

# Ecological discontinuity packages genes into discrete units of diversity

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# Authors

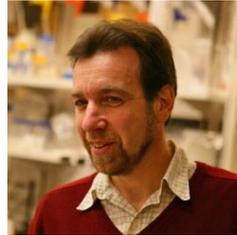
Romain Villoutreix



Clarissa Ferreira  
de Carvalho



Jeff Feder



Zach Gompert



Patrik Nosil



# Continuous vs discrete variation

*Continuous variation*

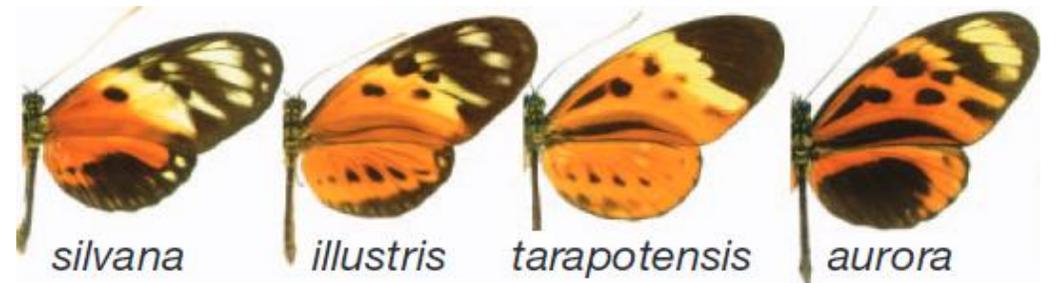
*Arctia plantaginis*



From Carita *et al.*, 2011, Behavioral Ecology.

*Discrete variation*

*Heliconius numata*



From Joron *et al.*, 2011, Nature.

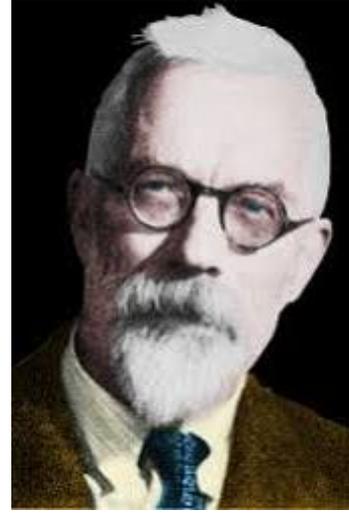
# Discrete morphs have fascinated biologists for a long time



Charles Darwin



Gregor Mendel

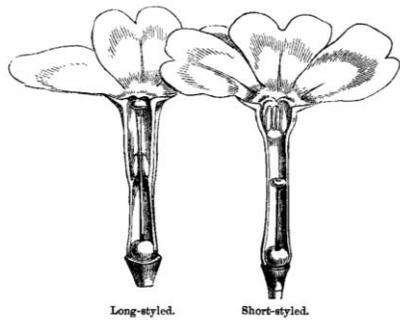


Ronald Aylmer Fisher



Edmund Brisco Ford

*Primula sp.*



*Pisum sativum*

Seed form	Seed color	Pod form	Pod color	Flower color	Flower position	Stem length
Round	Yellow	Inflated	Green	Purple	Axial	Tall
Wrinkled	Green	Constricted	Yellow	White	Terminal	Short

*Cepea nemoralis*

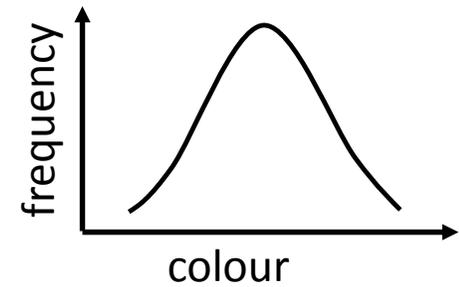
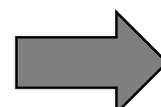
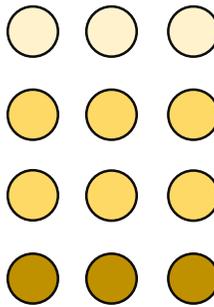
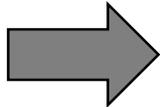
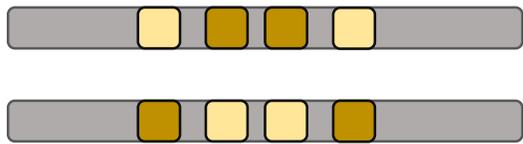
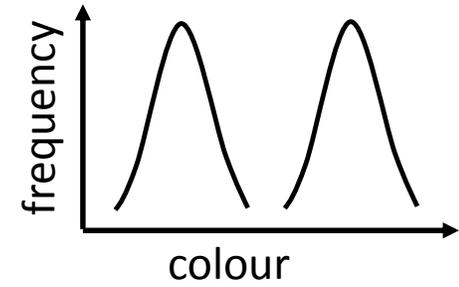
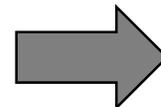
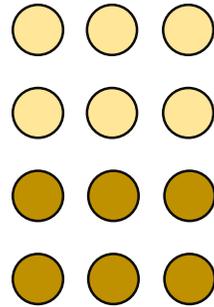
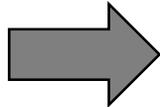
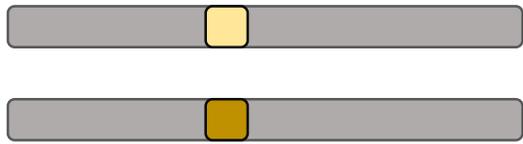


*Callimorpha dominula*



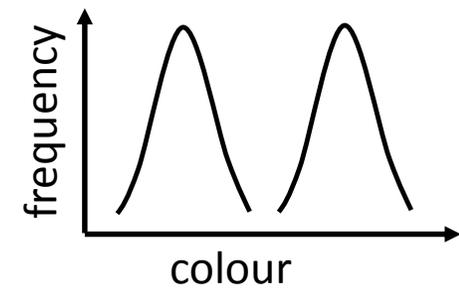
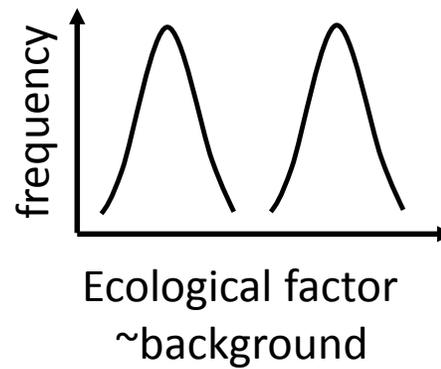
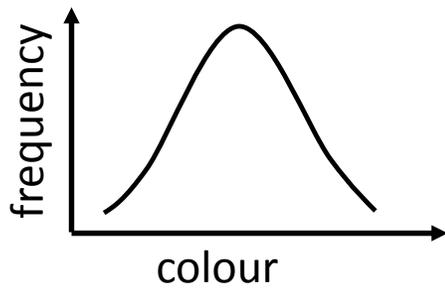
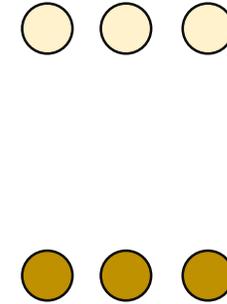
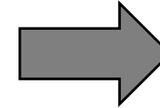
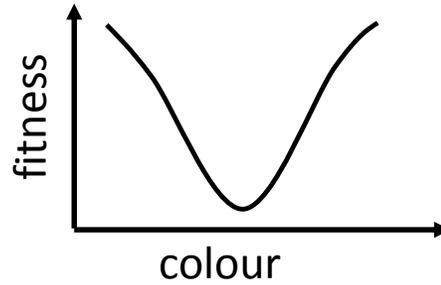
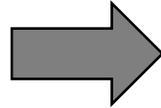
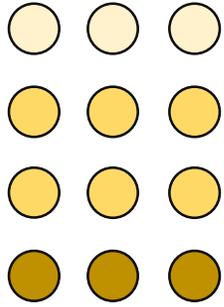
# Continuous vs discrete variation: genetic factors

Number of loci



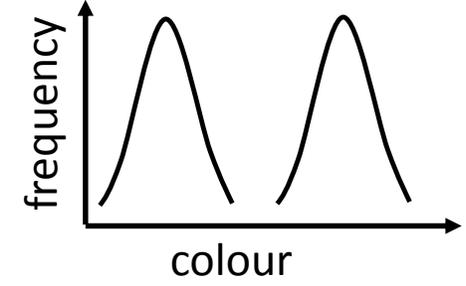
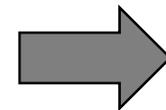
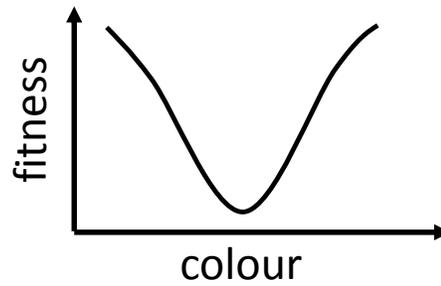
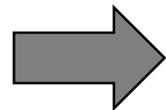
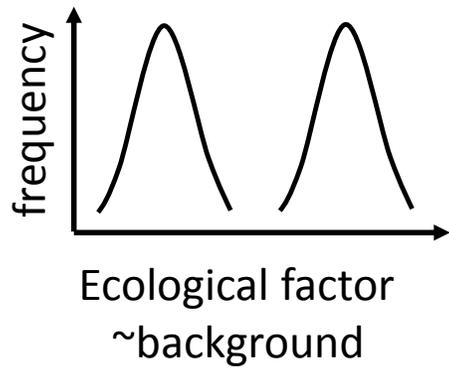
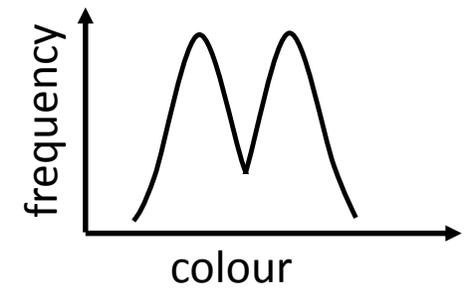
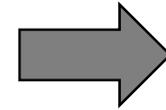
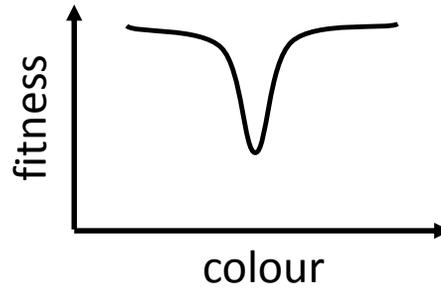
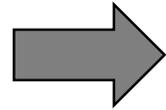
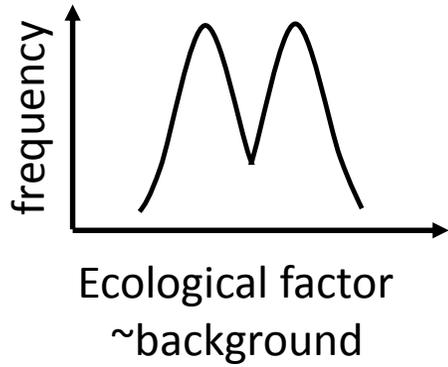
# Continuous vs discrete variation: ecological discontinuity

Disruptive selection



# Continuous vs discrete variation: ecological discontinuity

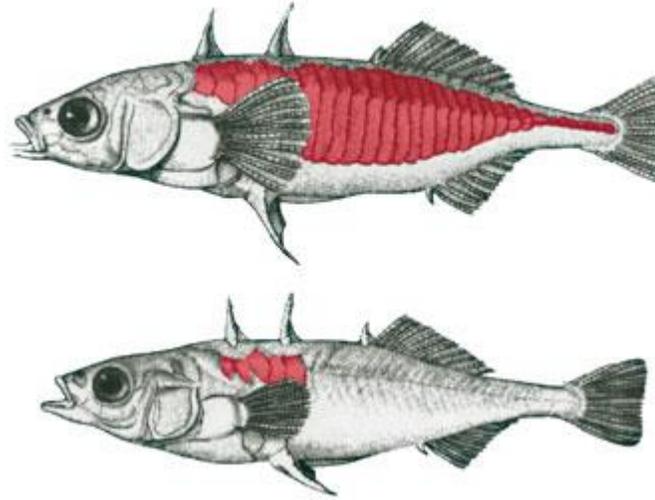
Expectations



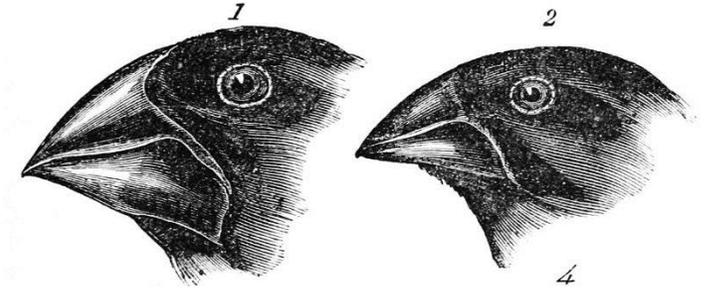
# Ecological discontinuity and disruptive selection



*Peromyscus sp.*



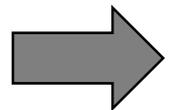
*Gasterosteus aculeatus*



*Geospiza sp.*

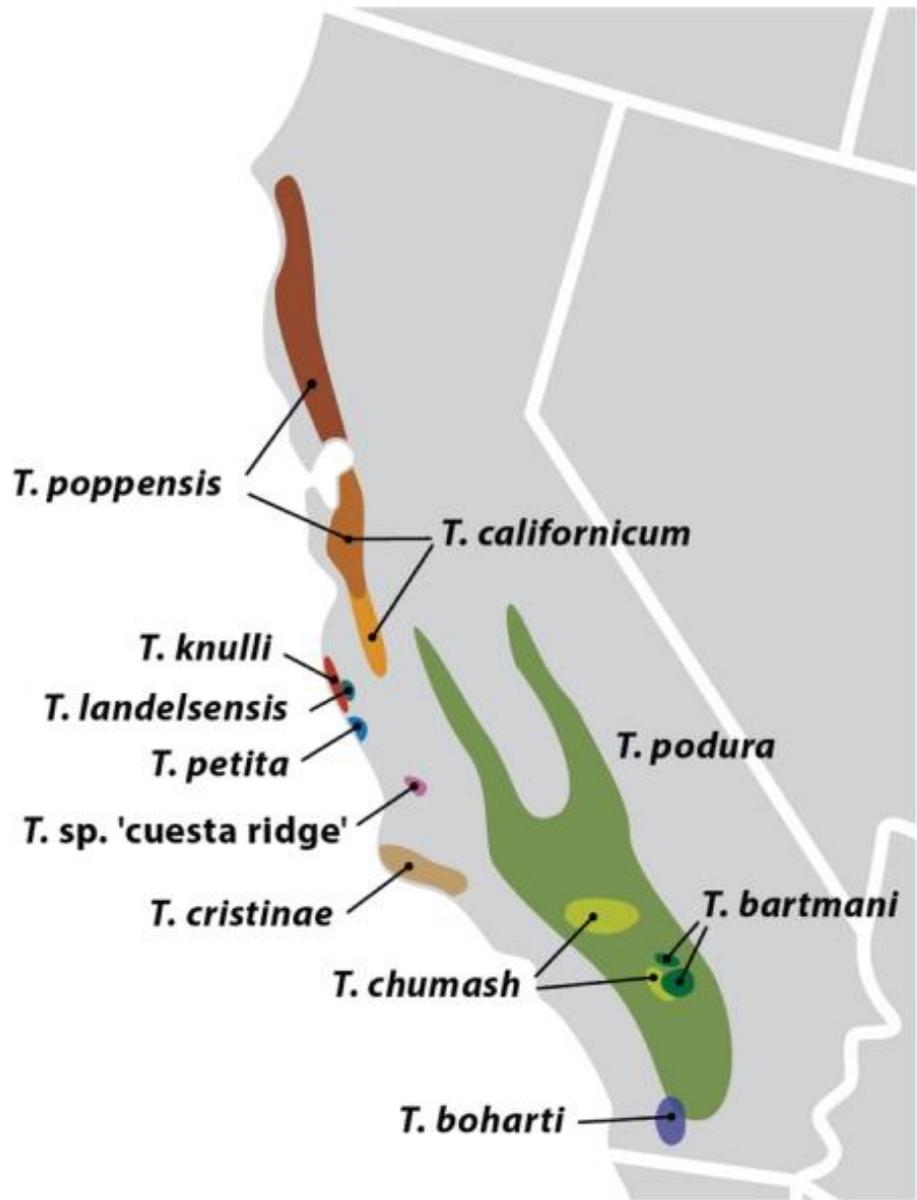
Ecological factor sometimes unknown

(Disruptive) selection inferred rather than estimated



A single level of ecological discontinuity studied





11 sexual species (root ~ 30Mya)



Coastal



Chaparral



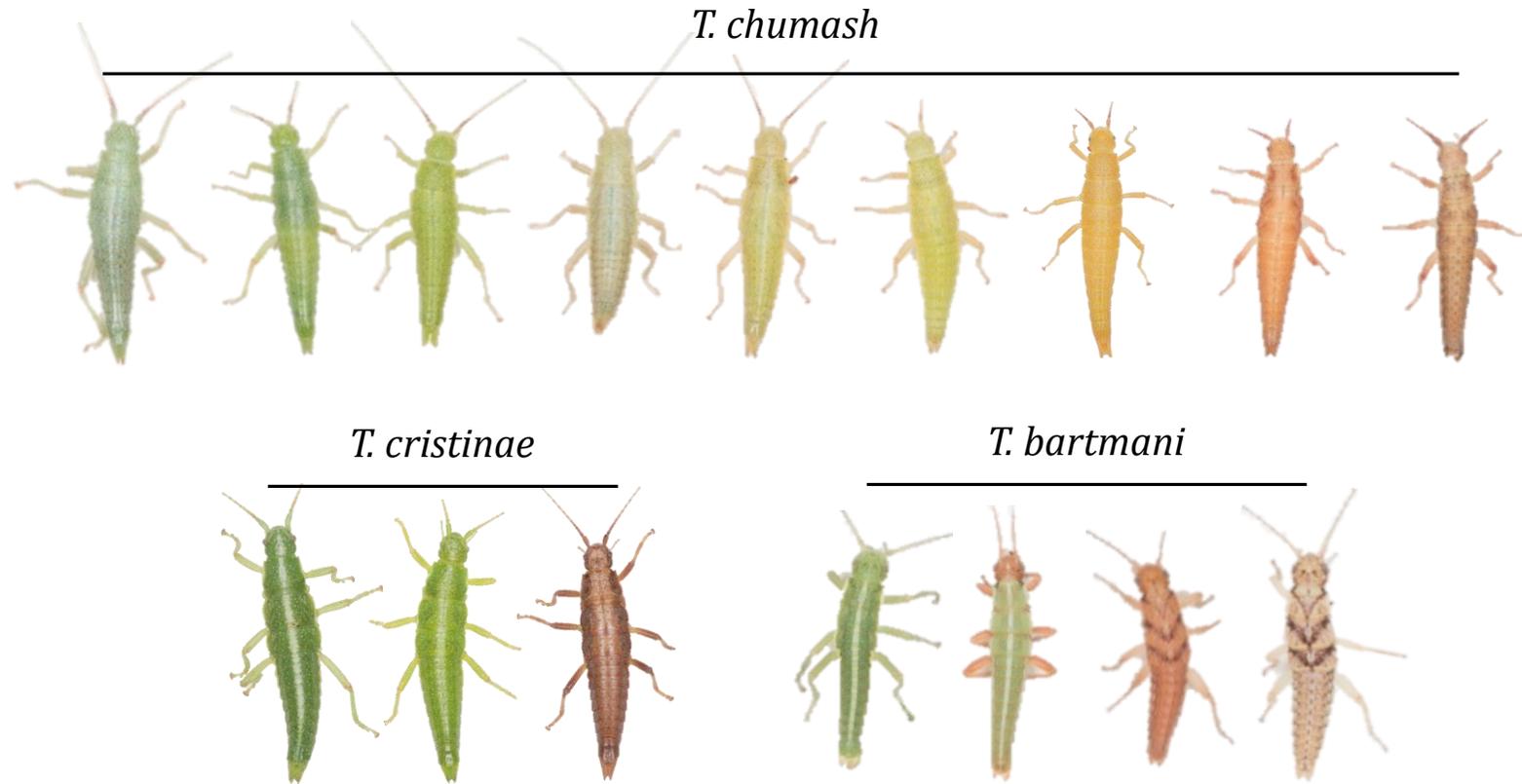
Alpine







# Body colouration in *Timema* sp.

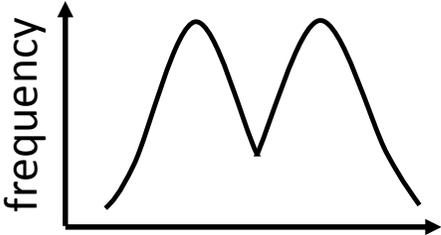
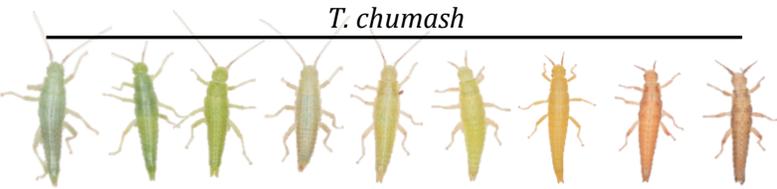


Genetically encoded (Villoutreix *et al.* Science 2020)

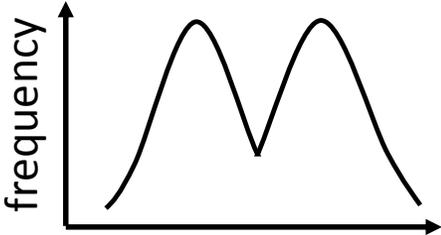
Different degrees of discontinuity, but never formally quantified

We never quantified host plant colouration (leaves vs stems)

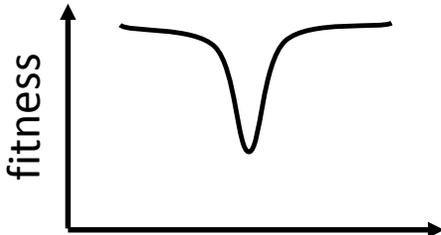
# Expectations in *Timema* sp.



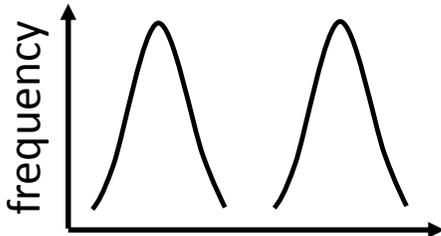
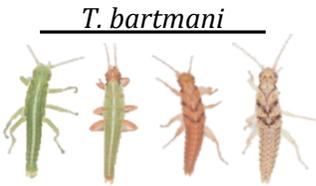
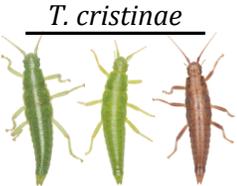
*Timema* colour  
Green to brown



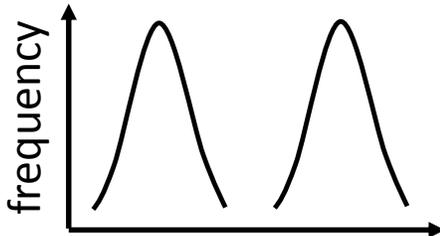
Hosts colour  
Green to brown



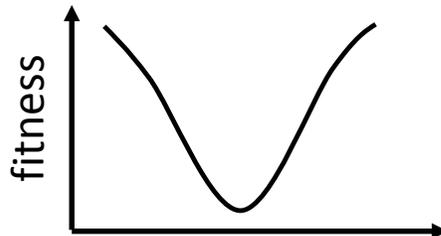
*Timema* colour



*Timema* colour  
Green to brown

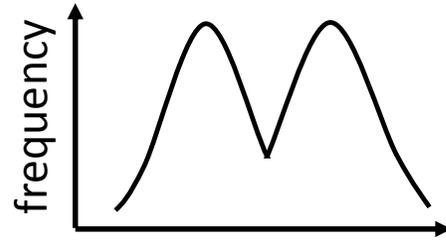
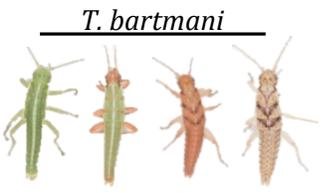
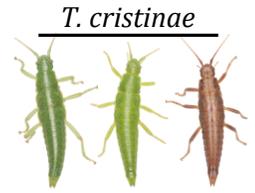
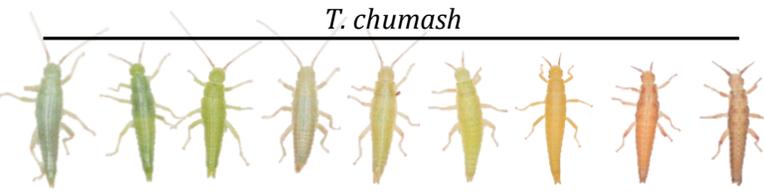


Hosts colour  
Green to brown

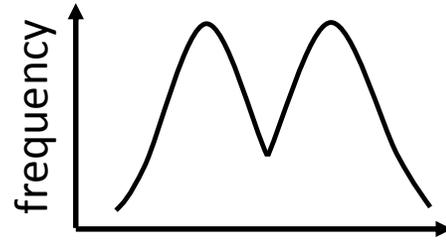


*Timema* colour

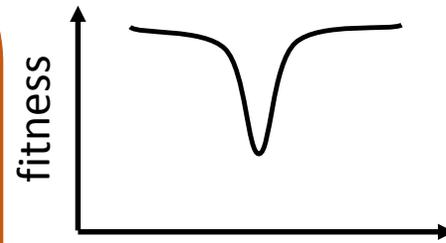
# Expectations in *Timema* sp.



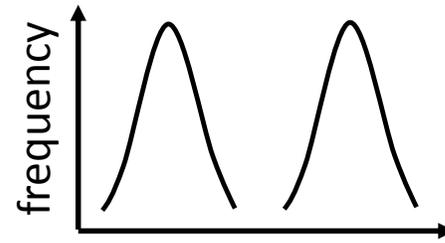
*Timema* colour  
Green to brown



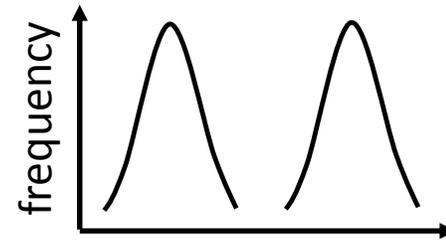
Hosts colour  
Green to brown



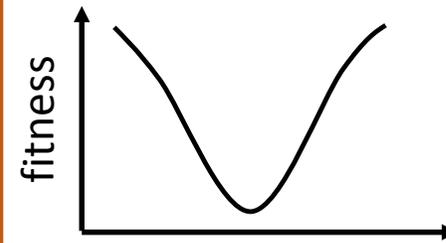
*Timema* colour



*Timema* colour  
Green to brown



Hosts colour  
Green to brown



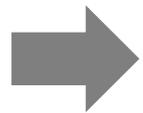
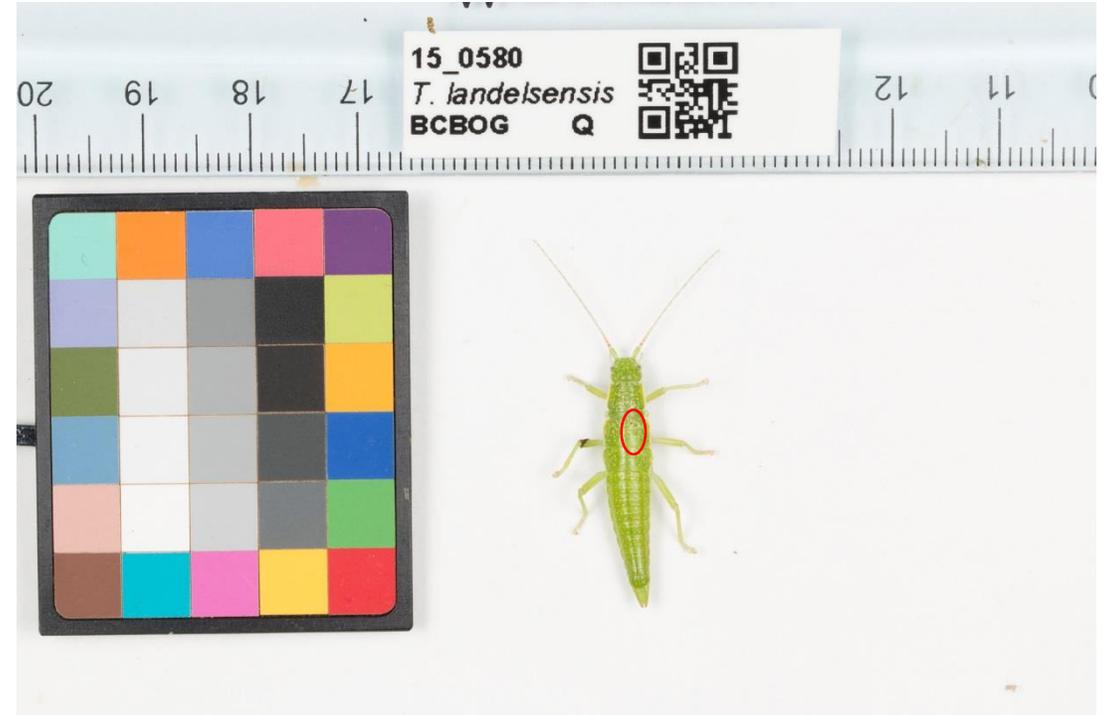
*Timema* colour

# Sampling of *Timema* natural populations



➔ Sampling of natural populations in 2015, plus previous sampling in 2013 (3 populations, 881 insects, 3 species)

# Quantification of colour in *Timema* sp.



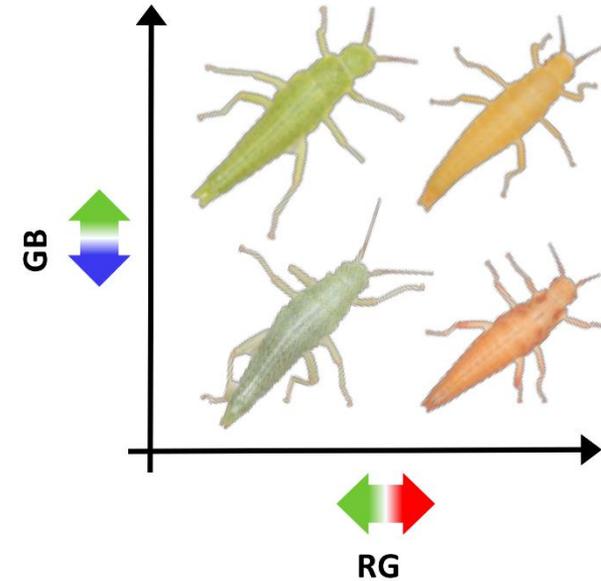
Standardized pictures

Amount of red, green and blue

# Quantification of colour in *Timema* sp.



(b) RG - GB color space

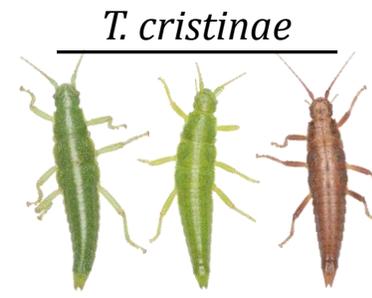
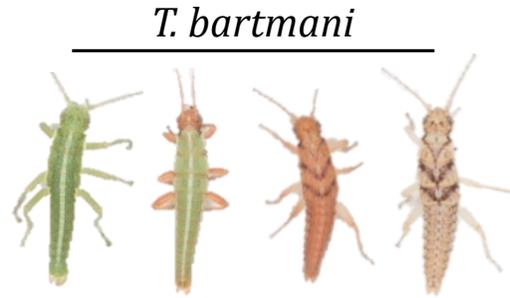
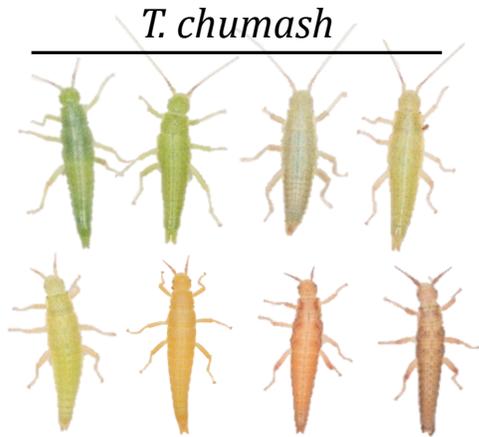
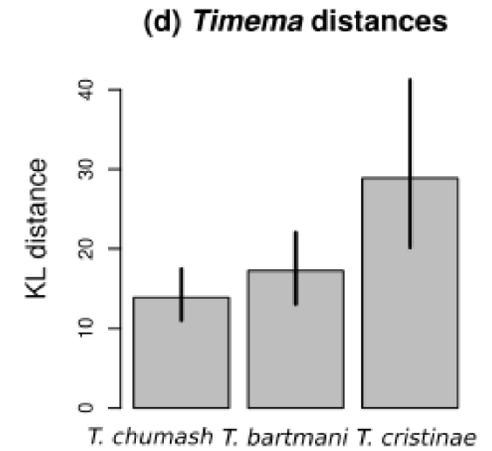
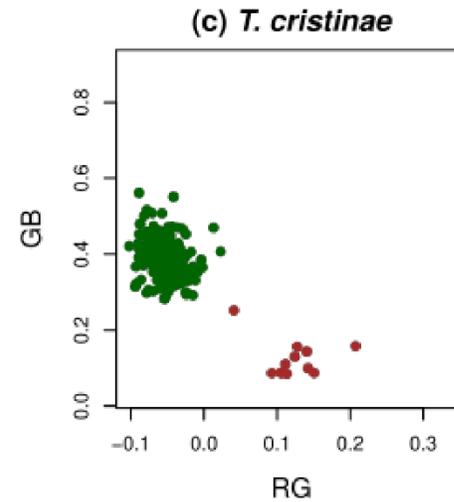
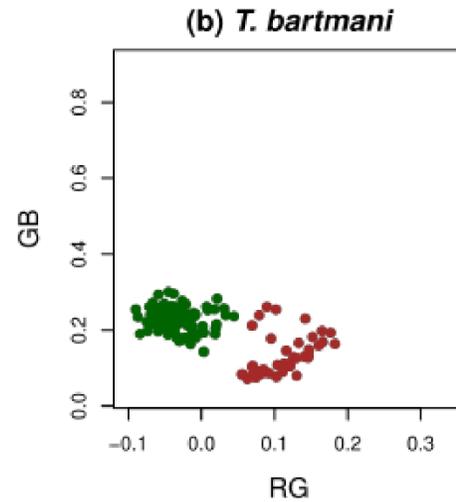
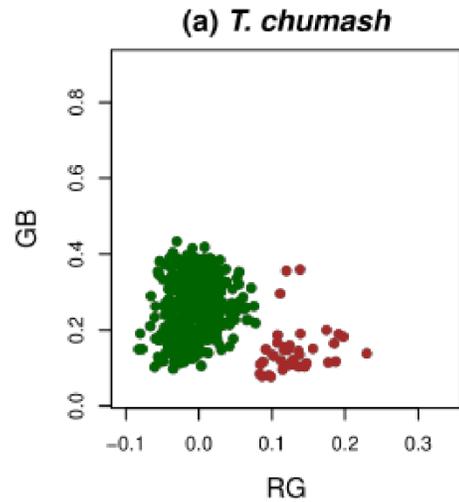


➔ Standardized pictures

Amount of red, green and blue colour

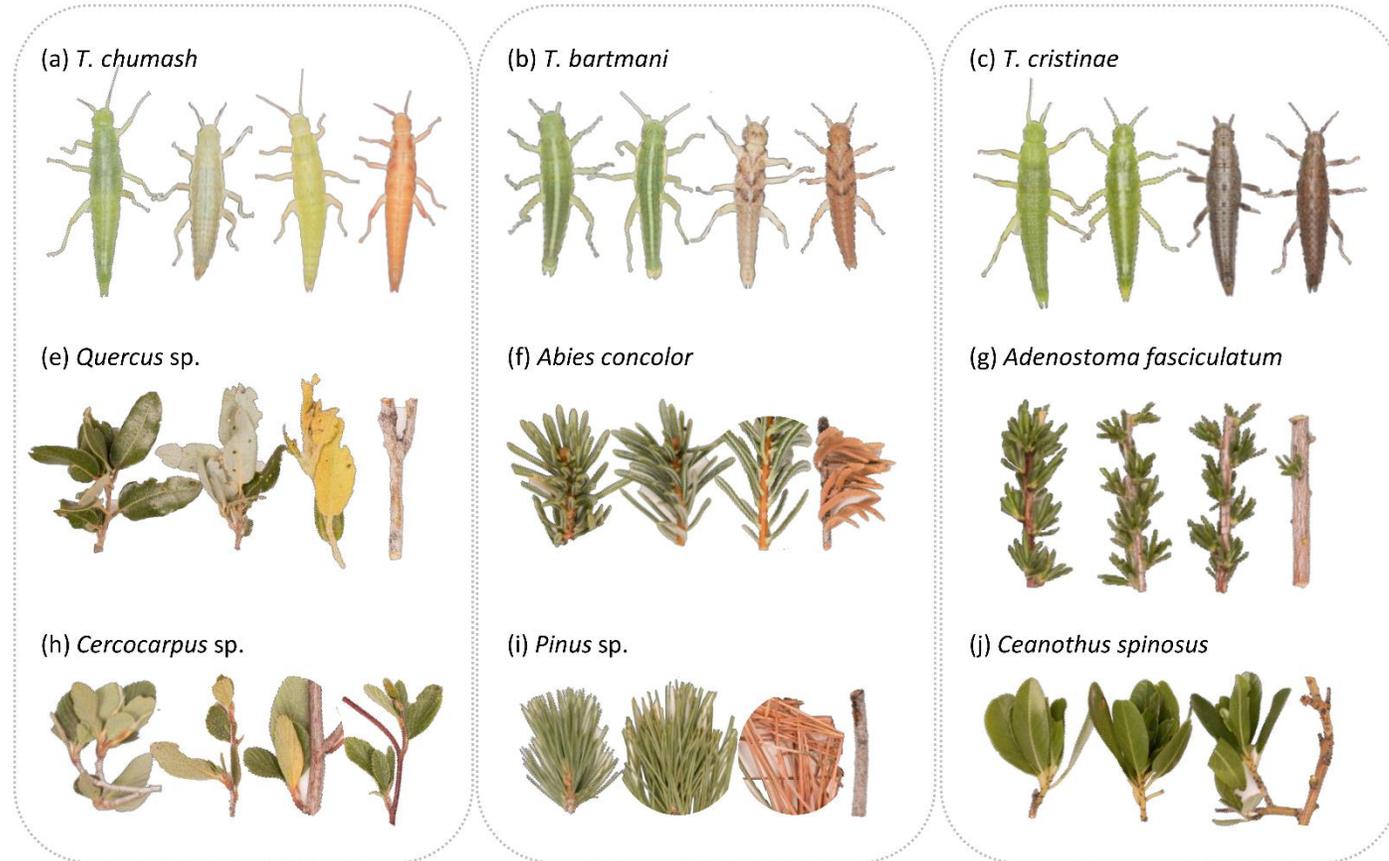
Colour space: Red/Green (RG) and Green/Blue (GB) ratios (Endler, 2012)

# Colour morphs are less discontinuous in *T. chumash*



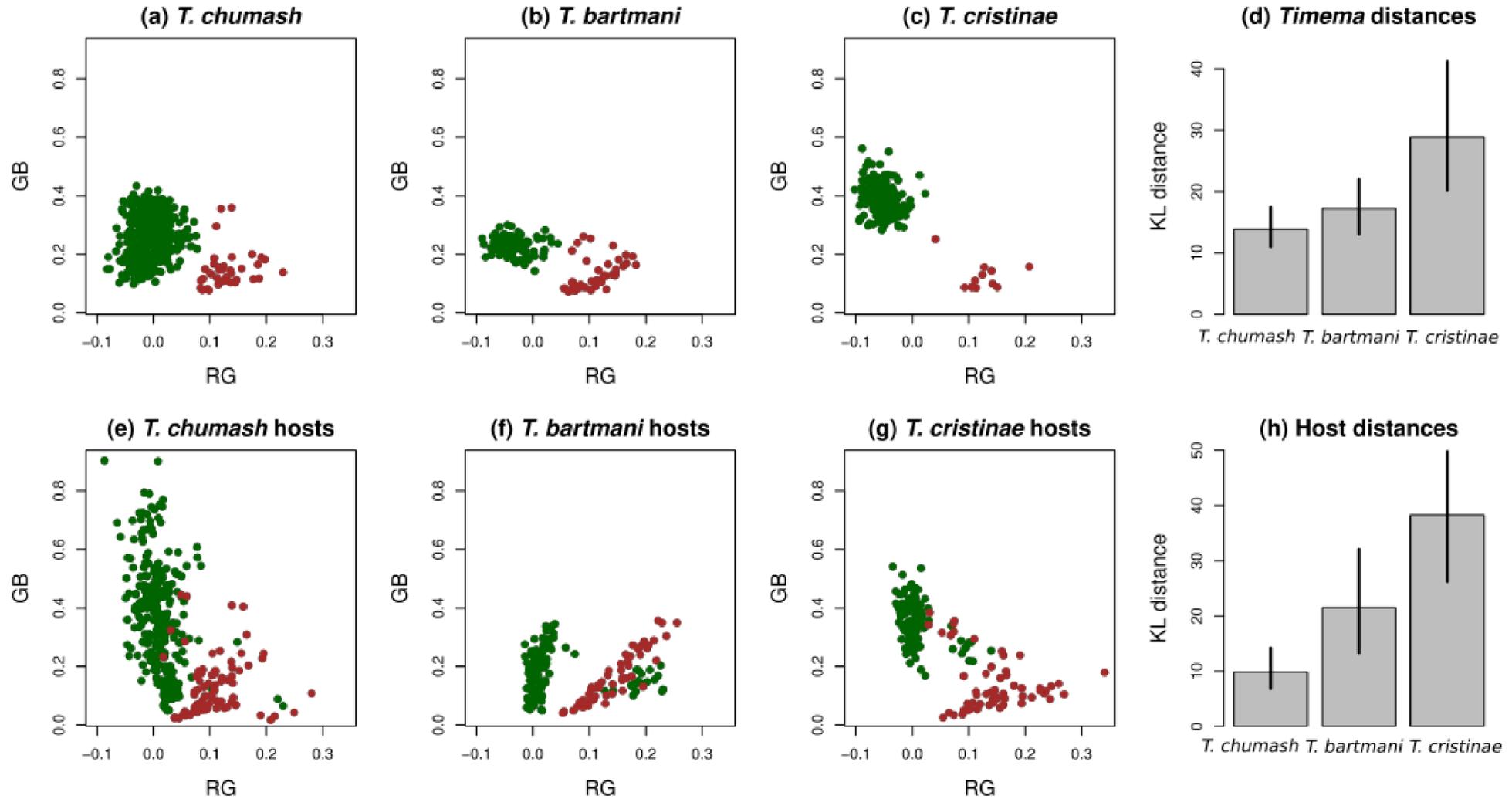
Are *T. chumash*'s host plants less differentiated in colour than *T. bartmani*'s and *T. cristinae*'s ?

# Quantification of host plants colour

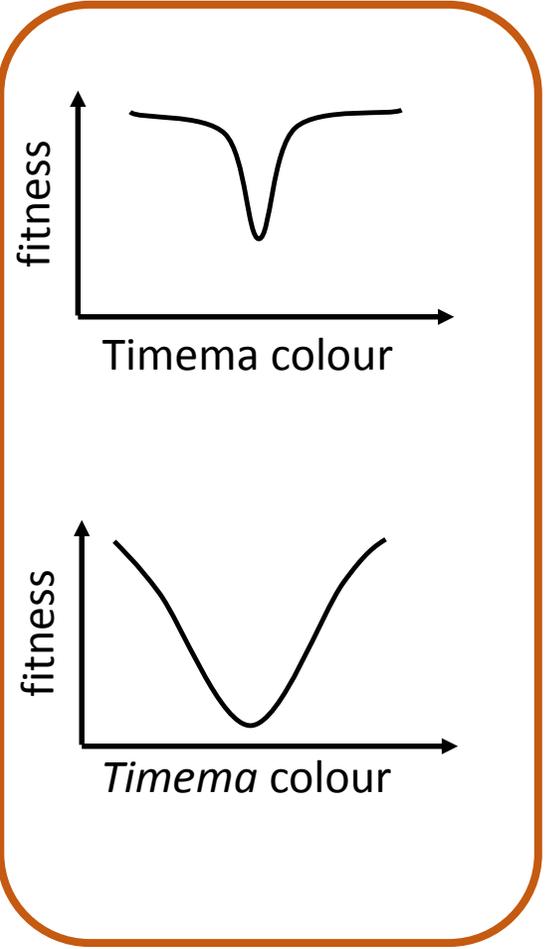
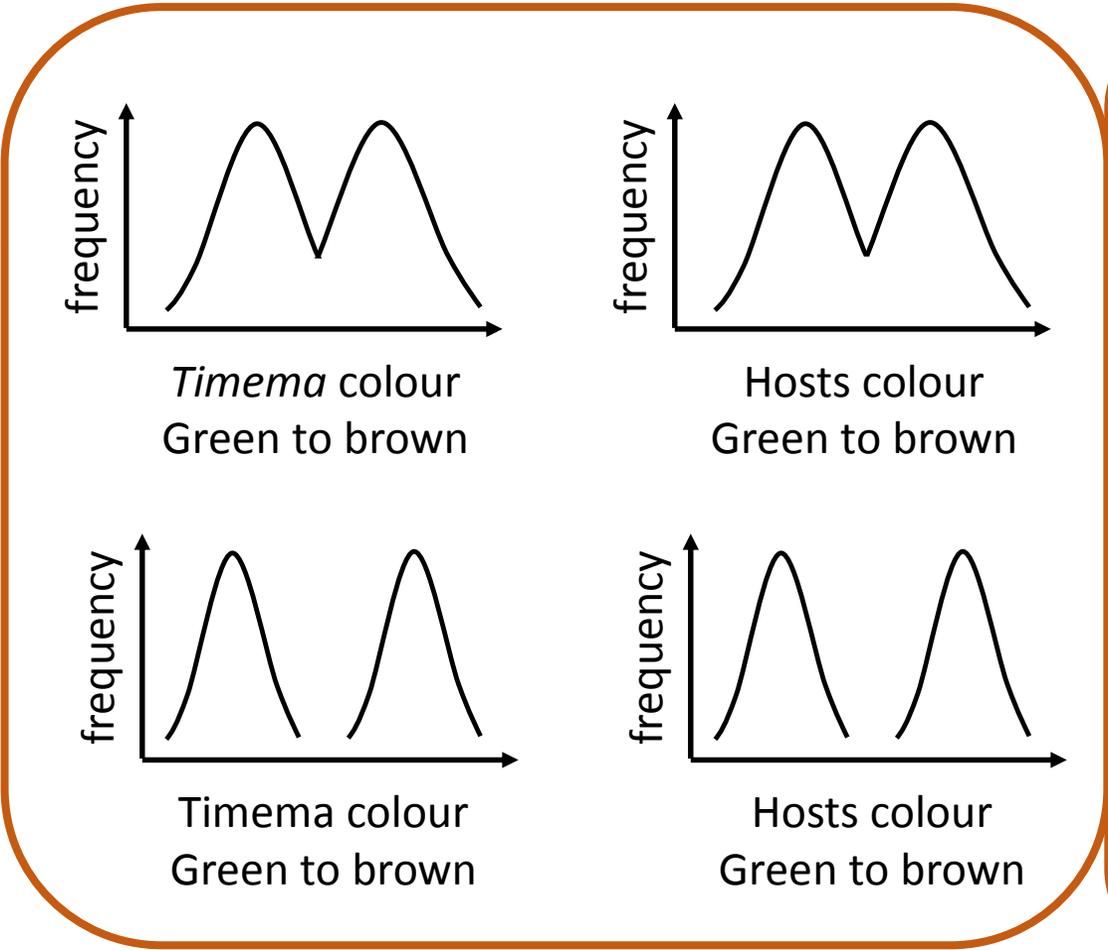
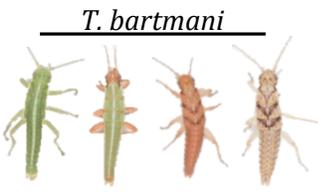
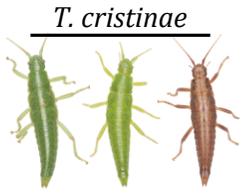
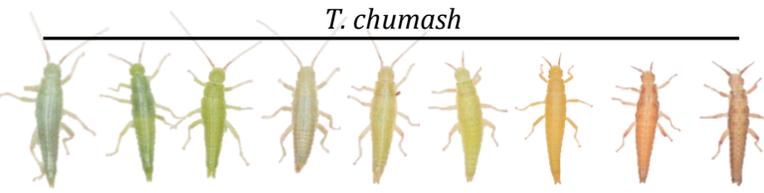


Approach similar to *Timema* for quantifying the colour of host plants (6 species, 203 samples, 781 measurements, both leaves and stems)

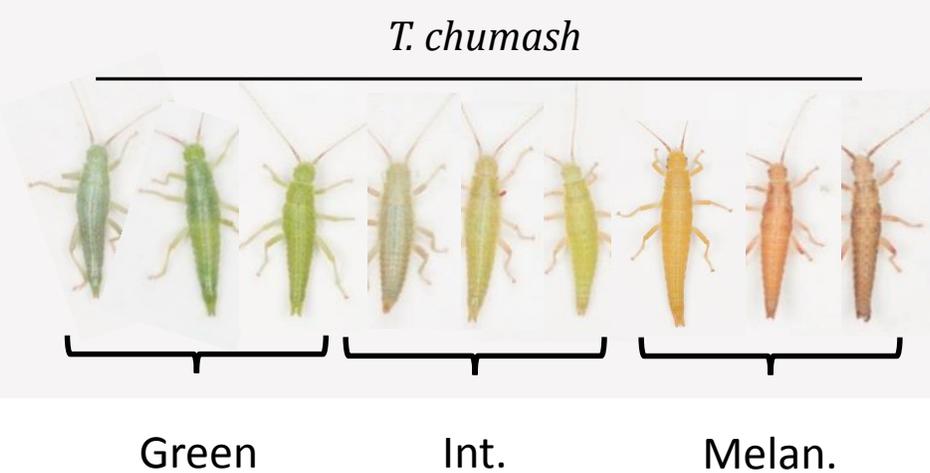
# *T. chumash's* hosts are less discontinuous



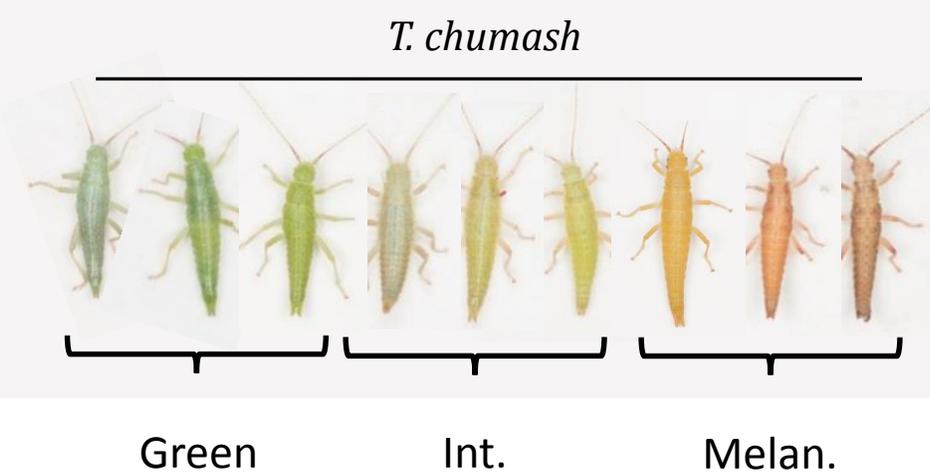
# Expectations in *Timema* sp.



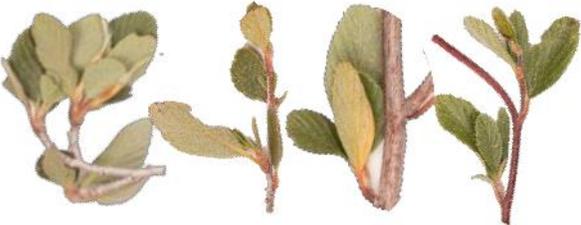
# Mark recapture on different host plants in *T. chumash*



# Disruptive selection varies between host plants



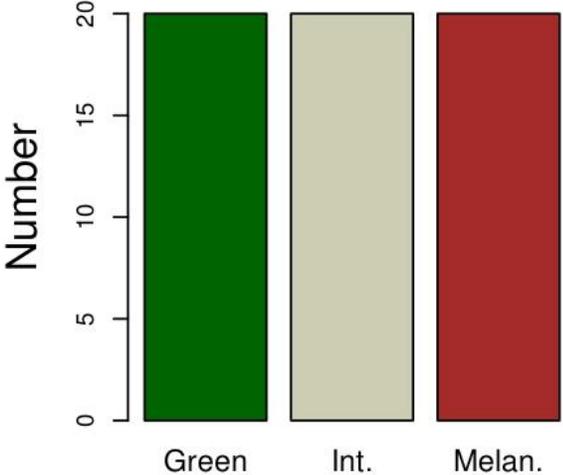
(h) *Cercocarpus* sp.



120 individuals in total

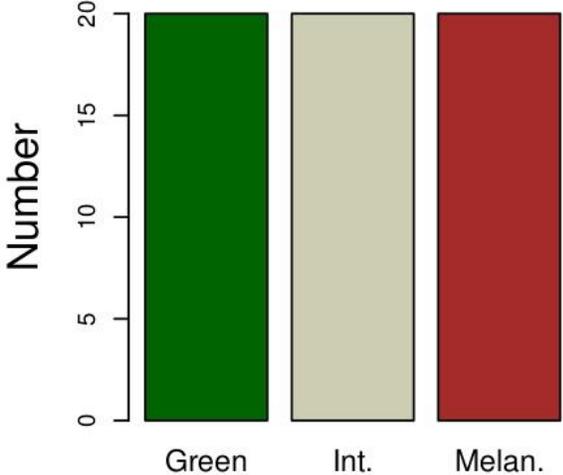
More continuous host plant

(a) Release MM



Highly discontinuous host plants

(b) Release A/C



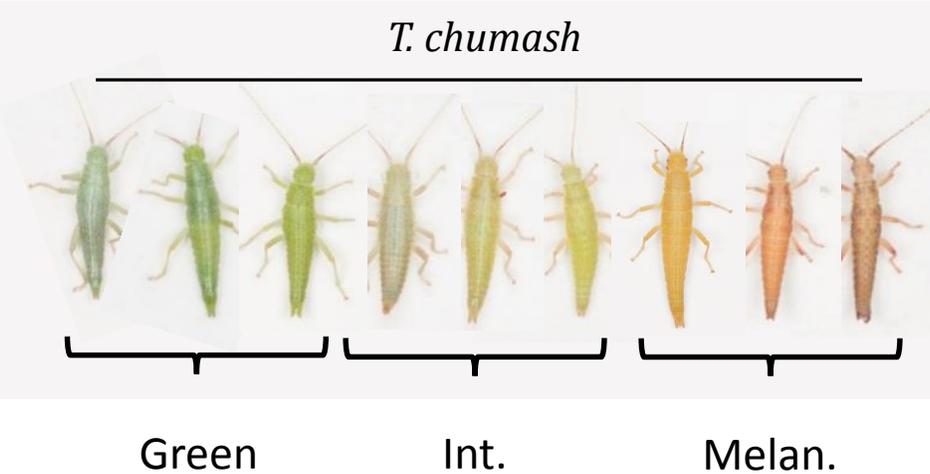
(g) *Adenostoma fasciculatum*



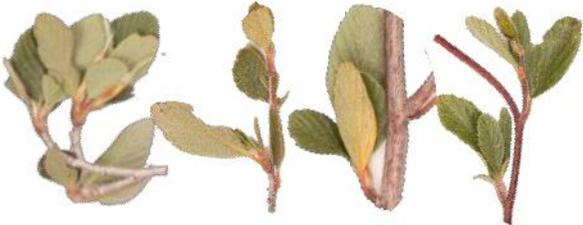
(j) *Ceanothus spinosus*



# Disruptive selection varies between host plants



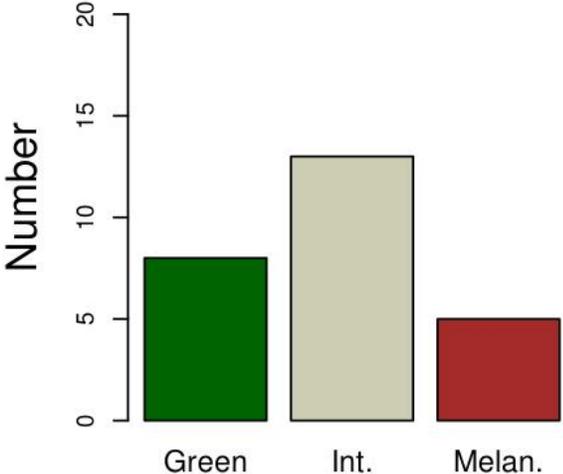
(h) *Cercocarpus* sp.



120 individuals in total  
42 recaptured (35%)

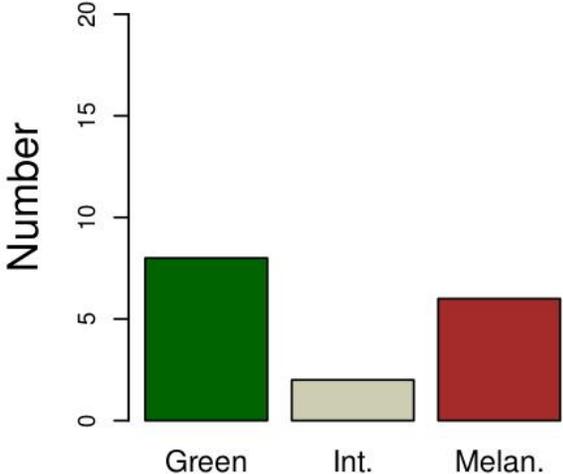
More continuous host plant

(c) Recapture MM



Highly discontinuous host plants

(d) Recapture A/C



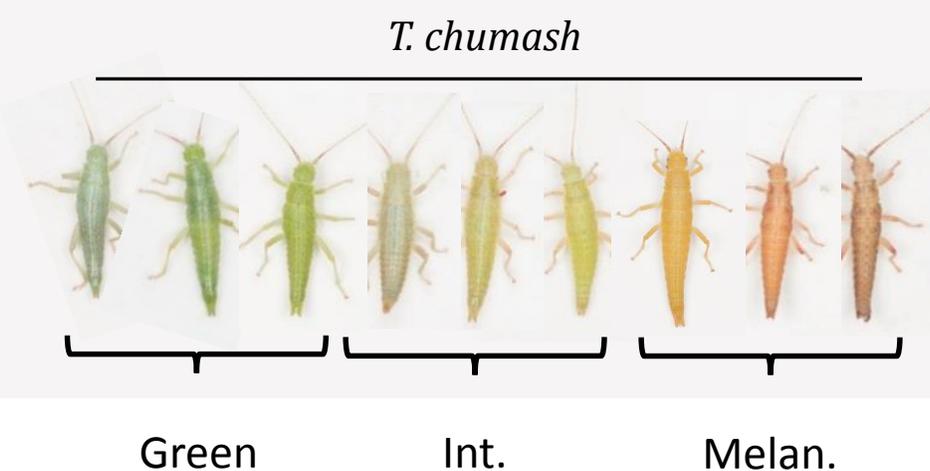
(g) *Adenostoma fasciculatum*



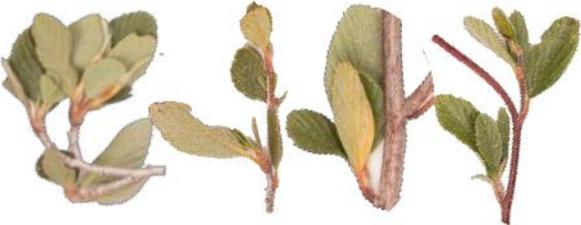
(j) *Ceanothus spinosus*



# Disruptive selection varies between host plants

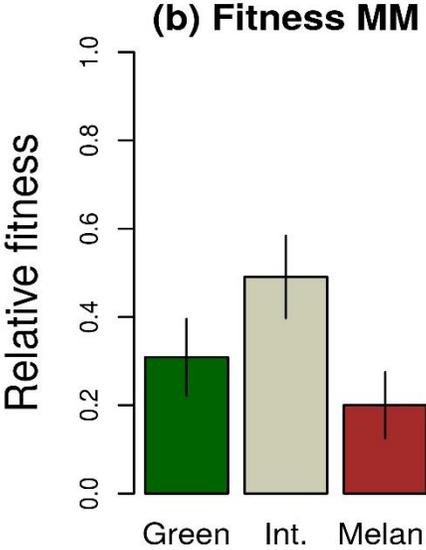


(h) *Cercocarpus* sp.

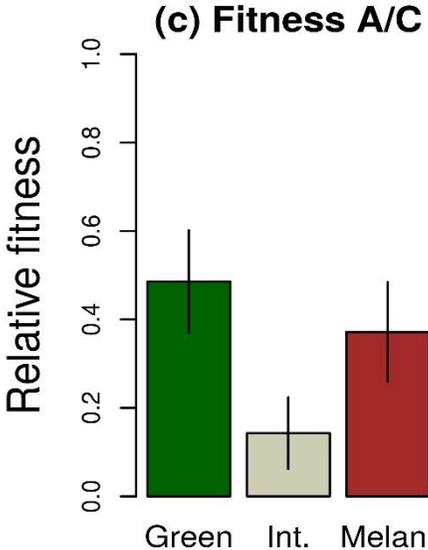


Intermediates survival MM > A/C.  
 P.P. = 0.99  
 (multinomial-Dirichlet model)

More continuous host plant



Highly discontinuous host plants



(g) *Adenostoma fasciculatum*



(j) *Ceanothus spinosus*



# Disruptive selection varies between host plants



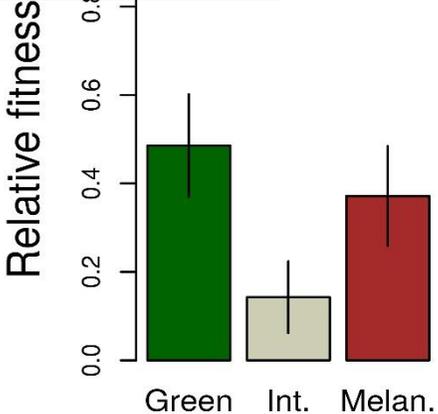
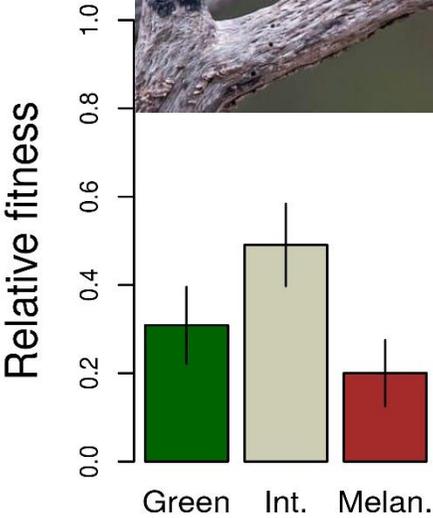
Thanks!



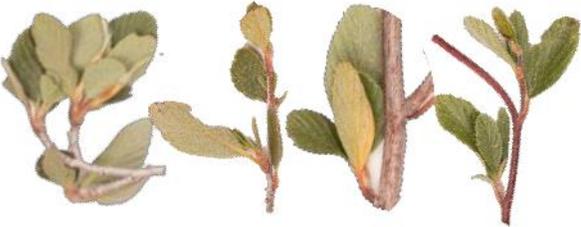
More co

ous host plants

less A/C



(h) *Cercocarpus sp.*



Intermediates survival MM > A/C.  
 P.P. = 0.99  
 (multinomial-Dirichlet model)

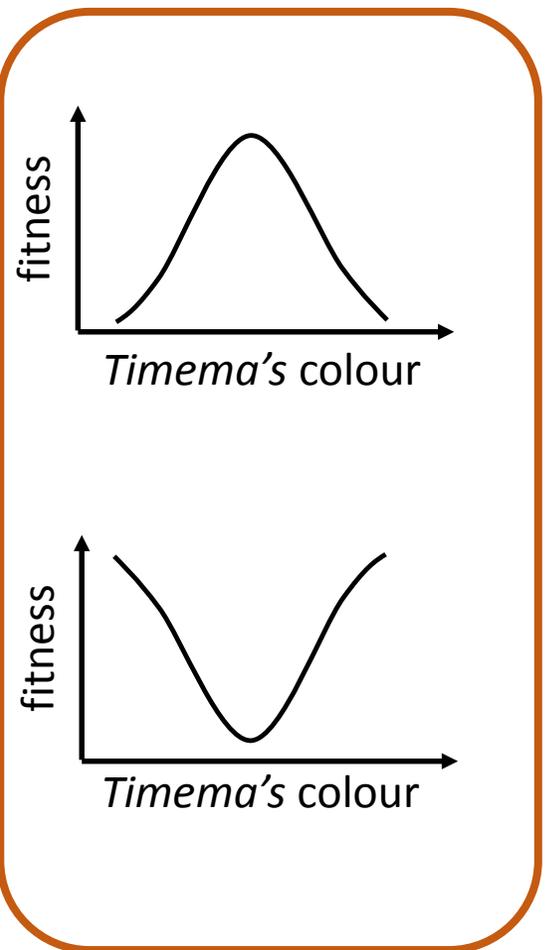
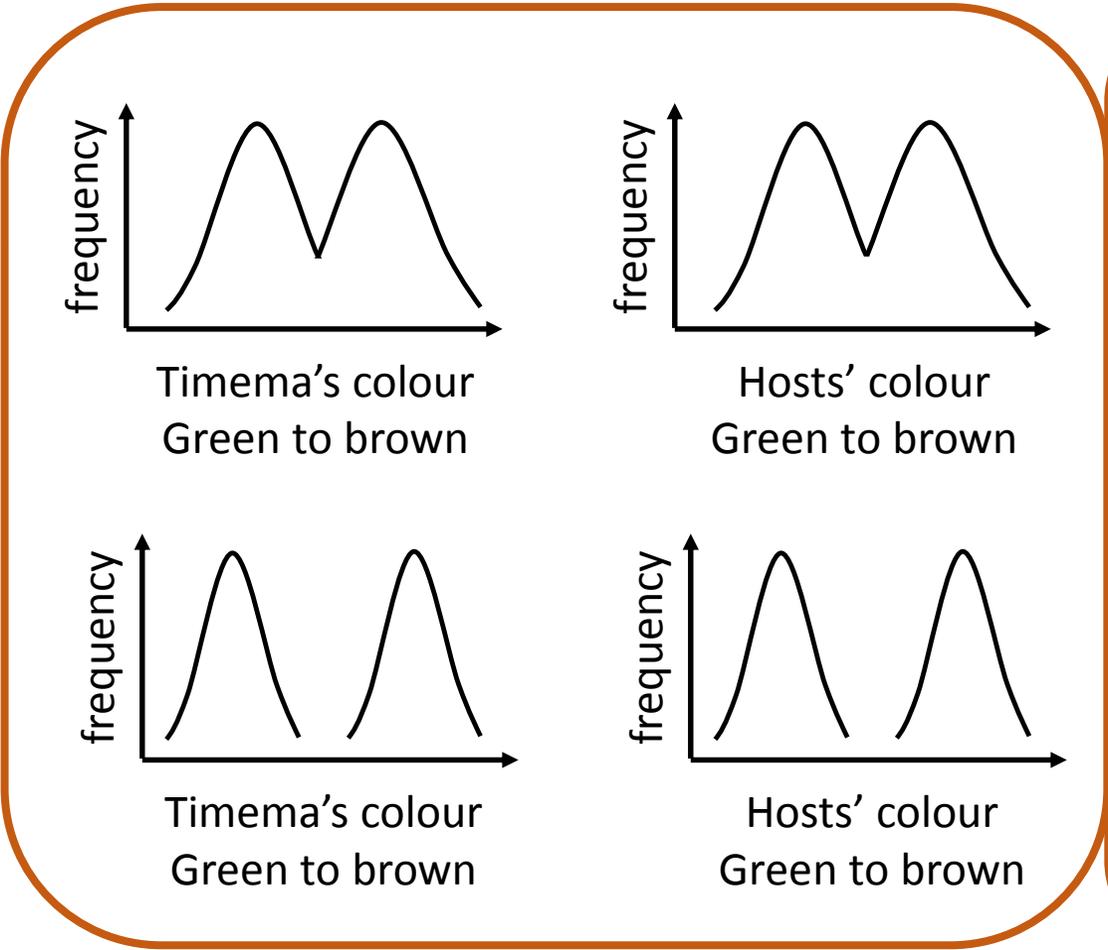
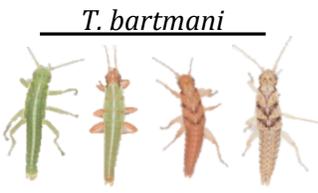
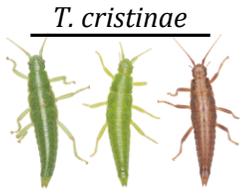
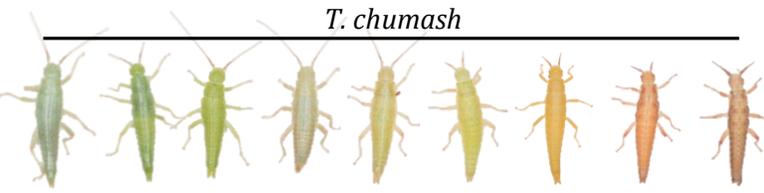
(g) *Adenostoma fasciculatum*



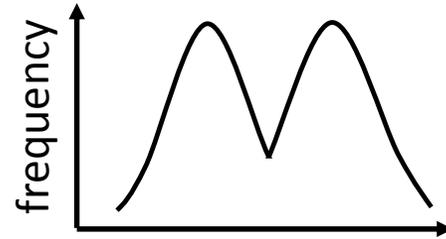
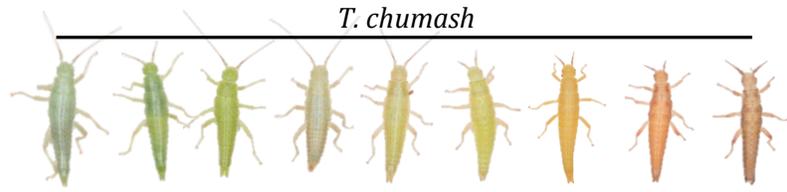
(j) *Ceanothus spinosus*



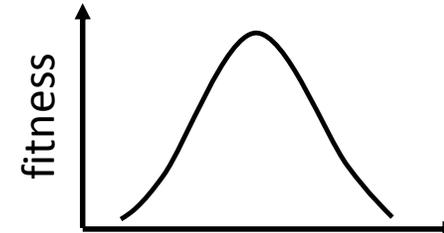
# Expectations in *Timema* sp.



# Expected genetic basis of colour in *Timema* sp.

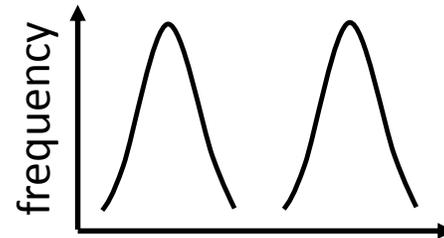
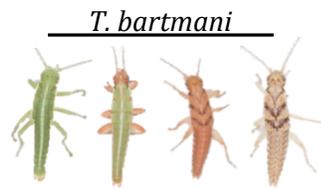
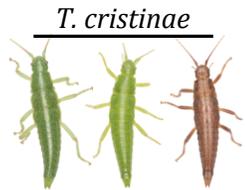


*Timema* colour  
Green to brown

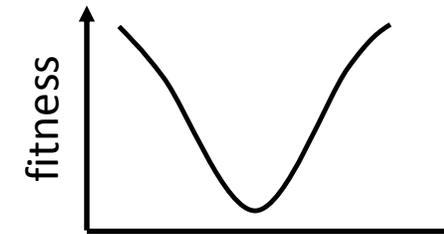


*Timema's* colour

Multiple loci



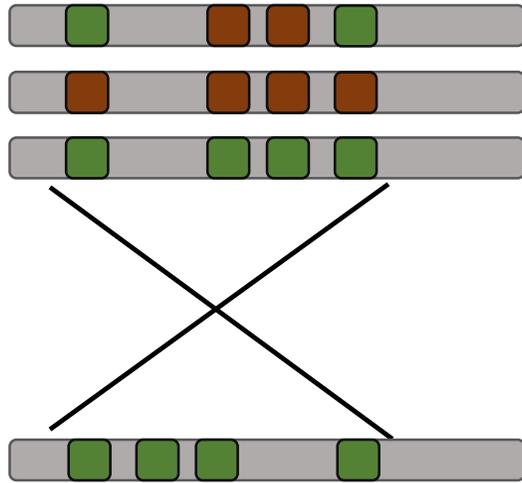
*Timema* colour  
Green to brown



*Timema's* colour

Single locus  
(supergenes)

# Why do supergenes evolve?



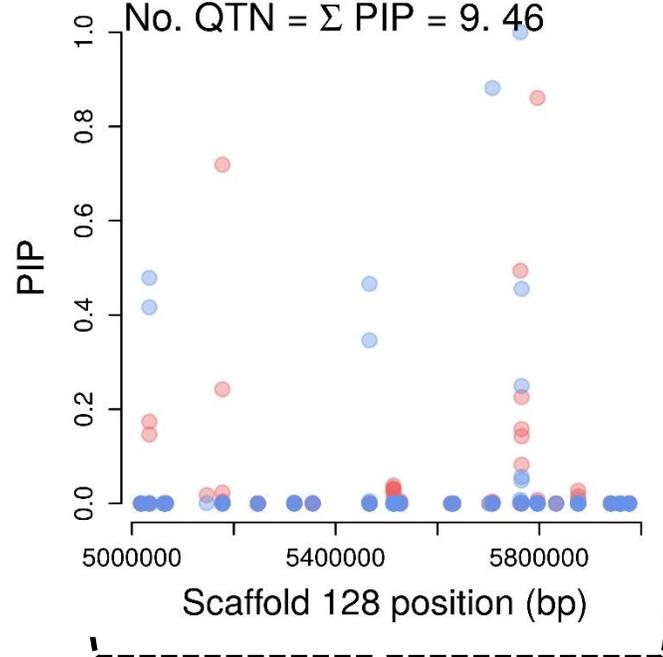
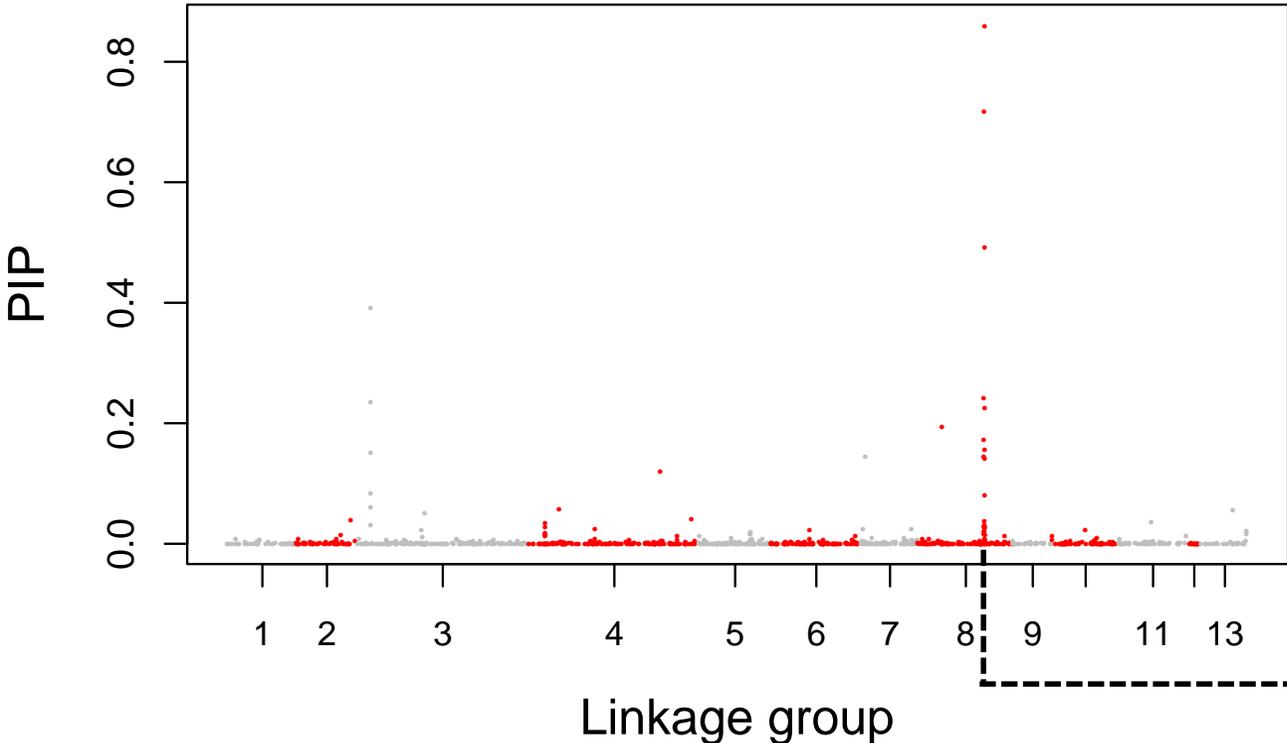
➔ Expected outcome of disruptive selection on a trait controlled by multiple loci located on the same chromosome (Charlesworth & Charlesworth 1976, Kirkpatrick & Barton 2006)

➔ Strongly reduce recombination in heterozygotes at this particular locus (Sturtevant 1921, Hoffmann & Rieseberg 2008, Stump et al. 2007).

Avoid the cost of producing offspring with 'unfit' allelic combinations  
Reduce the effect of gene flow  
Region segregates as a single locus

# Colour is polygenic in *T. chumash*

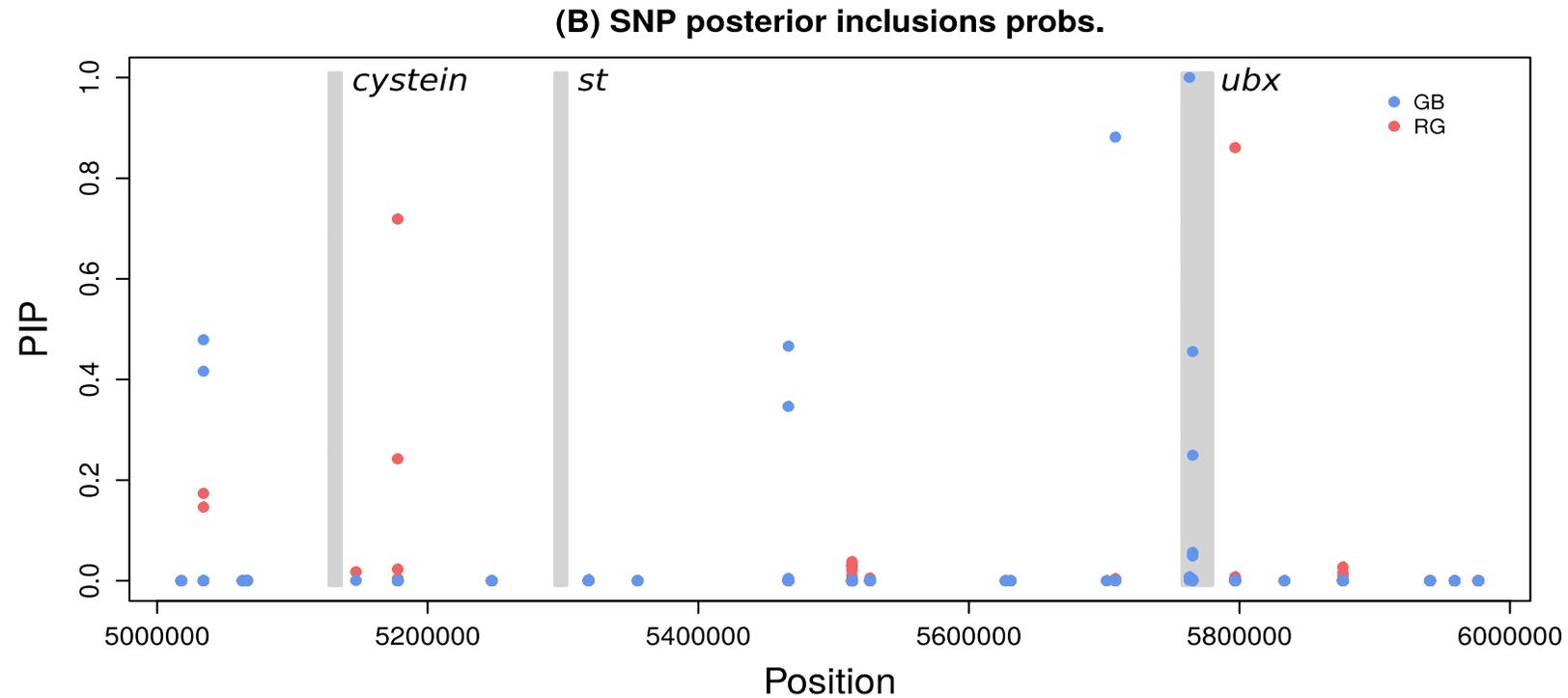
(A) *T. chumash*, RG



LD is low among top SNPs

~8-10 variants controlling color in *T. chumash*

# Colour is primarily associated with one region in *T. chumash*



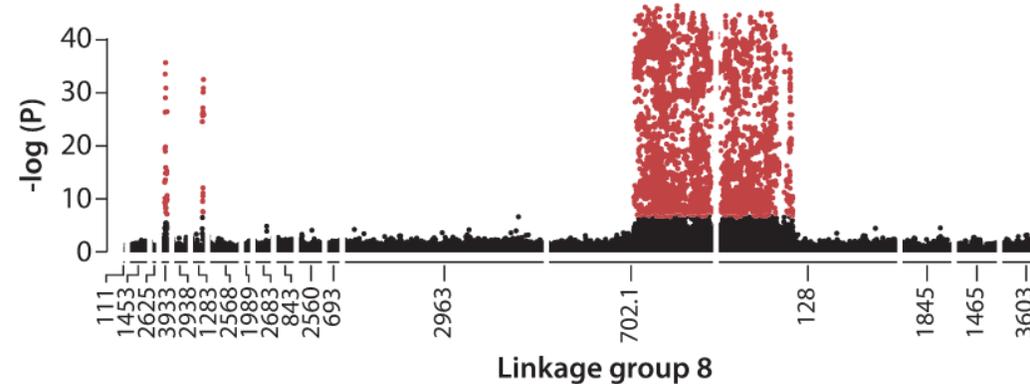
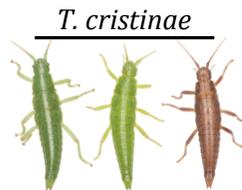
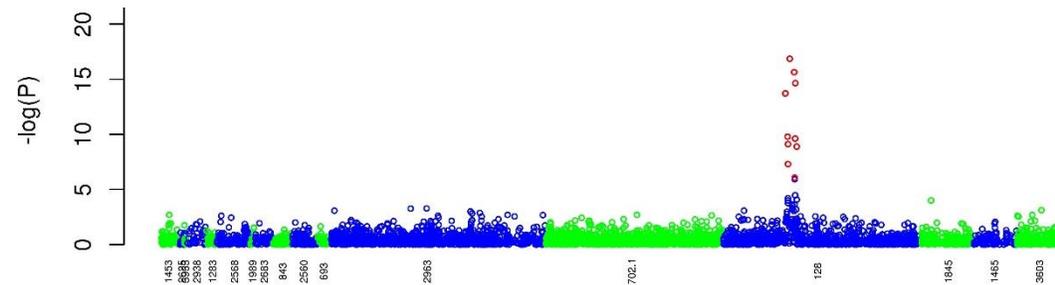
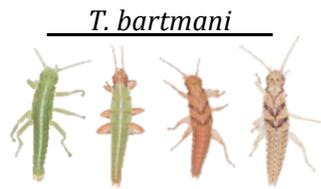
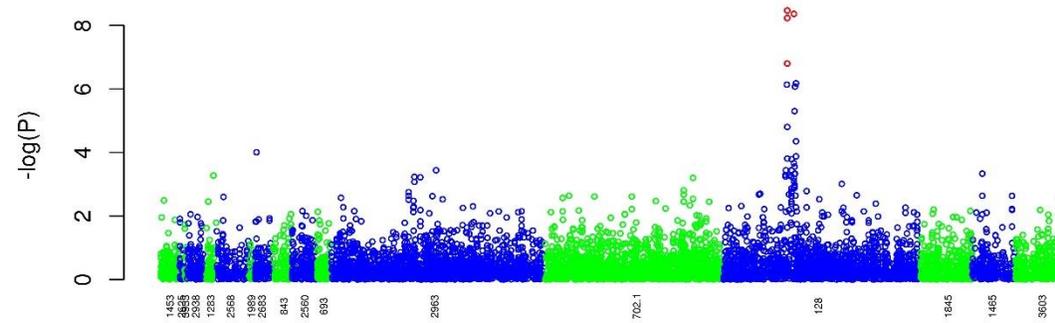
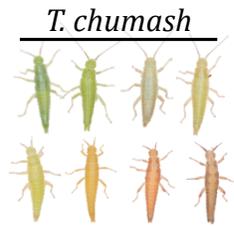
*st*: homolog of *st* gene in drosophila (scarlet membrane transporter)

*cystein*: Tyrosine kinase. Cell communication process. (*Haplochromini* cichlids)

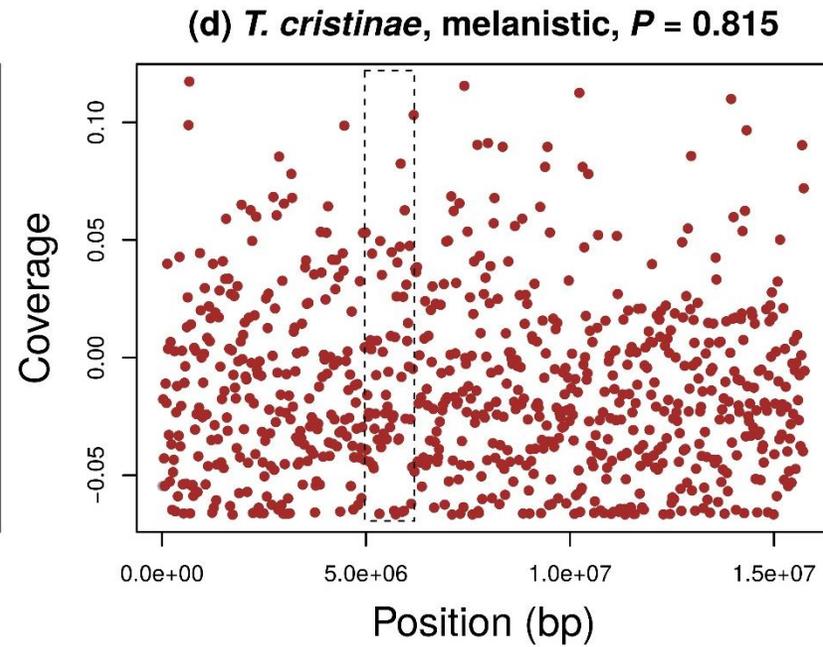
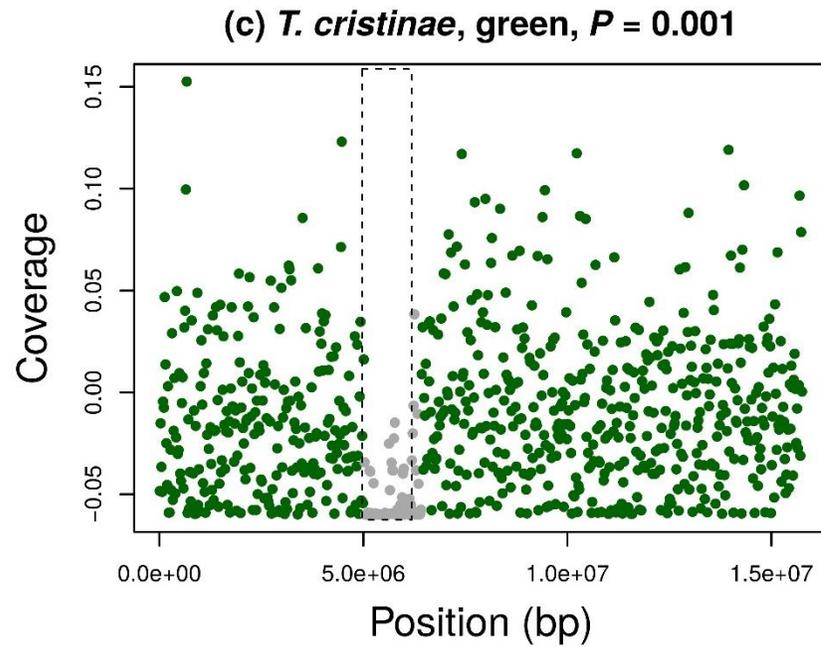
*ubx*: Protein activation. Activated by *cortex* (*Heliconius* and *Biston betularia*)

# Colour morph discontinuity is enhanced by structural variation...

... in all species studied but *T. chumash*.

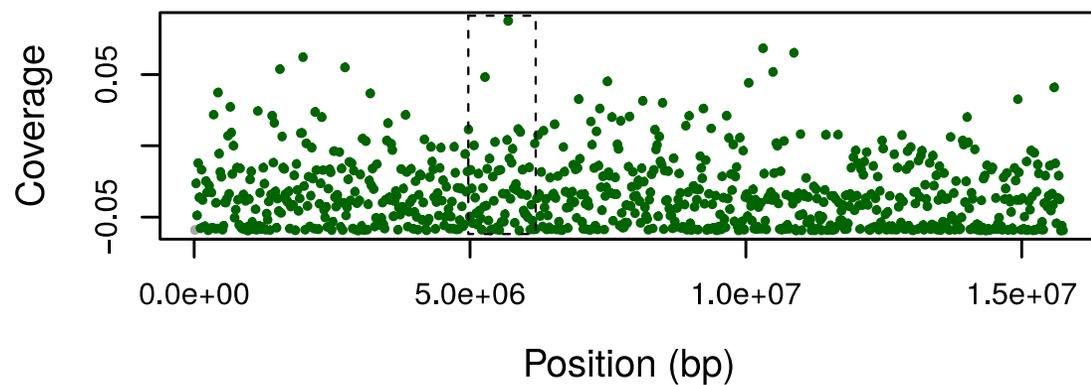


# Breakpoint mutation in *T. cristinae*

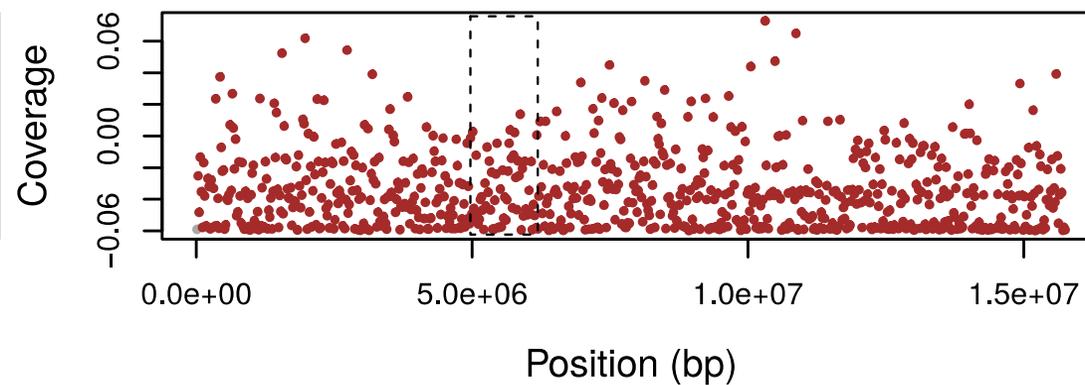


# Breakpoint mutation in *T. cristinae*

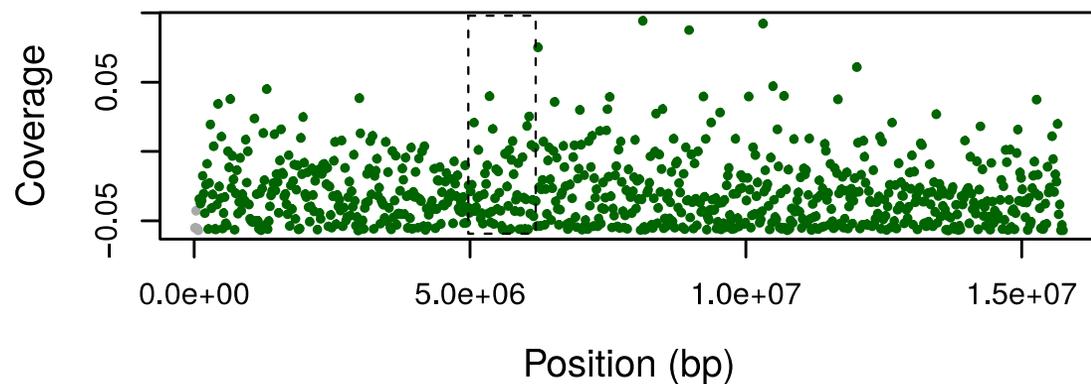
(M) *T. bartmani*, green,  $P = 0.807$



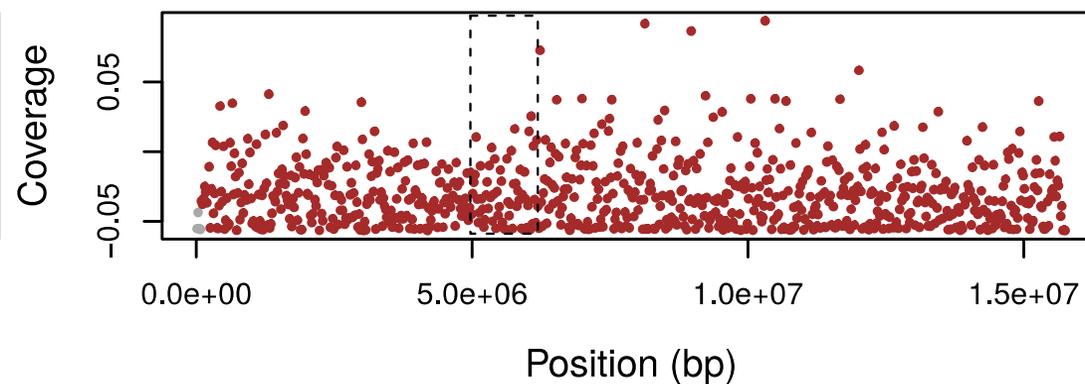
(N) *T. bartmani*, melanistic,  $P = 0.494$



(O) *T. chumash*, green,  $P = 0.711$



(P) *T. chumash*, melanistic,  $P = 0.511$



# In conclusion

➡ Host plant leaves and stems discontinuity drives colour morph discontinuity by generating disruptive selection

➡ Host plant colouration likely drives the evolution of supergene(s) in *Timema* sp..

➡ Plausibility of large or sudden evolutionary changes remains unclear.

Developmental biology: developmental switches involving gene regulation.

Here: conversion of polygenic variation into discrete phenotypic categories by **supergene evolution**.

➡ Reconcile ideas about **large evolutionary shifts** (**Punctuated equilibria** and **hopeful monsters**) with **polygenic adaptation** and **neo-darwinian gradualism**.

# Thanks!

## **Lab/fieldwork assistant:**

Óscar Mira Pérez

## **Undergraduate students:**

Lucy Lloyd

Josh Thakrar

## **Help with libraries:**

Anamaria Štambuk

## **IT support:**

CICs – University of Sheffield

HPC team (Iceberg)

## **Access to a lab during fieldwork:**

Todd Oakley

Emily Ellis

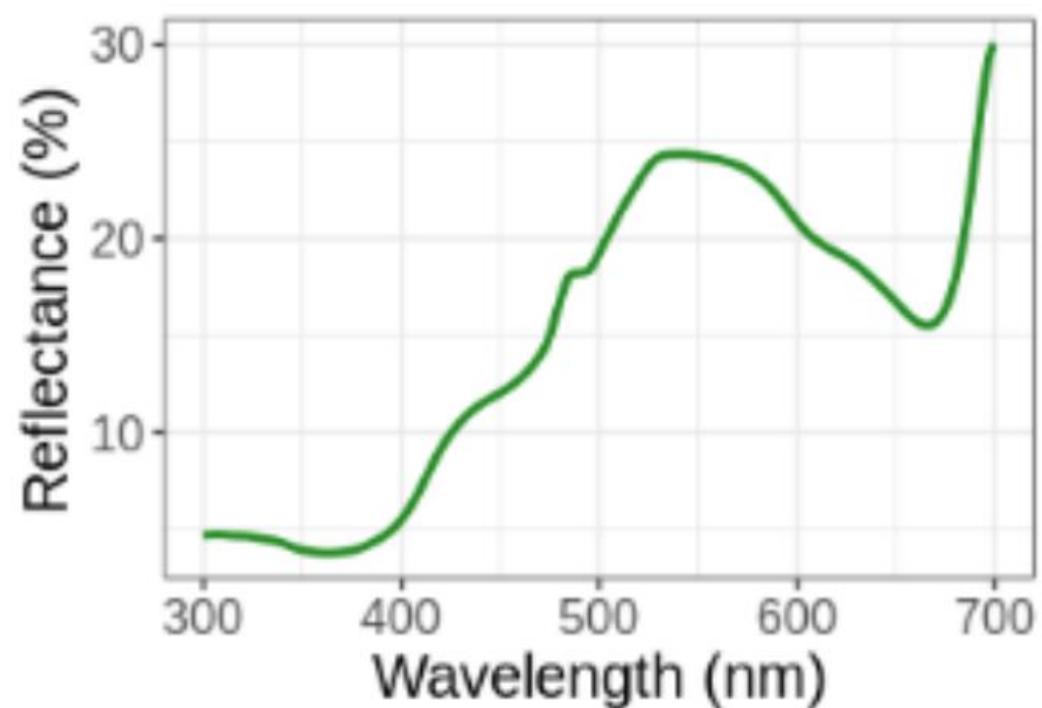
Morris Aguilar

## **Funding bodies:**

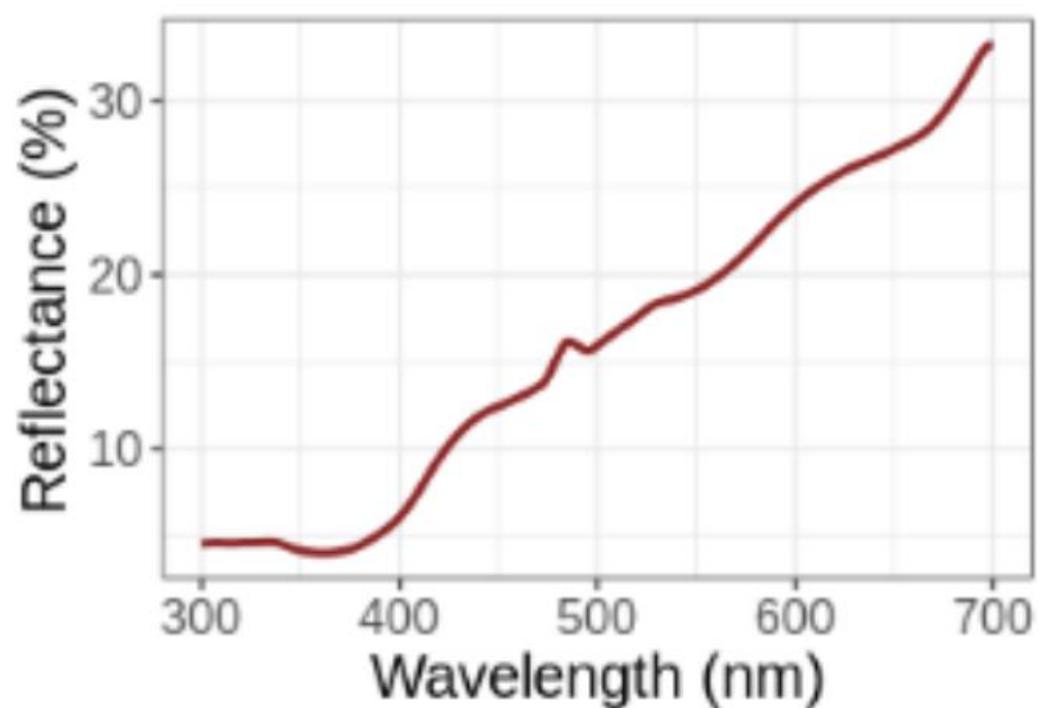
European research council



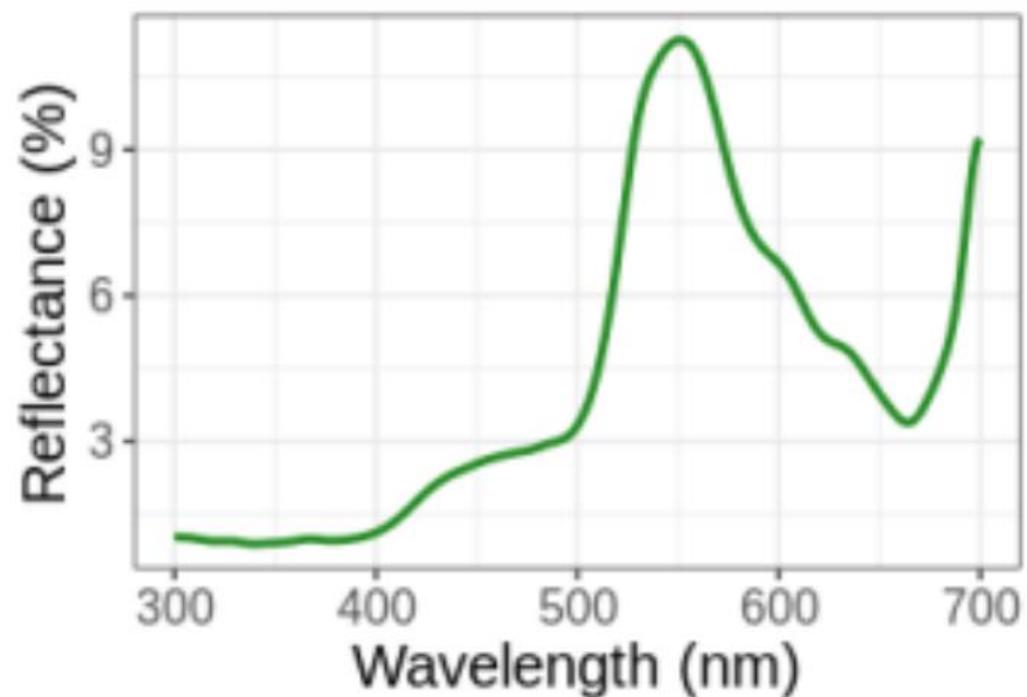
*T. bartmani* (green)



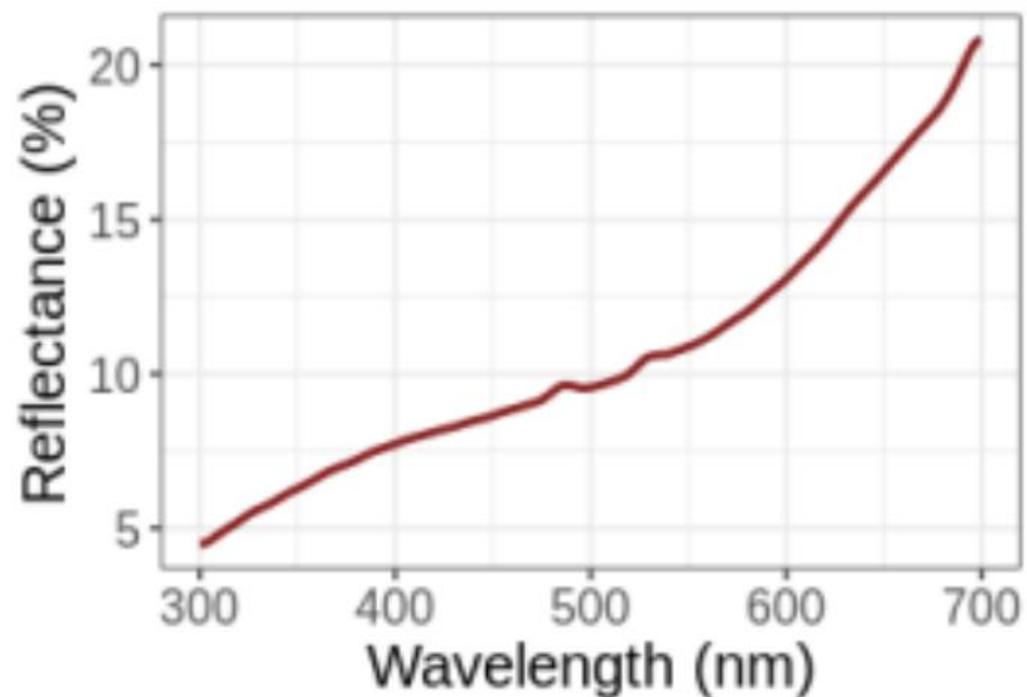
*T. bartmani* (melanistic)



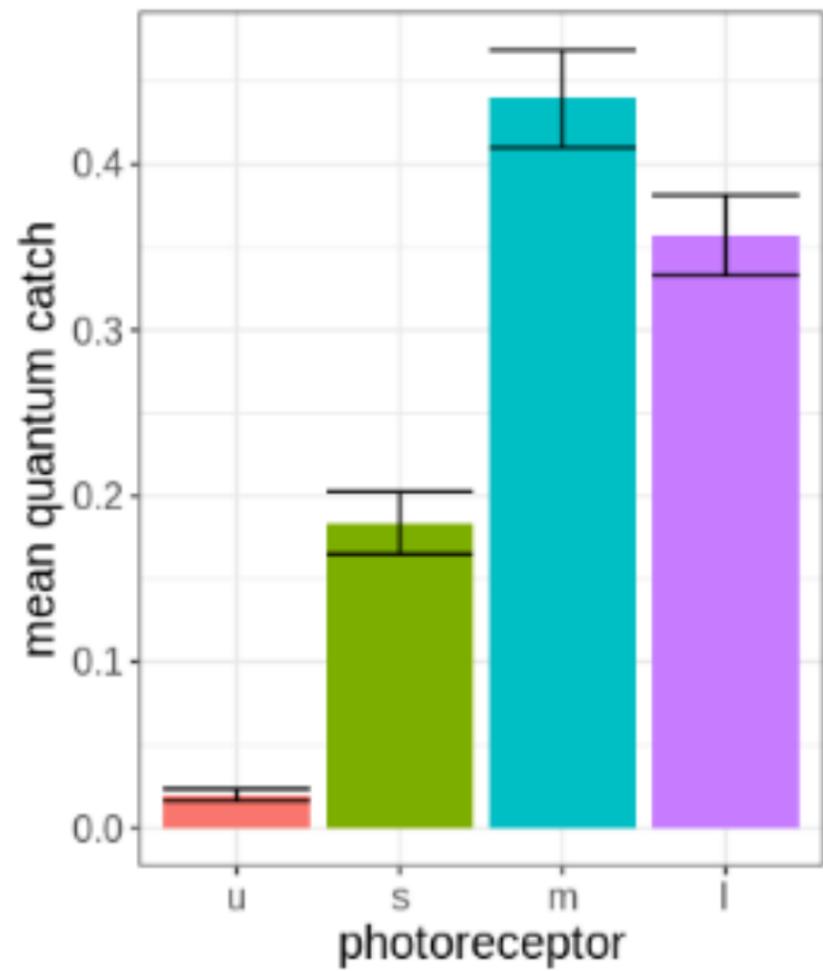
*Adenostoma* (green needles)



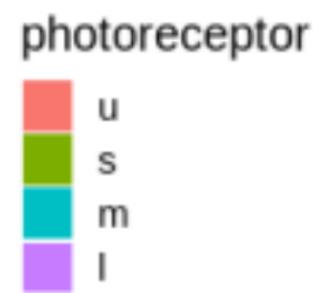
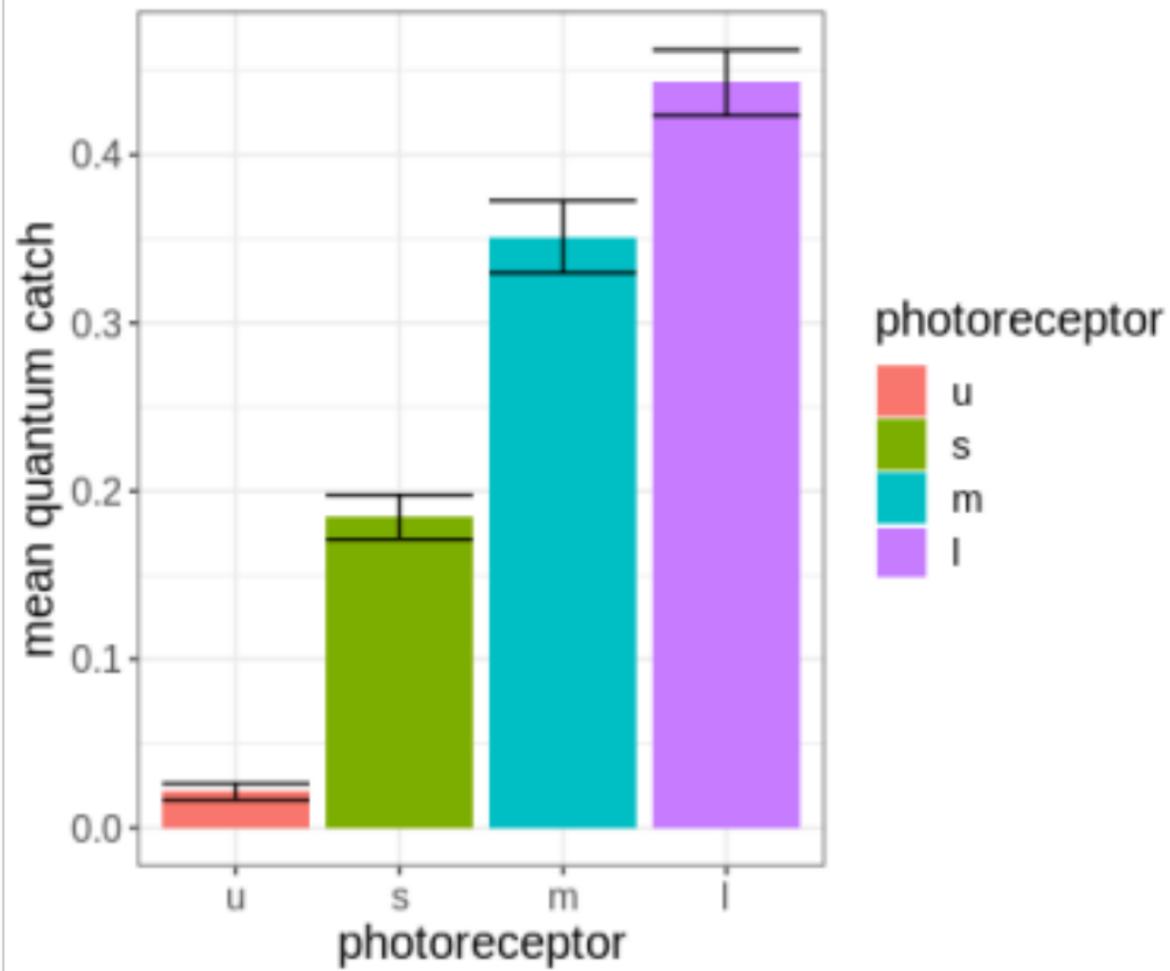
*Adenostoma* (stem)



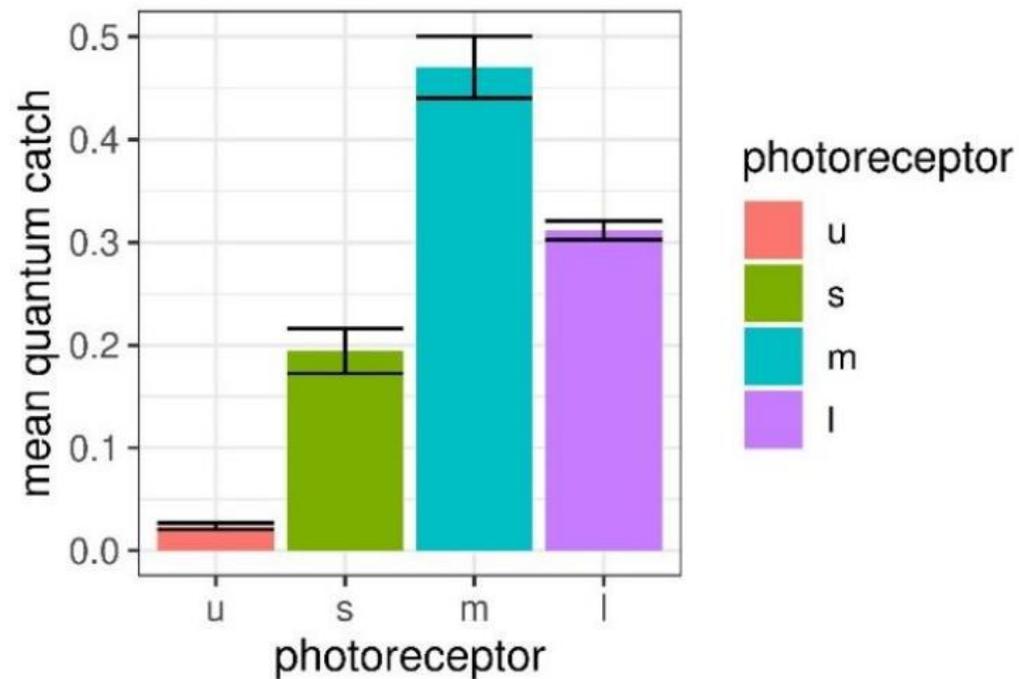
*Timema* sp (green)



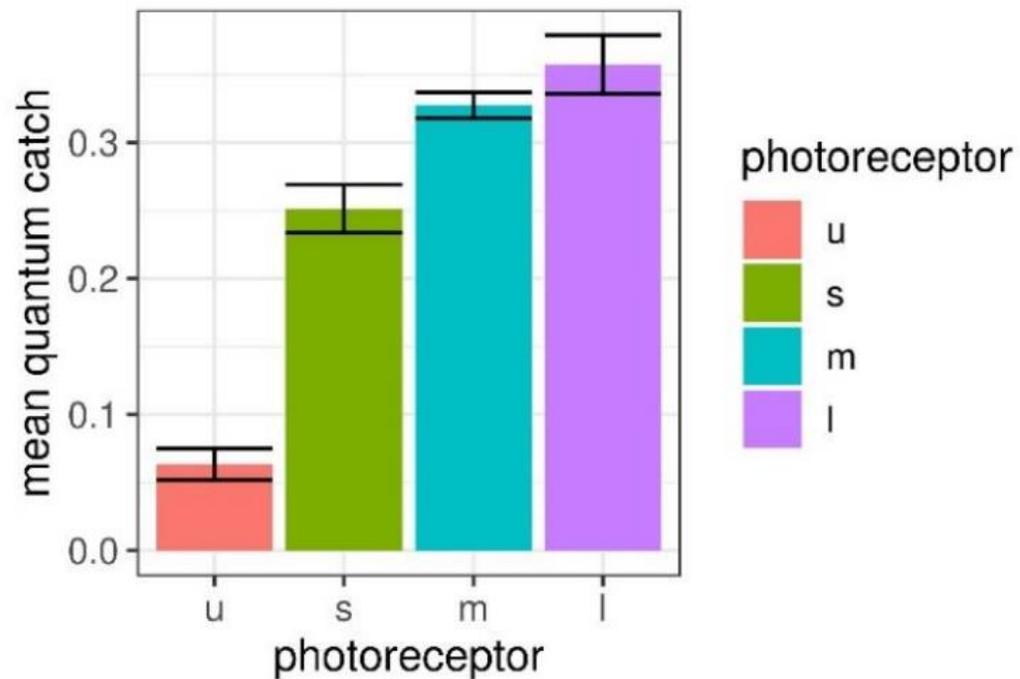
*Timema* sp (melanistic)



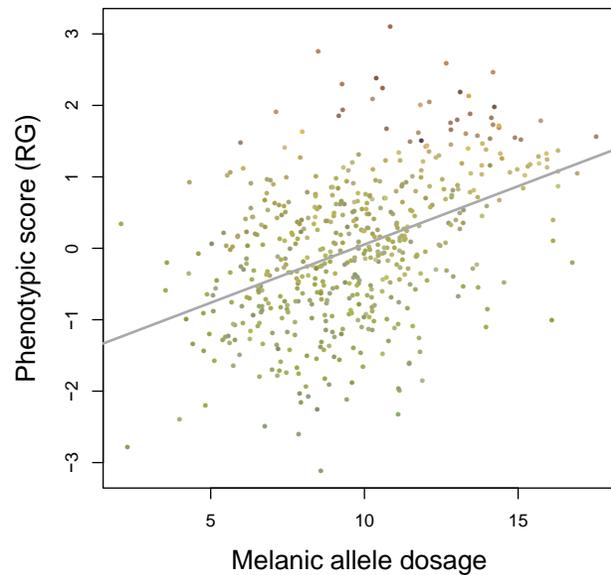
(a) *Cercocarpus* (green leaves)



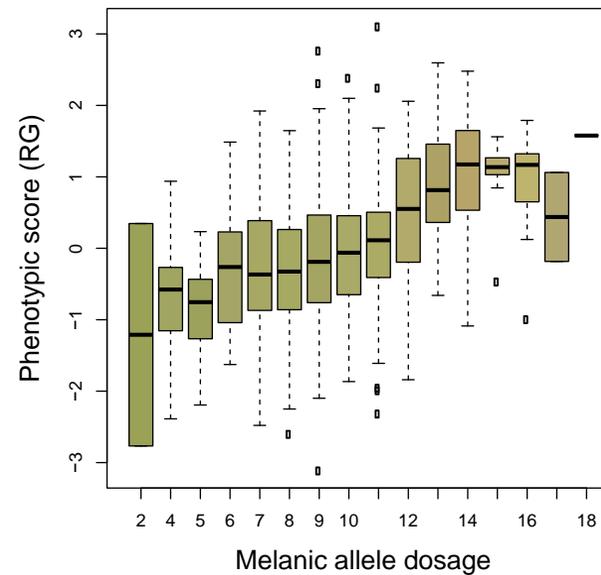
(b) *Cercocarpus* (stem)



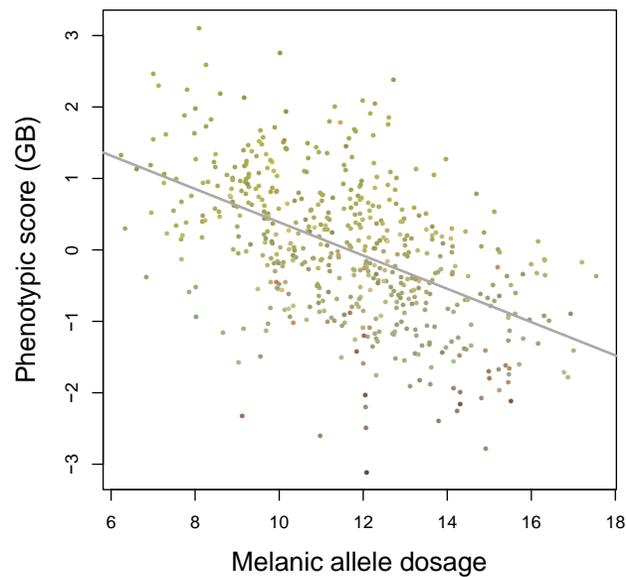
**(A) RG, mean genotype**



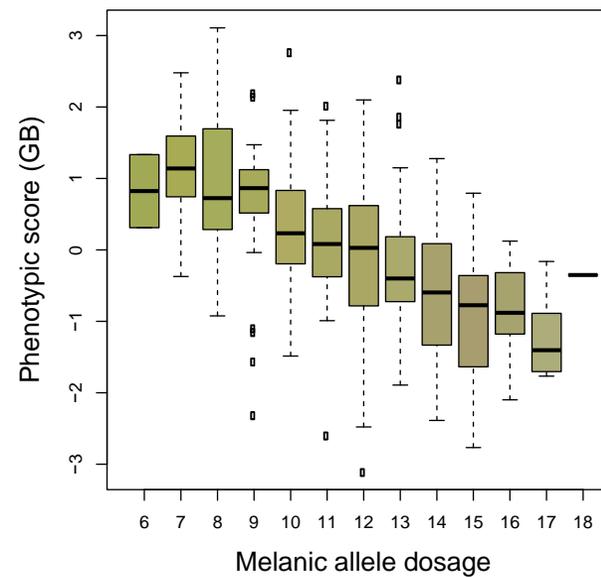
**(B) RG, binned genotype**



**(C) GB, mean genotype**



**(D) GB, binned genotype**



# Color map primarily to one region in *T. chumash* but is polygenic

