

Plant of the day!



Nepenthes rajah, the largest meat-eating plant in the world, growing pitchers that can hold two litres of water if filled to the brim.

It is dioecious

Pitchers have evolved 3 times in 3 independent groups, the Sarraceniaceae (the Americas), the Nepenthaceae (Asia), and the Cephalotaceae (Australia).

Carnivorous plants have evolved 6 times independently (~630 species)

Such species attract, trap and digest insects etc.. and derive nutrients from them (live in nutrient poor environments like bogs)



Adaptation

What is adaptation and local adaptation?

Why do we study local adaptation and how does it arise?

Can we measure selection in nature?

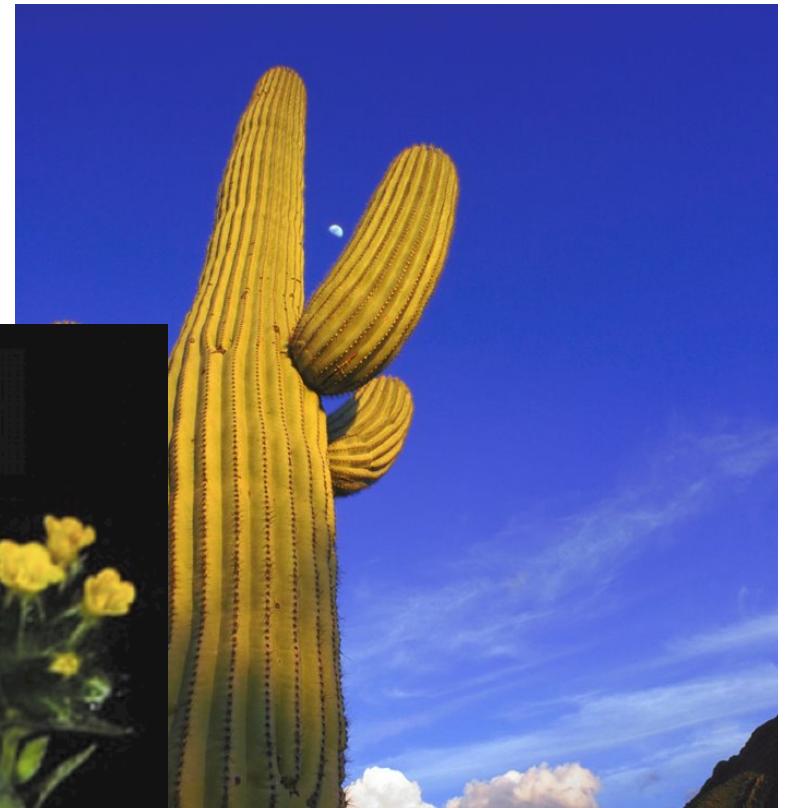
How do we assess quantitative genetic variation and why is it important?

How do we study local adaptation in nature?



Adaptation

A feature of an organism that has been favoured by natural selection because of that feature's positive effect on relative fitness





Local adaptation

What is local adaptation?

Evolution, through *divergent* natural selection, of traits that have high fitness in the environmental conditions specific to a population.

e.g. populations of sunflowers around the Great Salt Lake are highly salt tolerant there, but not elsewhere.



These adaptations are local in that they are NOT found throughout the whole species, having evolved through natural selection because they have high fitness in the *specific environments* of only certain populations of the species.



Local adaptation

Think – Pair – Share

Describe a scenario where you would want to know about local adaptation.

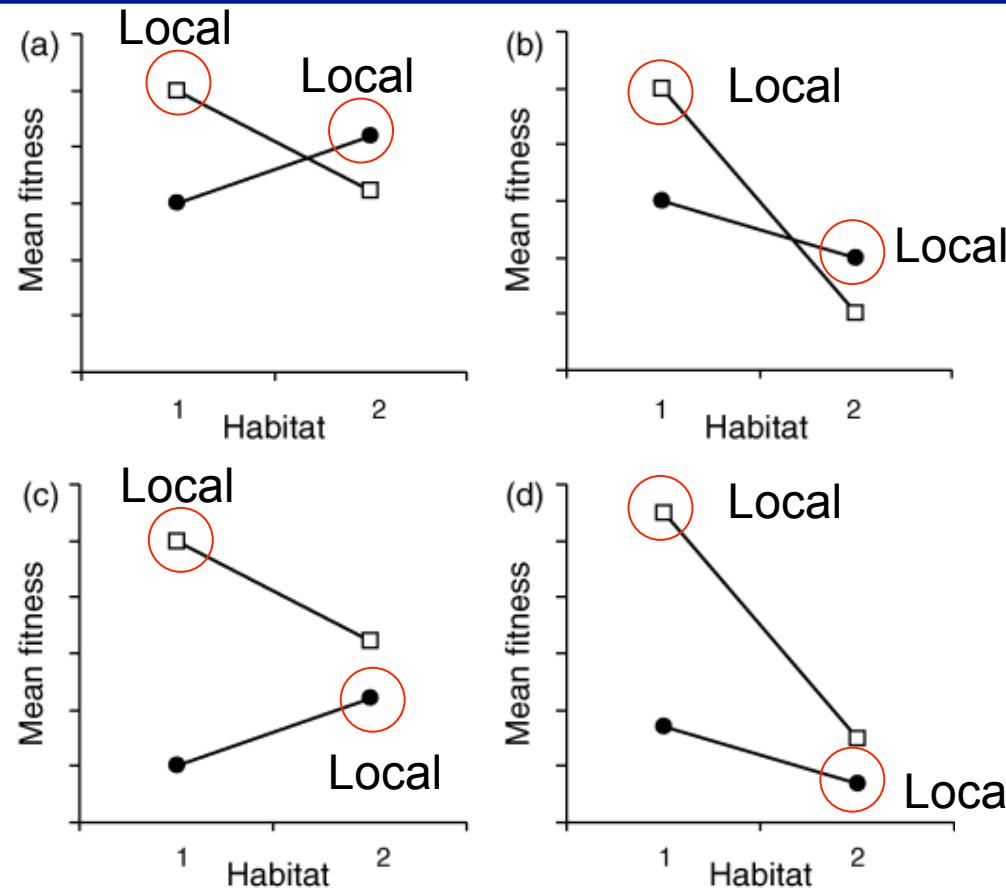
Write down 1-2 sentences.

Discuss with a neighbour.

Report back to class.



Which of these shows local adaptation?



“local” genotypes do better than “immigrant” at each site



Why study local adaptation?

Many adaptations are ancient, making it difficult to understand the selection pressures that led to their origins.

Local adaptation should be due to current or recent selection related to differences in environmental conditions experienced by different populations

- Can infer rate of adaptive evolution
- Is a mechanism that maintains genetic variation
- Can be crucial for initiating speciation



What might prevent local adaptation?

Weak/no divergent selection

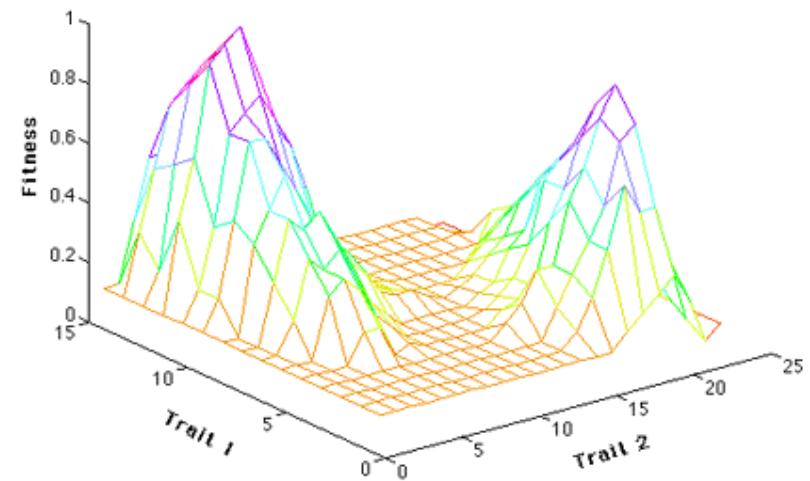
Gene flow can prevent divergence due to selection (e.g. dge center to edge)

Temporarily varying selection may lead to a “generalist” strategy

Drift can oppose selection

Alternative adaptive peaks

Lack of genetic variation





Natural selection

Natural selection: Individuals vary in traits that lead to differential fitness.

Fitness: An individual's contribution to the next generation. Determined by the probability of survival to reproduction and the number of offspring an individual produces. It is often expressed as a relative measure.

How can we measure fitness?

-difficult to measure in the field (especially for perennial and outcrossing plants)

Selection coefficient: A measure of the reduction in fitness compared with the best genotype in the population



Natural Selection

Natural selection:

More offspring are produced than can survive
Phenotypic variation in a trait
Differential fitness among phenotypes

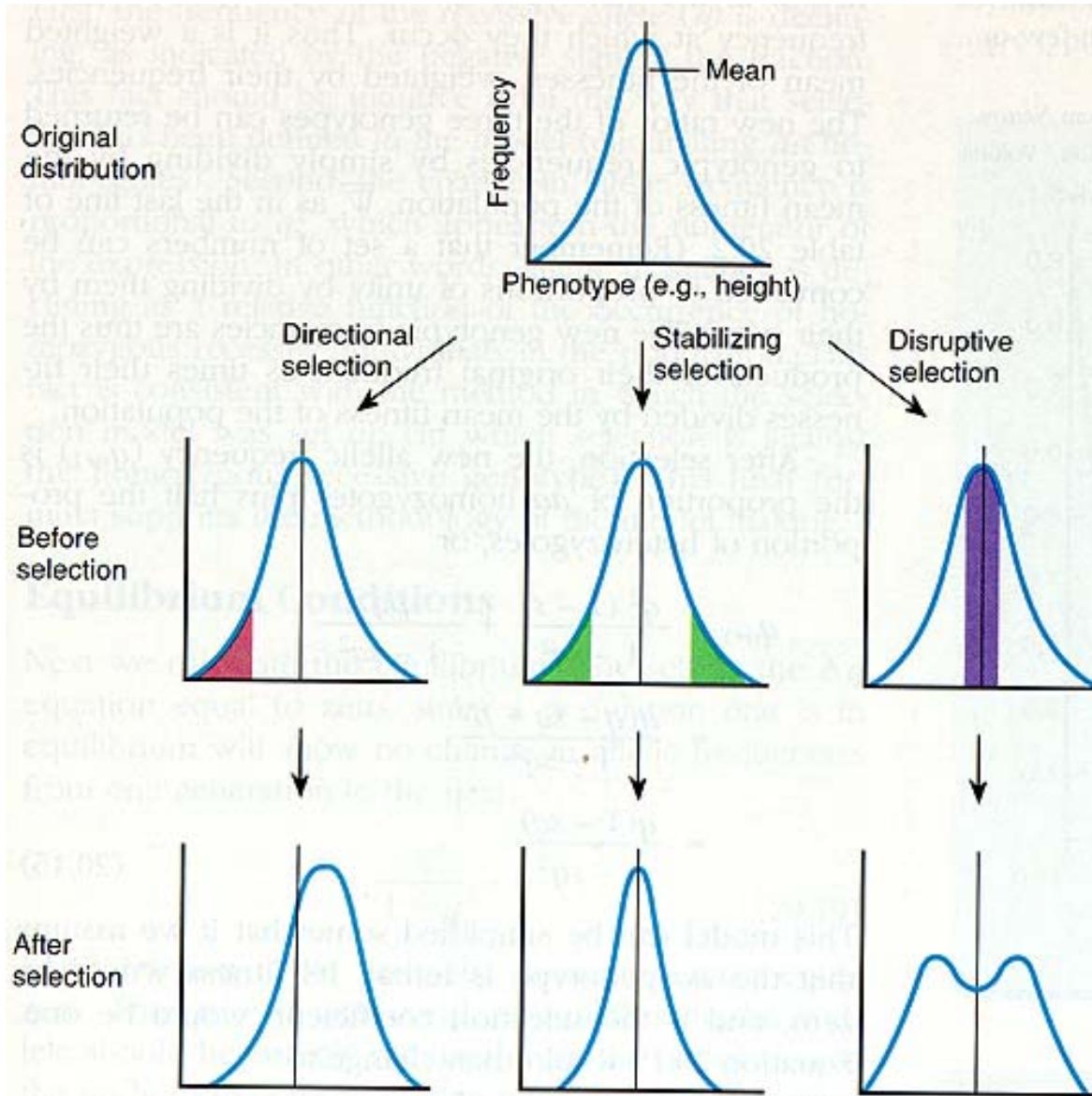
What else is required for a response to selection?

Genetic variation

-if these traits are heritable certain genotypes will produce more offspring leading to evolutionary change



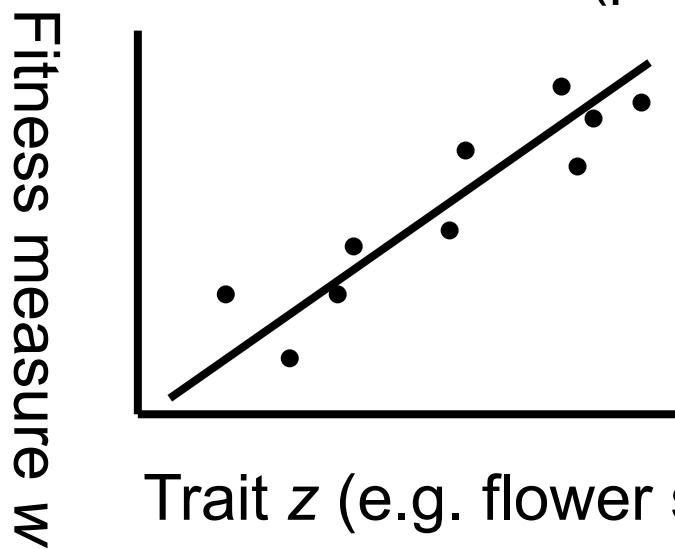
What are the different types of selection?





Modes of natural selection: Measuring selection on quantitative traits

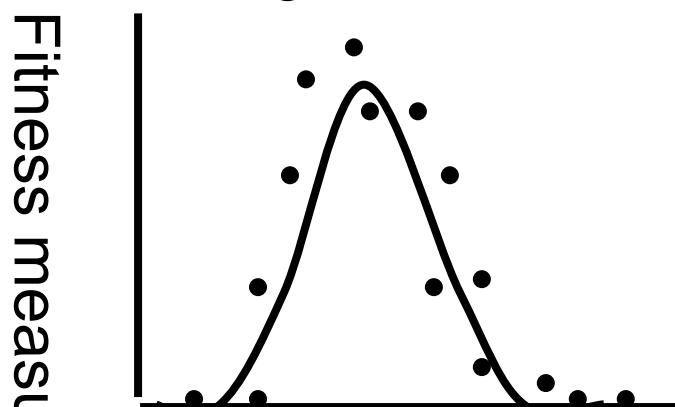
Directional selection (positive selection)



Slope of regression is estimate
of strength of selection

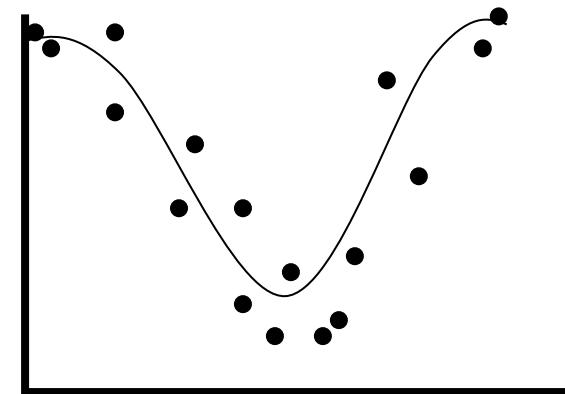
Trait z (e.g. flower size)

Stabilizing selection



Trait z (e.g. flower size)

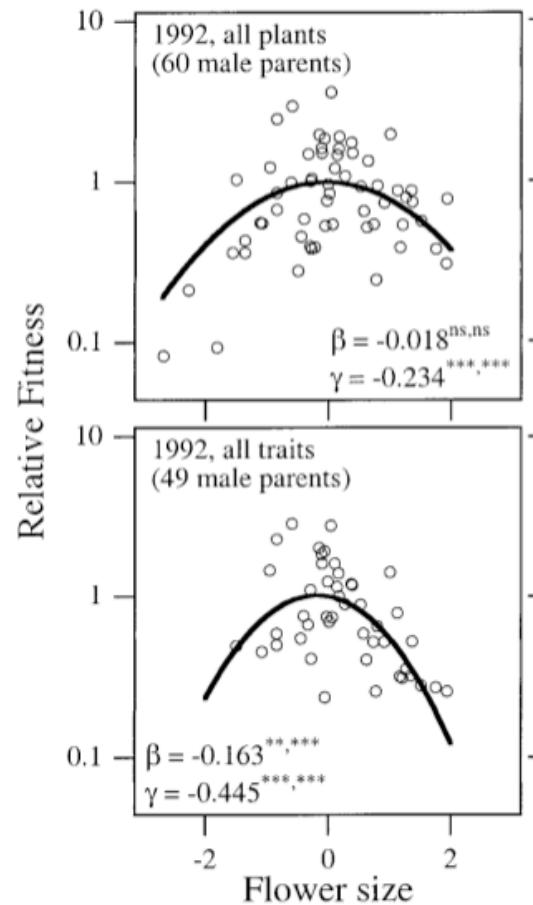
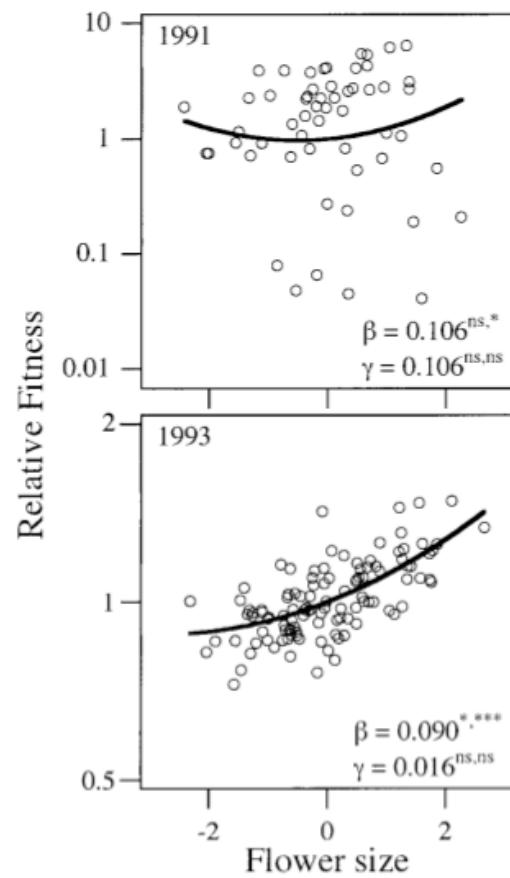
Disruptive selection



Trait z (e.g. flower size)



Measuring selection in wild populations



B = linear selection gradient (measures directional selection)

γ = quadratic selection gradient (measures stabilizing and disruptive selection)

Positive selection for larger flowers in 1993 through male function
Stabilizing selection for flower size in 1992 through male function

Morgan and Conner 2000



Genetic variation and response to selection

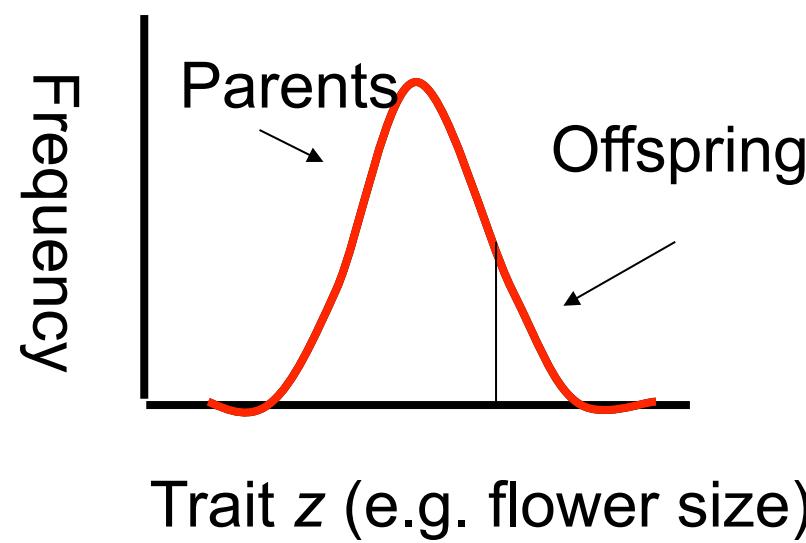
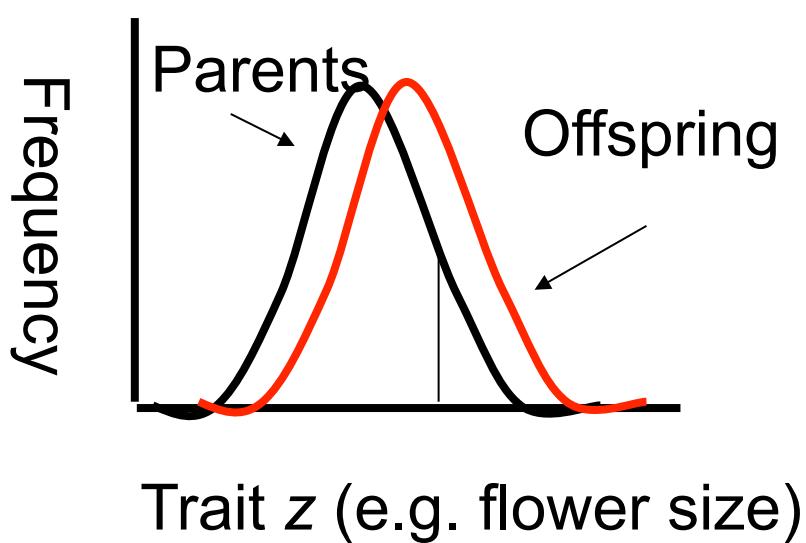
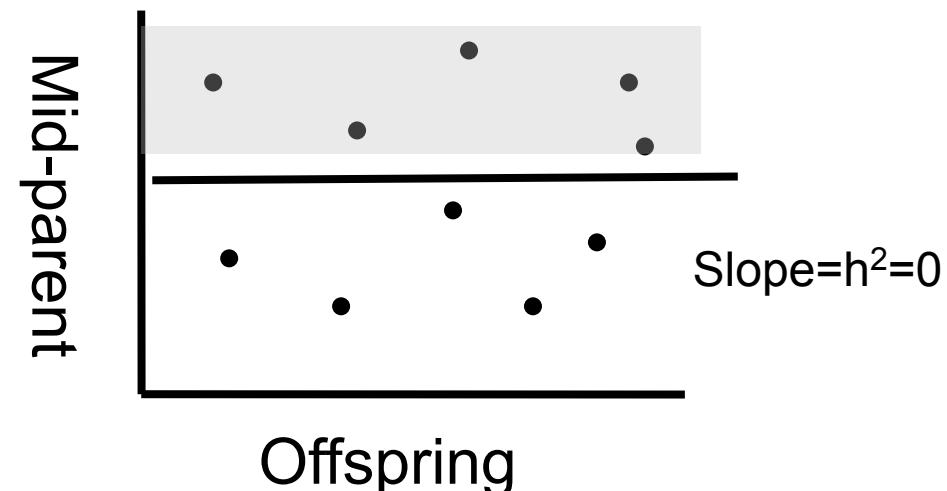
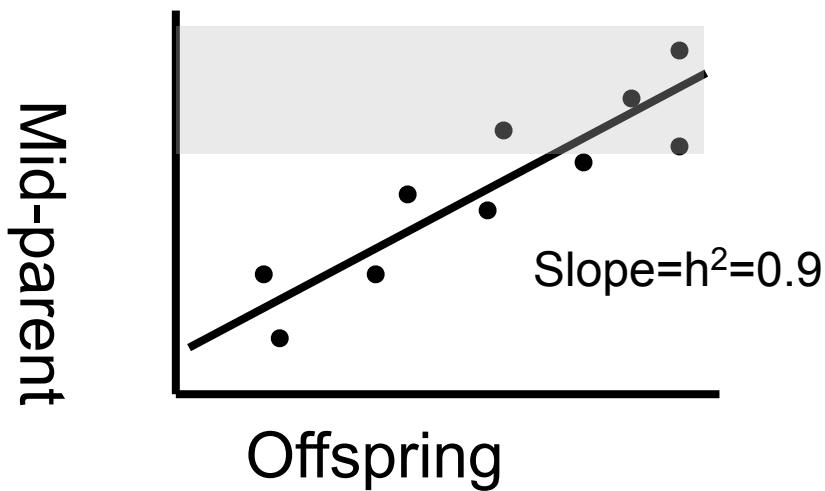
Provides the capacity for organisms to adapt

Population/species with no genetic variation can not respond to selection



How do we measure genetic variation in quantitative traits?

Parent offspring regression





How do we measure genetic variation in quantitative traits?

$$\text{Var}(P) = \text{Var}(G) + \text{Var}(E) + 2\text{Cov}(G,E)$$

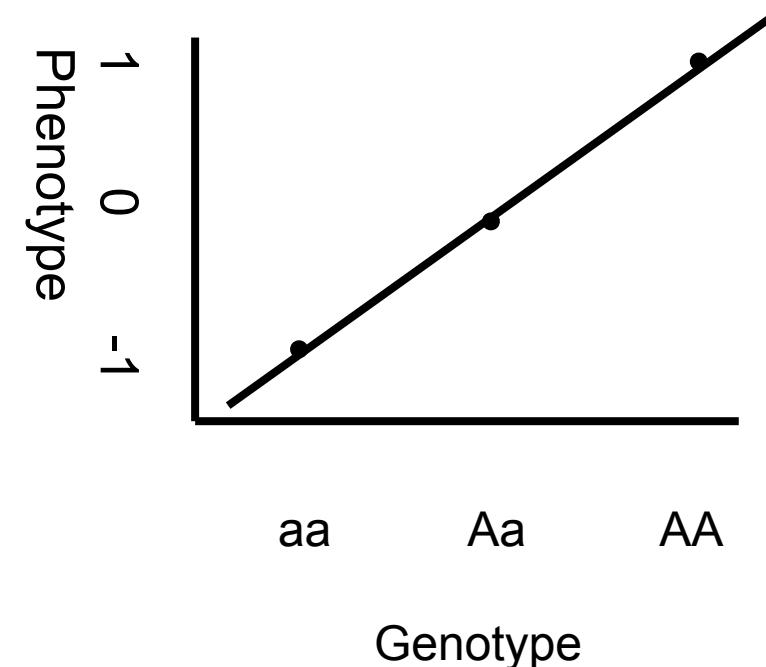
$$H^2 = \frac{\text{Var}(G)}{\text{Var}(P)}$$
 Broad Sense Heritability

$$\text{Var}(G) = \text{Var}(\text{add}) + \text{Var}(\text{dom}) + \text{Var}(\text{epi})$$

Additive effects = neither allele is dominant
(combined effect is equal to the sum of their individual effects)

Dominance = variation from interaction of alleles

Epistasis = variation from interaction of loci



Additive genetic variation is important for adaptation because this is the capacity of an individual to respond to selection (in a sexually reproducing outcrosser) as additive effects of genes are almost entirely responsible for the resemblance of parents and offspring.

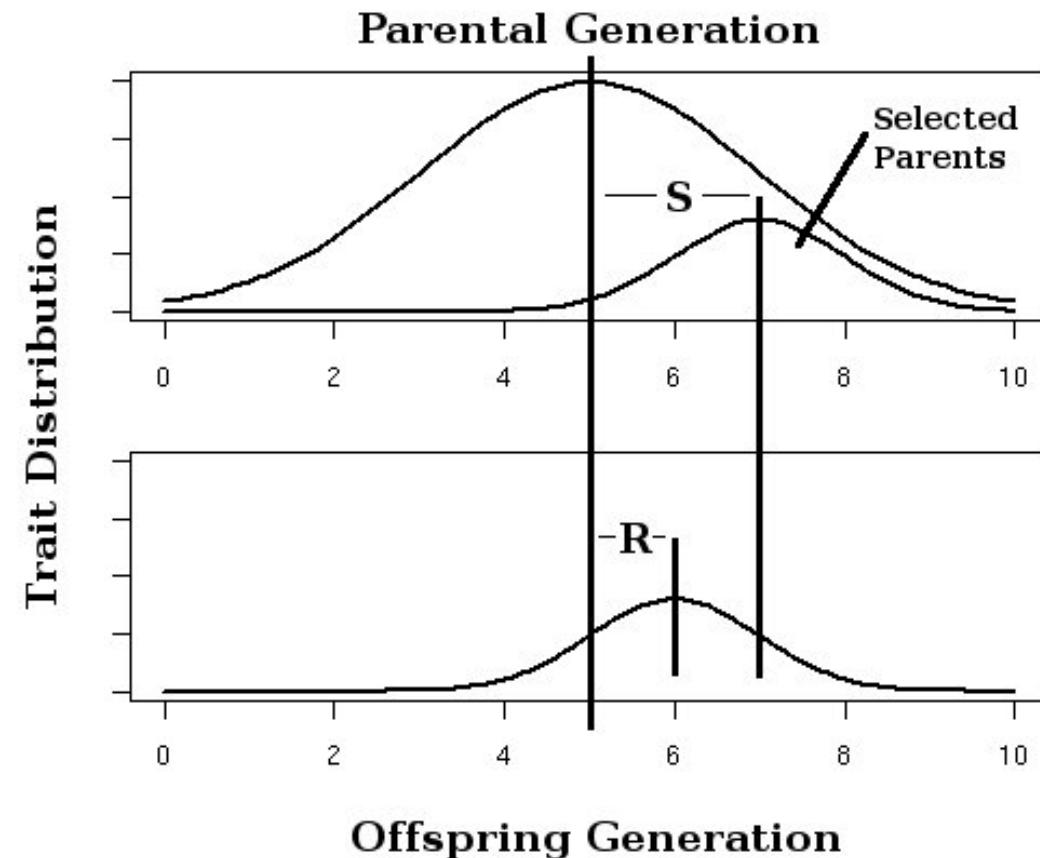


Genetic variation: quantitative traits and the breeder's equation

Narrow Sense Heritability

$$h^2 = \frac{\text{Var}(A)}{\text{Var}(P)} = \frac{R}{S}$$

$$R = h^2 S$$



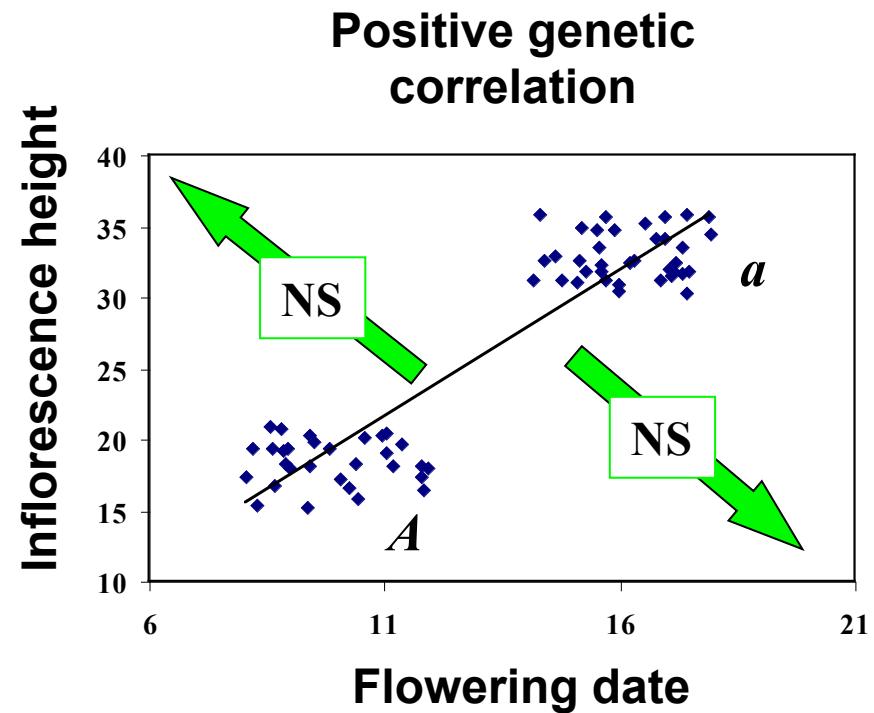
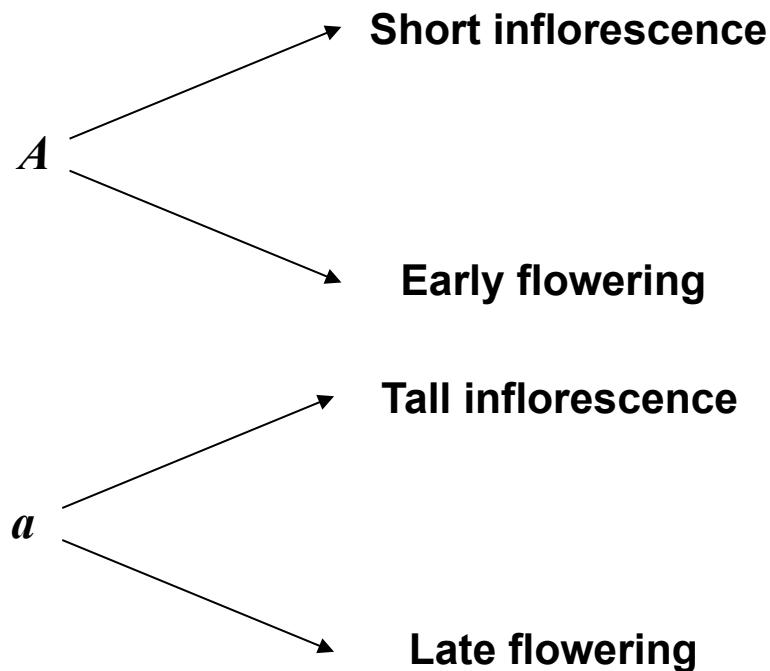
S = Selection differential
difference between selected parents
and the population as a whole (within a
generation)

R = response to selection
difference between selected offspring
and the unselected population (across
generations)



Genetic correlations can constrain adaptation

- Imagine a case where a single diallelic locus controls both inflorescence height and date of first flower

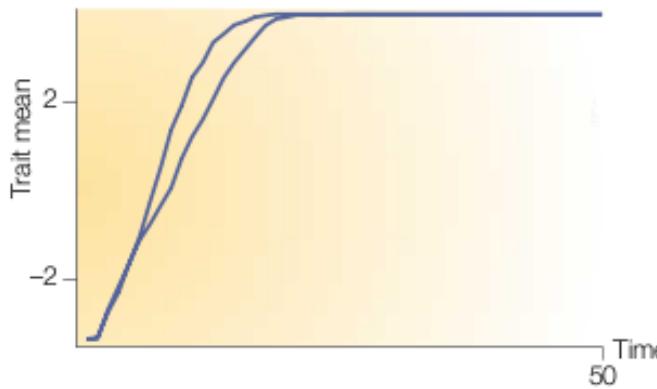


- Can natural selection lead to late flowering plants with short inflorescences?
- Can natural selection lead to early flowering plants with tall inflorescences?

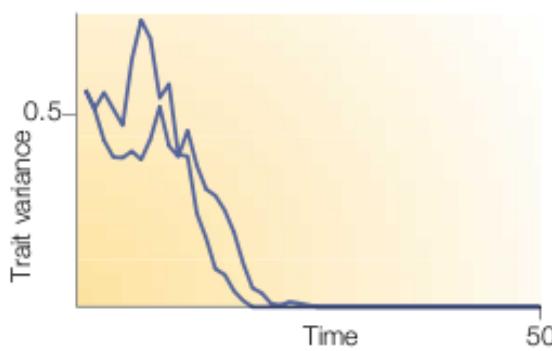


The depletion of genetic variation

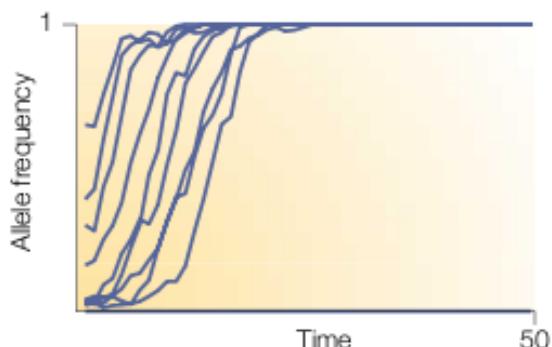
a



Over time additive variance for a trait is expected to be used up by selection

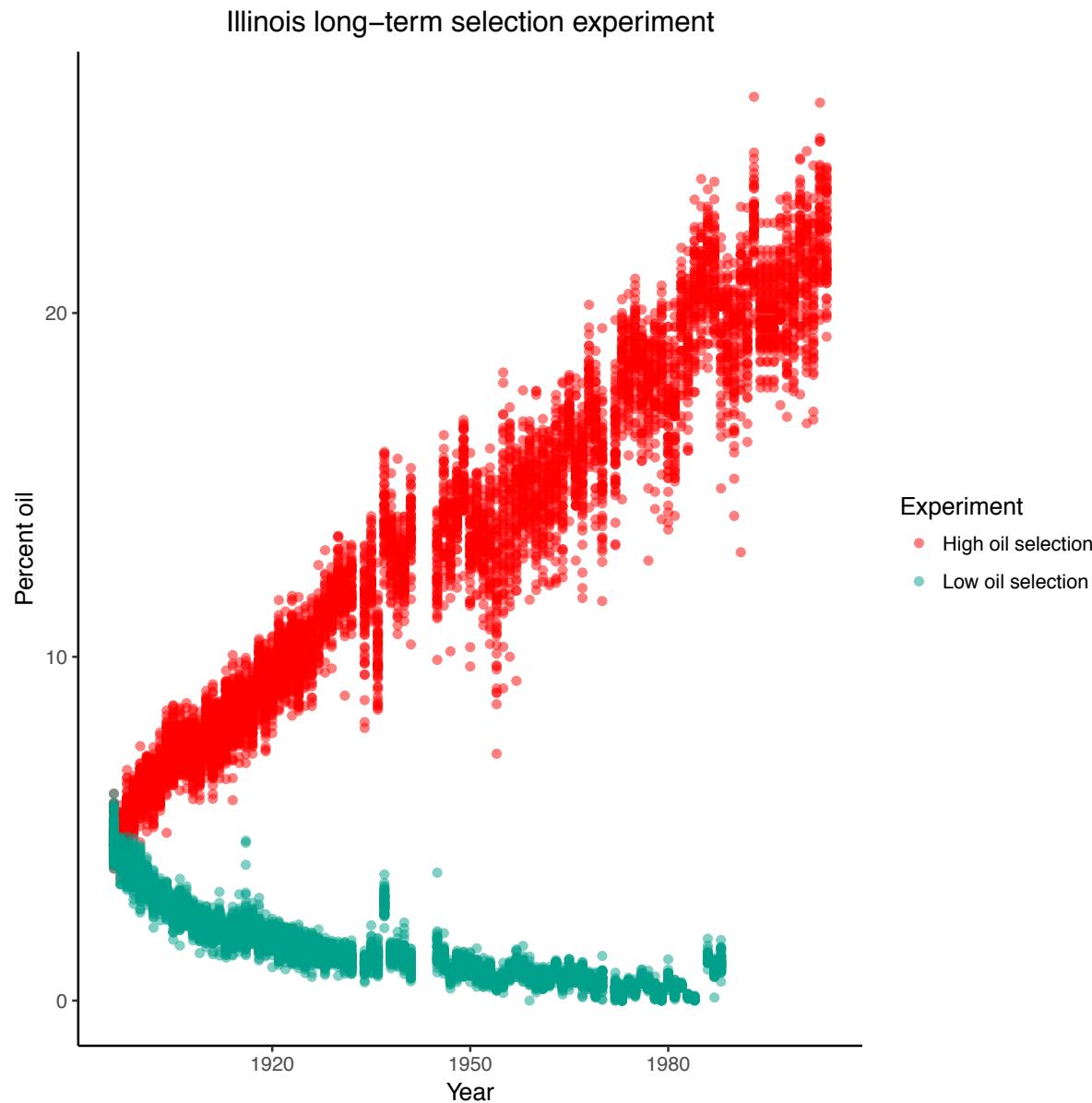


Population relies on new, beneficial mutations which may occur more frequently than expected as evidence by sustained responses to artificial selection



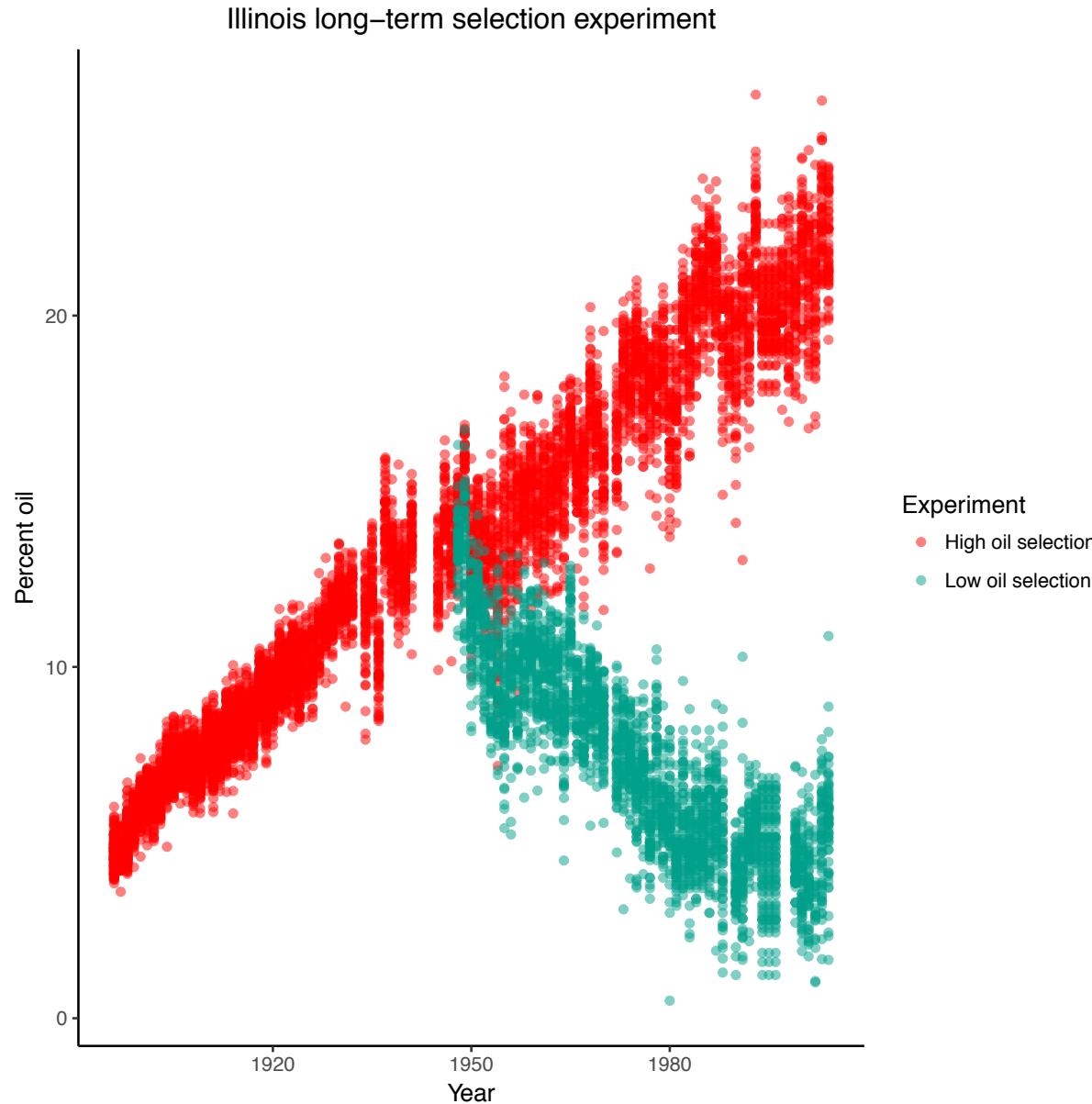


The depletion of genetic variation?





The depletion of genetic variation?





Finding evidence for local adaptation

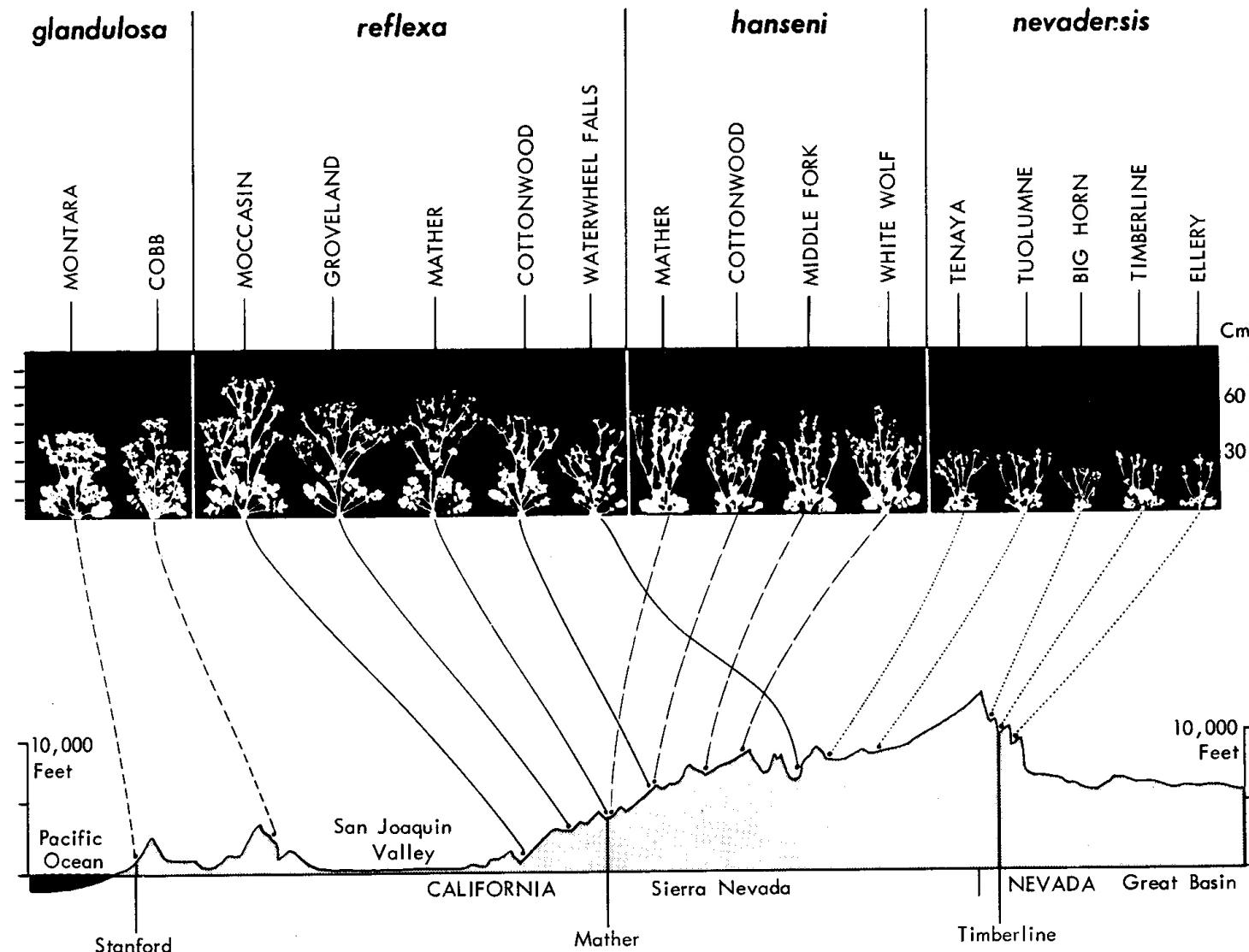
Common garden experiments/ reciprocal transplants

Clines

Q_{ST} (phenotypic differentiation) versus F_{ST} (genetic differentiation at neutral molecular markers)



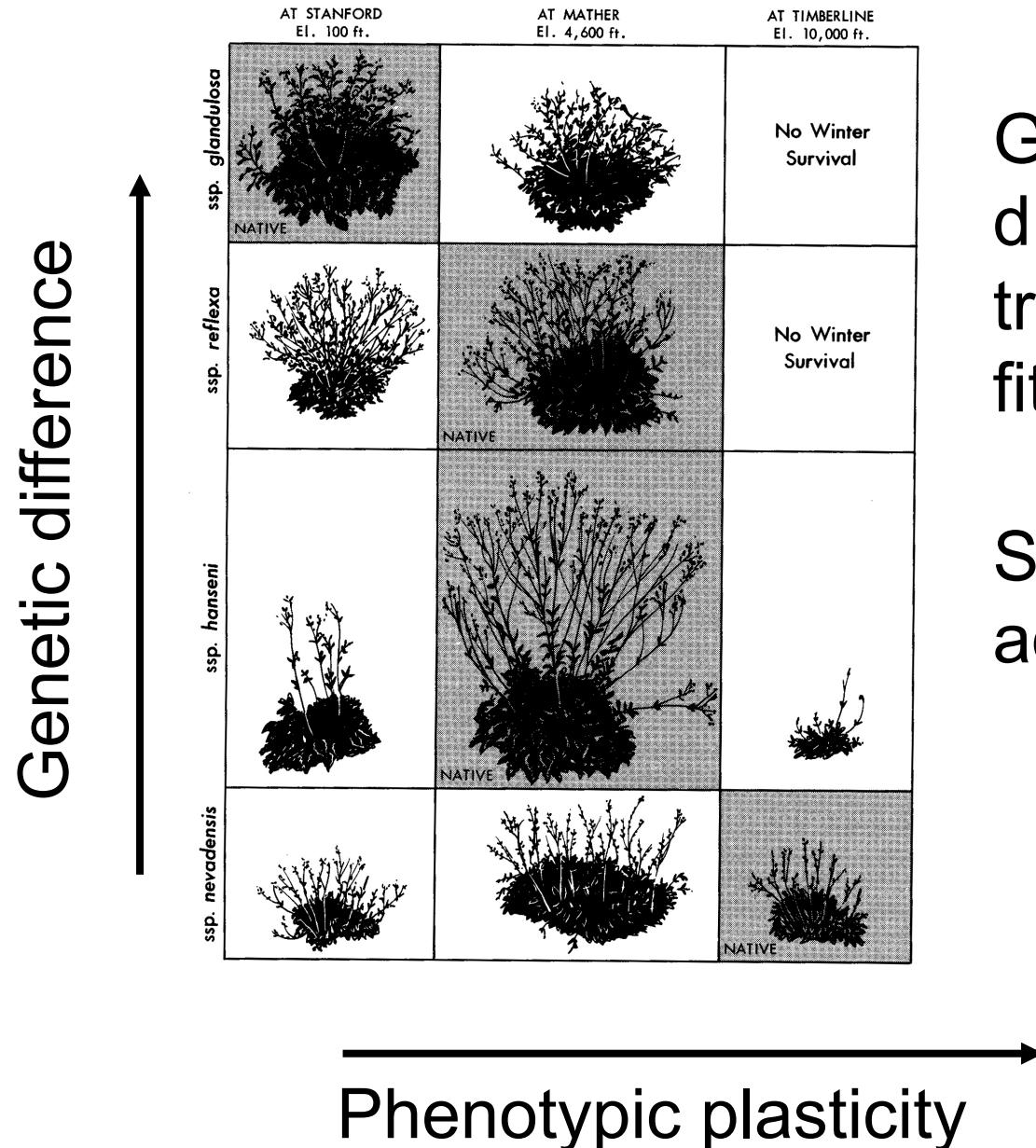
Common garden experiments



Potentilla glandulosa

Clausen, Keck, & Hiesey

Common garden experiments

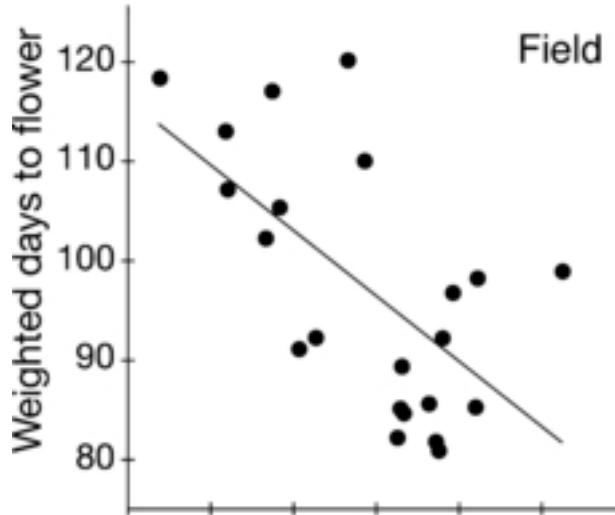


Genetic differentiation for traits related to fitness

Suggests local adaptation

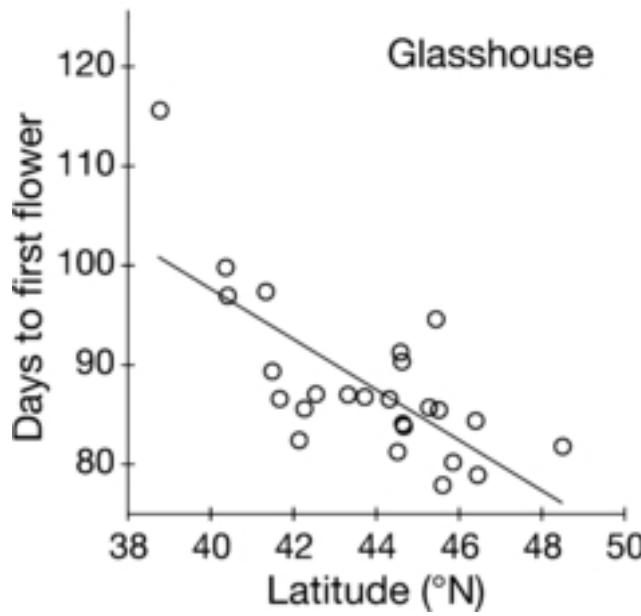


Identifying local adaptation: clinal variation



Clinal variation in traits (e.g. flowering time in purple loosestrife)

-suggests adaptation to local conditions



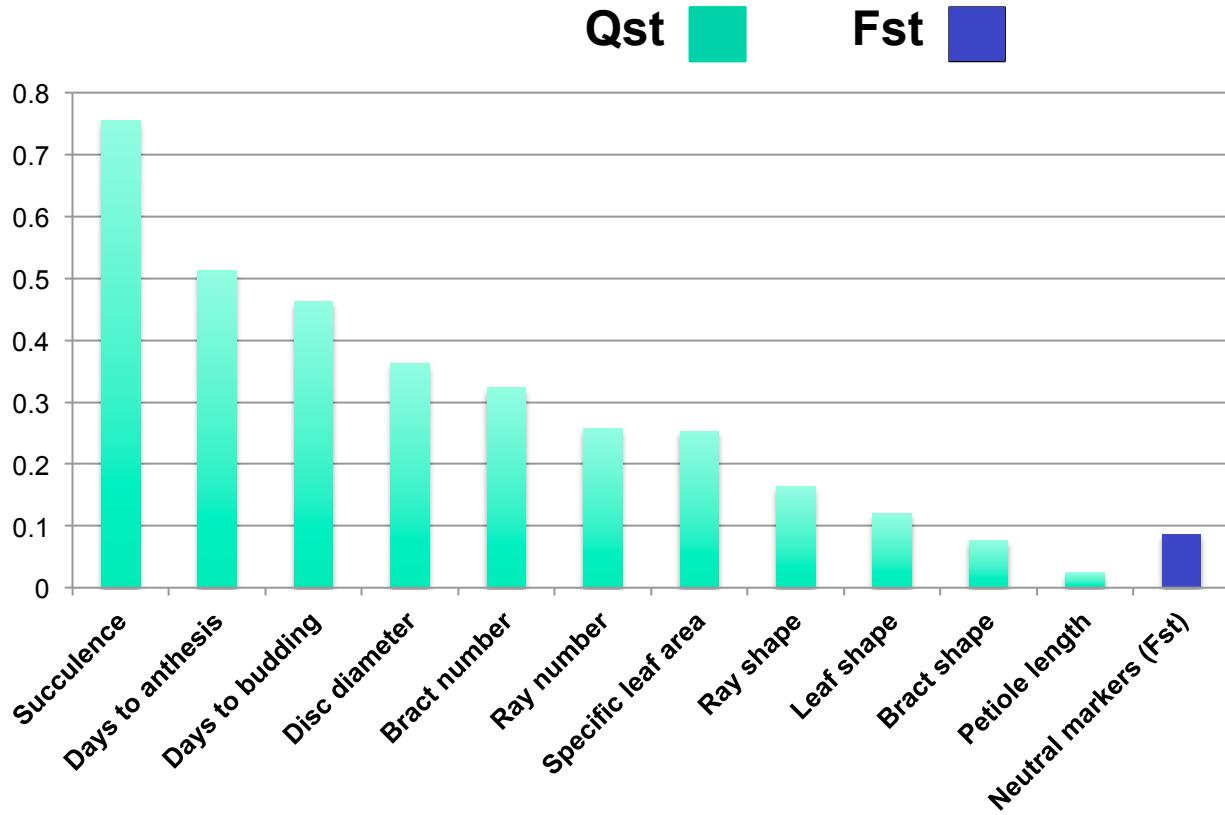
Why would we expect an earlier flowering time at higher latitudes?

MONTAGUE et al 2008





Is drift or selection driving patterns of genetic differentiation?



FST and QST values along latitudinal cline in common sunflower

FST=among population divergence in molecular markers

QST=among population variation in quantitative traits

QST>FST?

Suggests divergent selection rather than drift causing differences

QST<FST?

Suggests stabilizing selection



Identifying local adaptation: reciprocal transplants

Table 6.2. Population mean (standard error) reproductive biomass (g) of six populations of *Lythrum salicaria* grown at each of three common garden field site (South = Blandy, Mid = Newmarket and North = Timmins) in 2008. The population with the highest fitness at each field site is indicated in bold font.

Population ([°] N)	Field Site			
	North	Mid	South	
North	48.48	9.8 (1.32)	14.3 (1.26)	13.6 (1.30)
	46.43	16.3 (1.20)	33.9 (1.19)	22.5 (1.20)
Mid	45.49	6.3 (1.23)	22.1 (1.19)	8.9 (1.22)
	43.69	4.7 (1.22)	53.1 (1.20)	37.2 (1.20)
South	40.34	1.3 (1.23)	15 (1.20)	46.2 (1.21)
	38.75	2.6 (1.28)	15.6 (1.26)	23.3 (1.30)



This demonstrates local adaptation

But was is the mechanism underlying local adaptation? Can you think of some experiments to determine this?



Summary: local adaptation

Local adaptation is where local genotypes do better (have higher fitness) than immigrant genotypes

Divergent selection drives local adaptation but other factors such as gene flow can oppose it

Determining the traits underlying local adaptation and the agents of selection can be challenging

Additive genetic variation is required for an evolutionary response to selection



Unanswered Questions

How rapidly can populations evolve?

What sets the geographic limits of a species range?

What is the genetic architecture of adaptation?

- how many genes?
- what is the magnitude of their effects
- what is the relative importance of regulatory versus protein-coding changes?
- how repeatable is adaptation?