The plant of the day

Pinus longaeva

Pinus aristata

Today’s Topics

Non-random mating

Genetic drift

Population structure

Questions

- What are the causes and evolutionary consequences of non-random mating?
- What is genetic drift and what are its evolutionary consequences?
- How do we determine if these mechanisms are acting in a population?

Non-random mating

Assortative mating – mating with individuals that are similar or dissimilar for a given trait.

Positive Assortative Mating

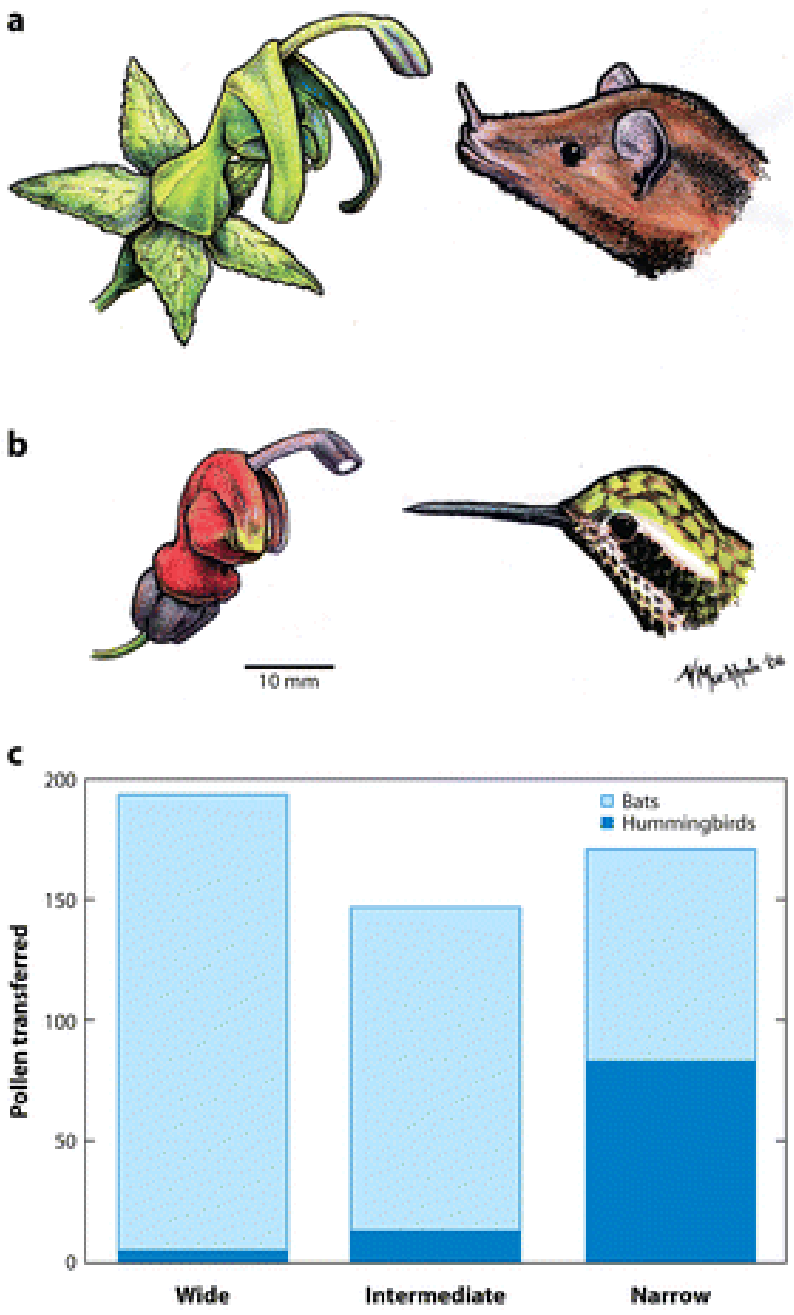
If a mating phenotype is genetically-based, what will **positive assortative mating** (mating with similar individuals) do to homozygosity at the loci affecting the trait?

AA	*Aa*	*aa*
red	**pink**	**blue**
|	|	|
AA	1/4 *AA*: 1/2 *Aa*: 1/4 *aa*	*aa*

Positive Assortative Mating

An example

In the genus *Burmeistera*, bats are more efficient at moving pollen between wide flowers, whereas hummingbirds excel at pollen transfer between narrow flowers.



Kay KM, Sargent RD. 2009.
Annu. Rev. Ecol. Evol. Syst. 40:637–56

Positive Assortative Mating

Sunflower ecotypes: *H. argophyllus*

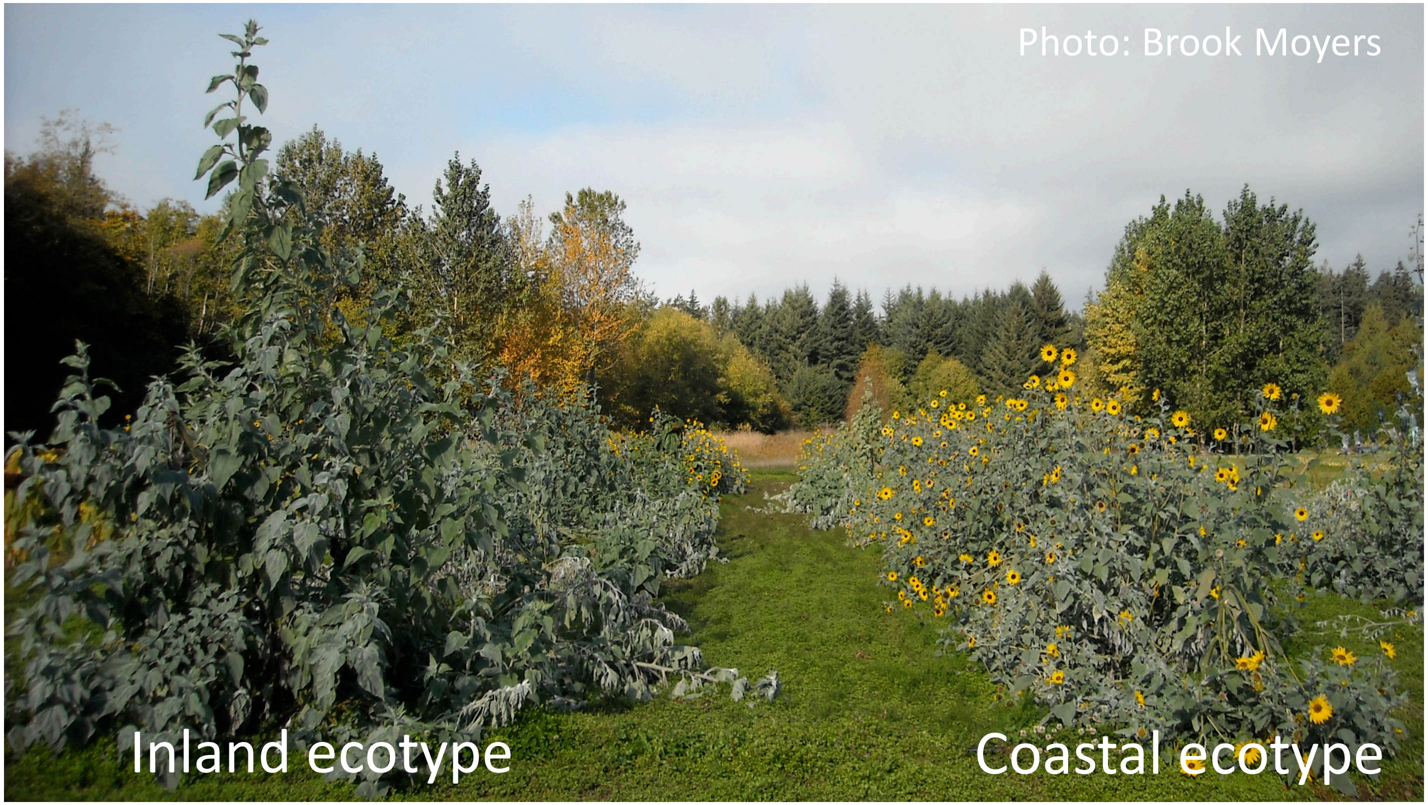
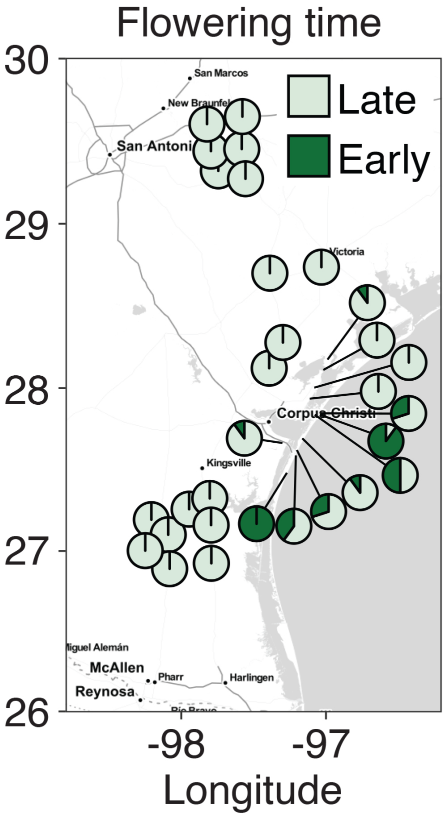


Photo: Brook Moyers



Negative Assortative Mating

Negative assortative mating is preferential mating with dissimilar individuals, which has the opposite effect on heterozygousity in a population.

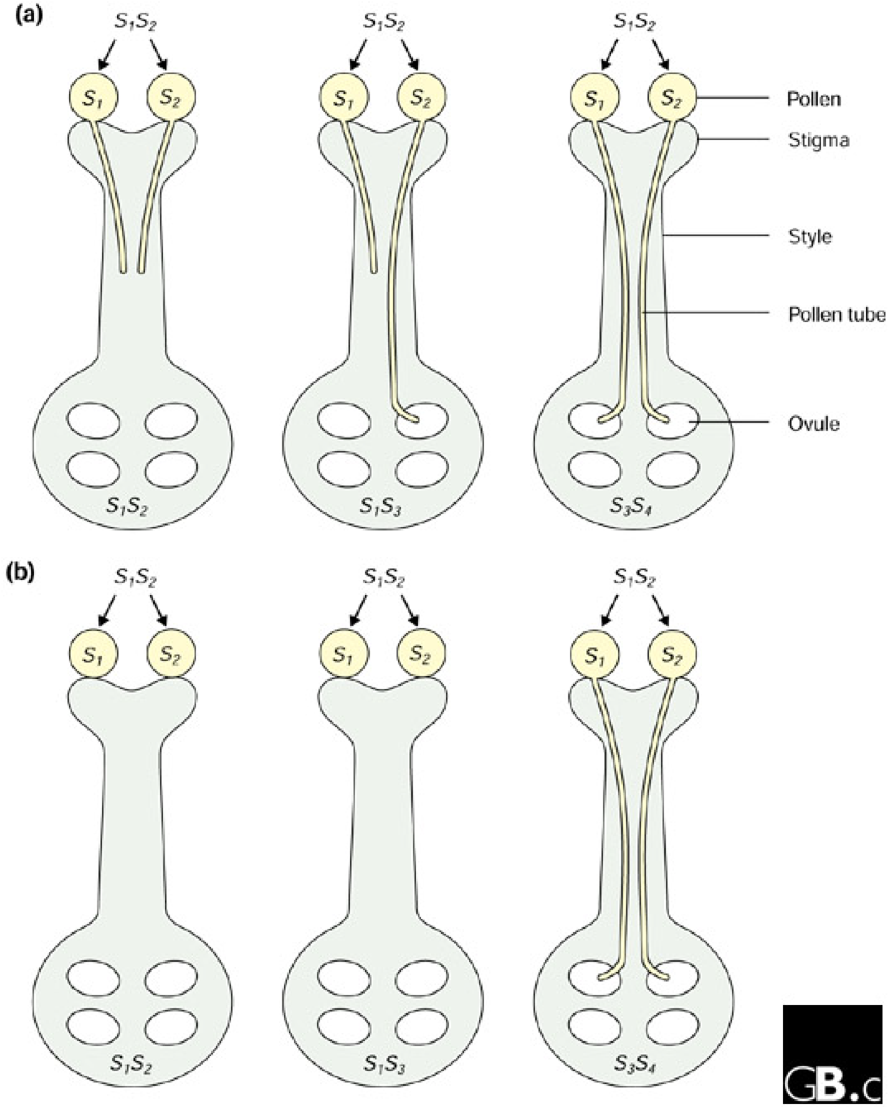
AA — *Aa* — *aa*

red pink blue

| | |

Aa 1/4 *AA*: 1/2 *Aa*: 1/4 *aa* *Aa*

Negative Assortative Mating



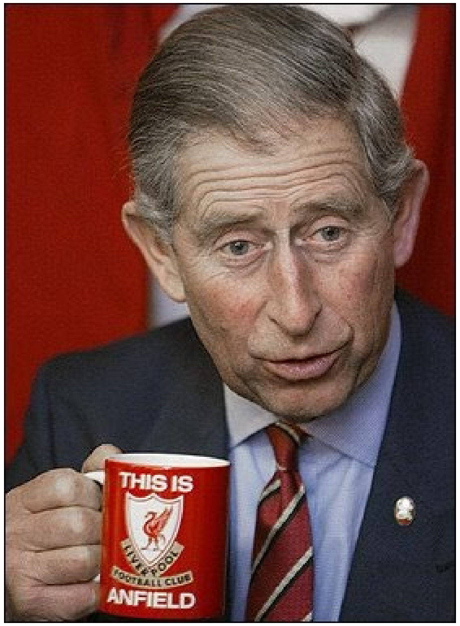
Plant self-incompatibility systems lead to negative assortative mating.

Examples: Sunflowers
Cocoa tree
Blue bells
Brassica rapa
(field mustard)

Inbreeding

Inbreeding: mating with a close relative

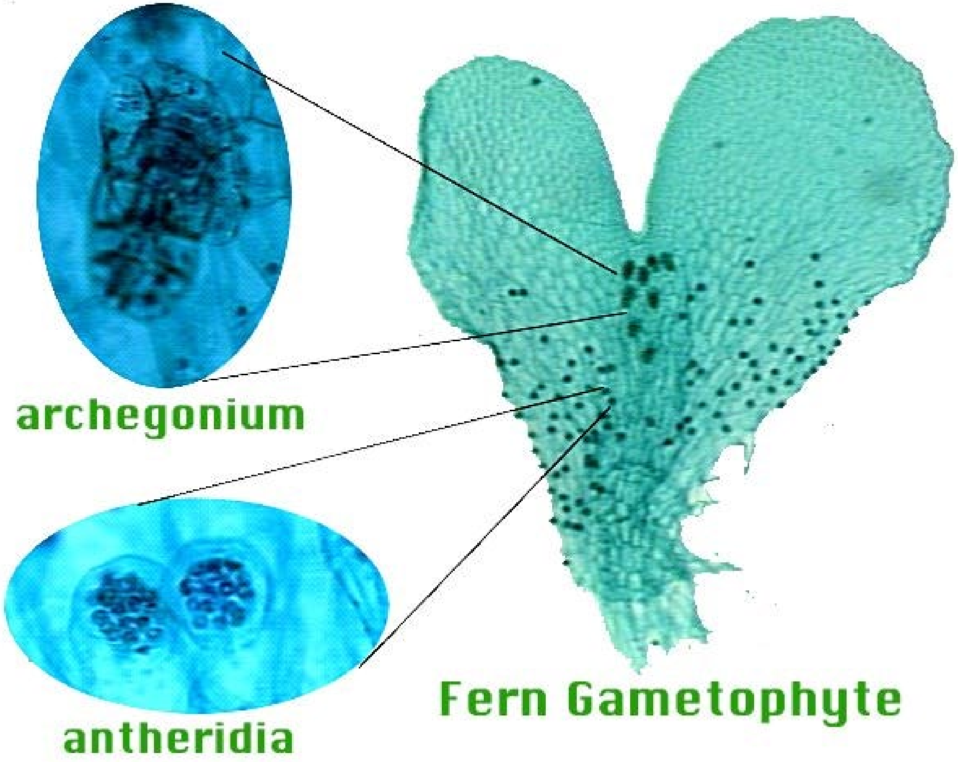
Biparental: two different individuals are involved



Extreme inbreeding

Intragametophytic selfing: mating between gametes produced from the same haploid individual

- 100% homozygosity in one generation!
- some ferns and mosses



Effect of inbreeding on genotype frequencies

Selfing

P:		Aa x Aa	
F1:	25% AA	50% Aa	25% aa
F2:	37.5% AA	25% Aa	37.5% aa
F3:	43.75% AA	12.5% Aa	43.75% aa

Fewer heterozygotes and more homozygotes

Is this evolution?

Inbreeding

Inbreeding does NOT change allele frequency by itself

Inbreeding coefficient or fixation index (*F*): measures the extent to which populations depart from the expectations of the Hardy-Weinberg equilibrium ($p^2+2pq+q^2=1$)

H_e = Expected heterozygosity, HW ($2pq$)
H_o = Observed heterozygosity

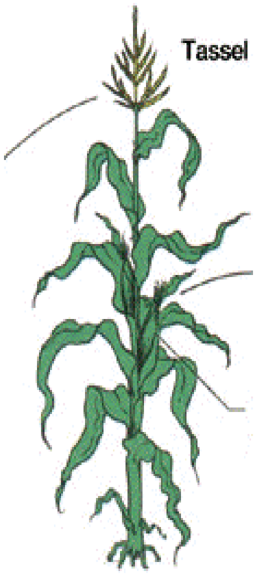
$$F = (H_e-H_o)/H_e$$

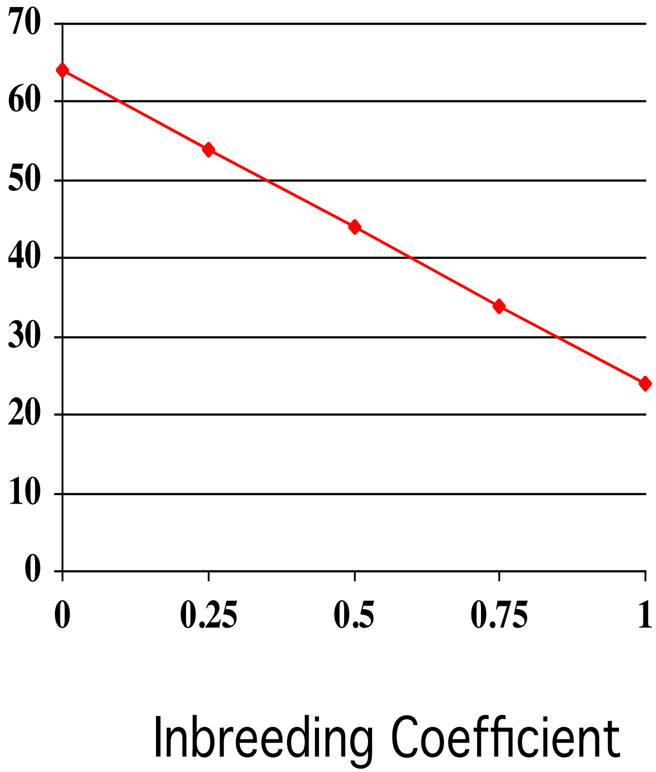
Evolutionary Consequences of Inbreeding

In large, random mating populations, most individuals carry recessive deleterious alleles as heterozygotes

Under inbreeding, increased homozygosity for these recessive deleterious alleles results in reduced population mean fitness

Corn yield in relation to Inbreeding





Evolutionary Consequences of Inbreeding

Discuss

When is inbreeding beneficial?
Discuss with members of breakout group.
Report back to class.

Genetic drift

Definition: Changes in the genotypic composition of populations due to random sampling.

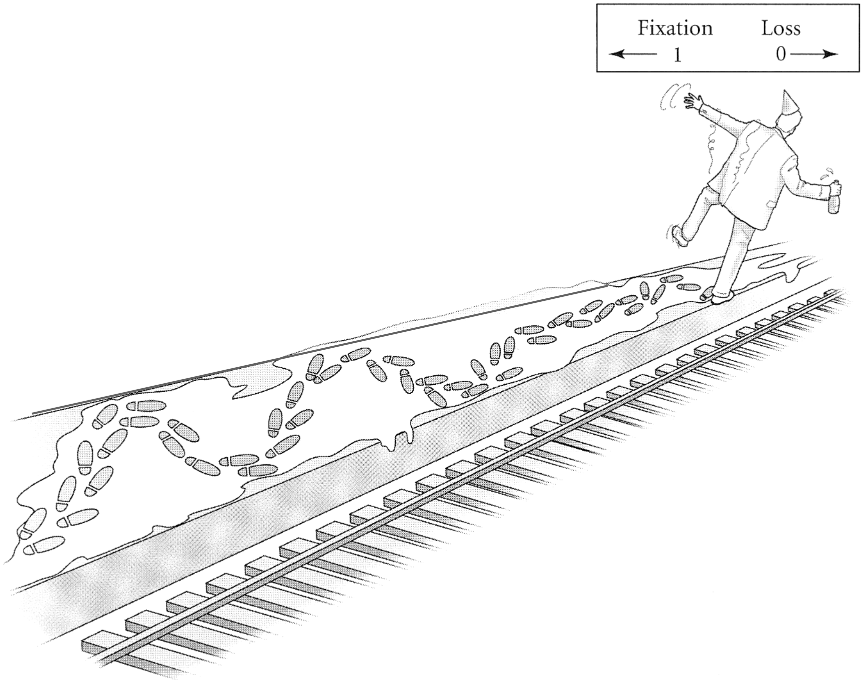
One of the requirements for the maintenance of stable allele frequencies in populations is a very large population size.

Genetic drift is the consequence of finite population size.

Genetic drift

Classic model:

Alleles that do not (necessarily) affect fitness fluctuate randomly in frequency, which eventually results in the loss of alleles from populations.



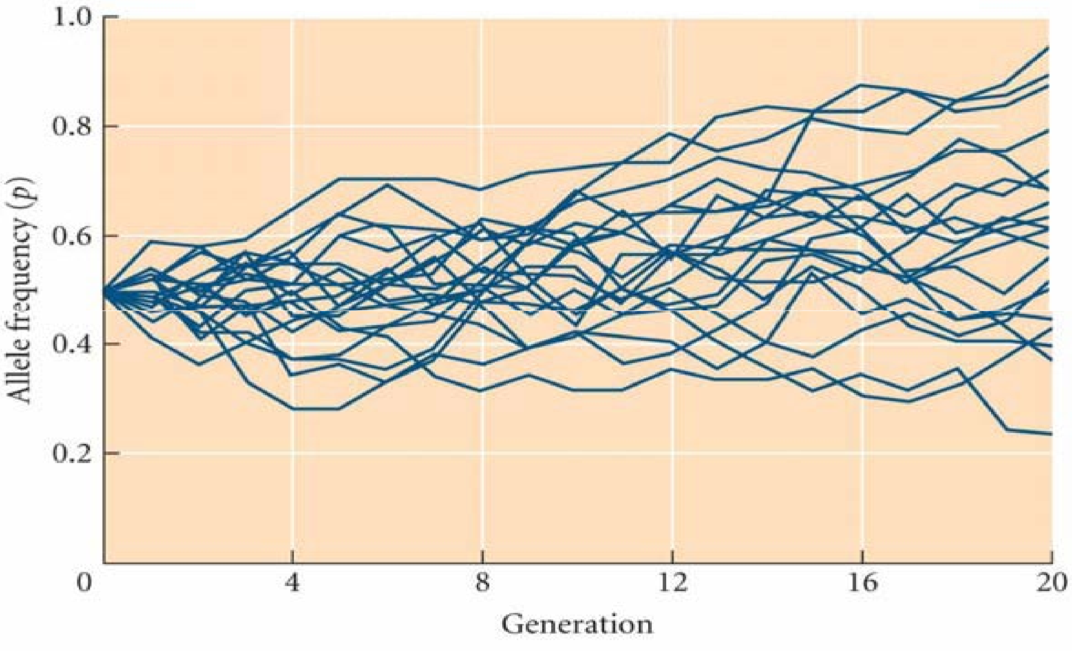
Futuyma *Evolution* 2009, fig. 10.2

Genetic drift

Different populations will lose different alleles.

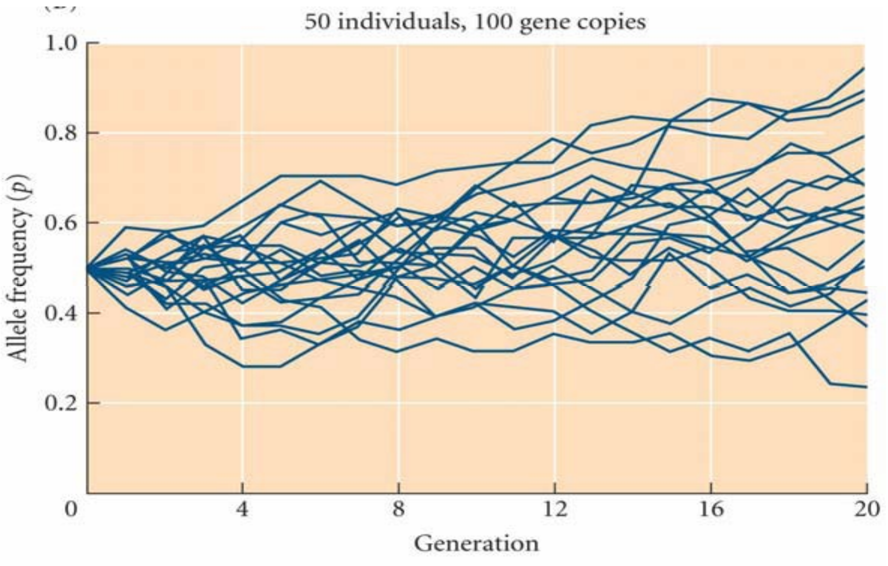
The probability that a particular allele will be fixed in a population in the future equals the frequency of the allele in the population.

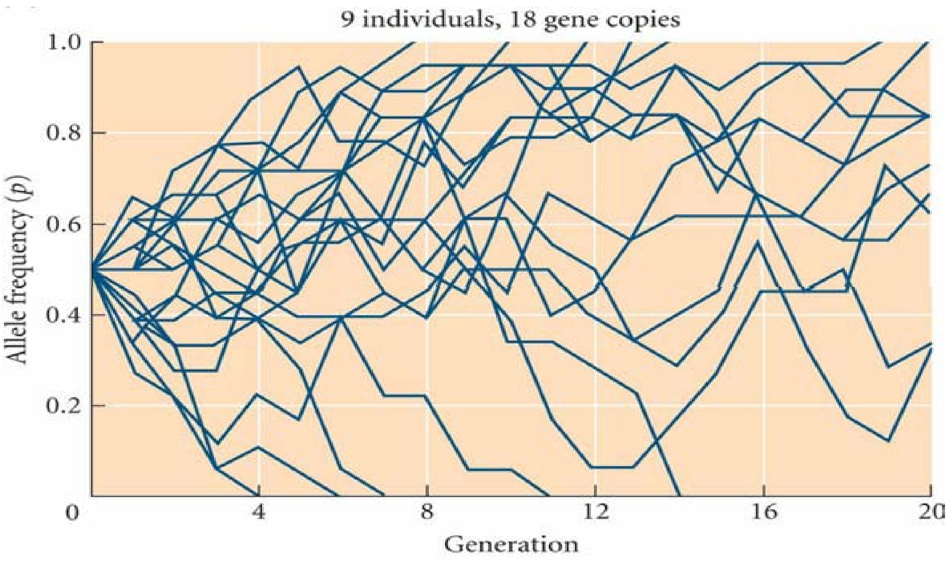
Futuyma *Evolution* 2009, fig. 10.3b



Genetic drift

(Population) size matters. Why?





Effective population size, N_e

- number of individuals in the population that successfully pass genes to the next generation

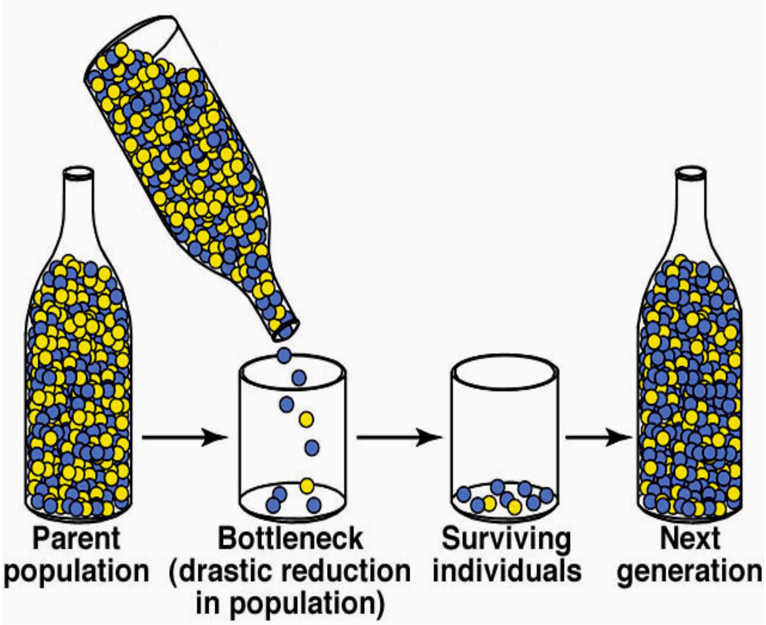
- usually smaller than the actual population (census) size

- affected by biological parameters other than the number of breeding individuals in the population

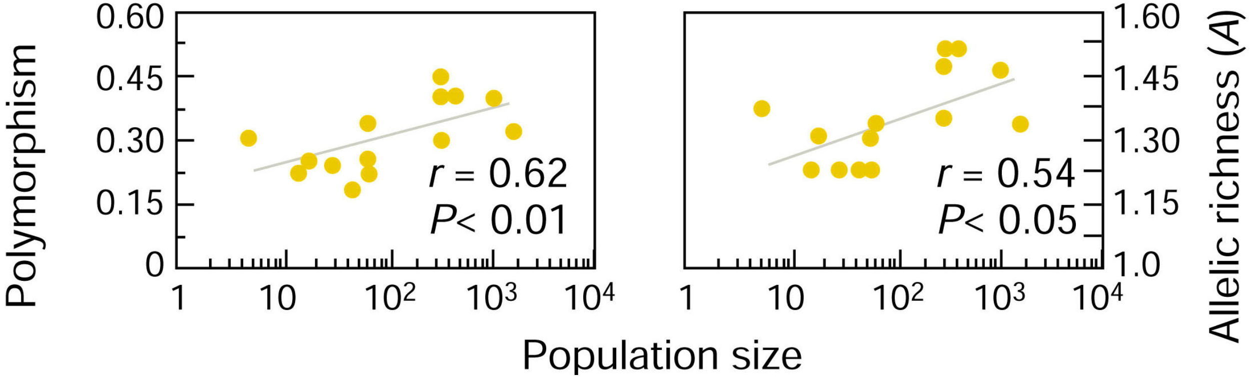
Effective population size

Factors that affect N_e:

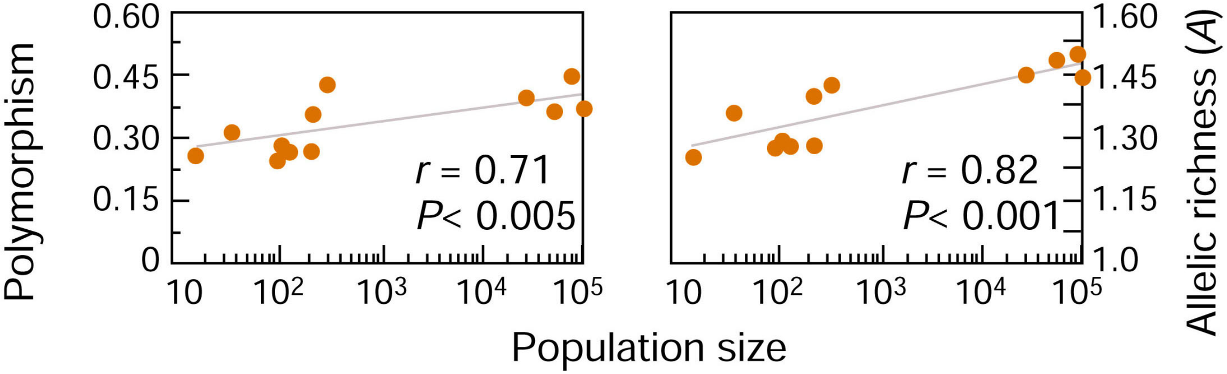
- Variation in offspring number among individuals
- Natural selection
- Uneven sex ratios
- Inbreeding (reduces the number of different copies of a gene passed to the next generation)
- Fluctuations in population size



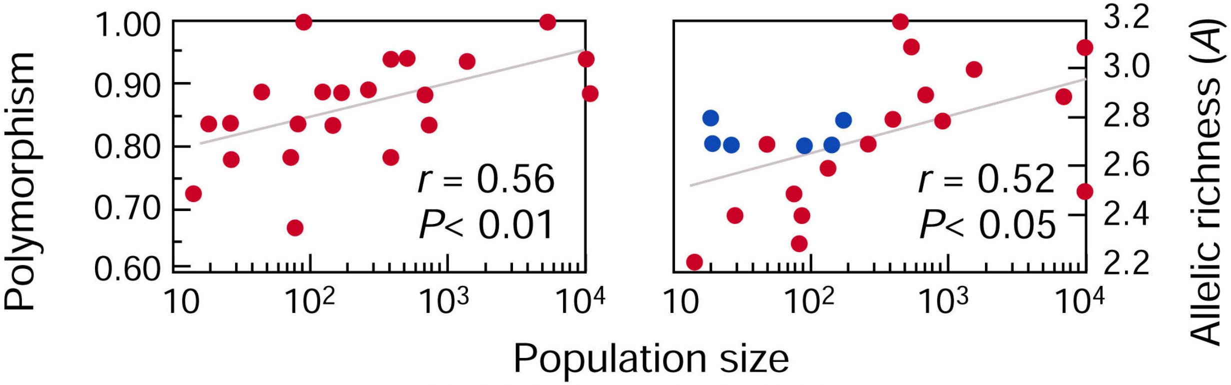
(a) *Salvia pratensis*



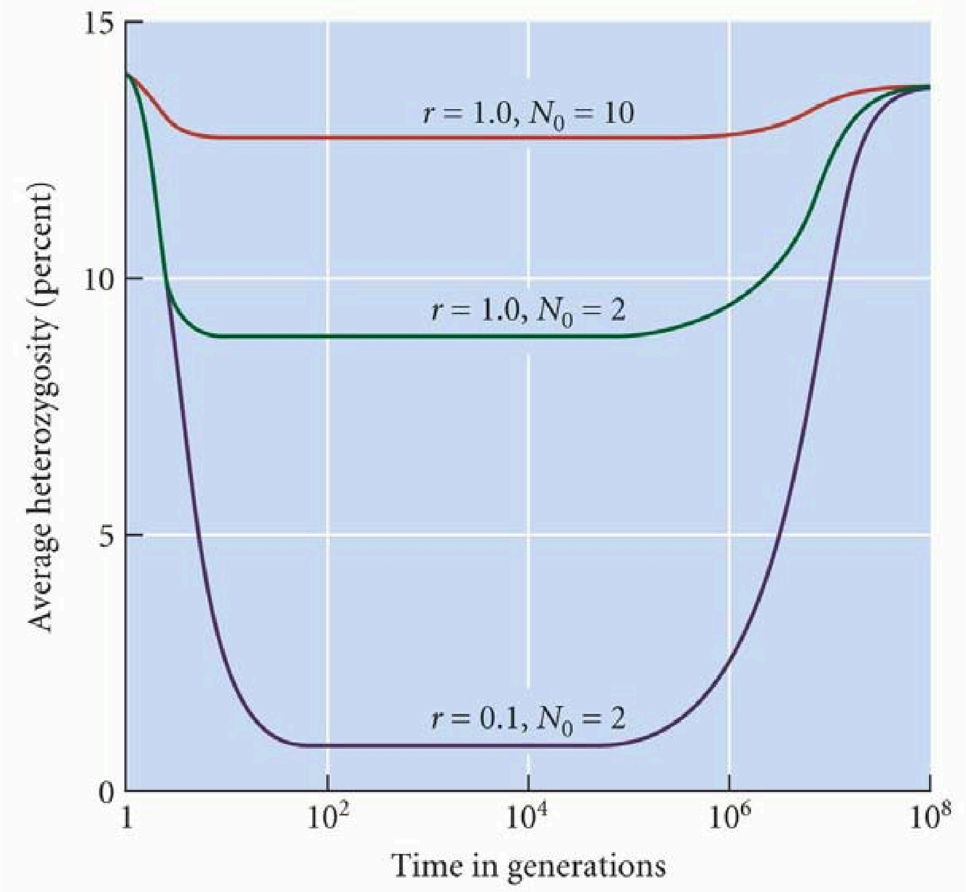
(b) *Scabiosa columbaria*



(c) *Eucalyptus albens*



Founder effects

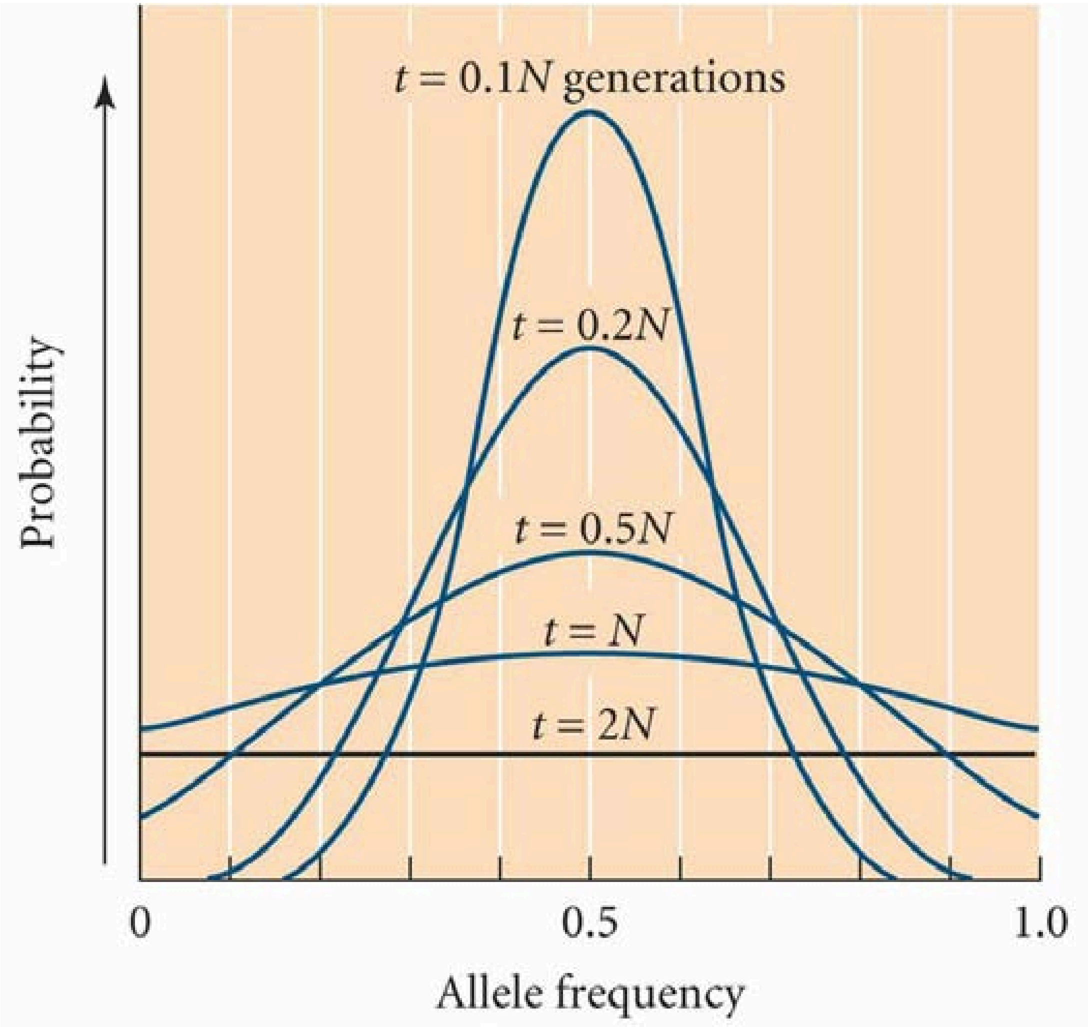


When a small number of individuals from a source population establish a new population, genetic variation can be lost.

Fewer founders and a small population growth rate (*r*) result in greater loss of genetic diversity.

Eventually, genetic variation will be restored in a founding population. Why?

Genetic drift

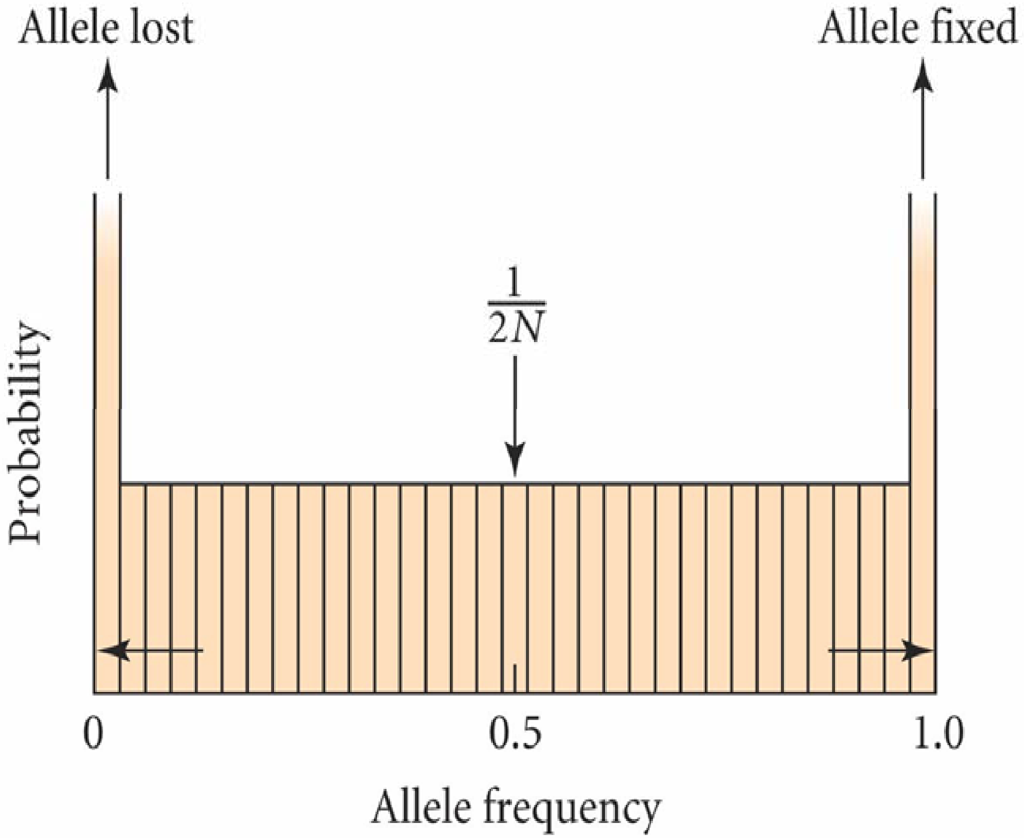


Futuyma *Evolution* 2009, fig. 10.4a

The likely magnitude of divergence from initial frequencies (here as $p = q = 0.5$) increases with time and scales to population size (N_e).

Genetic drift

After 2*N* generations, all allele frequencies between 0 and 1 are equally likely. Fixation or loss, however, are more likely.



Futuyma *Evolution* 2009, fig. 10.4b

Genetic drift

In a finite population, allele frequencies are simultaneously affected by **both** selection and drift.

If *s* (the strength of selection) or N_e are small, then an allele will primarily evolve via genetic drift.

The theoretical critical value is $4N_es$
($4N_es < 1$, alleles are **nearly neutral**).

Genetic Drift

- Within populations
  - Changes allele frequencies
  - Reduces genetic variation due to loss of rare alleles
  - Can still predict genotype frequencies from allele frequencies using Hardy-Weinberg expectations

- Among populations (if there are many)
  - Does NOT change allele frequencies
  - Does NOT degrade diversity
  - Causes a deficiency of heterozygotes compared to Hardy-Weinberg expectations (if all populations are pooled), like inbreeding.

Genetic drift: why is it important?

- Erodes genetic variation within populations
- Causes population differentiation
- Strength is dependent on effective population size
- Can oppose selection (e.g. conservation implications)
- Provides a “neutral” model for evolutionary change based on the assumption that most molecular changes are effectively neutral

The neutral theory of molecular evolution

Observations:

- Many loci are polymorphic (Lewontin and Hubby, 1966)
- Proteins evolve at similar rates in different lineages (Kimura, 1968)

Debate: How much of evolution is neutral (i.e. via drift)?

Partial Resolution? The neutral theory proposes that the majority of mutations that are fixed are effectively neutral. If so, most genetic variation evolves via genetic drift (and at a relatively constant rate). HOWEVER, this does not propose that the majority of *phenotypic* variation is neutrally evolved.

Effective population size matters: The proportion of fixed mutations that are adaptive can be as high as 50% in species with large effective population sizes, but not significantly different from zero for species with low effective population sizes.

Population structure

How do we measure population genetic structure?

Sewall Wright

Wright's fixation index (F)

F is referred to as the fixation index because of the increase in homozygosity, or fixation, that results from inbreeding.

It can also be used to measure genetic differentiation by comparing heterozygosity at different hierarchical levels. For example:

$$F_{ST} = (H_T - H_S)/H_T$$

H_T: The overall expected HW heterozygosity for the **T**otal set of (sub)populations

H_S: The average expected HW heterozygosity among organisms within (**S**ub)populations

Linanthus parryae population structure

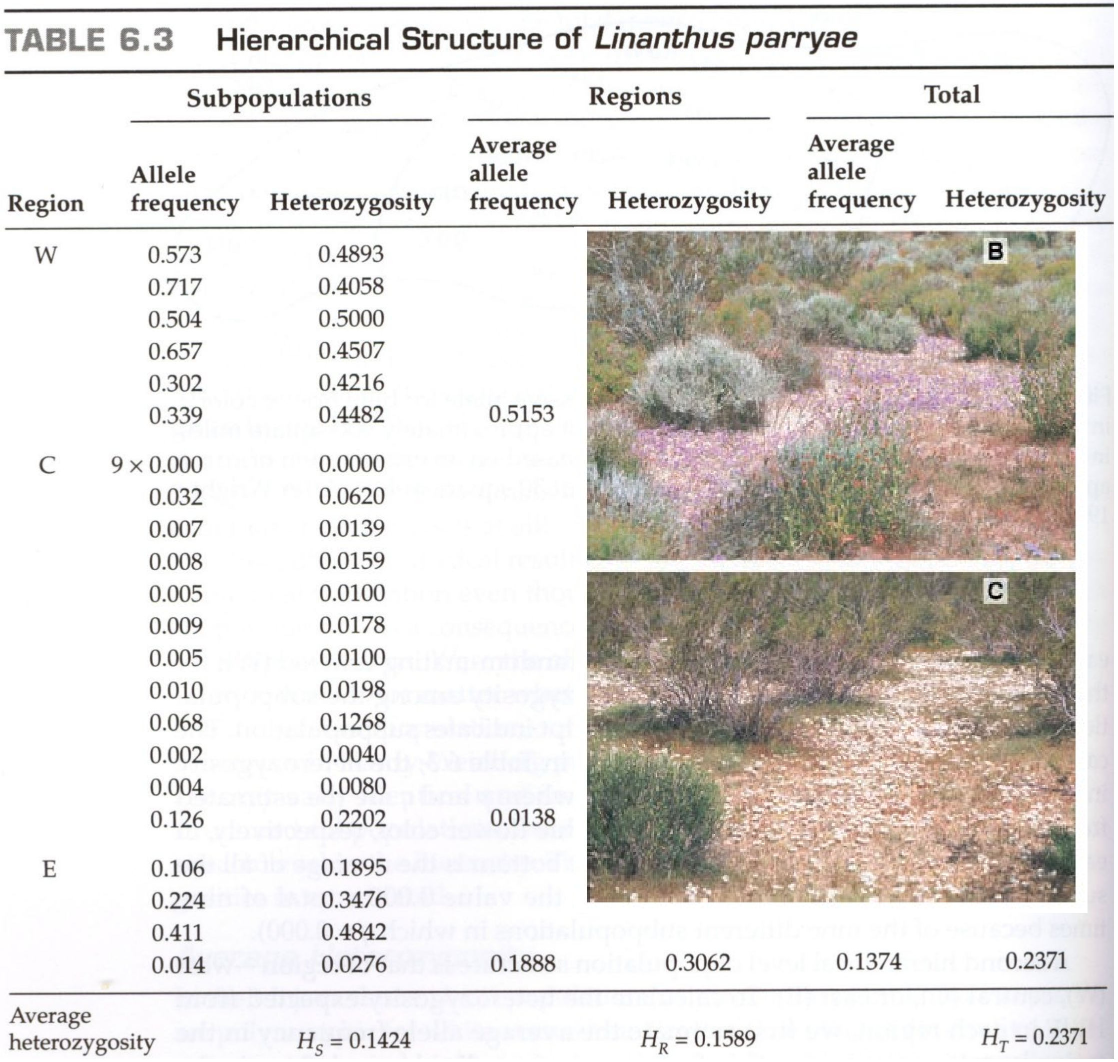


TABLE 6.3 Hierarchical Structure of *Linanthus parryae*

	Subpopulations		Regions		Total	
Region	Allele frequency	Heterozygosity	Average allele frequency	Heterozygosity	Average allele frequency	Heterozygosity
W	0.573	0.4893				
	0.717	0.4058				
	0.504	0.5000				
	0.657	0.4507				
	0.302	0.4216				
	0.339	0.4482	0.5153			
C	9 × 0.000	0.0000				
	0.032	0.0620				
	0.007	0.0139				
	0.008	0.0159				
	0.005	0.0100				
	0.009	0.0178				
	0.005	0.0100				
	0.010	0.0198				
	0.068	0.1268				
	0.002	0.0040				
	0.004	0.0080				
	0.126	0.2202	0.0138			
E	0.106	0.1895				
	0.224	0.3476				
	0.411	0.4842				
	0.014	0.0276	0.1888	0.3062	0.1374	0.2371
Average heterozygosity		$H_S = 0.1424$		$H_R = 0.1589$		$H_T = 0.2371$

What could be causing the divergence in flower colour among the sub populations?

$$F_{ST} = (H_T - H_S)/H_T$$

$$= (0.2371-0.1424)/0.2371$$

$$=0.40$$

Unresolved Questions

- How important is genetic drift (versus natural selection) in creating patterns of genetic variation within species and between species?
- What proportion of new mutations are fixed via natural selection versus genetic drift?