# PLANT OF THE DAY!

*Camellia sinensis* – tea

Native to East and South Asia

tea consumption dates to the 10th century BC

# Big Questions

- What is speciation?
- What kinds of reproductive barriers can isolate plant species?
- Which kinds of barriers are most important during speciation?
- How do reproductive barriers evolve?

# Outline

1. Speciation – what is it?
2. Reproductive isolation
3. Drift versus Selection
4. Geography of Speciation

# Speciation: What is it?

> "Under the BSC*, the nebulous problem of 'the origin of species' is instantly reduced to the more tractable problem of the evolution of isolating barriers."
>
> Coyne and Orr 2004

*Biological Species Concept

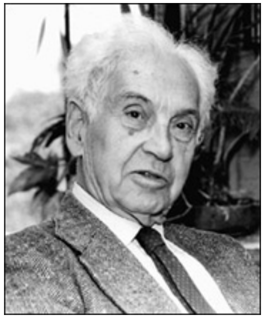
# Speciation: What is it?

<u>For our purposes:</u>

Speciation refers to the evolution of barriers to gene flow between previously interbreeding populations.

These barriers are thought to evolve primarily as the by-product of genetic drift or selection.

# Reproductive Isolation

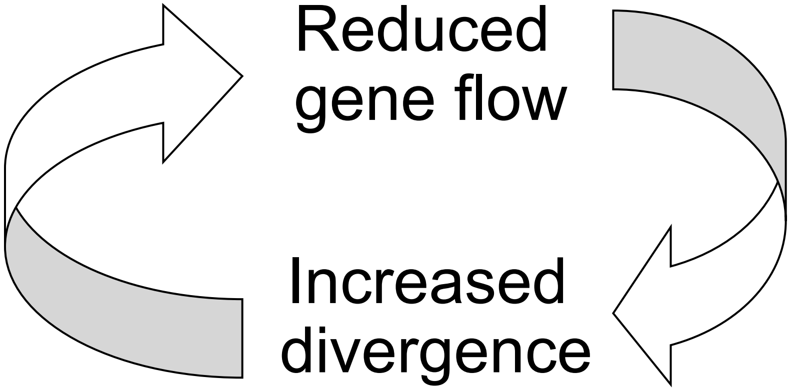


**a.k.a. barriers to gene flow**

**Definition:** “Biological properties of individuals which prevent the interbreeding of populations that are actually or potentially sympatric” (Mayr 1970).

**Role:** Reduce interspecific gene flow, thereby facilitating the accumulation of genetic differences through drift or selection.

FEEDBACK LOOP:



Reduced gene flow

Increased divergence

# Barrier Components

**Prepollination barriers** limit the transfer of pollen from individuals of one species to styles of another.

**Postpollination prezygotic barriers** prevent heterospecific pollen from successfully fertilizing ovules.

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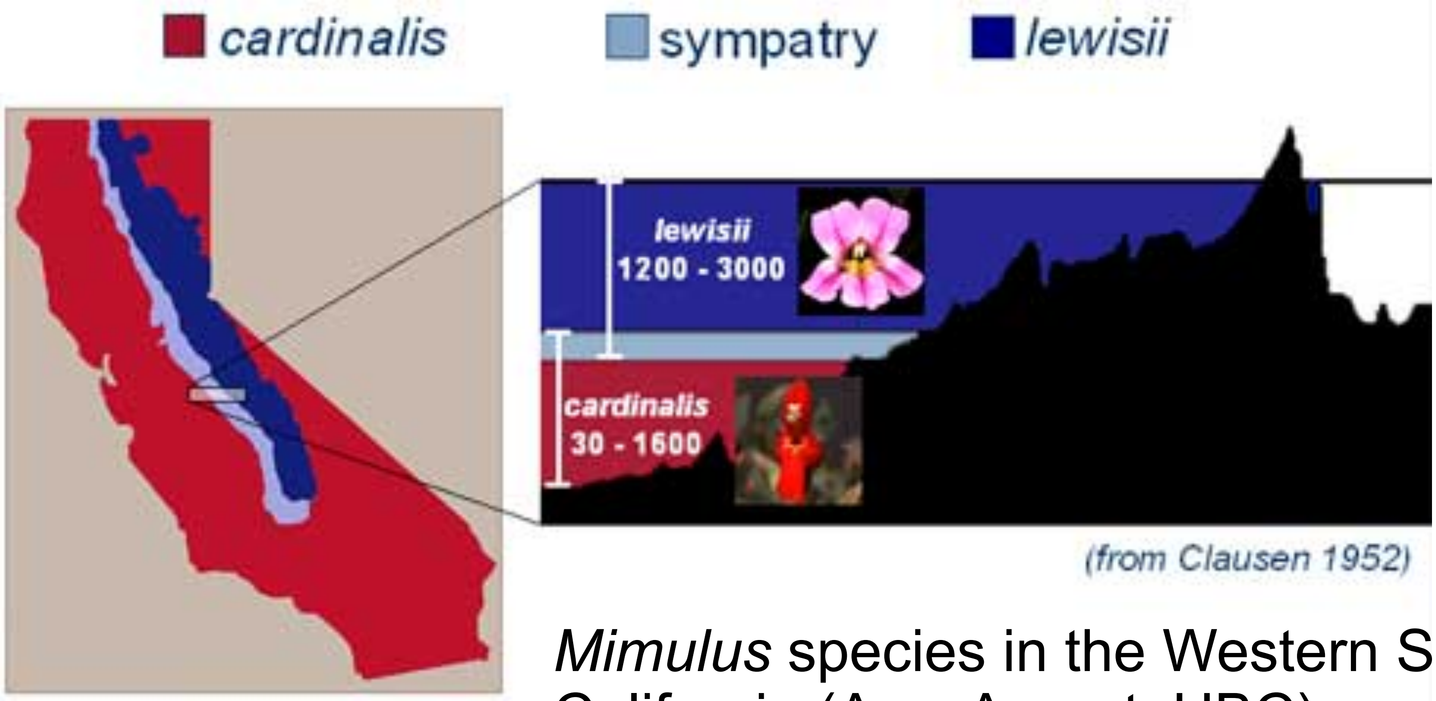
**Intrinsic postzygotic barriers** result from genetic incompatibilities and are mostly independent of the environment (e.g., hybrid sterility or breakdown).

**Extrinsic postzygotic barriers** result from genotype by environment interactions (e.g., ecological isolation).

# Ecogeographic Isolation/ Immigrant Inviability

Ecological divergence often contributes to spatial isolation.
This is probably most important reproductive barrier in plants.



(from Clausen 1952)

(from Hickman 1993)

*Mimulus* species in the Western Sierras of California (Amy Angert, UBC)

# Temporal Isolation

Can be seasonal, diurnal, etc.

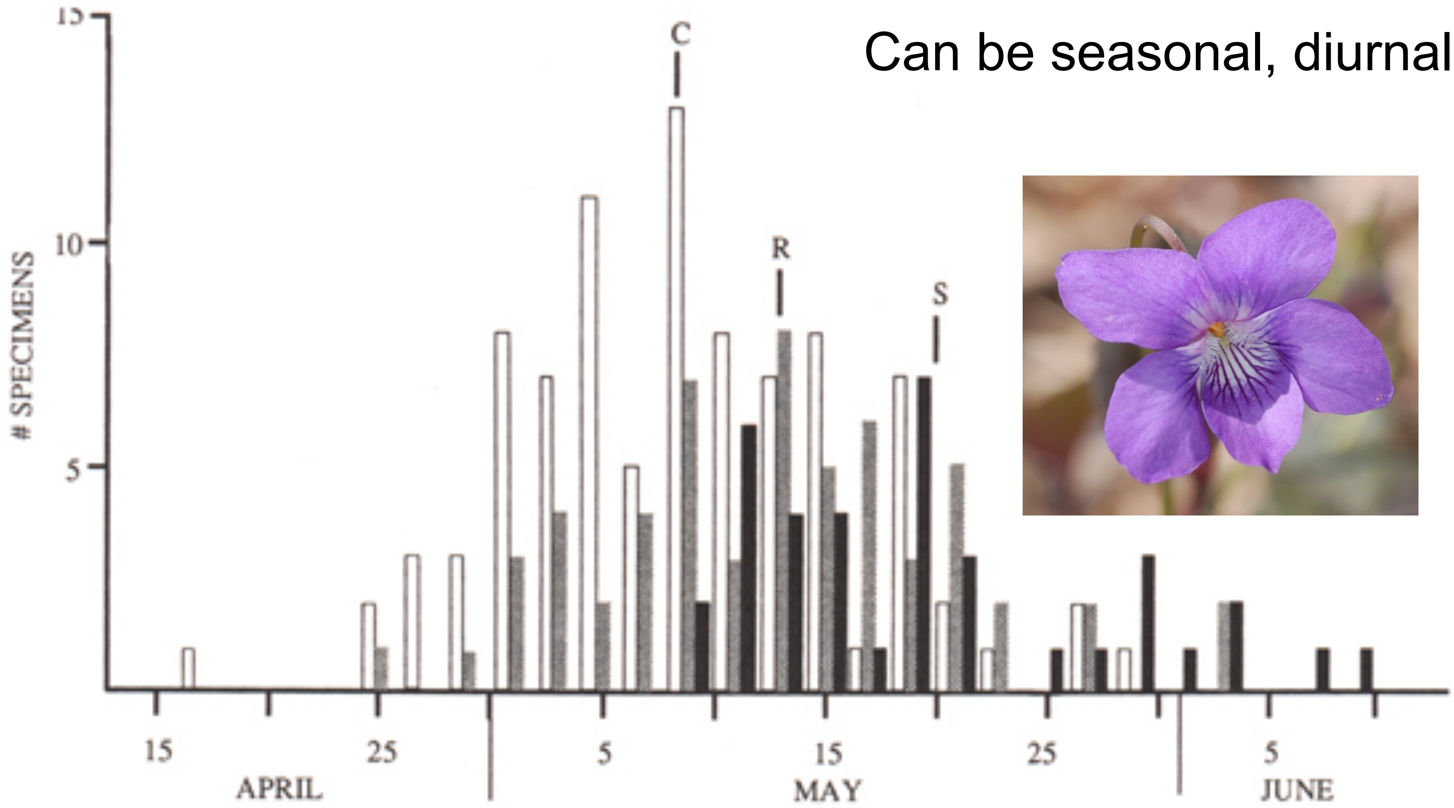
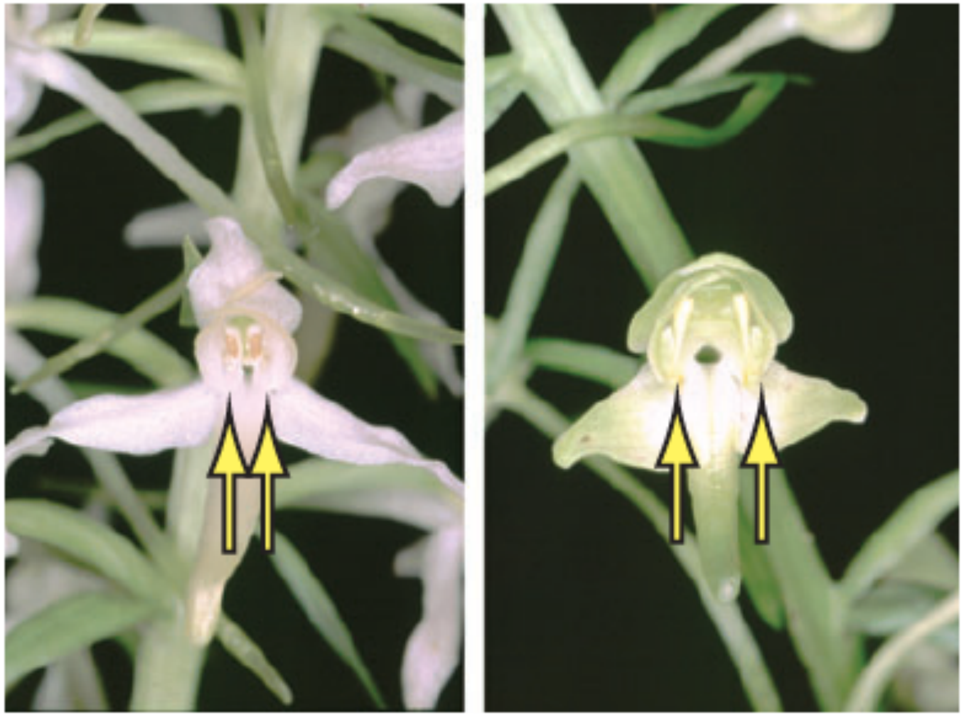


FIGURE 4. Phenology of *V. conspersa* (white), *V. rostrata* (gray), and *V. striata* (black) based on specimens at MICH from south-central Michigan; initials of specific epithets indicate means of collection dates for each species.

# Mechanical Isolation

Mechanical isolation occurs because the sexual organs (e.g. flower structures) of different species are incompatible.



*Platanthera bifolia* *Platanthera chlorantha*

Schiestl and Schlüter 2009

# Pollinator Isolation

*Mimulus cardinalis*

*Mimulus lewisii*

Bradshaw and Schemske 2003

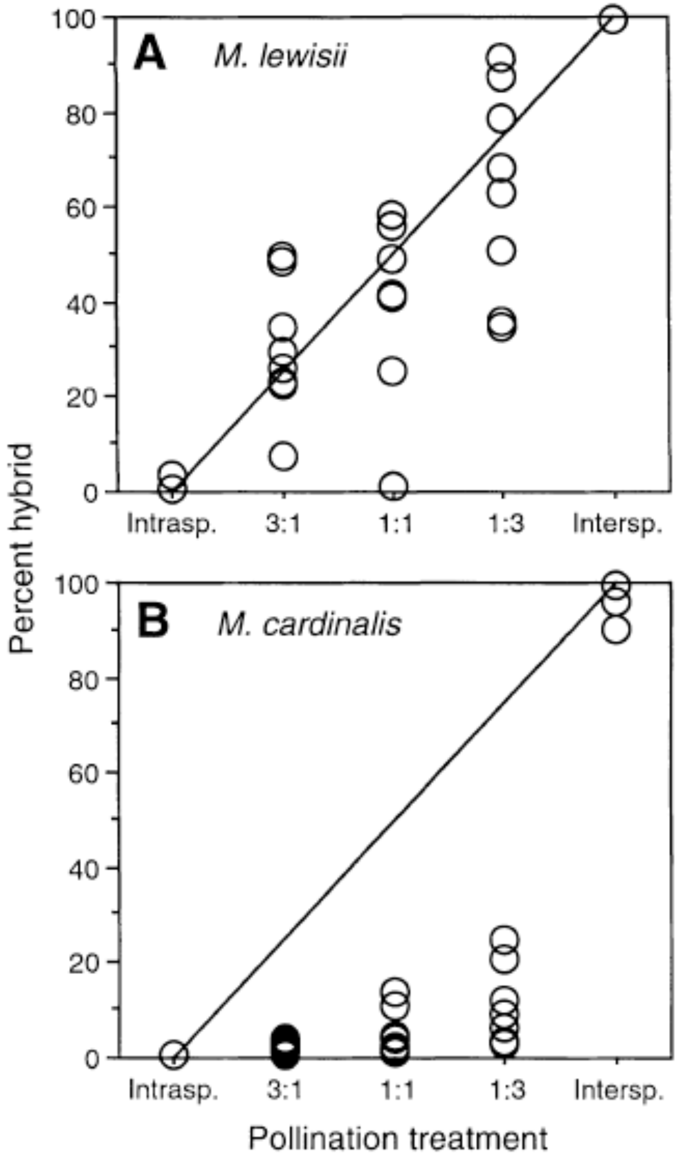
# Mating System Isolation

*Mimulus guttatus*

*Mimulus nasutus*

Martin and Willis 2007

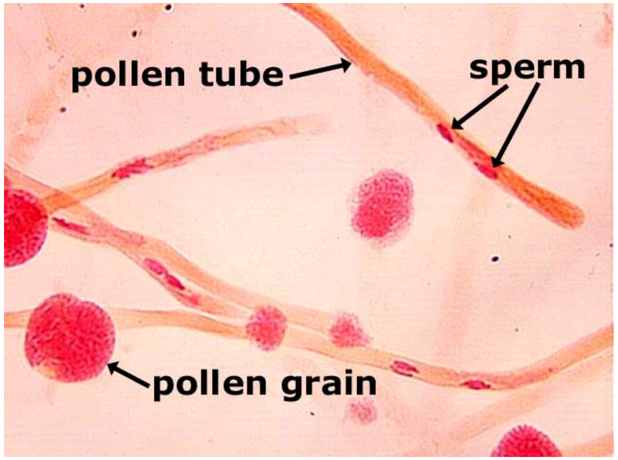
# Post-pollination, Prezygotic Isolation



Ramsey et al. 2003

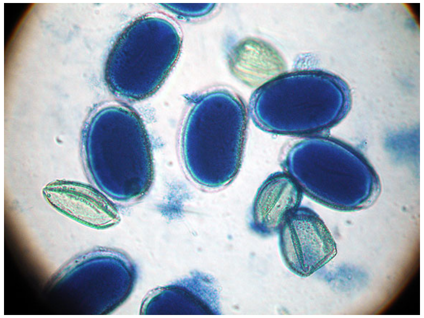
**Conspecific pollen precedence**
conspecific pollen often outcompetes heterospecific pollen (perhaps due to sexual selection).

**Pollen-ovule incompatibilities**



# (Intrinsic) Postzygotic Isolation

**Hybrid sterility:** hybrids have reduced fertility

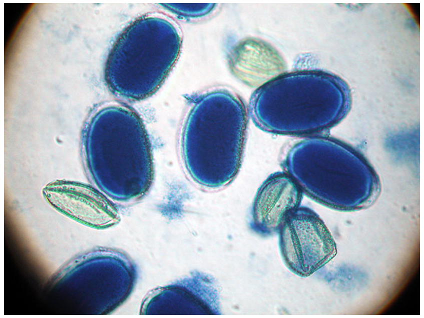


Hybrid pollen sterility

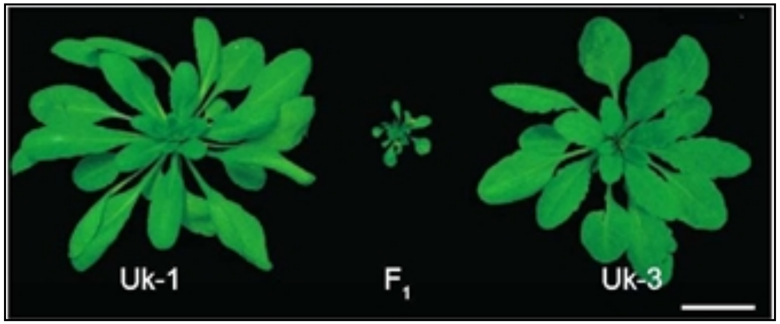
# (Intrinsic) Postzygotic Isolation

**Hybrid sterility:** hybrids have reduced fertility

**Hybrid inviability**: hybrids have reduced viability



Hybrid pollen sterility



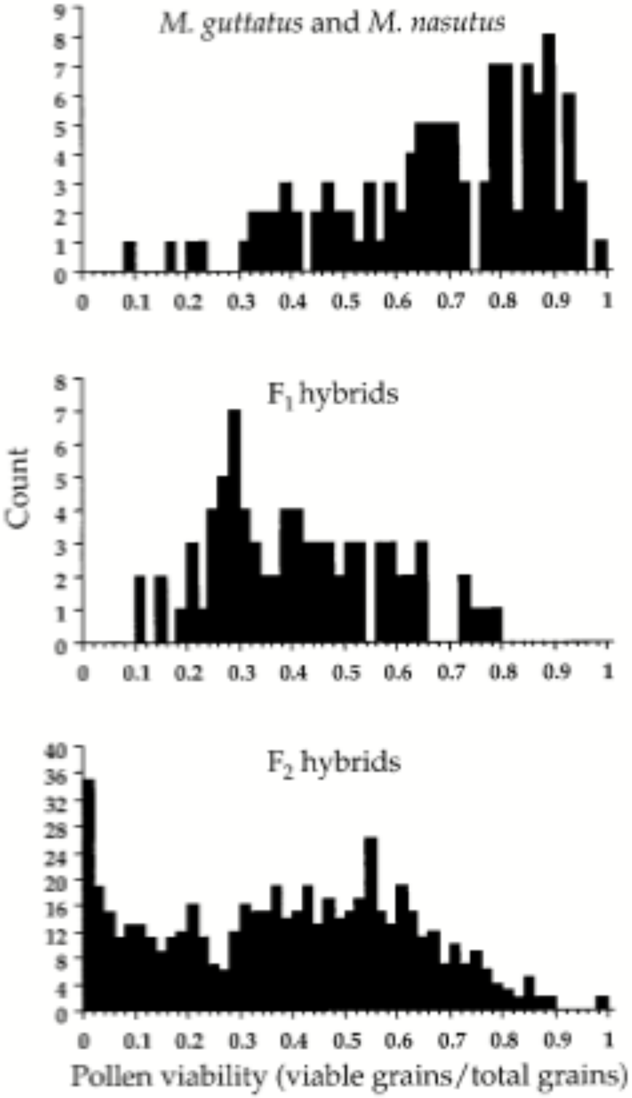
Hybrid inviability (Bomblies et al. 2007)

# (Intrinsic) Postzygotic Isolation

**Hybrid sterility:** hybrids have reduced fertility

**Hybrid inviability**: hybrids have reduced viability

**Hybrid breakdown:** later generation hybrids have reduced viability or fertility



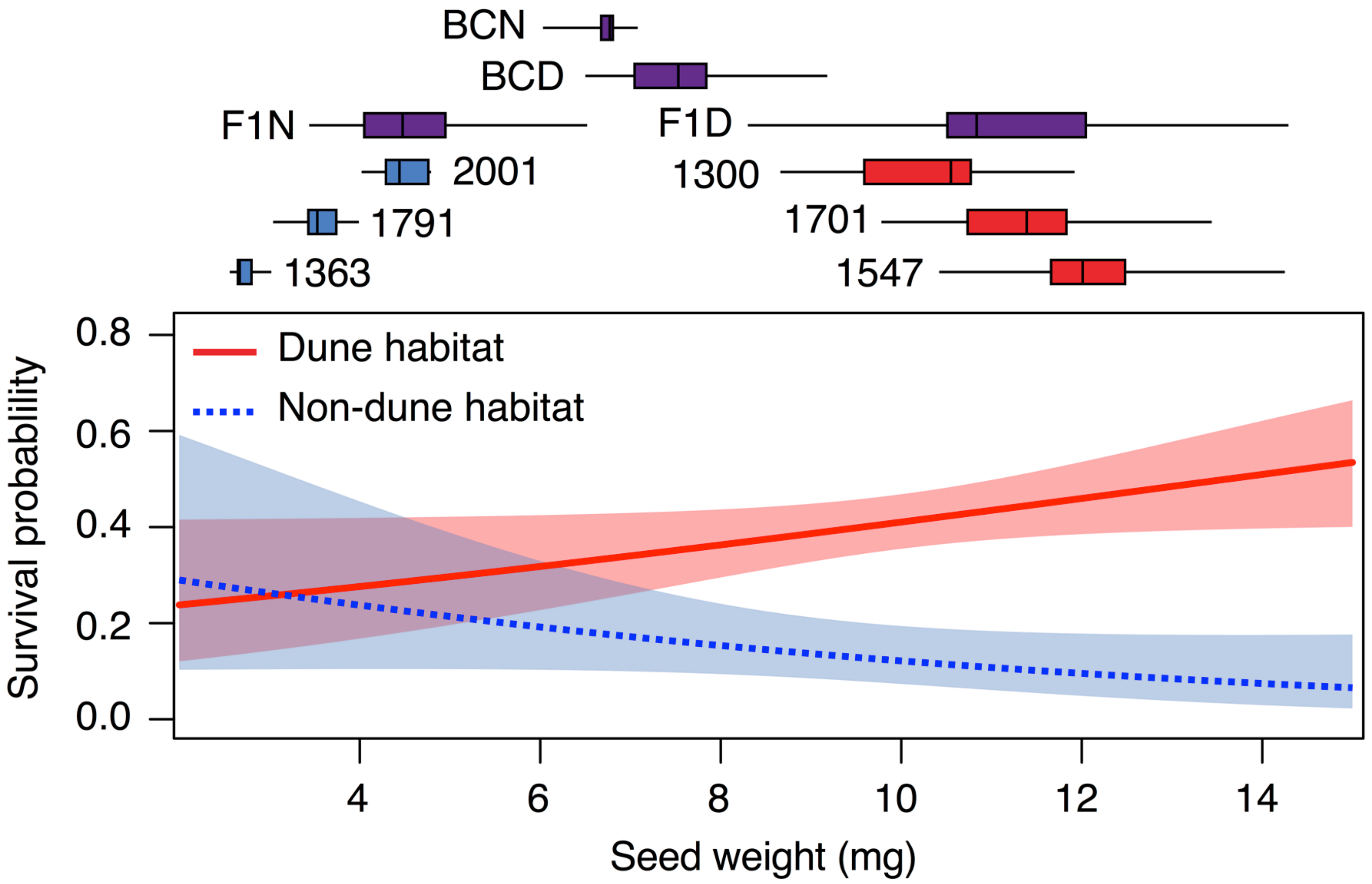
Fishman and Willis 2001

# (Extrinsic) Postzygotic Isolation

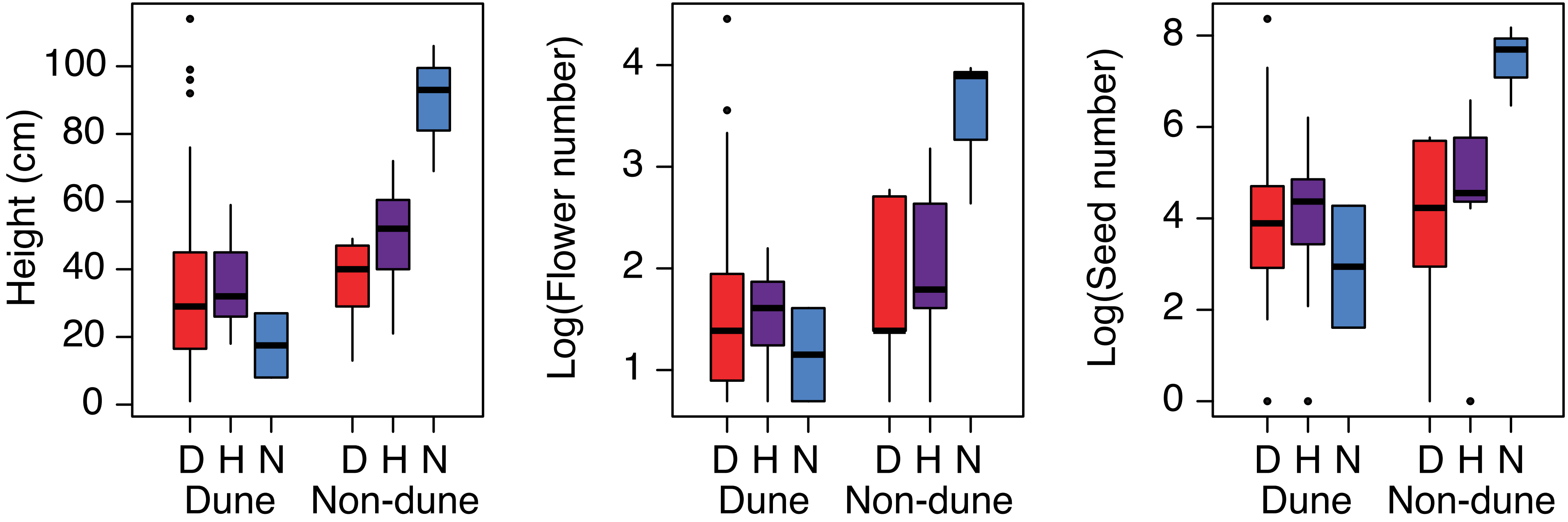
**Ecological isolation**: hybrids are not as fit (have reduced fertility or viability) as parents in parental environments.

Ostevik et al. 2016

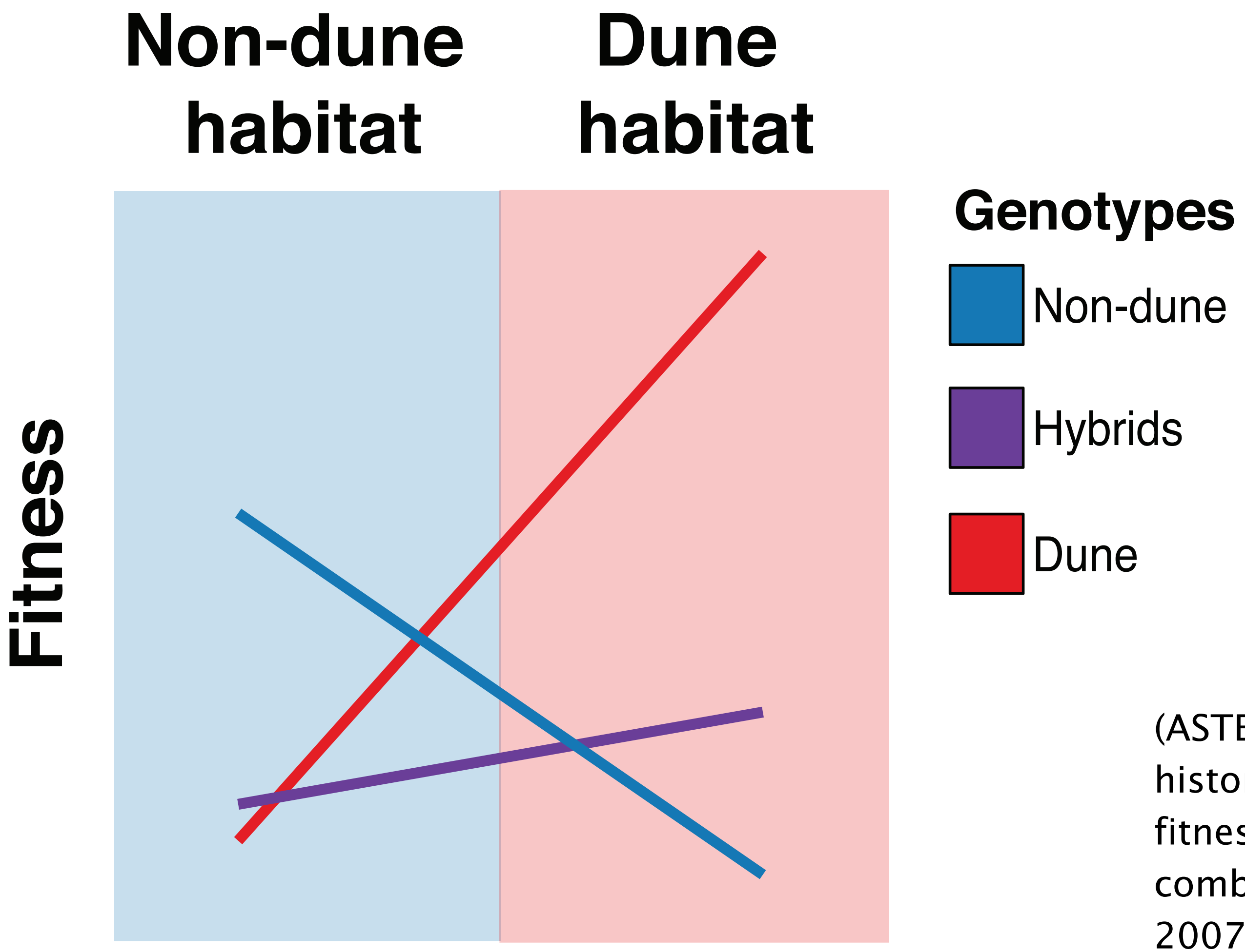
# Large Seeds Favored in Dune Habitat



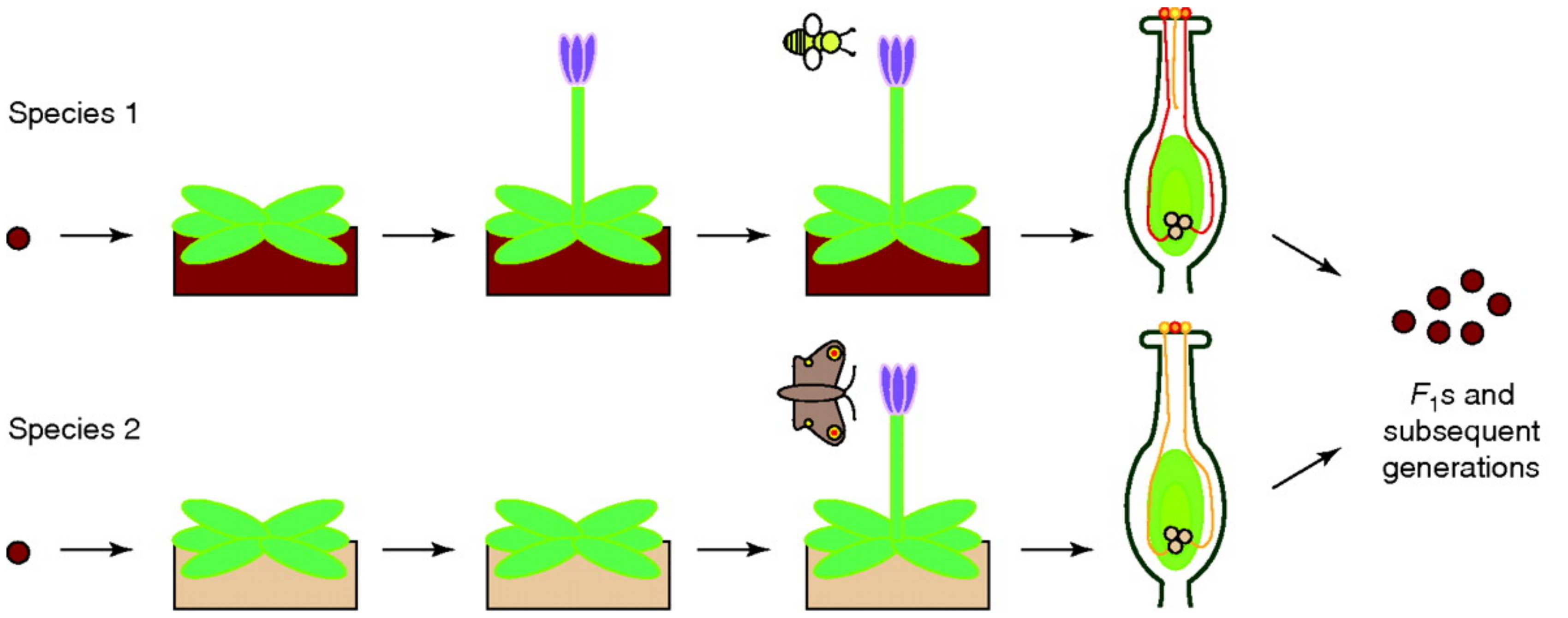
# But, non-dune plants produce more flowers and seeds on sand sheet



# And hybrids are selected against in both parental habitats



(ASTER models for life history analysis allow fitness components to be combined: Geyer et al. 2007)



*Pre-pollination*
*Prezygotic*

- Habitat isolation
- Temporal isolation
- Pollinator isolation
- Mechanical isolation
- Mating system divergence

*Post-pollination*
*Prezygotic*

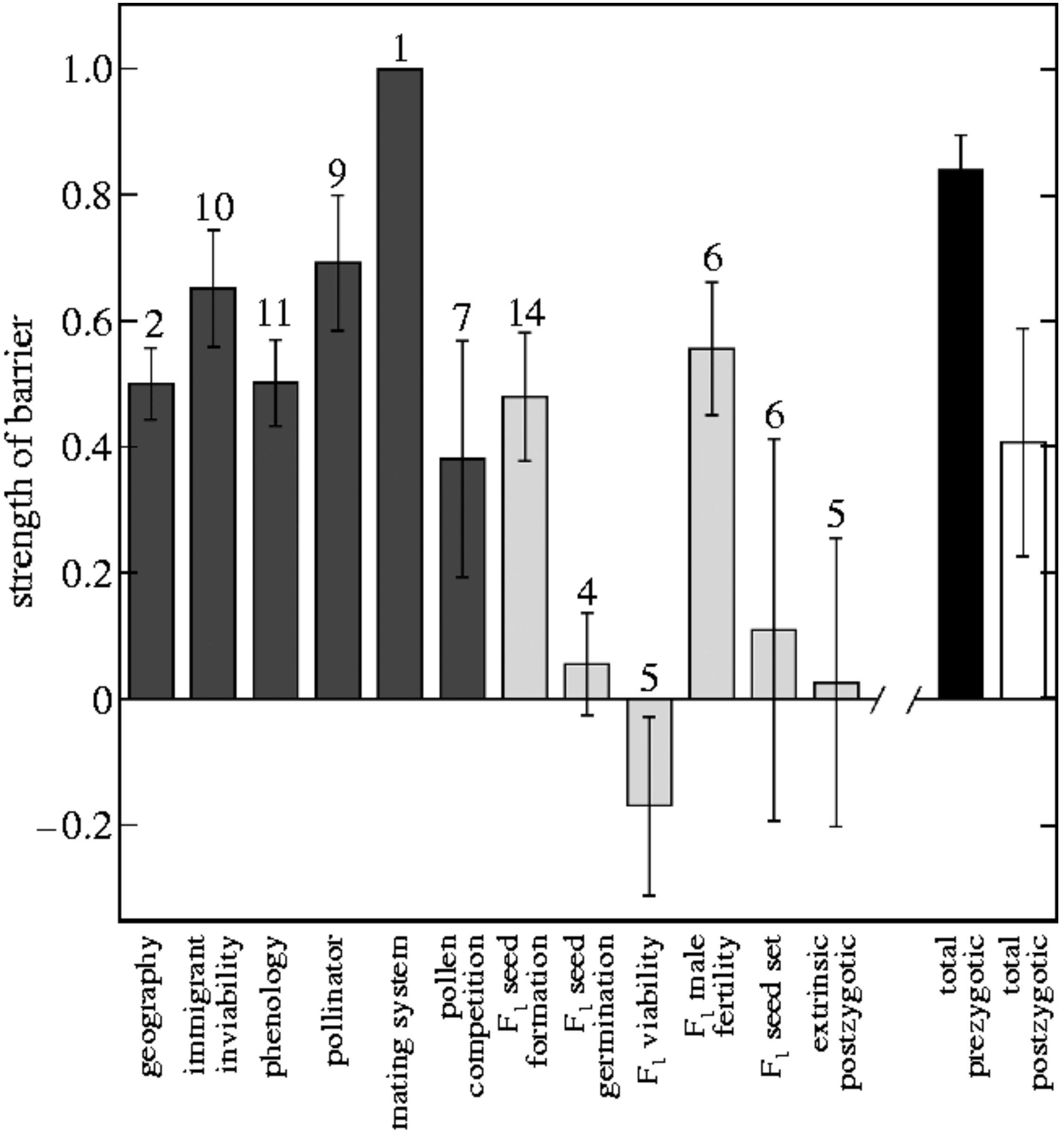
- Conspecific pollen precedence
- Unilateral incompatibility

*Postzygotic*

- *Extrinsic*
  - Ecological inviability
  - Behavioral sterility
- *Intrinsic*
  - Hybrid inviability
  - Hybrid sterility

All else being equal, early-acting reproductive barriers will contribute more to isolation than late-acting barriers

Rieseberg and Blackman 2010



Prezygotic isolation is approximately twice as strong as postzygotic isolation in flowering plants.

Also, post-mating barriers are much more likely to be asymmetric than pre-mating barriers.

Lowry et al. 2008

Which reproductive barriers were important during speciation?

Which reproductive barriers are important during speciation?

- e.g. Find out which barriers arise early by looking at incipient species

Incipient species are populations that are in the process of diverging to the point of speciation but can still exchange genes

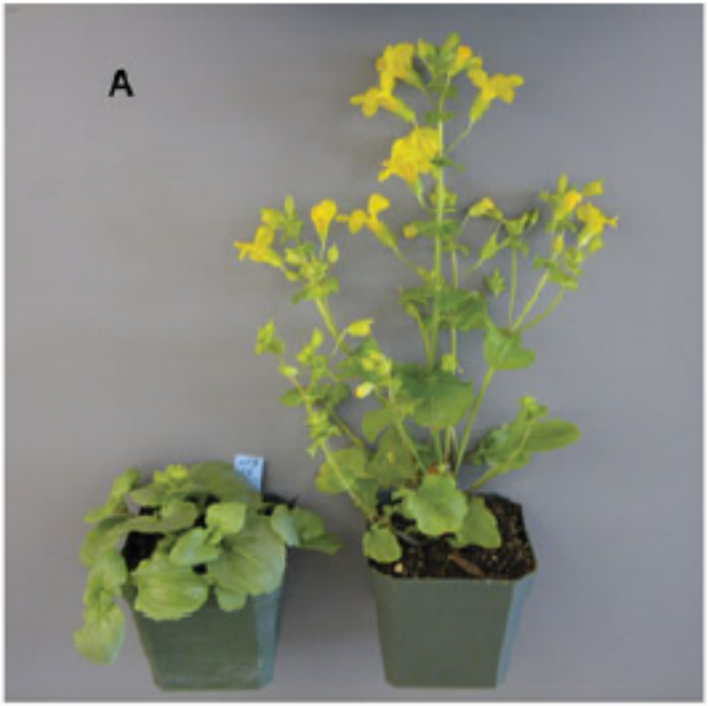
Coyne and Orr 2004

# ECOLOGICAL REPRODUCTIVE ISOLATION OF COAST AND INLAND RACES OF *MIMULUS GUTTATUS*

David B. Lowry,[1,2,3] R. Cotton Rockwood,[4] and John H. Willis[1,2]

| Isolating barrier | Strength of barrier | |
|---|---|---|
| | Coast | Inland |
| Temporal flowering isolation among habitats ($RI_{FA}$) | 1.000 | 1.000 |
| Selection against immigrants ($RI_I$) | 0.874 | 0.999 |
| Temporal flowering isolation in sympatry ($RI_{FS}$) | 0.895 | 0.00[1] |
| Intrinsic postzygotic isolation ($RI_{IP}$) | 0.023 | 0.023 |
| Extrinsic postzygotic isolation ($RI_{EP}$) | −1.801 | 0.233 |

[1] This was calculated for one surviving coast plant in inland habitat.



Lowry *et al*. 2008

# How do these barriers evolve?

# Drift versus Selection

## Laboratory Experiments: Divergent Selection (no gene flow)

| Taxon | Isolation* | Reference |
|---|---|---|
| *Drosophila pseudoobscura* | prezygotic | Ehrman, 1964, 1969 |
| *Drosophila pseudoobscura* | prezygotic | del Solar, 1966 |
| *Drosophila melanogaster* | prezygotic | Barker & Cummins, 1969 |
| *Drosophila melanogaster* | prezygotic | Grant & Mettler, 1969 |
| *Drosophila* | postyzgotic | Robertson, 1966a,b |
| *Drosophila melanogaster* | prezygotic | Burnet & Connolly, 1974 |
| *Musca domestica* | prezygotic | Soans et al., 1974 |
| *Musca domestica* | prezygotic | Hurd & Eisenberg, 1975 |
| *Drosophila willistoni* | both | de Oliveira & Cordeiro, 1980 |
| *Drosophila melanogaster* | prezygotic | Kilias et al., 1980 |
| *Drosophila simulans* | postzygotic | Ringo et al., 1985 |
| *Drosophila mojavensis* | prezygotic | Koepfer, 1987 |
| *Drosophila pseudoobscura* | prezygotic | Dodd, 1989 |

*Prezygotic isolation failed to evolve in four other experiments;
postzygotic isolation failed to evolve in one other experiment.

From Rice and Hostert 1993

# Drift versus Selection

## Laboratory Experiments: Drift / Population Bottlenecks (no selection and no gene flow)

| Taxon | Isolation | Reference |
|---|---|---|
| *Drosophila melanogaster* | weak prezygotic | Koref-Santibanez et al., 1958 |
| *Drosophila pseudoobscura* | none | Powel & Morton, 1979 |
| *Drosophila melanogaster* | none | Averhoff & Richardson, 1974 |
| *Drosophila pseudoobscura* | pre (3/8) | Powell, 1979* |
| *Drosophila silvestris* | none | Ahearn, 1980 |
| *Drosophila pseudoobscura* | pre (1/8) | Dodd and Powell, 1985* |
| *Drosophila simulans* | pre (1/8) | Ringo et al., 1985* |
| *Musca domestica* | pre (1/16) | Meffert & Bryant, 1991** |
| *Drosophila pseudoobscura* | pre (4/628)<br>retests (0) | Moya et al., 1995 |
| *Drosophila melanogaster* | none (0/50) | Rundle et al., 1998 |
| *Drosophila pseudoobscura* | none (0/78) | Rundle, 2003 |

*hybrid base population
**not significant after correction for multiple tests

From Rice and Hostert 1993

# Genetics of Speciation

Darwin’s Dilemma: How could something as maladaptive as hybrid sterility or inviability evolve by natural selection?

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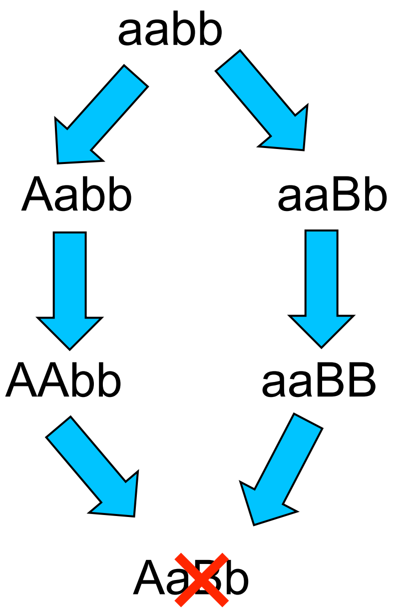
Darwin’s Dilemma: How could something as maladaptive as hybrid sterility or inviability evolve by natural selection?



aabb

Aabb

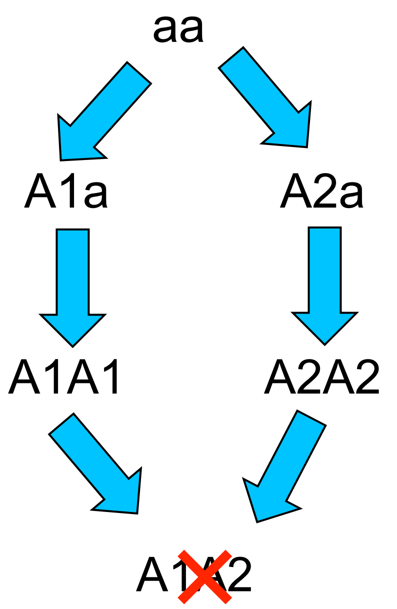
aaBb

AAbb

aaBB

AaBb

two locus model



aa

A1a

A2a

A1A1

A2A2

A1A2

one locus model

Bateson-Dobzhansky-Muller (BDM) incompatibilities

# Examples of BDM incompatibilities

| Phenotype / Organism(s) | Genes / Characteristics | References |
|---|---|---|
| Hybrid Seed lethality<br>Arabidopsis | *PHERES1,* a MADS-box gene<br>*TTG2, WRKY* transcription factor | Josefsson et al. 2006<br>Dilkes et al. 2008 |
| Cytoplasmic male sterility<br>*Oryza, Helianthus, Mimulus*, etc. | > 15 genes cloned / chimeric orfs in mtDNA | Hanson & Benolila 2004 |
| Restoration of CMS<br>Maize, *Oryza, Petunia,* raidish | 7 genes cloned; mitochondria-targeting PPR proteins | Hanson & Benolila 2004 |
| Hybrid inviability (hybrid necrosis)<br>*Arabidopsis,* tomato, lettuce | Disease resistance genes | Bomblies et al. 2007<br>Kruger et al. 2002 |

**Cytoplasmic male sterility in *Petunia hybrida***

**Hybrid necrosis in tomato**

# Genetics of Speciation

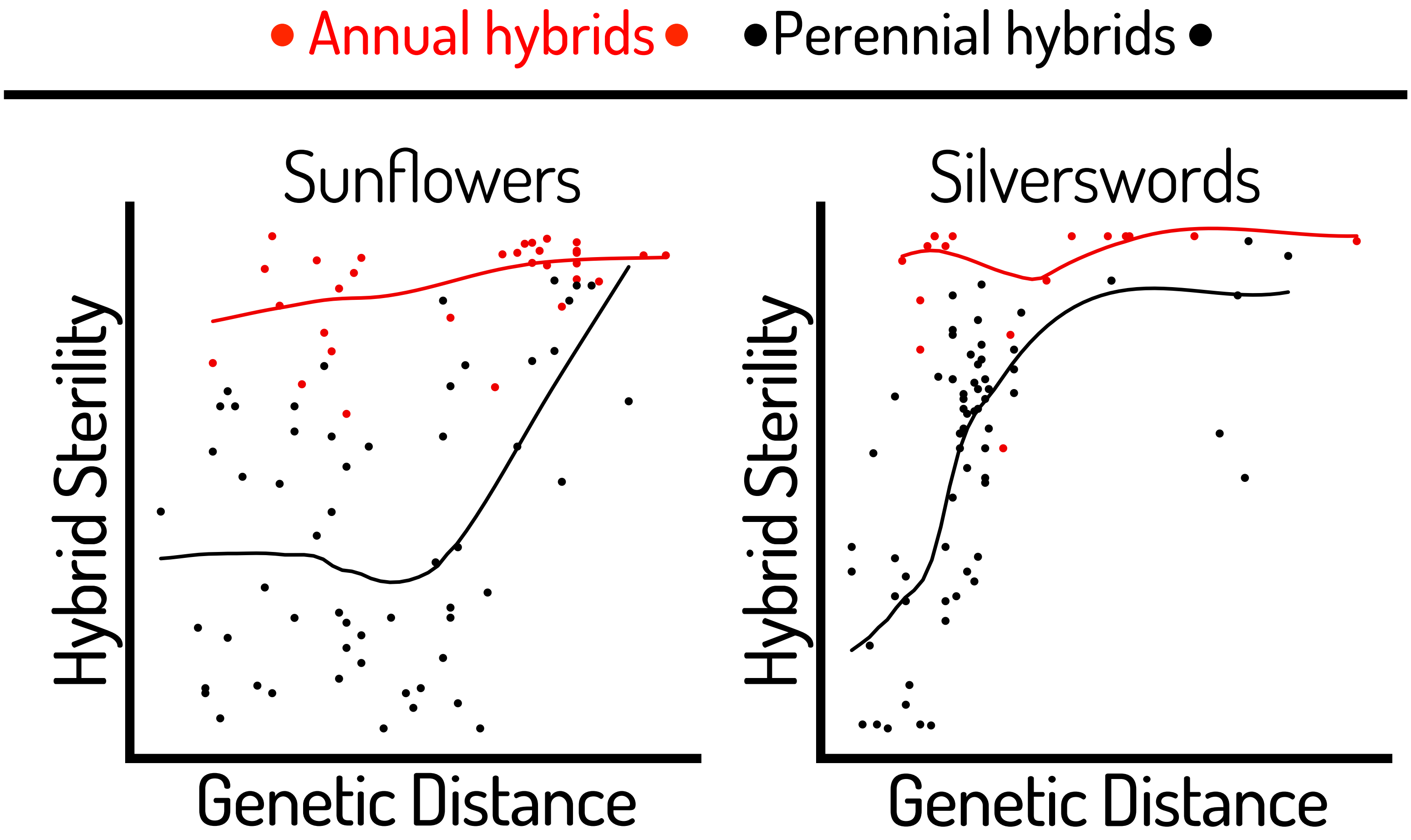
Speciation genes – genes that contribute to the cessation of gene flow between populations

Some generalizations from speciation genes found in plants so far:

- Disease resistance genes often involved (e.g., NBS-LRR family)
- Loss of function mutations are surprisingly frequent (e.g., PPR genes)
- Cytoplasmic factors frequently involved (e.g., CMS)
- Divergence mainly due to positive selection (either balancing or directional)
- Substantial intraspecific variation

Rieseberg and Blackman 2010

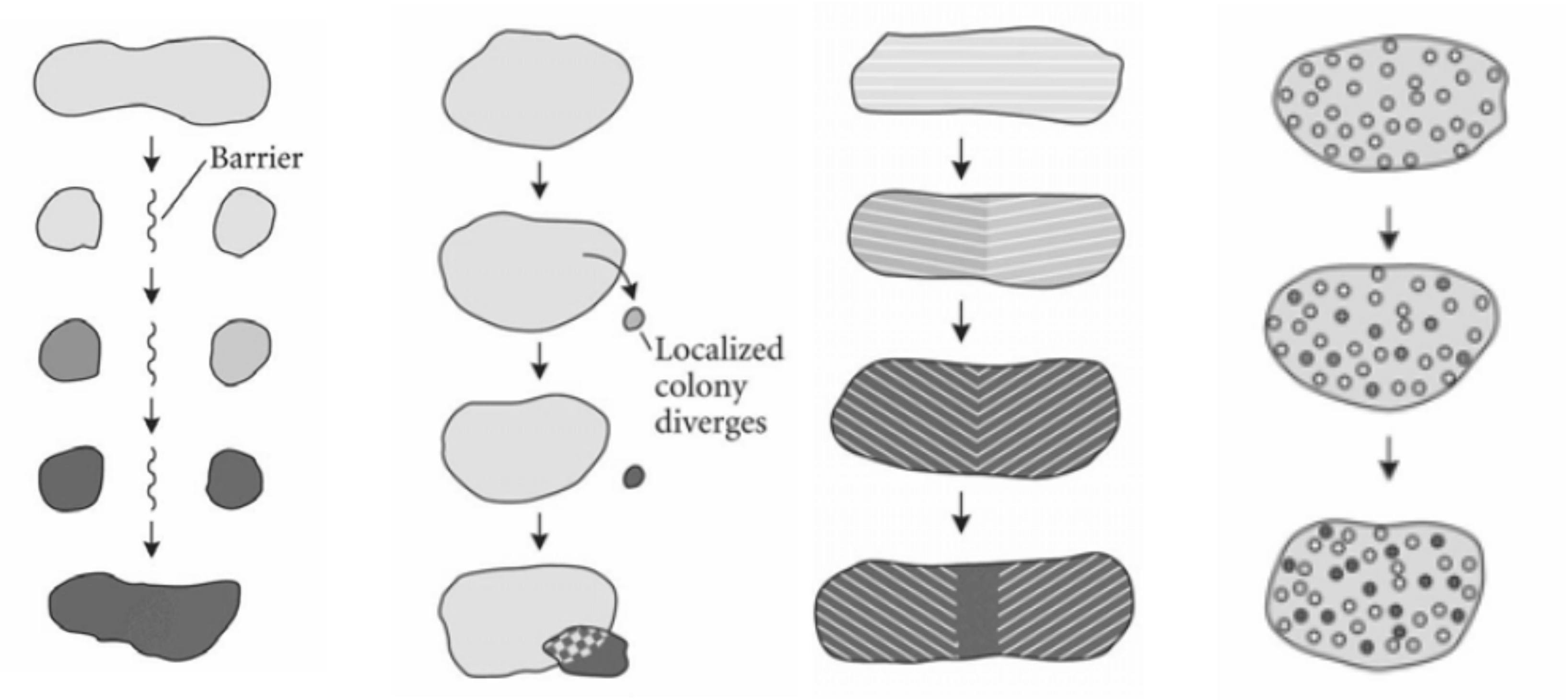
# Other patterns in the evolution of reproductive isolation



$p < 0.002$ ANOVA $p < 0.00005$

Owens and Rieseberg 2013

# Geography of Speciation



| Allopatric (vicariance) | Peripatric | Parapatric | Sympatric |
|---|---|---|---|
| $m = 0$ | $m = 0$ | $0 < m < 0.5$ | $m = 0.5$ |

*m* is the initial level of gene flow

Futuyma 2009

# Geography of Speciation

Allopatric and parapatric speciation are common (Wallace)

Sympatric speciation is controversial (Darwin)

Example of allopatric speciation in Datisca

http://plants.usda.gov/

# Sympatric Speciation

Problems:

1. Antagonism between selection and recombination — recombination breaks up associations between alleles under disruptive natural selection and those causing assortative mating.

2. Sympatric species must coexist.

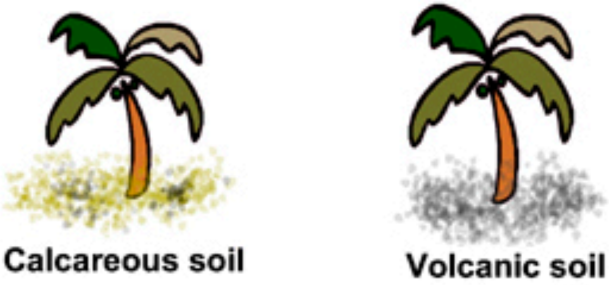
3. Hard to prove that currently sympatric species have not been allopatric in past.

One of the best examples of sympatric speciation is palms on Lord Howe Island

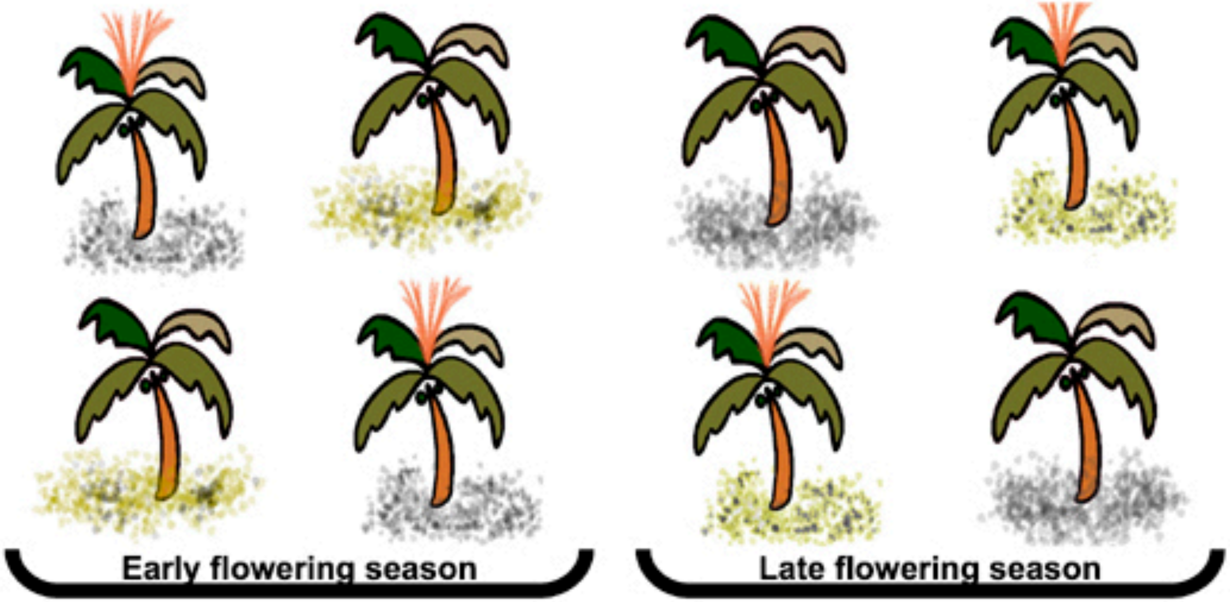
Savolainen et al. 2006

**Disruptive selection**

Some palms survive better in volcanic acidic soils whereas others perform better in basic calcareous soils



**Assortative mating**



Palms growing in calcareous soil tend to flower later than palms growing in volcanic soils

Sympatric speciation occurs most easily when traits under disruptive selection (e.g. soil preference) and assortative mating (e.g. flowering time) are correlated genetically.

When assortative mating and disruptive selection are combined in the same trait, it is called a **magic trait.**

# (somewhat) Unanswered Questions

- Is there a pattern to the genetic architecture of reproductive isolation (e.g. many vs. few loci, under selection or evolving neutrally)?
- Which reproductive barriers are most important early in speciation? Late in speciation?
- How often do reproductive barriers evolve as a by-product of selection? By drift? By direct selection (e.g. reinforcement)?