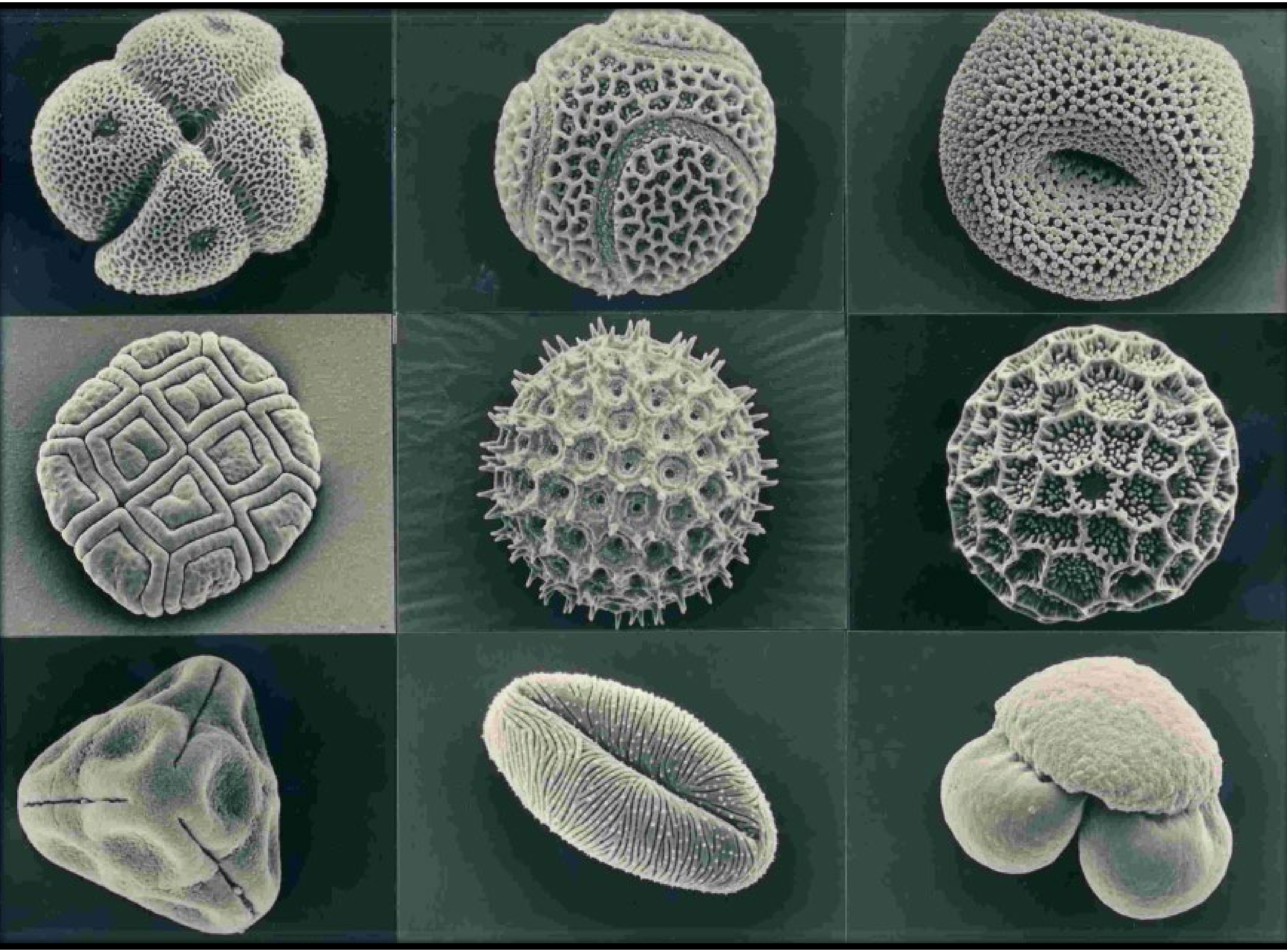
Plant of the Day

Drosera rotundifolia

... a miniscule, carnivorous sundew living in Camosun bog.



Gene flow

Gene flow is the transfer of genetic material between populations resulting from the movement of individuals (**migration**) or their gametes.

Gene flow may add new alleles to a population or change the frequencies of alleles already present

Gene flow connects the populations of a species, enabling them to evolve collectively (as a unit).

Reductions in gene flow may lead to speciation.

Gene flow: lecture outline

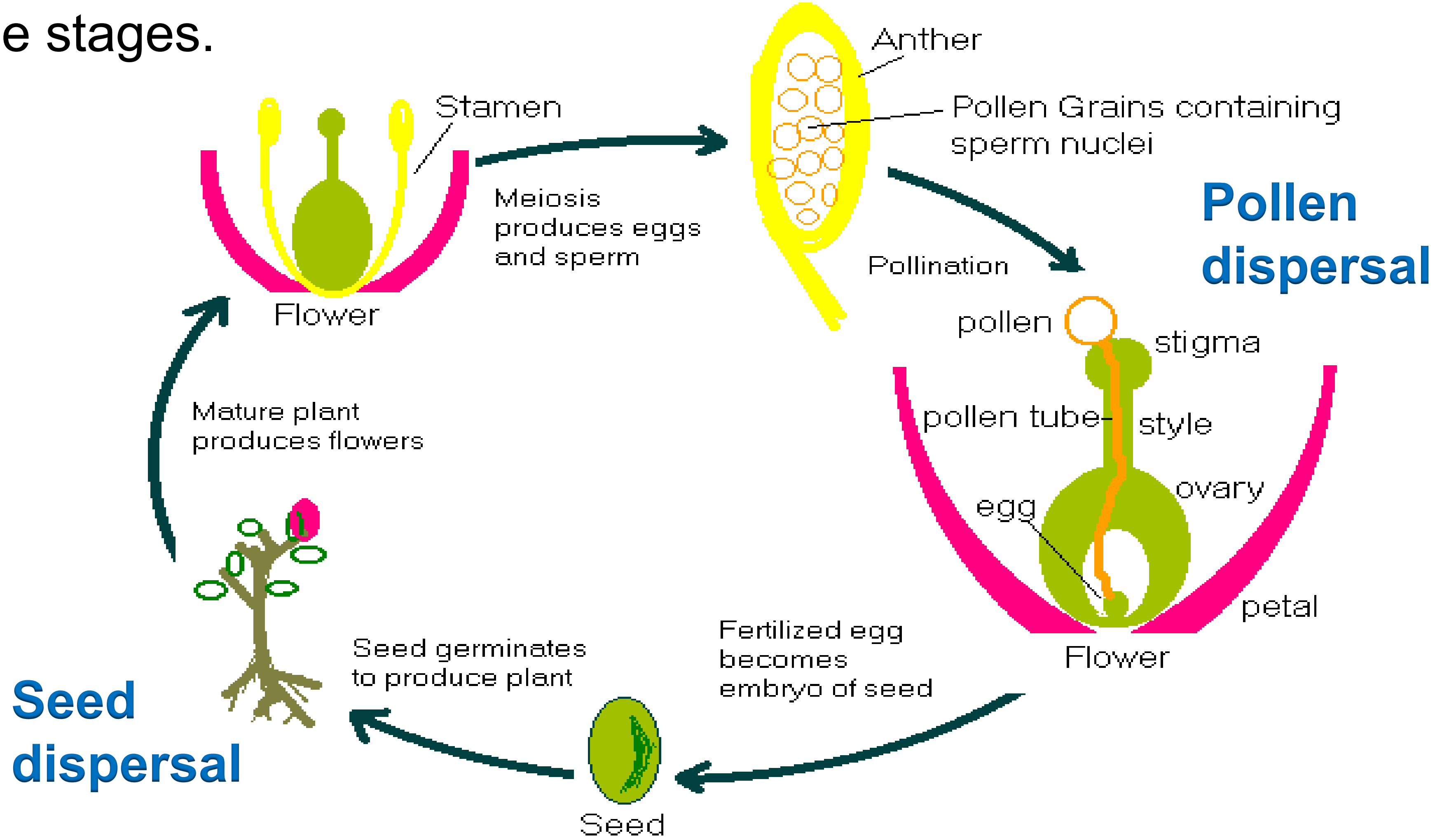
- Gene flow in plants
  - Dispersal mechanisms
  - Measuring gene flow directly & indirectly
  - Pollen versus seed dispersal

- Gene flow and evolution
  - From species cohesion to speciation
  - The spread of beneficial alleles

- Applications
  - Conservation implications
  - Transgene escape

Gene flow in plants

Plants disperse their genes during two independent life cycle stages.



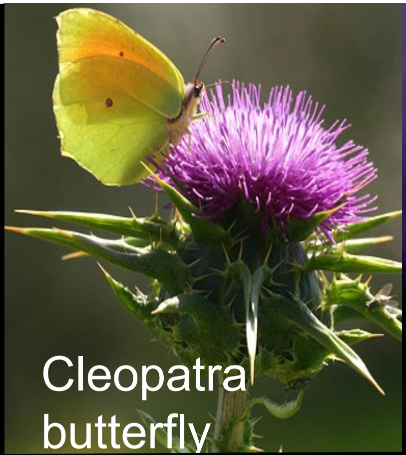
Pollen dispersal agents: biotic

Bees

Lepidoptera

Vertebrates

Solitary bee



Cleopatra butterfly

Hawkmoth

Sunbird

Honey possum

Other insects

Thynnid wasp

Tchinid fly

Beetle

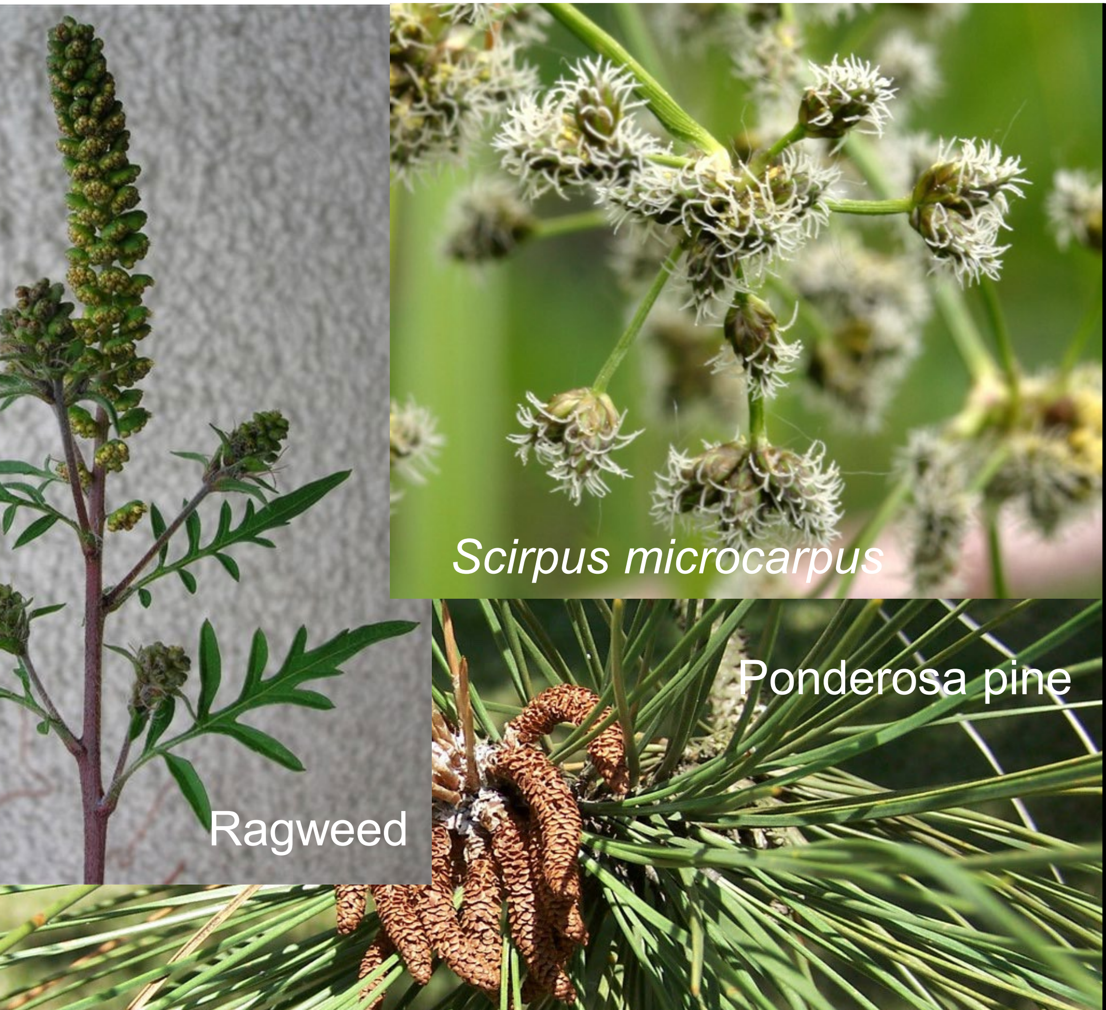
Long-nosed bat

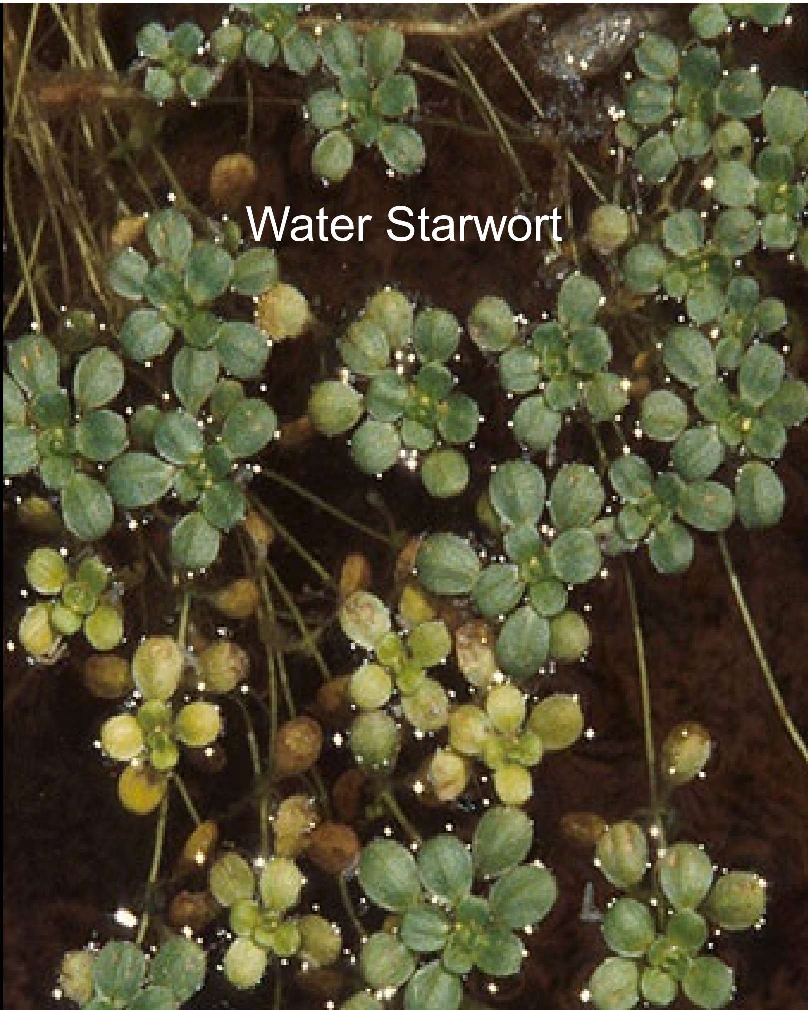
Hummingbird

Pollen dispersal agents: abiotic

Wind

Water





Seed dispersal agents

Animal

Blackberry

Water

Pond iris

Impatiens

Wind

Dandelion

Explosive

Gorse

Measuring gene flow: direct methods

(1) Observe movement of dispersal agents

- *Shortcomings: may e.g. underestimate dispersal because of pollen carryover. Can’t tell if pollen is successfully incorporated into new population or if seed grows into reproductively successful individuals.*

(2) Mark pollen with dyes, paint, rare earth magnets or radioactive tracers and monitor movement

- *Alternative: naturally polymorphic pollen.*
- *Shortcomings: marking may affect dispersal. Can’t tell if pollen is successfully incorporated into new population.*

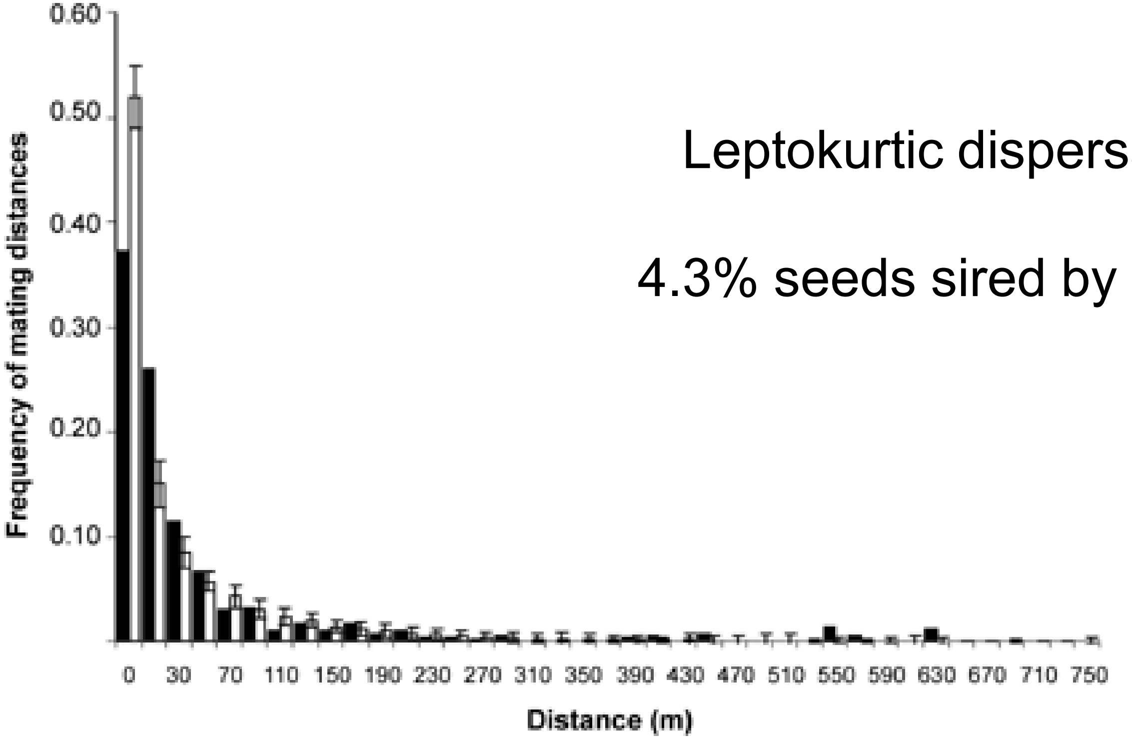
Measuring gene flow: direct methods

(3) Track unique molecular marker from source plant(s) in progeny of nearby plants

Data from first three methods indicates that most pollen and seeds are dispersed close to source. These results suggested that gene flow rates between plant populations were very low (< 1% per gen.).

Measuring gene flow: direct methods

(4) **Parentage analyses**: highly polymorphic markers are used to screen seeds to determine what fraction of seeds had fathers or mothers from outside the population.



Leptokurtic dispersal curve in Scots Pine

4.3% seeds sired by individuals outside of the population

Robledo-Arnuncio & Gi 2005

Measuring gene flow: direct methods

Paternity analyses suggest that populations spatially isolated by hundreds or thousands of meters are not genetically isolated and gene flow rates often are high (> 1% per gen.)

How to resolve this conflict?

Measuring dispersal from a source (i.e. as in Methods 1-3) misses rare, long distance dispersal events. The tails of these dispersal curves were missing.

Measuring gene flow: direct methods

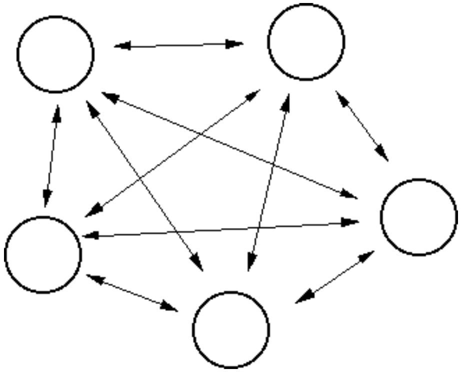
Final caveat: all direct methods provide contemporary estimates of gene flow only and are not easily related to historical gene flow levels, which is what we really care about from an evolutionary standpoint.

Measuring gene flow: indirect methods

Historical gene flow can be inferred from population genetic structure (e.g. from Fst). Greater genetic differentiation implies lower gene flow and vice versa.

Statistical methods exist to relate genetic distance estimates to a parameter called Nm, which is the average number of immigrants per generation.

Wright's Fst



Island model

$$Fst = \frac{1}{4Nm + 1}$$

Measuring gene flow: indirect methods

Nm is a critical value because it tells us how much gene flow is required to overcome the effects of genetic drift.

Nm > 4 gene flow wins
Nm < 1 genetic drift wins and populations diverge
Nm between 1 and 4 (neither prevails)

Caveats:

1) Tells us about historical gene flow not contemporary gene flow.
2) The real world is not like the island model (assumptions of equal population size, equal contributions to migrant pool, no spatial structure, everything is at equilibrium, no selection, and no mutation all are violated in all species).

Thus, indirect estimates must be viewed with caution.

Measuring gene flow: indirect methods

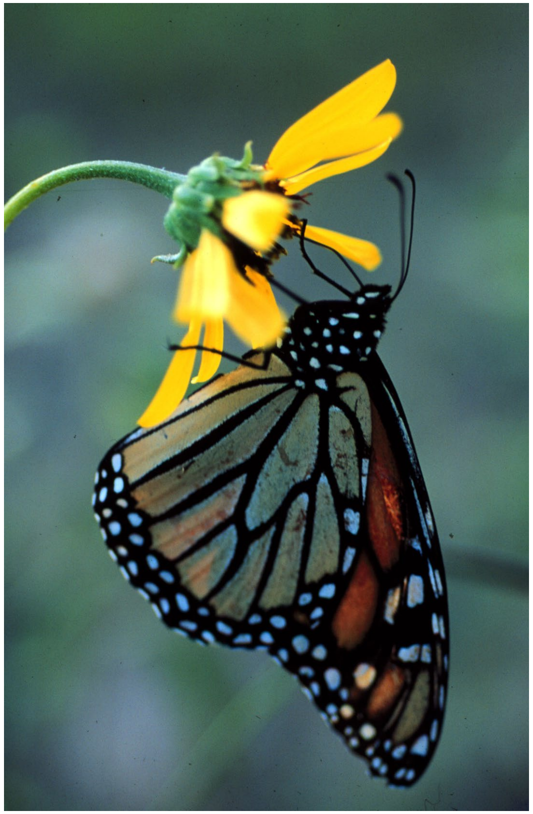
Nm=0.24

Selfers

Nm=0.90

Mixed maters

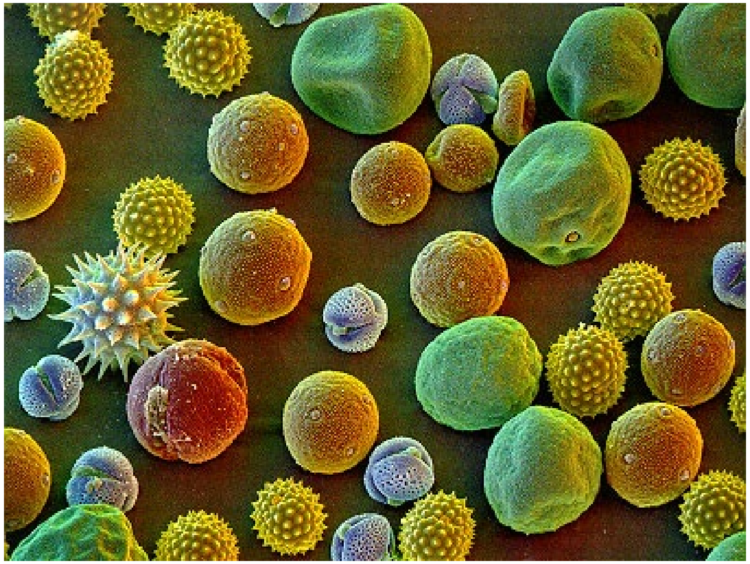
Nm=1.43



Outcrossers

Hamrick and Godt 1996

Pollen versus seed dispersal



- Most direct estimates of gene flow measure pollen dispersal only

- Indirect estimates measure both, but do not discriminate between them.

Pollen versus seed dispersal

Direct estimates from parentage analyses have generally documented fairly high rates of seed immigration rates, ranging from 2.1% in honey locust to 40% in Magnolias

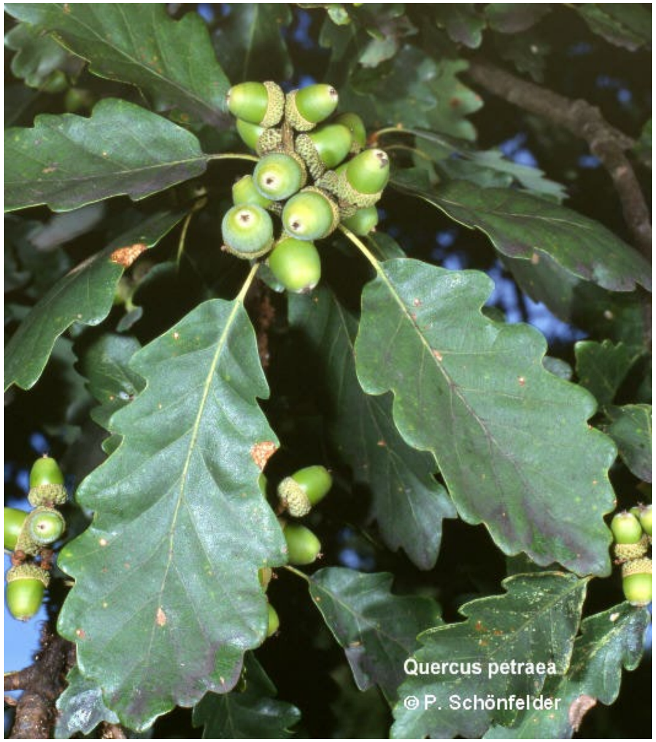
Contribution of seed dispersal to overall gene flow can be estimated by comparing levels of interpopulational differentiation (e.g. Fst or Gst) for maternal versus biparentally inherited genes

Chloroplast and mitochondrial are typically inherited maternally in plants, whereas nuclear genes are inherited through both parents.

Pollen versus seed dispersal

Ratios of pollen to seed flow from indirect measures (i.e., Gst or Fst) range from 4 (for selfing annual, wild barley) to 400 for wind-pollinated sessile oak.

wild barley



Quercus petraea

© P. Schönfelder

Evolution and gene flow

CONSERVATIVE ROLE:

Prevents differentiation due to random processes (i.e. genetic drift) unless the number of migrants (Nm) between populations is < 1 per generation.

Prevents adaptive genetic differentiation if m>s.

CREATIVE ROLE:

Enables the spread of favorable mutations.

Gene flow: unifying effects

How strong is gene flow in nature?

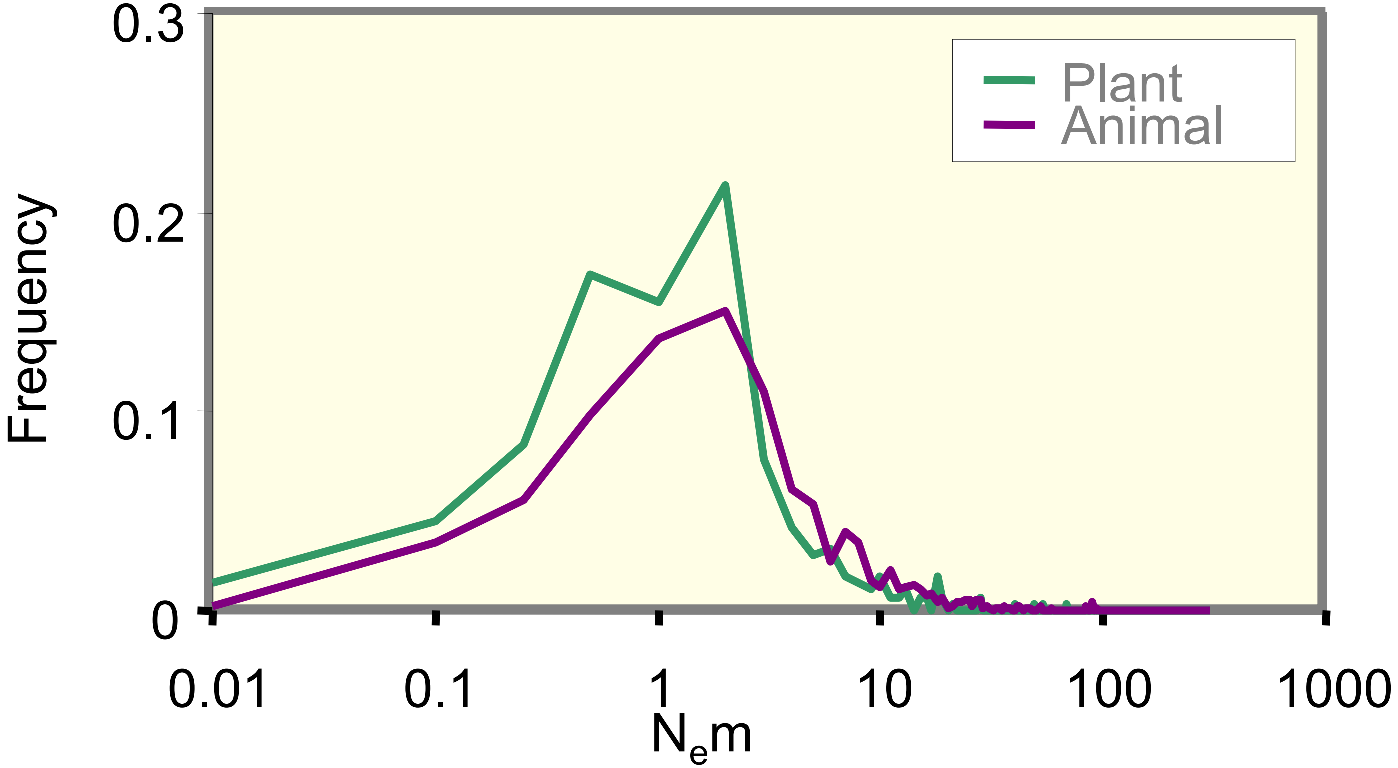
Traditional View:

- Species held together by gene flow (Mayr, Dobzhansky)

Opposing View (Ehrlich and Raven, 1969):

- Species-wide gene flow is too low
- Populations are the units of evolution
- Species are merely aggregates of evolving units

Gene flow: unifying effects

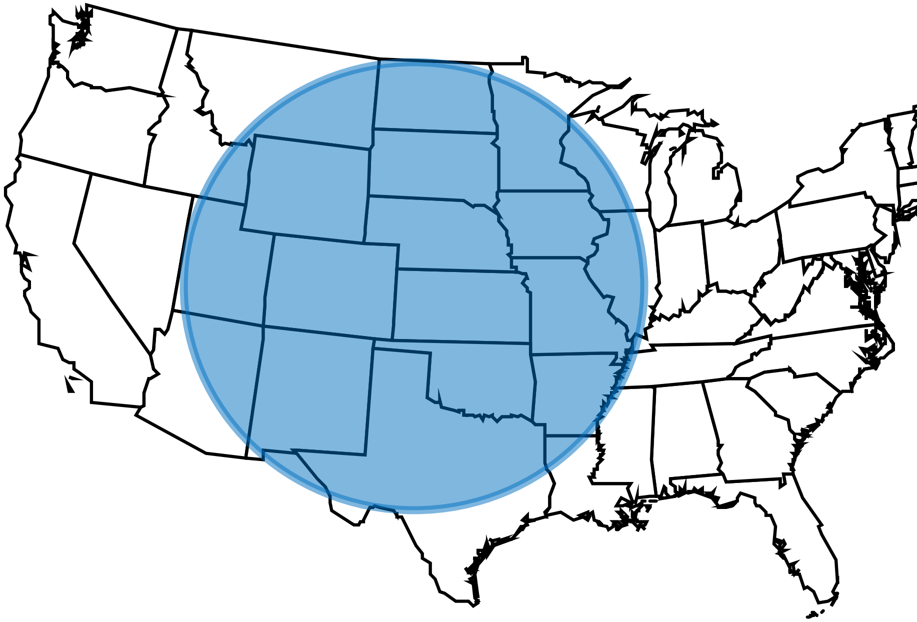


Conclusion: in many species, gene flow is not high enough to prevent differentiation at neutral loci.

Morjan & Rieseberg 2004

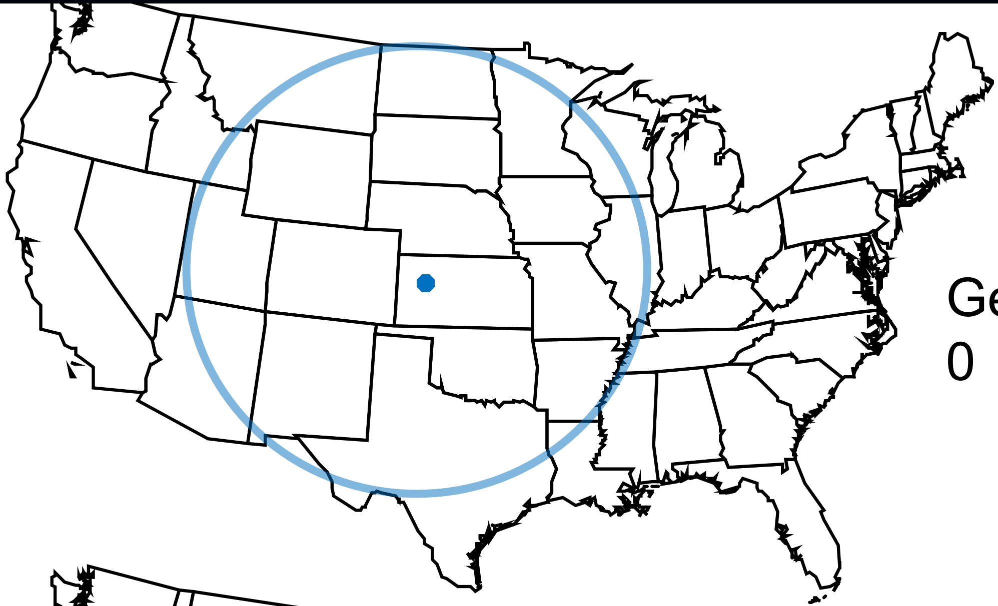
Gene flow: how favorable mutations are spread

Common sunflower, *Helianthus annuus,* and its primary dispersal agent



Prehistorical range of common sunflower

Spread of mutant alleles across the range of a widespread species



Advantageous mutation

Strength of selection
$S = 0.10$

Number of migrants
Nm = 1

Generation
0

Near neutral mutation

Strength of selection
$S = 0.0001$

Number of migrants
Nm = 1

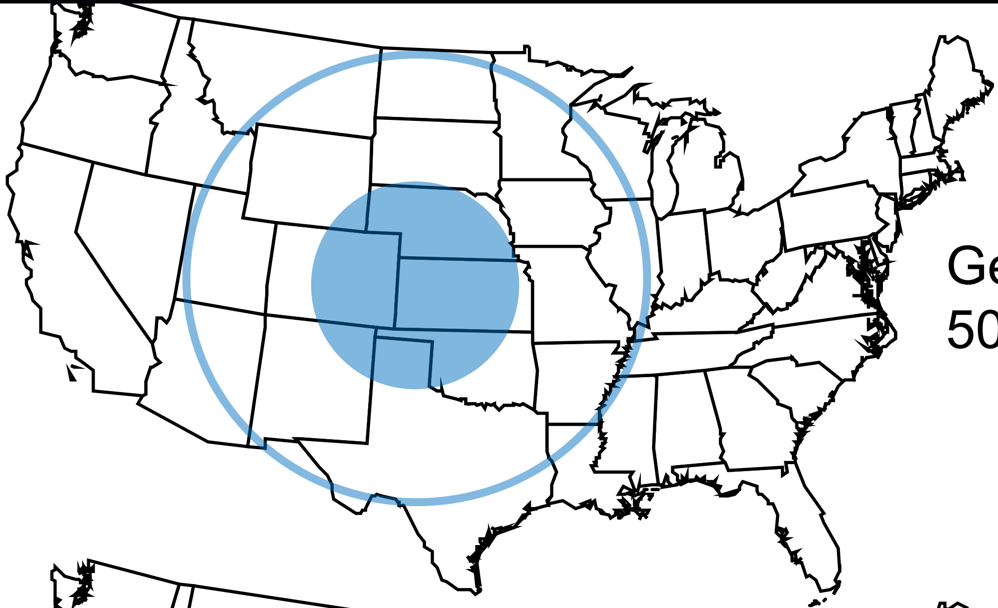
Generation
0

Spread of mutant alleles across the range of a widespread species

Advantageous mutation

Strength of selection
$S = 0.10$

Number of migrants
Nm = 1



Generation
50

Near neutral mutation

Strength of selection
$S = 0.0001$

Number of migrants
Nm = 1

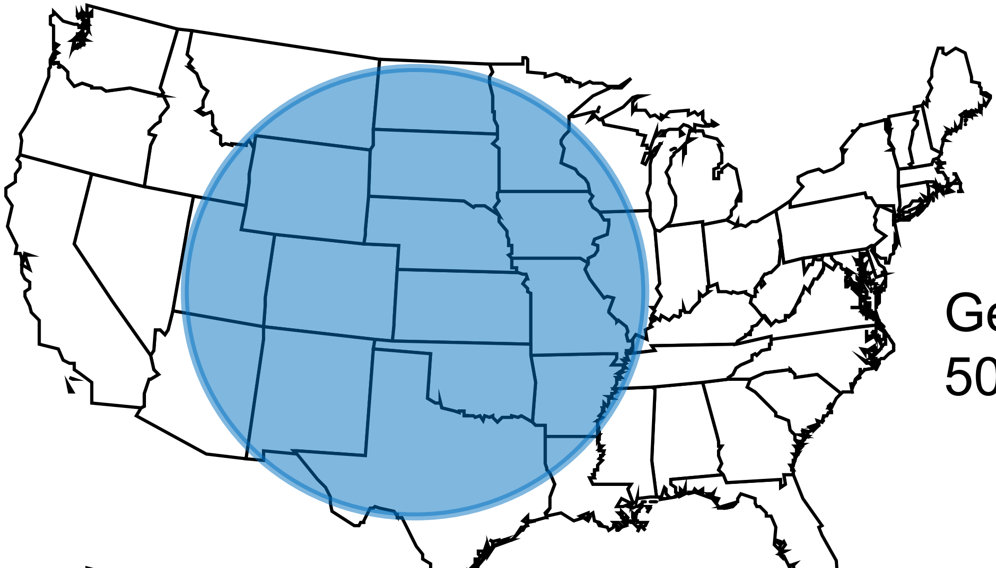
Generation
50

Spread of mutant alleles across the range of a widespread species

Advantageous mutation

Strength of selection
S = 0.10

Number of migrants
Nm = 1

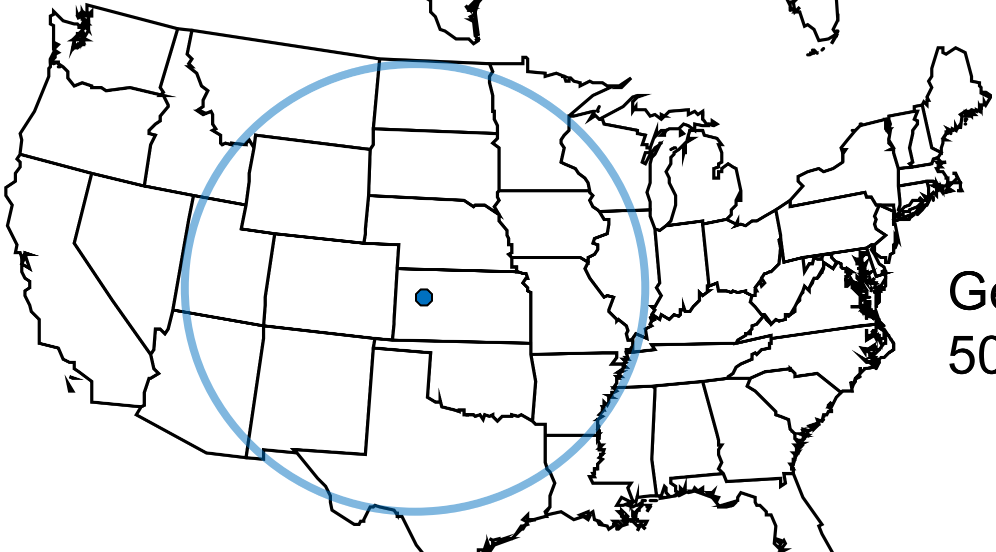


Generation
500

Near neutral mutation

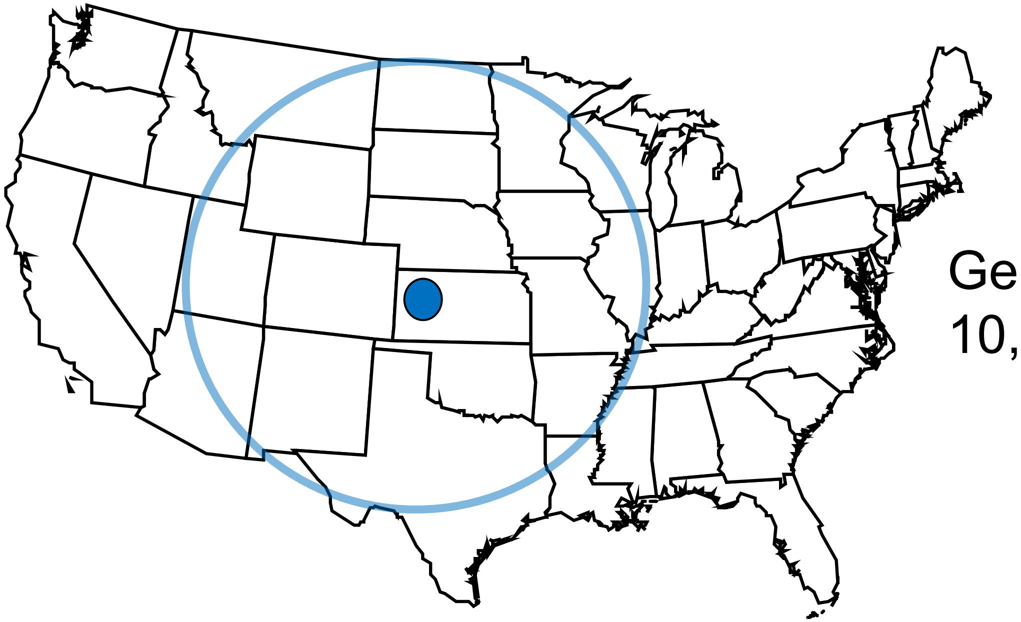
Strength of selection
S = 0.0001

Number of migrants
Nm = 1



Generation
500

Spread of mutant alleles across the range of a widespread species



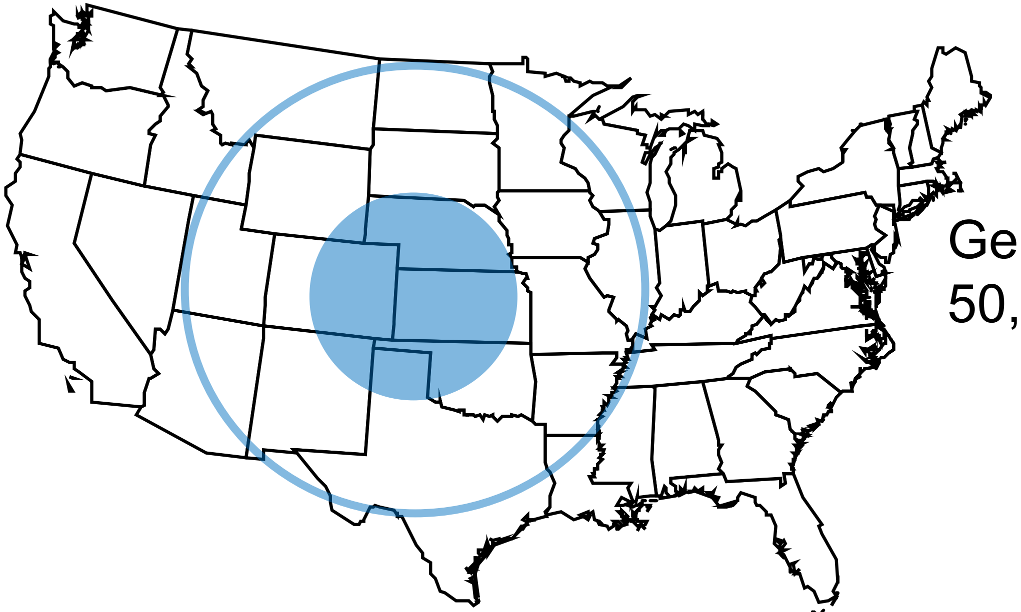
<u>Near neutral mutation</u>

Strength of selection
S = 0.0001

Number of migrants
Nm = 1

Generation
10,000

Spread of mutant alleles across the range of a widespread species



Near neutral mutation

Strength of selection
S = 0.0001

Number of migrants
Nm = 1

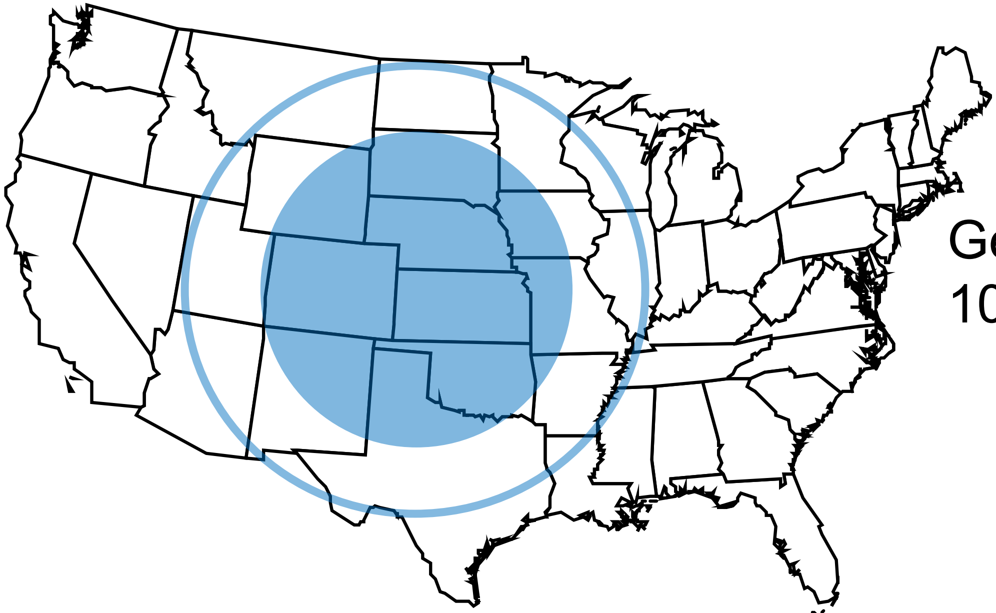
Generation
50,000

Spread of mutant alleles across the range of a widespread species

<u>Near neutral mutation</u>

Strength of selection
S = 0.0001

Number of migrants
Nm = 1



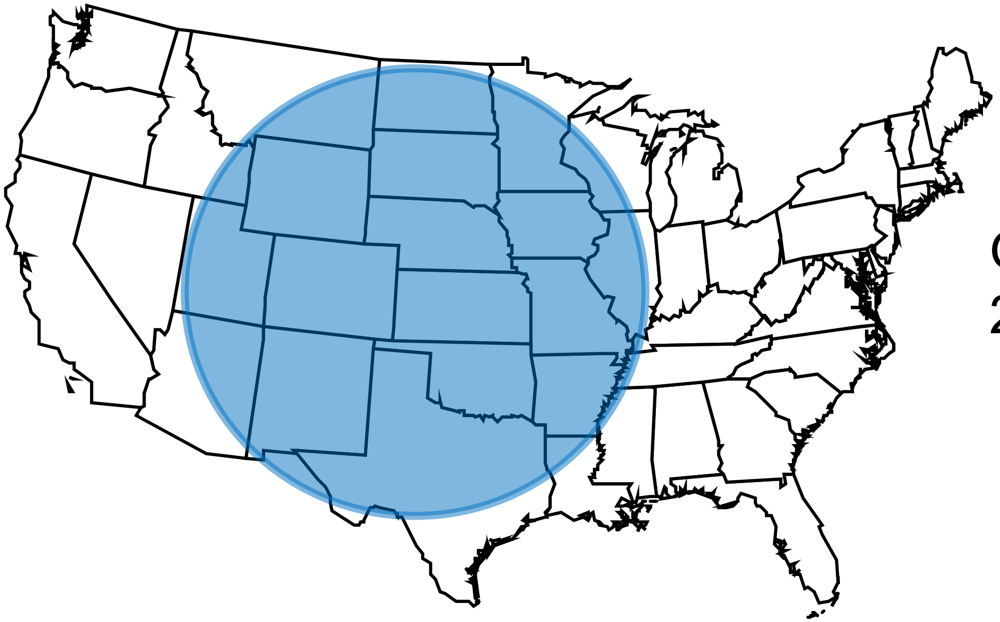
Generation
100,000

Spread of mutant alleles across the range of a widespread species

<u>Near neutral mutation</u>

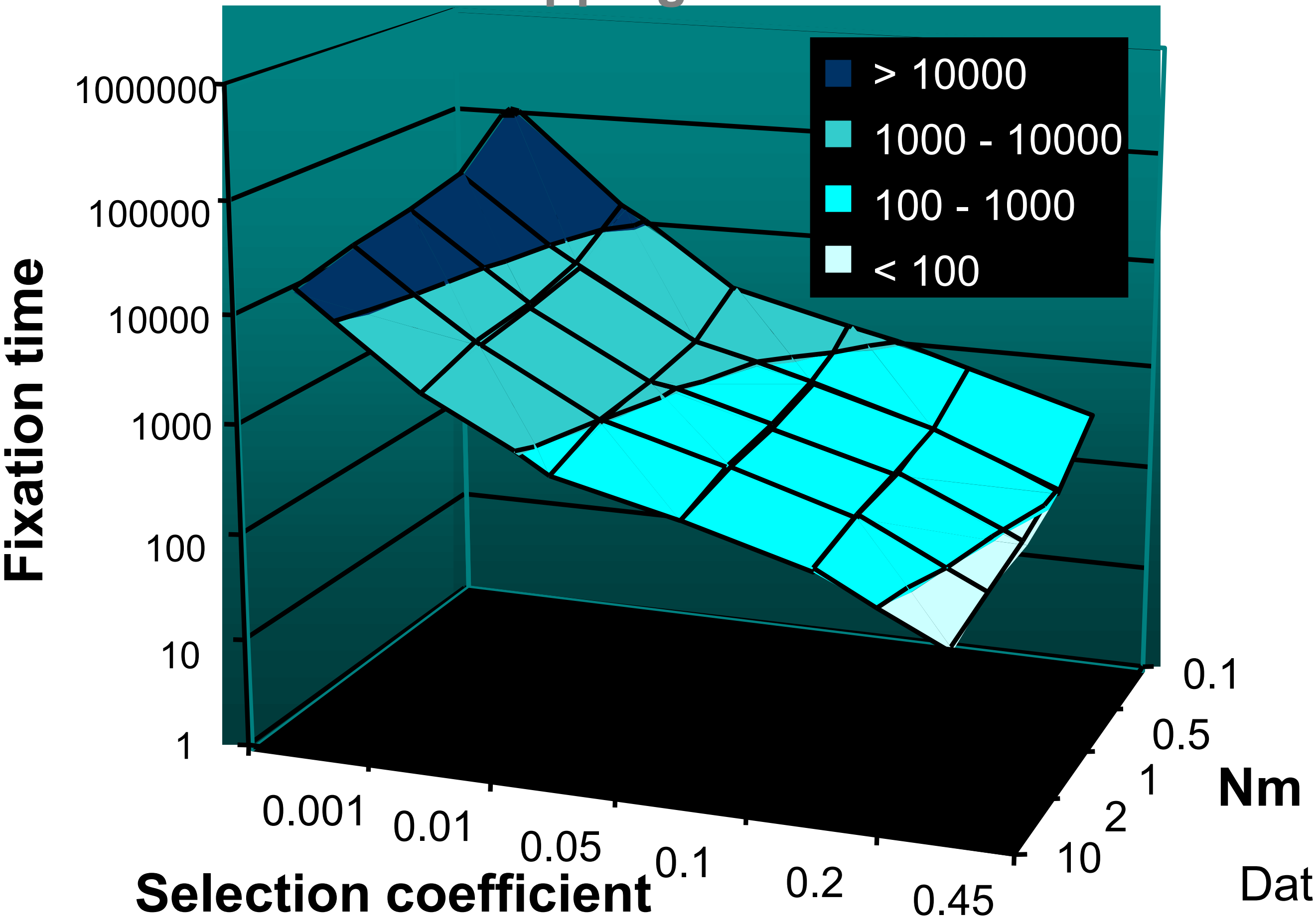
Strength of selection
S = 0.0001

Number of migrants
Nm = 1



Generation
200,000

Time to fixation of a beneficial allele in a stepping stone model



Data from Slatkin 1976

Conclusion: Gene flow is high enough in virtually all species to allow spread of advantageous mutations.

Unresolved Questions

- What are the evolutionary forces responsible for the diversity of pollen and seed shapes and sizes?
- Are local adaptation and speciation often constrained by gene flow?
- What is the geography of selective sweeps of adaptive alleles?
- Are species-wide sweeps of adaptive alleles frequent enough to hold species together?