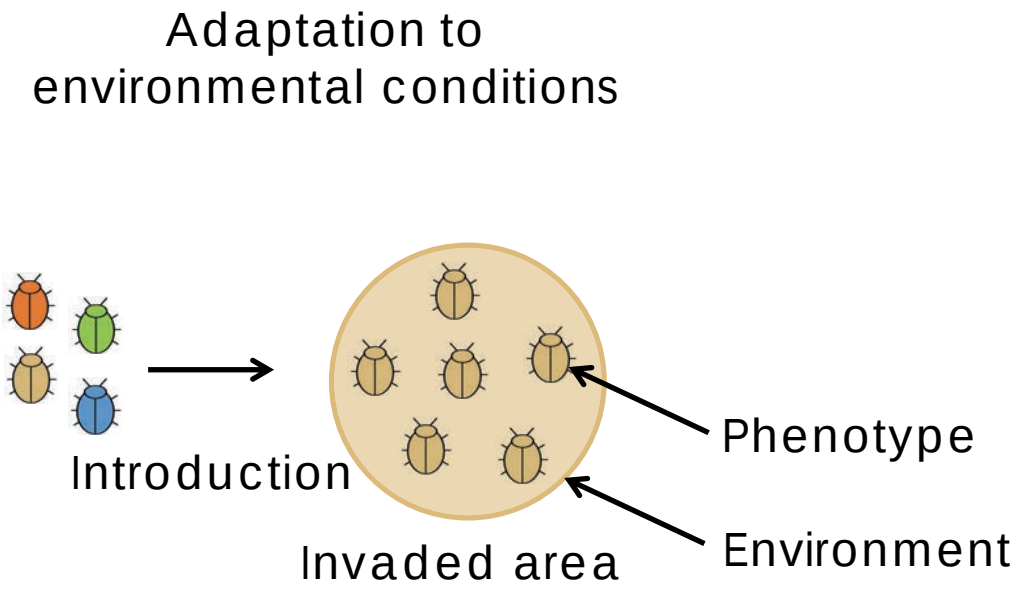
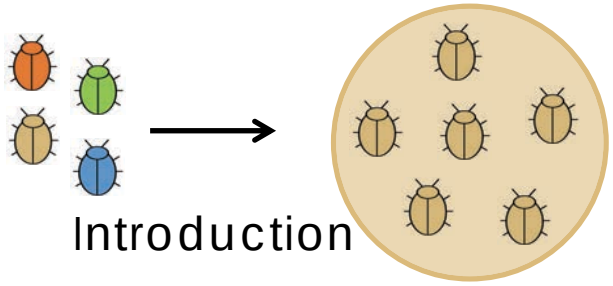
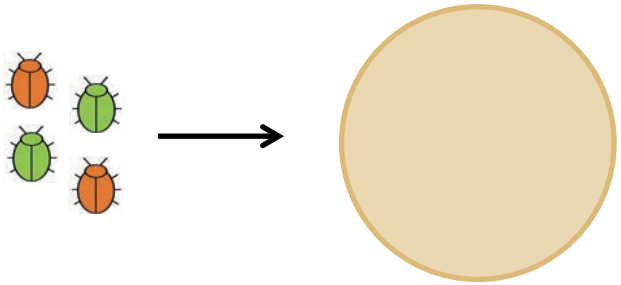


What factors promote invasion success?

Adaptation to
environmental conditions





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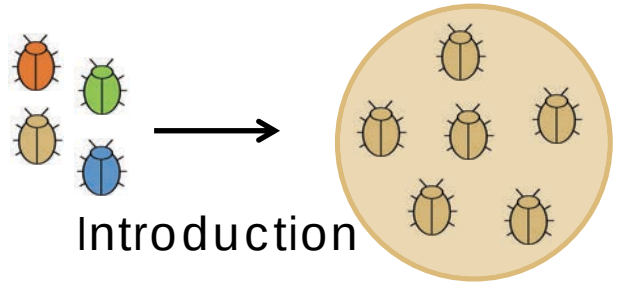
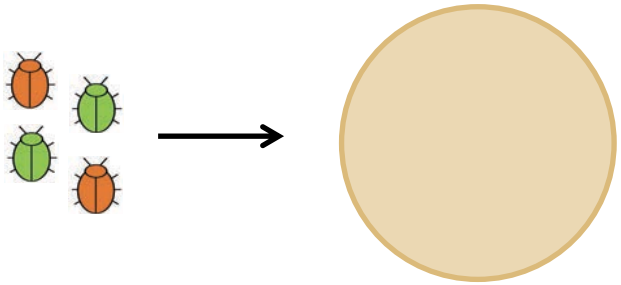
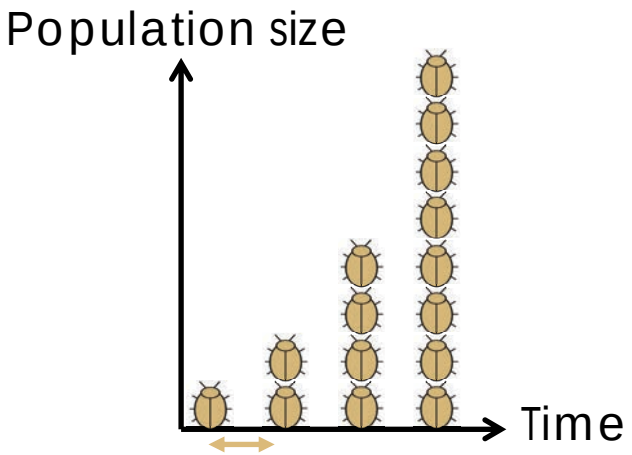
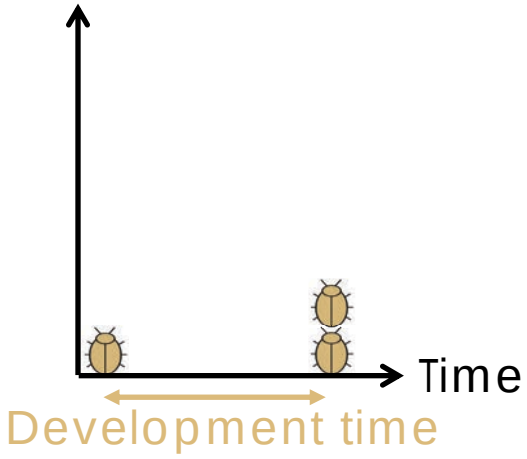




Demographic processes





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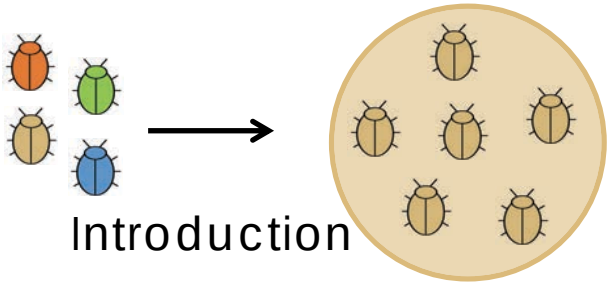
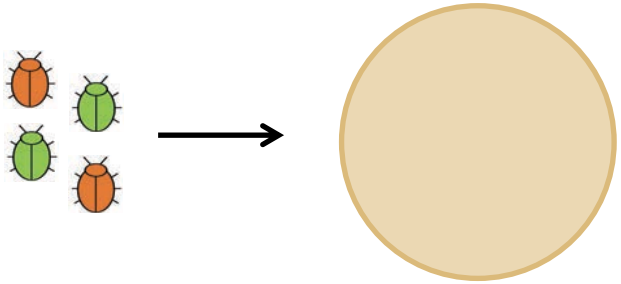
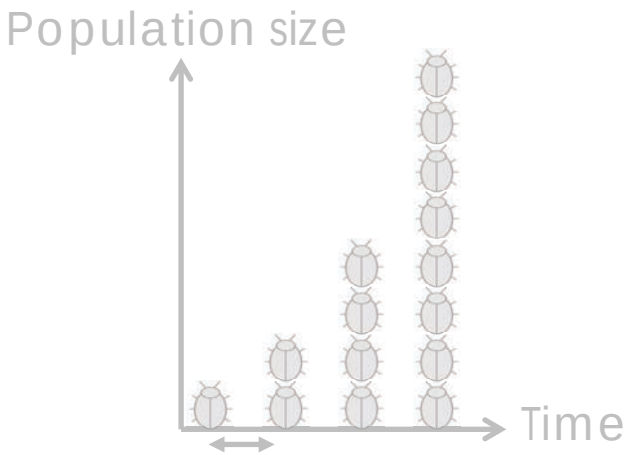


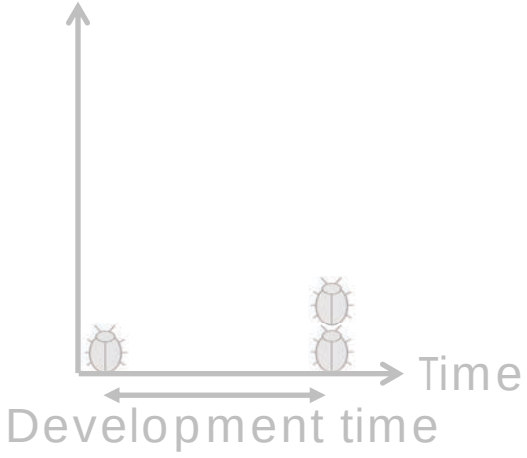
Introduction



Invaded area

Demographic processes





Invasion success and degree of specialization

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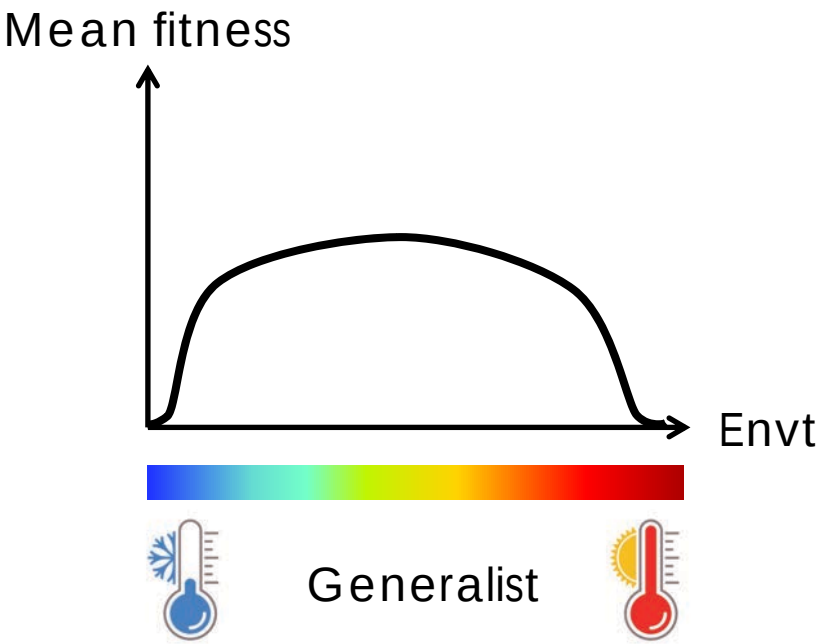
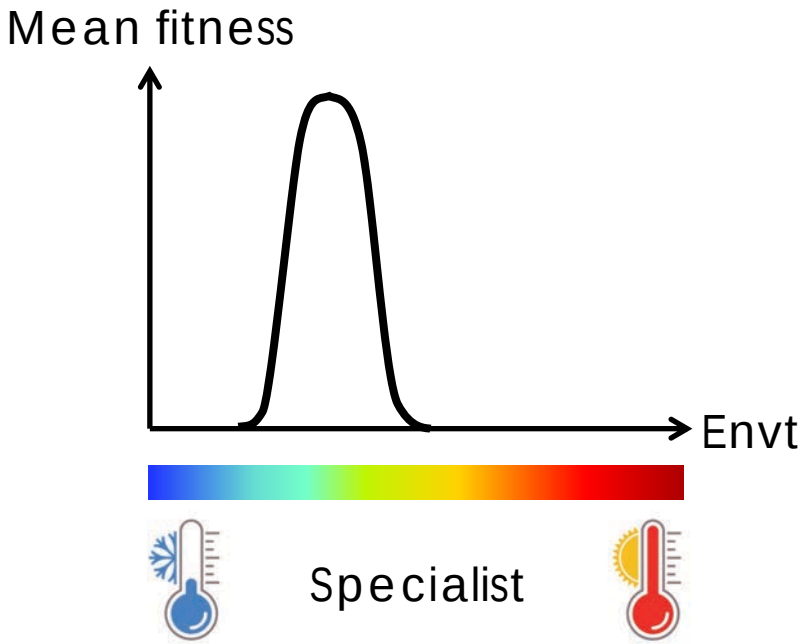
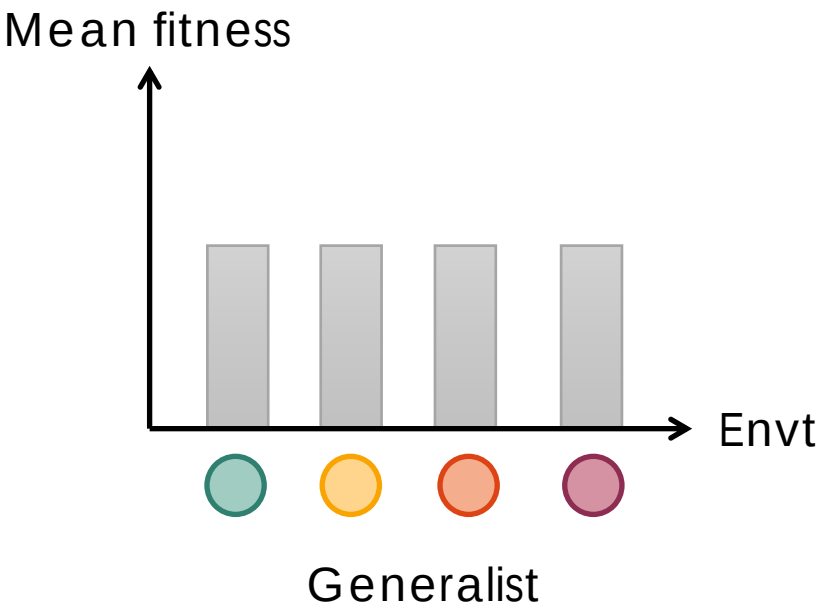
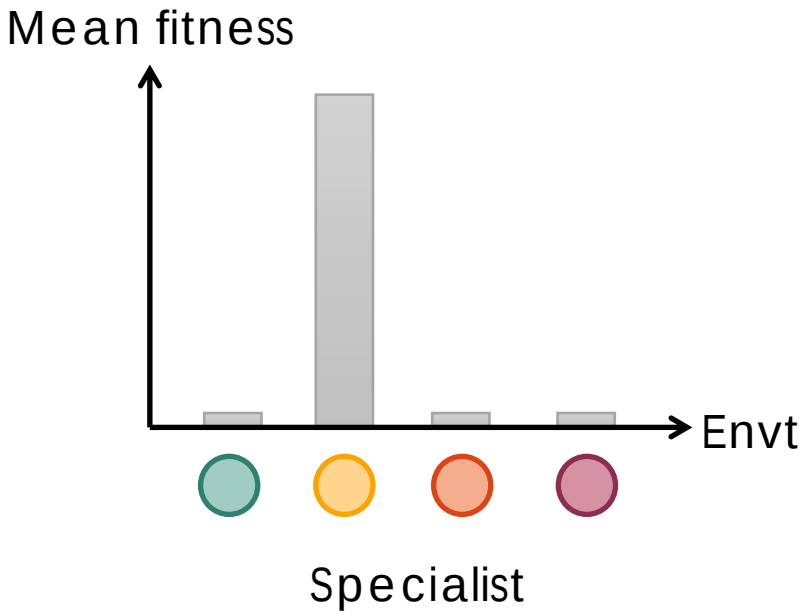




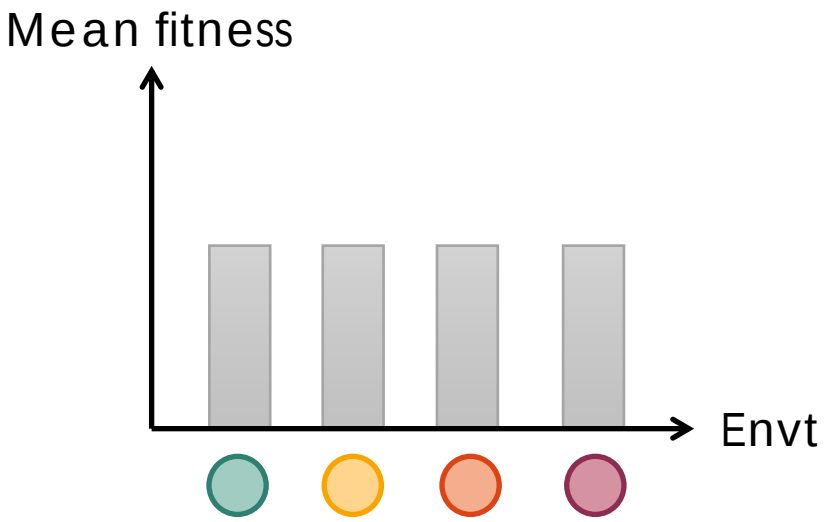
Invasion success and degree of specialization





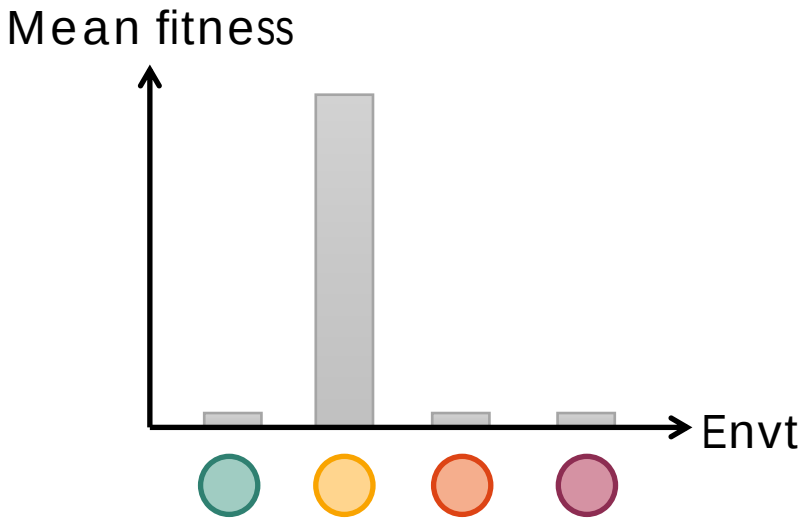
Invasion success and degree of specialization

Drosophila simulans



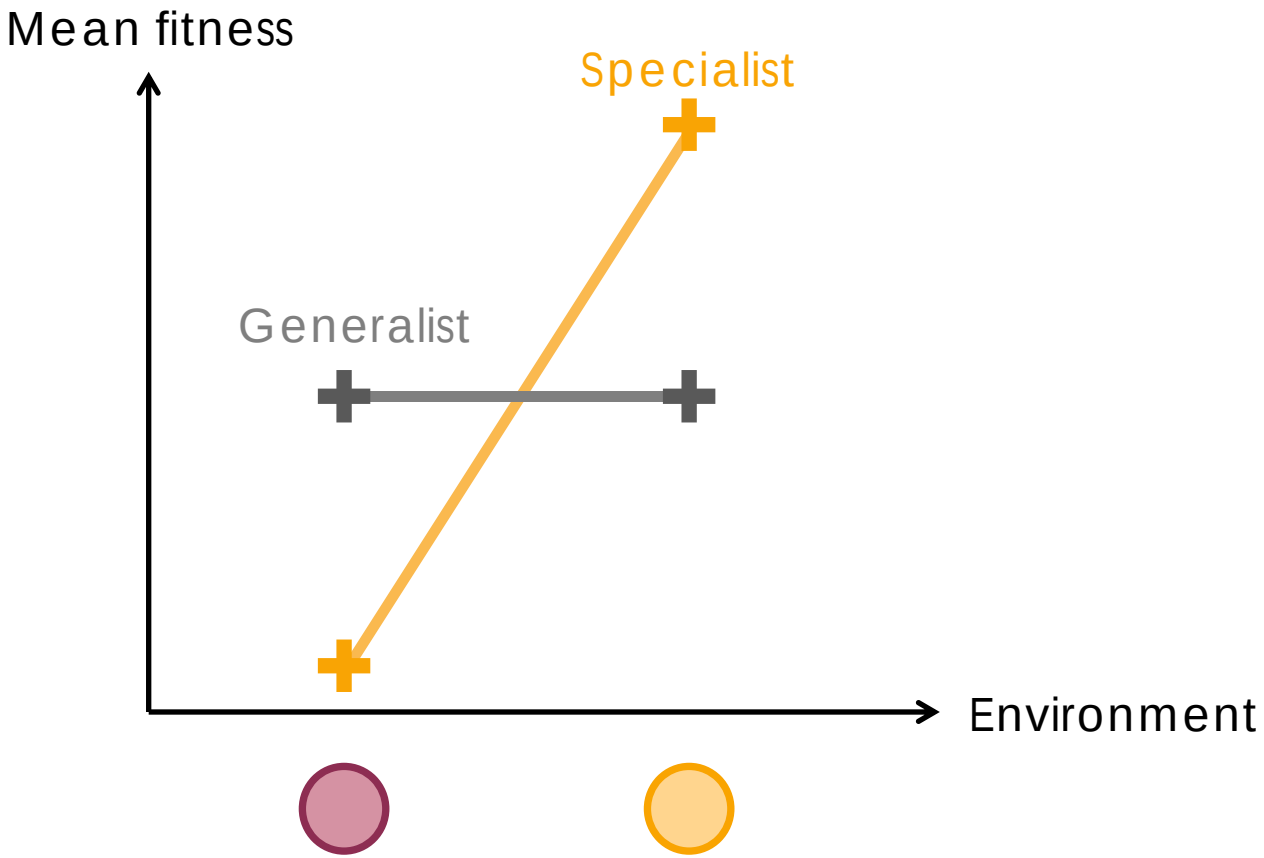
Rotten fruits

Drosophila yakuba

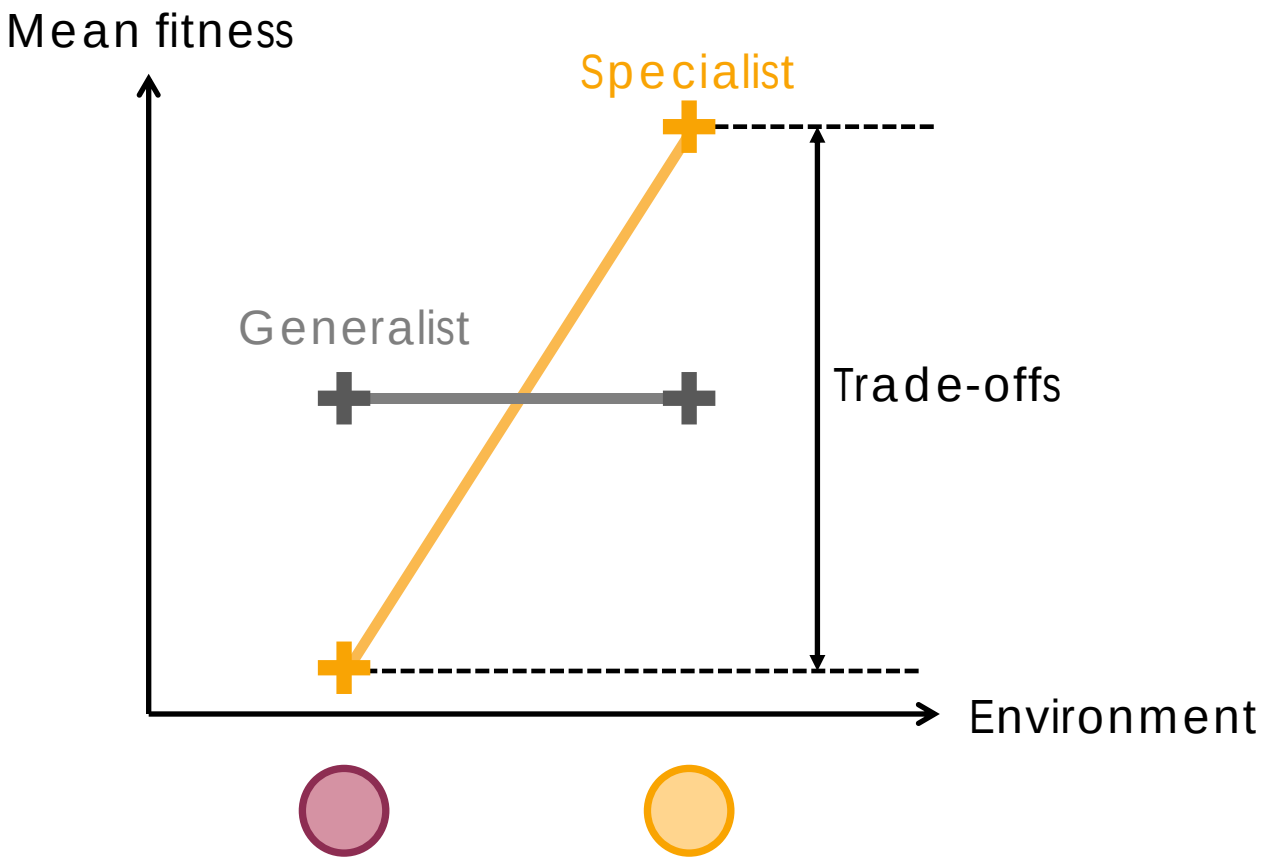


Nono fruit

Invasion success and degree of specialization



Invasion success and degree of specialization



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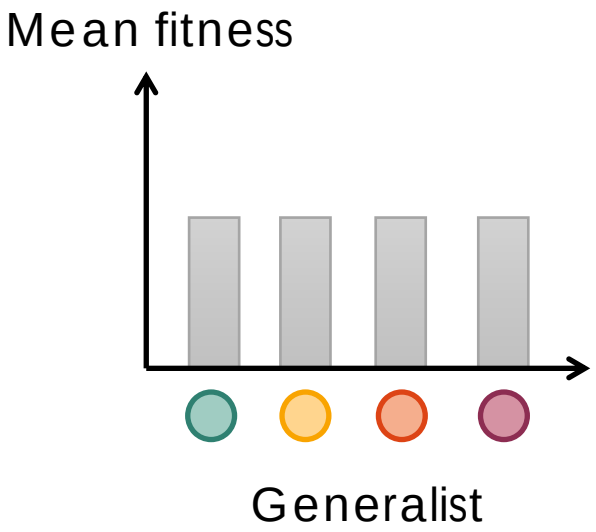
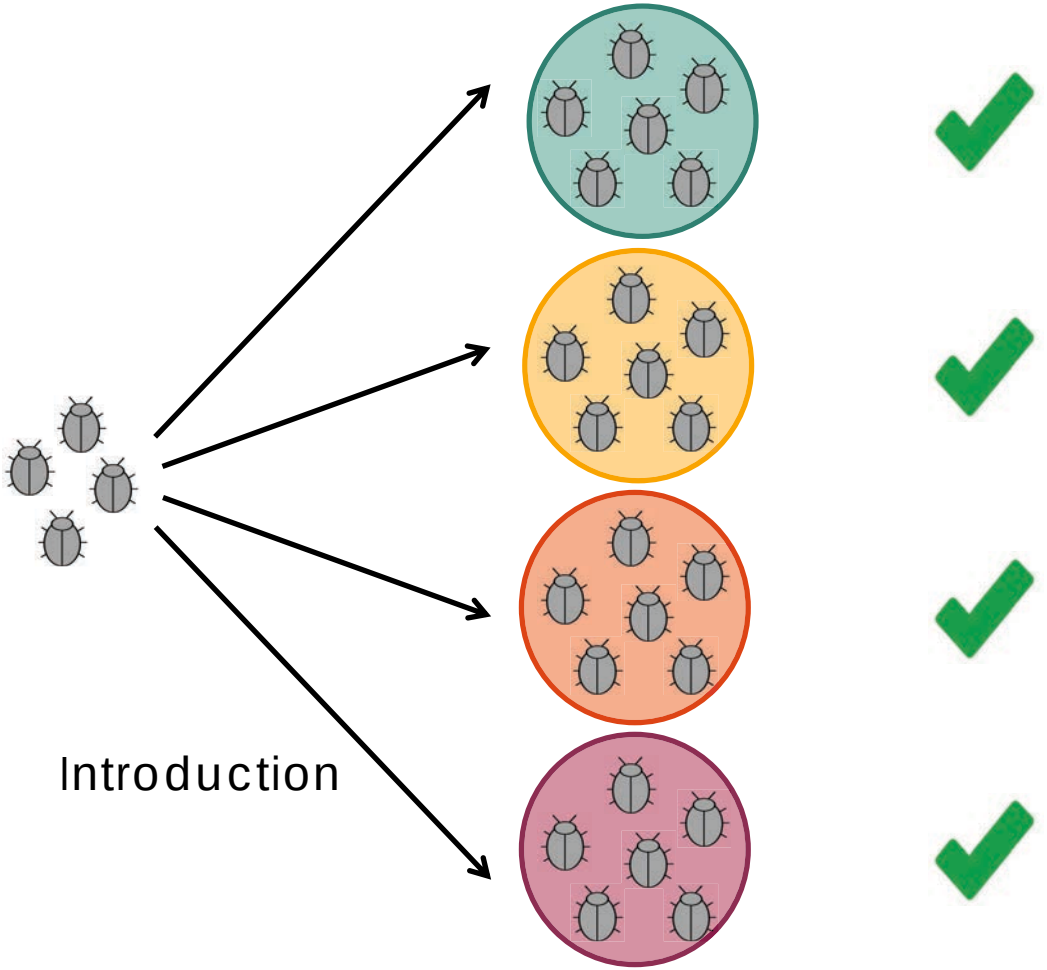


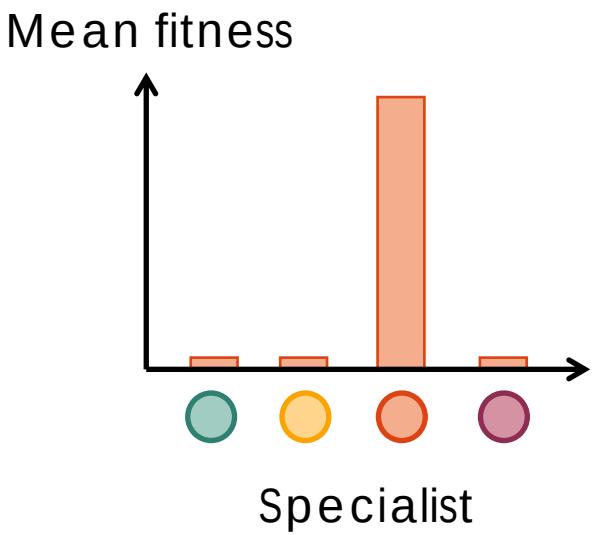


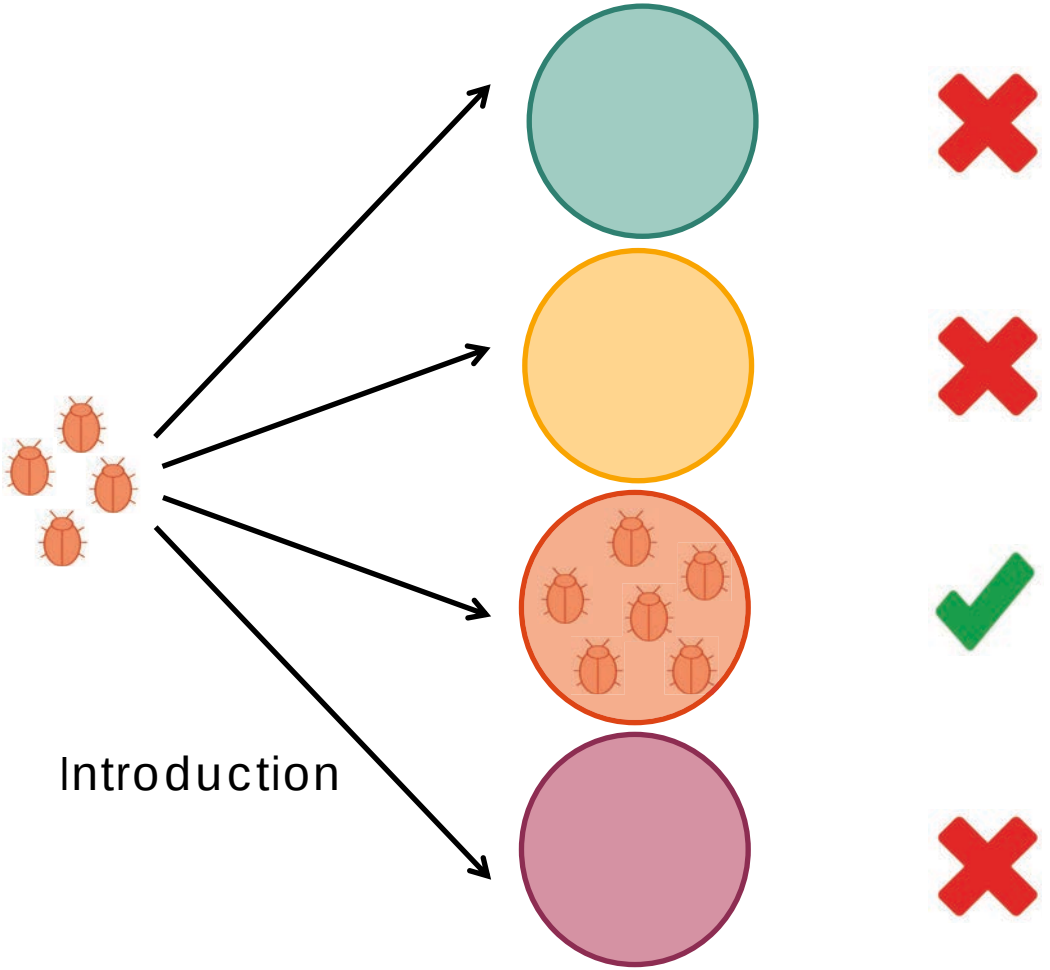
[Vazquez, 2006]

Invaded area

Invasion success

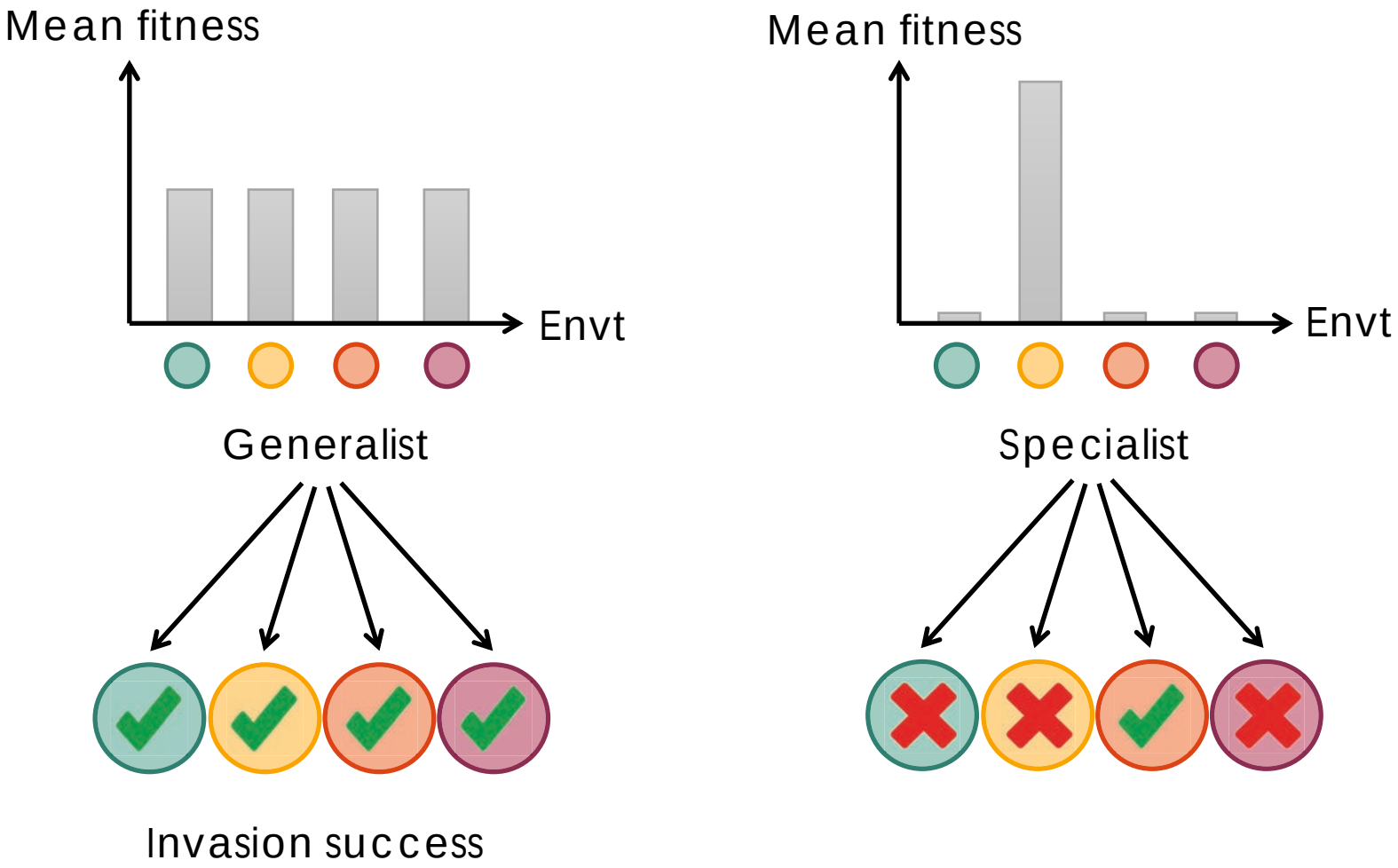
Invasion success and degree of specialization





[Vazquez, 2006]

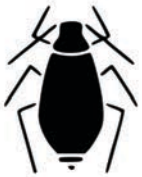
Invasion success and degree of specialization

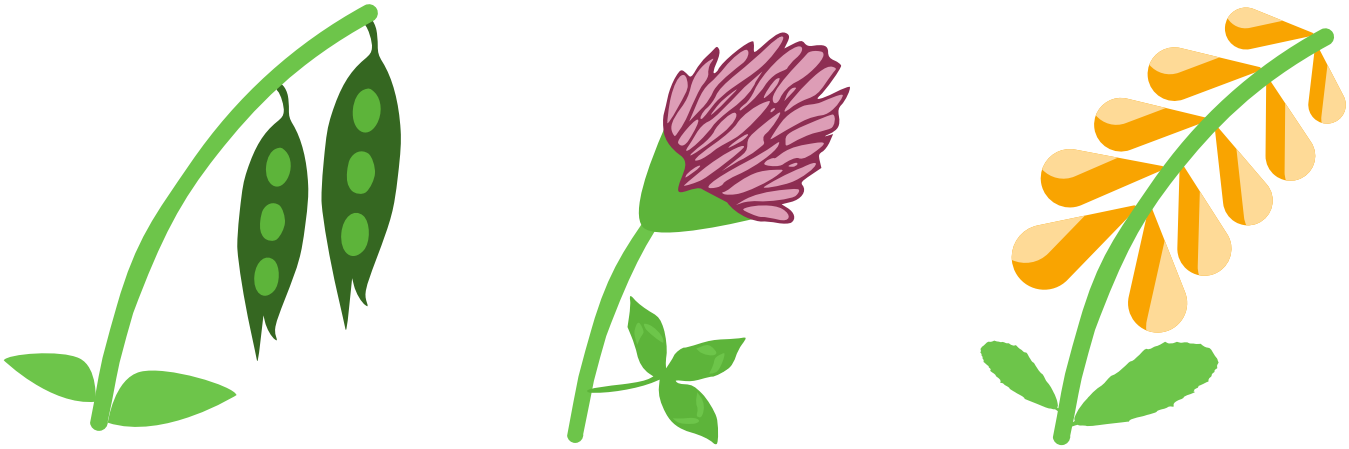


[Vazquez, 2006]

Generalist population

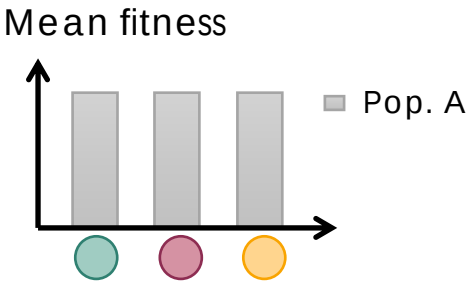
Pea aphid





[Eastop, 1971]

Generalist population



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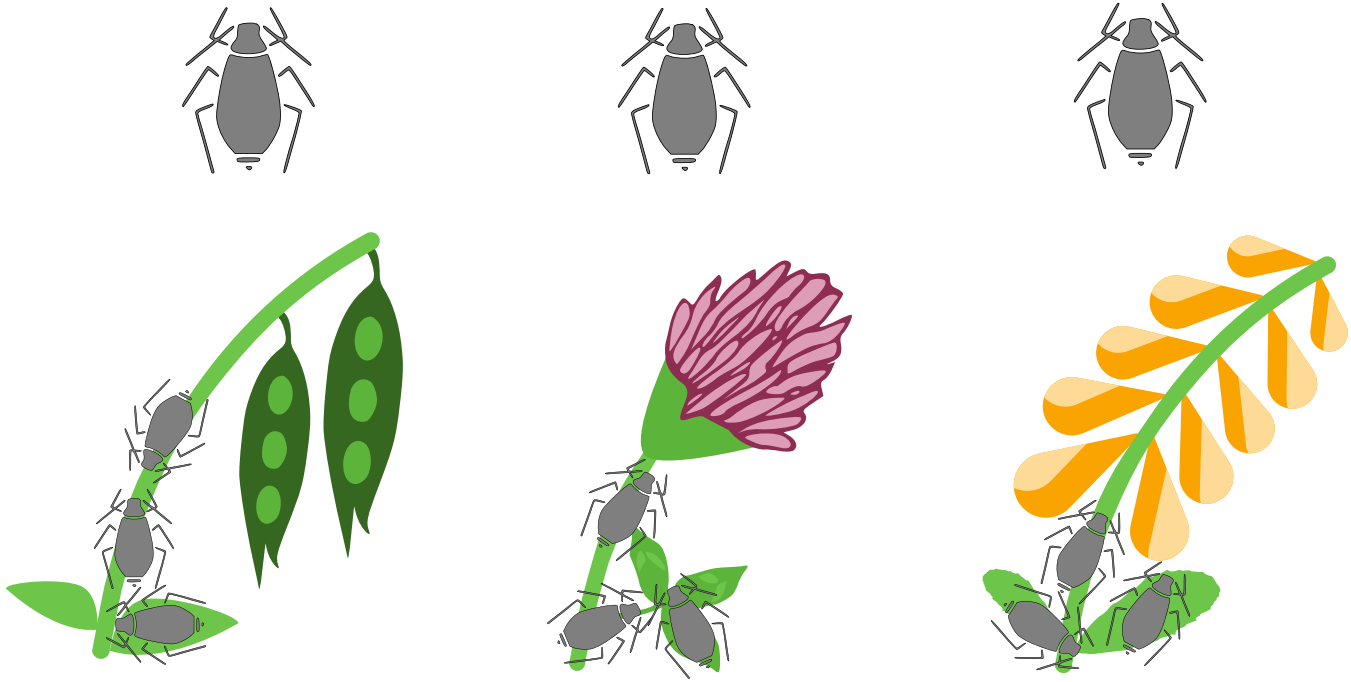

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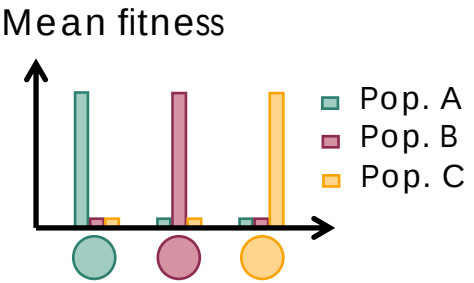

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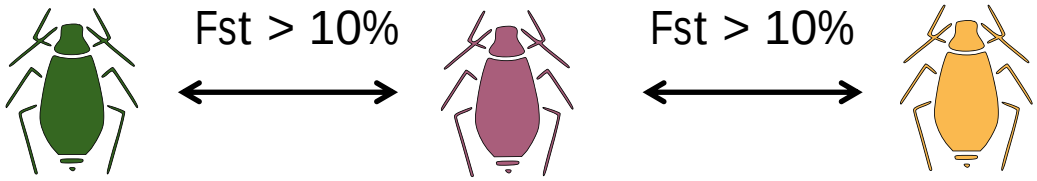
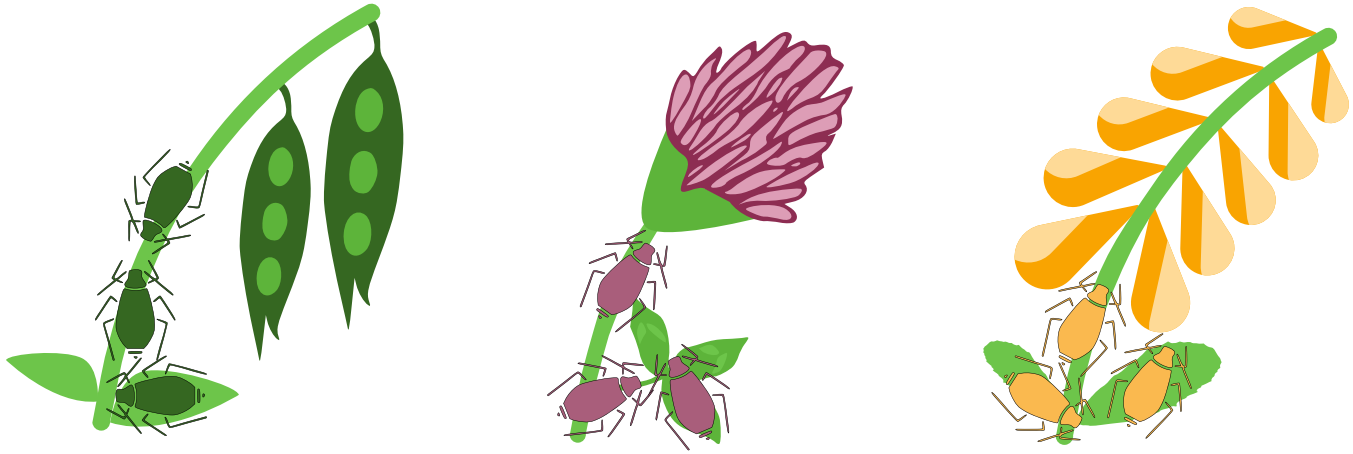
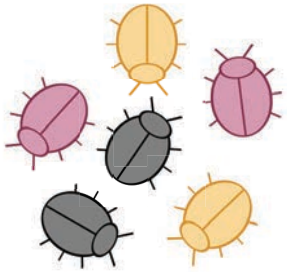




[Peccoud et al., 2009; Nouhaud et al., 2018]

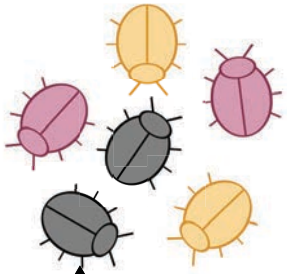
Process of adaptation

Population



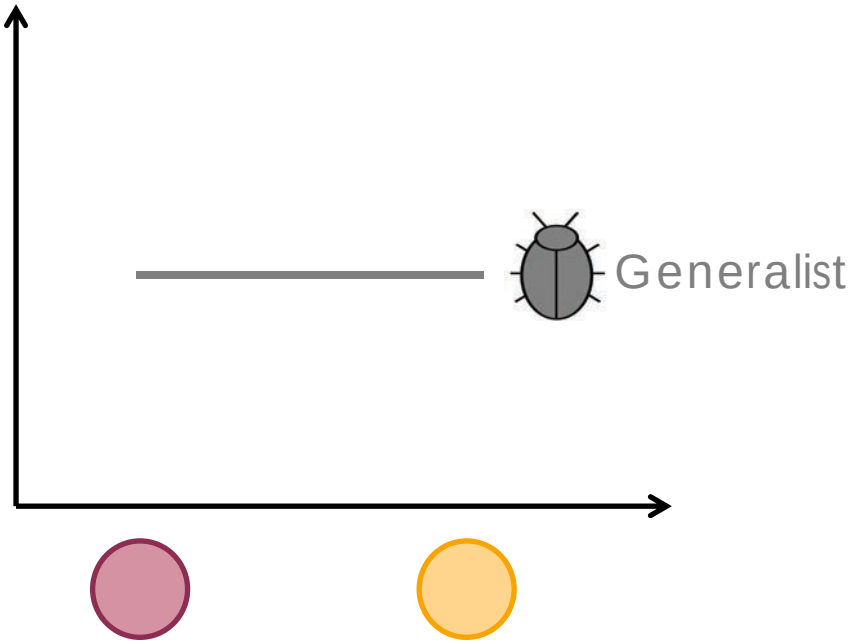
Process of adaptation

Population



Genotype
generalist

Fitness (genotype)



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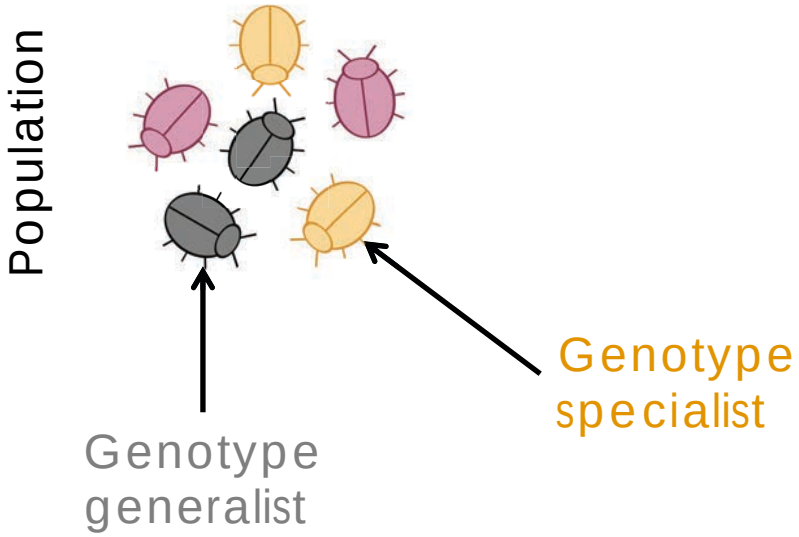

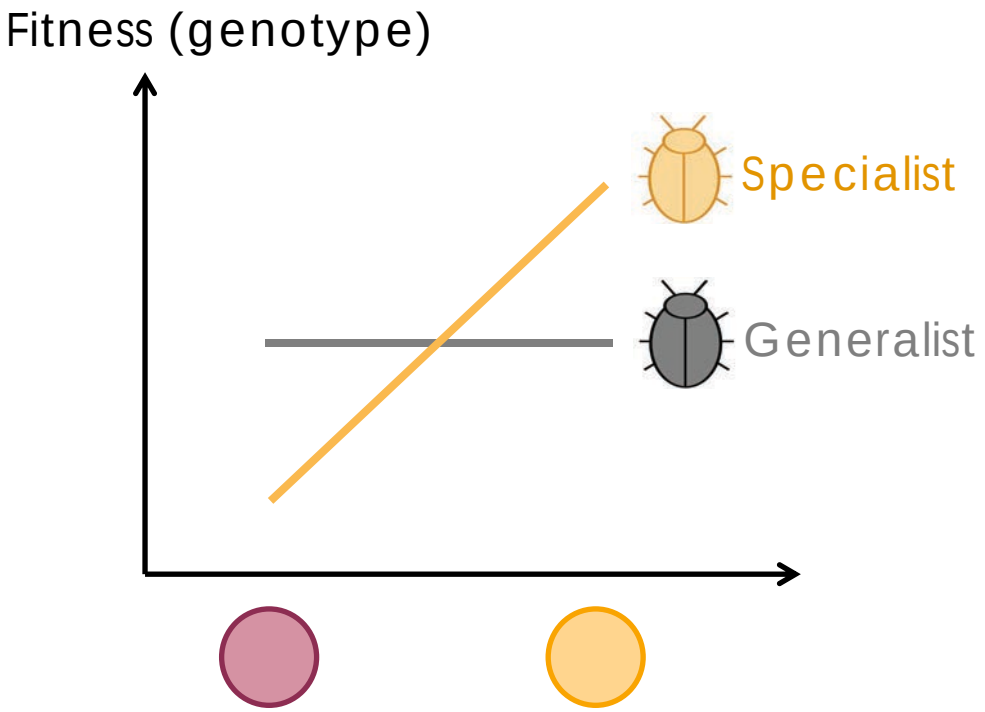

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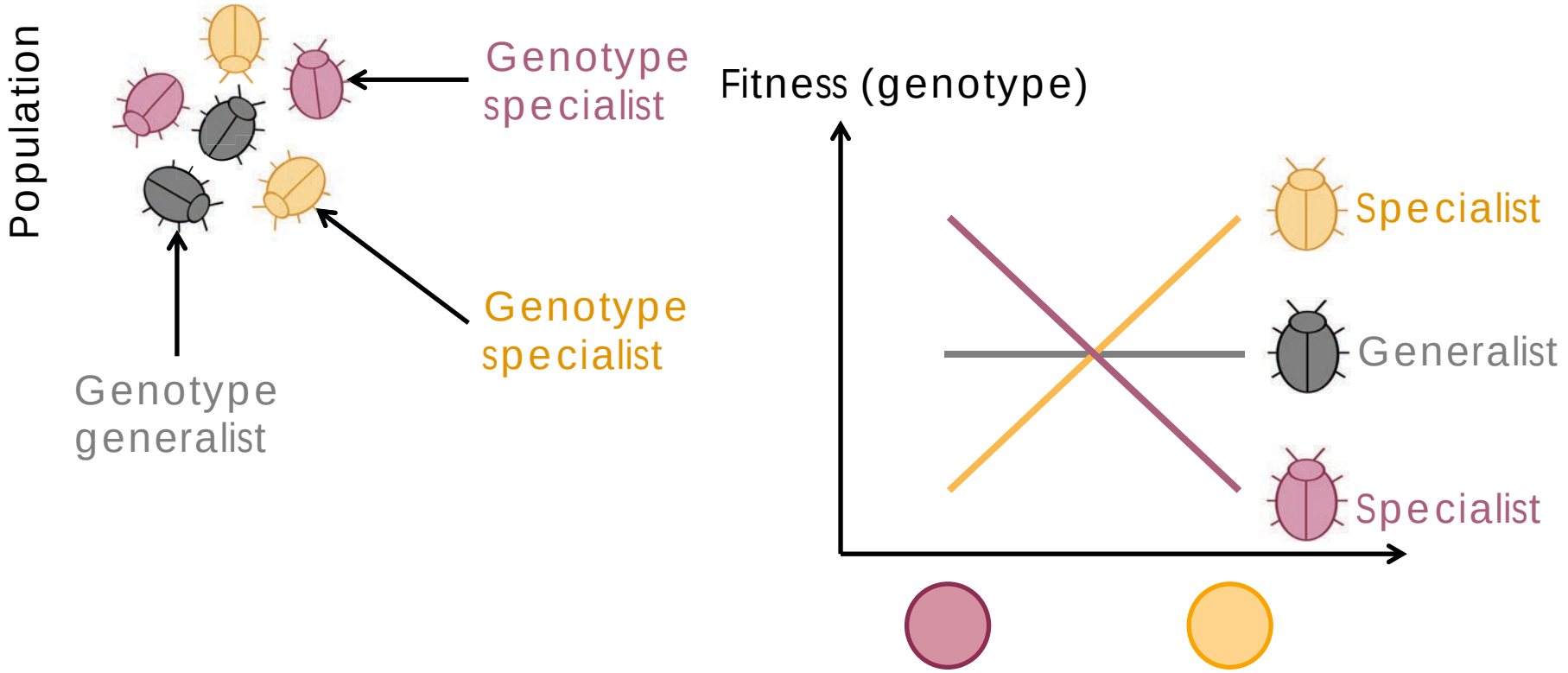

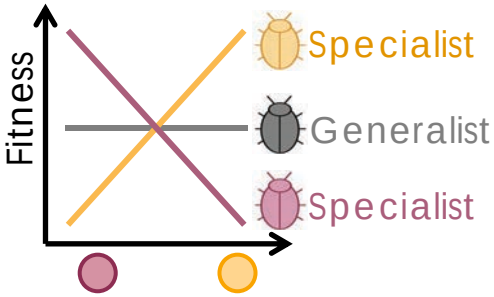

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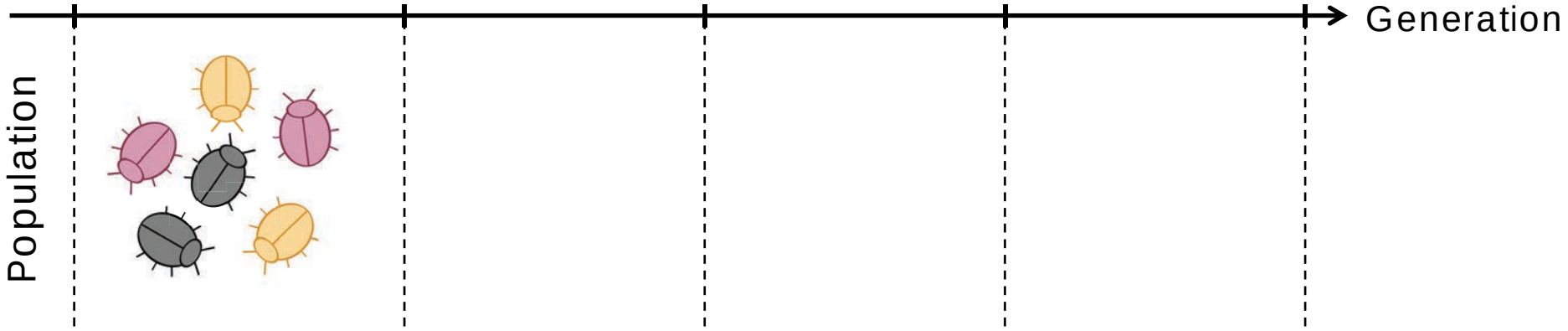

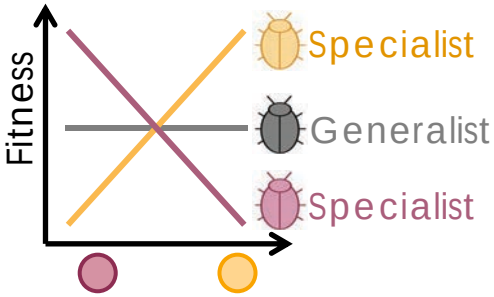

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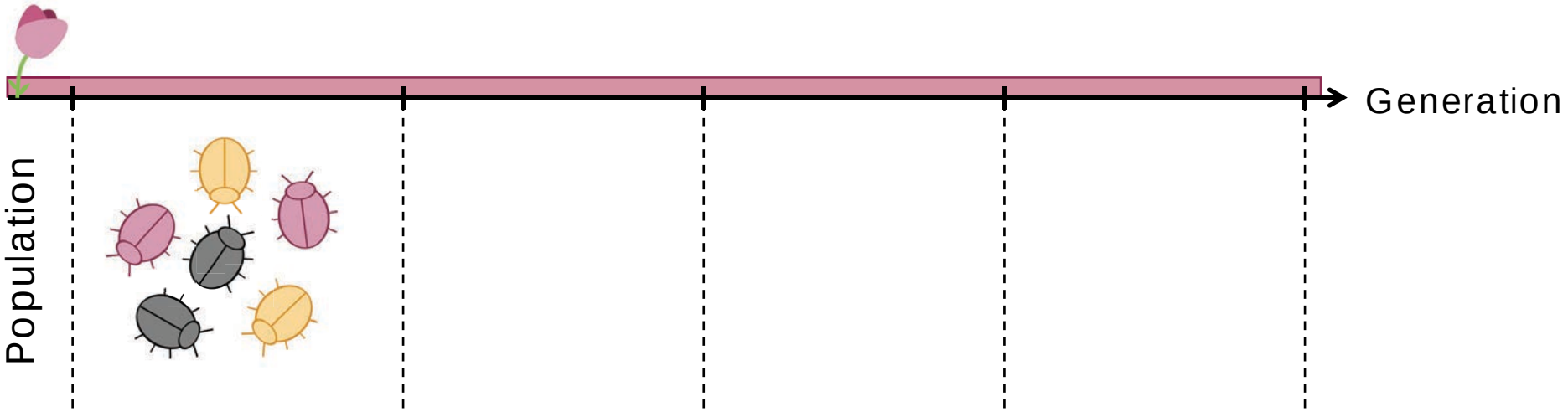
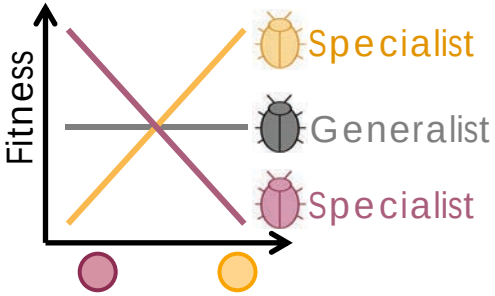
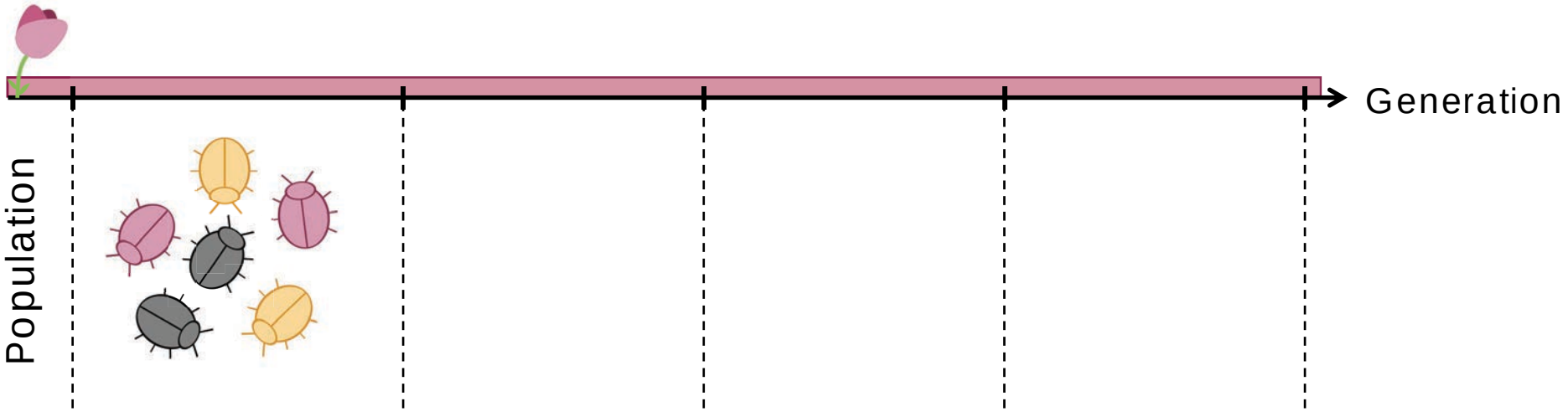
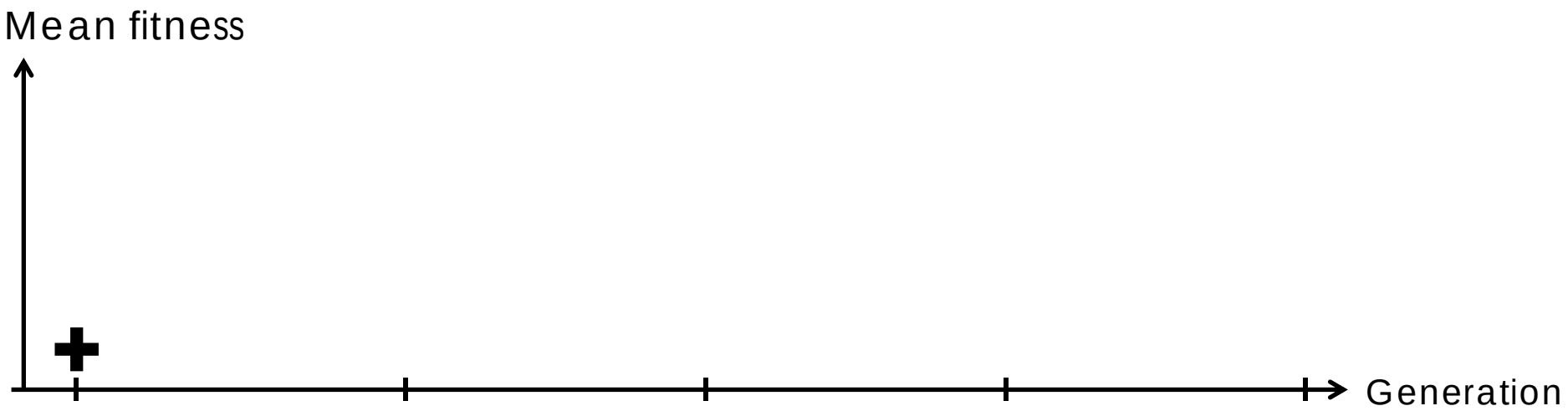
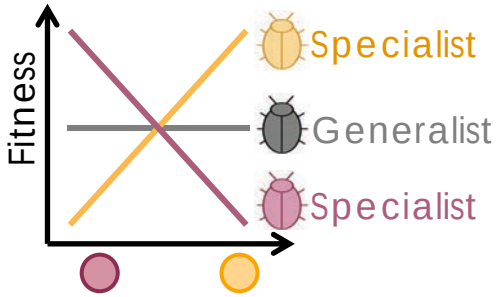




Process of adaptation







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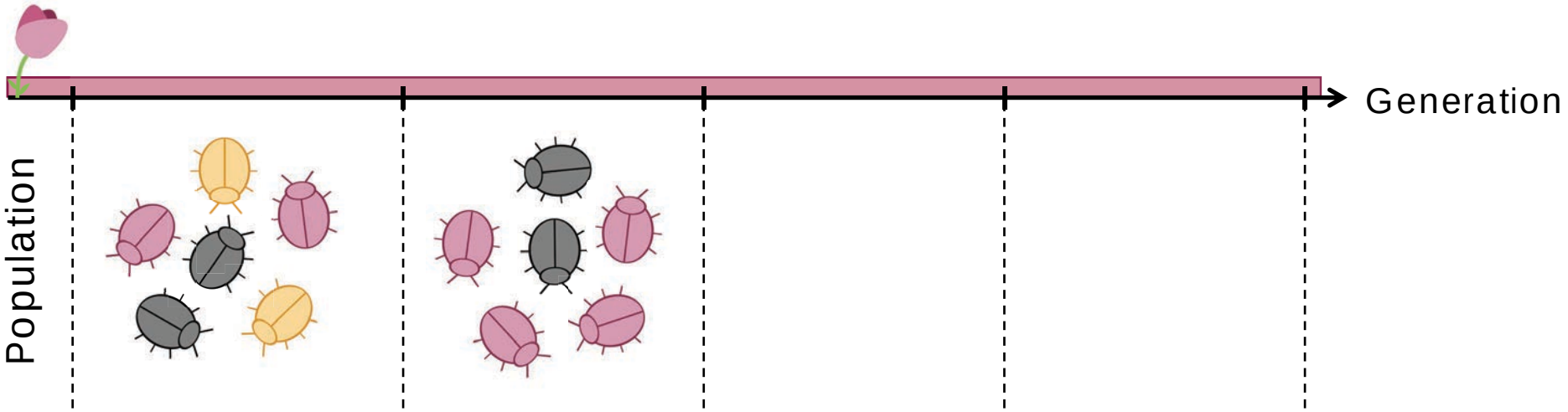

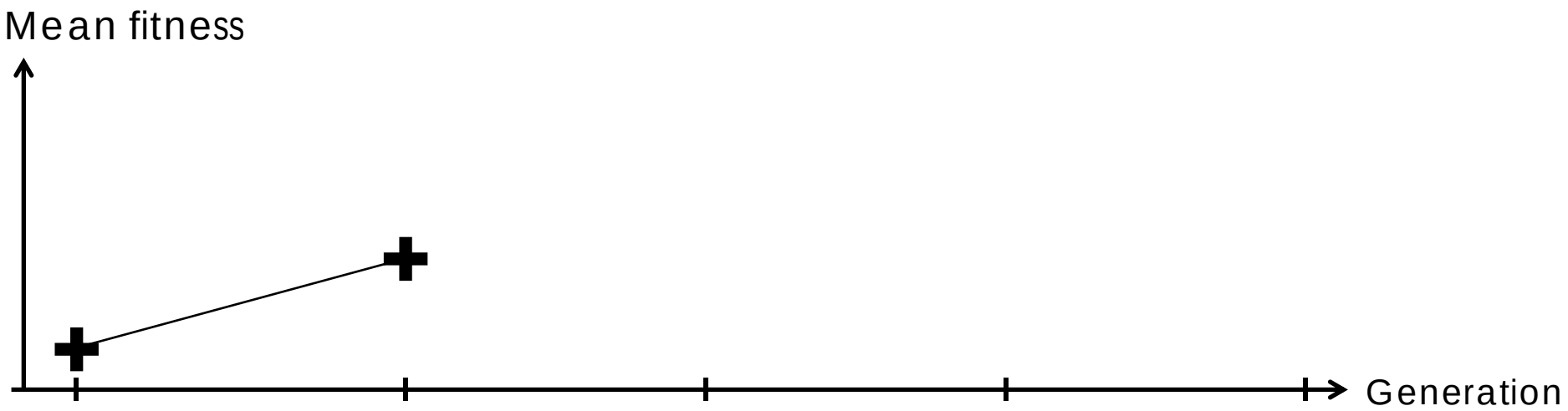

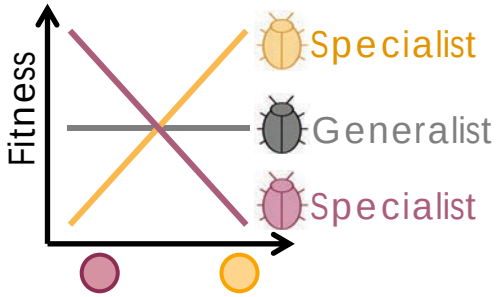

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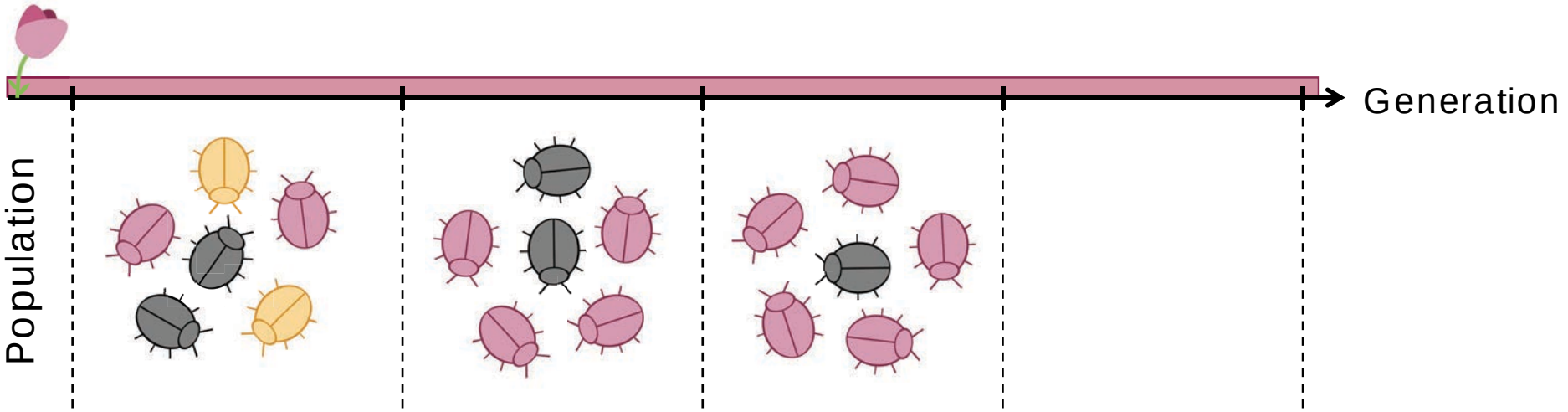

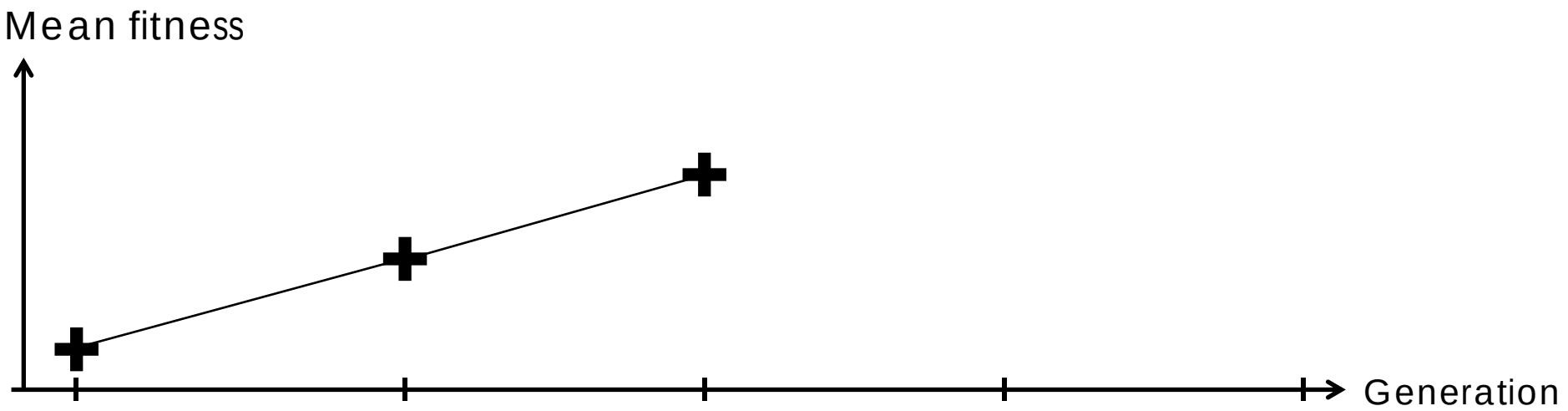

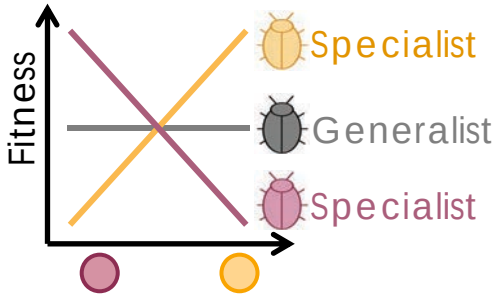

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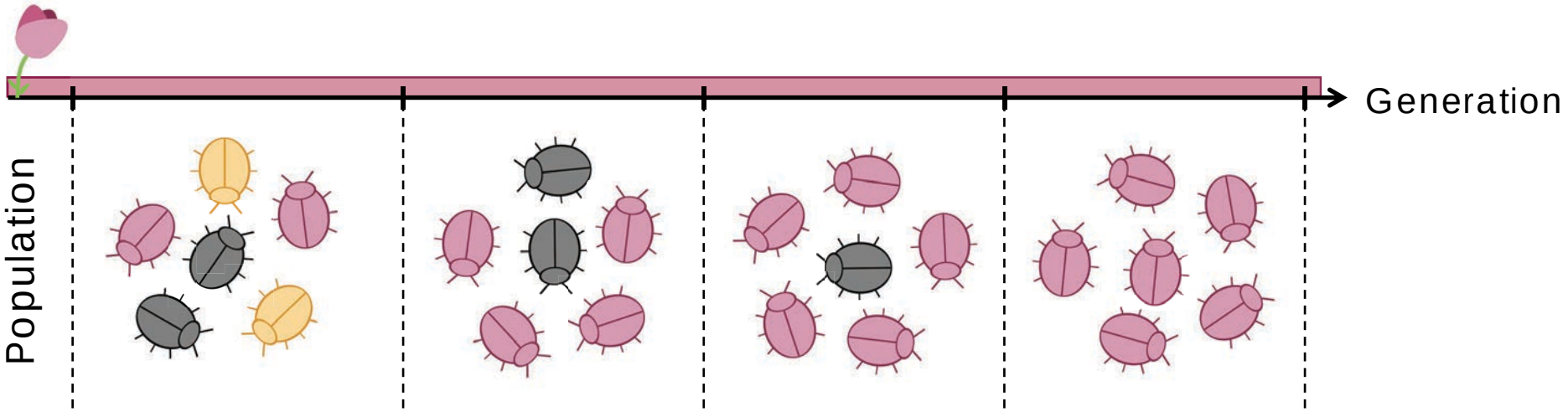

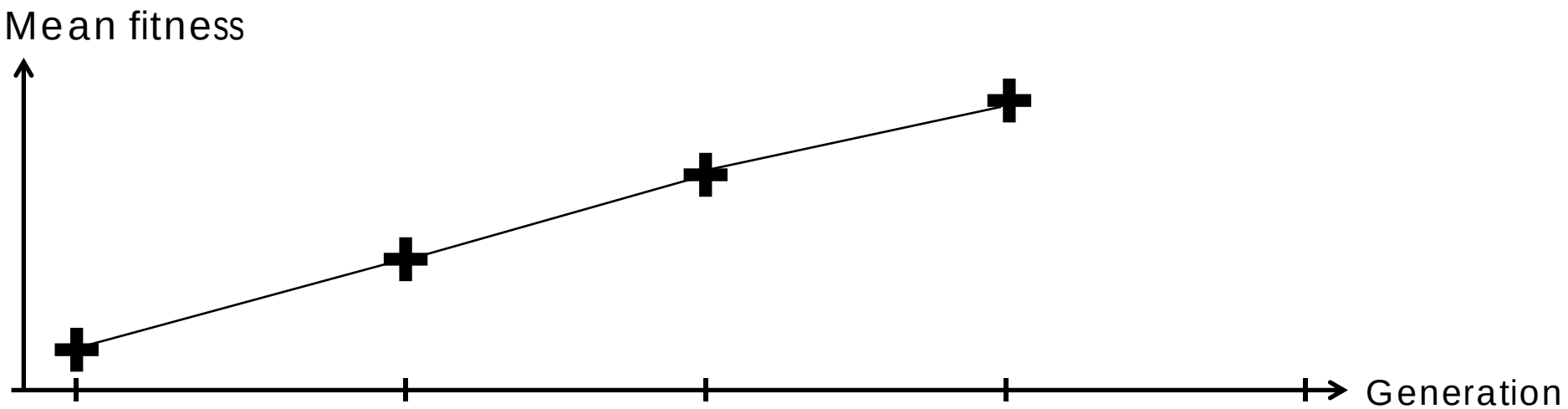

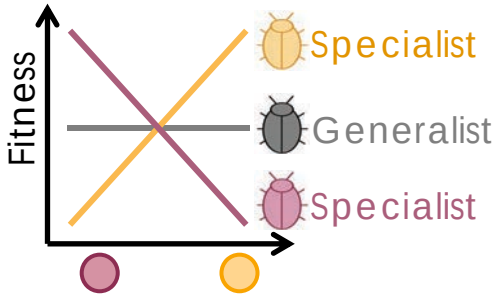

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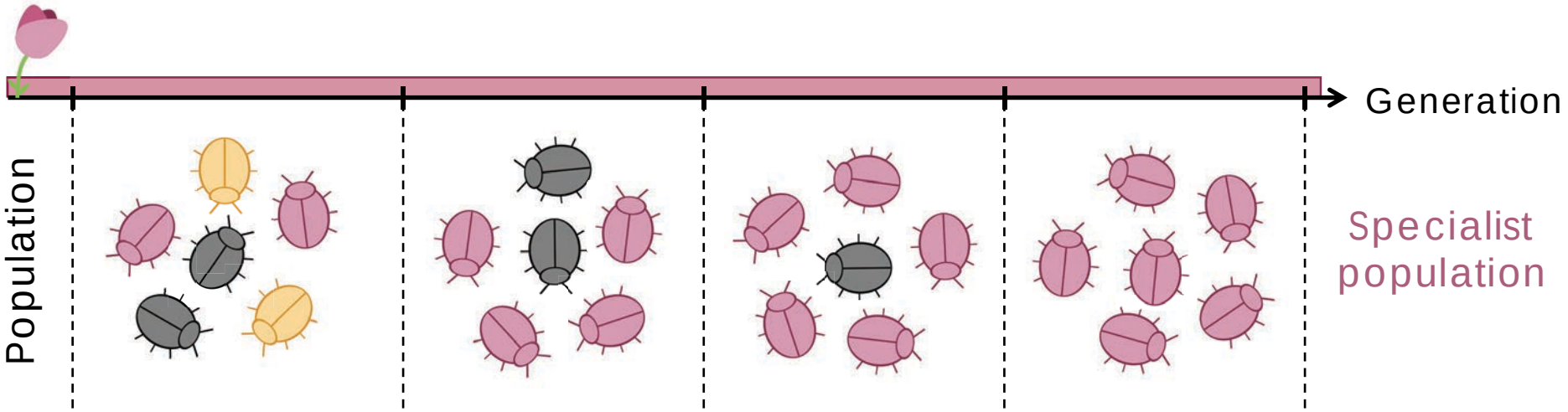
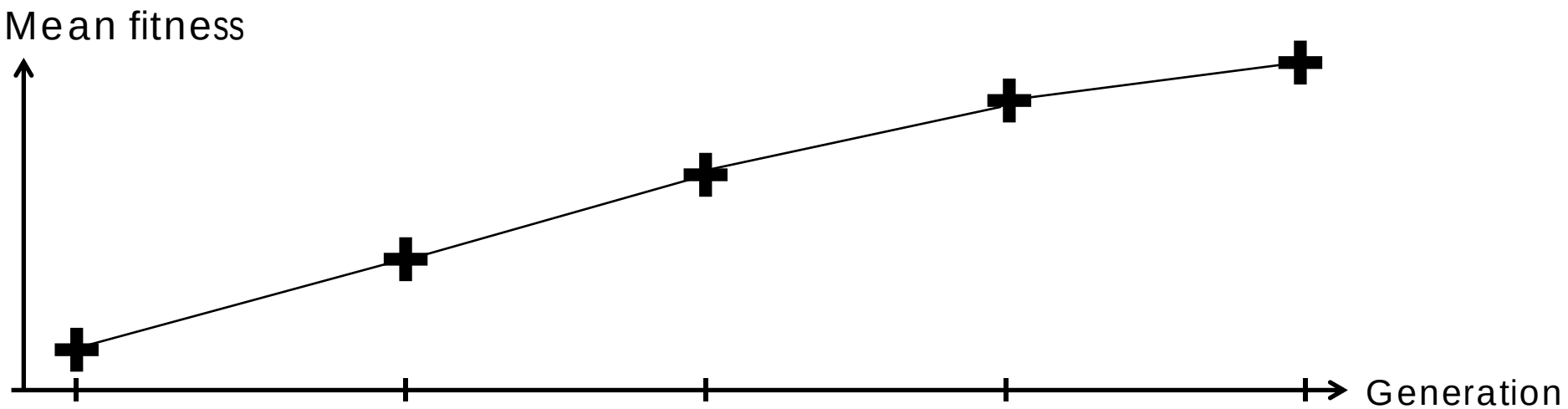
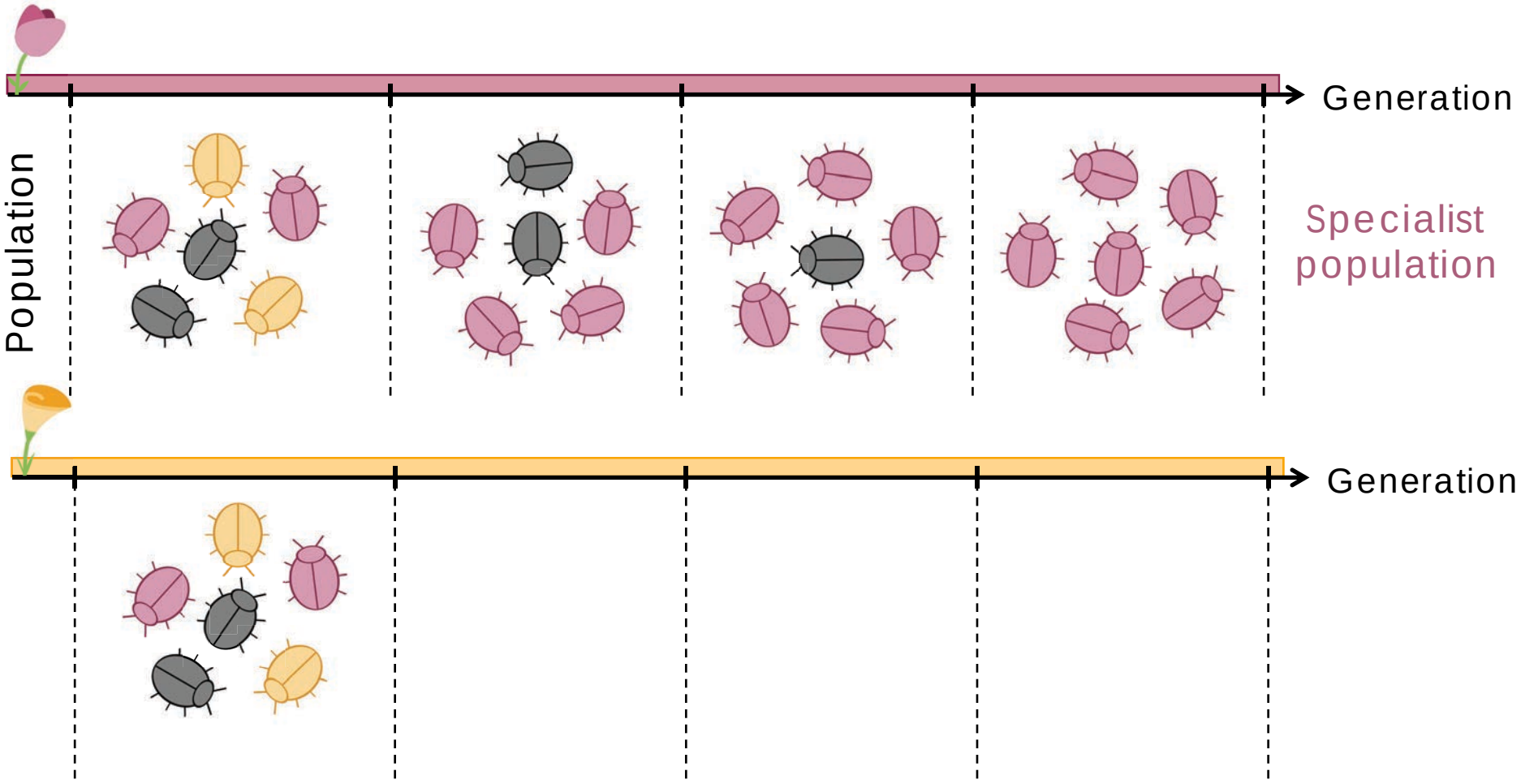




Environmental heterogeneity

[Levins 1968; Kassen 2002]

Environmental heterogeneity



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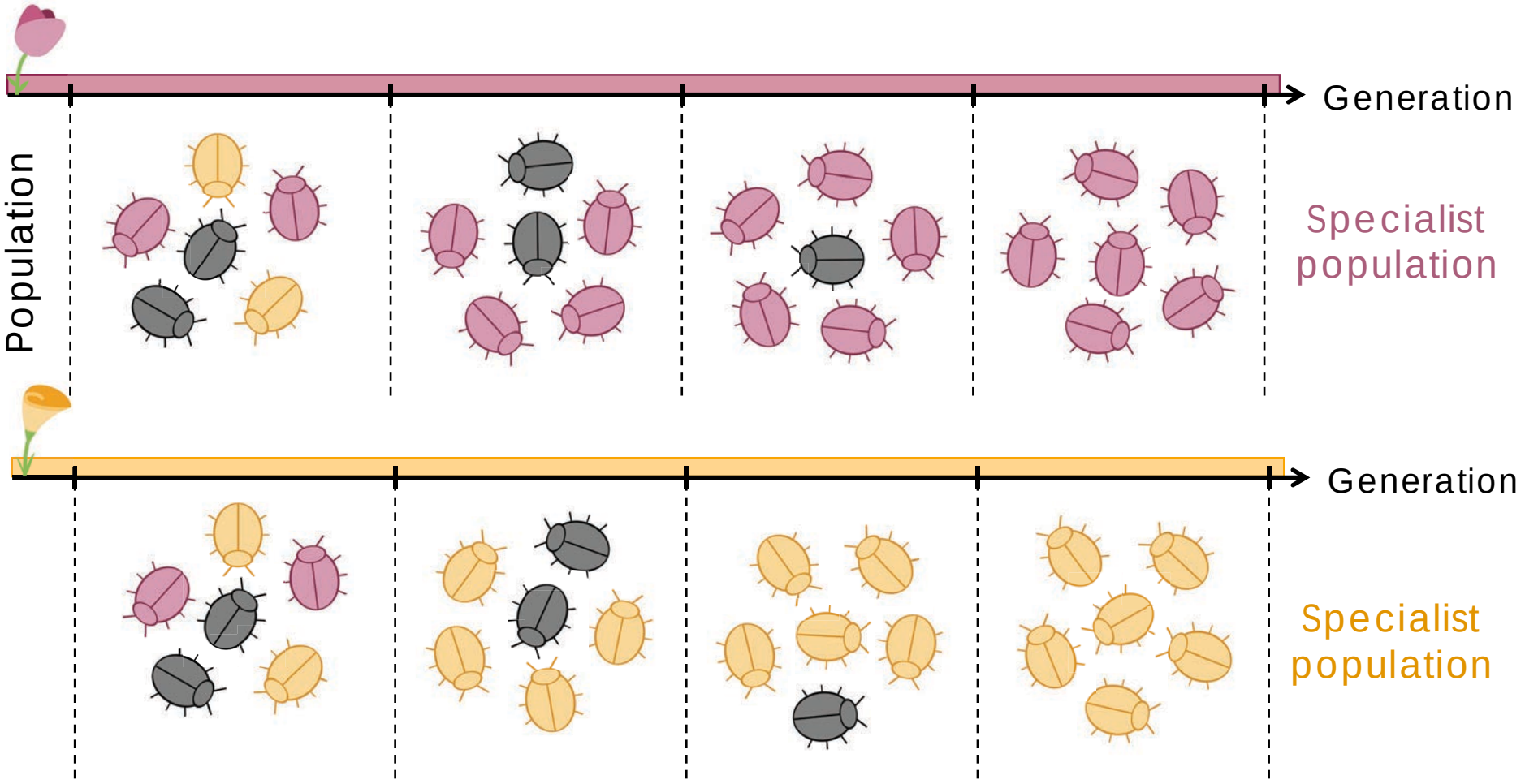

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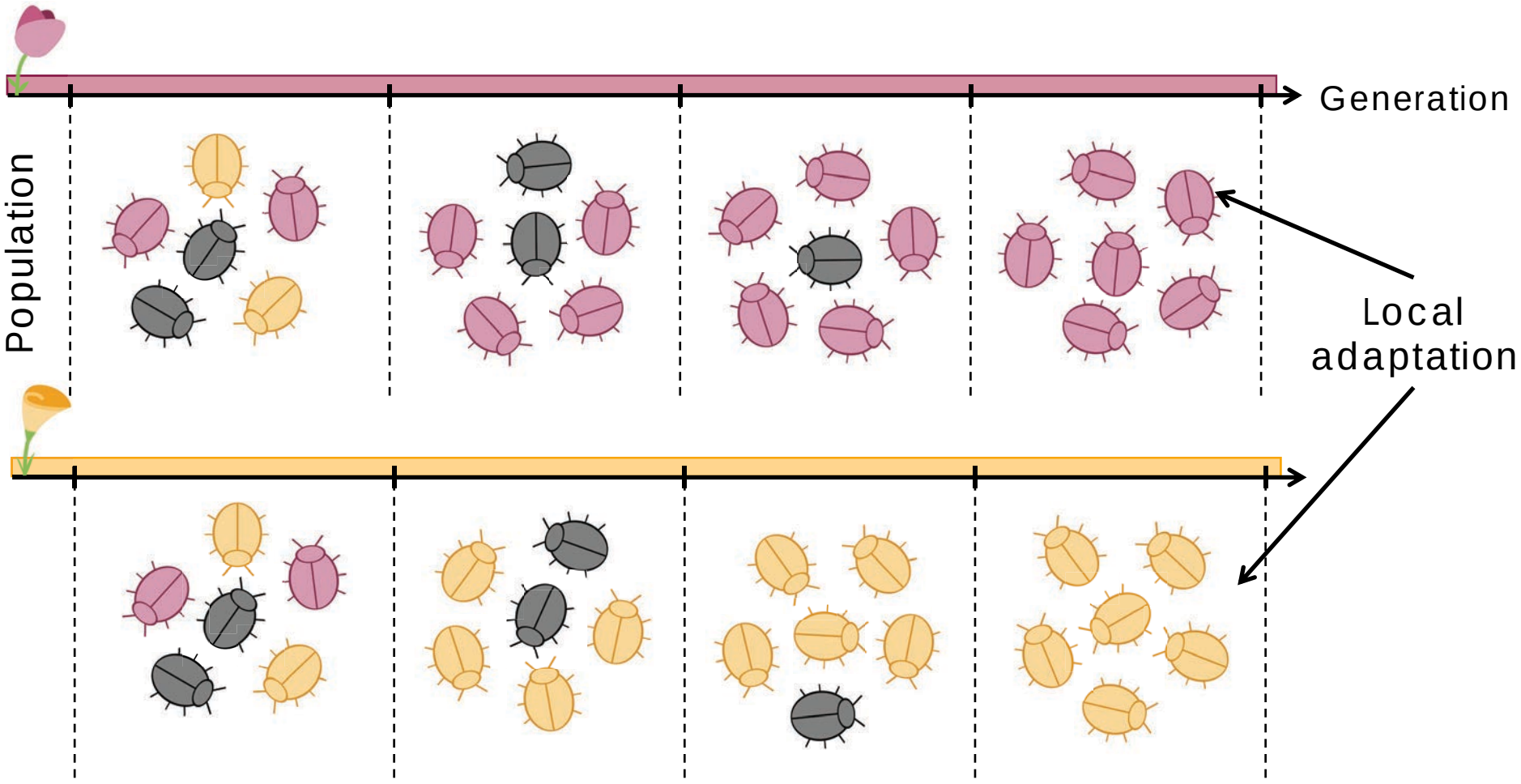
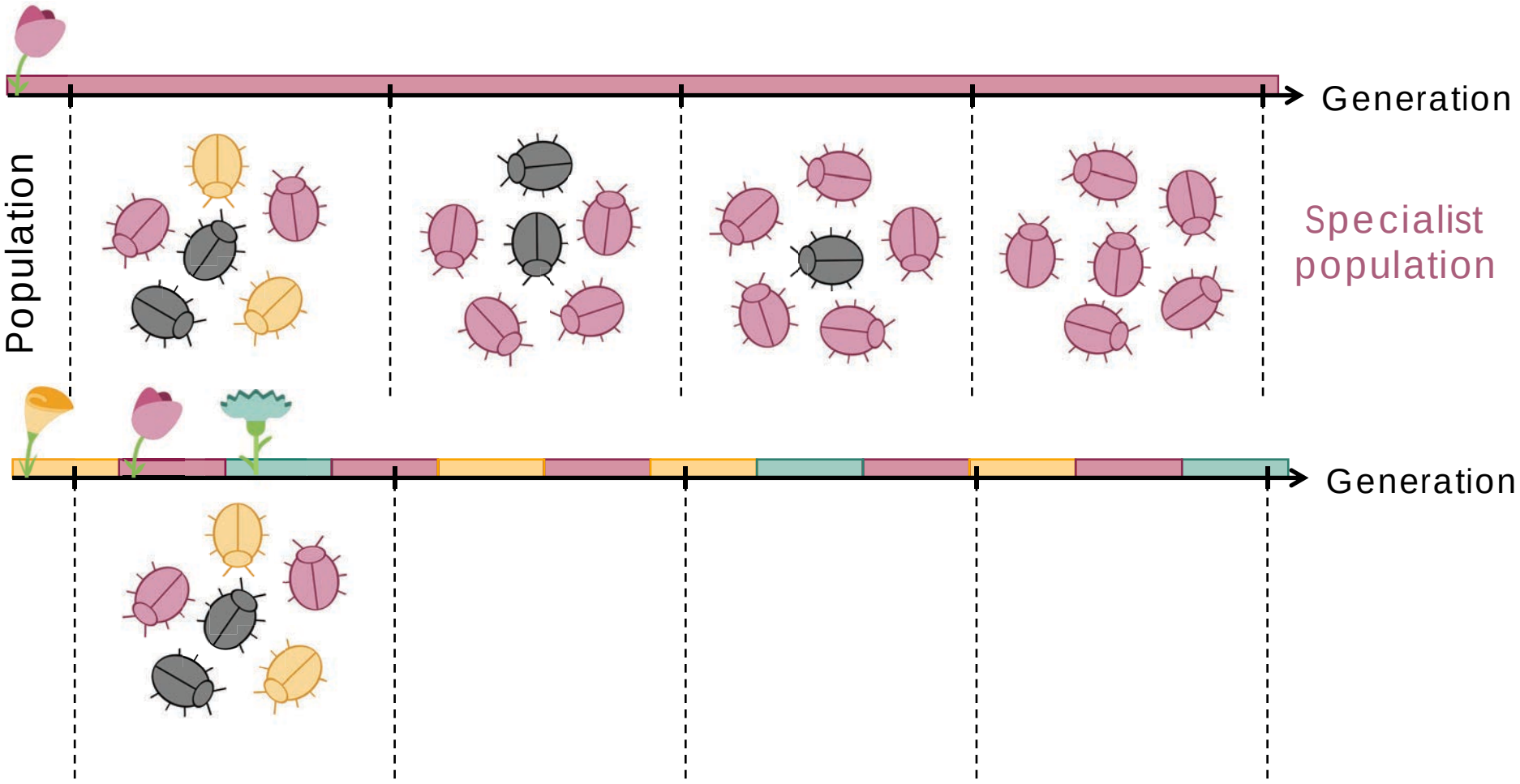


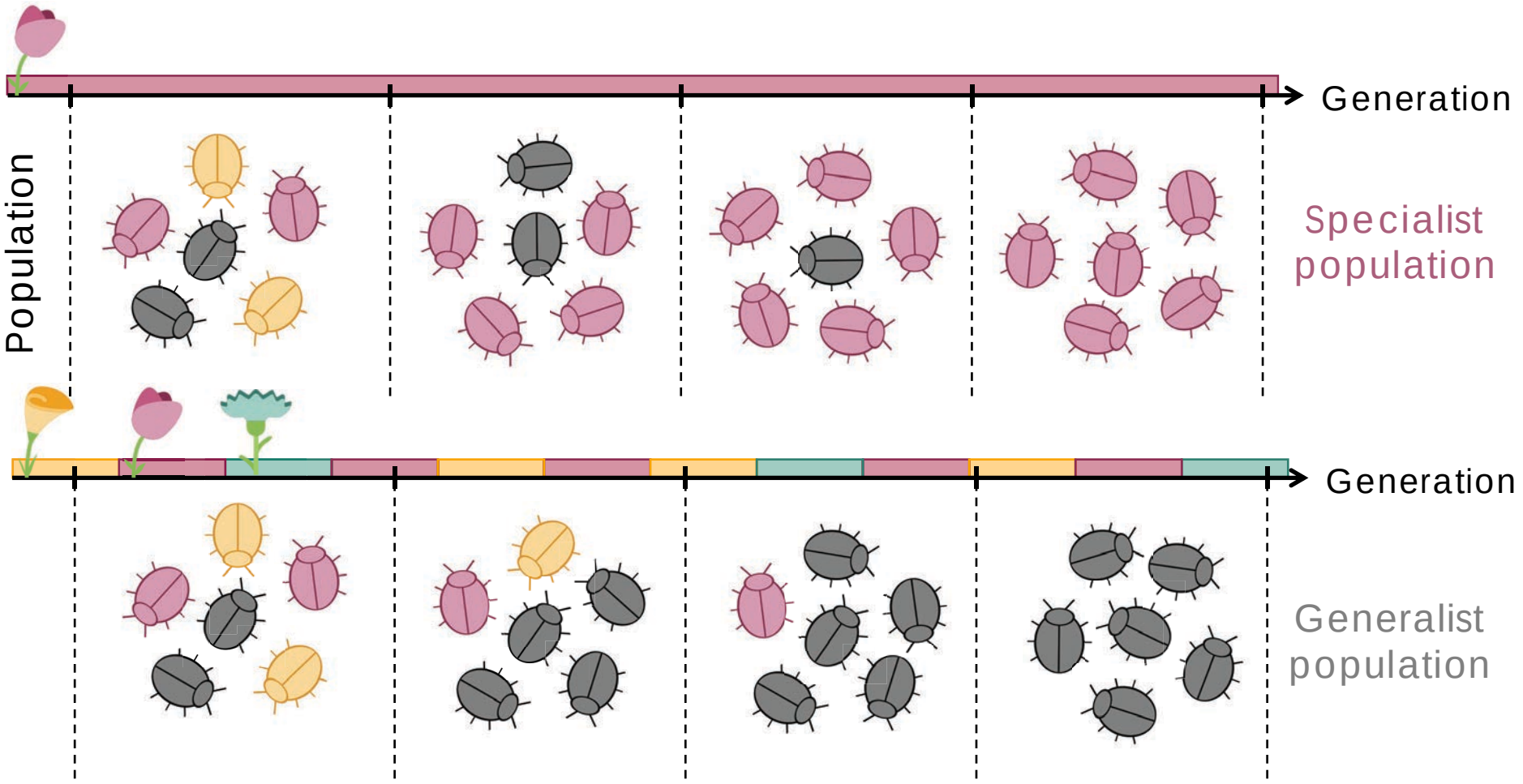
[Levins 1968; Kassen 2002]

Environmental heterogeneity



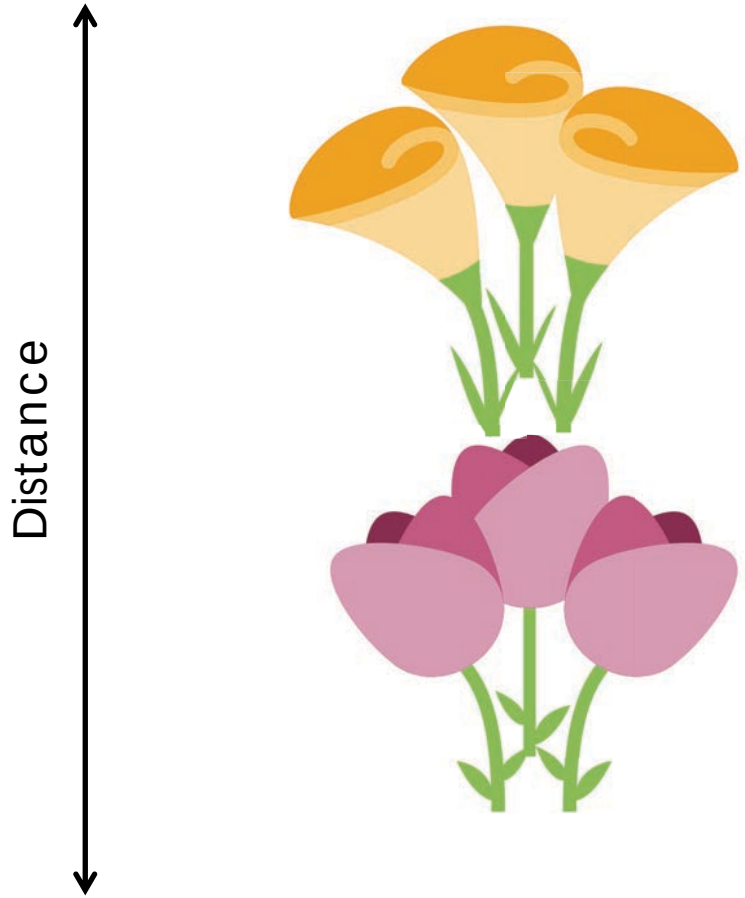
[Levins 1968; Kassen 2002]

Environmental heterogeneity



[Levins 1968; Kassen 2002]

Environmental heterogeneity

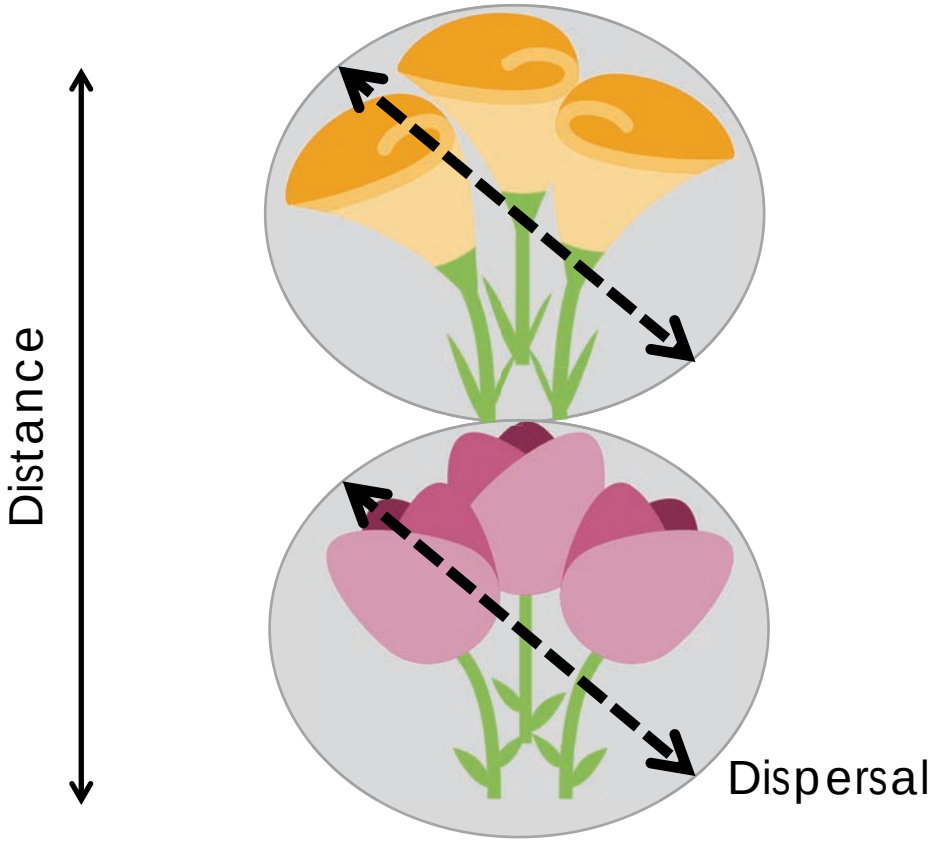


[Levins 1968; Kassen 2002]

Environmental heterogeneity

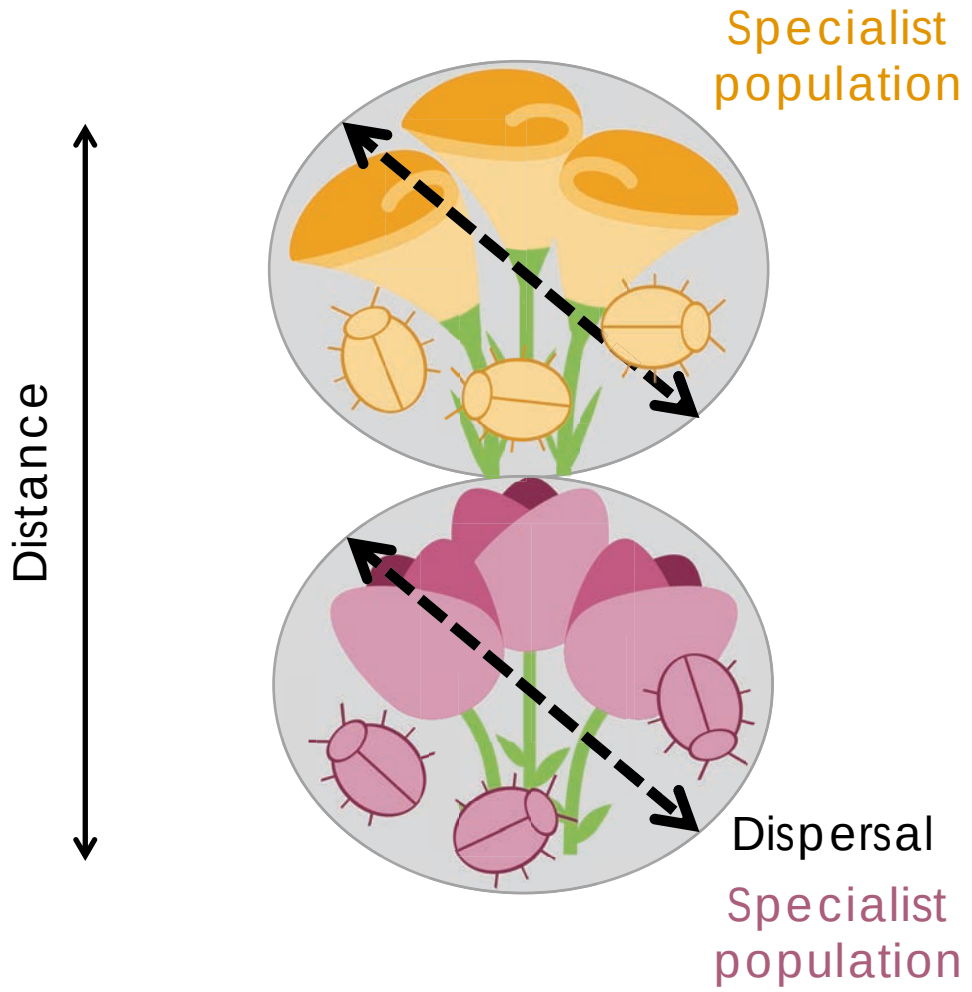
[Levins 1968; Kassen 2002]

Environmental heterogeneity



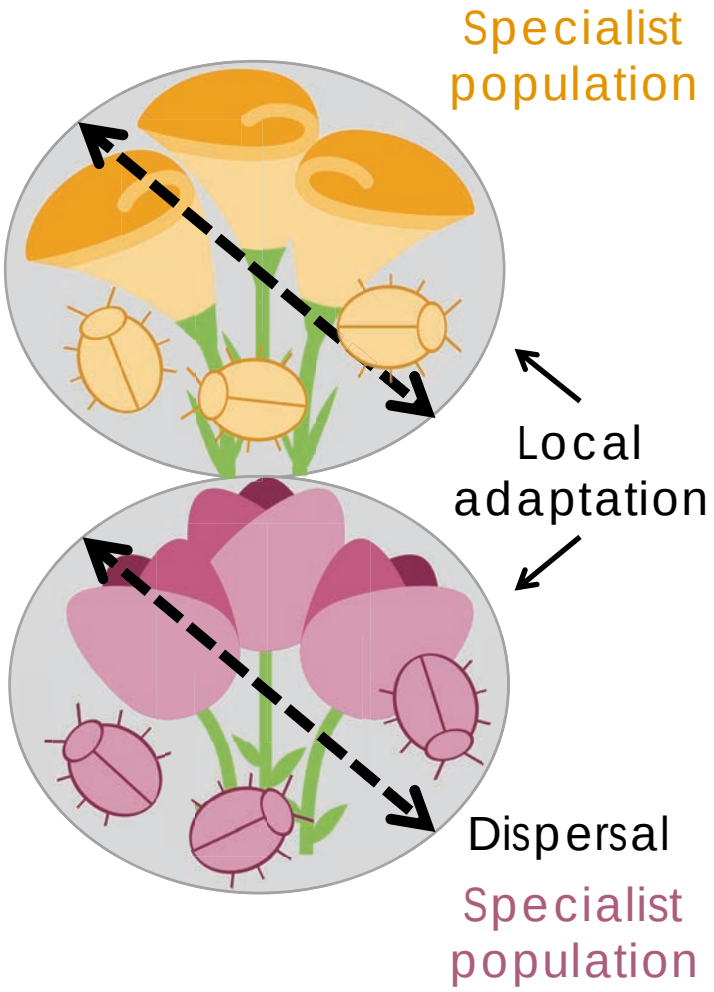
[Levins 1968; Kassen 2002]

Environmental heterogeneity



[Levins 1968; Kassen 2002]

Environmental heterogeneity

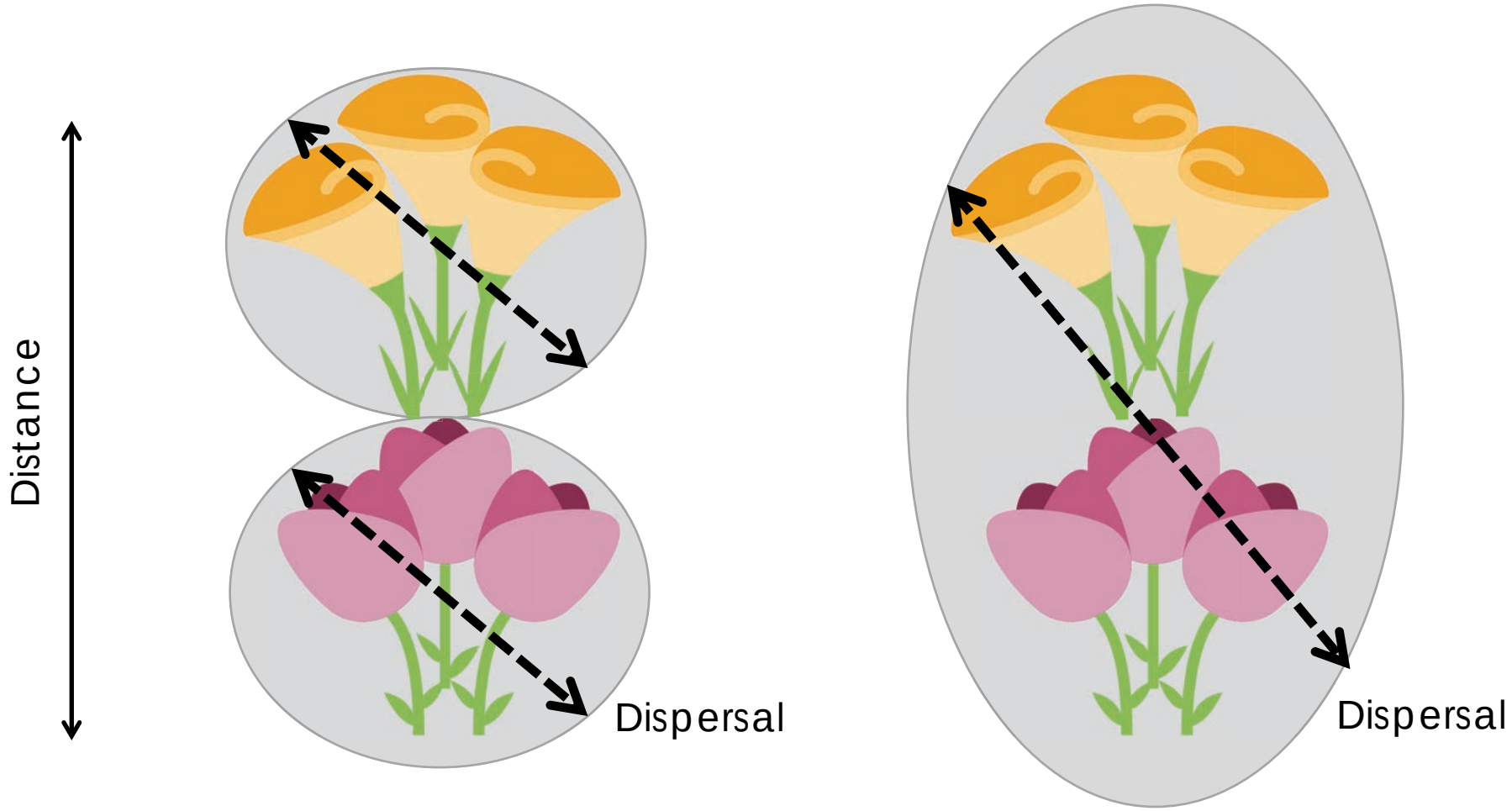


[Levins 1968; Kassen 2002]

Environmental heterogeneity

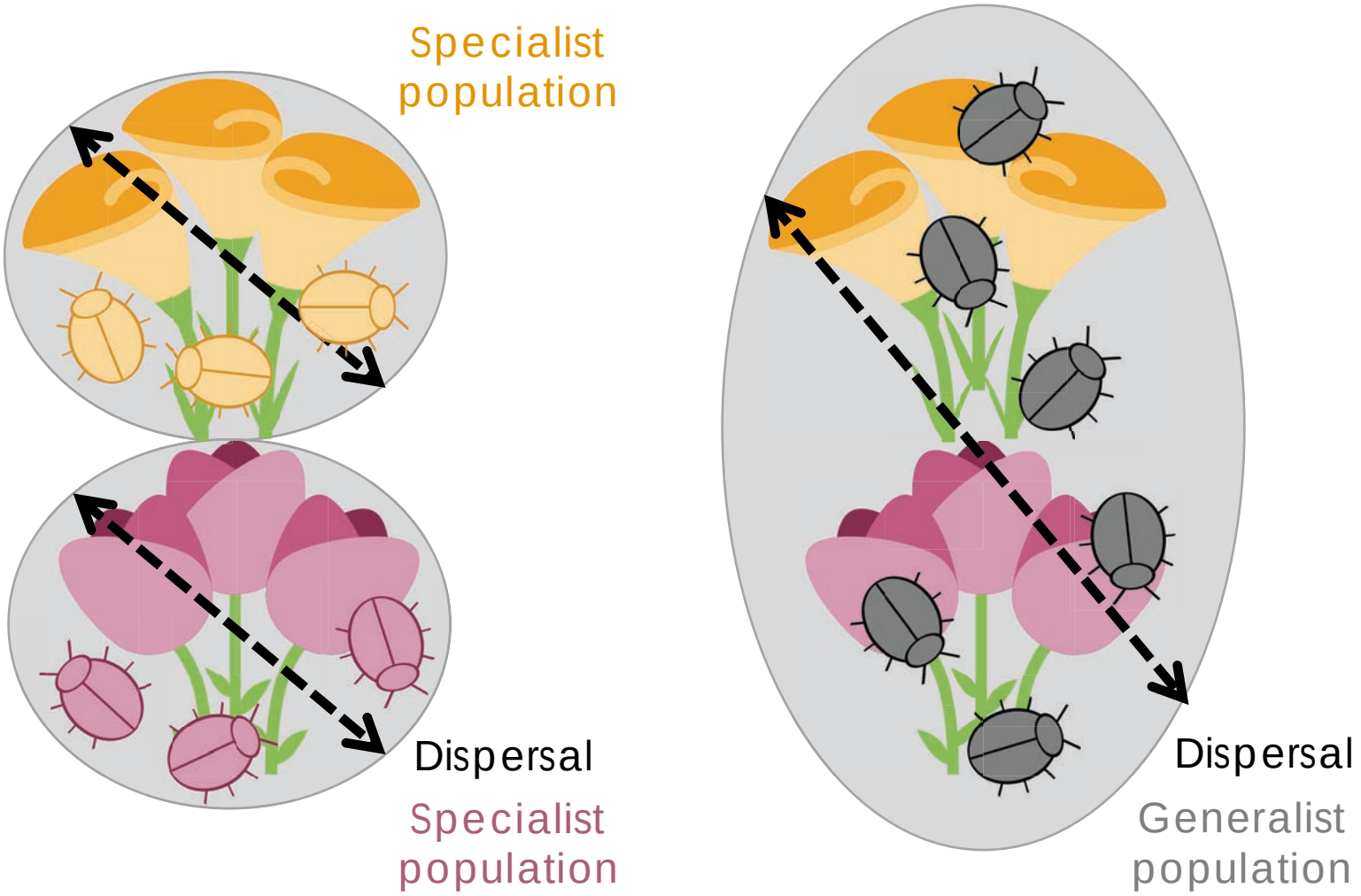
[Levins 1968; Kassen 2002]

Environmental heterogeneity



[Levins 1968; Kassen 2002]

Environmental heterogeneity

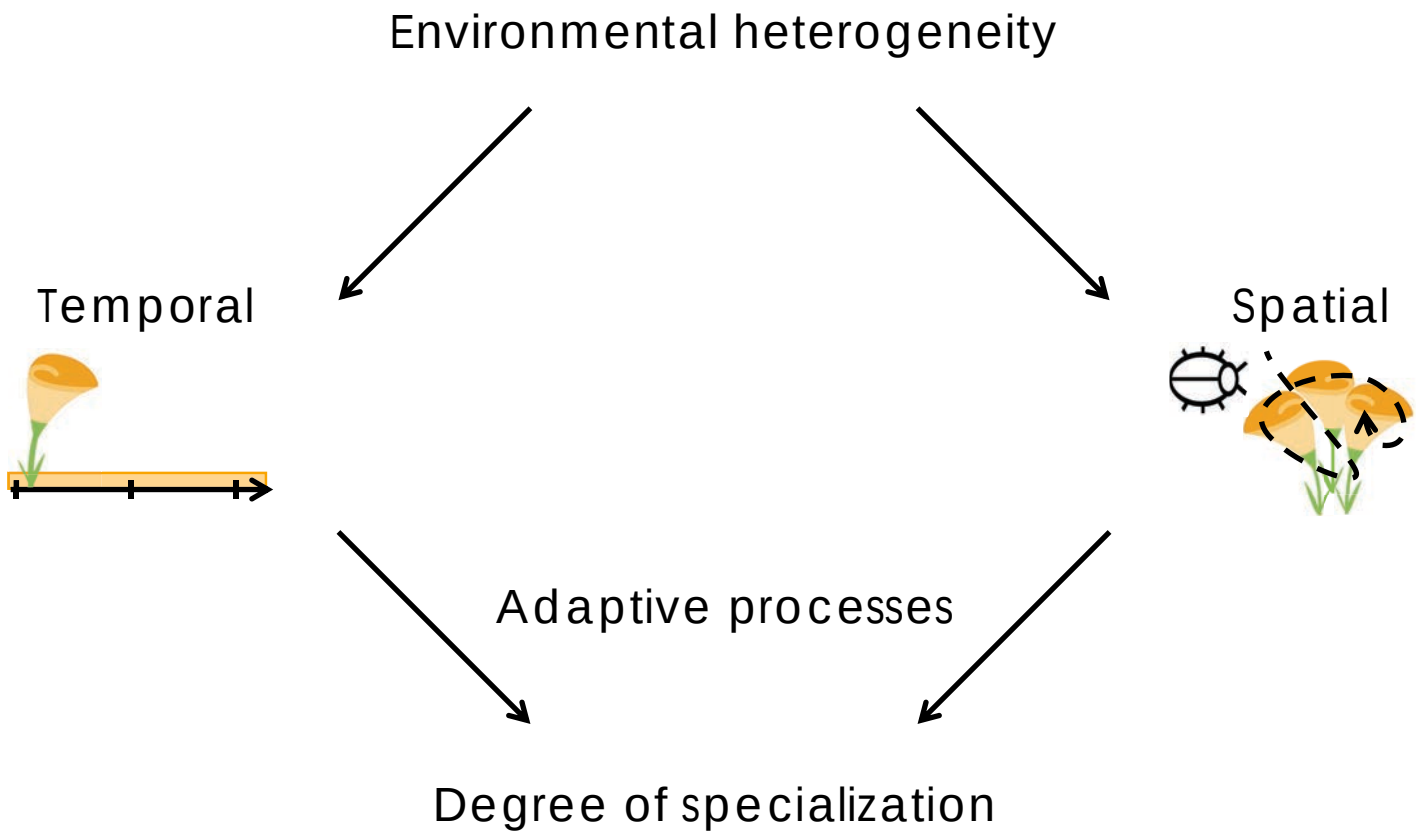


[Levins 1968; Kassen 2002]

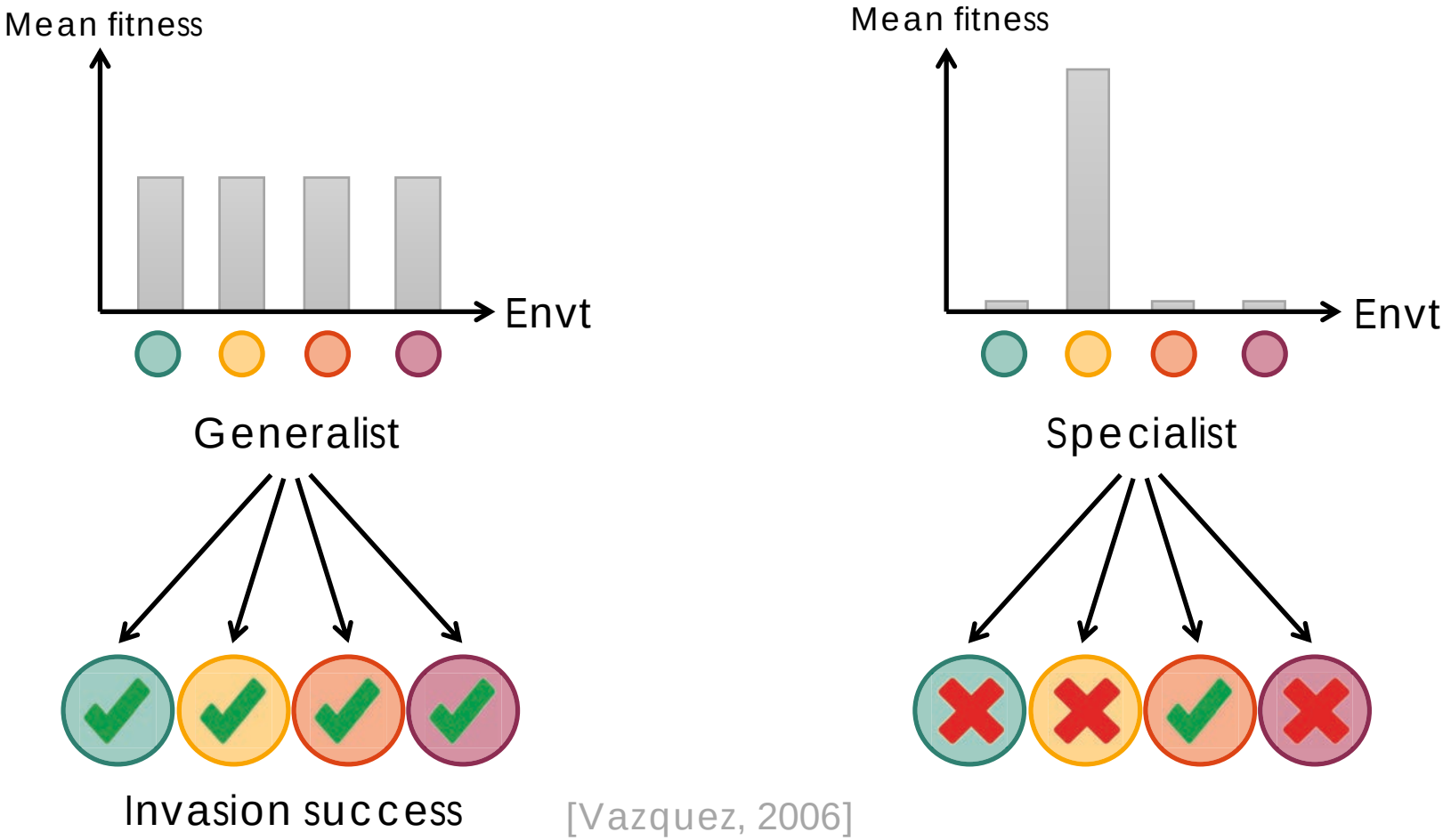
Invasion success and degree of specialization

Degree of specialization

Invasion success and degree of specialization

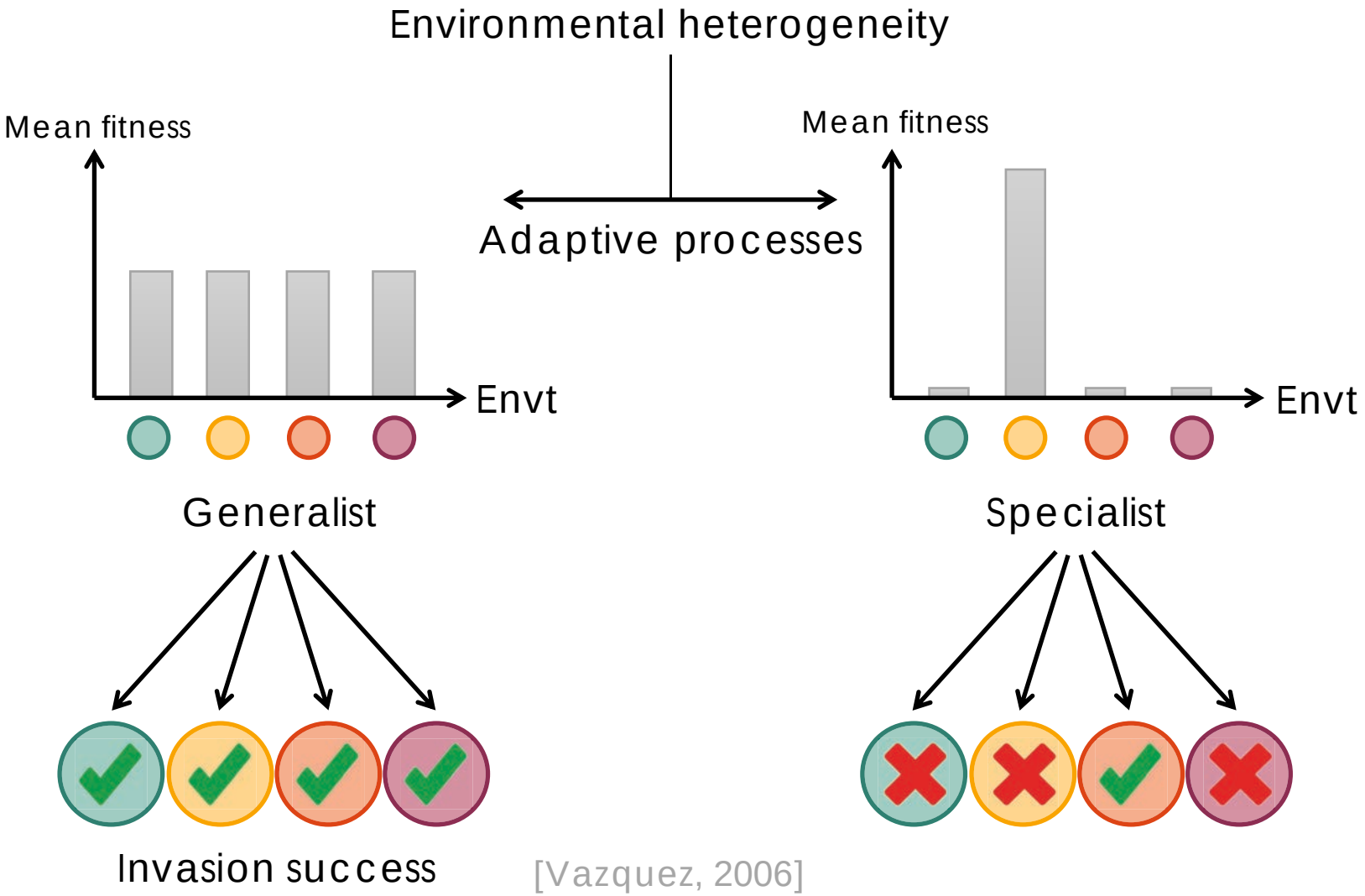


Invasion success and degree of specialization



[Vazquez, 2006]

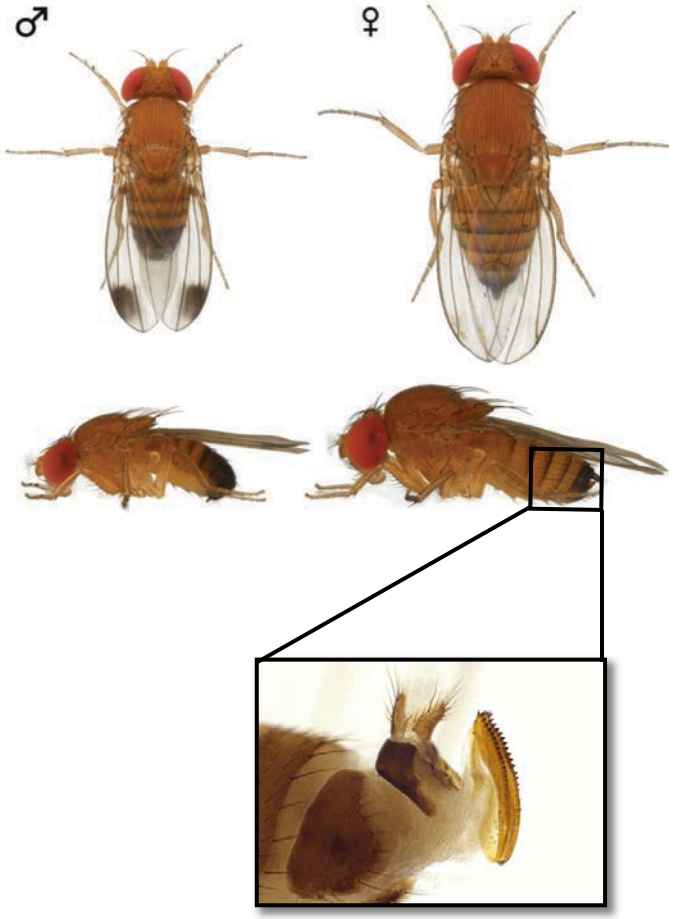
Invasion success and degree of specialization



[Vazquez, 2006]

Drosophila suzukii

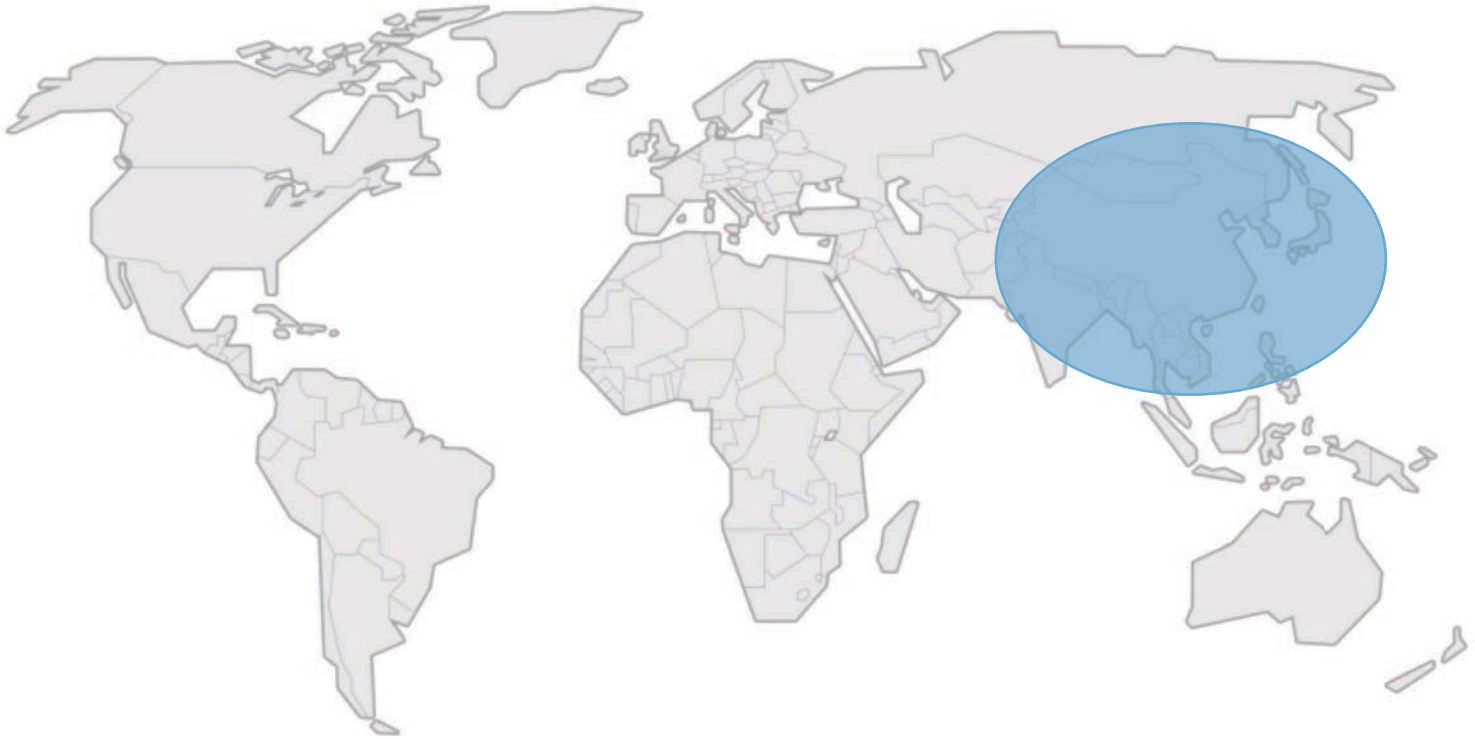
© Yann Le Poul



© Nicolas Gompel

Drosophila suzukii

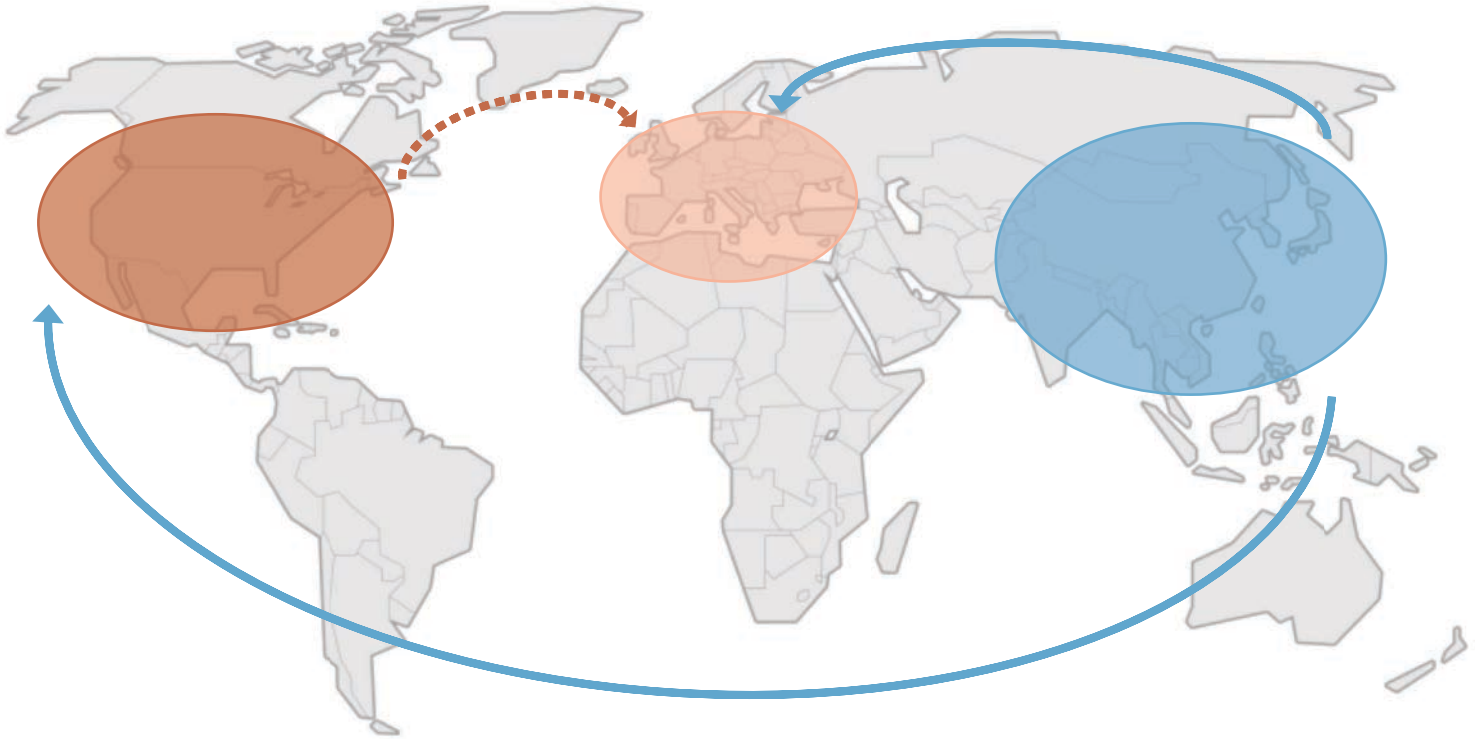
Invasive species



[Fraimout et al., 2017]

Drosophila suzukii

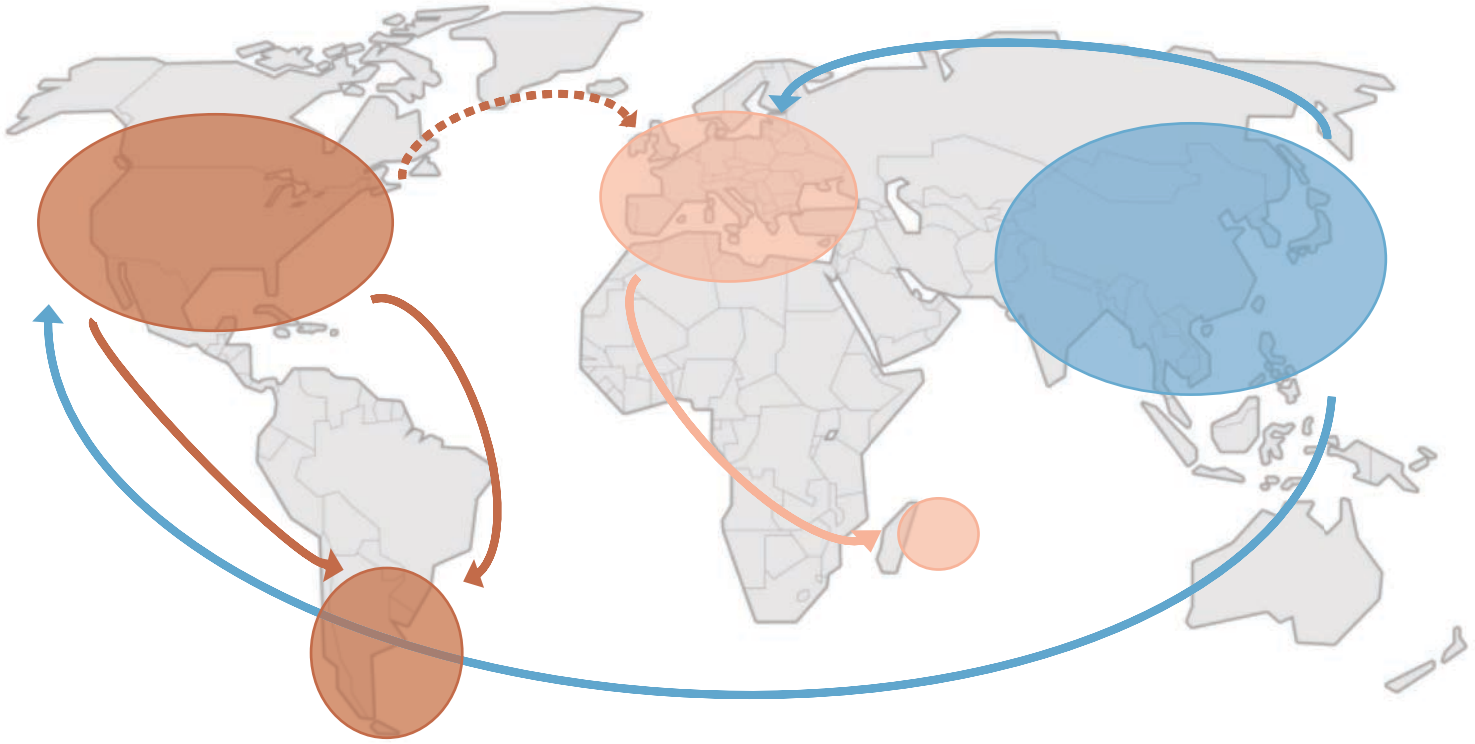
Invasive species



[Fraimout et al., 2017]

Drosophila suzukii

Invasive species



[Fraimout et al., 2017; Andreazza et al., 2017]

Drosophila suzukii

Invasive species

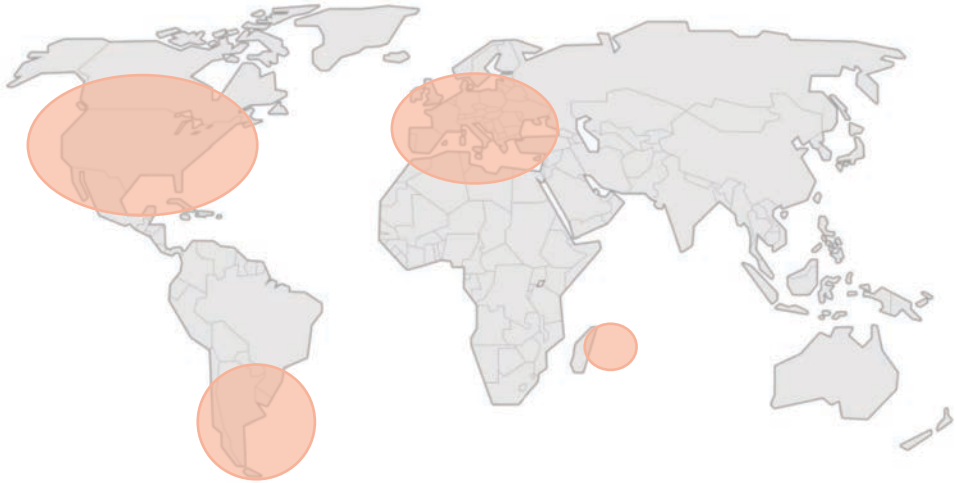
Generalist species

[Kanzawa 1939; Kimura et al., 1977; Nishiharu 1980; Mitsui et al. 2006, 2010; Lee et al. 2011]

Drosophila suzukii

Invasive species

Generalist species: crop pest species in invaded area



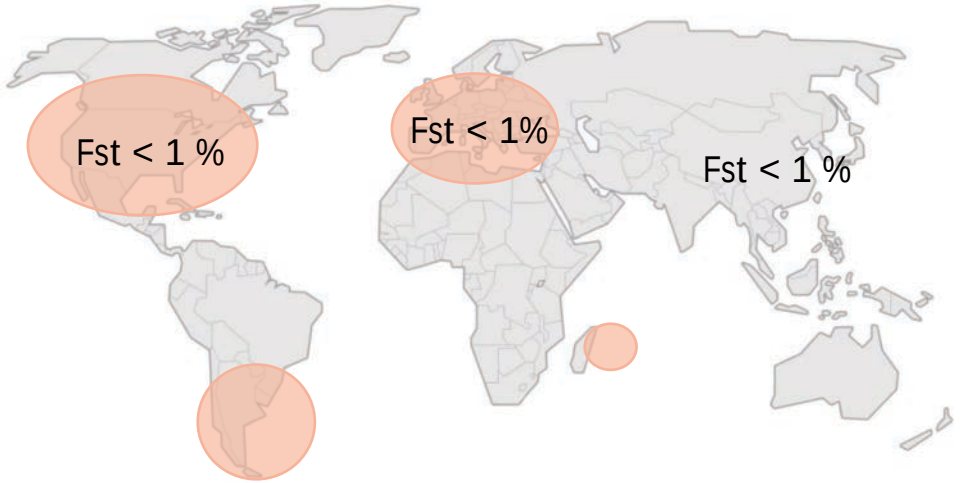
[Lee et al, 2011; Walsh et al., 2011]

Drosophila suzukii

Invasive species

Generalist species: crop pest species in invaded area

Low level of small-scale genetic differentiation

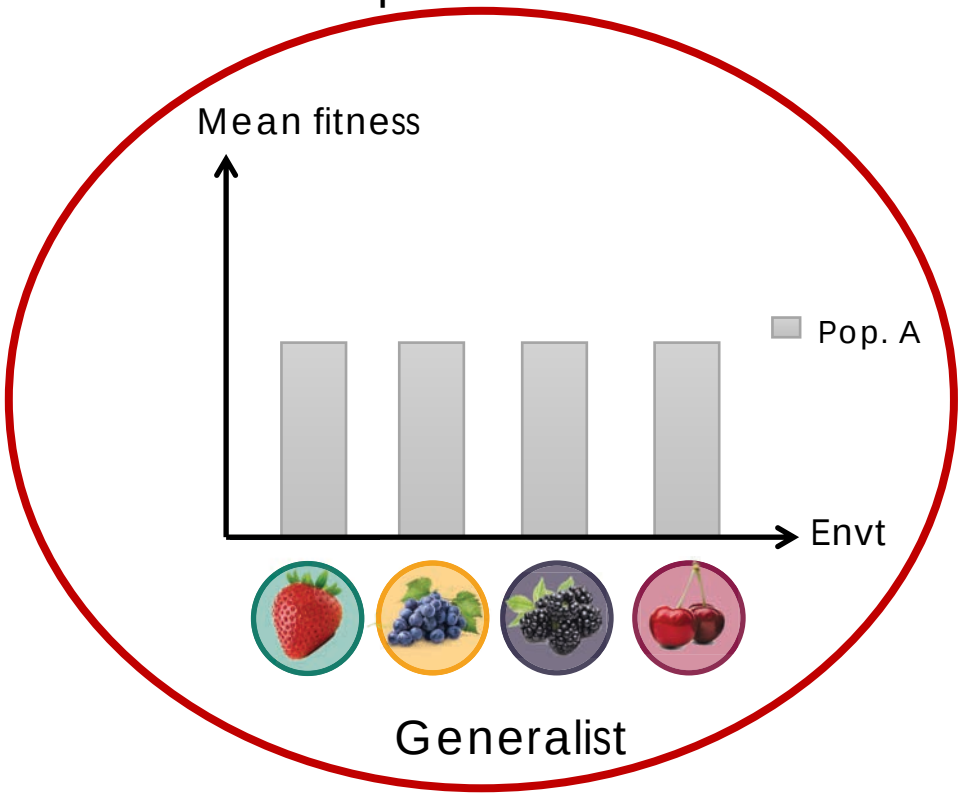


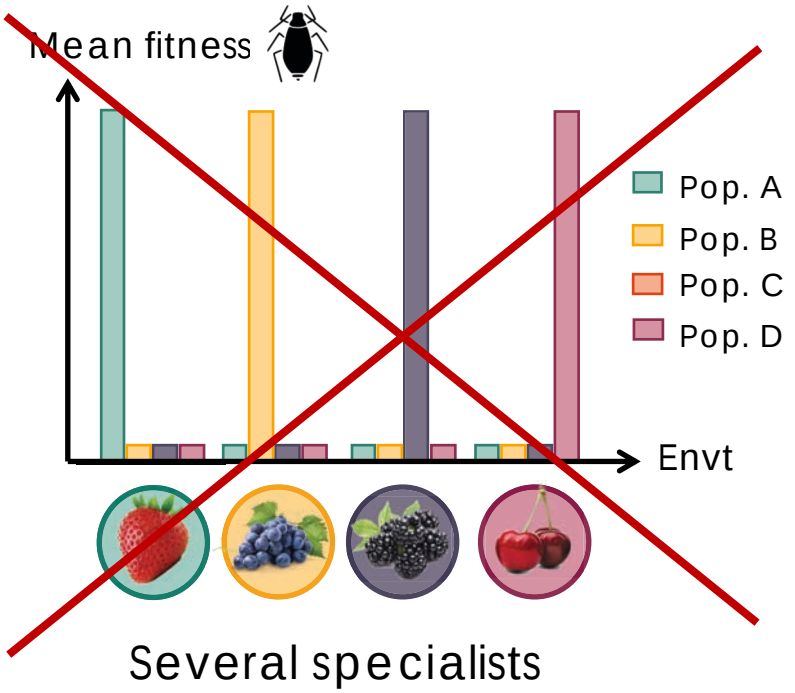
[Fraimout et al., 2017; Pers. Com.]

Drosophila suzukii

Invasive species

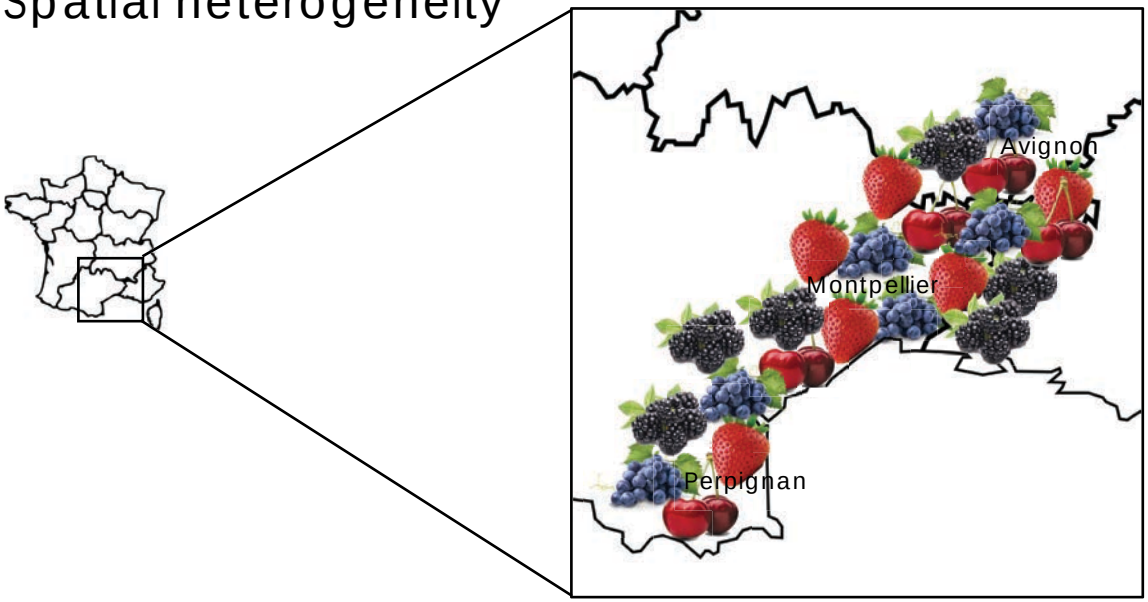
Generalist species



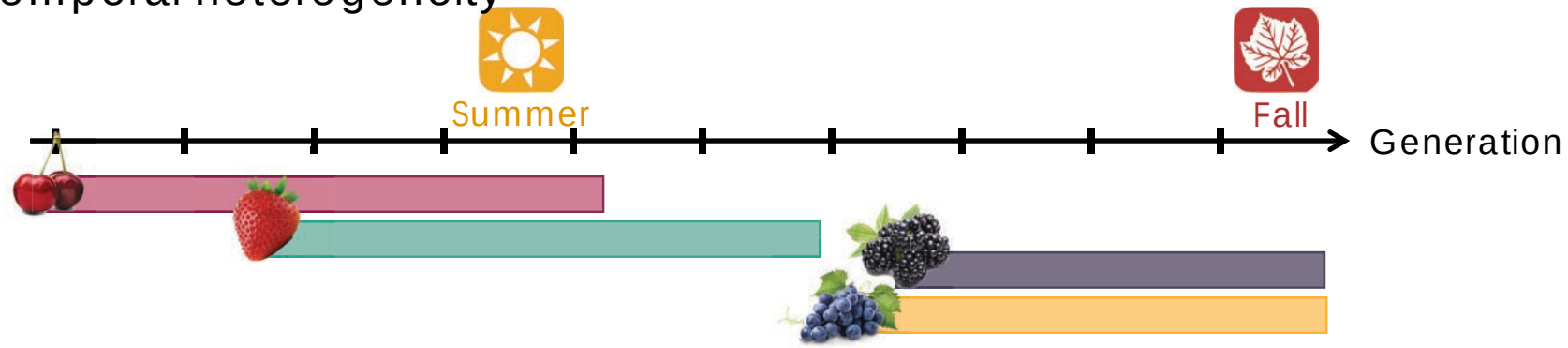


D. suzukii: environmental heterogeneity

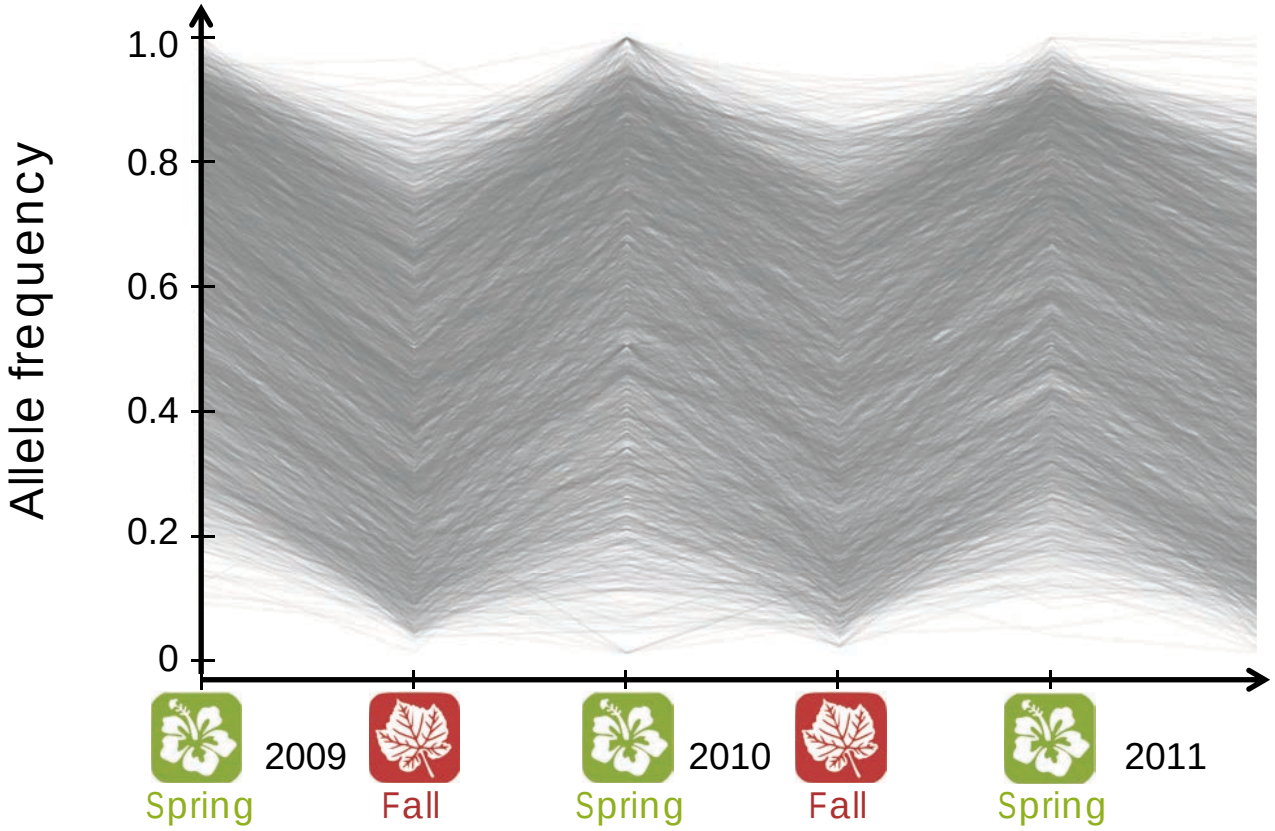
Spatial heterogeneity



Temporal heterogeneity



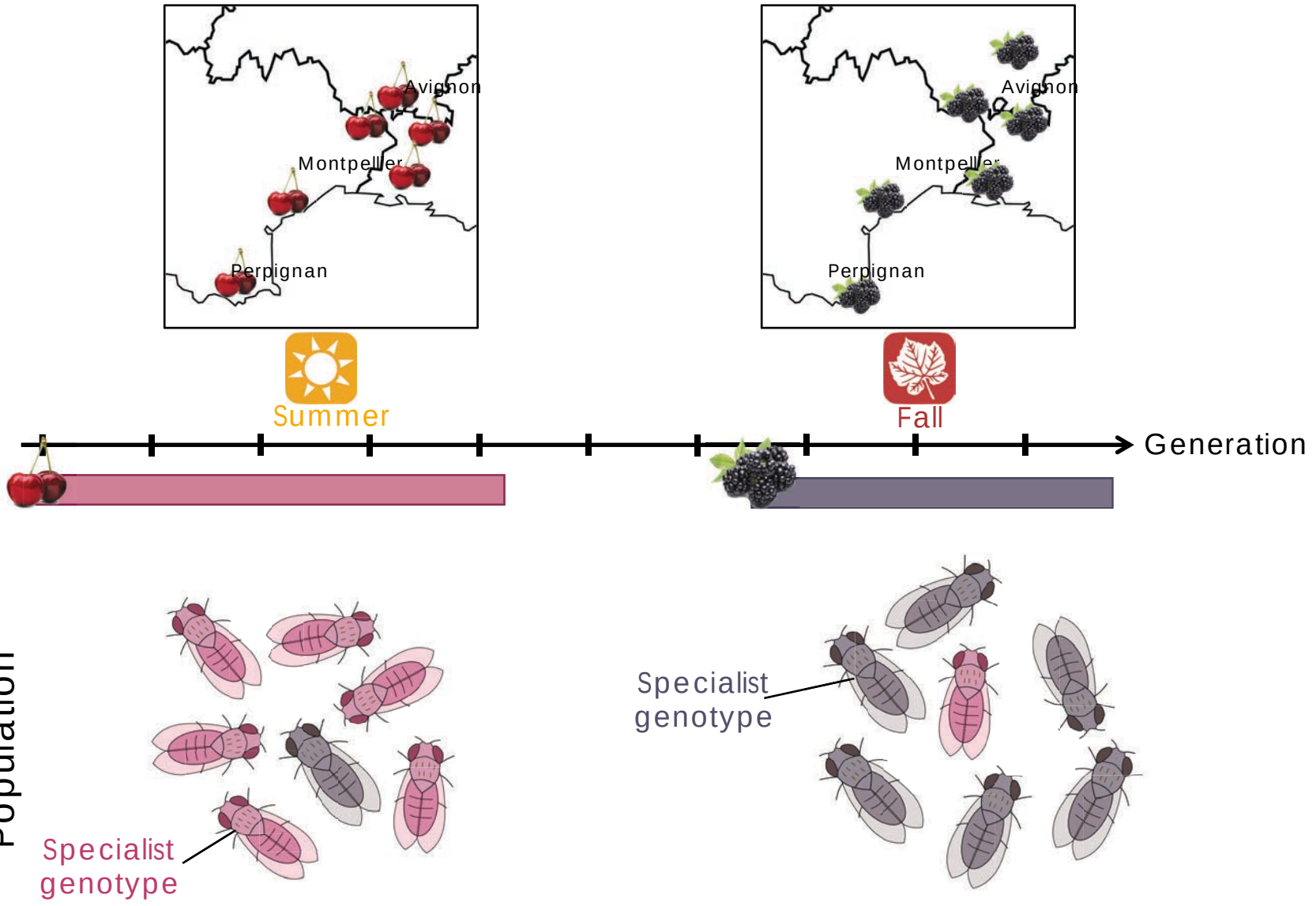
Genetic responses to seasonal variation in *Drosophila*



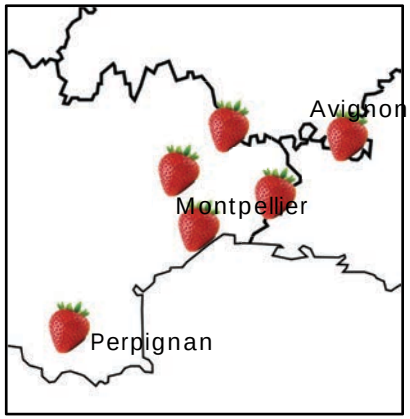
[Bergland et al., 2014]

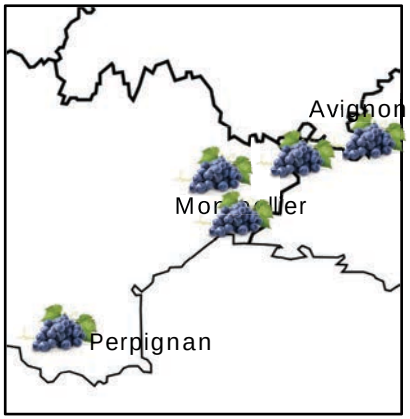
Response to host plant selective pressures?

Response to host plant selective pressures?



Response to host plant selective pressures?





Summer

Fall

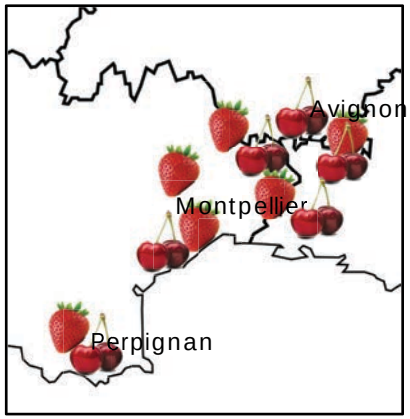
Generation

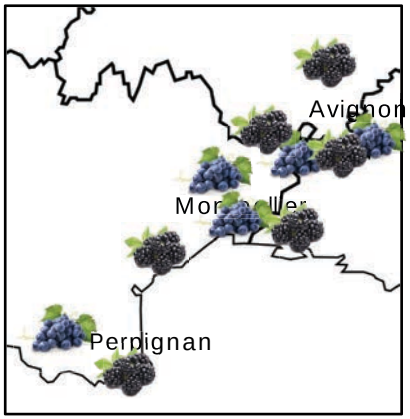
Population

Specialist genotype

Specialist genotype

Response to host plant selective pressures?



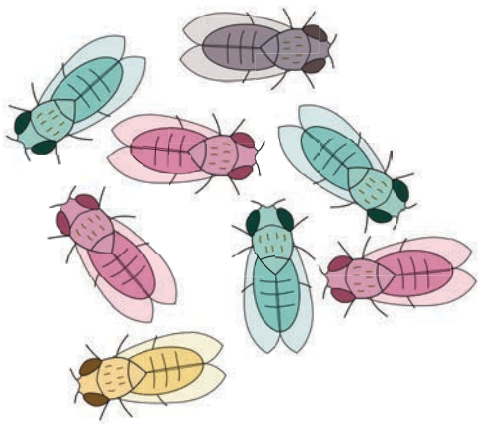


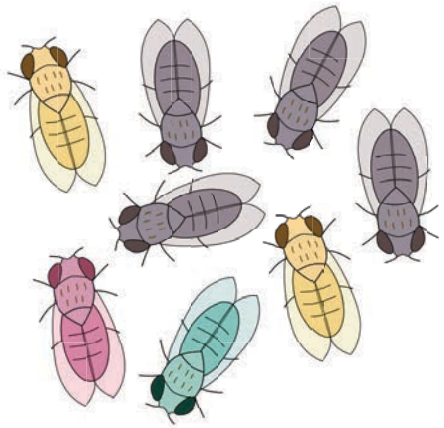
Summer

Fall

Generation

Meta-population



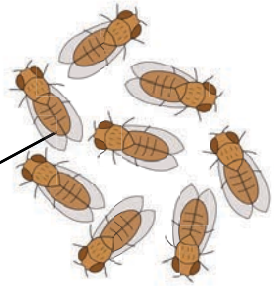


Generalist populations

Summer

Fall

Without polymorphism



Generalist genotype

Generalist genotypes

OR

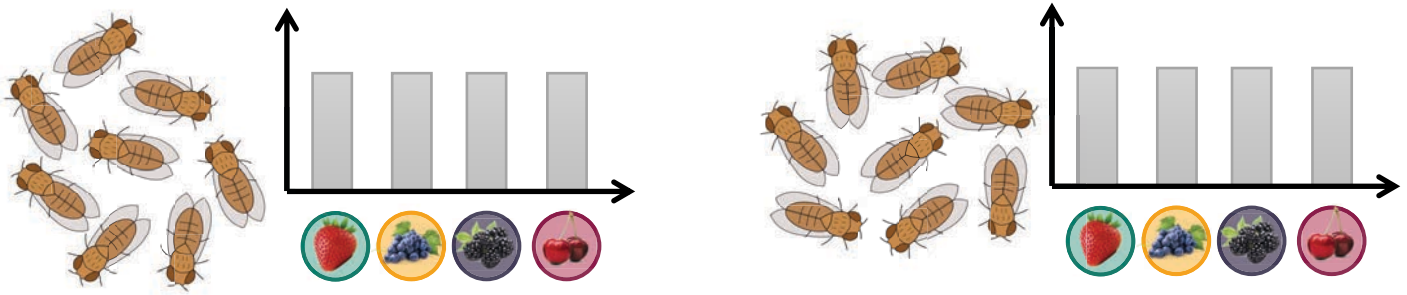
With polymorphism

Generalist populations

Summer

Fall

Without polymorphism



Generalist genotypes

OR

With polymorphism

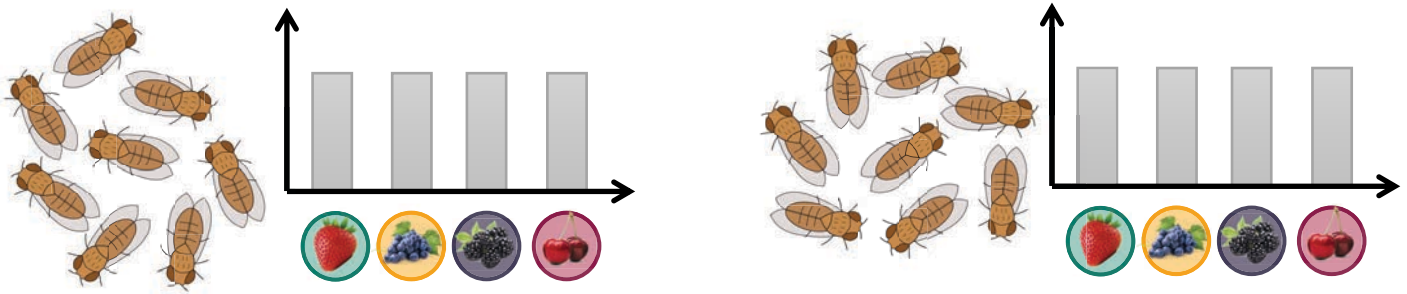
Pool of specialist genotypes

Generalist populations

Summer

Fall

Without polymorphism



Generalist genotypes

OR

With polymorphism

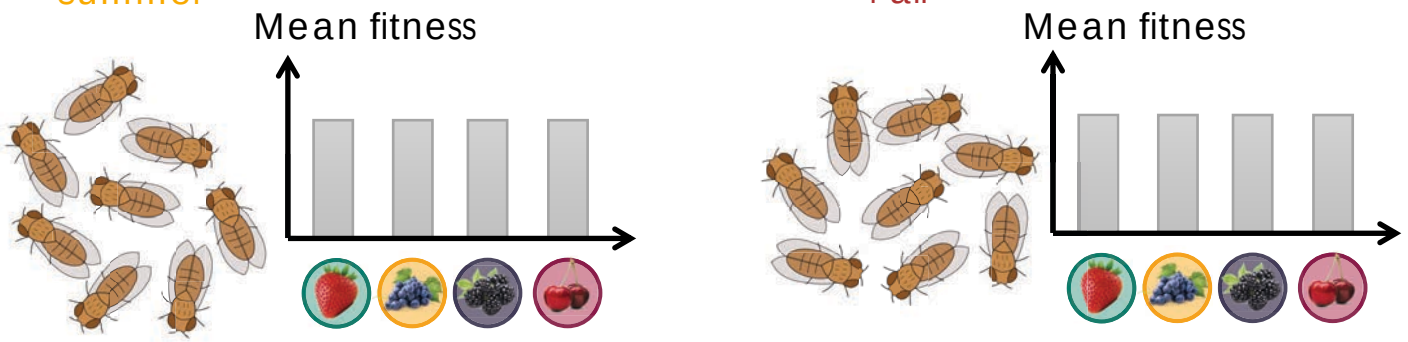
Pool of specialist genotypes

Generalist populations

Summer

Fall

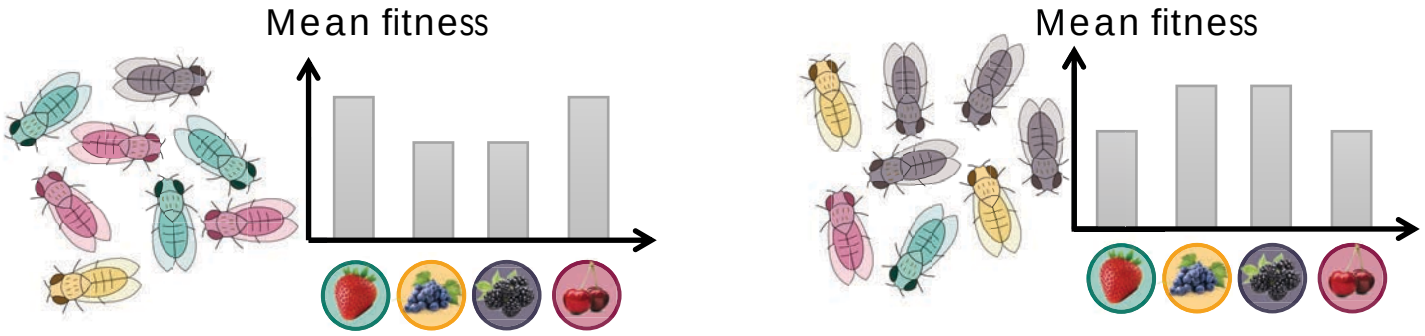
Without polymorphism



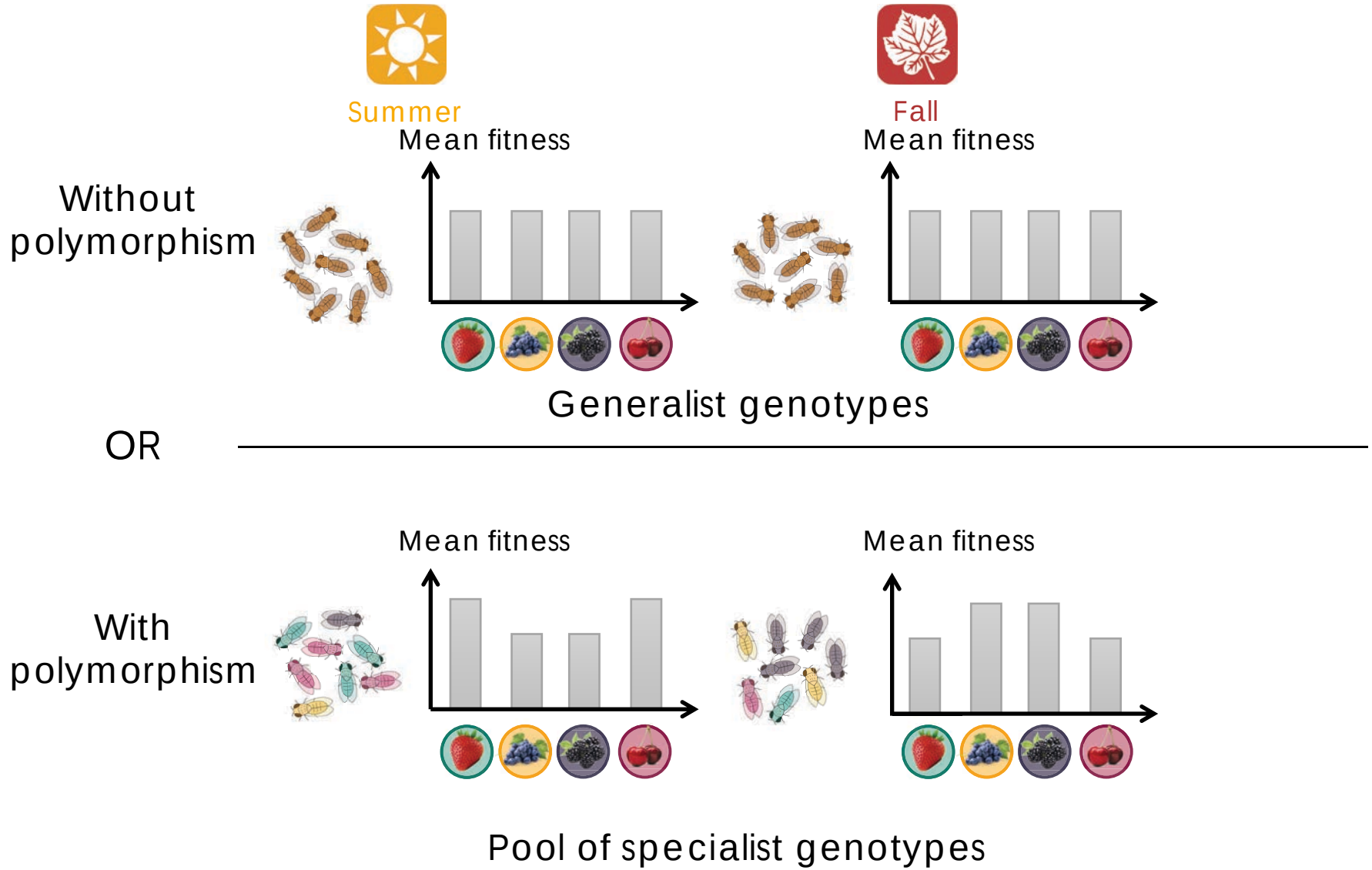
Generalist genotypes

OR

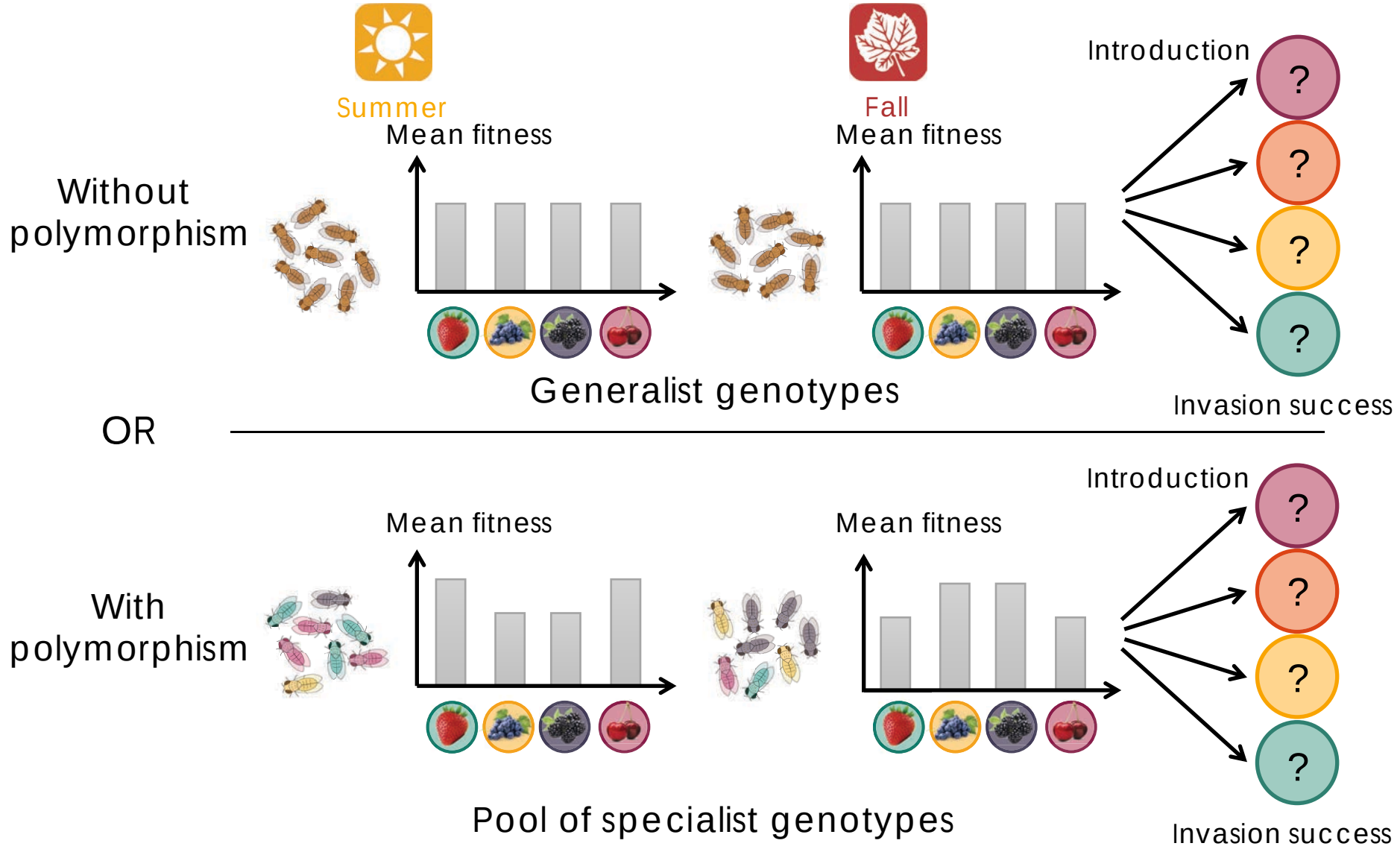
With polymorphism

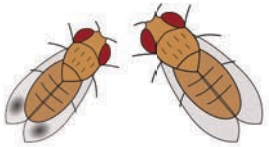


Pool of specialist genotypes

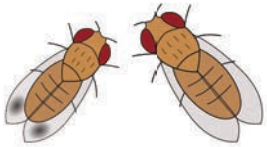

Summer
Fall
Mean fitness
Mean fitness
Without polymorphism
Generalist genotypes
OR
Mean fitness
Mean fitness
With polymorphism
Pool of specialist genotypes

Effect on invasion success?



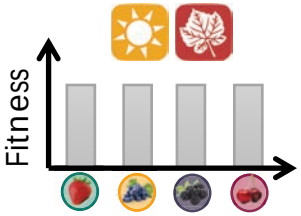


Adaptive responses of *Drosophila suzukii*

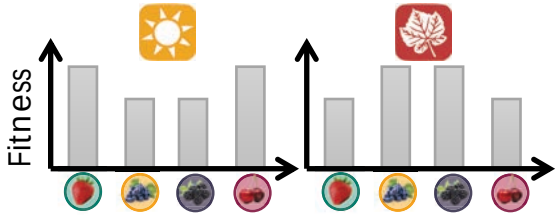


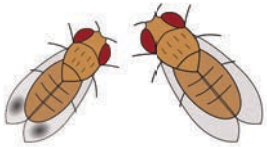
Adaptive responses of *Drosophila suzukii*

What kind of generalist?



OR





Adaptive responses of *Drosophila suzukii*

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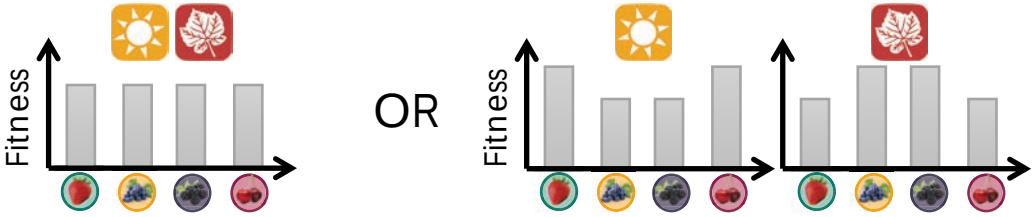
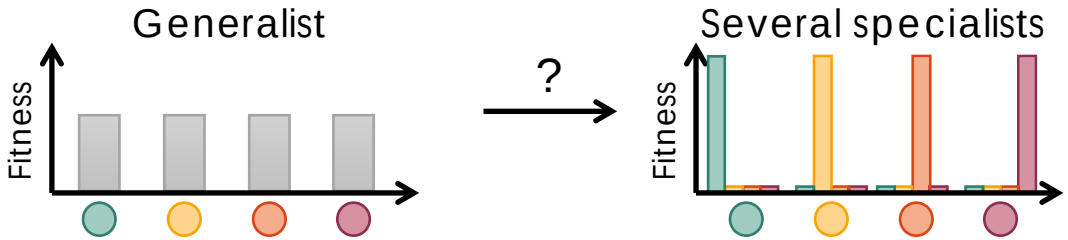
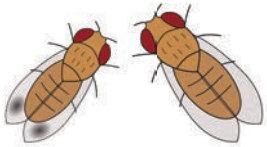


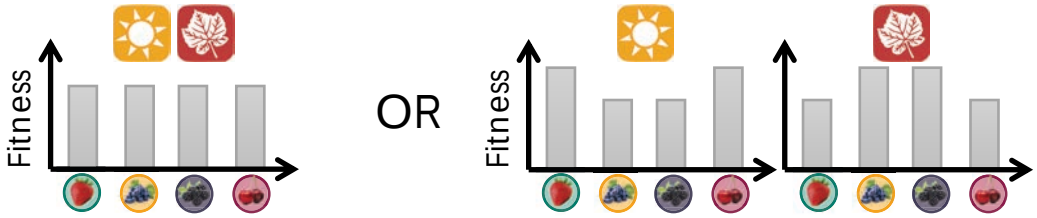
Can we select for specialization?



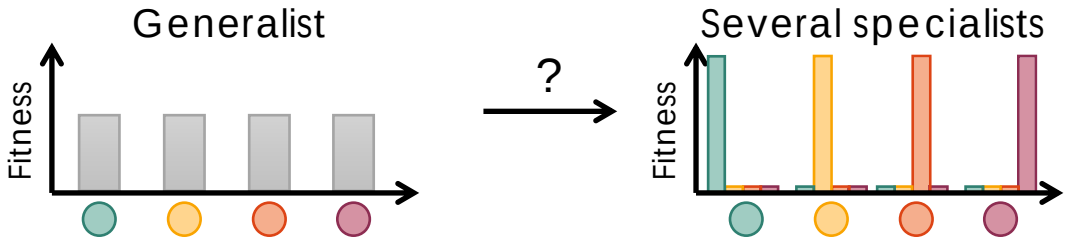


Adaptive responses of *Drosophila suzukii*

What kind of generalist?

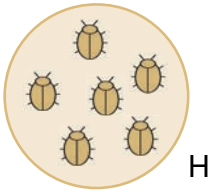


Can we select for specialization?



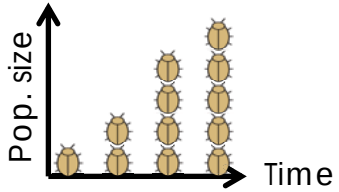
Factors promoting invasion success?

Environmental conditions



OR

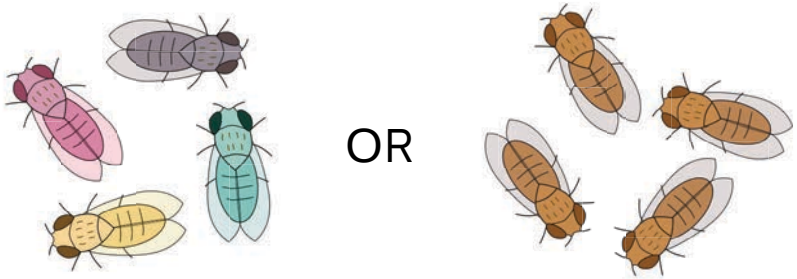
Demographic processes



Generalist with polymorphism *in natura*: heterogenous environment

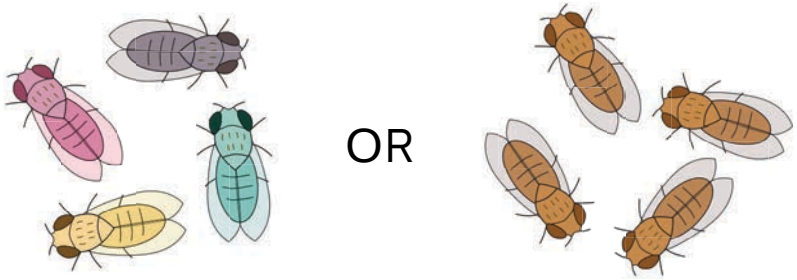
What kind of generalist?

Goal:
Is there any phenotypic variability in fruit exploitation?



What kind of generalist?

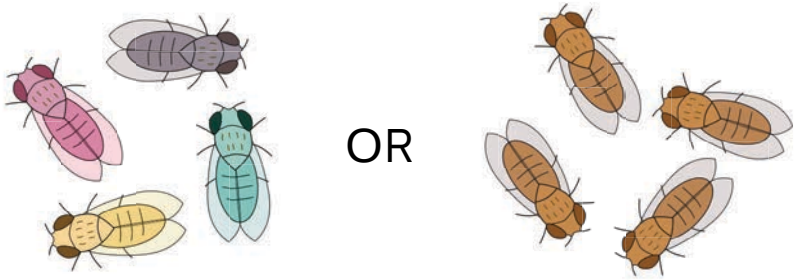
Goal:
Is there any phenotypic variability in fruit exploitation?



Expectation:
Local adaptation evolve with genetic and non-genetic effects

What kind of generalist?

Goal:
Is there any phenotypic variability in fruit exploitation?



Expectation:
Local adaptation evolve with genetic and non-genetic effects

Approach:
Reciprocal transplant experiments with wild populations

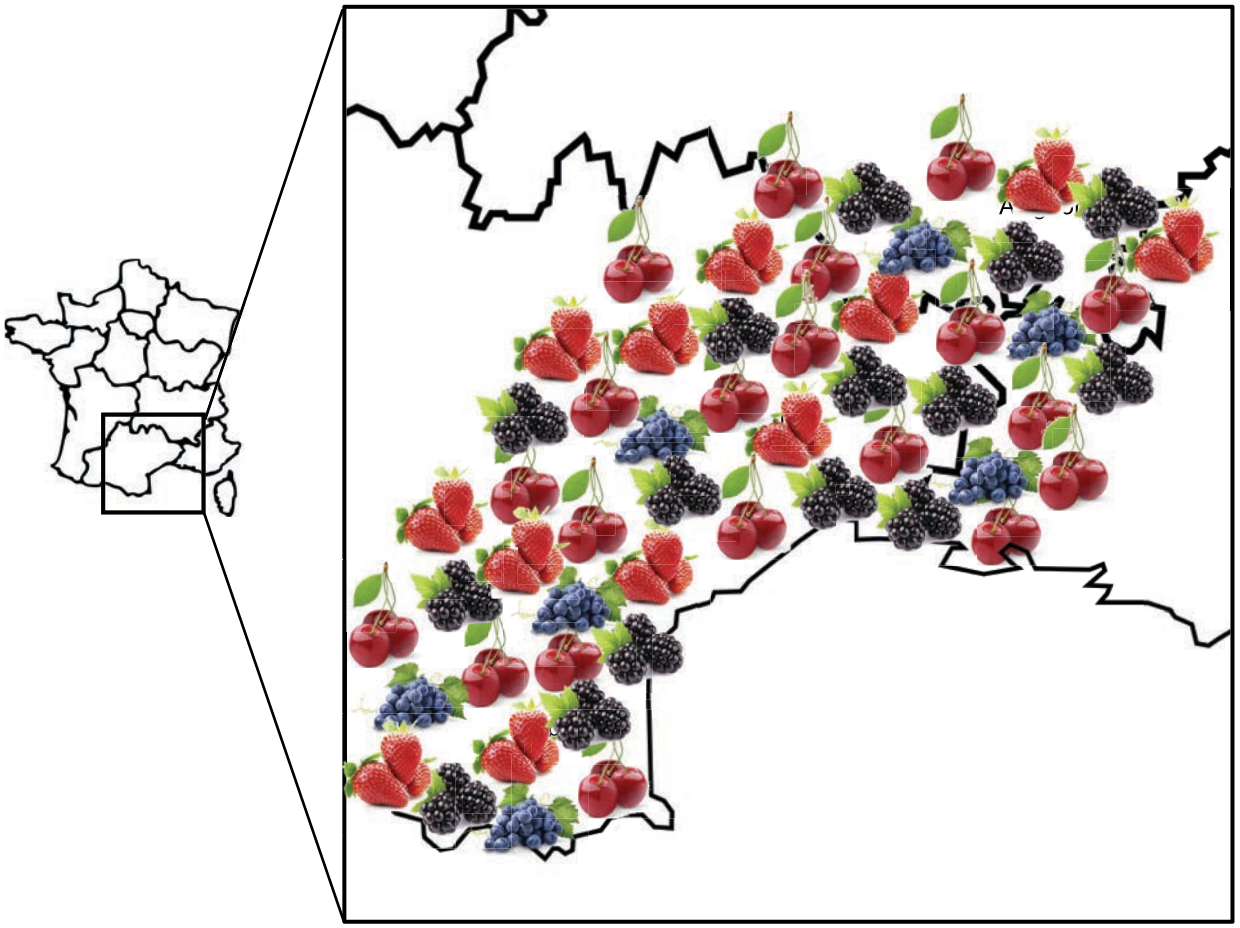
Strawberry

Cherry

Blackberry

Grape

Sampling fly populations



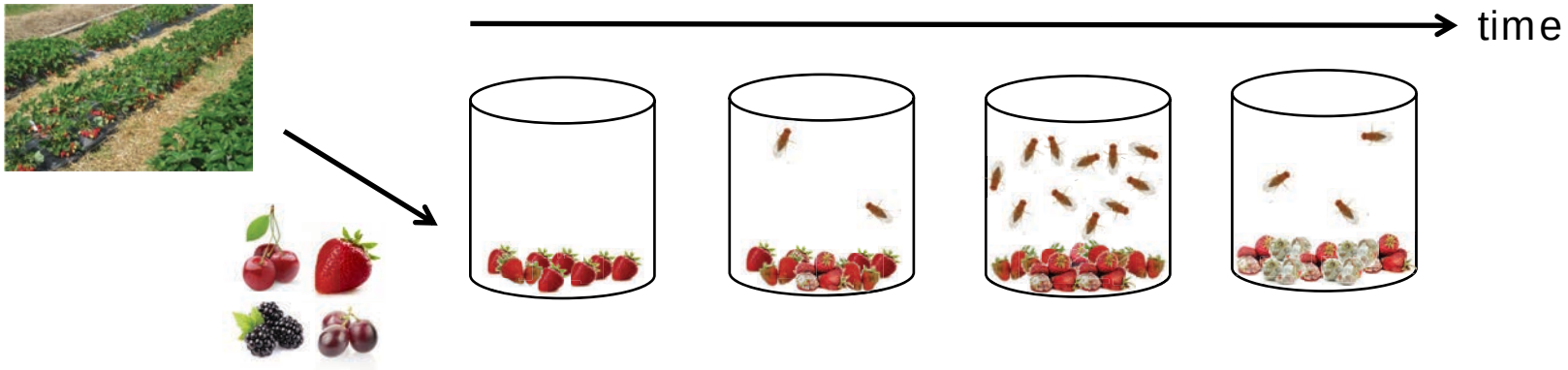
12 locations for

20 locations for

15 locations for

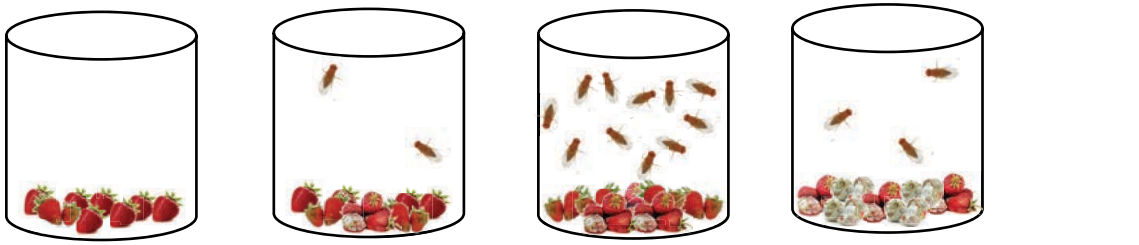
7 locations for

Sampling fly populations



More than 200 containers
During 8 months

Sampling fly populations



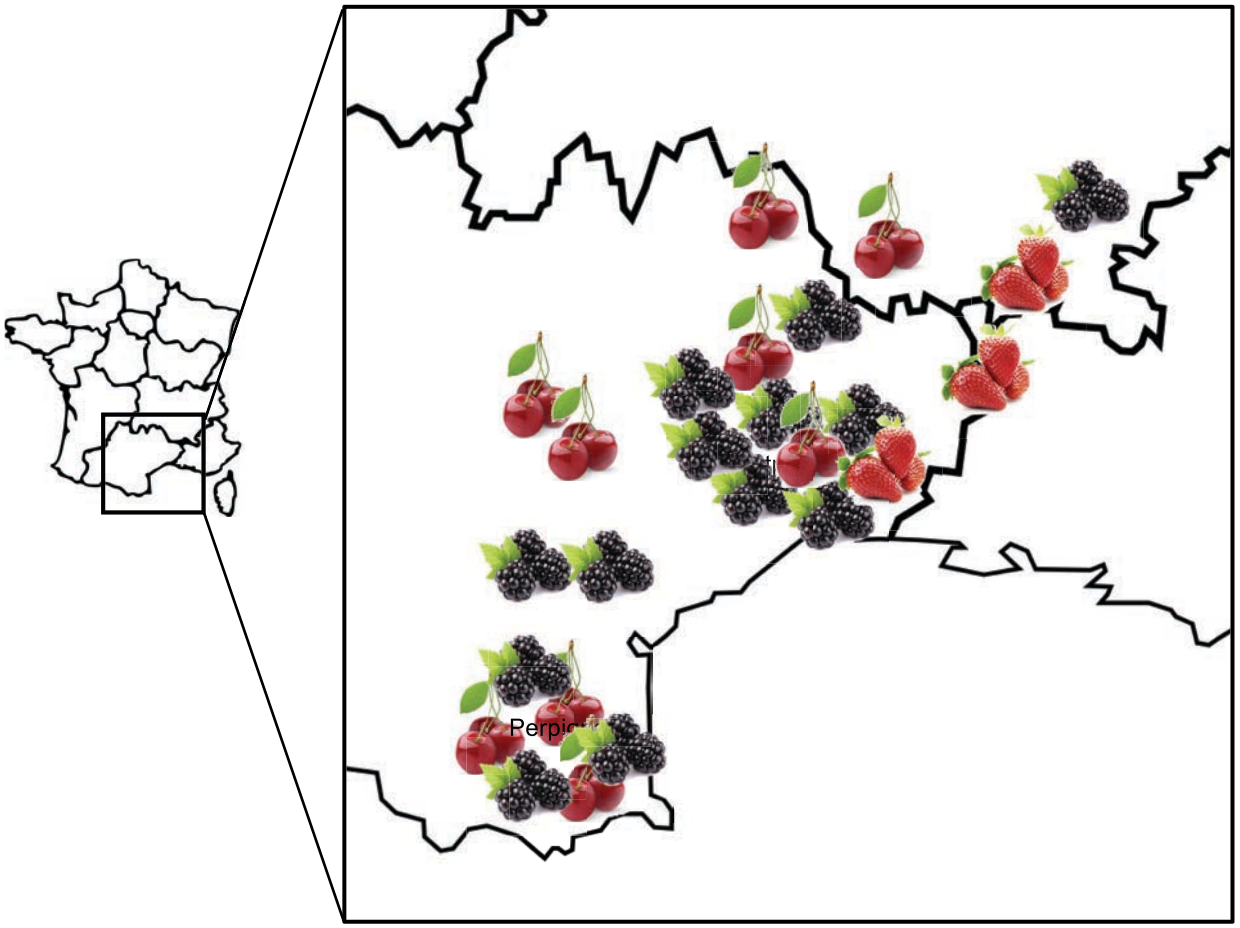
3/12 fly populations

9/20 fly populations

13/15 fly populations

0/7 fly population

Sampling fly populations



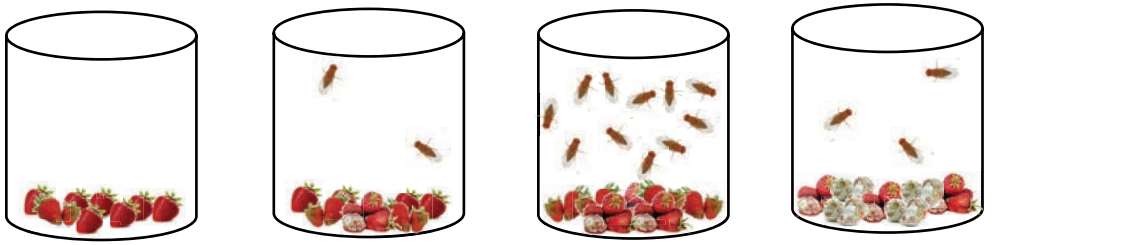
3 locations for

9 locations for

13 locations for

0 locations for

Sampling fly populations



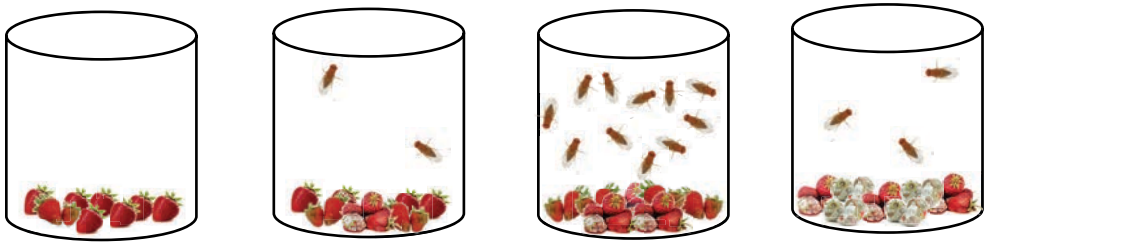
3/12 fly populations

9/20 fly populations

13/15 fly populations

0/7 fly population

Sampling fly populations



3/12 fly populations

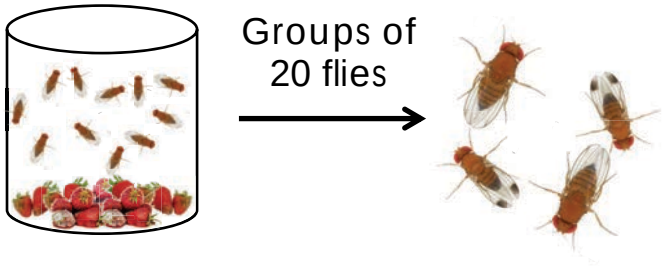
9/20 fly populations

13/15 fly populations

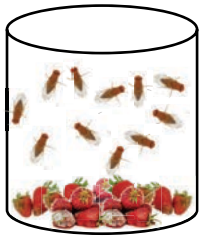
0/7 fly population

Reciprocal transplant experiments

Reciprocal transplant experiments



Reciprocal transplant experiments



Groups of
20 flies

Emergence rate

Fruits purees:
Cherry
Strawberry
Blackberry

Number of eggs
Number of adults

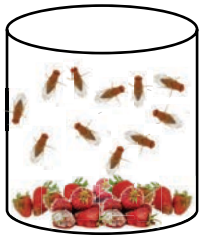
Oviposition preference

Apricot
Blackberry
Blackcurrant
Cherry
Cranberry
Fig

Grape
Kiwi
Raspberry
Rose Hips
Strawberry
Tomato

Number of eggs

Reciprocal transplant experiments

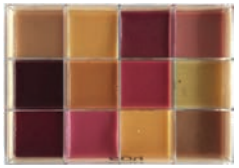


Groups of
20 flies

G1

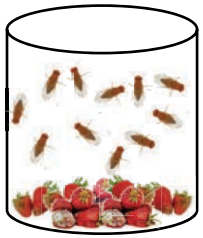
Genetic + non-
genetic effects

Emergence
rate



Number of
eggs laid

Reciprocal transplant experiments



Groups of
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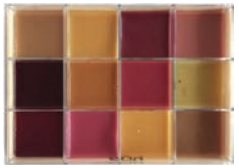
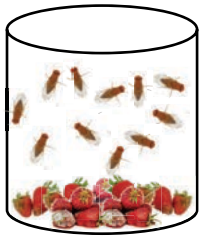


Number of
eggs laid

Two generations in a common garden

G3

Reciprocal transplant experiments

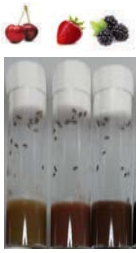


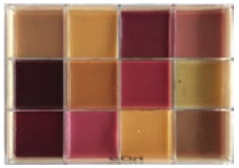
Groups of 20 flies

G1

Genetic + non-genetic effects

Emergence rate





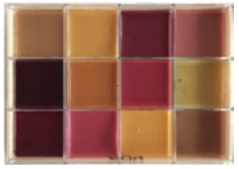
Number of eggs laid

Two generations in a common garden

G3

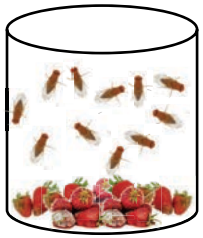
Genetic effects

Emergence rate



Number of eggs laid

Reciprocal transplant experiments

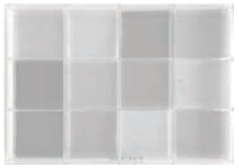


Groups of 20 flies

G1

Genetic + non-genetic effects

Emergence rate



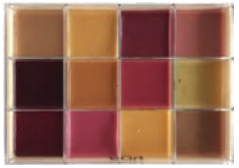
Number of eggs laid

Two generations in a common garden

G3

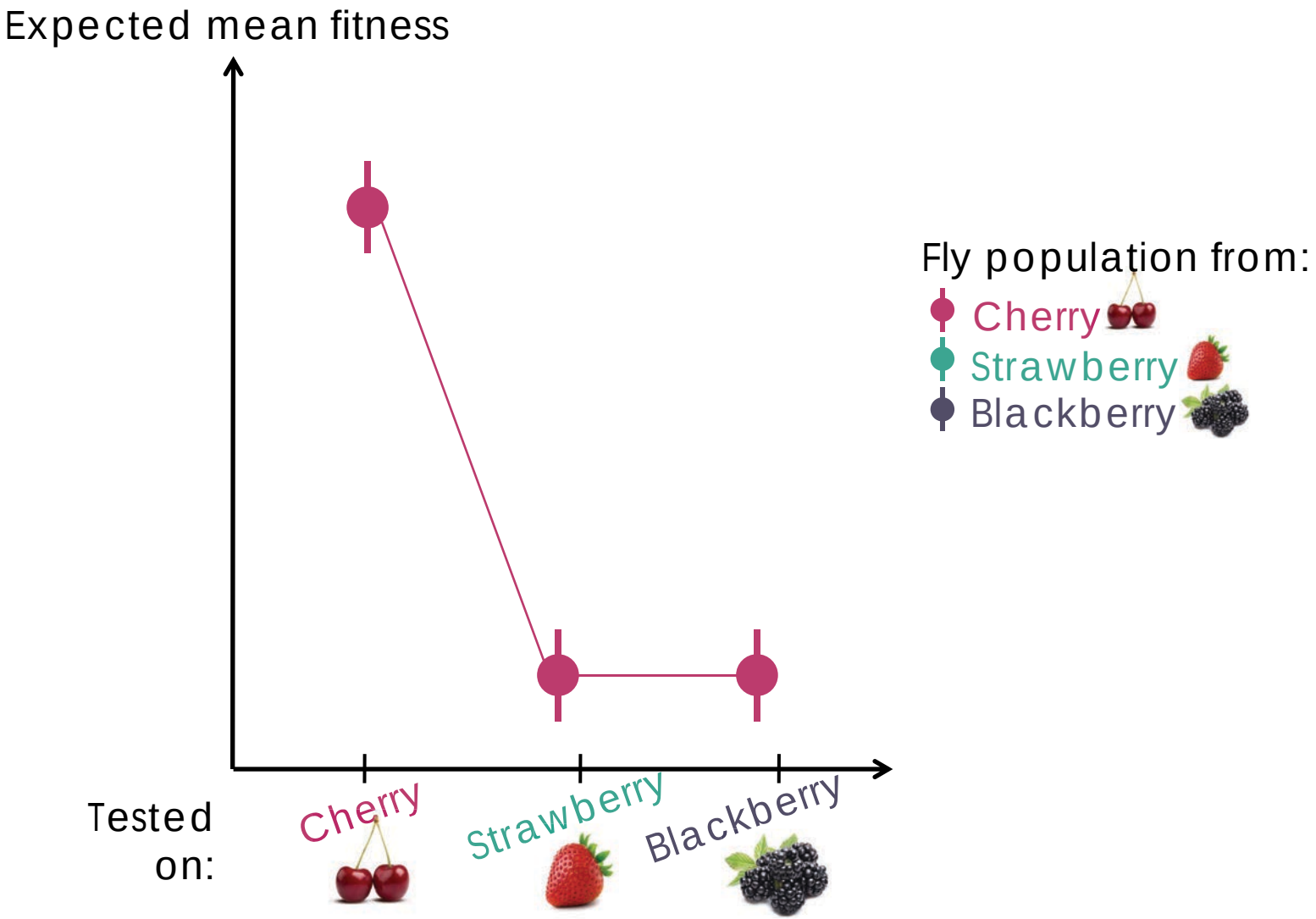
Genetic effects

Emergence rate

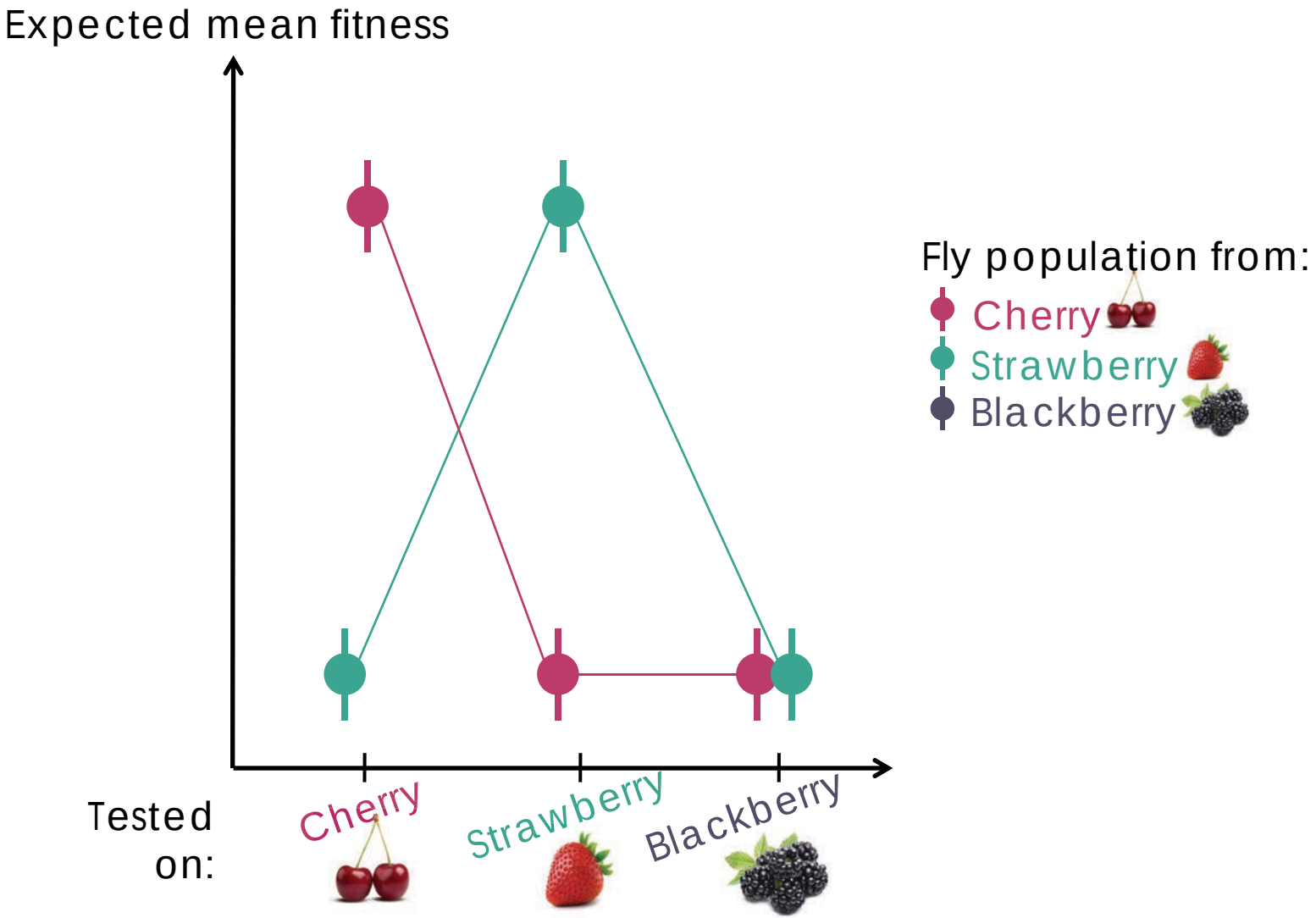


Number of eggs laid

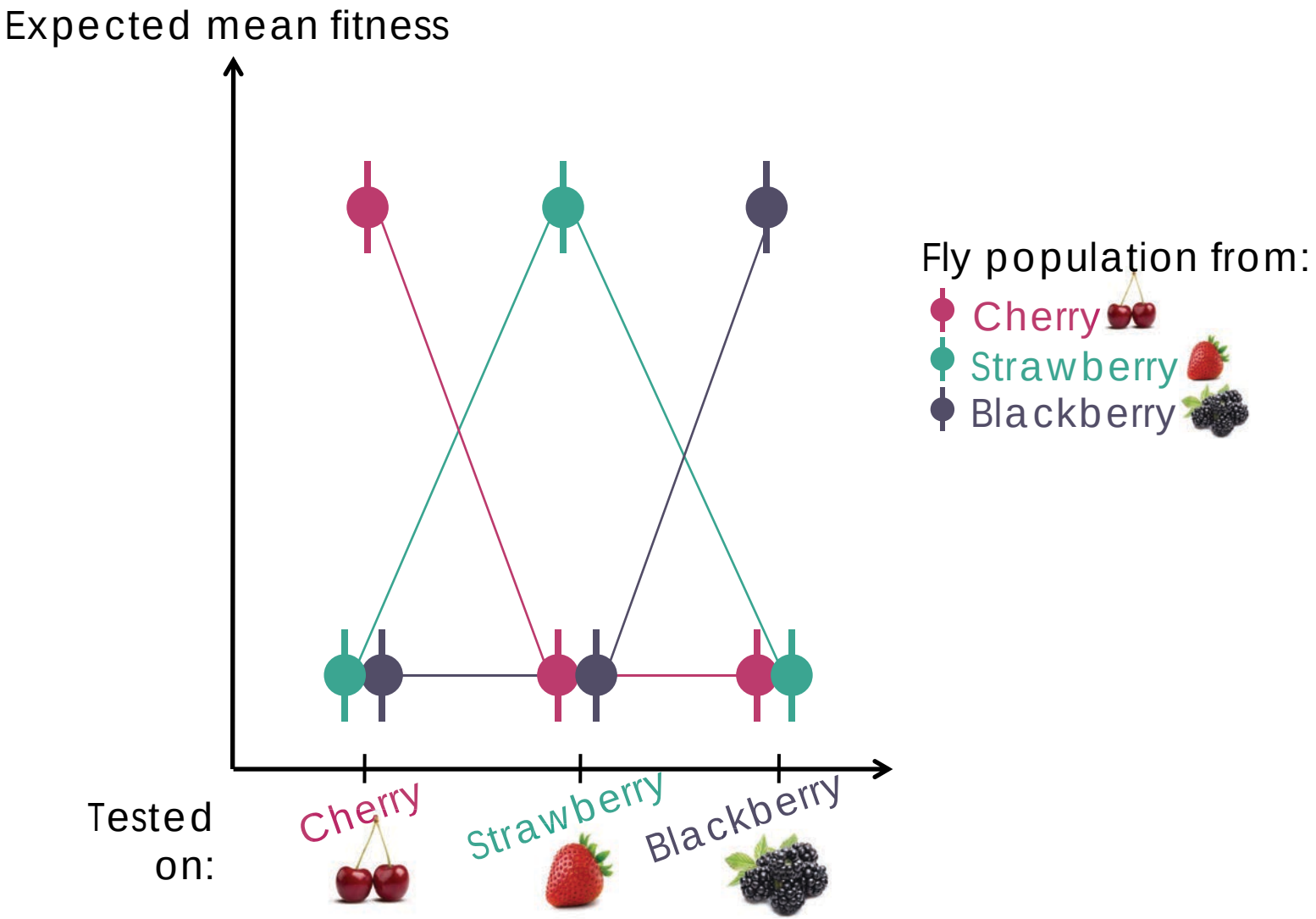
Expectations: Local adaptation



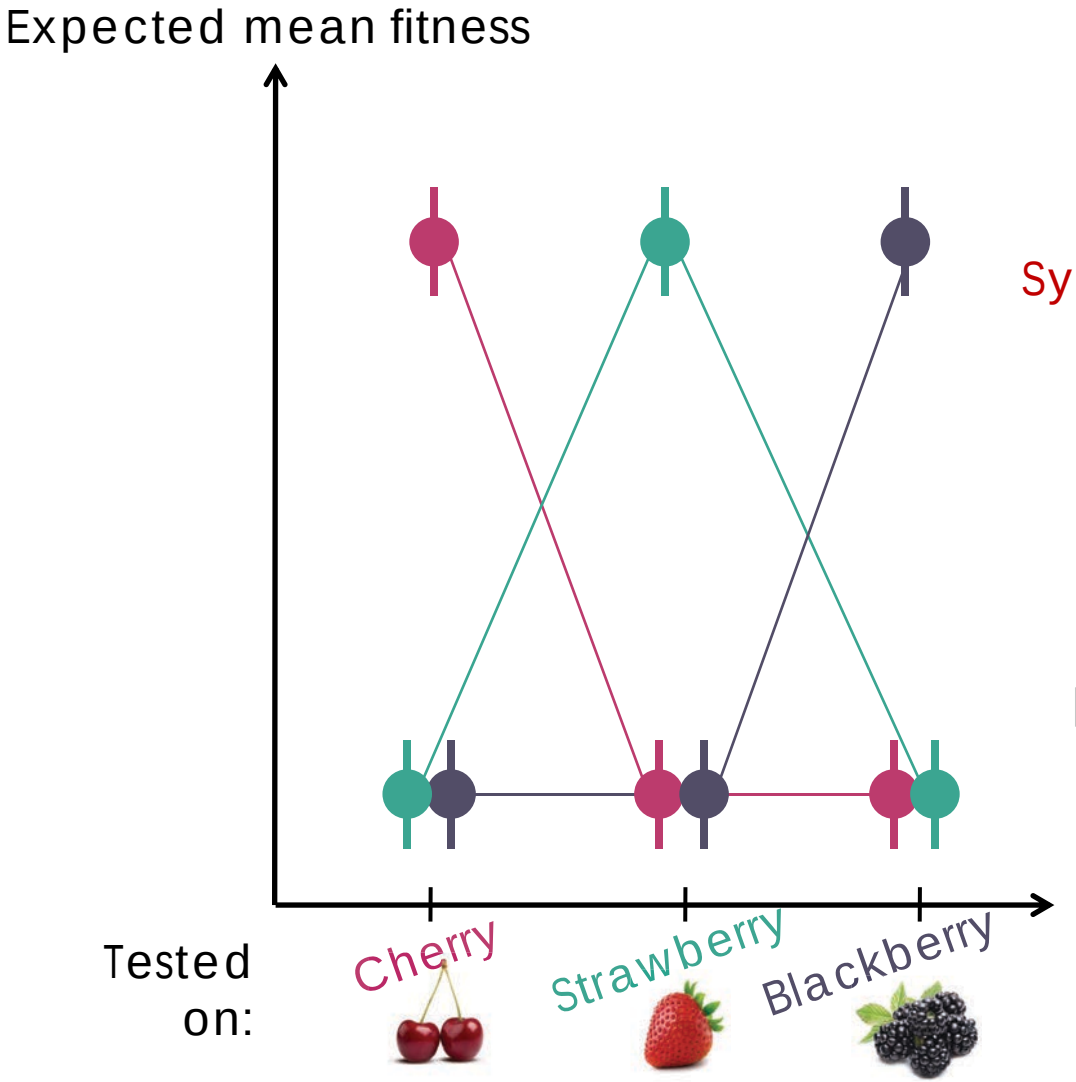
Expectations: Local adaptation



Expectations: Local adaptation



Expectations: Local adaptation

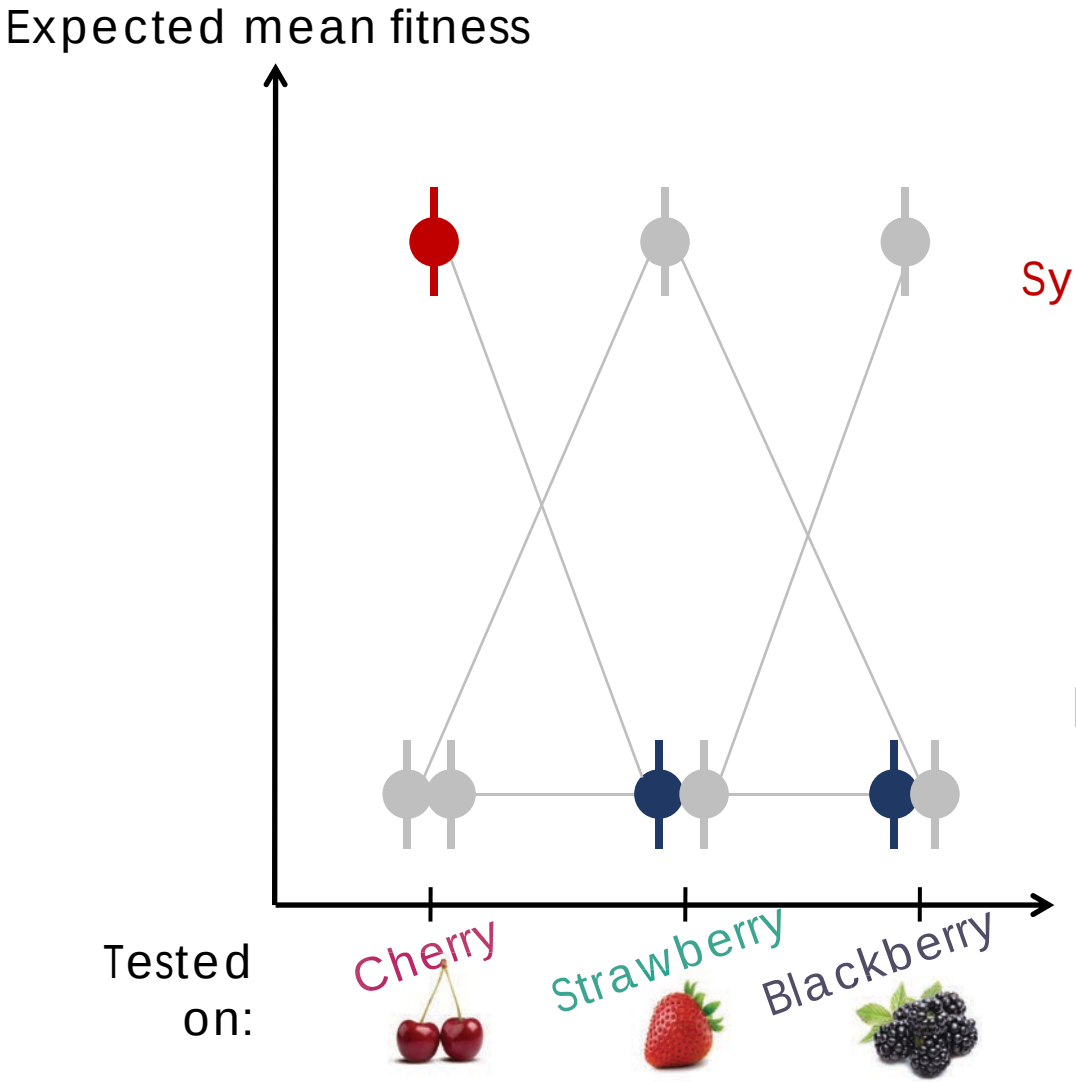


Statistical test:

Sympatric *vs.* Allopatric

[Blanquart et al., 2013]

Expectations: Local adaptation

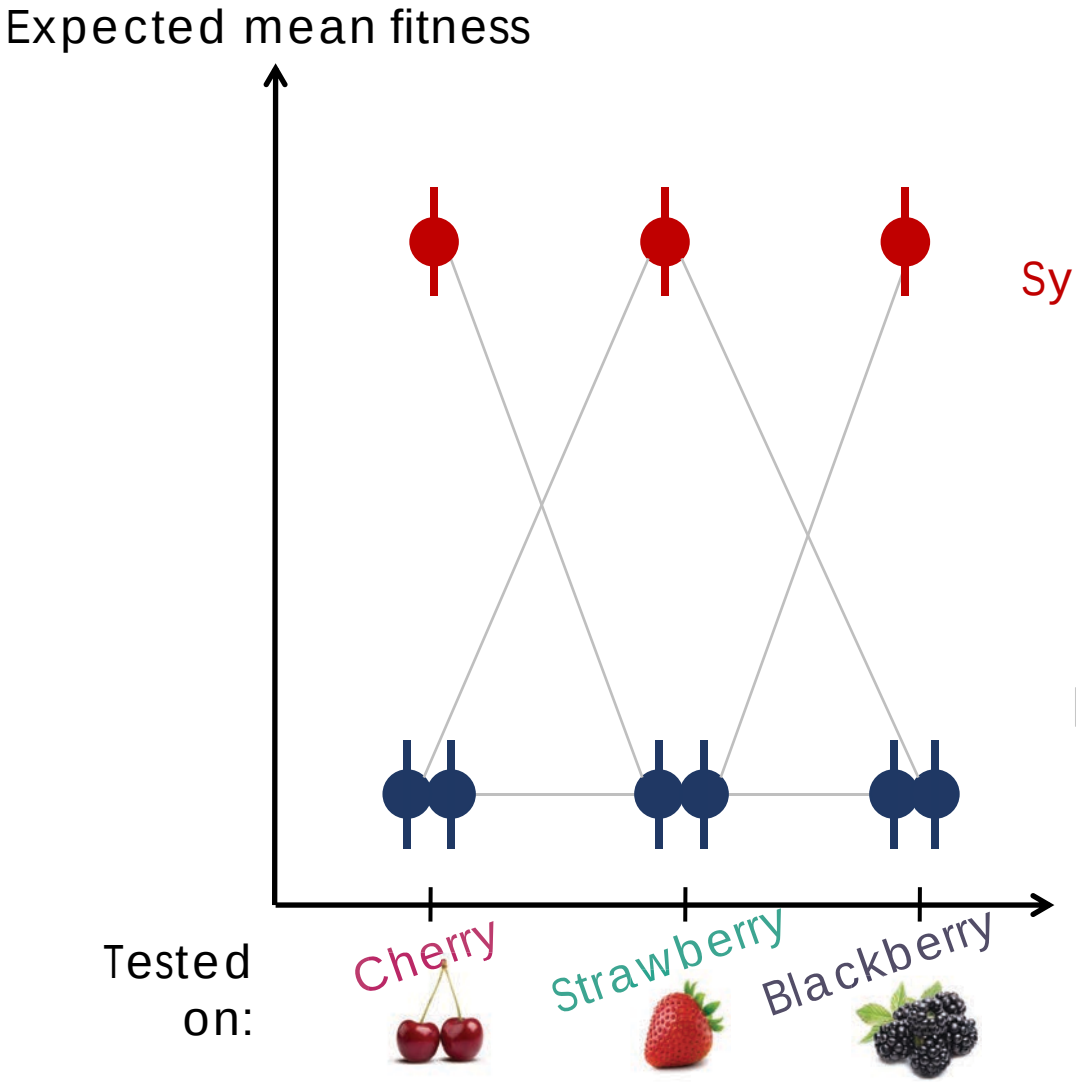


Statistical test:

Sympatric *vs.* Allopatric

[Blanquart et al., 2013]

Expectations: Local adaptation

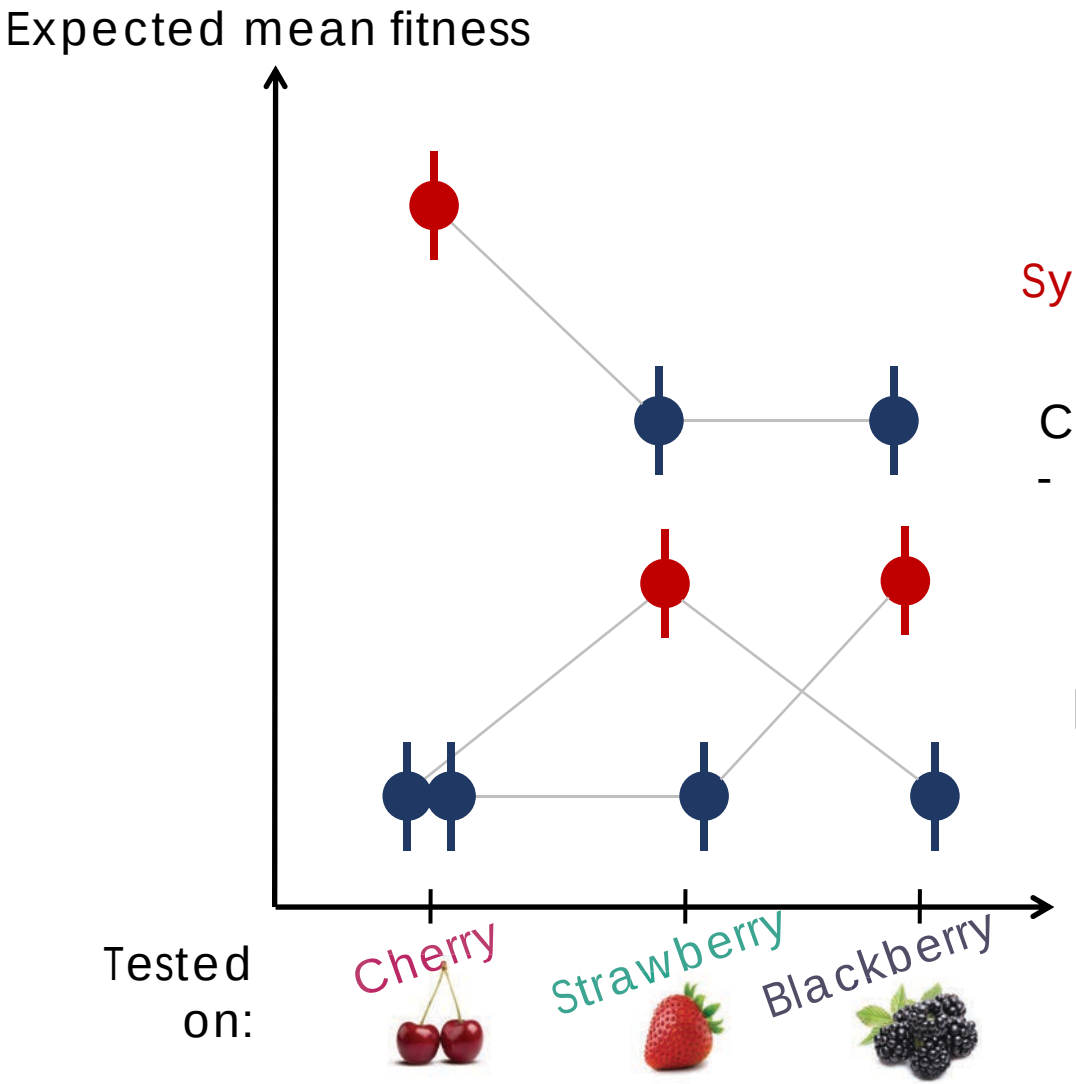


Statistical test:

Sympatric *vs.* Allopatric

[Blanquart et al., 2013]

Expectations: Local adaptation



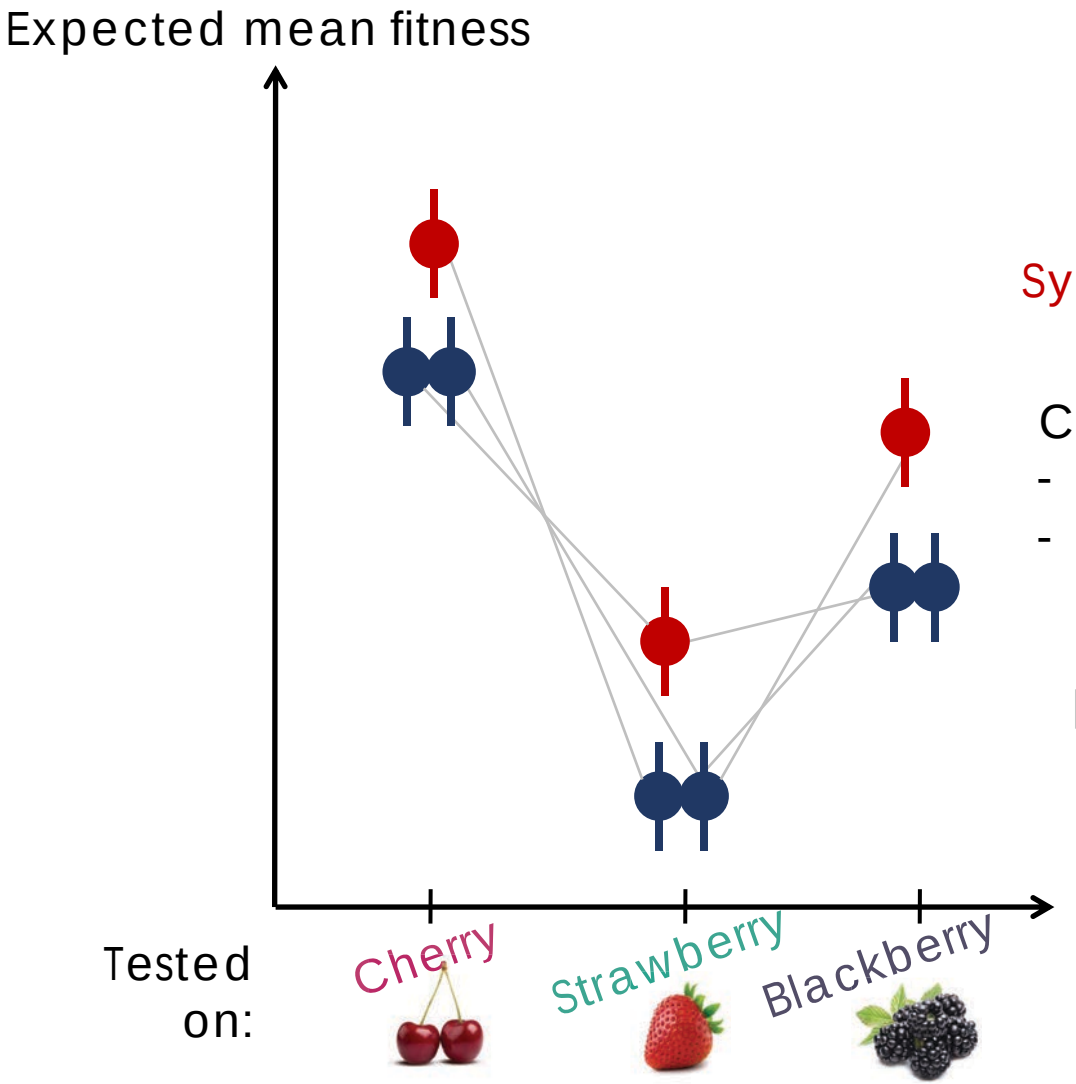
Statistical test:

Sympatric *vs.* Allopatric

Control:
- Population effect

[Blanquart et al., 2013]

Expectations: Local adaptation



Statistical test:

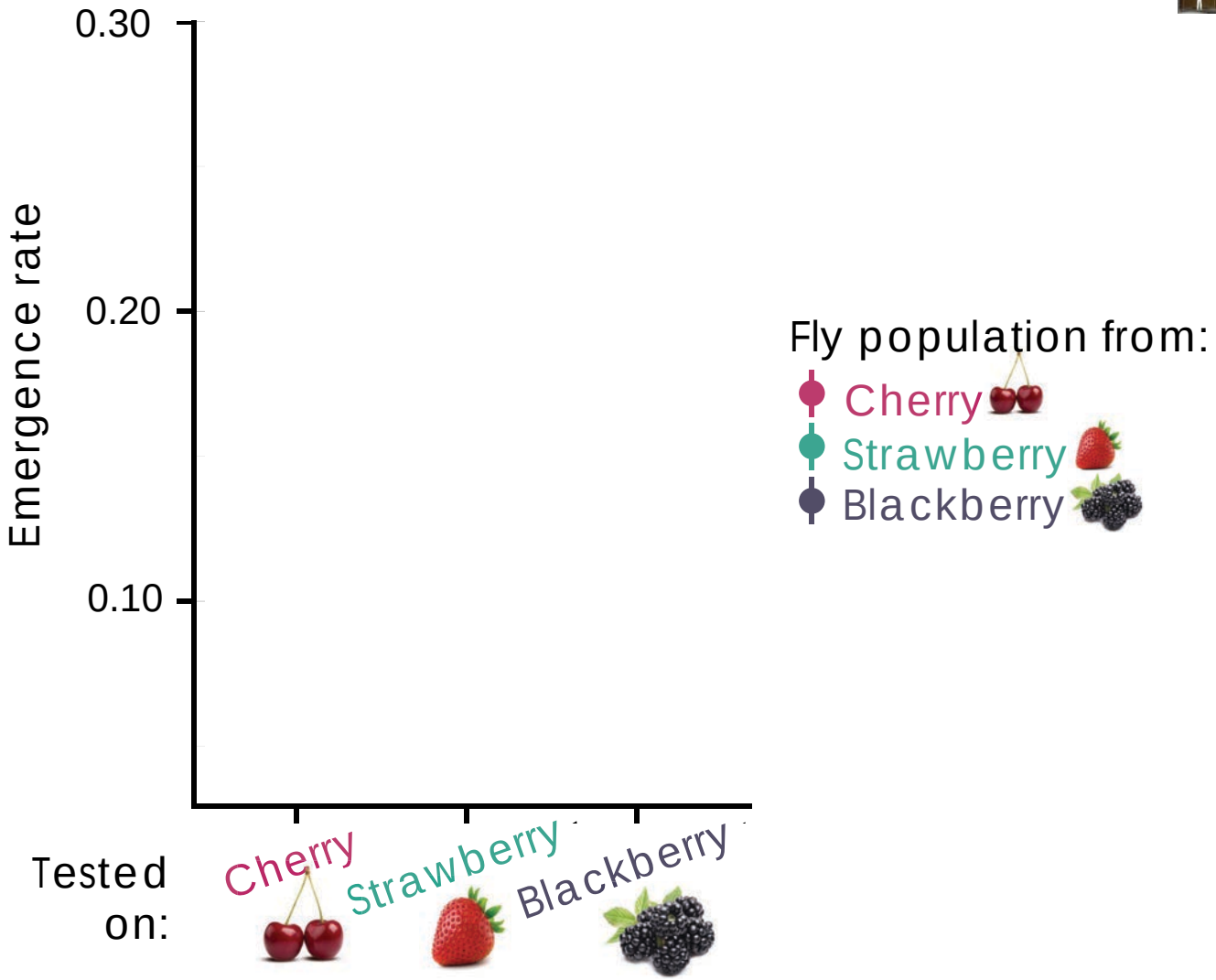
Sympatric *vs.* Allopatric

Control:
- Population effect
- Quality environment

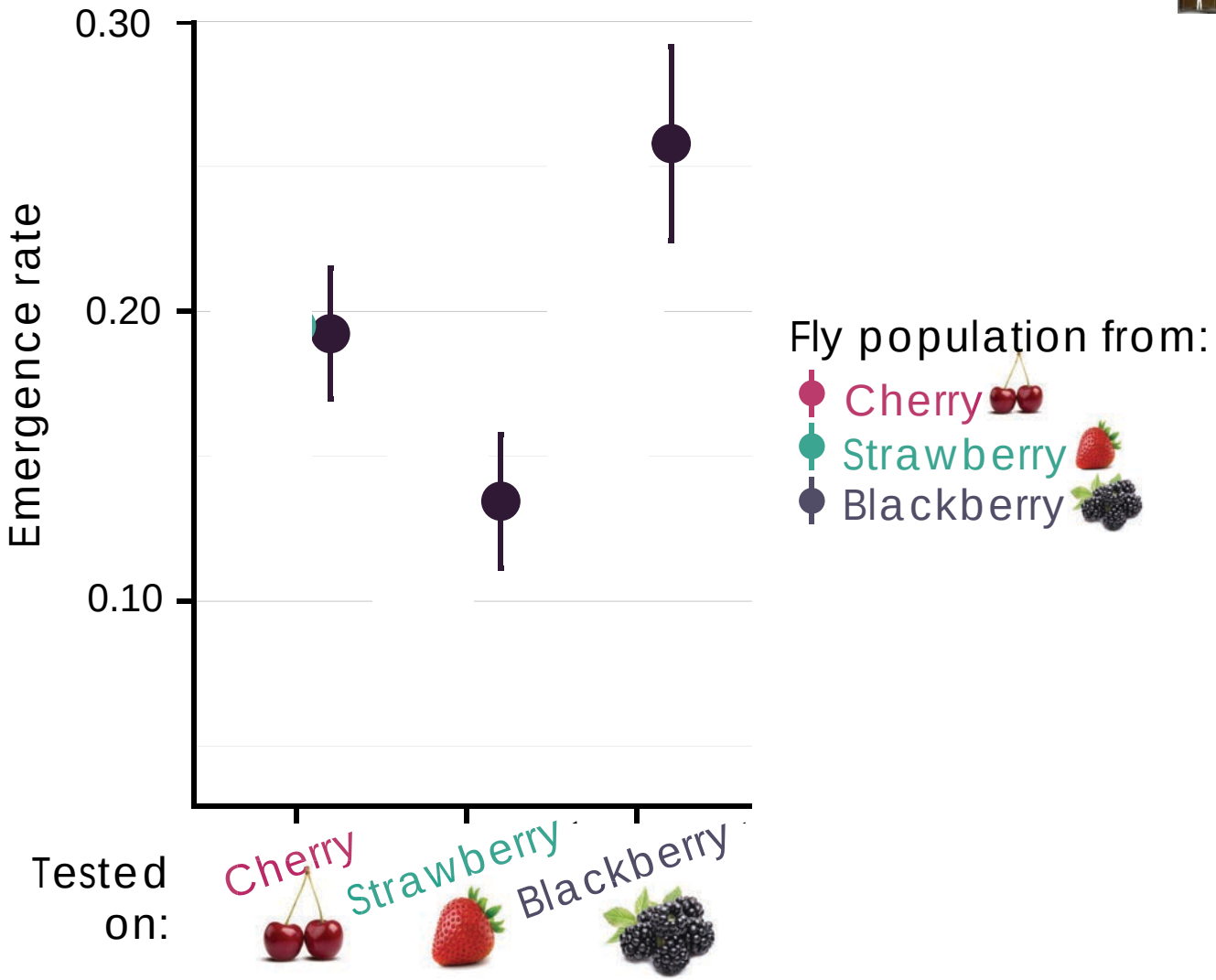
[Blanquart et al., 2013]

Emergence rate (G3)

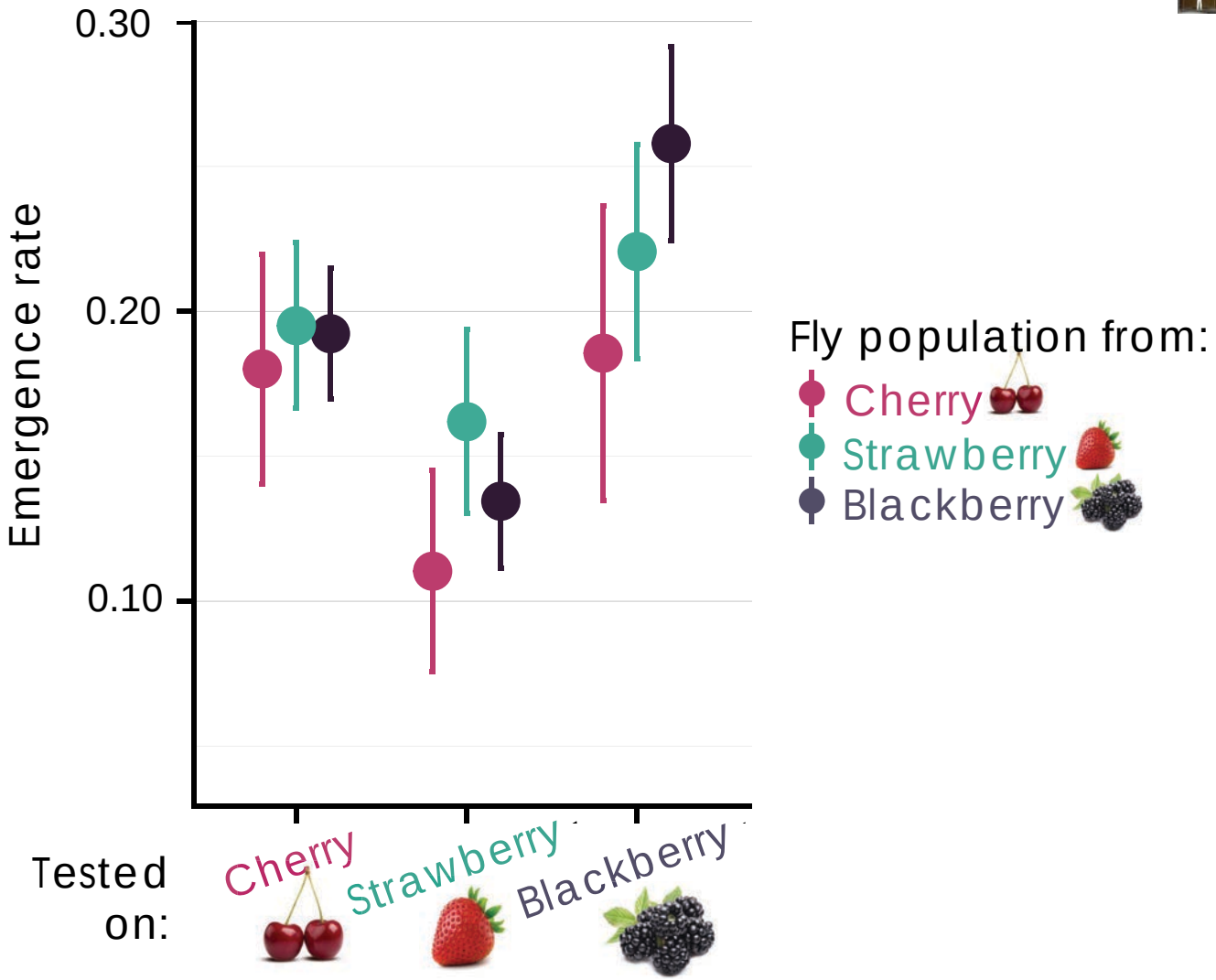
Emergence rate (G3)



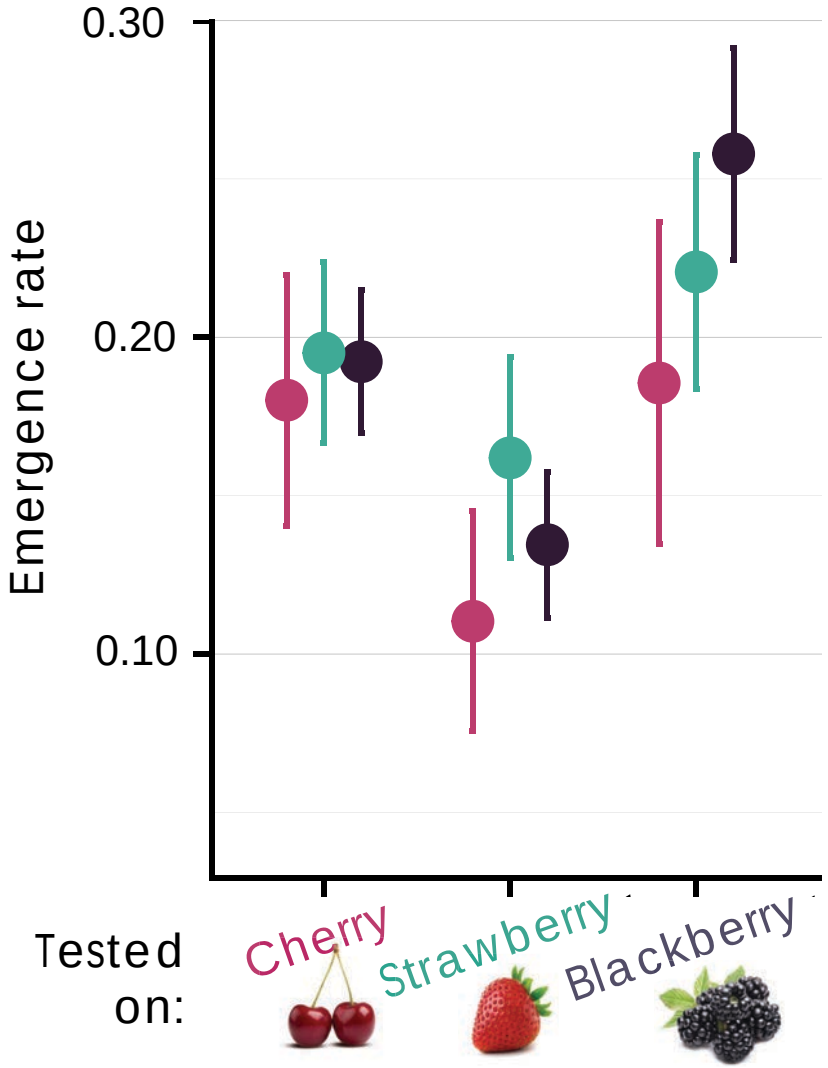
Emergence rate (G3)



Emergence rate (G3)



Emergence rate (G3)



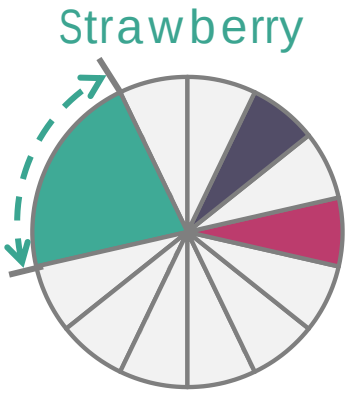
Fly population from:

- Cherry
- Strawberry
- Blackberry

Local adaptation
P = 0.005

Expectations: Local preference

Fly populations from:

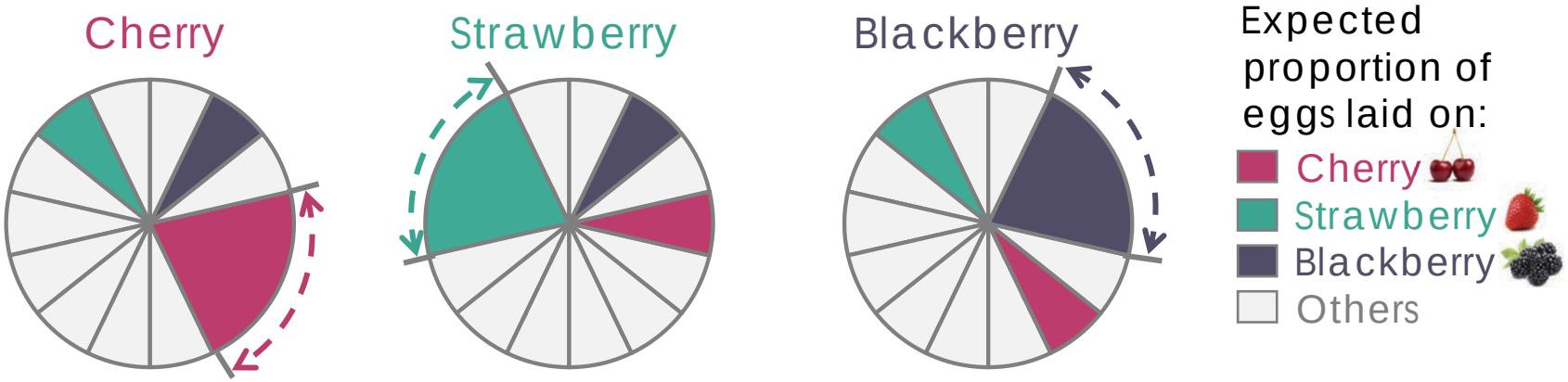


Expected proportion of eggs laid on:

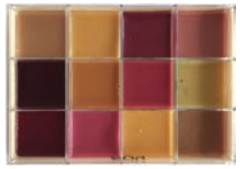
- Cherry
- Strawberry
- Blackberry
- Others

Expectations: Local preference

Fly populations from:



Oviposition preference (G3)



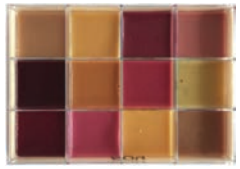
Fly populations from:

Cherry Strawberry Blackberry

Proportion of eggs laid on:

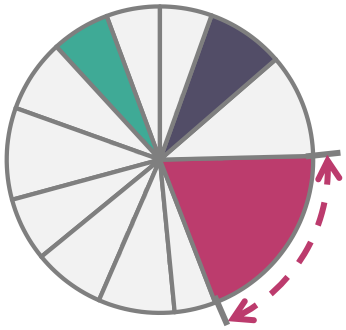
- Cherry
- Strawberry
- Blackberry
- Others

Oviposition preference (G3)

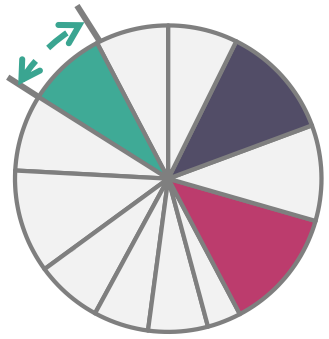


Fly populations from:

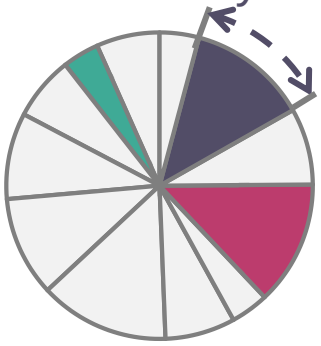
Cherry



Strawberry



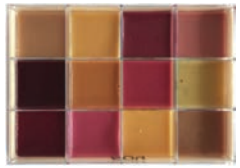
Blackberry



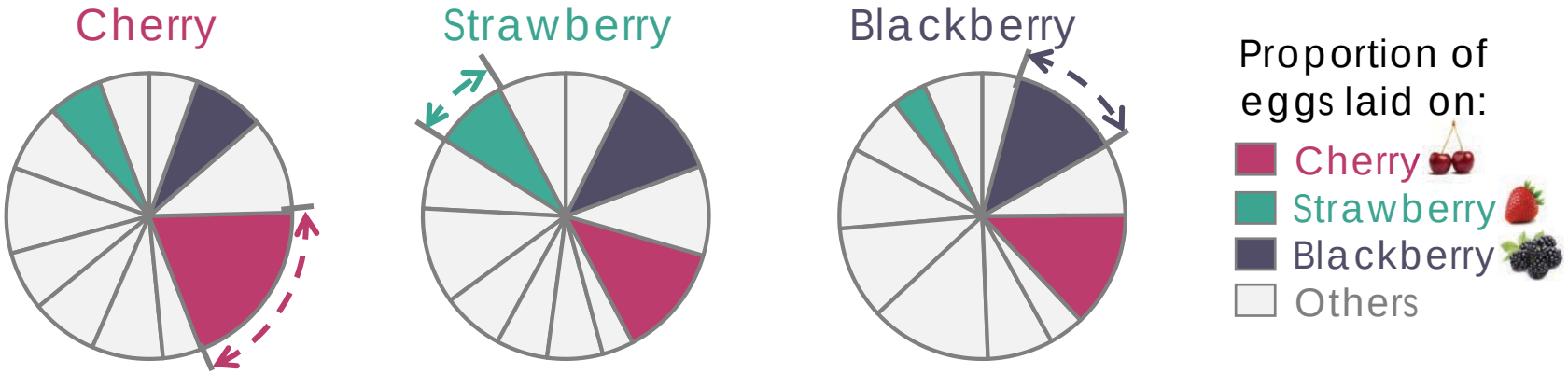
Proportion of eggs laid on:

- Cherry
- Strawberry
- Blackberry
- Others

Oviposition preference (G3)

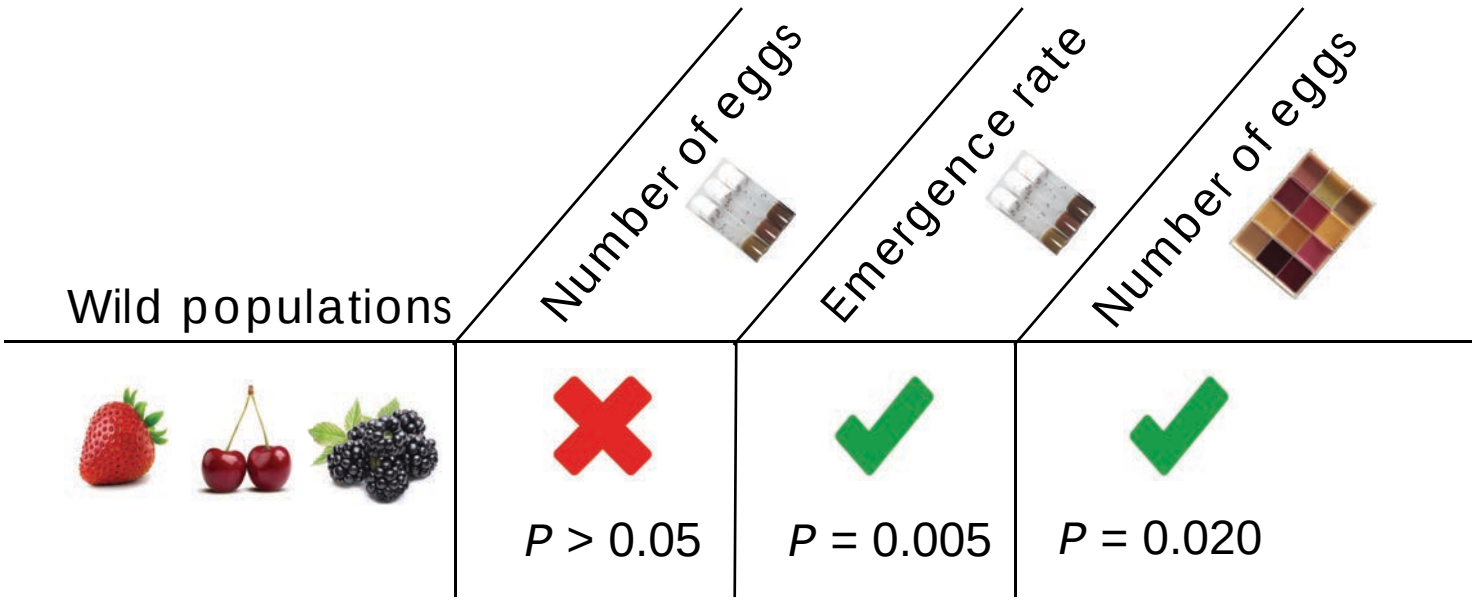


Fly populations from:



Local preference
$P = 0.020$

What kind of generalist?



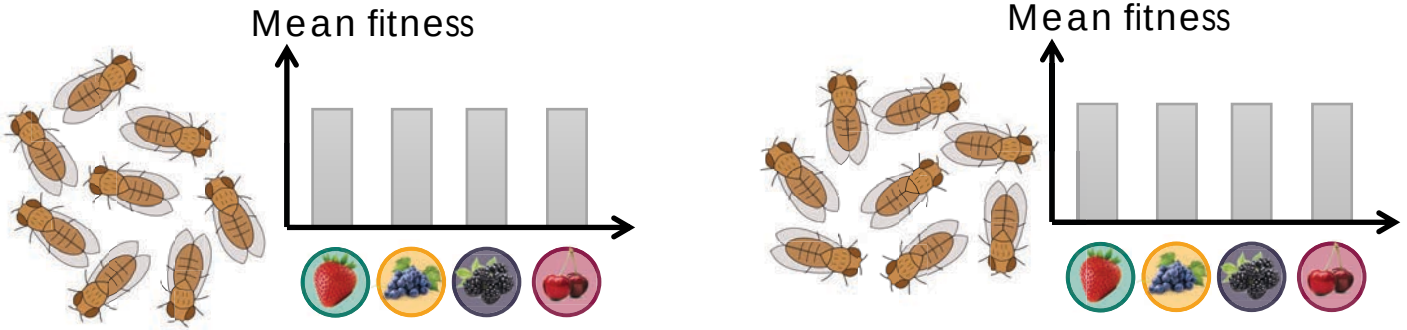
What kind of generalist?

What kind of generalist?

Summer

Fall

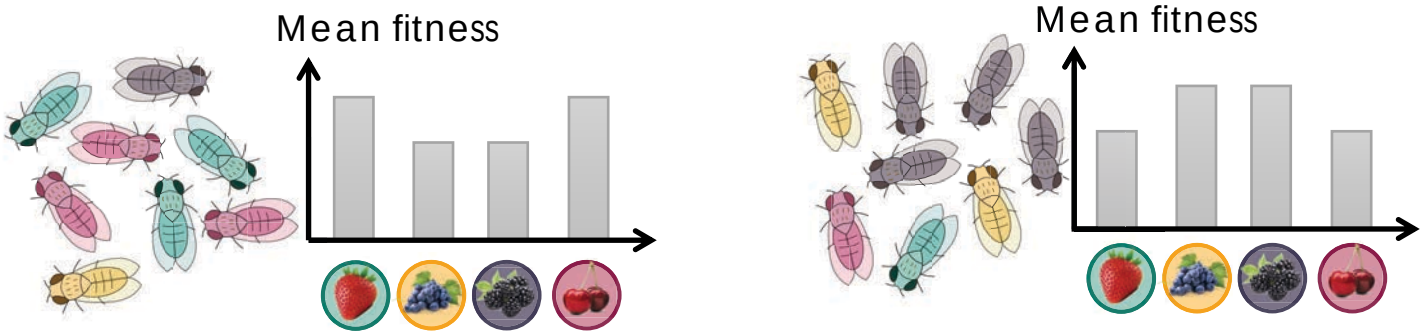
Without polymorphism



Generalist genotypes

OR

With polymorphism



?

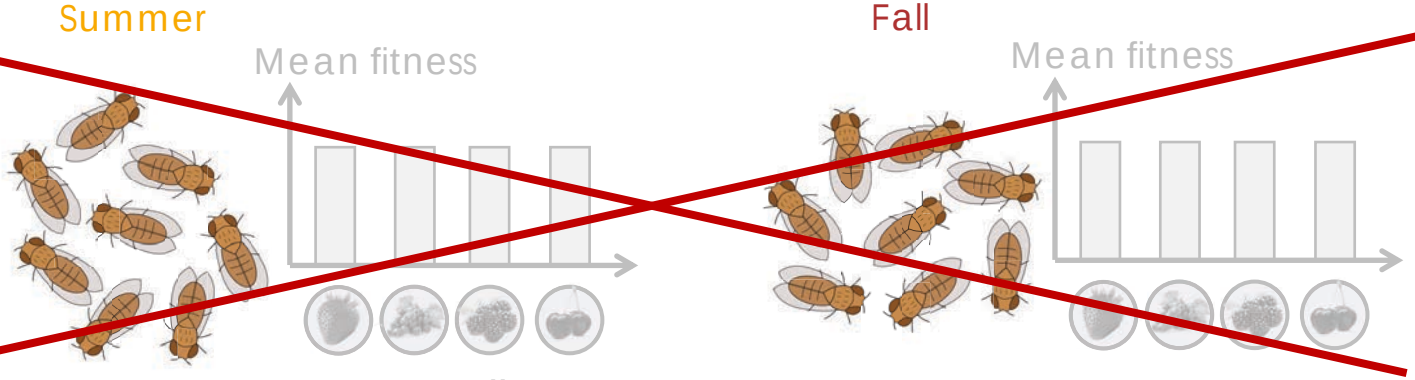
Pool of specialist genotypes

What kind of generalist?

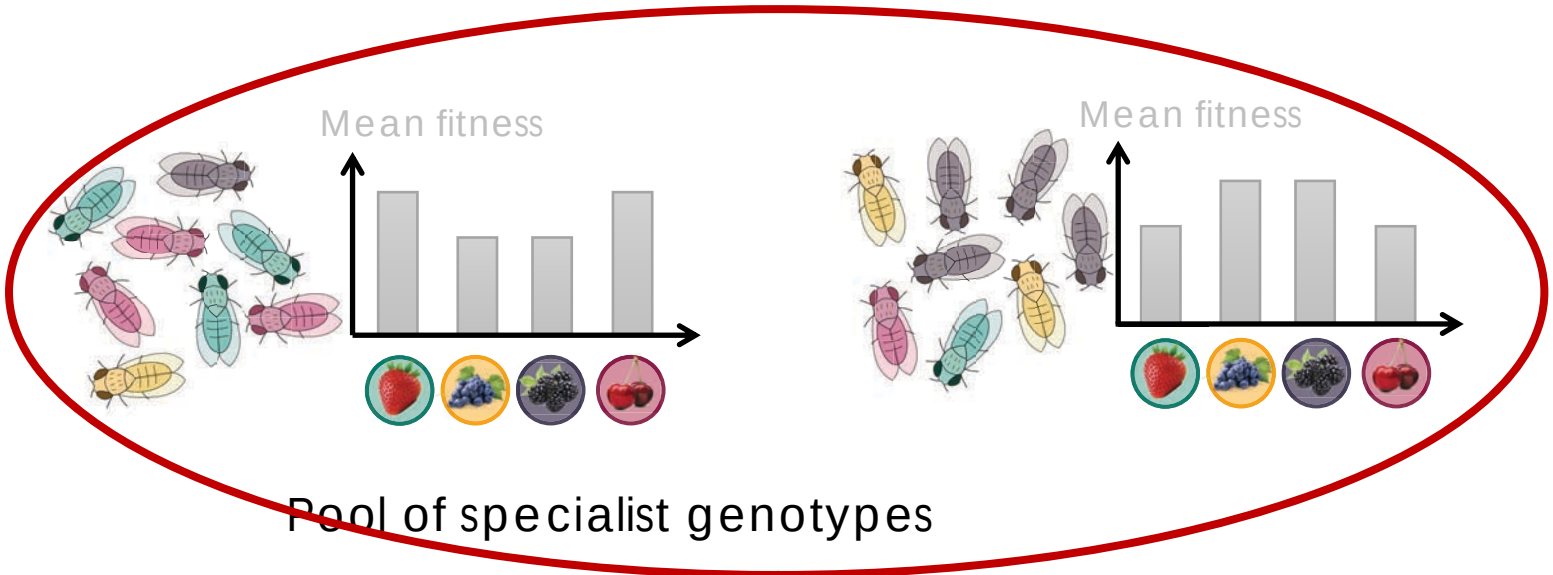
Summer

Fall

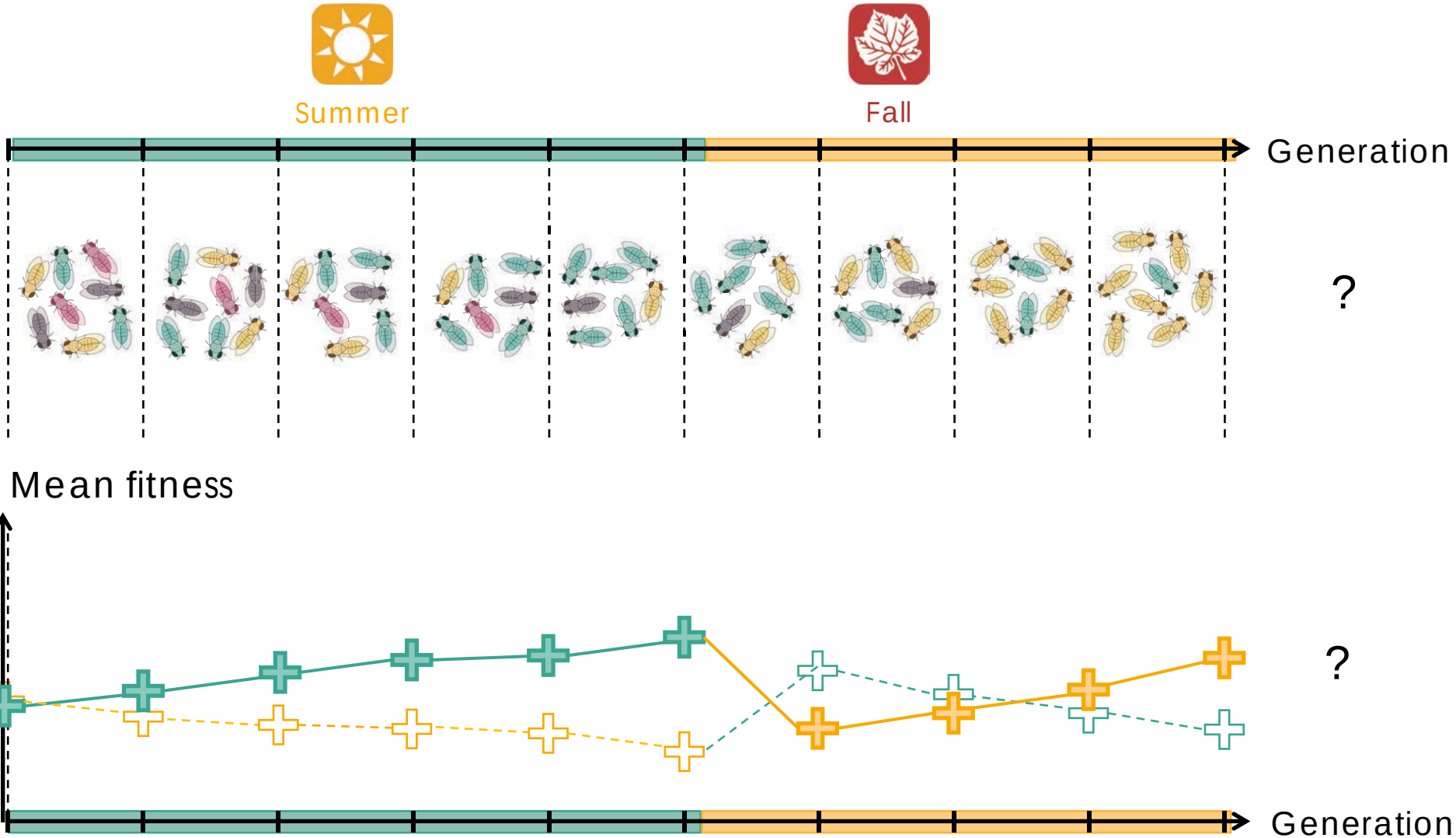
Without polymorphism



With polymorphism



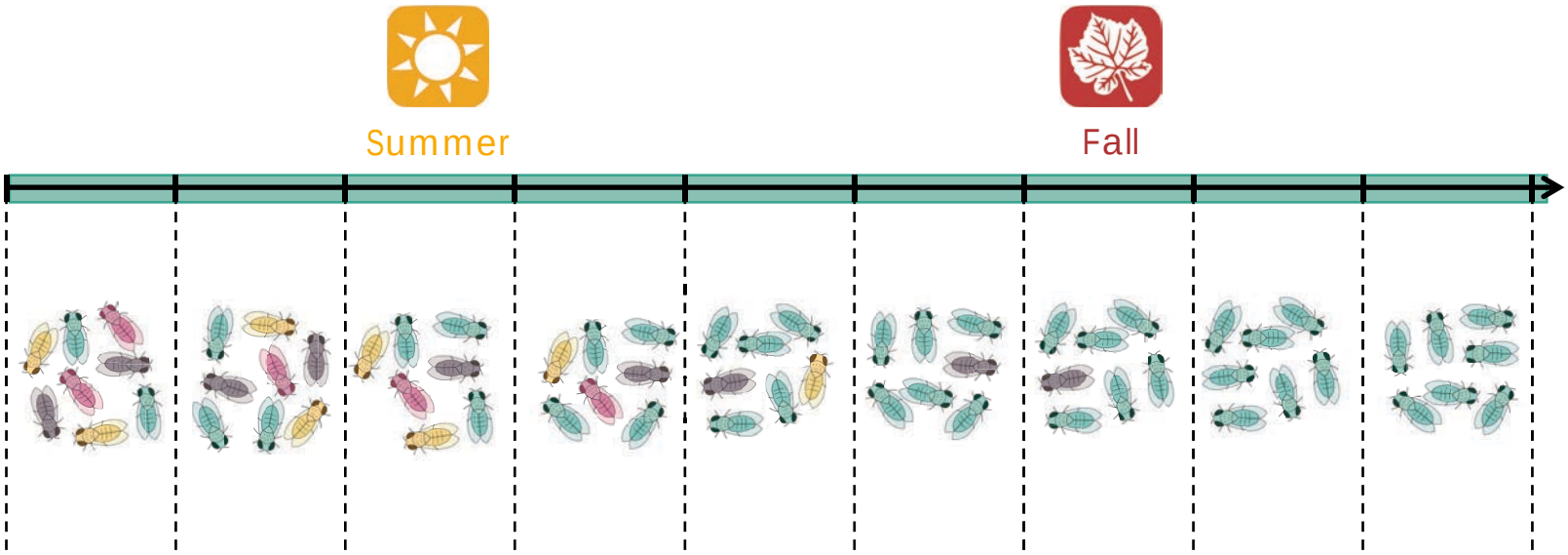
Transitional adaptation phase?

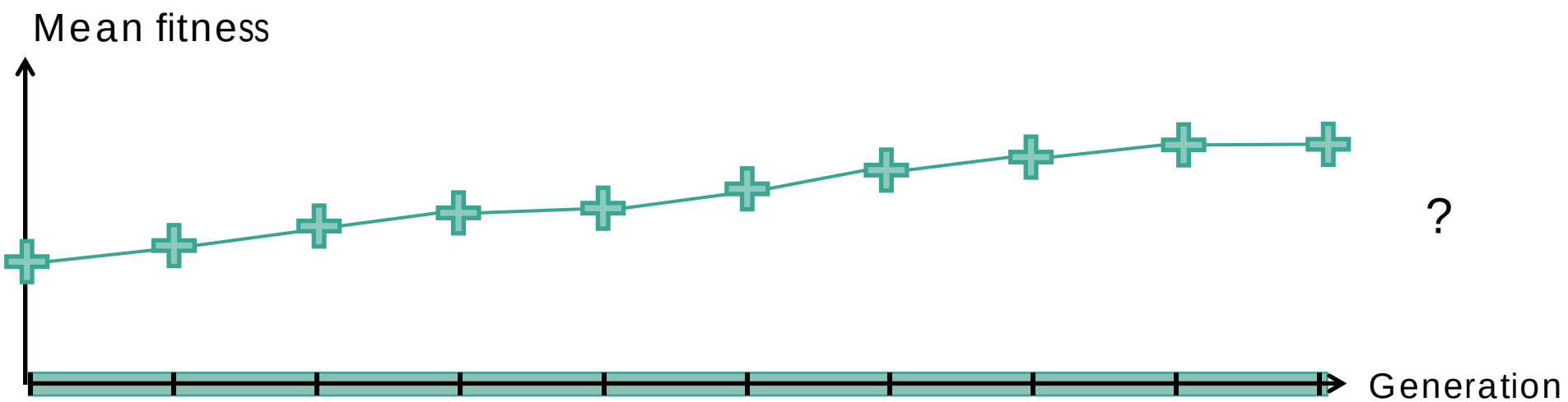


Consequences of homogeneous environment?

Watsonville strawberry fields, USA, 2012

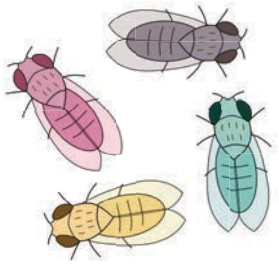
Consequences of homogeneous environment?





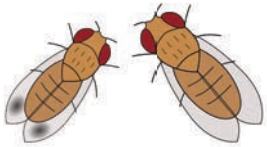
Conclusion: generalist with polymorphism

- Phenotypic variability in fruit exploitation



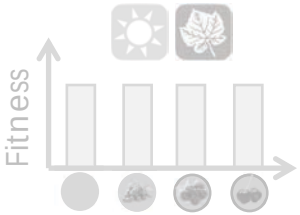
- Maintenance of genetic diversity throughout the year

- Does specialization evolve in homogeneous environments?

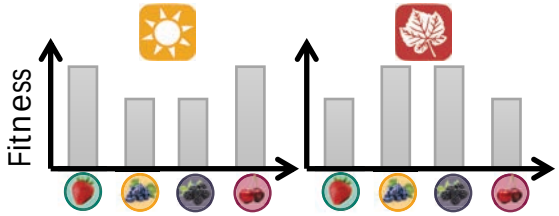


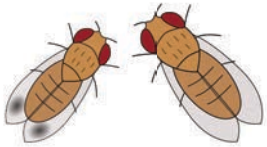
Adaptive responses of *Drosophila suzukii*

Generalist with polymorphism:



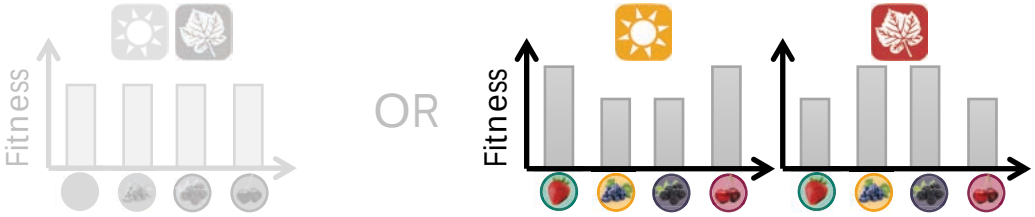
OR



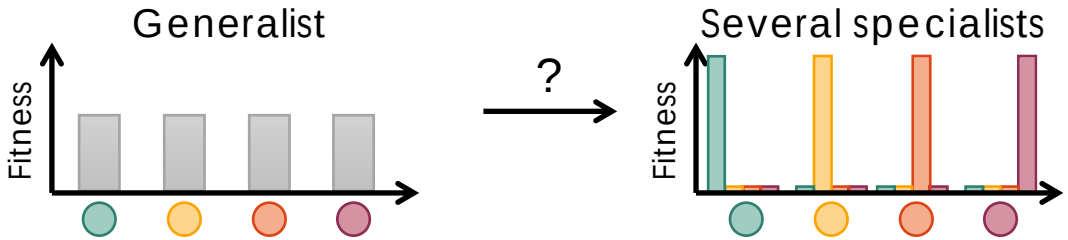


Adaptive responses of *Drosophila suzukii*

Generalist with polymorphism:



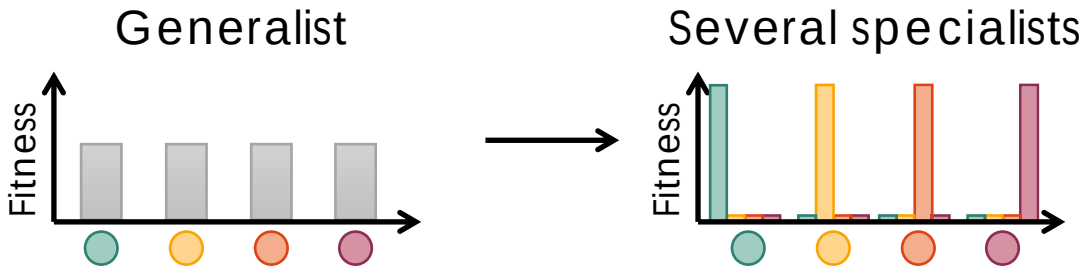
Can we select for specialization?



Specialization in homogeneous environments in the laboratory

Evolution of specialization?

Goal:
Specialization can evolve when conditions are optimal



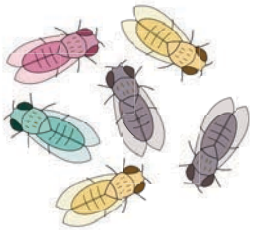
Expectation:
Local adaptation can be detected after five generations

Approach:
Evolution on homogeneous environments

Approach:

Sampling: population with polymorphism

End of fall



1000 ind

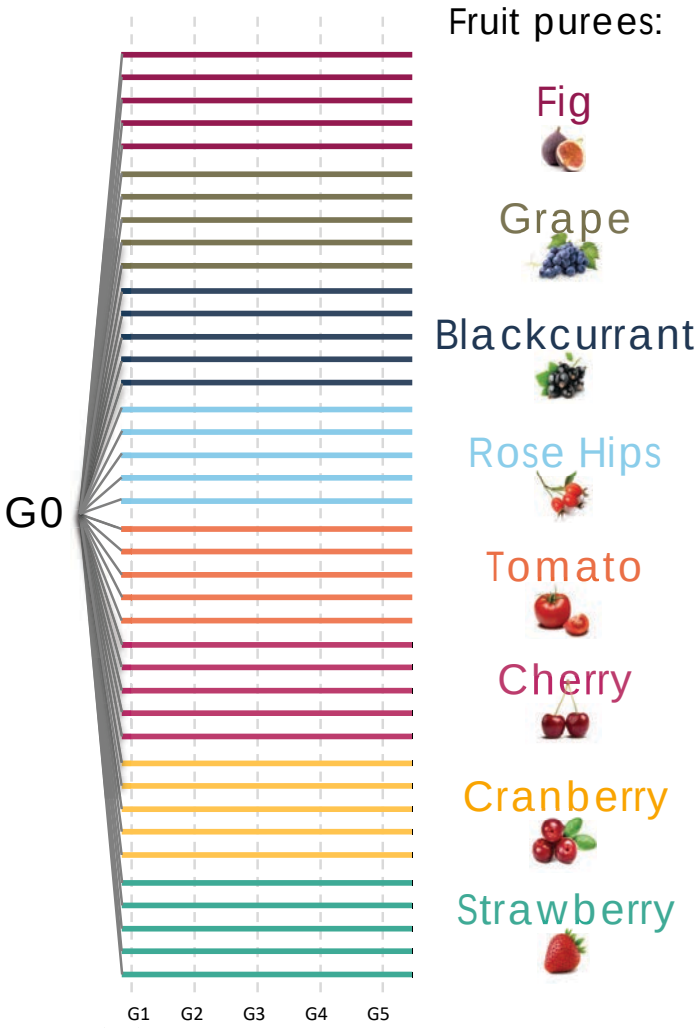
Adaptation to lab conditions with standard medium

2000 ind

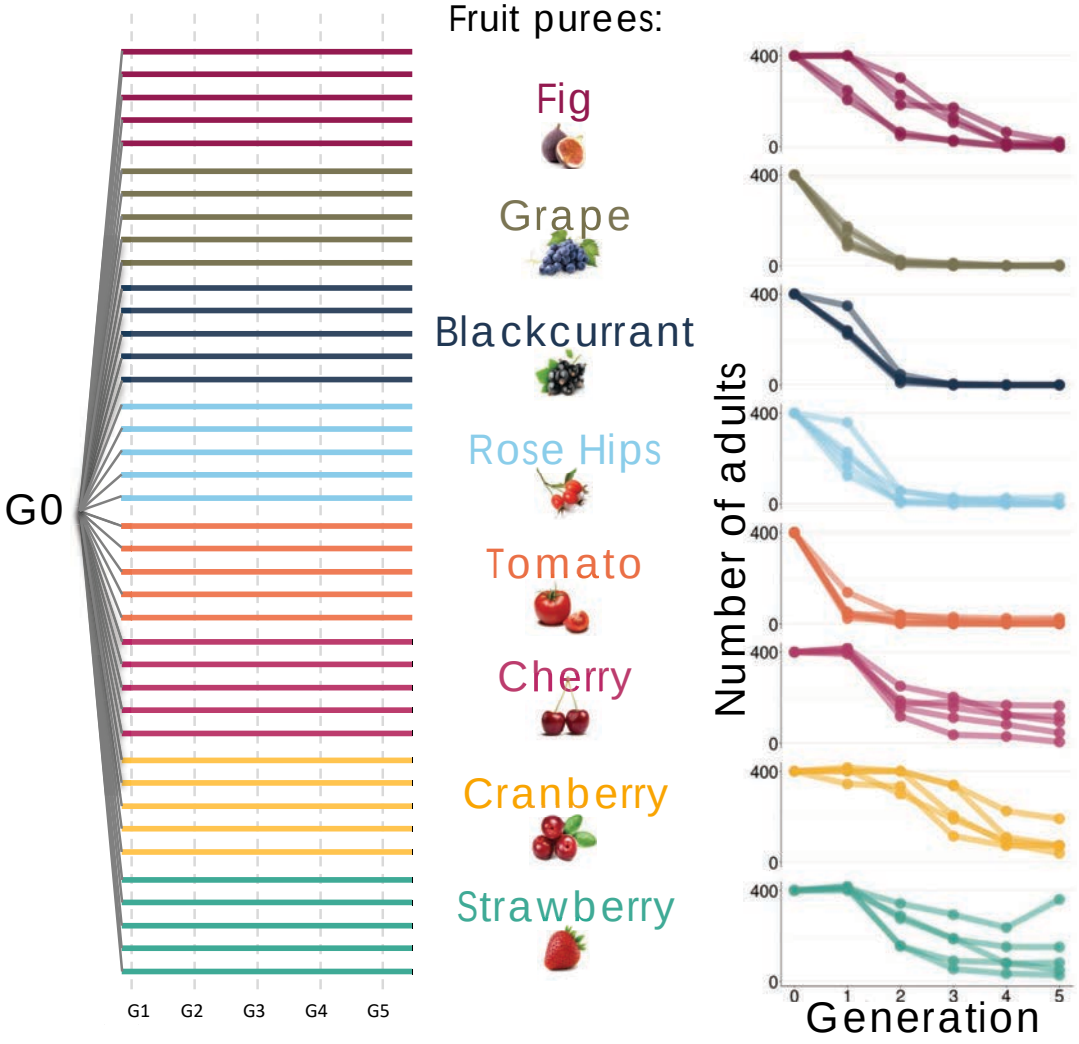
Experimental evolution: evolution on homogeneous environments

Strawberry Cranberry Cherry Tomato Rose Hips Blackcurrant Grape Fig

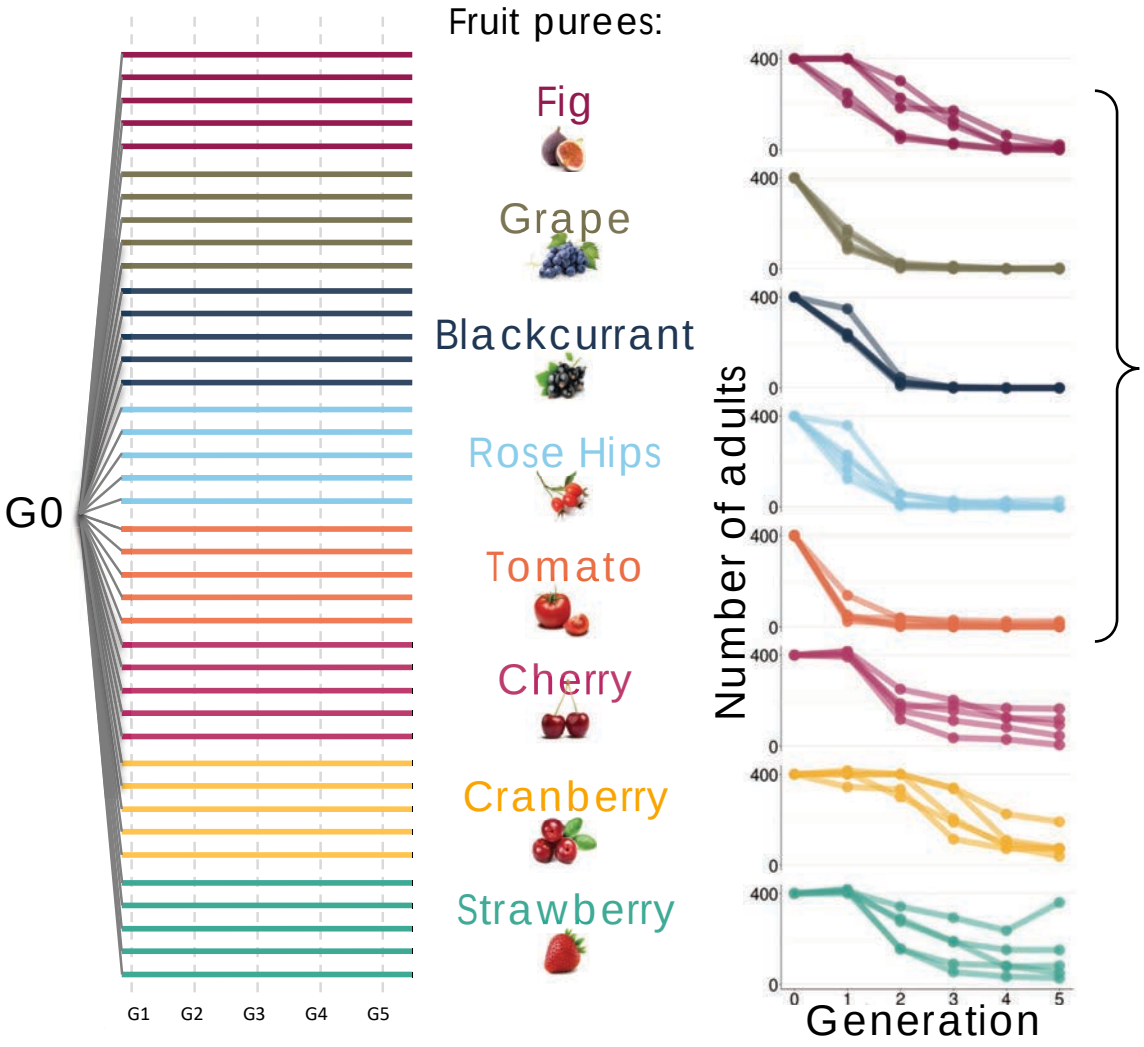
Experimental evolution



Experimental evolution



Experimental evolution

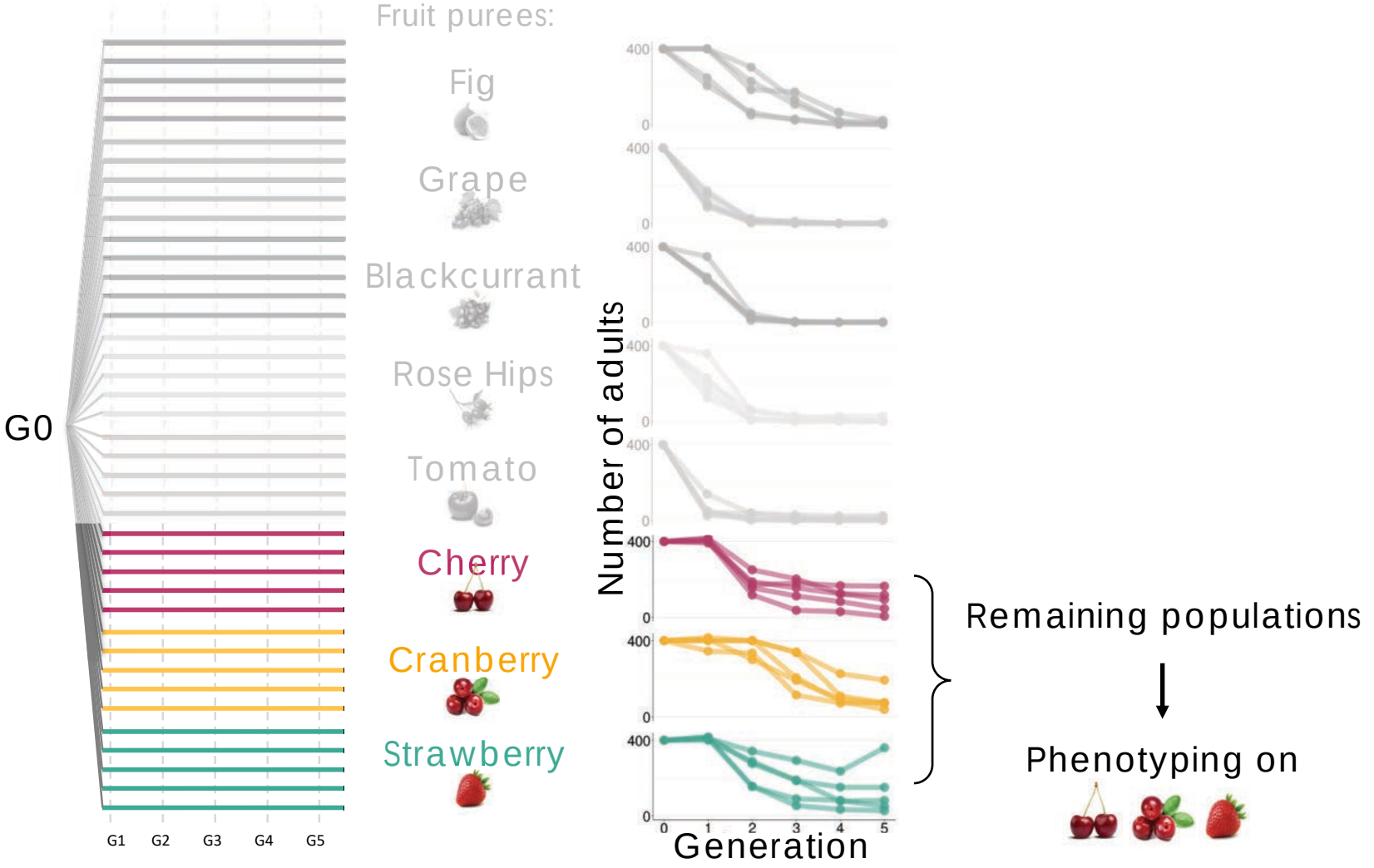


Experimental populations crashed

↓

Multigeneration development not possible

Experimental evolution



Phenotyping

Groups of
20 flies

Fitness

Fruits
purees:
Cherry
Cranberry
Strawberry

Number of adults

Oviposition preference

Apricot
Blackberry
Blackcurrant
Cherry
Cranberry
Fig

Grape
Kiwi
Raspberry
Rose Hips
Strawberry
Tomato

Number of eggs

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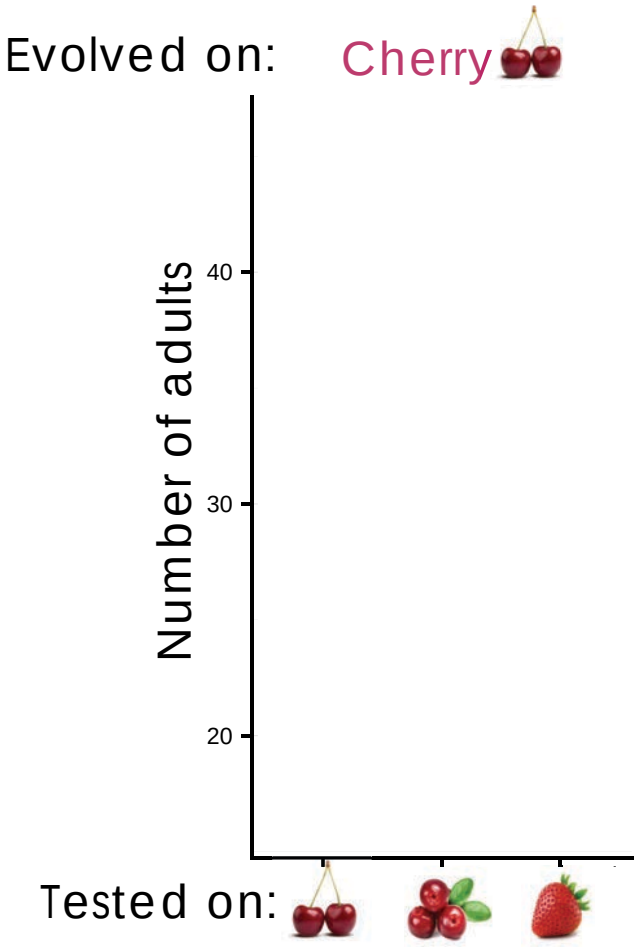
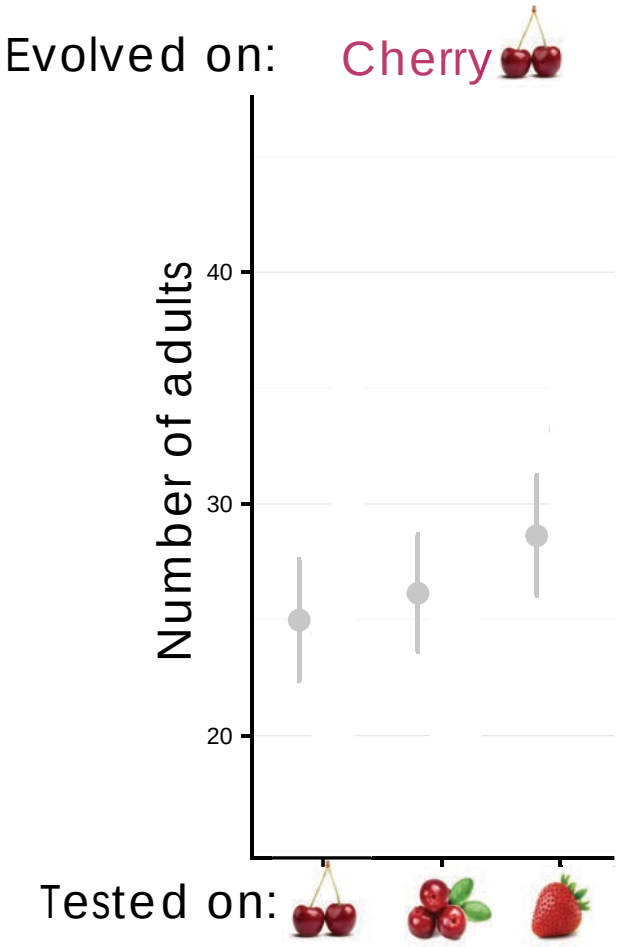
Number of eggs

Phenotyping: fitness



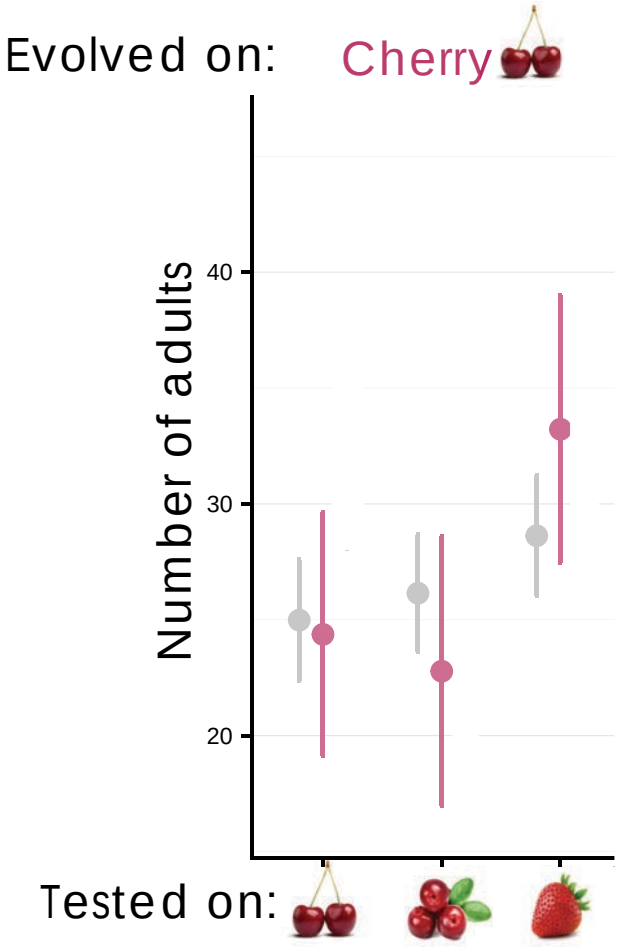
Phenotyping: fitness



Phenotyping

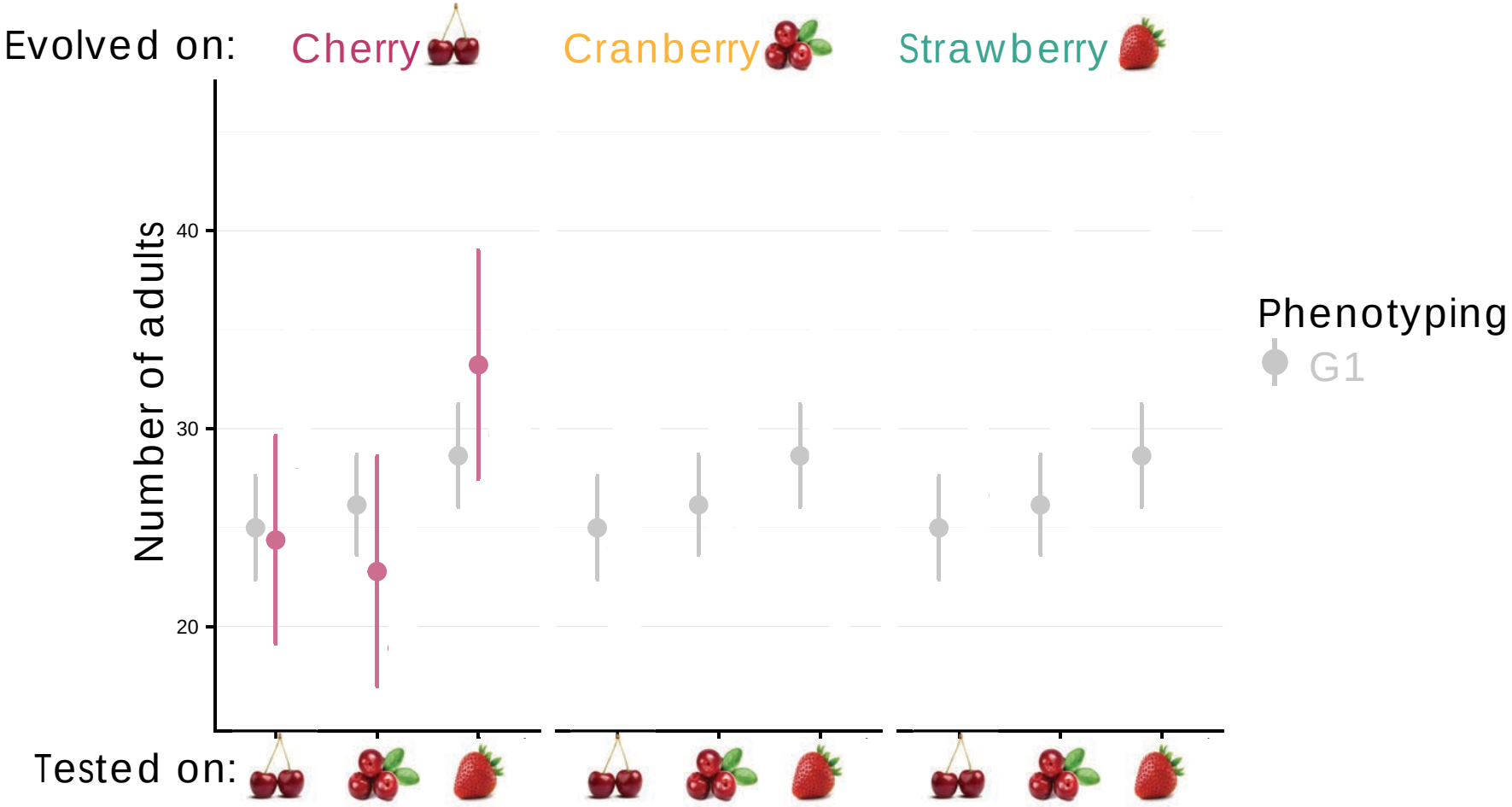
G1

Phenotyping: fitness

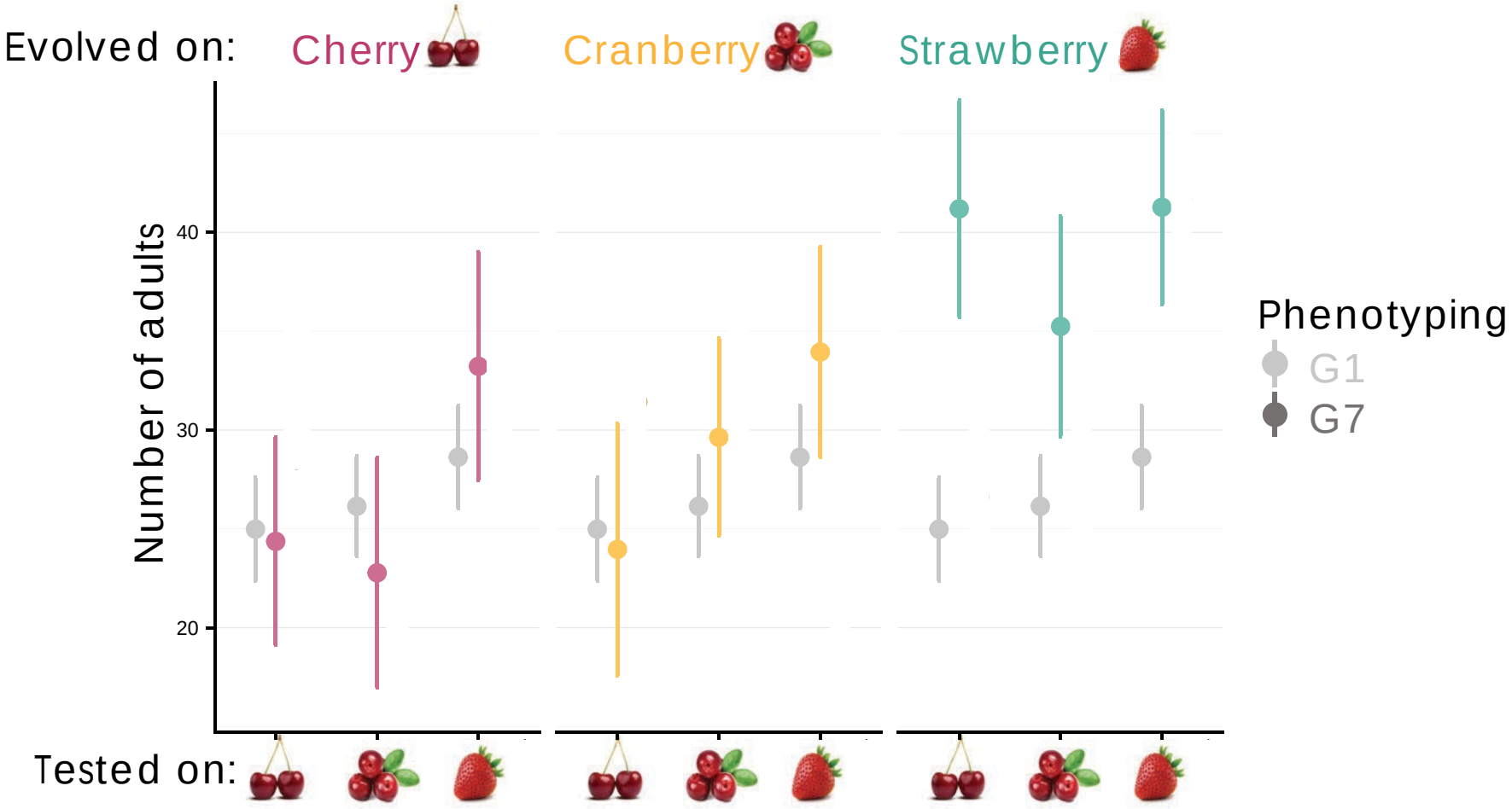


Phenotyping
G1
G7

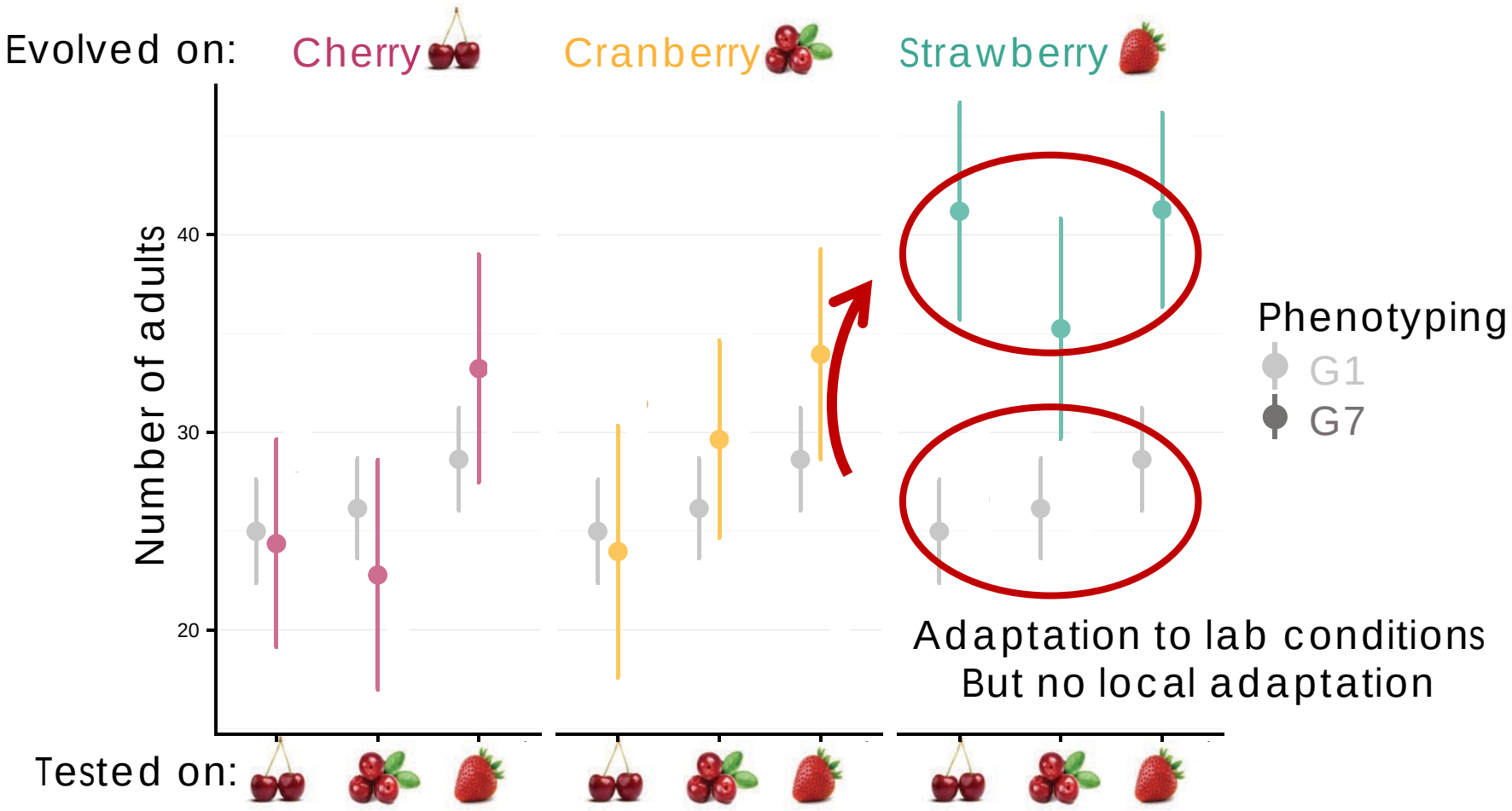
Phenotyping: fitness



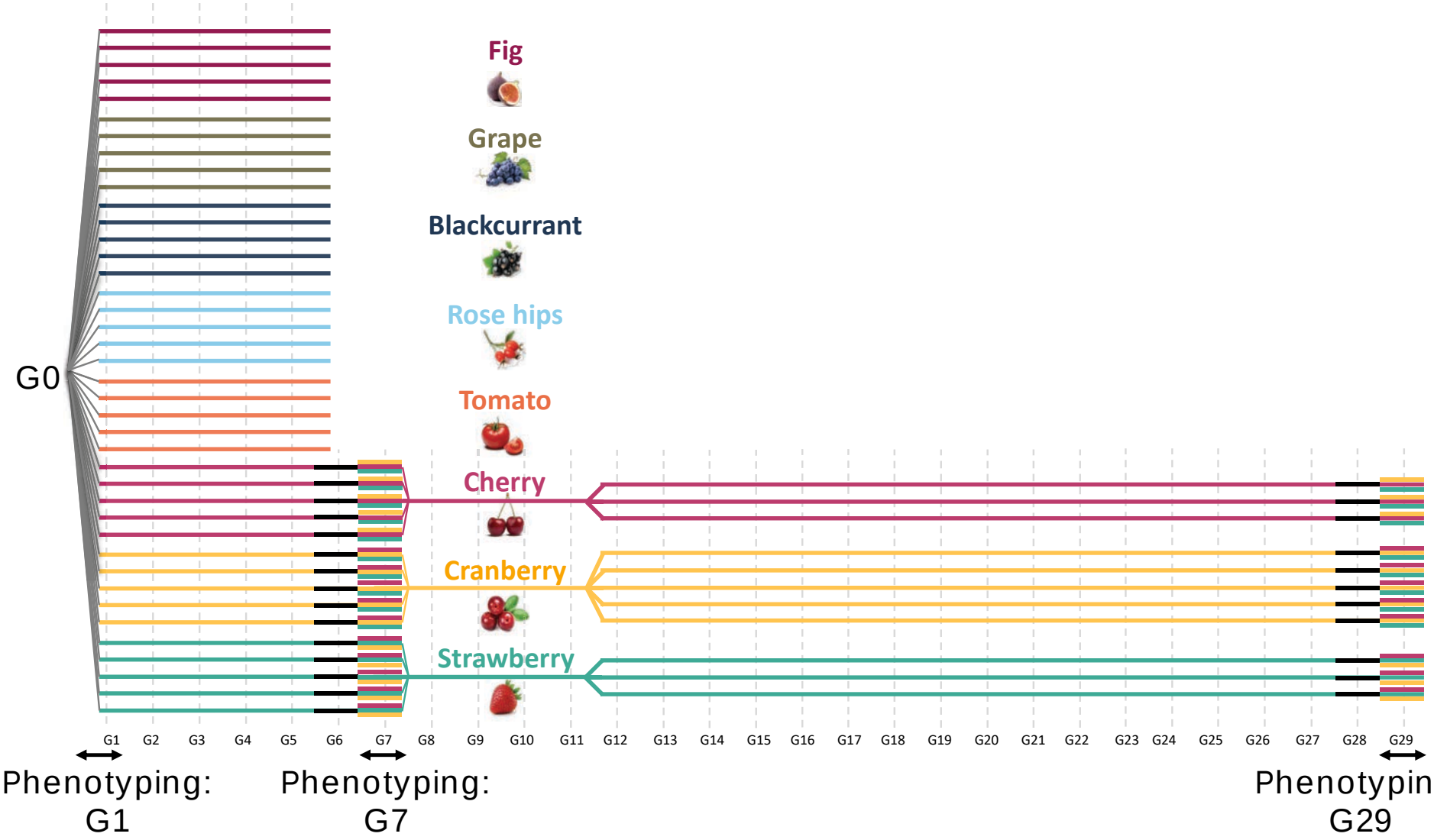
Phenotyping: fitness



Phenotyping: fitness

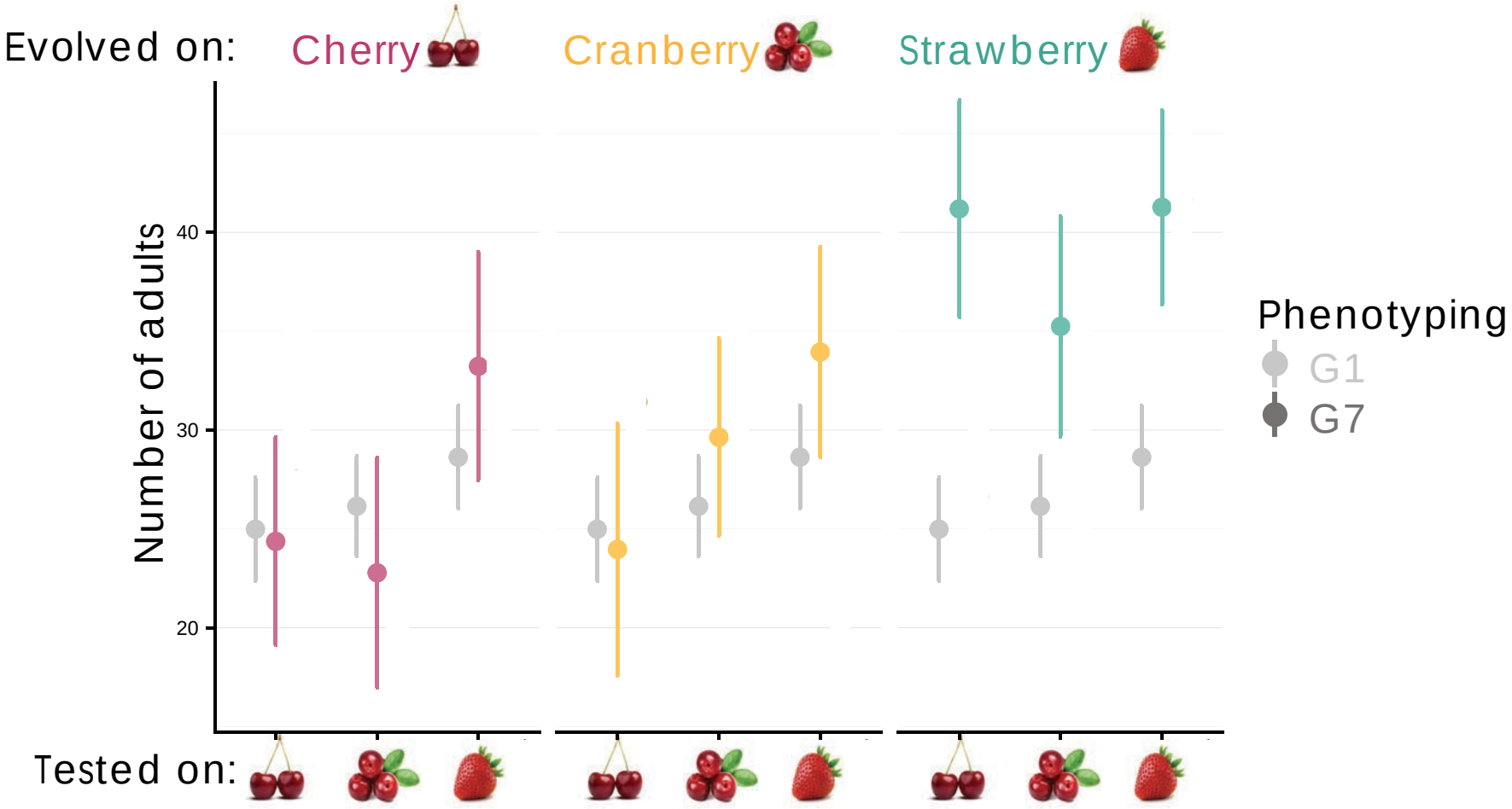


Experimental evolution

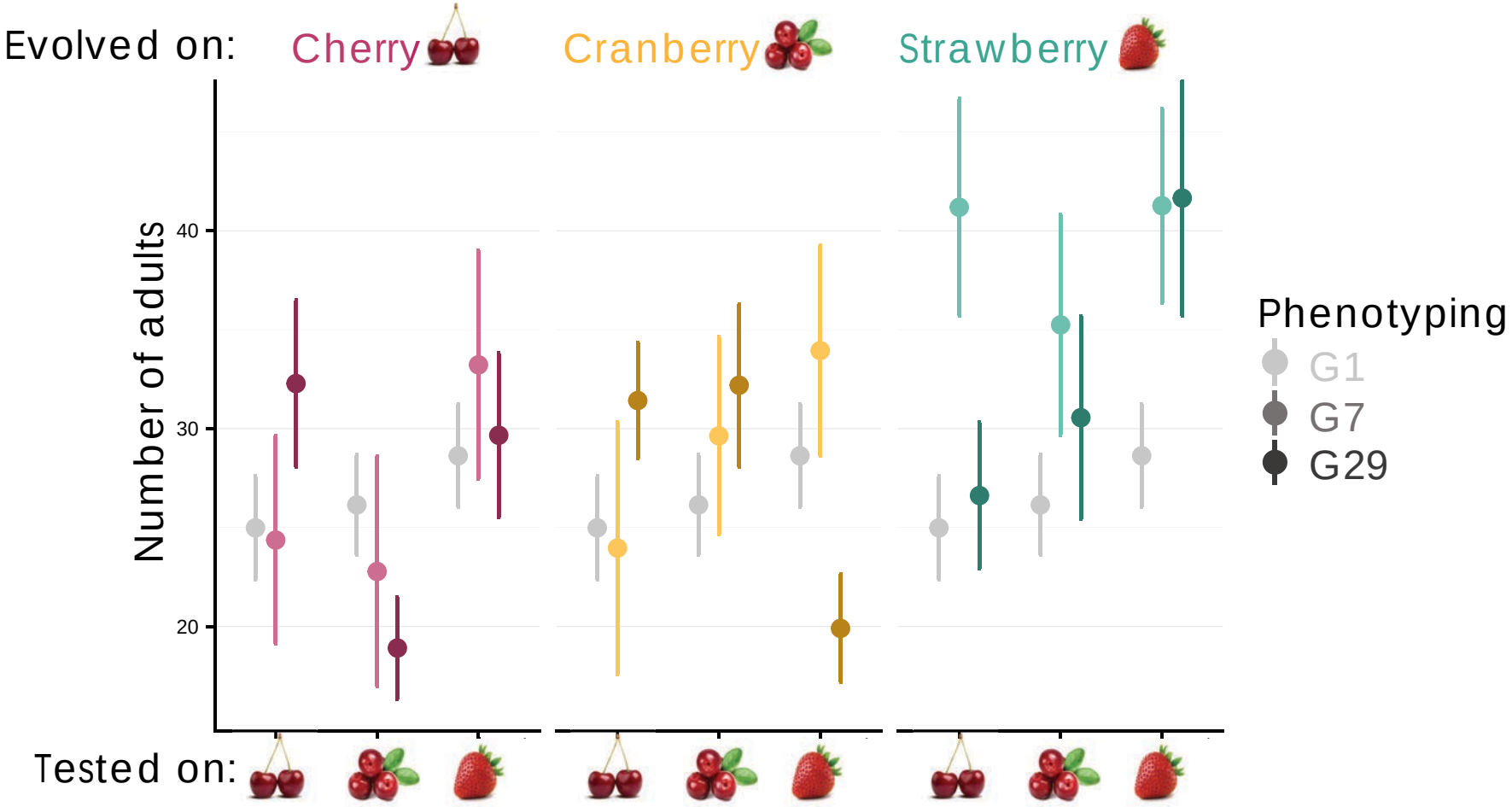


More than
200,000 flies
During 2 years

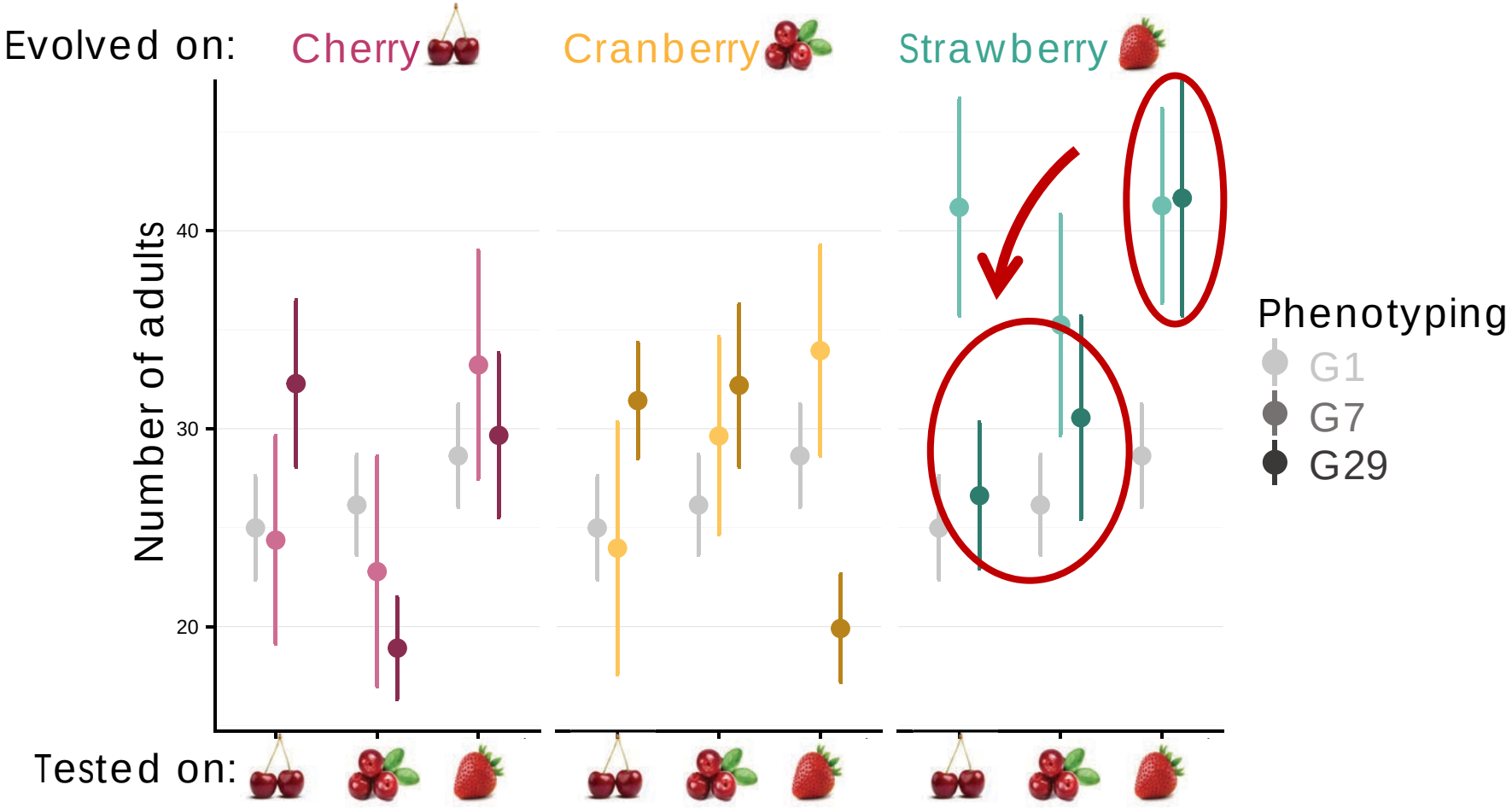
Phenotyping: fitness



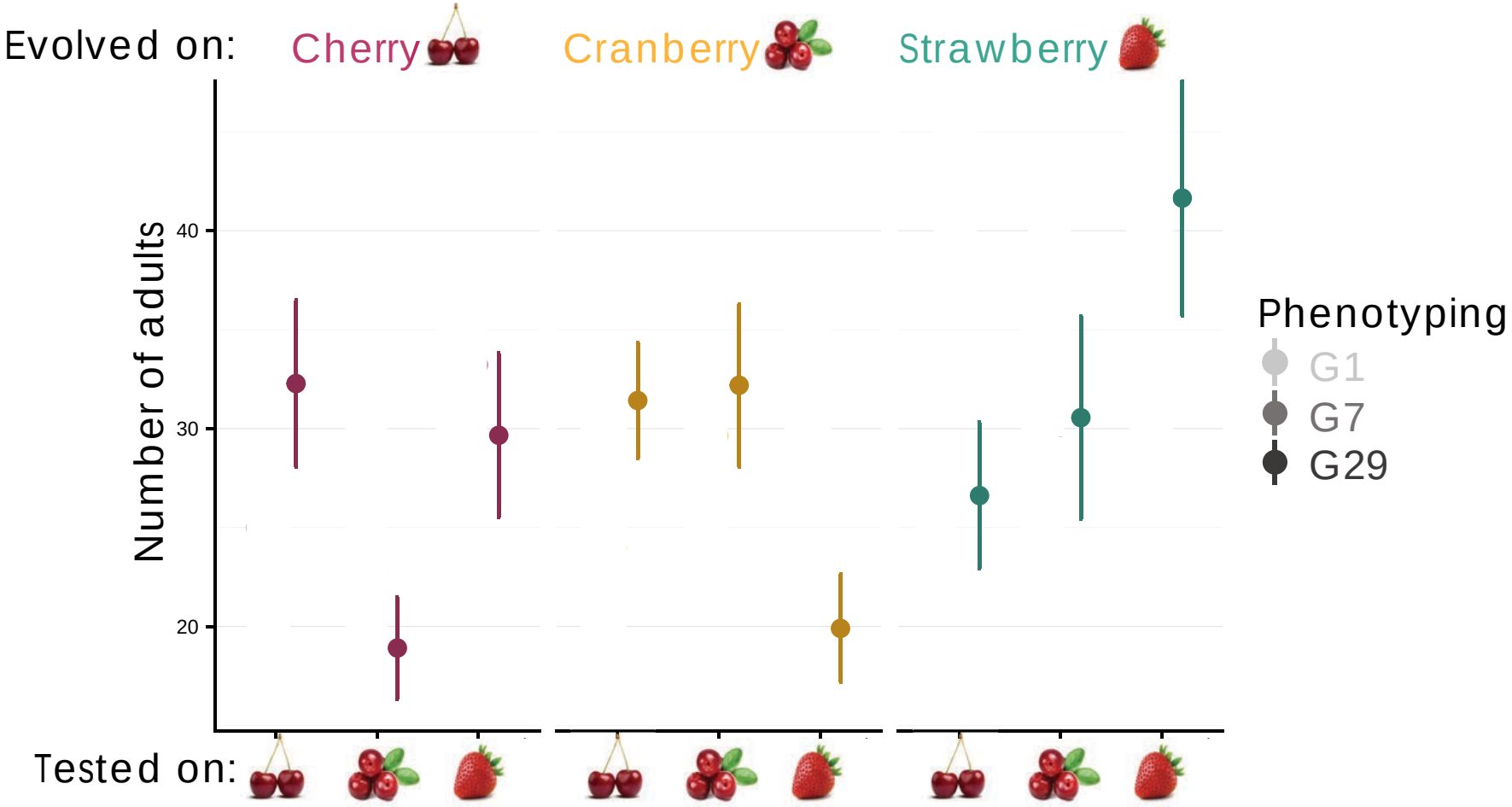
Phenotyping: fitness



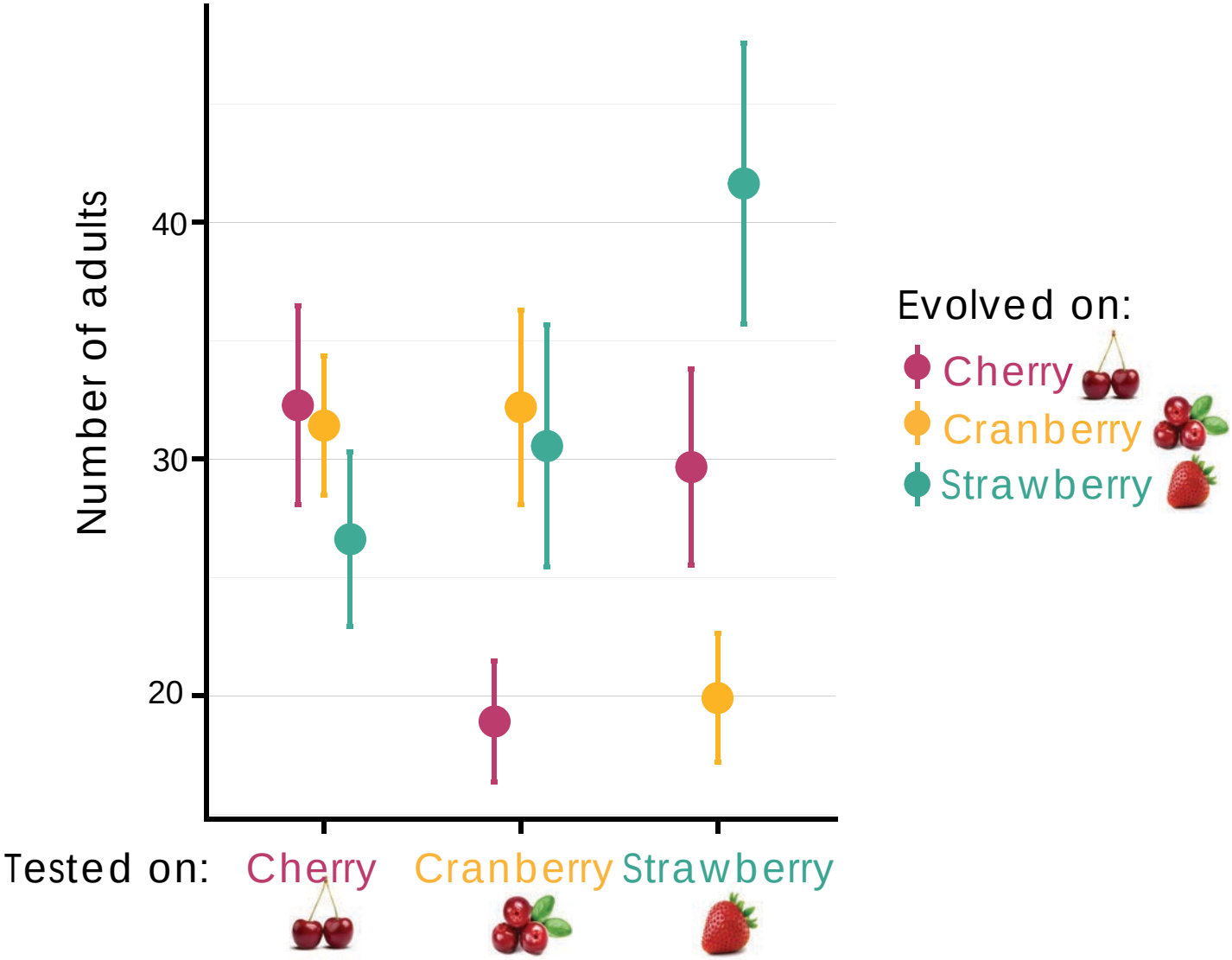
Phenotyping: fitness



Phenotyping: fitness



Phenotyping: fitness (G29)



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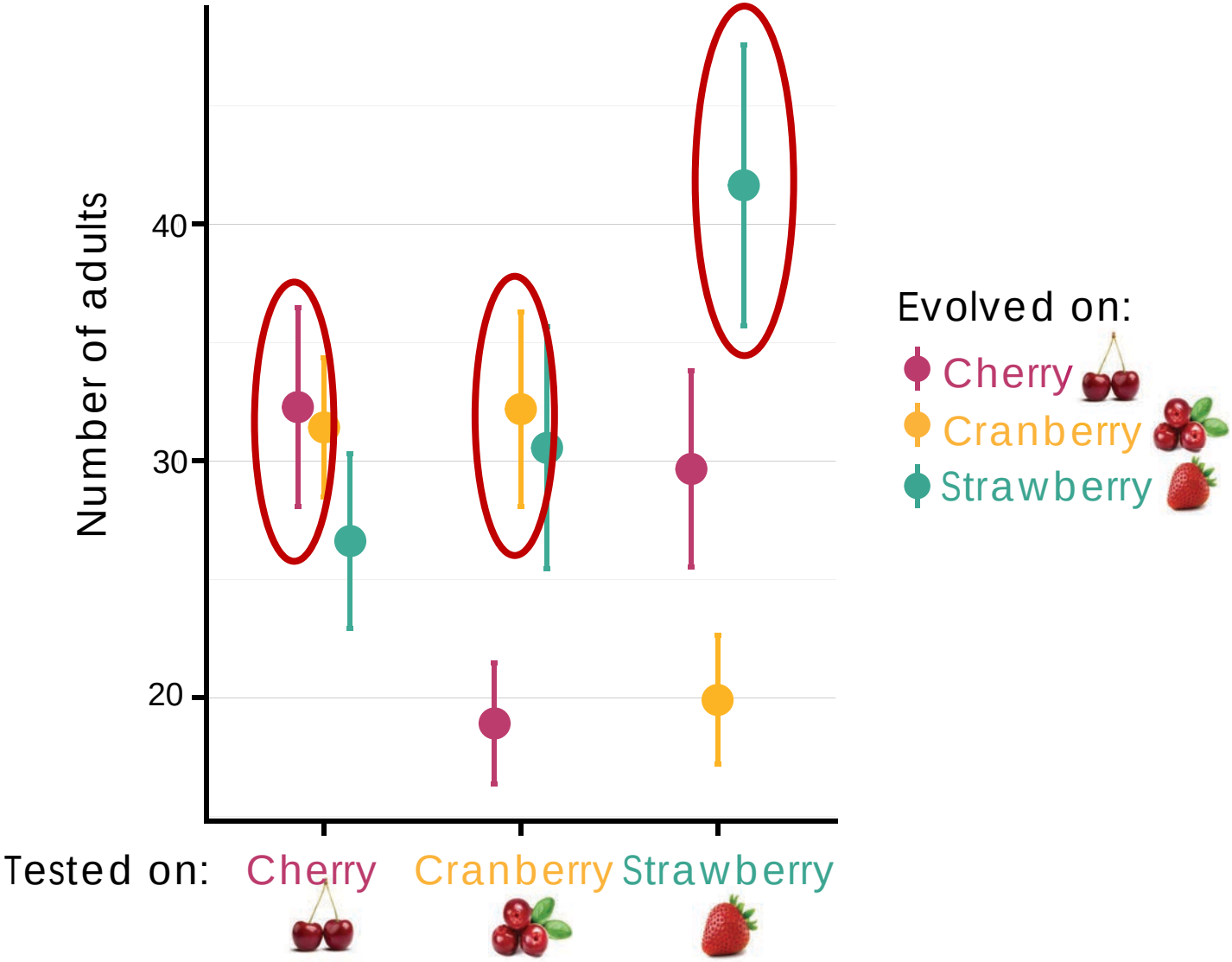
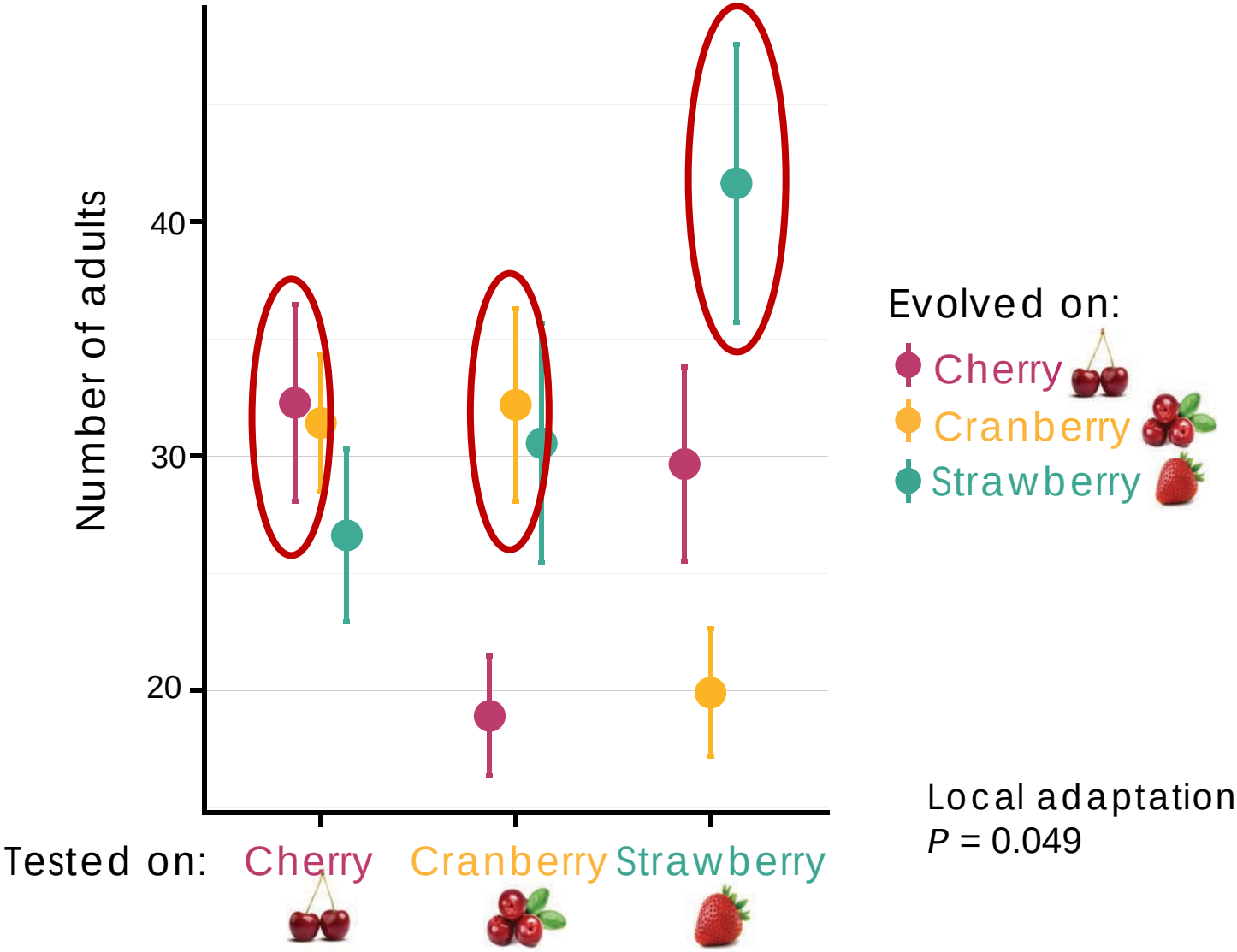
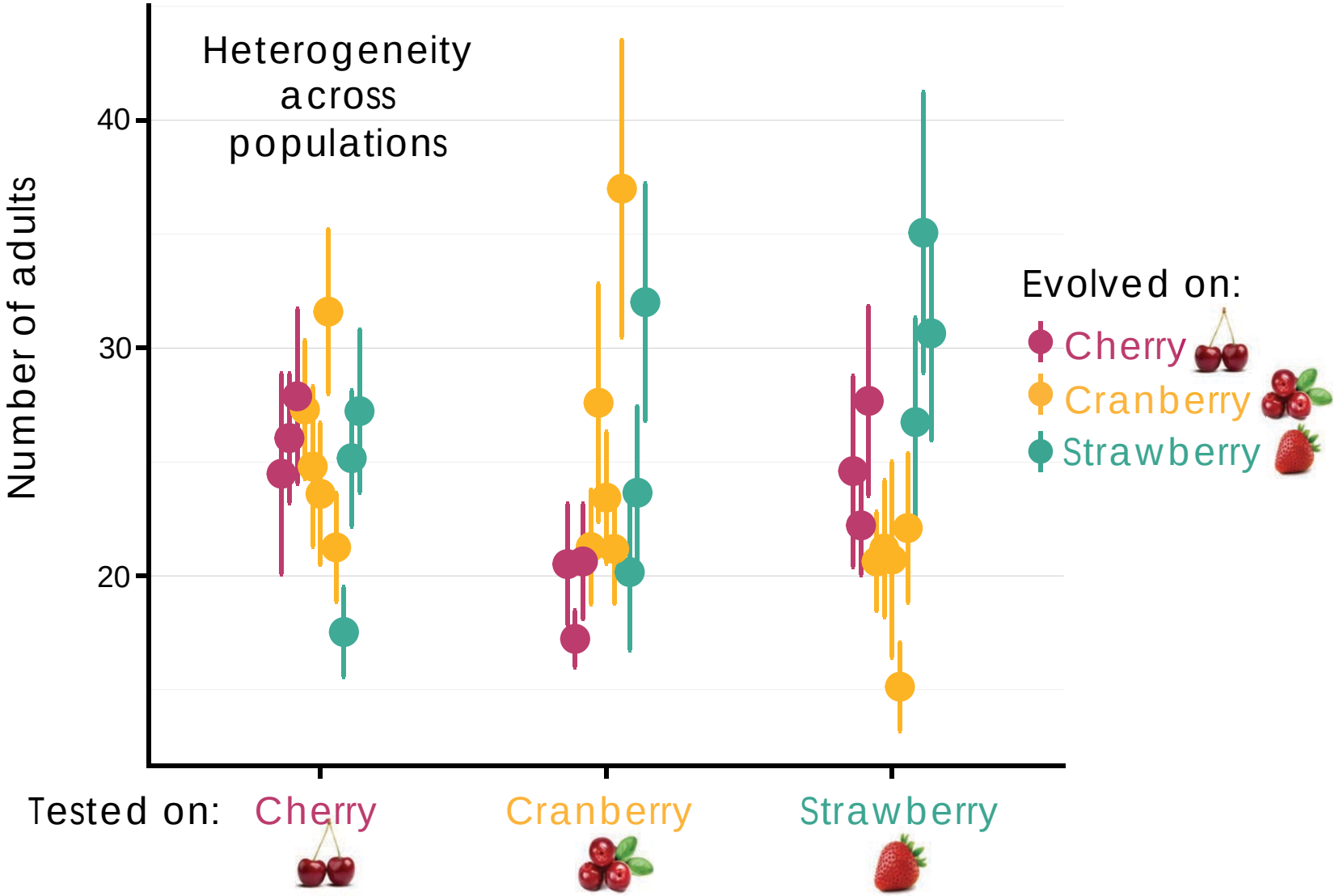


Phenotyping: fitness (G29)



Local adaptation
$P = 0.049$

Phenotyping: fitness (G29)



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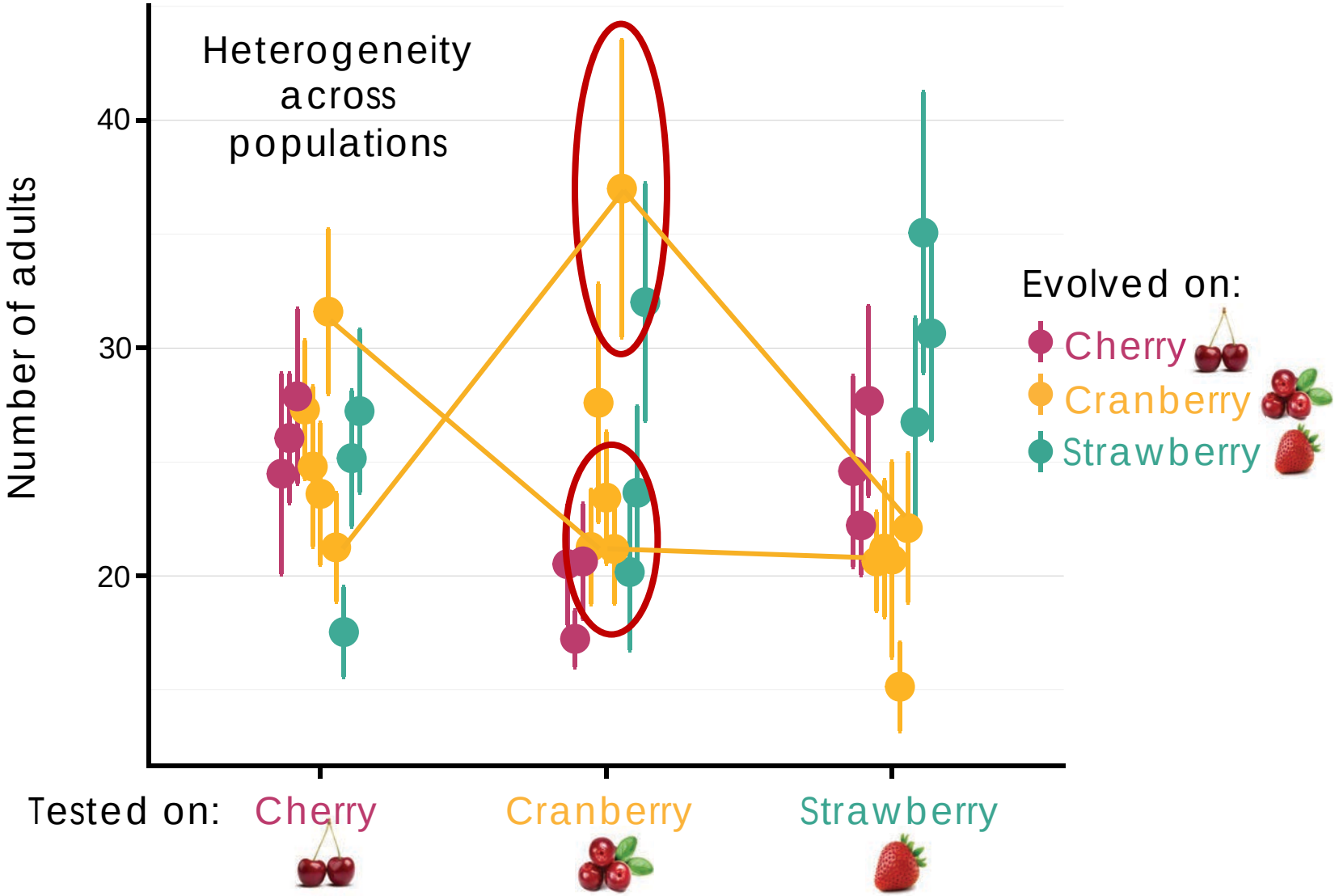


Phenotyping

Groups of
20 flies

Fitness

Cherry
Cranberry
Strawberry

Number of adults

Oviposition preference

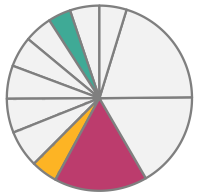
Apricot
Blackberry
Blackcurrant
Cherry
Cranberry
Fig

Grape
Kiwi
Raspberry
Rose Hips
Strawberry
Tomato

Number of eggs

Phenotyping: oviposition preference

Ancestral

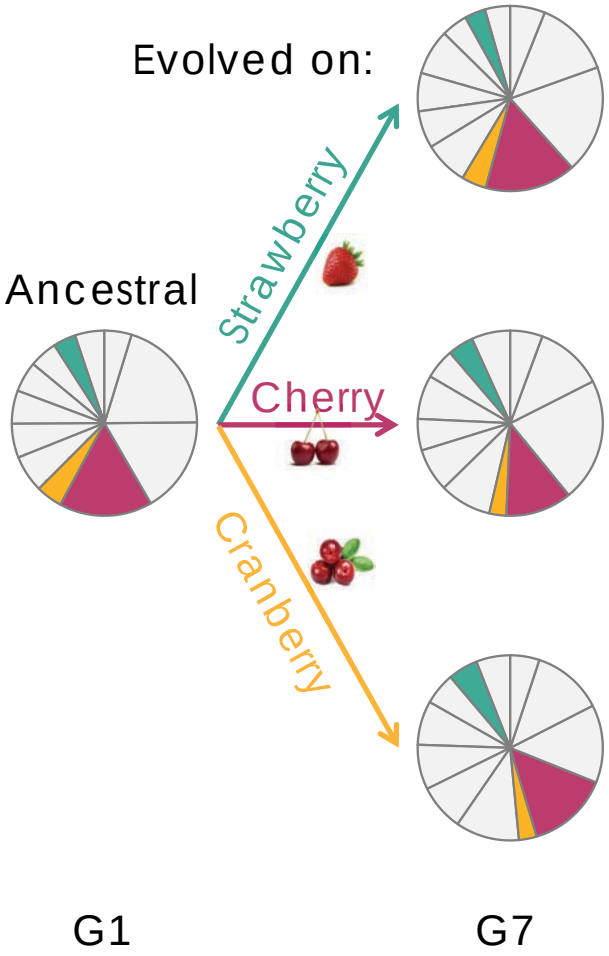


Proportion of eggs laid on:

- Cherry
- Cranberry
- Strawberry
- Others

G1

Phenotyping: oviposition preference

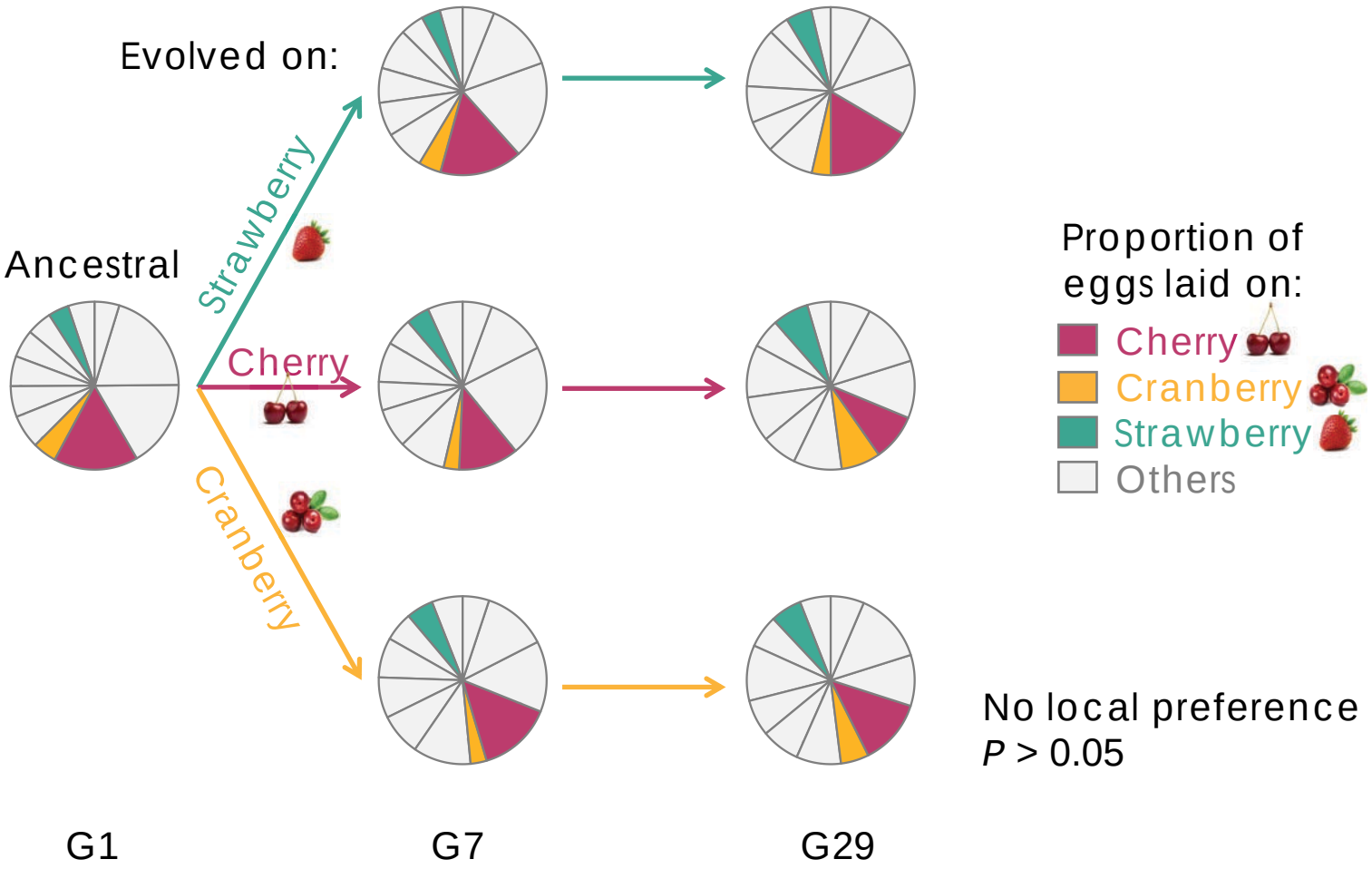


Proportion of eggs laid on:

- Cherry
- Cranberry
- Strawberry
- Others

No local preference
$P > 0.05$

Phenotyping: oviposition preference



Conclusion: evolution of specialization

- In some fruits: adaptation not possible

Tomato  Rose Hips  Blackcurrant  Grape  Fig 

Source-sink dynamic
or
Strong selective pressures in the lab
?

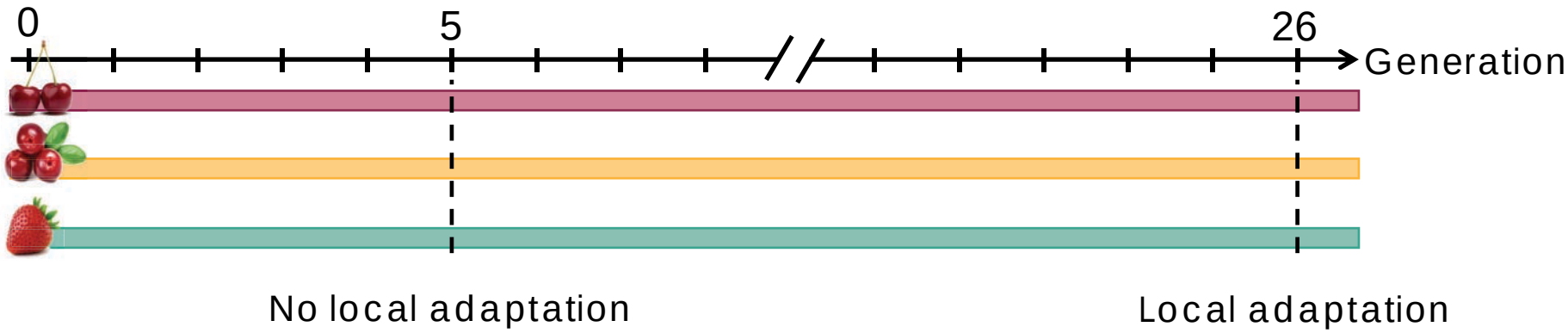
Conclusion: evolution of specialization

- In some fruits: adaptation not possible

Tomato  Rose Hips  Blackcurrant  Grape  Fig 

- Two-step evolution:
  - First: Lab adaptation
  - Second: Local adaptation

Strawberry  Cranberry  Cherry 



Conclusion: evolution of specialization

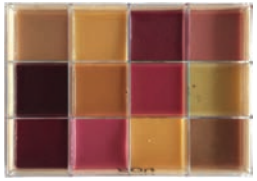
- In some fruits: adaptation not possible

Tomato 
Rose Hips 
Blackcurrant 
Grape 
Fig 

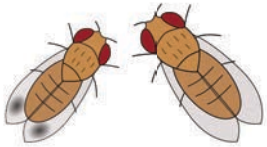
- Two-step evolution:
  - First: Lab adaptation
  - Second: Local adaptation

Strawberry 
Cranberry 
Cherry 

- No evolution of oviposition preference in choice environment

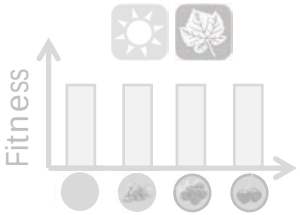


Preference and performance not genetically correlated?

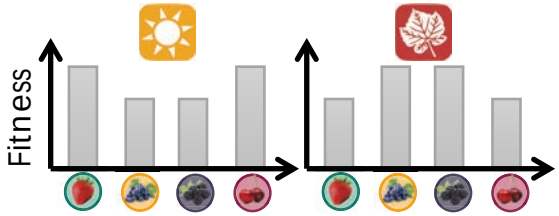


Adaptive responses of *Drosophila suzukii*

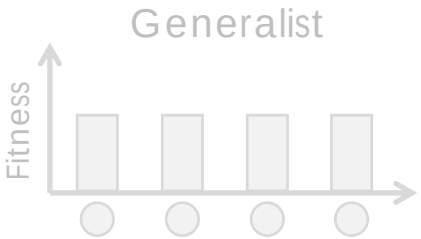
Generalist with polymorphism:

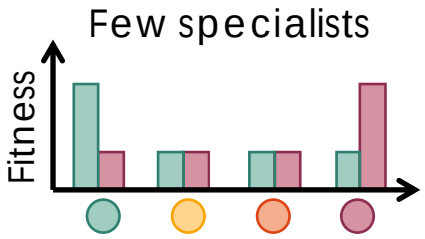


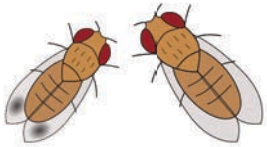
OR



Initialization of specialization:







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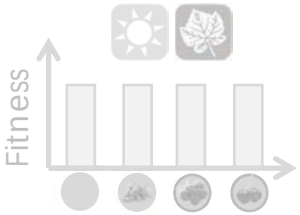

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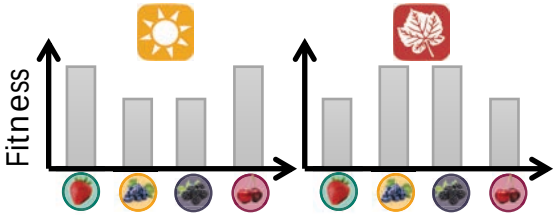
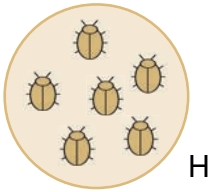


Initialization of specialization:

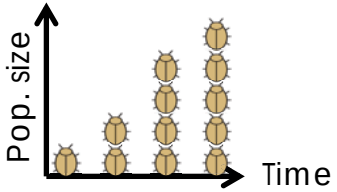
Factors promoting invasion success?

Environmental conditions



OR

Demographic processes



Genomic basis of adaptation associated with invasion success

Factors promoting invasion success?

Goal:
Invasion success due to adaptive processes?
Which traits are decisive in invasion success?

Factors promoting invasion success?

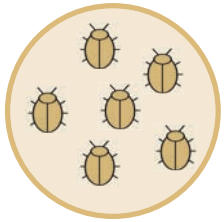
Goal:
Invasion success due to adaptive processes?
Which traits are decisive in invasion success?

Expectation: Traits involved in

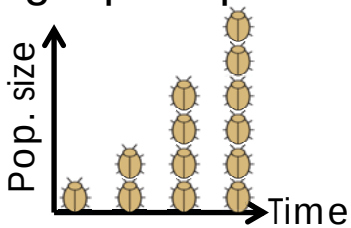
Environmental conditions

Traits associated with host use?

Ex. Olfactory receptor



Demographic processes



Ex. Development time
Ex. Diapause

Factors promoting invasion success?

Goal:
Invasion success due to adaptive processes?
Which traits are decisive in invasion success?

Expectation: Traits involved in

Environmental conditions

Traits associated with host use?

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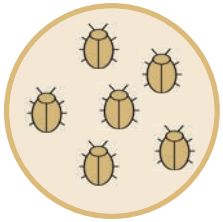
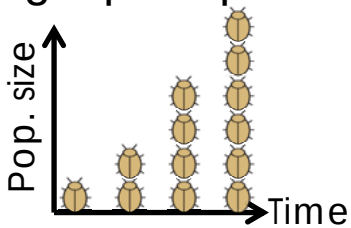


Demographic processes

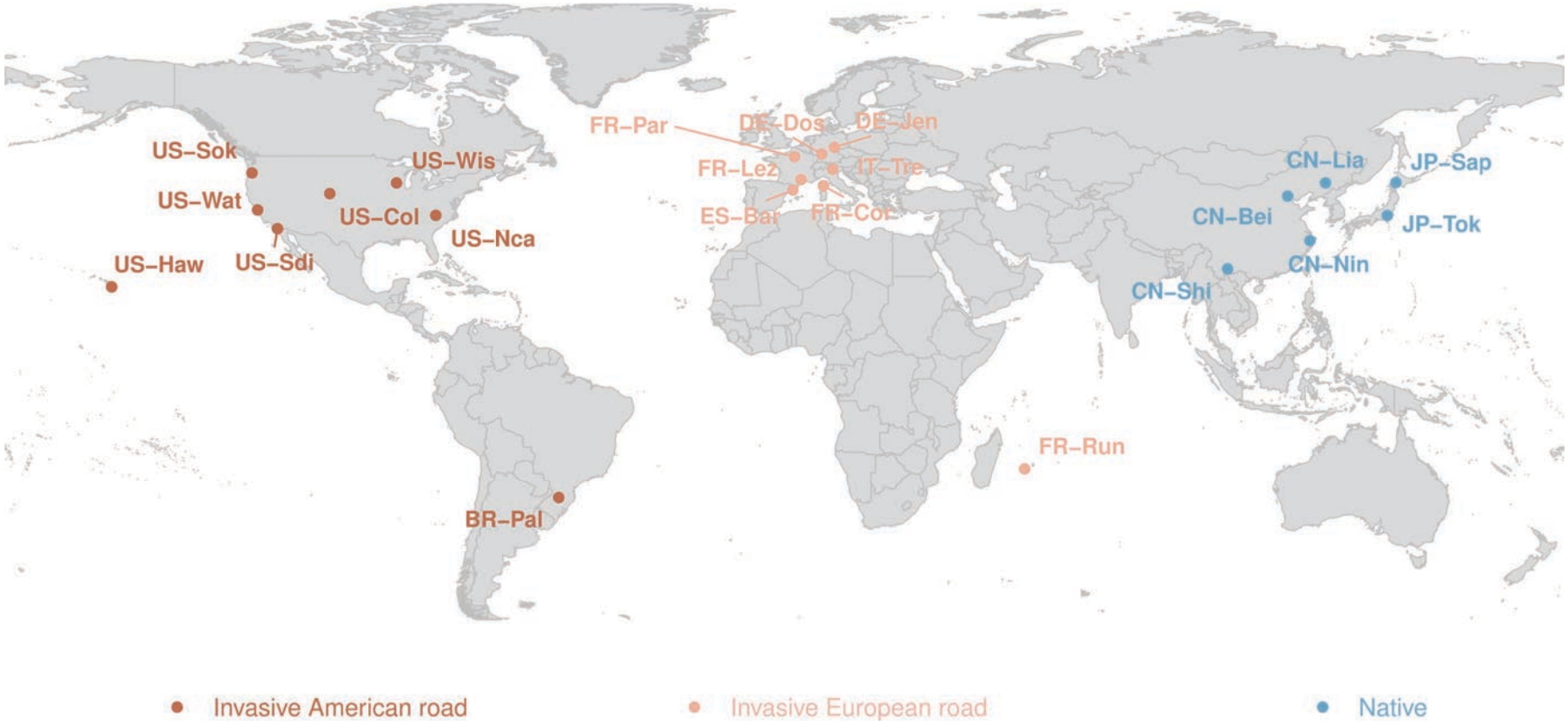


Ex. Development time
Ex. Diapause

Approach:
Indirect approaches: Genetic data —Genome scan→ Gene —Annotation→ Trait
Populational association analysis with invasive *vs.* native status

Methods

Sampling of 22 populations



Methods

Sampling of 22 populations

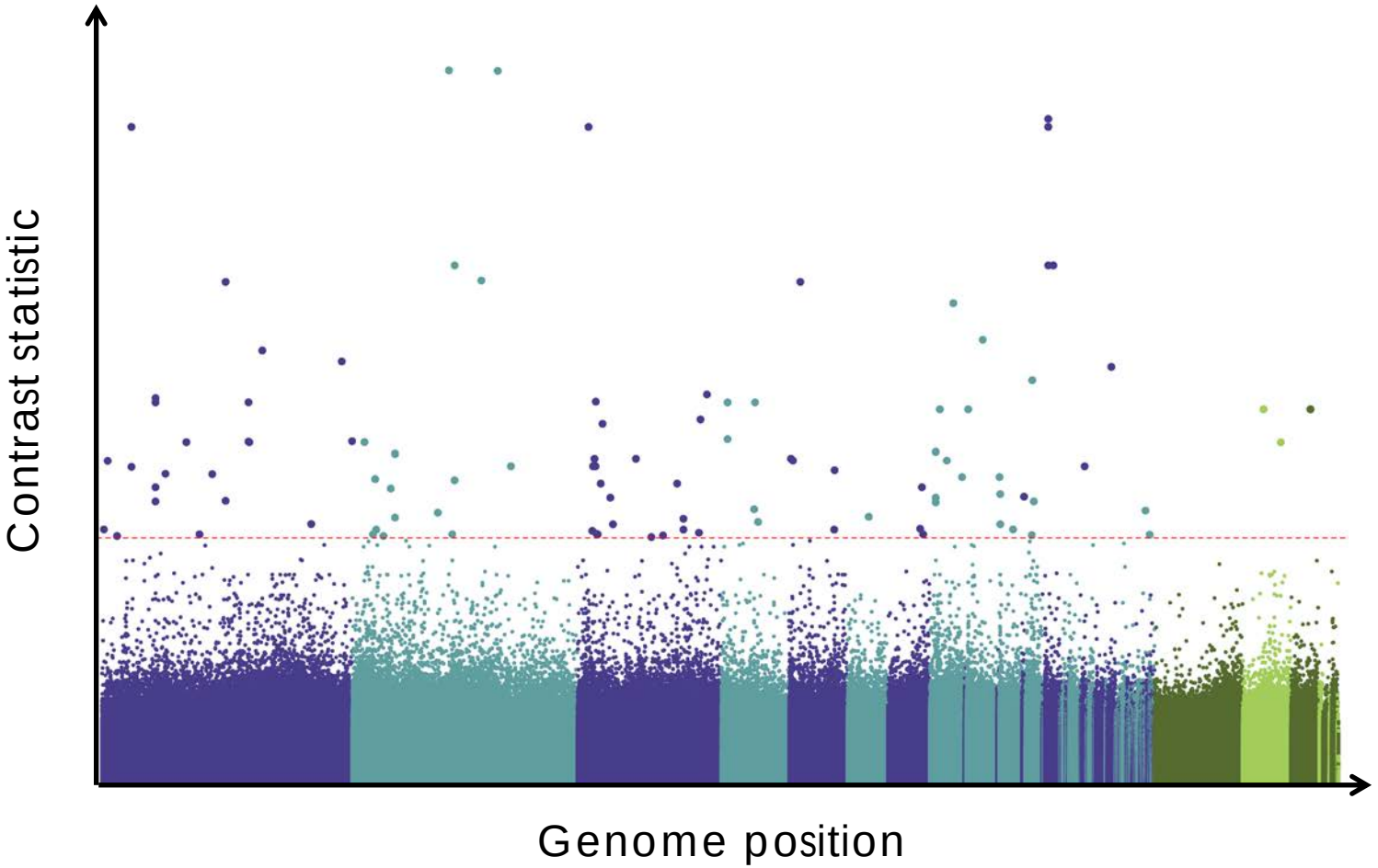
Whole genome sequencing of 22 pools

11,564,472 SNP on autosomal chromosome
1,966,184 SNP on X chromosome

Contrast analysis: Baypass Software

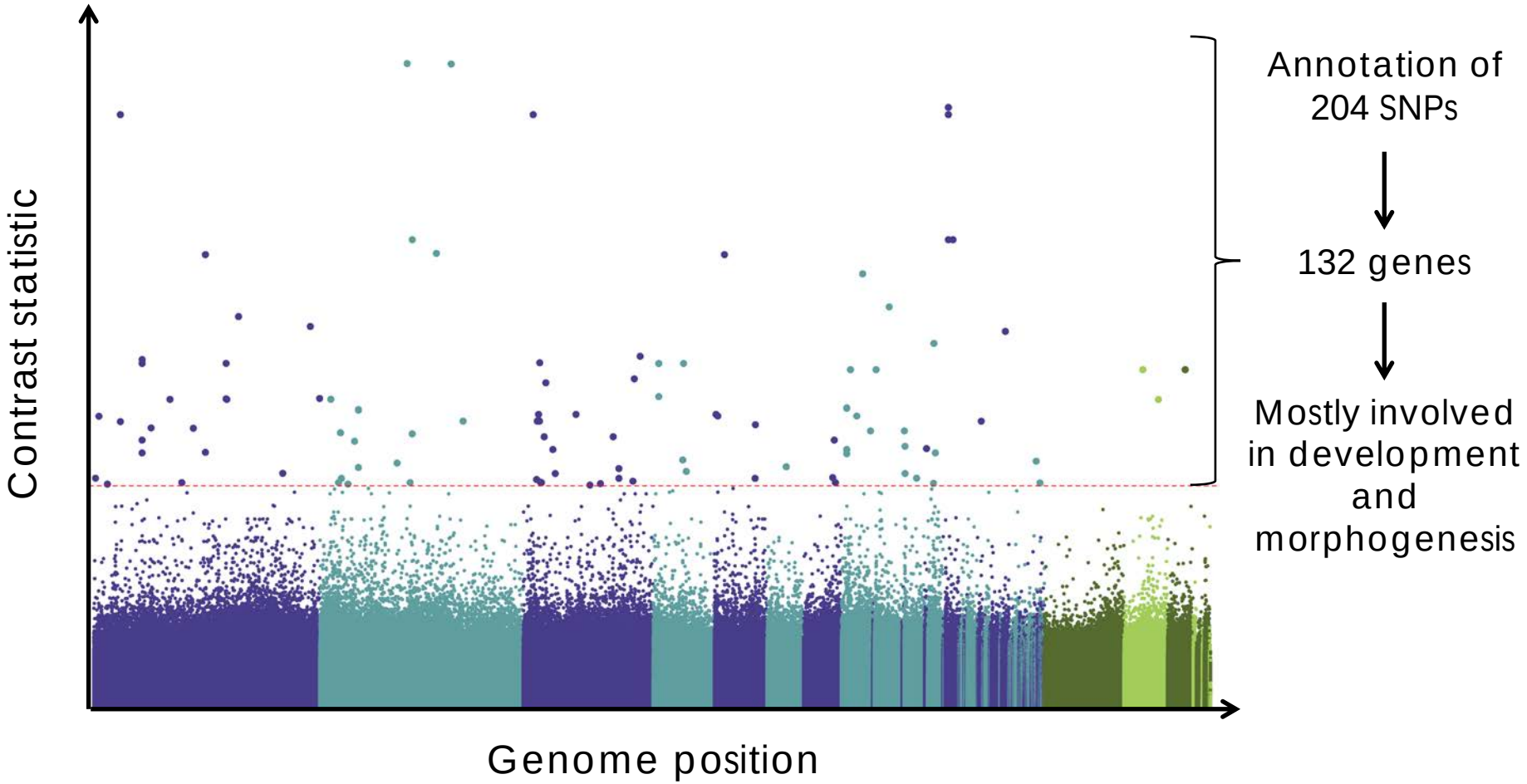
Invasive *vs.* native populations

Results



[Olazcuaga et al., submitted]

Results



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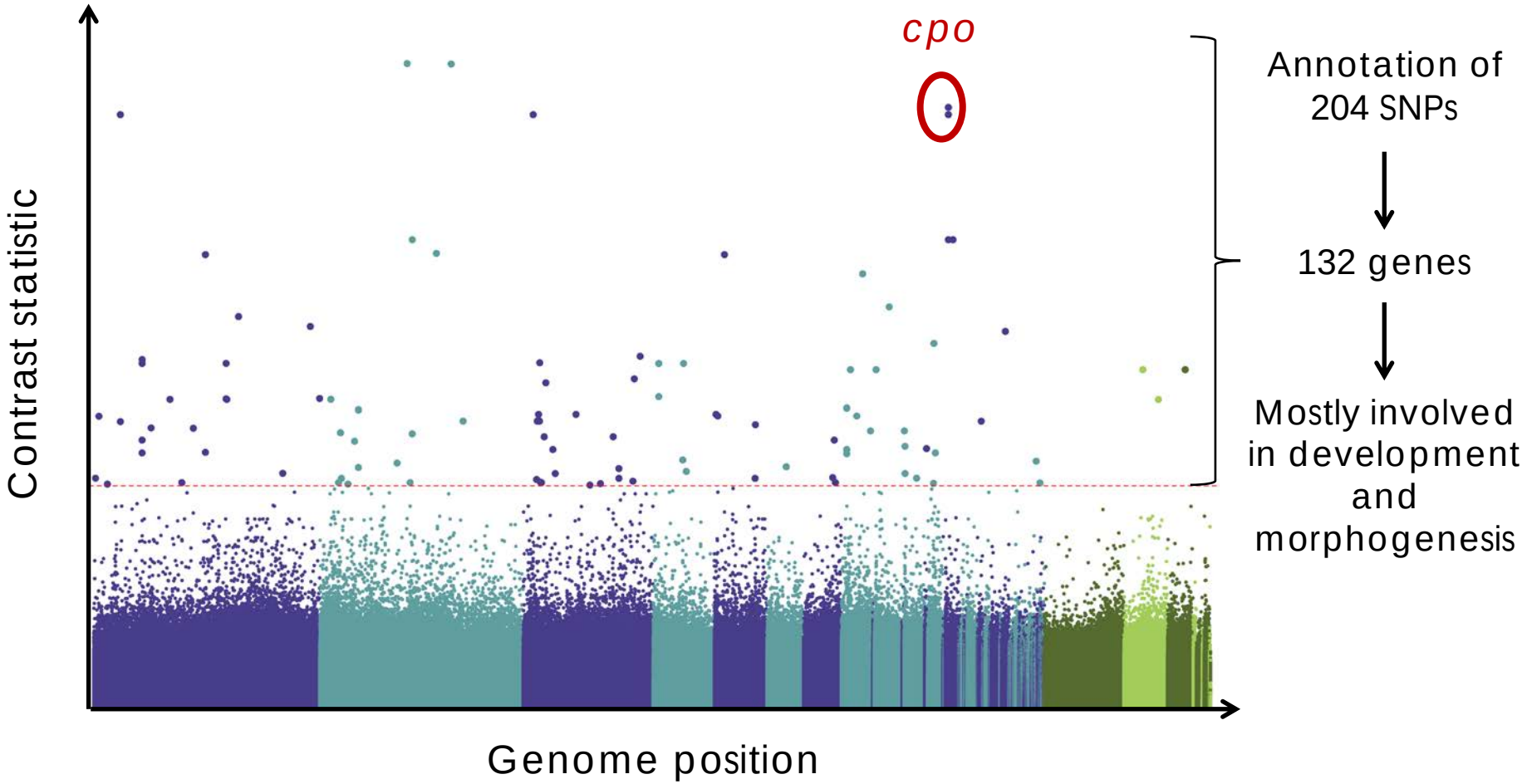
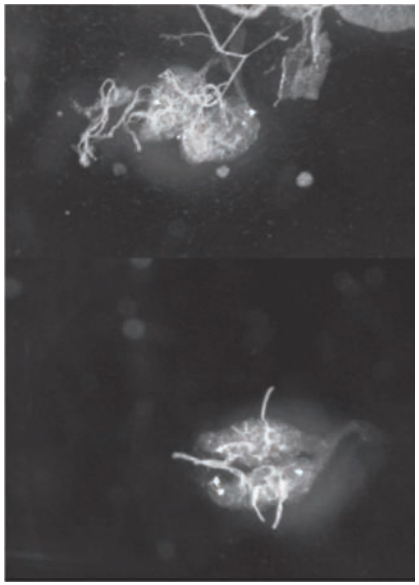
Results



[Olazcuaga et al., submitted]

cpo involved in diapause phenotype?

D. melanogaster: 11°C development



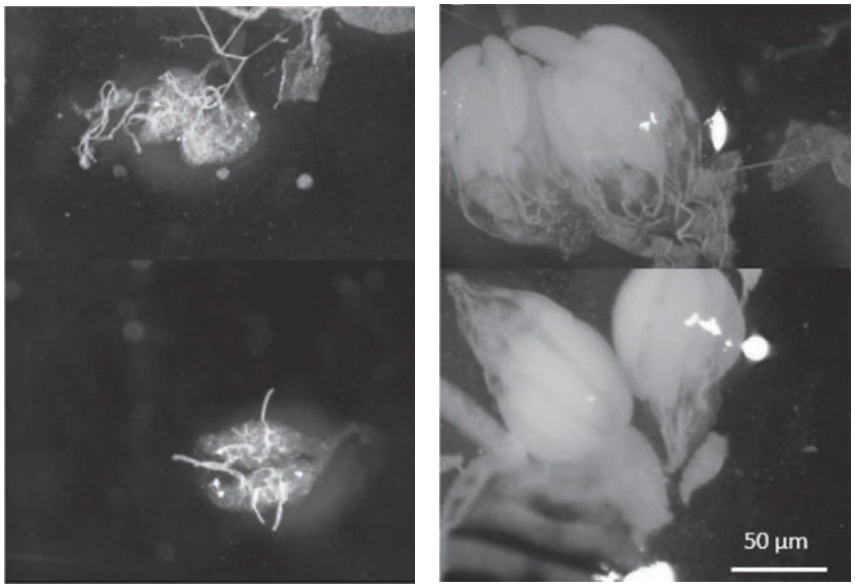
No ovarian development

[Schmidt et al., 2005]

cpo involved in diapause phenotype?

D. melanogaster: 11°C development

cpo: alternative allele



No ovarian development

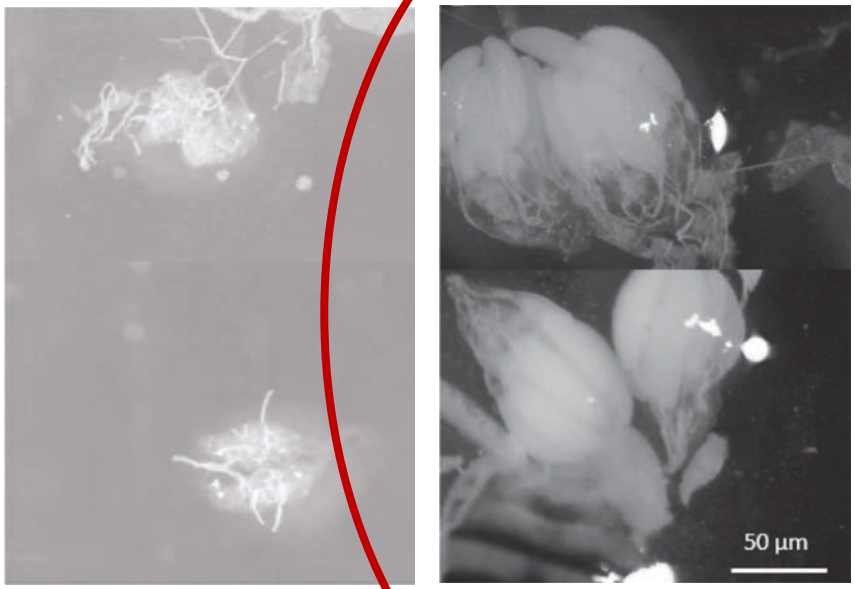
Full ovarian development

[Schmidt et al., 2005]

cpo involved in diapause phenotype?

D. melanogaster: 11°C development

cpo: alternative allele



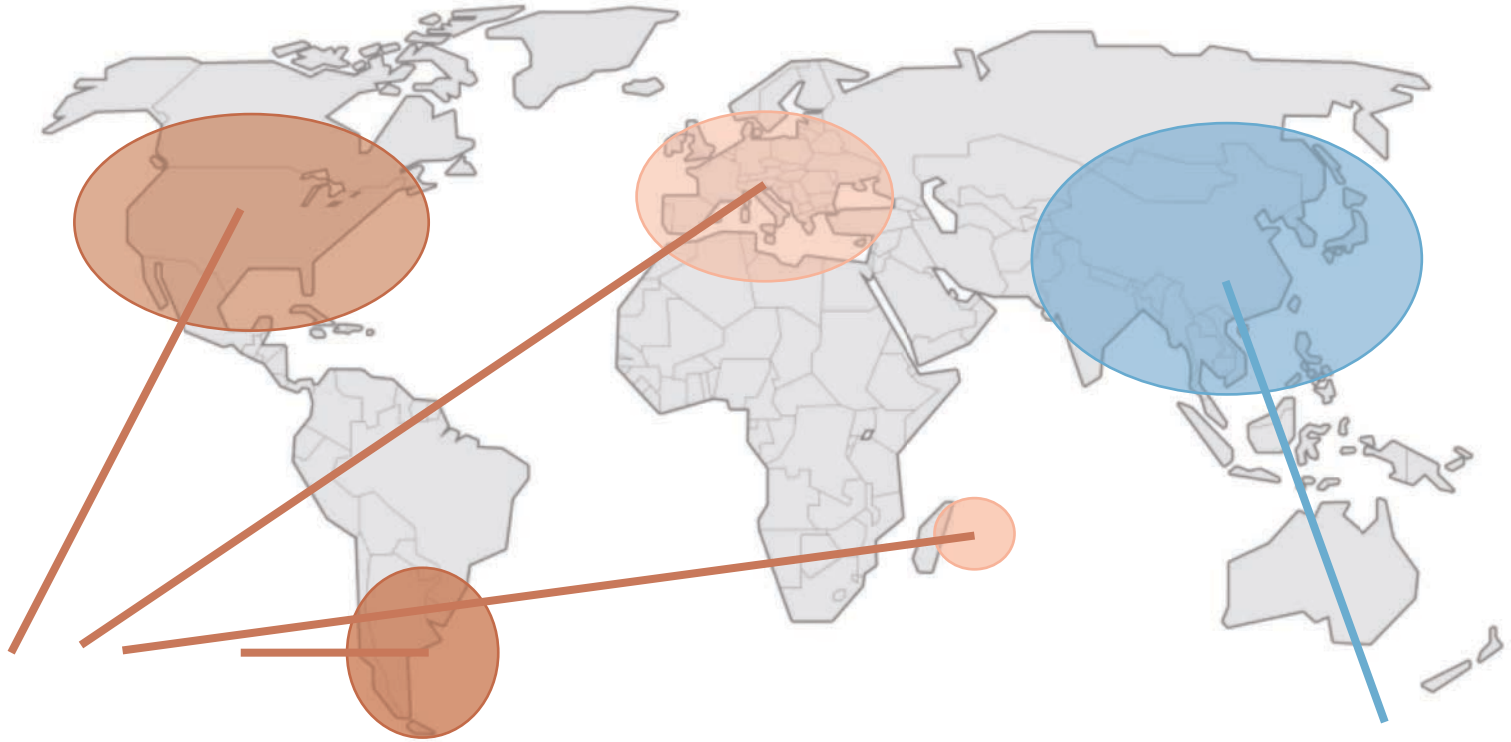
No ovarian development

Full ovarian development

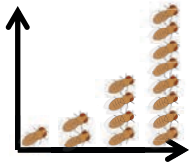
Selected during invasion?

[Schmidt et al., 2005]

Demographic processes?

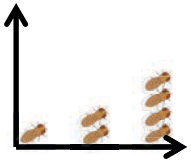


Shorter development time?



Non-equilibrium

Longer development time?



Equilibrium

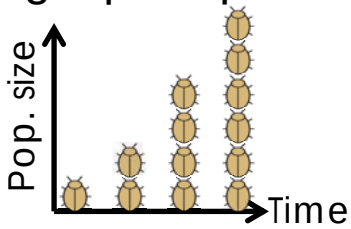
Conclusion: factors promoting invasion success?

- Invasion success due to traits involved in:

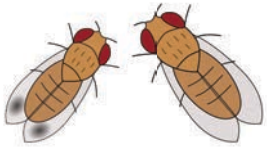
Environmental conditions

No evidence for candidat traits associated with host use

Demographic processes

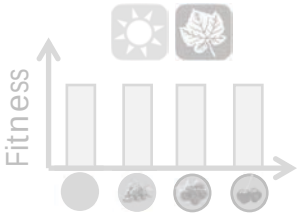


Diapause?
Development time?



Adaptive responses of *Drosophila suzukii*

Generalist with polymorphism:



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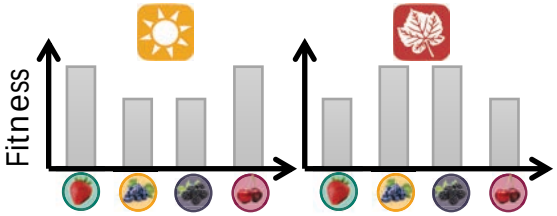
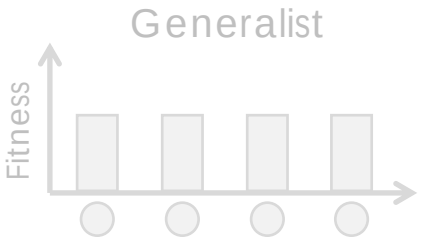
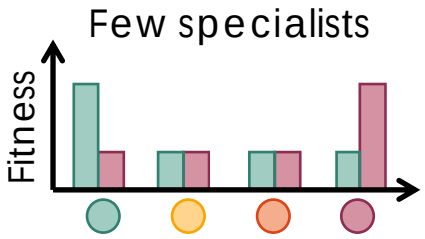


Initialization of specialization:



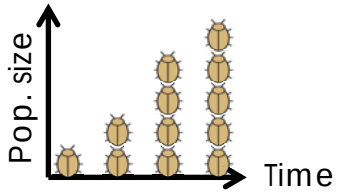


Factors promoting invasion success:

Environmental conditions

OR

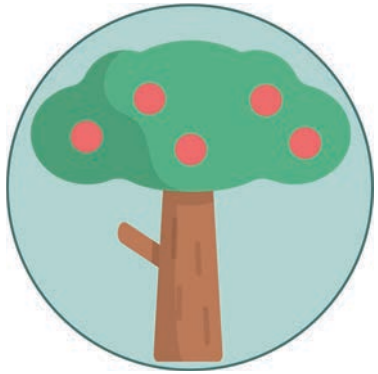
Demographic processes



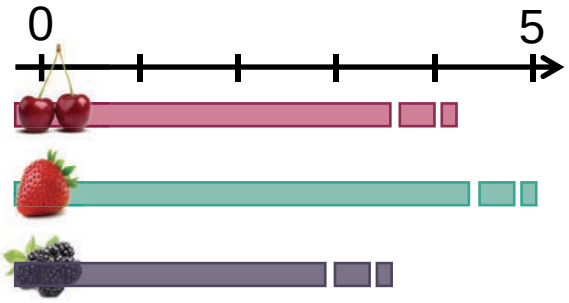
Discussion and perspectives

Experimental populations *vs.* wild populations

Evolution *in natura*



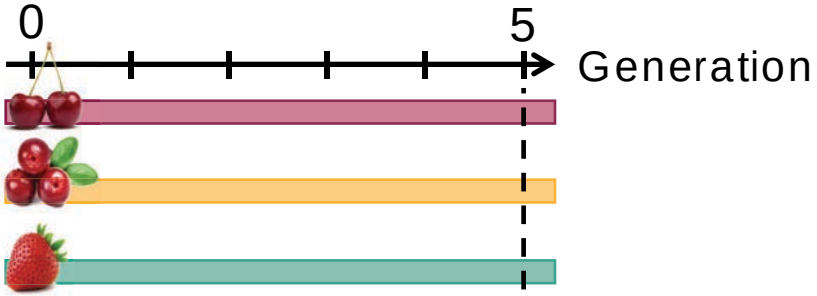
Heterogeneous environment



Local adaptation

Experimental evolution

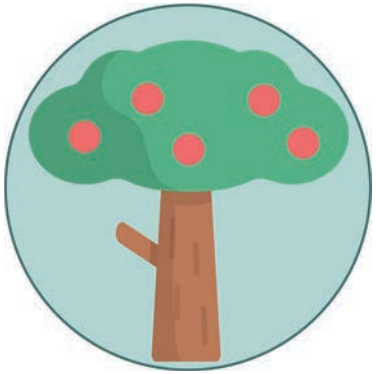
Homogeneous environments



No local adaptation

Experimental populations *vs.* wild populations

Evolution *in natura*



Large population size

Microbiota community

Experimental evolution

Small population size

Less diverse microbiota

Lab selective pressures > Fruit selective pressures

Evolution *in natura*: a dynamic and complex process

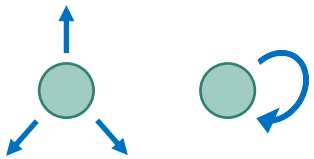
Heterogeneity of environment ⟶ Evolution of local adaptation

Evolution *in natura*: a dynamic and complex process

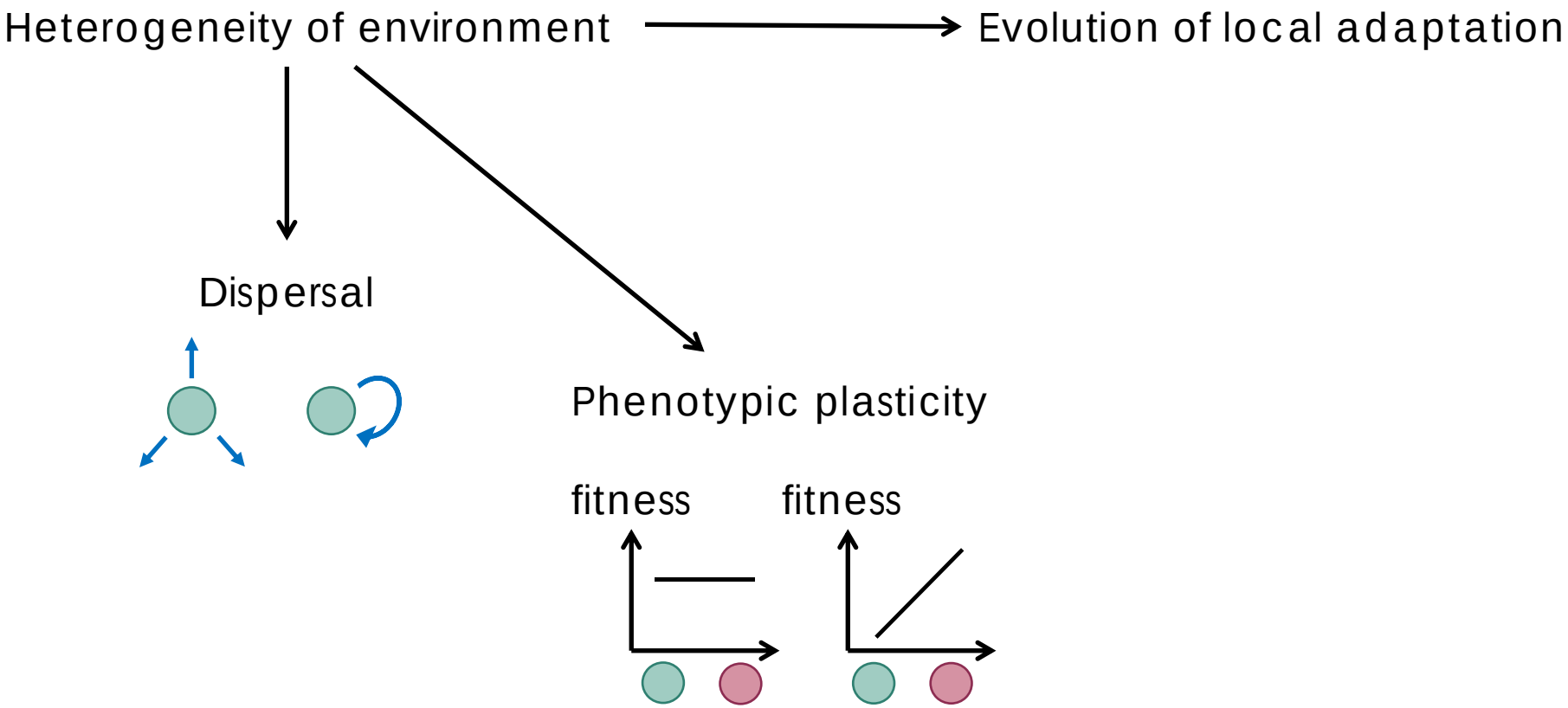
Heterogeneity of environment → Evolution of local adaptation

↓

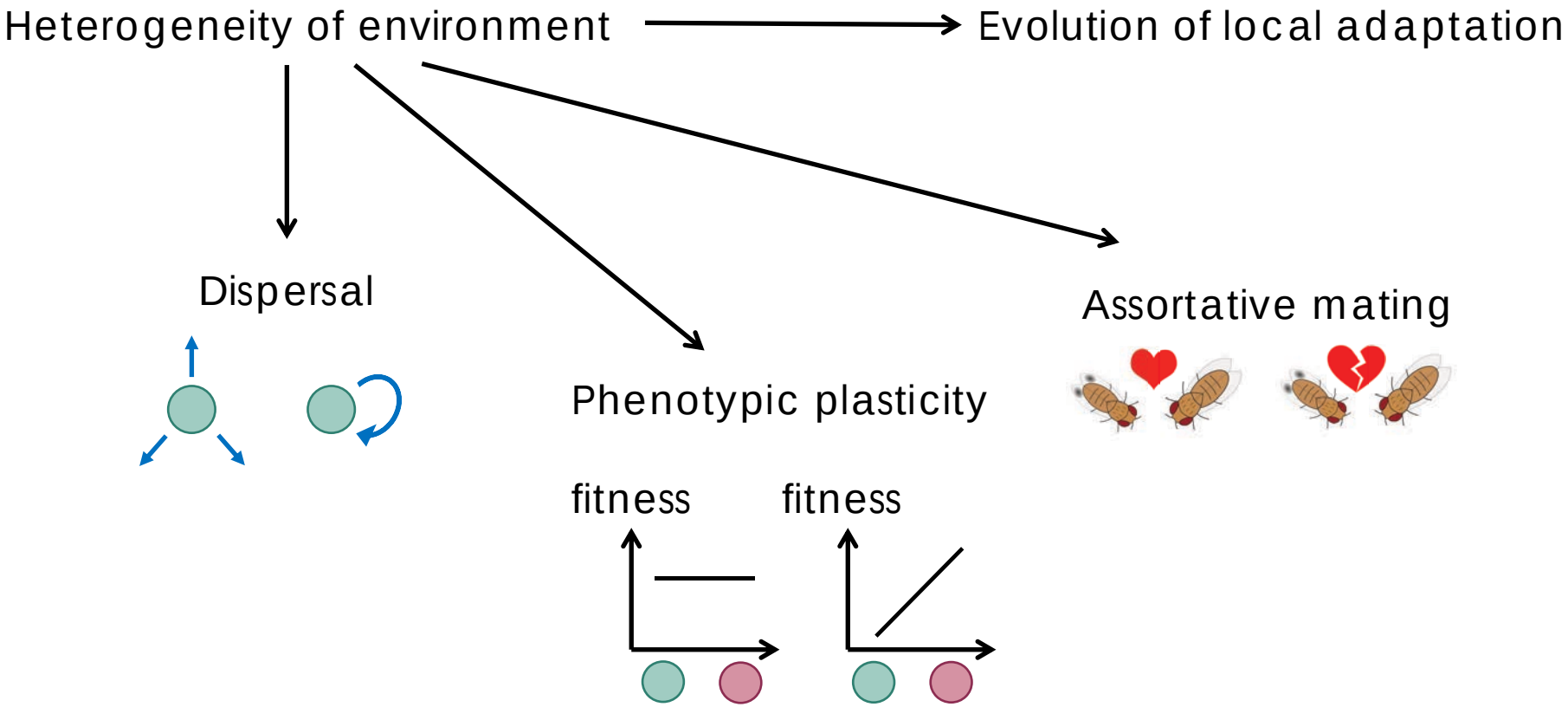
Dispersal



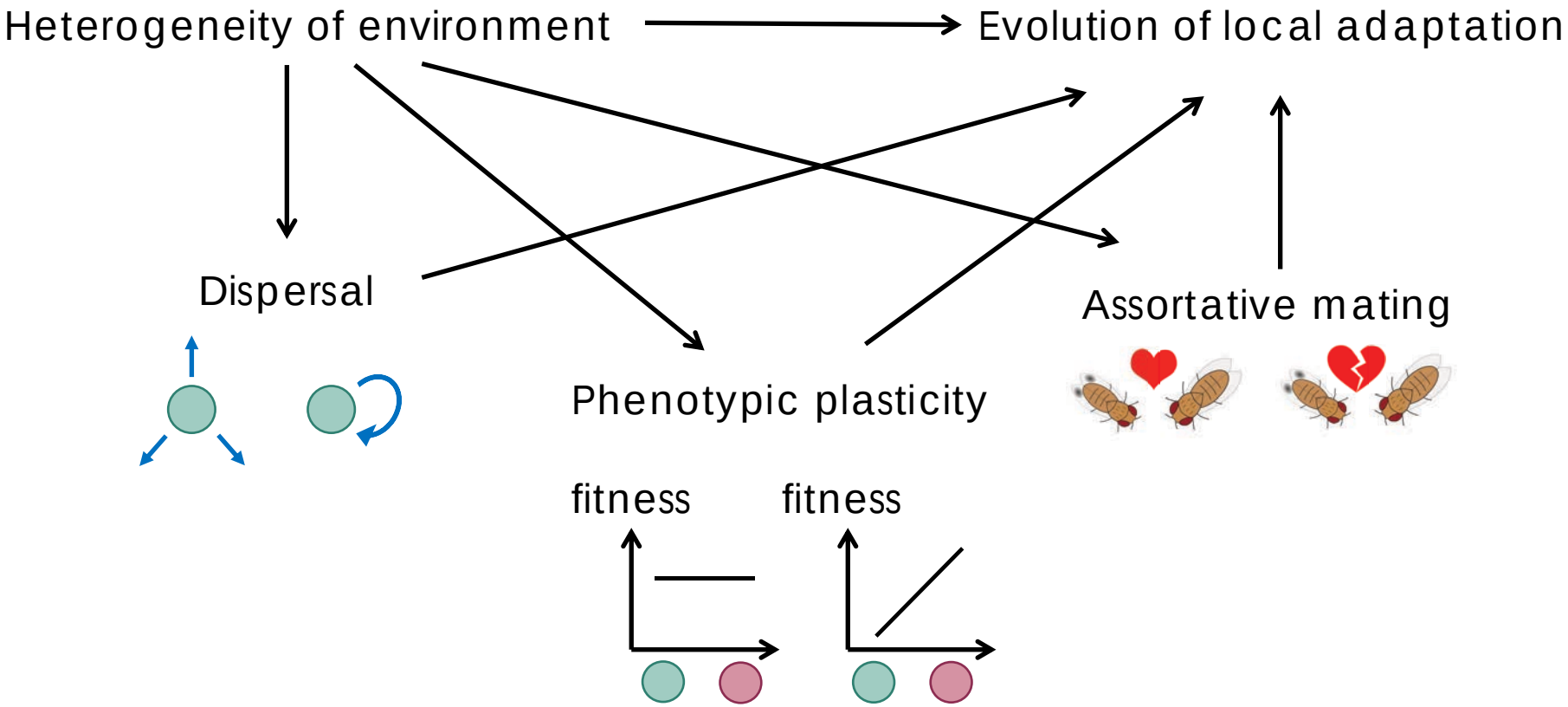
Evolution *in natura*: a dynamic and complex process



Evolution *in natura*: a dynamic and complex process

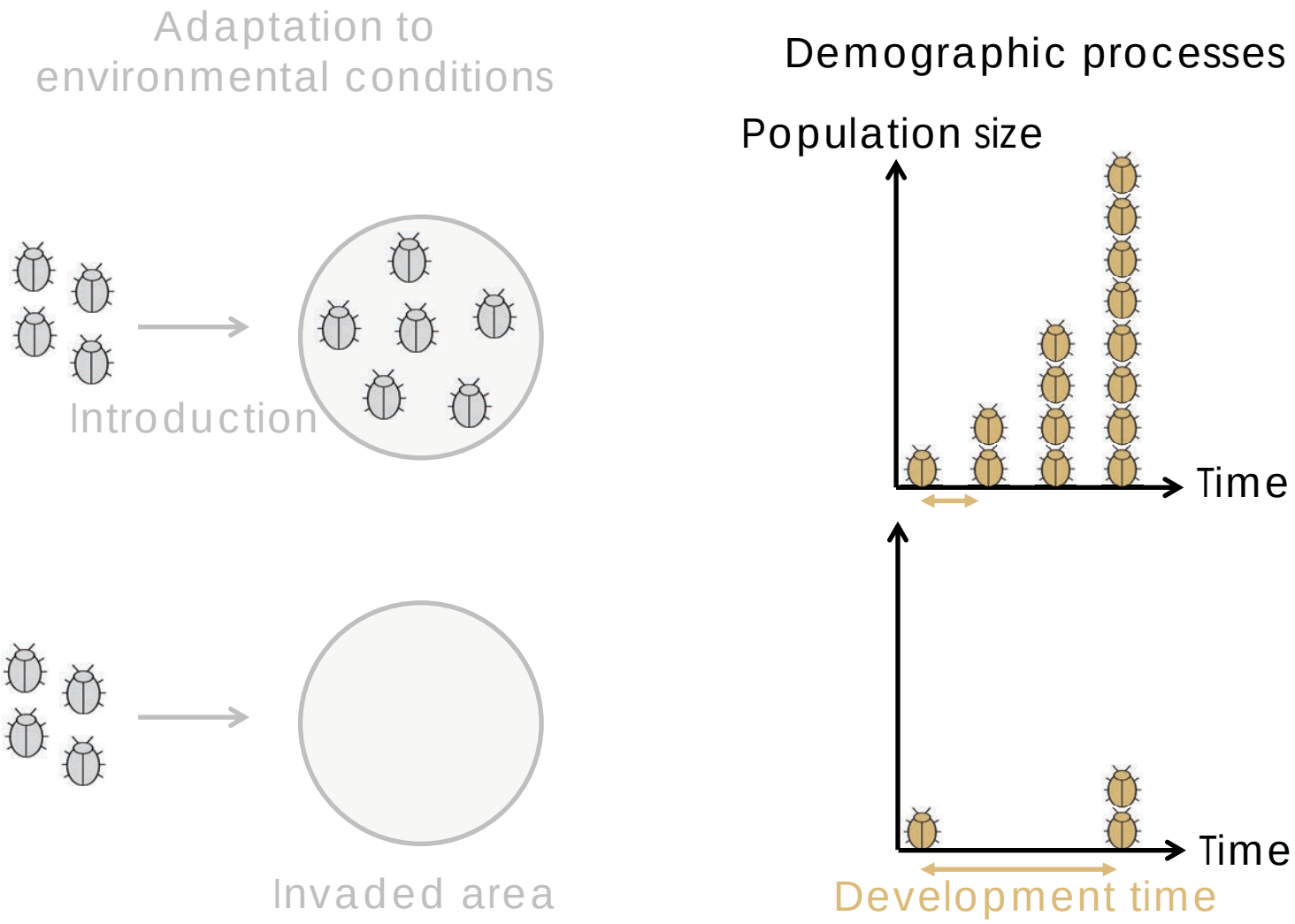


Evolution *in natura*: a dynamic and complex process

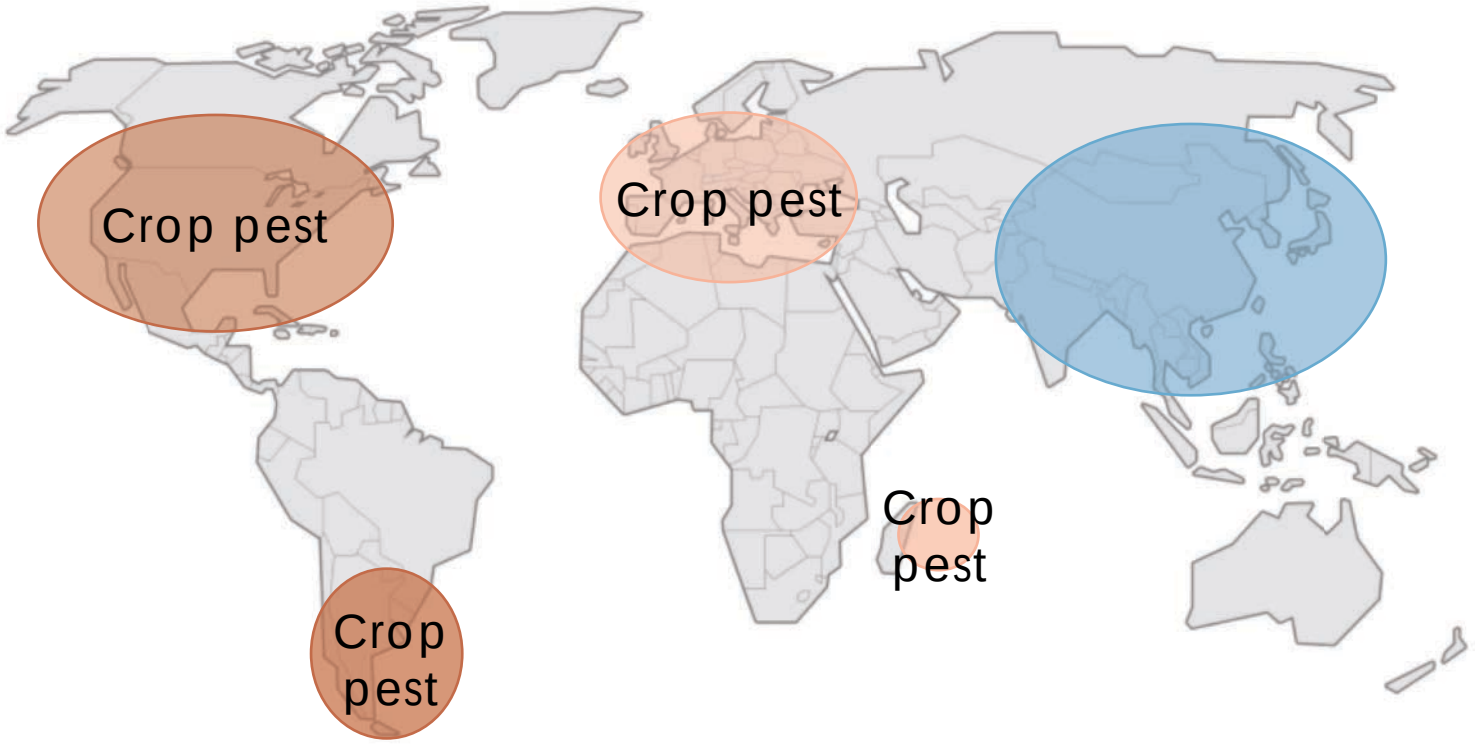


What factors promote invasion success?

What factors promote invasion success?



Why is *D. suzukii* a crop pest only in invaded area?



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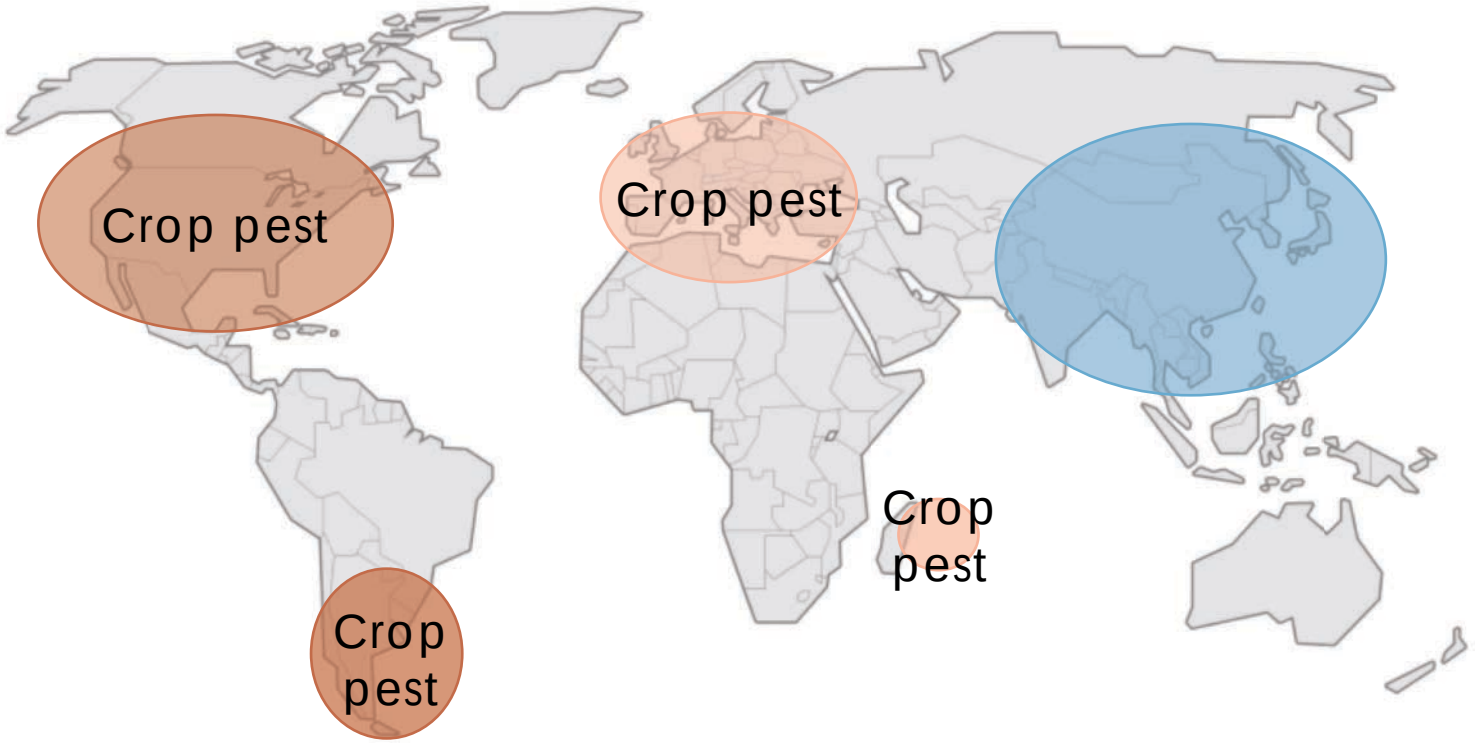
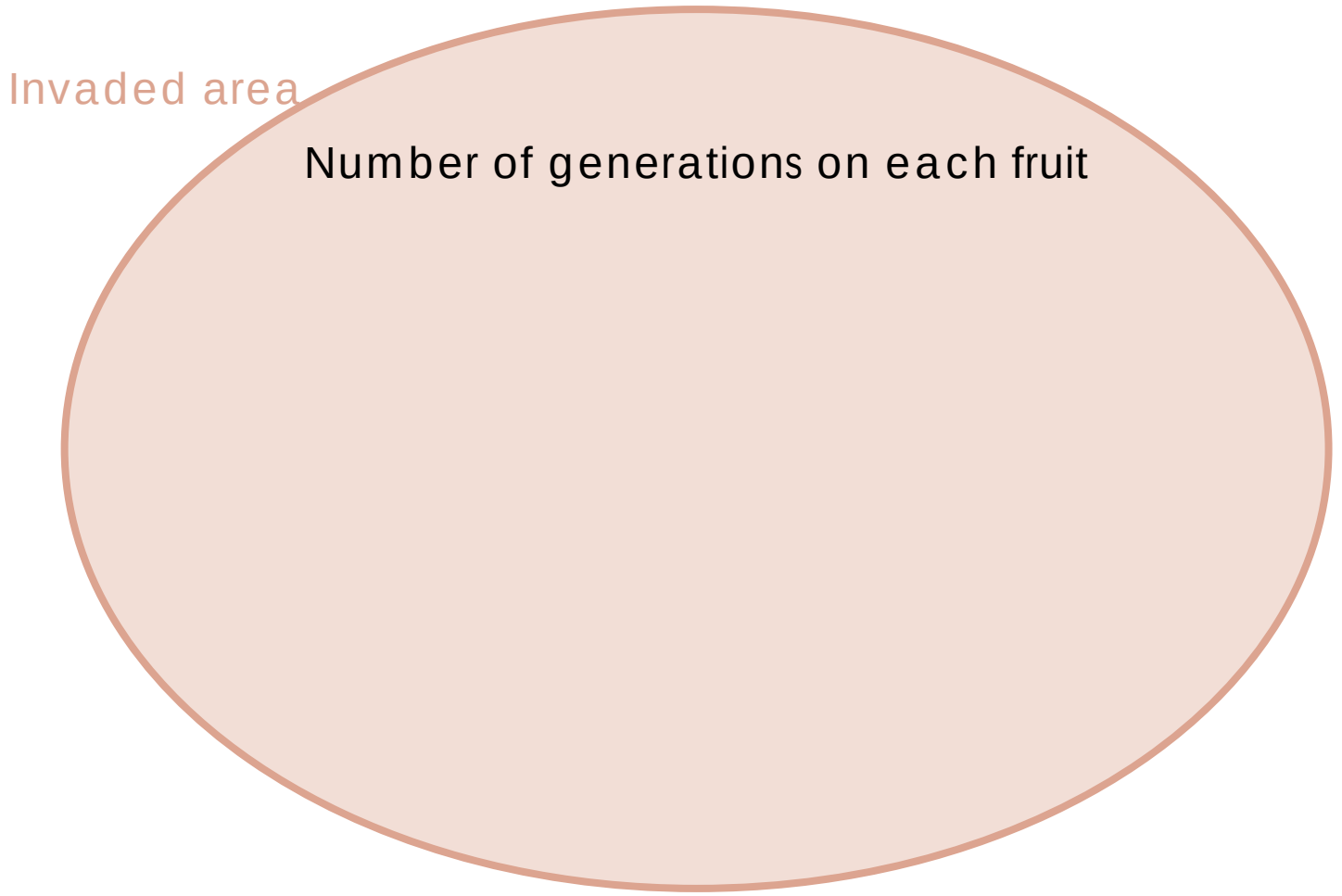


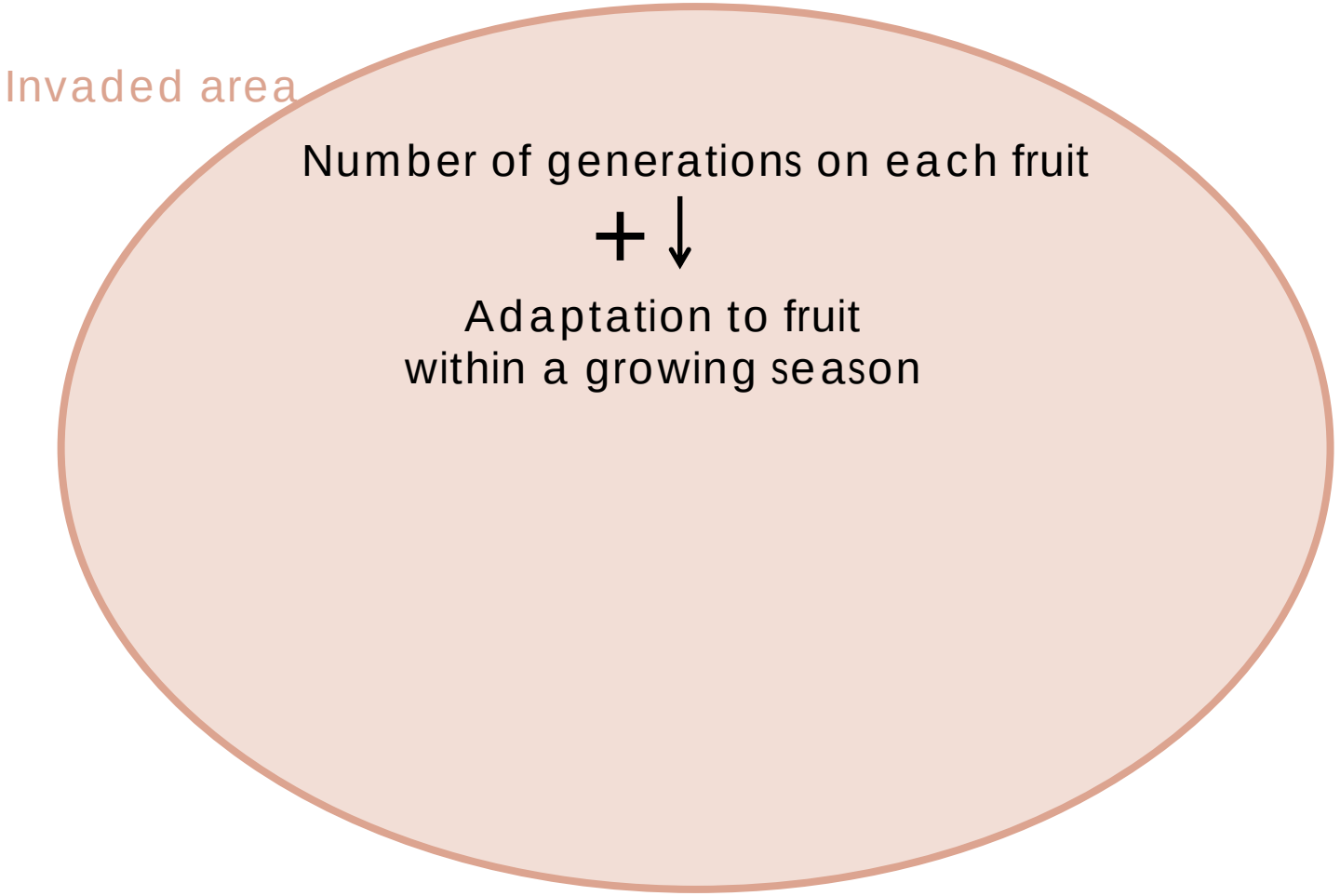
Current hypothesis: ‘‘Enemy Release Hypothesis’’

[Chabert et al., 2012]

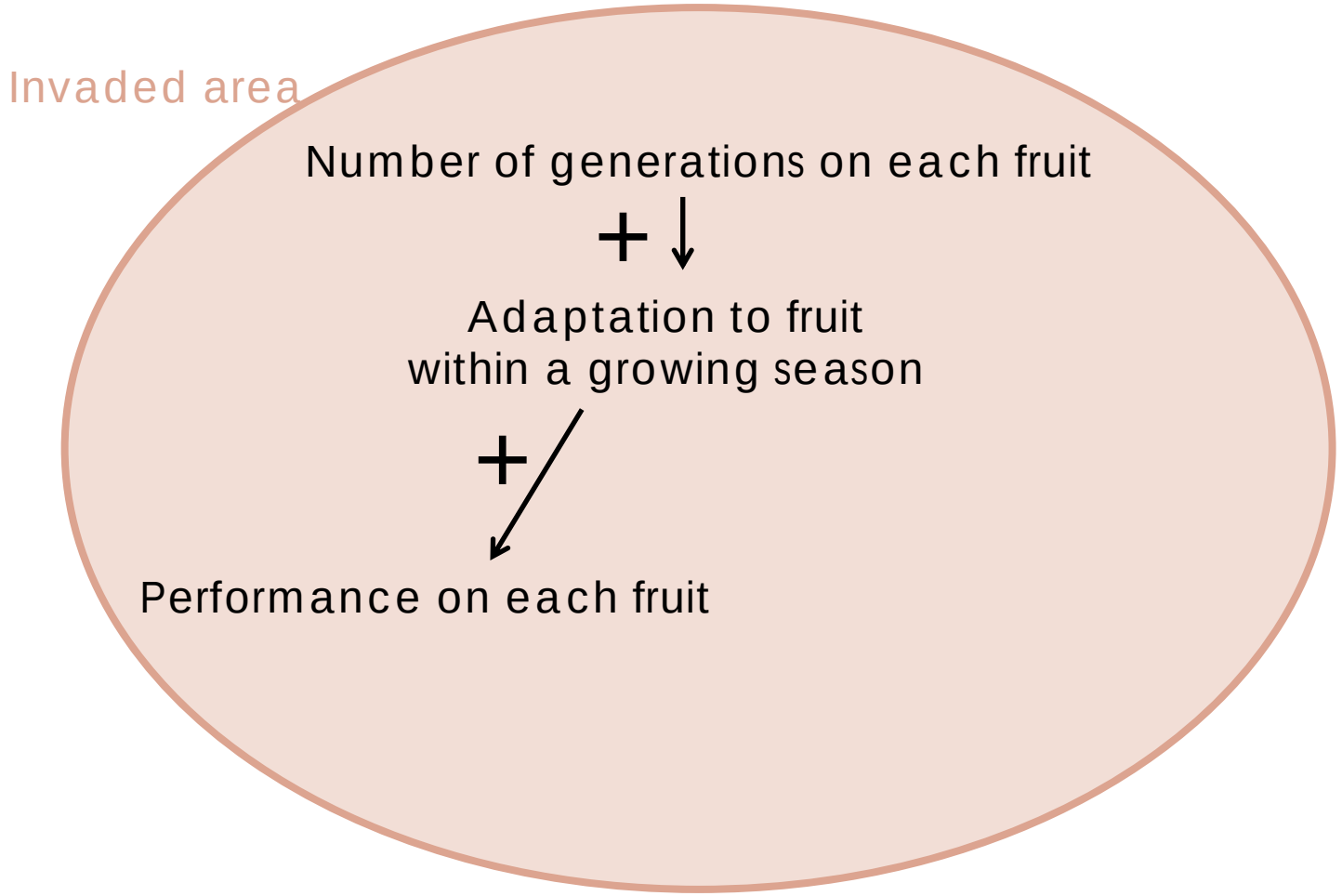
Alternative hypothesis: Phenology involved



Alternative hypothesis: Phenology involved



Alternative hypothesis: Phenology involved



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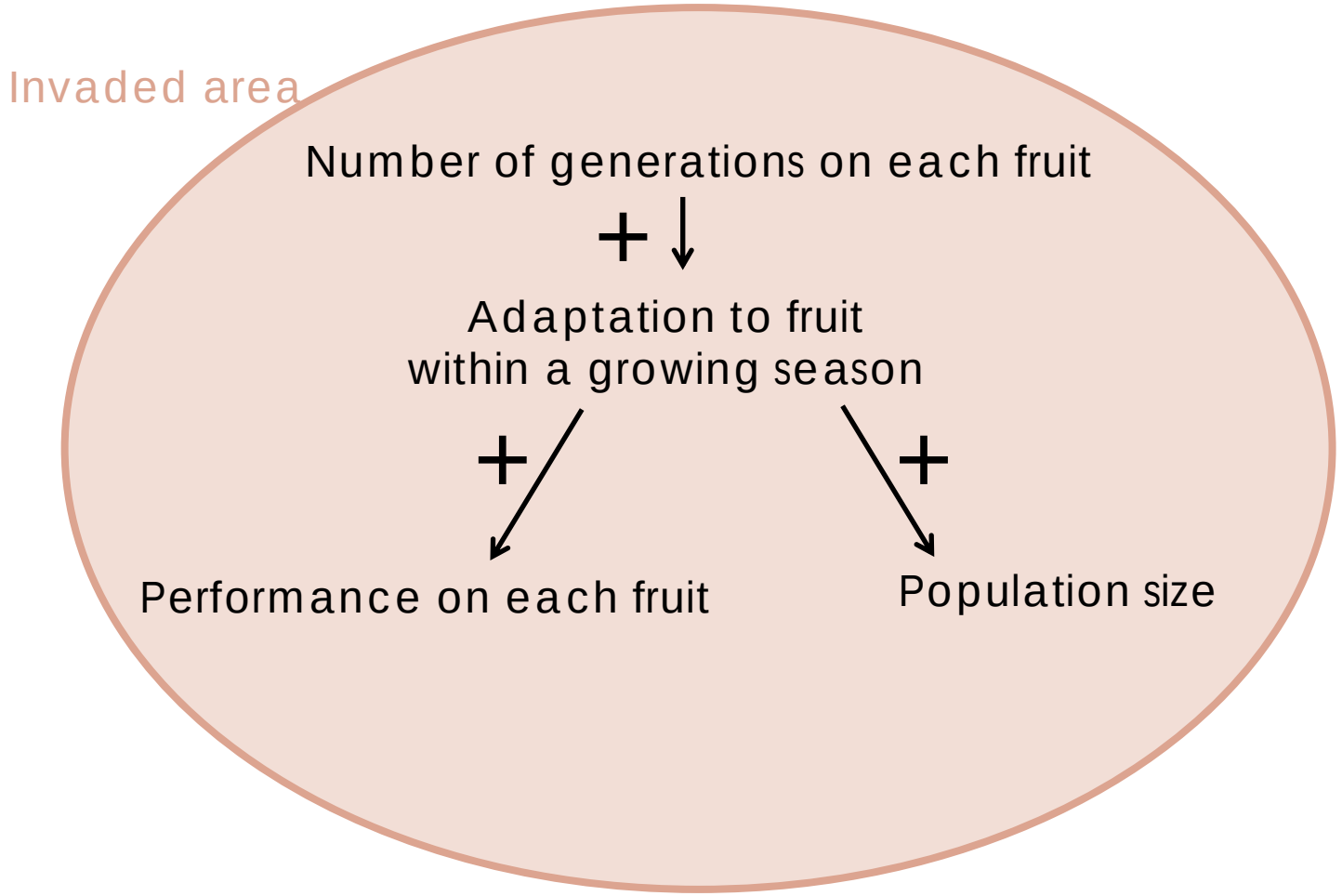
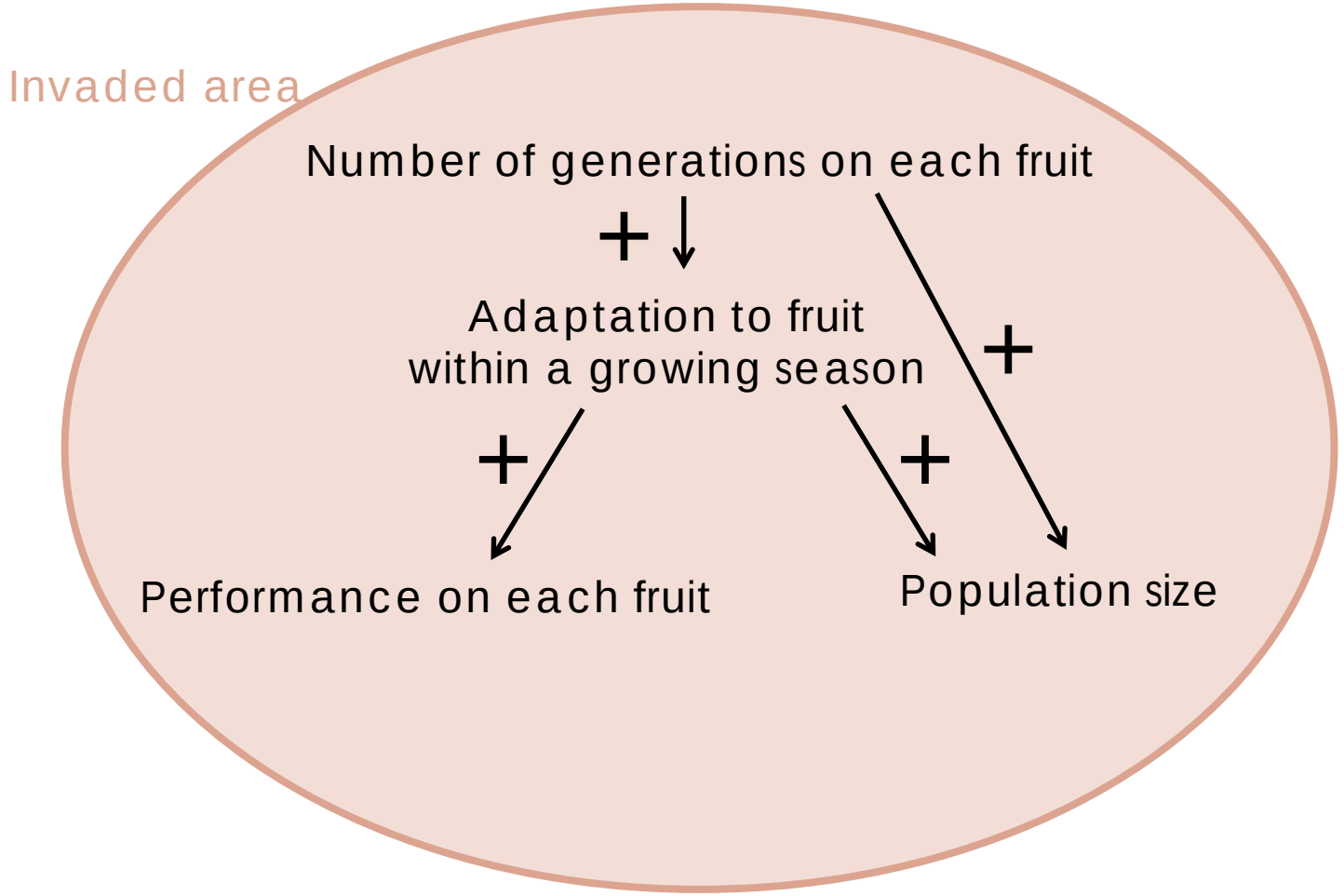


Alternative hypothesis: Phenology involved



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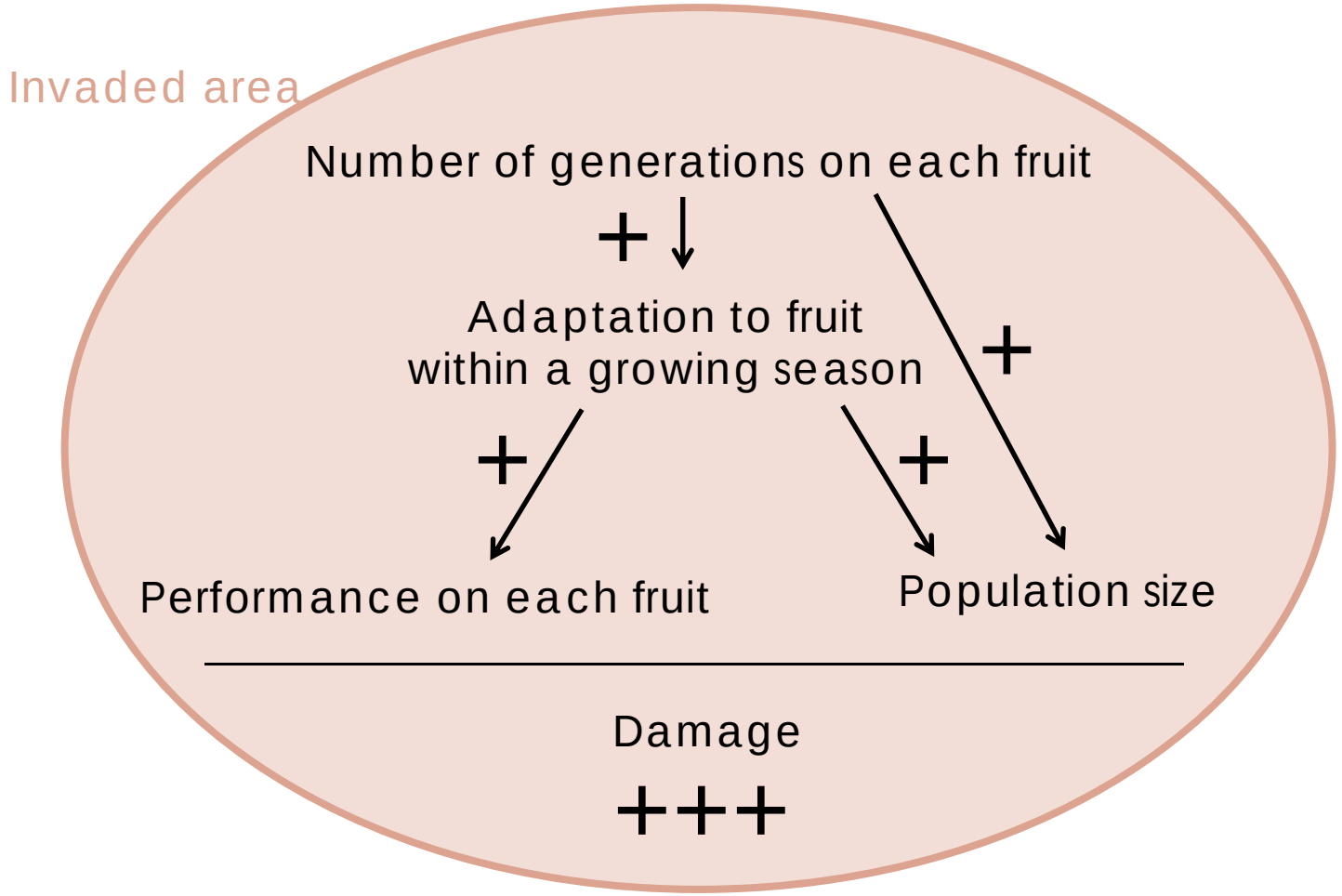
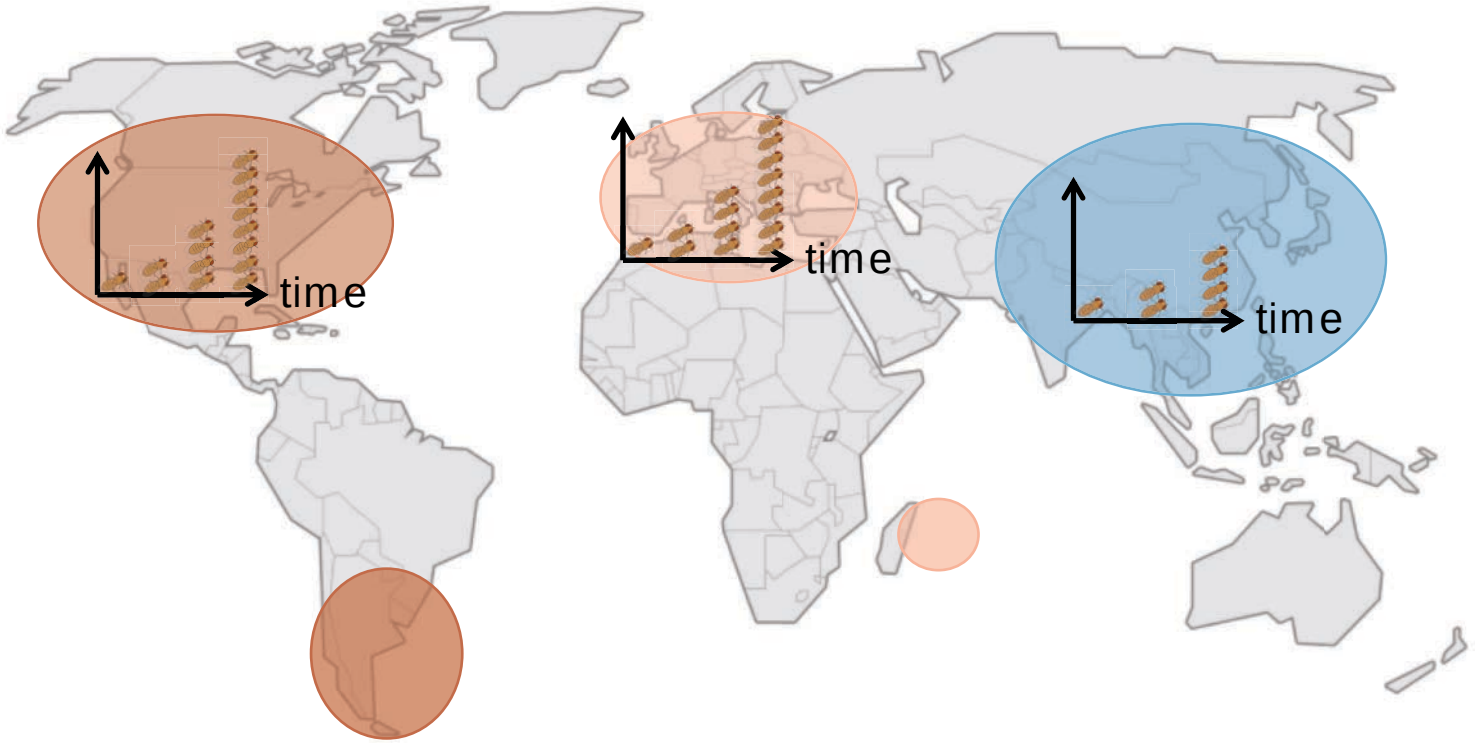


Candidat traits impacted by demographic processes?

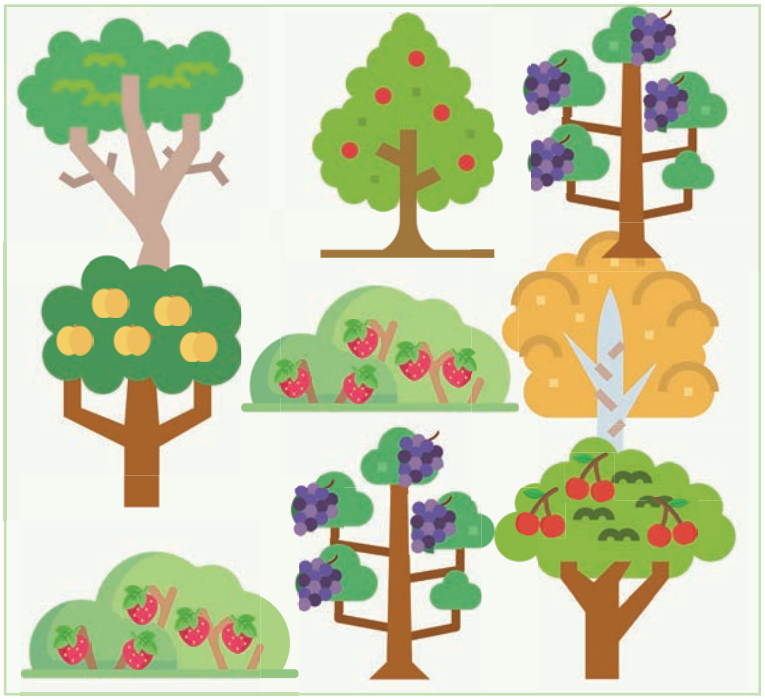


Direct approach: phenotypic study of candidats traits

Integrated pest management

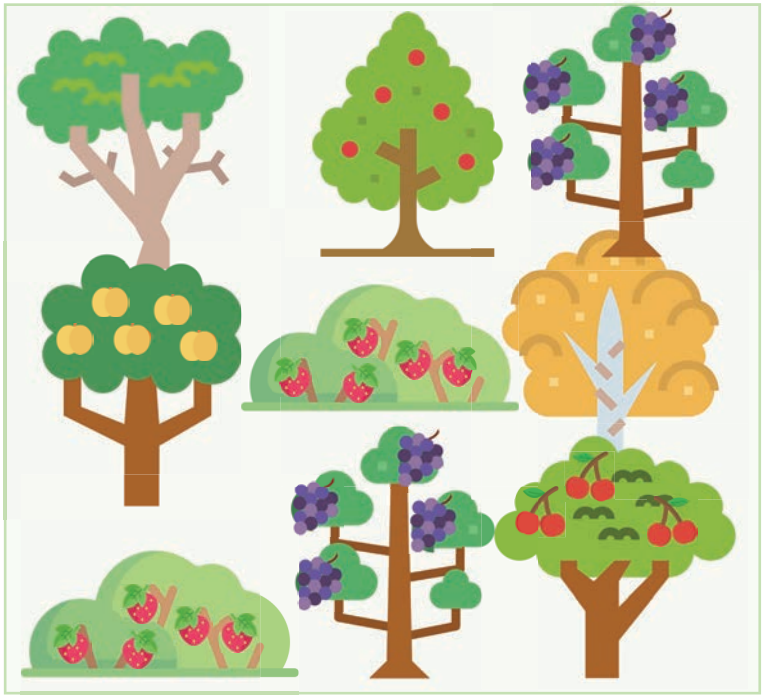
Integrated pest management

Polyculture

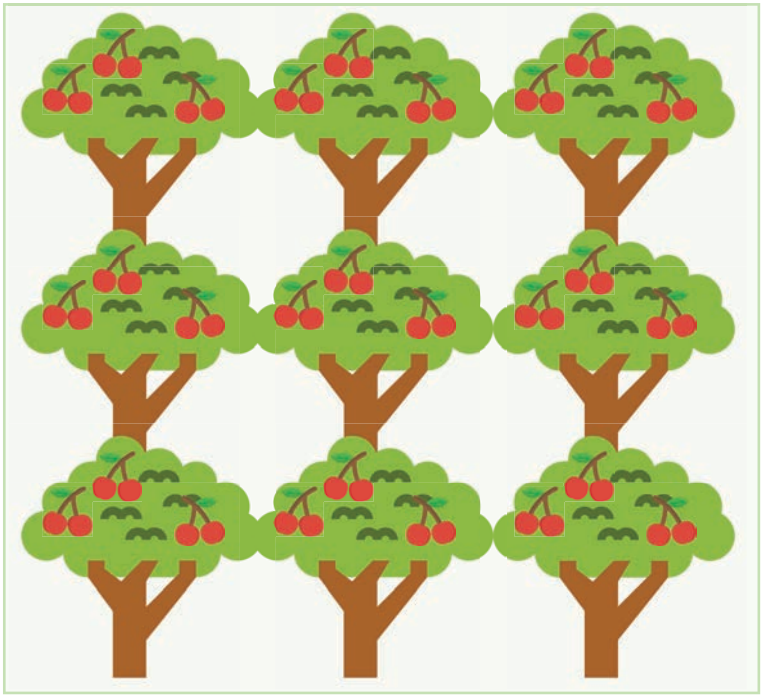


Integrated pest management

Polyculture



Monoculture



More damages?

Adaptive responses of *Drosophila suzukii*, a generalist invasive species

Laure Olazcuaga

13 December 2019

Supervision: Arnaud Estoup and Mathieu Gautier