

The plant of the day



Today's Topics

Non-random mating

Genetic drift

Population structure

Big 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.

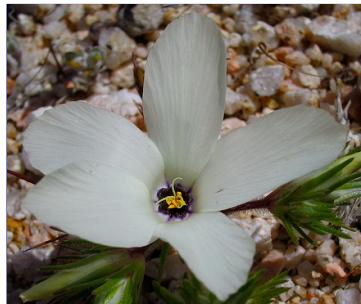




Positive Assortative Mating

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

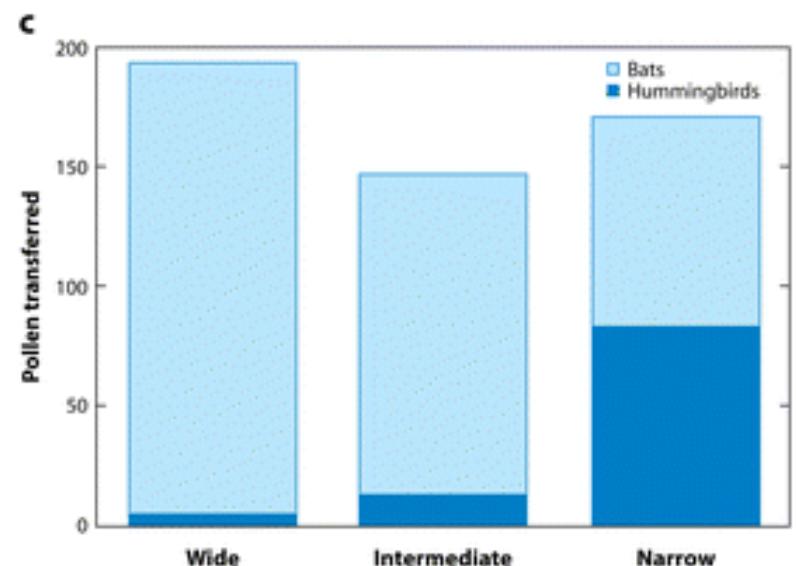
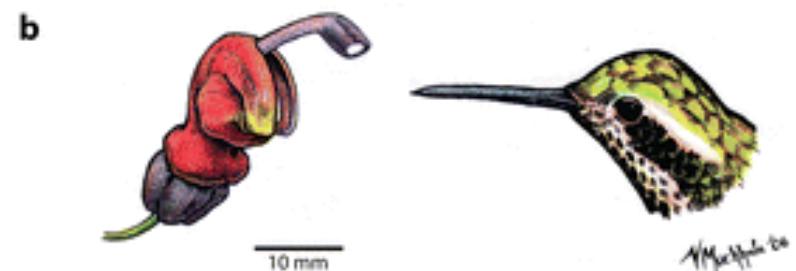
<u>AA</u>	<u>Aa</u>	<u>aa</u>
red	pink	blue
AA	$1/4 AA: 1/2 Aa: 1/4 aa$	aa



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



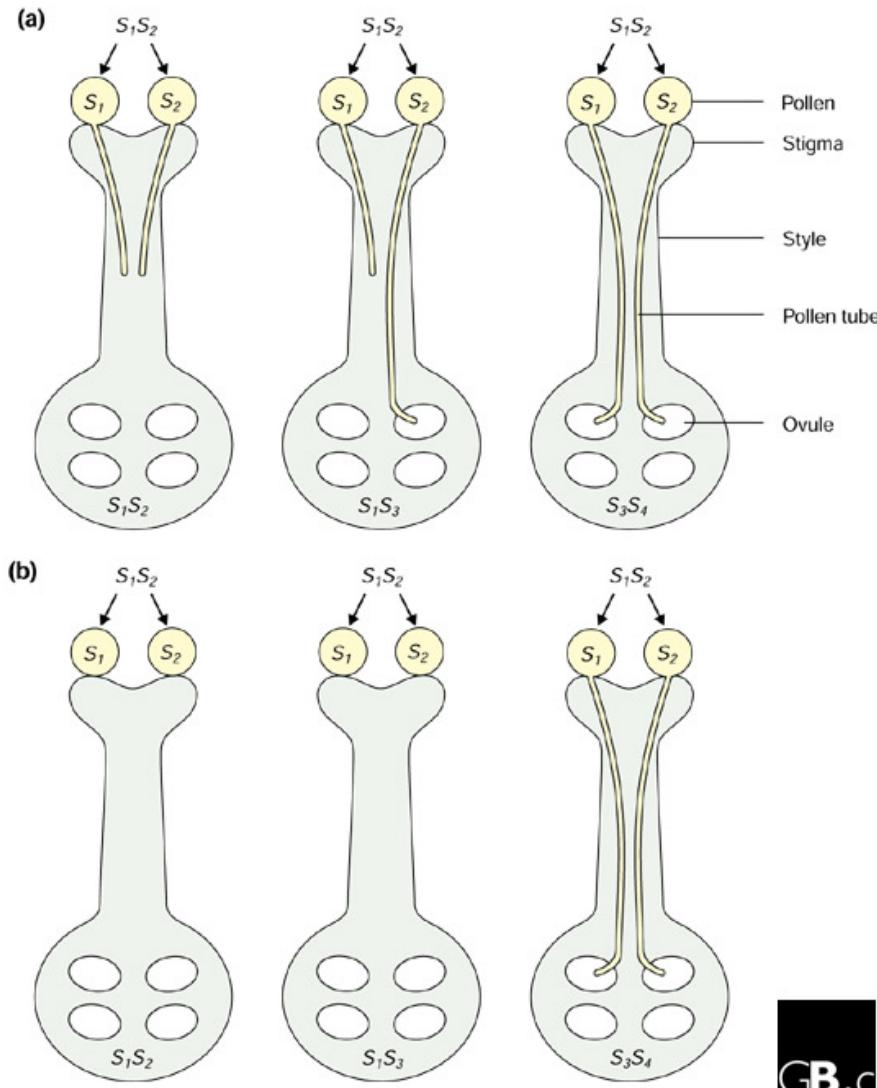
Negative Assortative Mating

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





Negative Assortative Mating



Plant self-incompatibility systems lead to negative assortative mating.

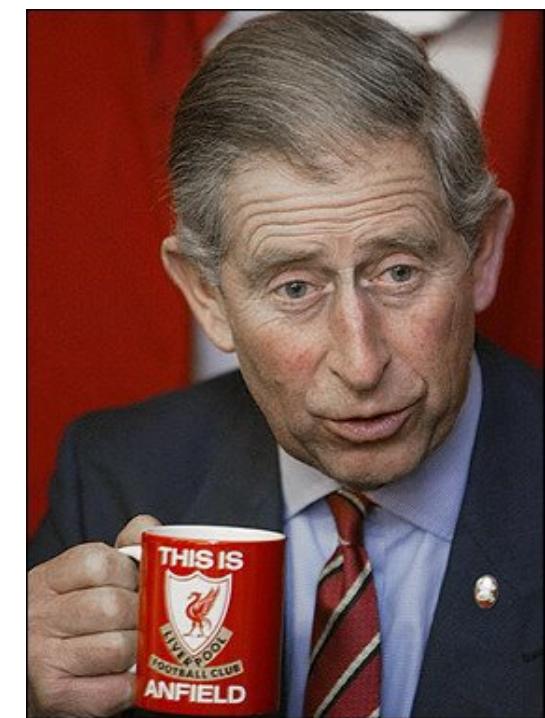
Examples: Sunflowers
Cocoa tree
Blue bells
Brassica rapa
(field mustard)



Inbreeding

Inbreeding: mating with a close relative

Biparental: two different individuals are involved

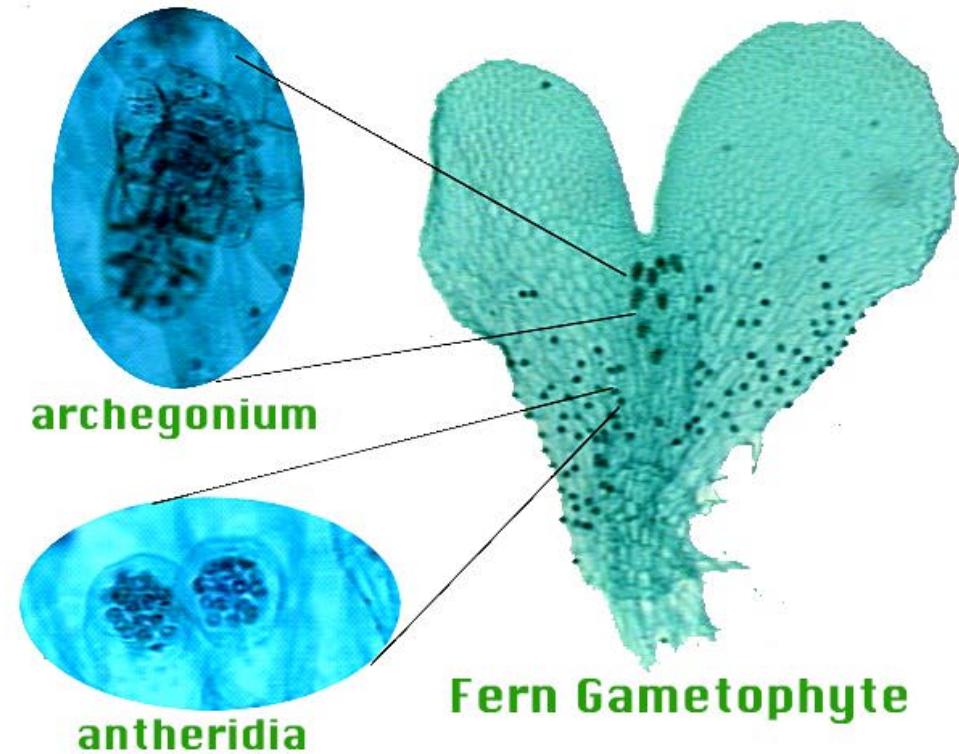




Extreme inbreeding

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

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





The effects of inbreeding on genotype and allele frequencies

Selfing

P: $Aa \times Aa$

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 (F):

measures the extent to which populations depart from the expectations of the Hardy-Weinberg equilibrium

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

H_o = Observed heterozygosity

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

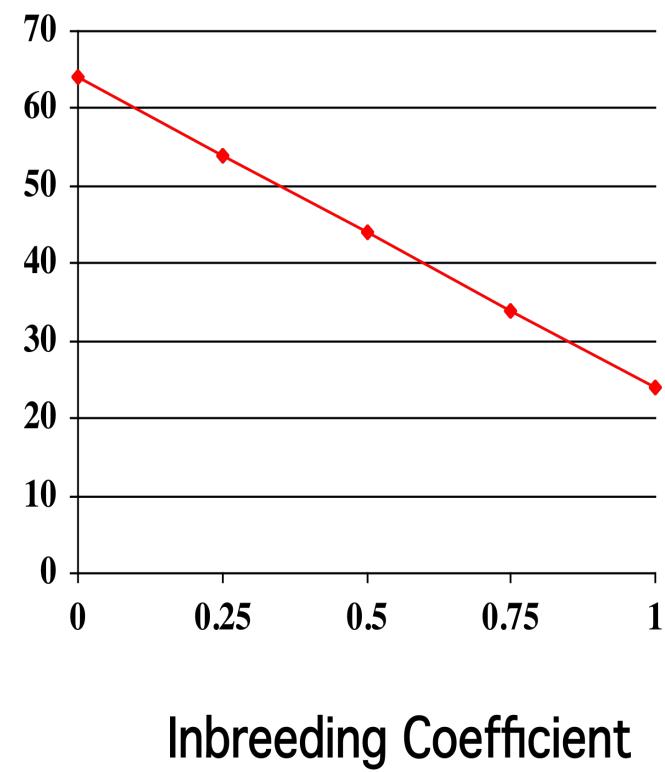
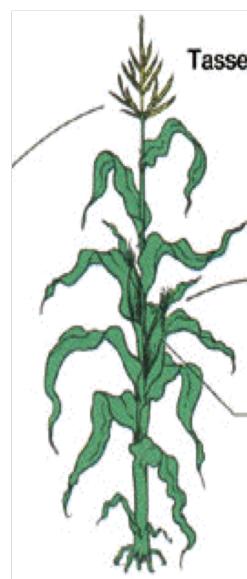


Evolutionary Consequences of Inbreeding

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





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.

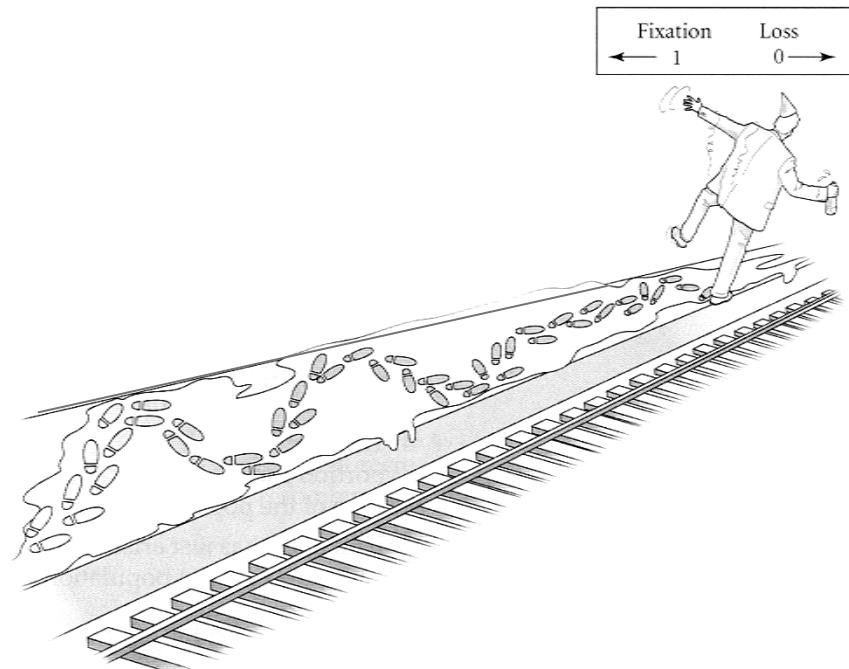
Genetic drift is the consequence of finite population size.



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

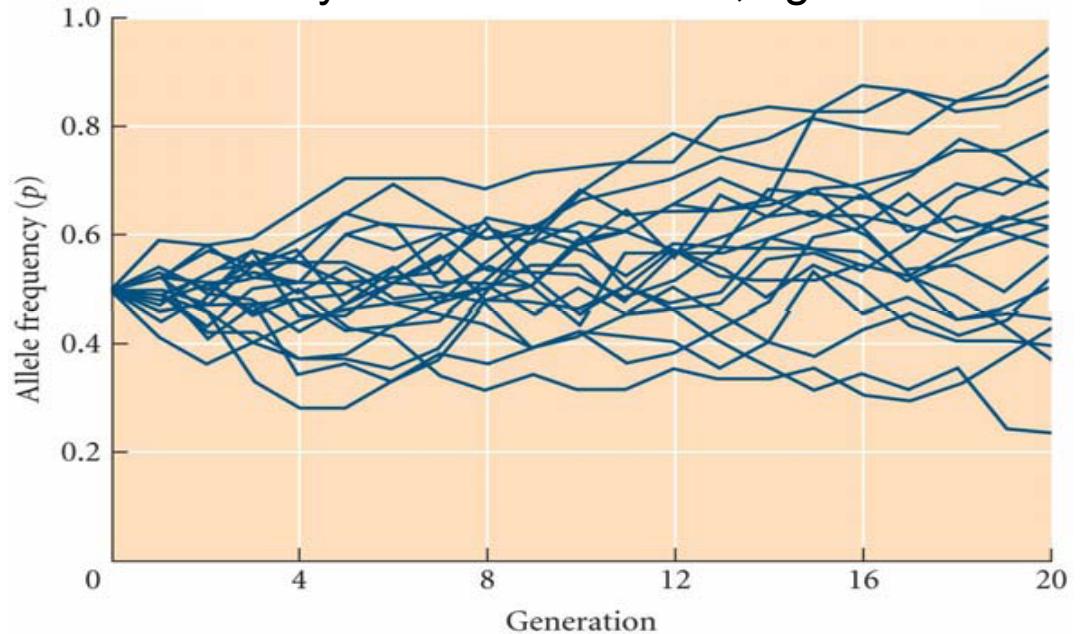


Genetic drift

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.

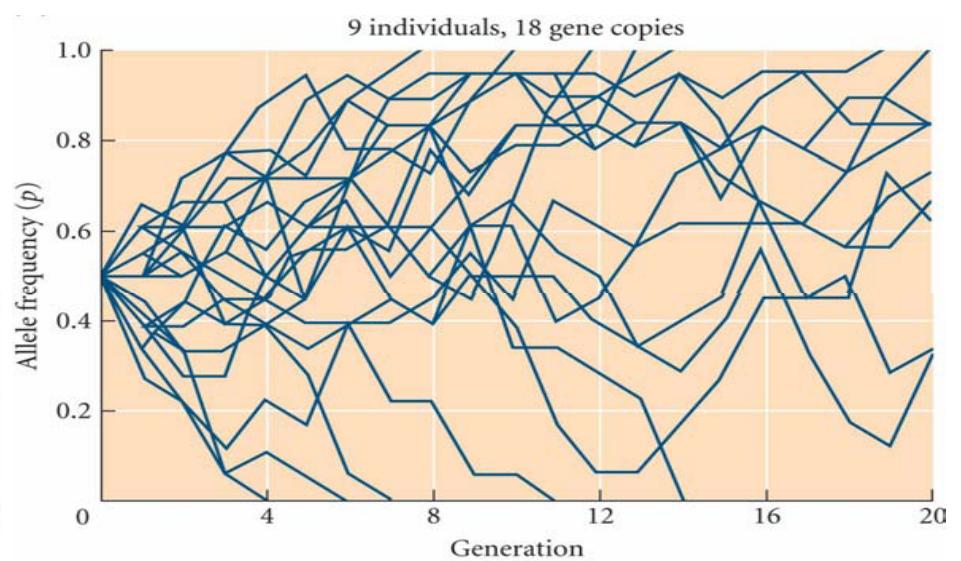
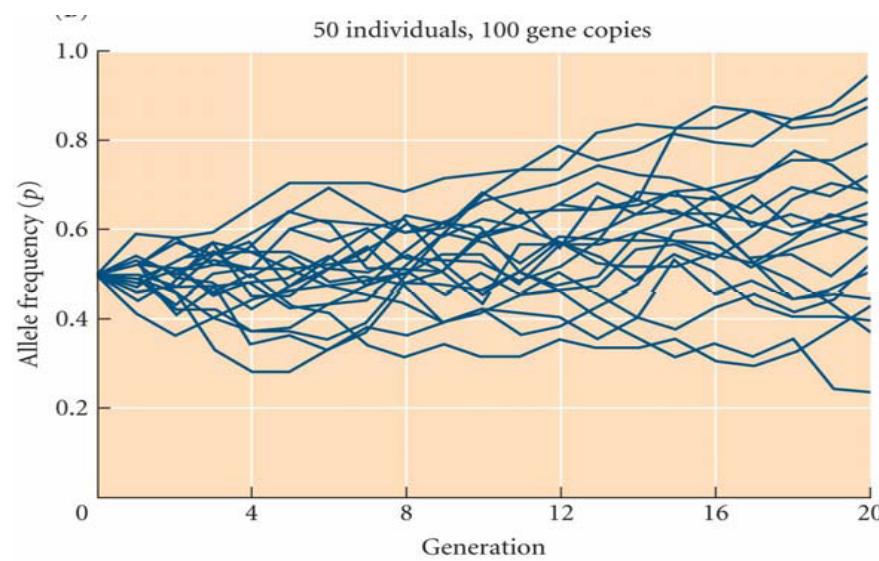
Futuyma *Evolution* 2009, fig. 10.3b





Genetic drift

(Population) size matters. Why?





Effective population size, N_e

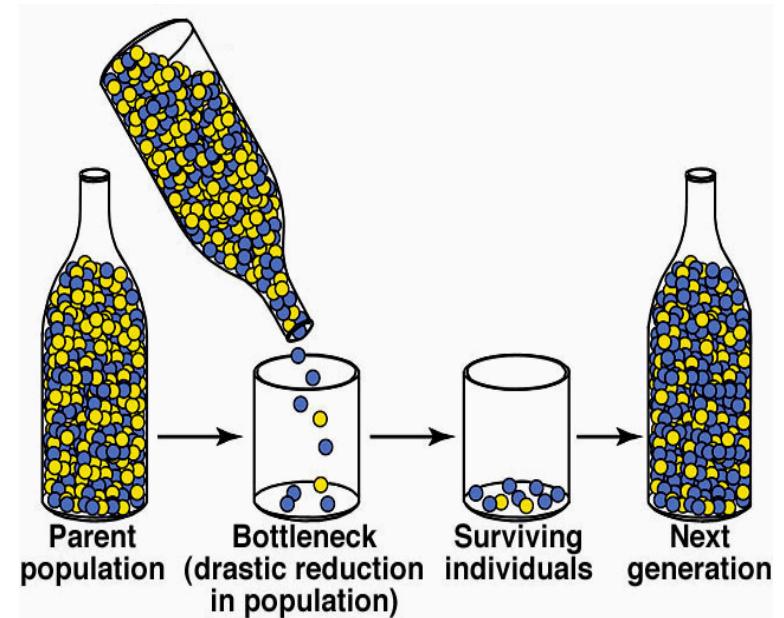
- number of individuals in the population that successfully pass genes to the next generation
- usually smaller than the actual population (census) size
- affected by biological parameters other than the number of breeding individuals in the population



Effective population size

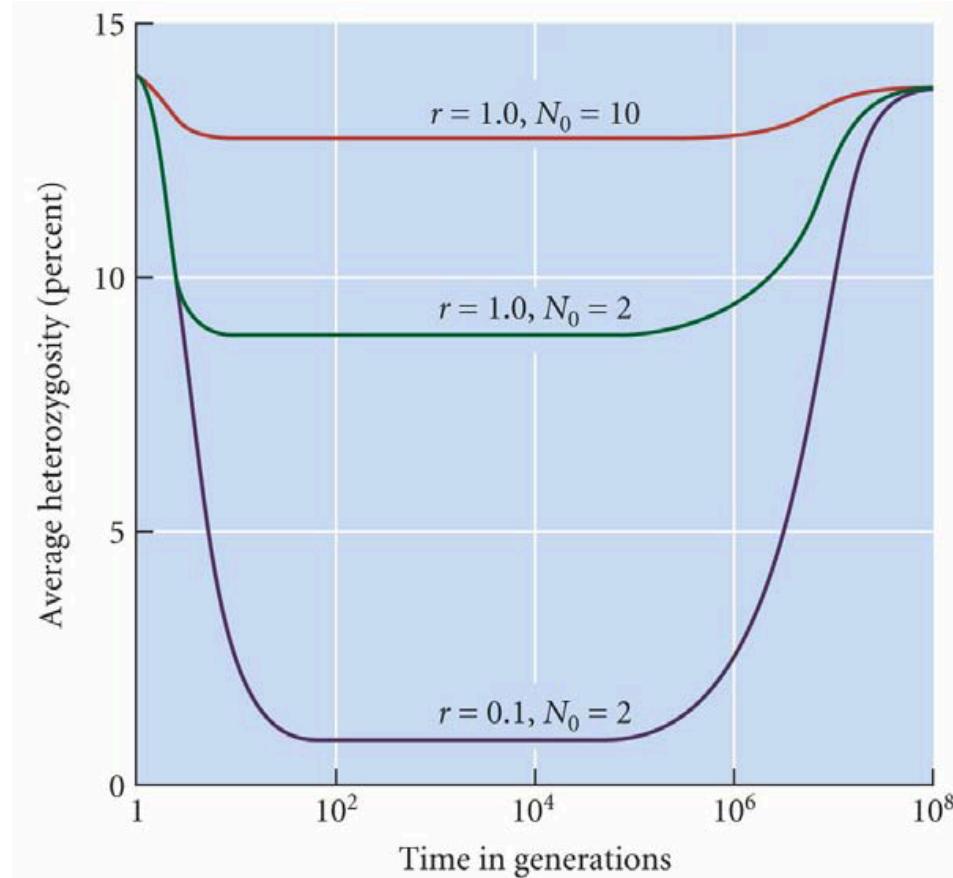
Factors that affect N_e :

- 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





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, mutation will restore genetic variation in a founding population.

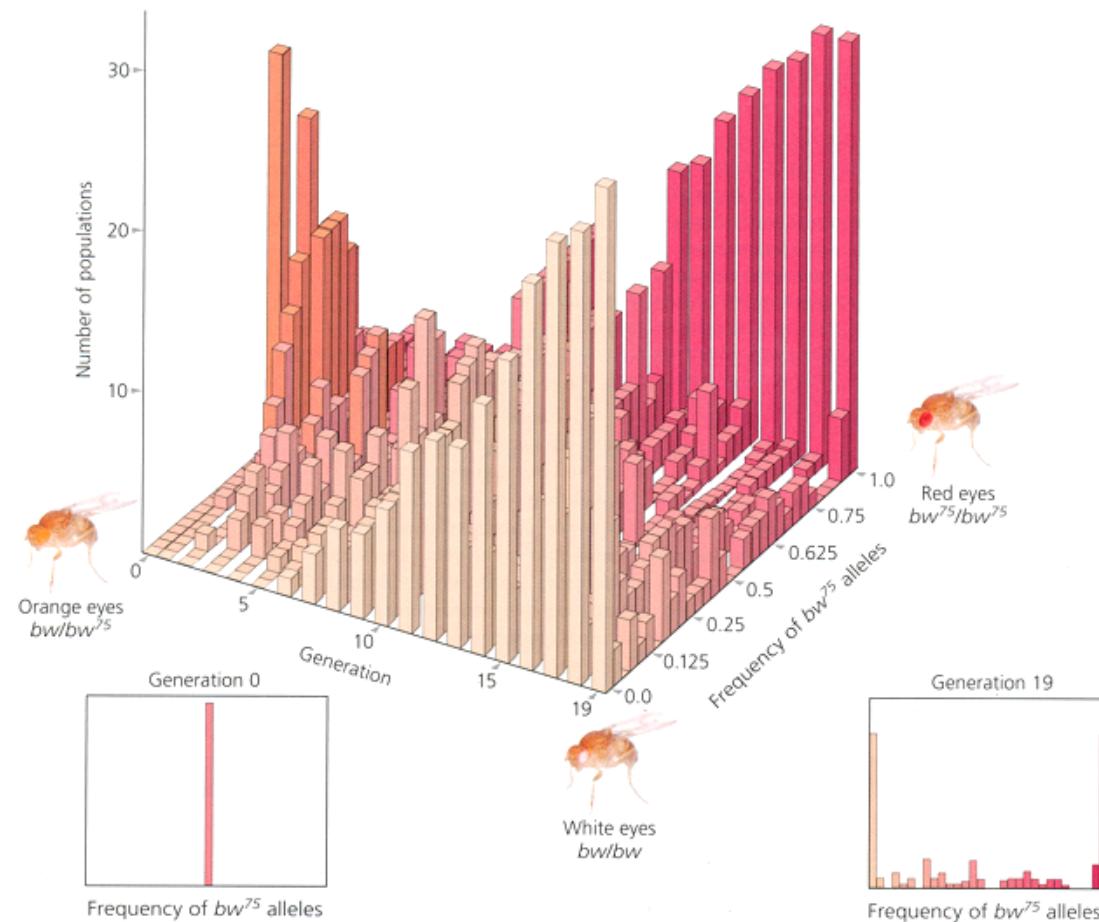


Genetic drift

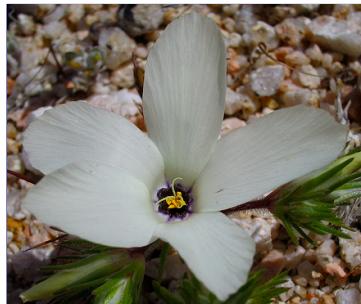
What is the approximate probability of fixation of a new neutral mutation that arises in an effective population of 1500 diploid *Arabidopsis thaliana* individuals?



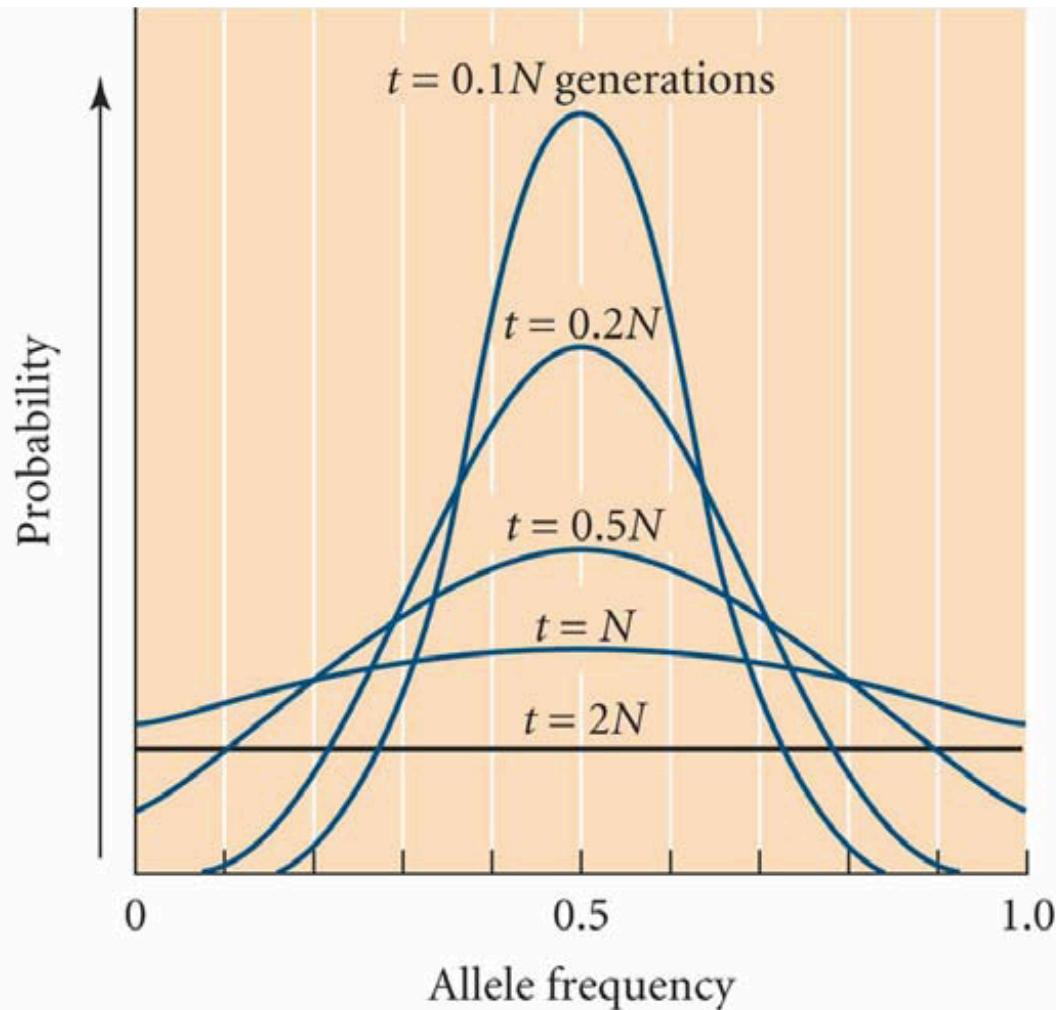
Genetic drift



Zimmer and Emlen *Evolution* 2013, fig. 6.4



Genetic drift



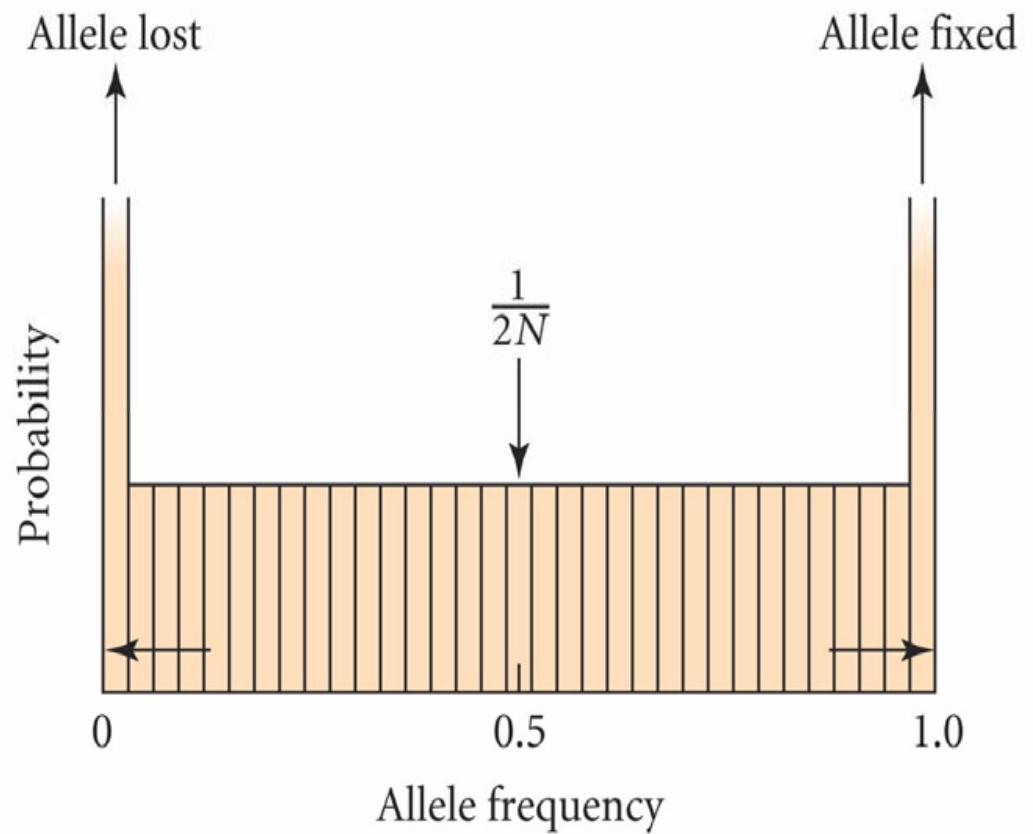
The likely magnitude of divergence from initial frequencies (here as $p = q = 0.5$) increases with time and scales to population size (N_e).

Futuyma *Evolution* 2009, fig. 10.4a



Genetic drift

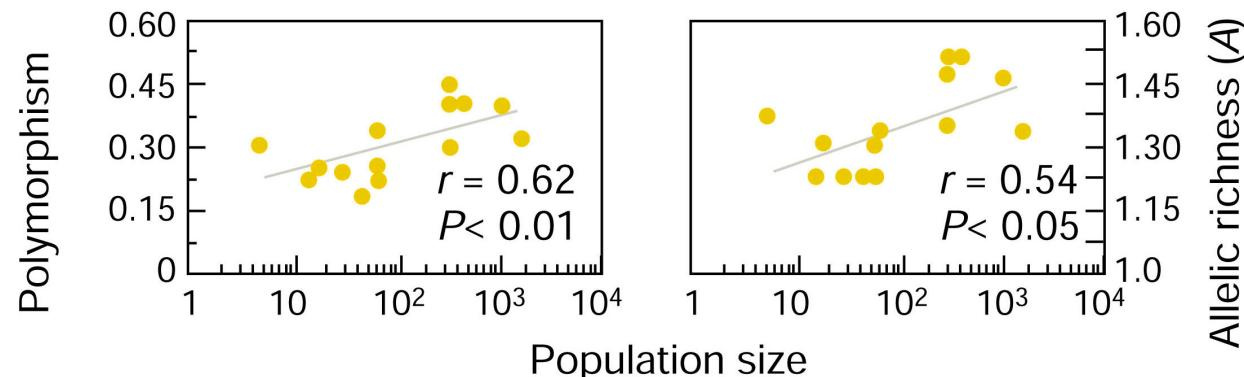
After $2N$ generations, all allele frequencies between 0 and 1 are equally likely. Fixation or loss, however, are more likely.



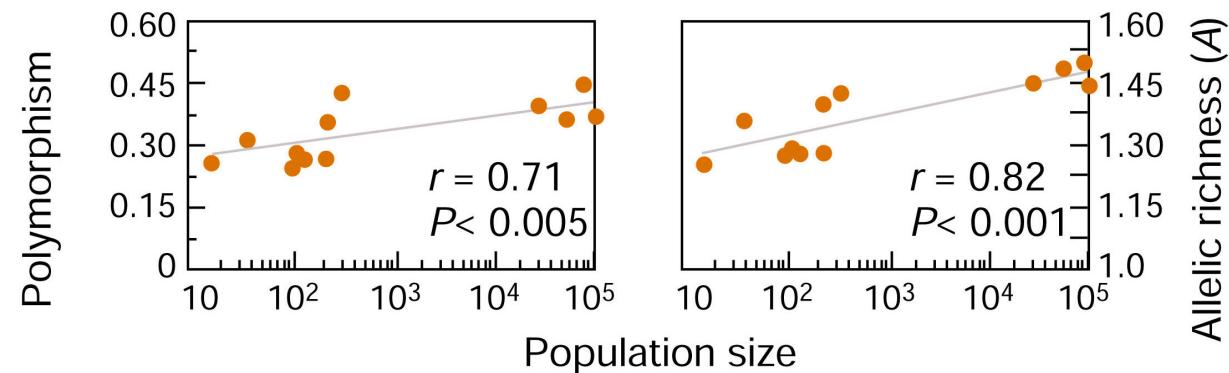
Futuyma *Evolution* 2009, fig. 10.4b



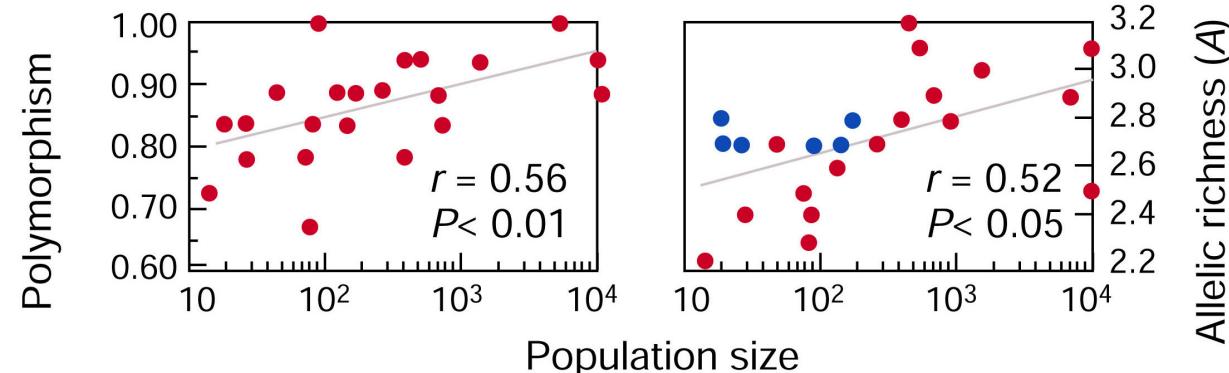
(a) *Salvia pratensis*



(b) *Scabiosa columbaria*



(c) *Eucalyptus albens*





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 $4N_e s$
($4N_e s < 1$, alleles are **nearly neutral**).



Genetic Drift

- Within populations
 - Changes allele frequencies
 - Reduces variance among individuals
 - 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 population size
- The demographic history of populations effects patterns of genetic variation
- Can oppose selection (e.g. conservation implications)
- Provides a “neutral” model for evolutionary change and 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)?

Resolution? The neutral theory proposes that the majority of mutations that are fixed are effectively neutral. Therefore, 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.

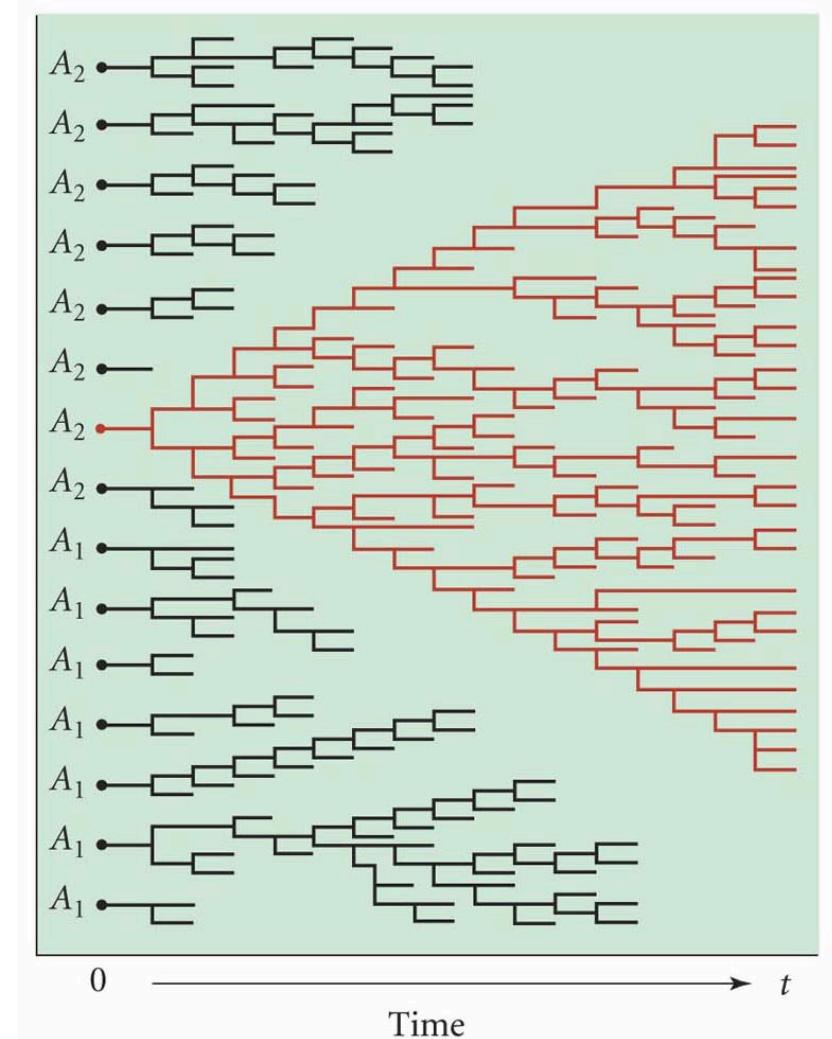


Coalescence

All gene copies in a population ultimately are descended from a single ancestral copy

(Or, all gene copies **coalesce** back to a single common ancestor)

Futuyma *Evolution* 2009, fig. 10.1





Population structure

How do we measure population genetic structure?



Sewall Wright



Wright's fixation index

Fixation index (F) is a measure of genetic differentiation among populations

Compares heterozygosity at different hierarchical levels. For example:

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

H_T : The overall expected HW heterozygosity for the total area

H_S : The average expected HW heterozygosity among organisms within populations



Linanthus parryae population structure

TABLE 6.3 Hierarchical Structure of *Linanthus parryae*

Region	Subpopulations		Regions		Total	
	Allele frequency	Heterozygosity	Average allele frequency	Heterozygosity	Average allele frequency	Heterozygosity
W	0.573	0.4893	0.5153	 	0.1374	0.2371
	0.717	0.4058				
	0.504	0.5000				
	0.657	0.4507				
	0.302	0.4216				
	0.339	0.4482				
C	9 × 0.000	0.0000	0.0138	 	0.1374	0.2371
E	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				

Average heterozygosity $H_S = 0.1424$ $H_R = 0.1589$ $H_T = 0.2371$

What is the genetic divergence among sub populations (F_{ST})?

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

Unresolved Questions

- How often does genetic drift (versus natural selection) create patterns of genetic variation within species?
- What proportion of new mutations are fixed via natural selection versus genetic drift?