PLANT OF THE DAY!

Wolfia borealis – northern watermeal

One of smallest plants on planet

Aquatic – found in Canadian lakes

Edible – good protein source

Outline

- Measuring the strength of reproductive isolation
- How do reproductive barriers evolve
- Genetics of speciation
- Geography of speciation
- Speciation with gene flow

Measuring Reproductive Barrier Strength

Focus is mainly on sister species that have sympatric or parapatric populations

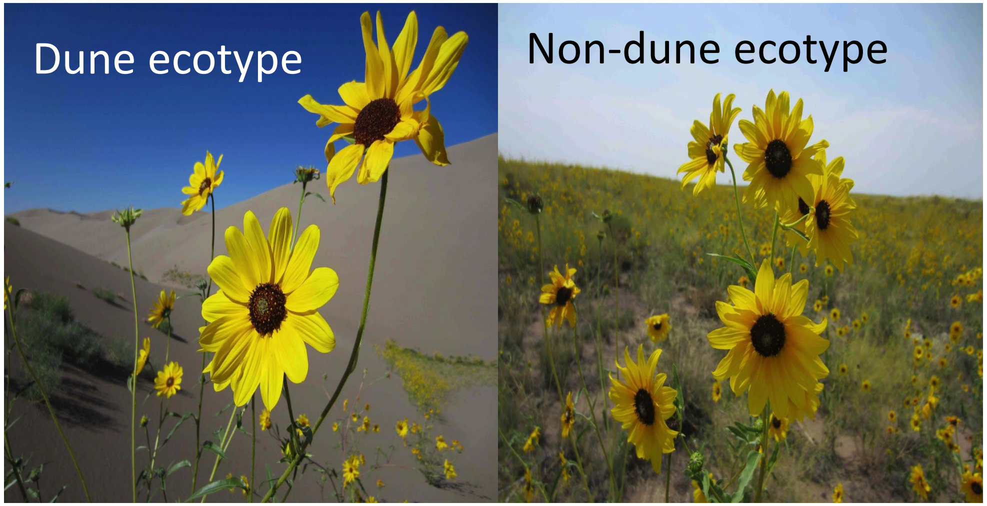
Reproductive isolation is measured for as many barriers as possible using the following equation:

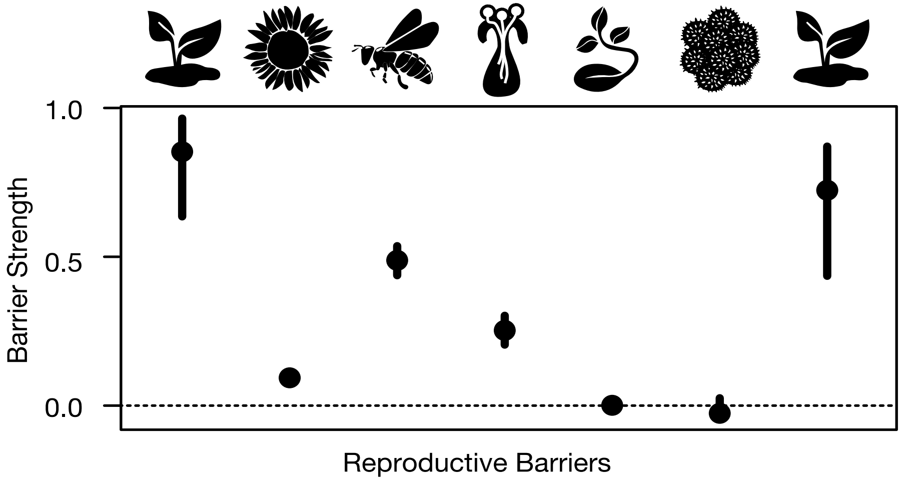
$$\mathrm{RI} = 1 - 2 \times \left(\frac{H}{H+C}\right)$$

H and *C* represent heterospecific and conspecific fitness, respectively.

Metric bounded by 1 (complete isolation) and 0 (no isolation).

RI can be measured with respect to each parent species or averaged between them.

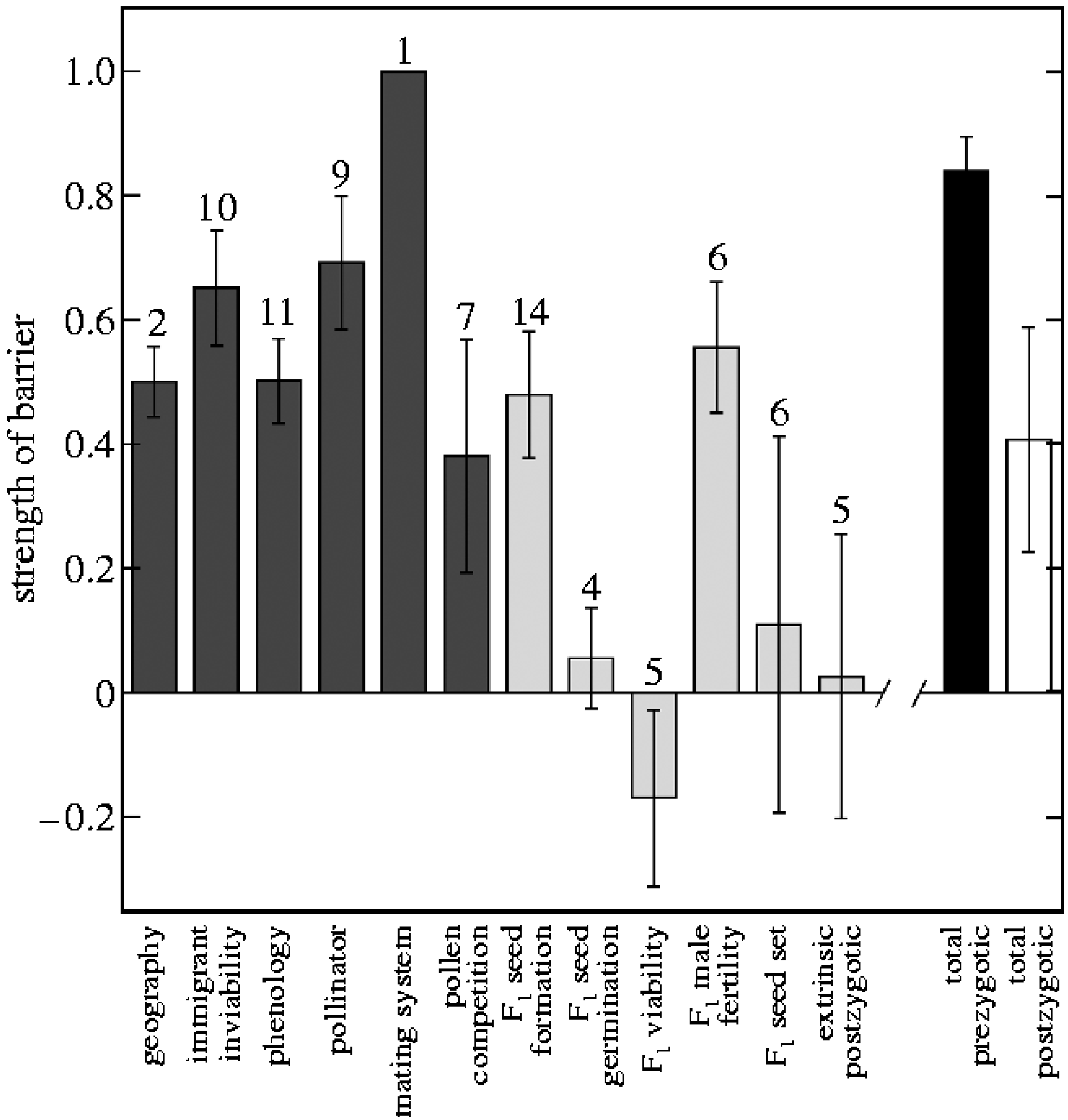




Total RI = 0.993 to 0.996

Ostevik et al. (2016)

Measuring Reproductive Barrier Strength



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

Why is barrier strength for F1 viability negative?

Lowry et al. 2008

Measuring Reproductive Barrier Strength

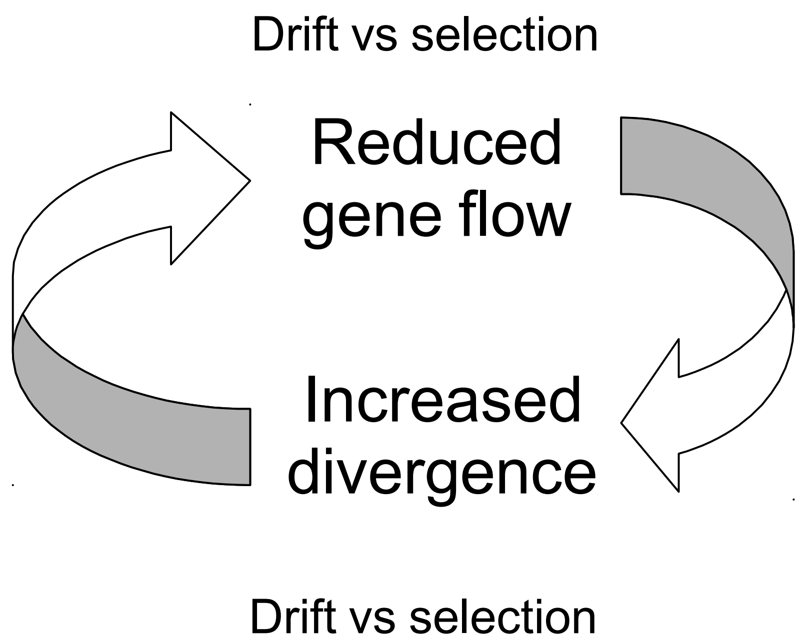
How would you determine which reproductive barriers contribute importantly to speciation versus those that arose after speciation?

Measuring Reproductive Barrier Strength

How would you determine which reproductive barriers contribute importantly to speciation versus those that arose after speciation?

Find out which barriers arise early by looking at young species.

How do these barriers evolve?



- Reproductive isolation through to arise as a byproduct of differentiation through genetic drift or natural selection
- Which process is more important?

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) 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

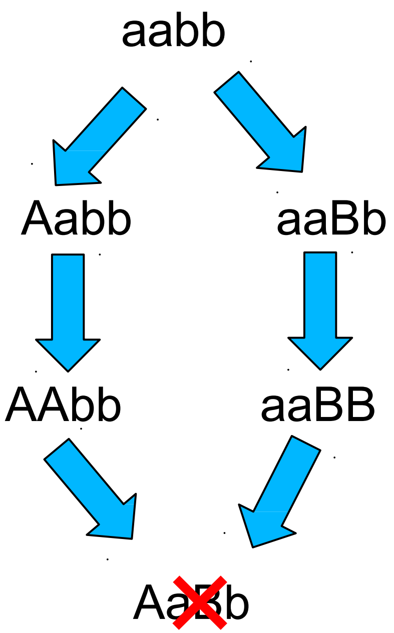
From Rice and Hostert 1993

Genetics of Speciation

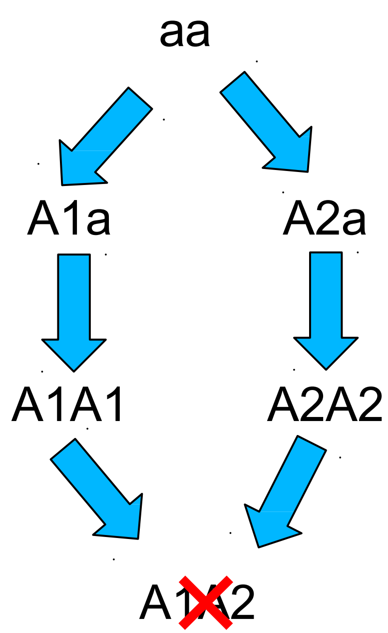
Darwin’s Dilemma: How could something as maladaptive as hybrid sterility or inviability evolve by natural selection?

Genetics of Speciation

Solution was independently discovered by William Bateson, Theodosius Dobzhansky, and Herman Muller



two locus model



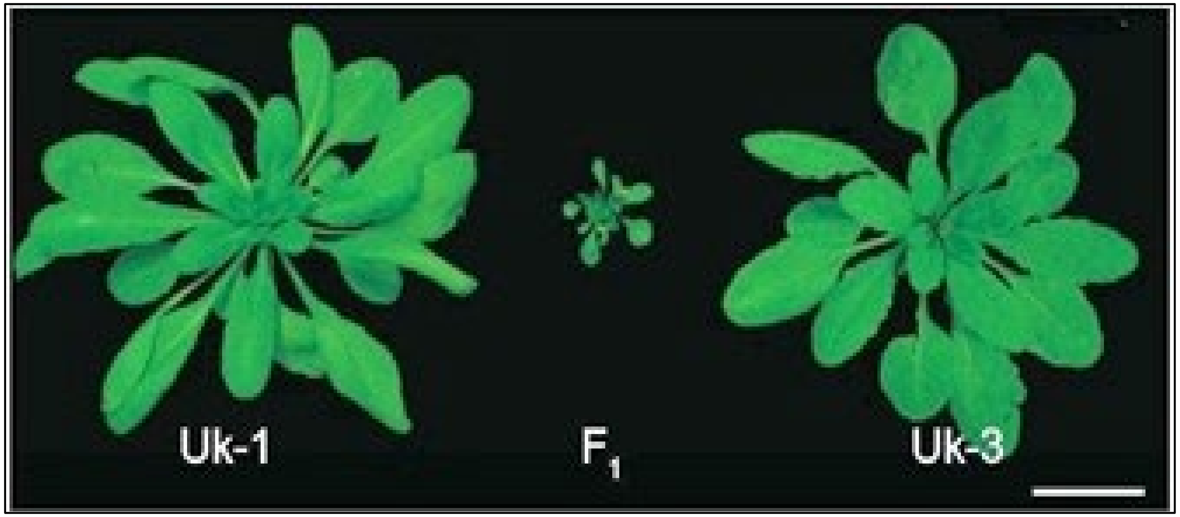
one locus model

Bateson-Dobzhansky-Muller (BDM) incompatibilities

Example of BDM incompatibilities

Disease resistance (R-genes): Typically consist of a nucleotide binding domain (NB) and a leucine rich repeat (LRR) domain(s) and are often referred to as (NB-LRR) R-genes or NLRs.

Hybrid inviability (Arabidopsis)
(Bomblies et al. 2007)



Hybrid necrosis (tomato)
Kruger et al. 2002

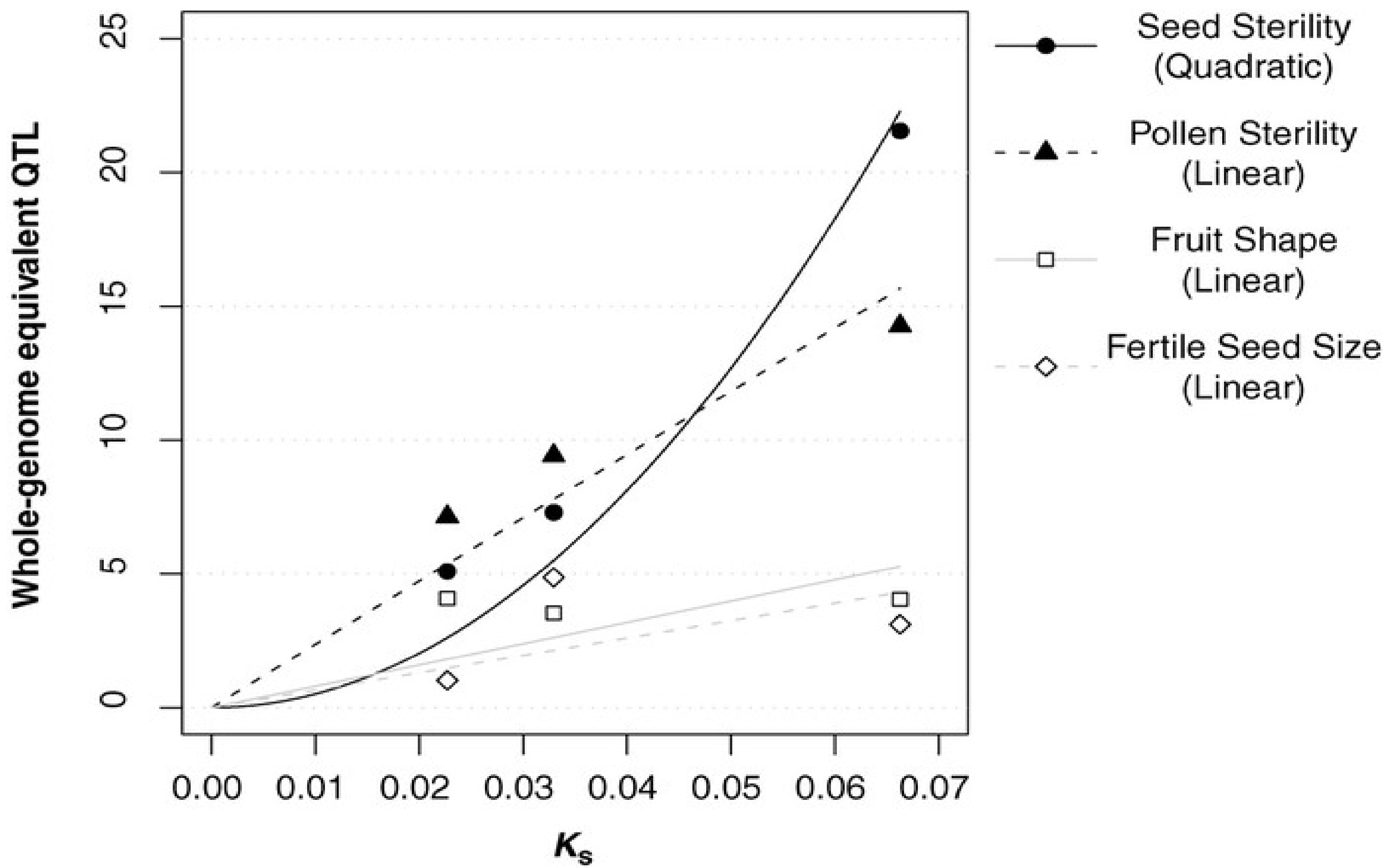
Often under balancing selection

The Snowball Effect

Prediction:

BDM incompatibilities expected to accumulate at a faster than linear rate (Orr, 1995).

Some evidence for this in tomato



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Hybrid incompatibilities can also arise via selfish evolution

Example:

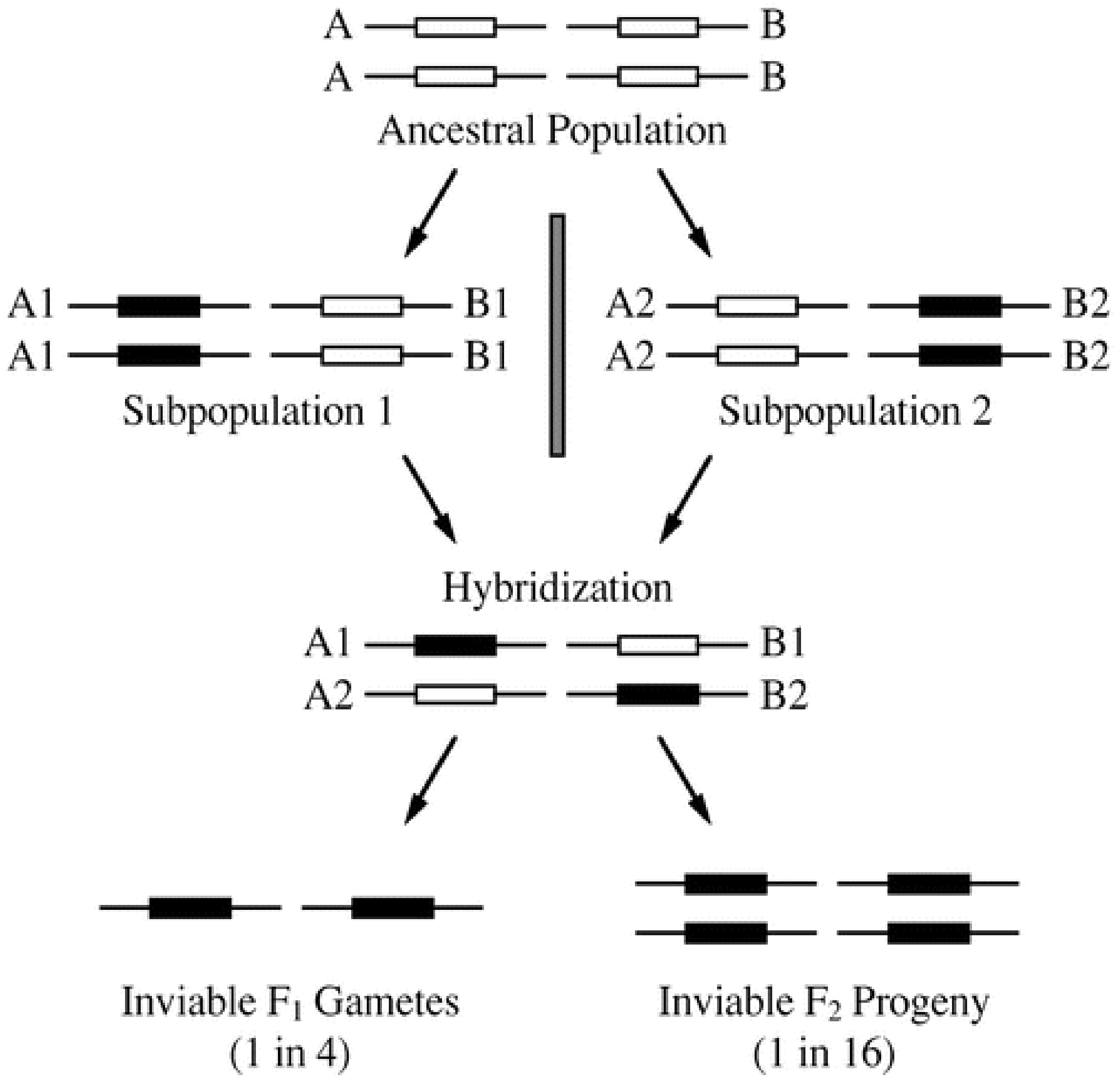
- <u>Cytoplasmic male sterility</u> (plant is unable to produce pollen due to a cytonuclear incompatibility)
- Spreads through seed despite reduction in male fertility
- Found in numerous species, including Oryza, Petunia, Helianthus, Mimulus, etc.
- Often used for hybrid production in crops
- >15 genes cloned (all chimeric genes in mitochondrial genomes)

Cytoplasmic male sterility in *Petunia*

- <u>Restorers of cytoplasmic male sterility</u>
- Strongly favored by selection
- >7 genes cloned, mostly mitochondria-targeting pentatricopeptide repeat (PPR) gene family

Rieseberg and Blackman, 2010

Hybrid incompatibilities can also arise via divergent resolution of duplicate genes



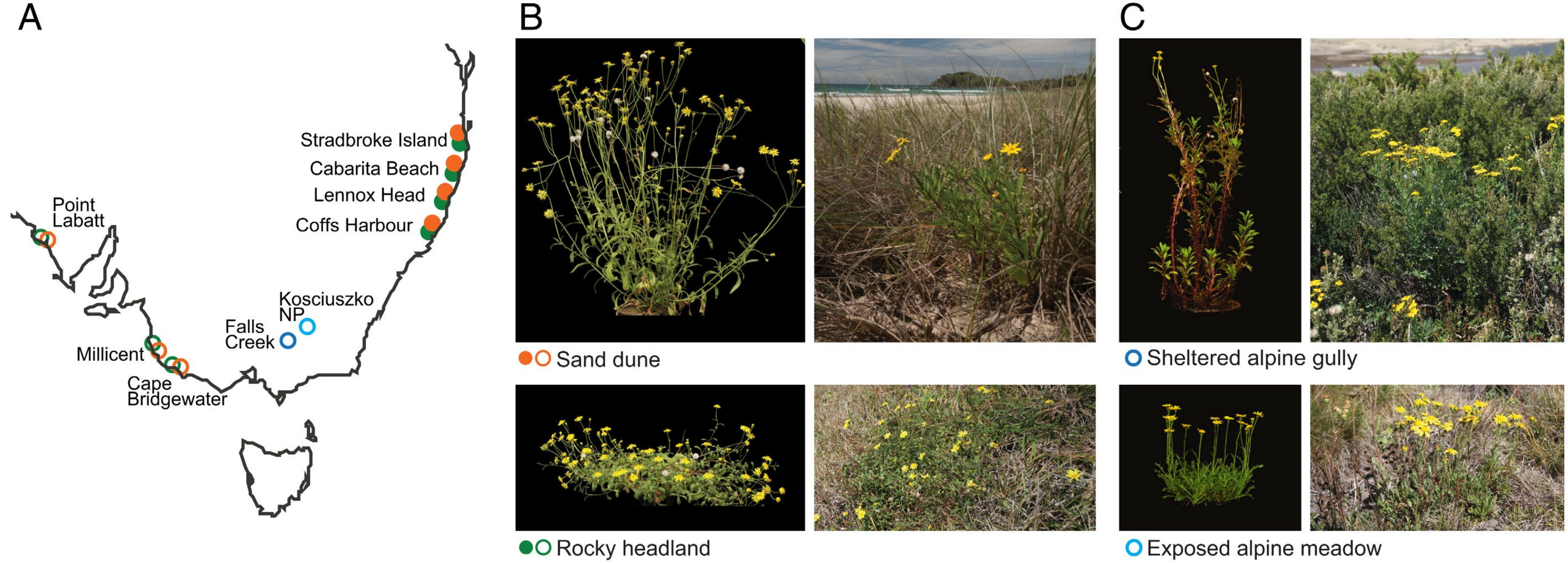
Burke and Arnold 2001

Phenotypic divergence and the genetics of postzygotic isolation

Are the genes causing hybrid sterility/inviability the same as those underlying phenotypic differences between species?

Examples:

- Many cases of hybrid necrosis caused by interactions between divergent NLR plant-immune genes in interpopulation hybrids
- Shoot gravitropism, which differs between ecotypes of *Senecio lautus* is associated with partial hybrid sterility caused by variation at an underlying gene, *ABA3* (Wilkinson et al. 2021)



Phenotypic divergence and the genetics of postzygotic isolation

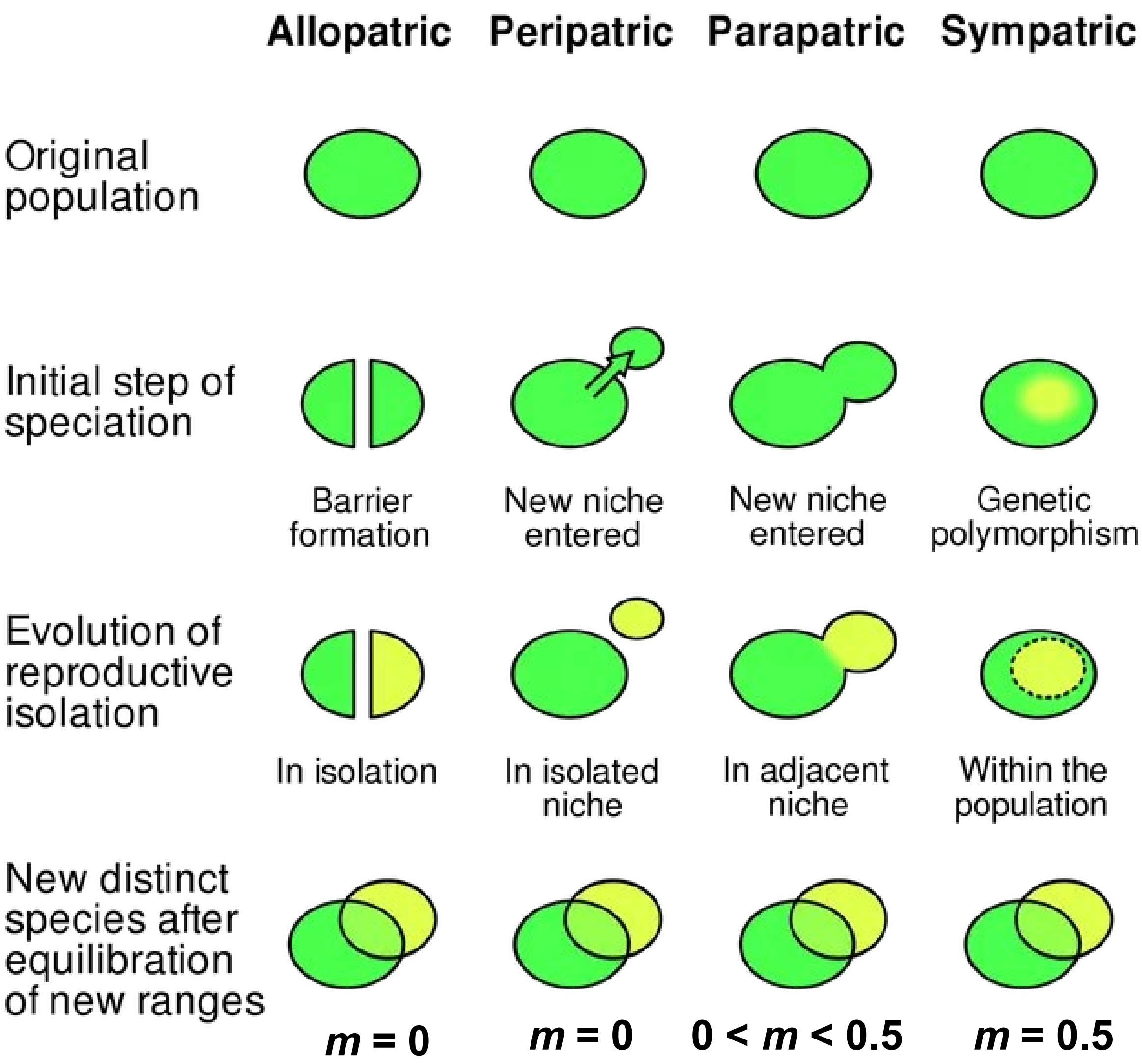
Are the genes causing hybrid sterility/inviability the same as those underlying phenotypic differences between species?

Counter examples:

- Lethality of offspring between *Mimulus guttatus* adapted to copper mine tailings and off-mine plants due to linkage rather than pleiotropy (Wright et al. 2013)
- Selfish evolution (e.g., cytoplasmic male sterility)
- Divergent resolution of duplicated genes (Zuellig and Sweigart 2018)

White seedlings segregate in 1:15 in reciprocal F2 hybrids of *M. guttatus* due to segregation of functional copy of *pTAC14*

Geography of Speciation



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)

M. cupriphilis

M. guttatus

Sympatric Speciation

Problems:

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

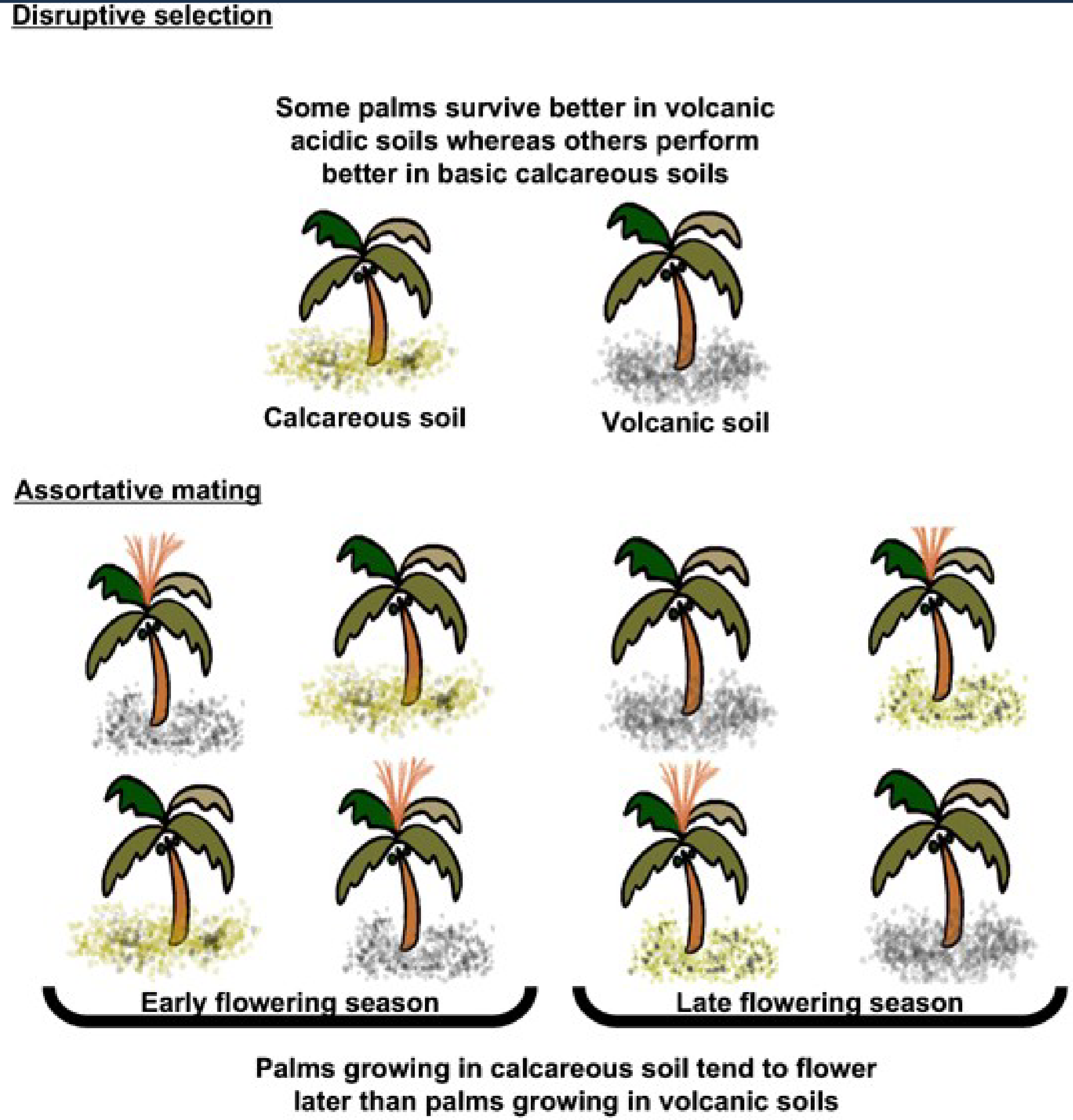
Sympatric species must coexist- resource use

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

Sympatric Speciation



Magic Traits

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

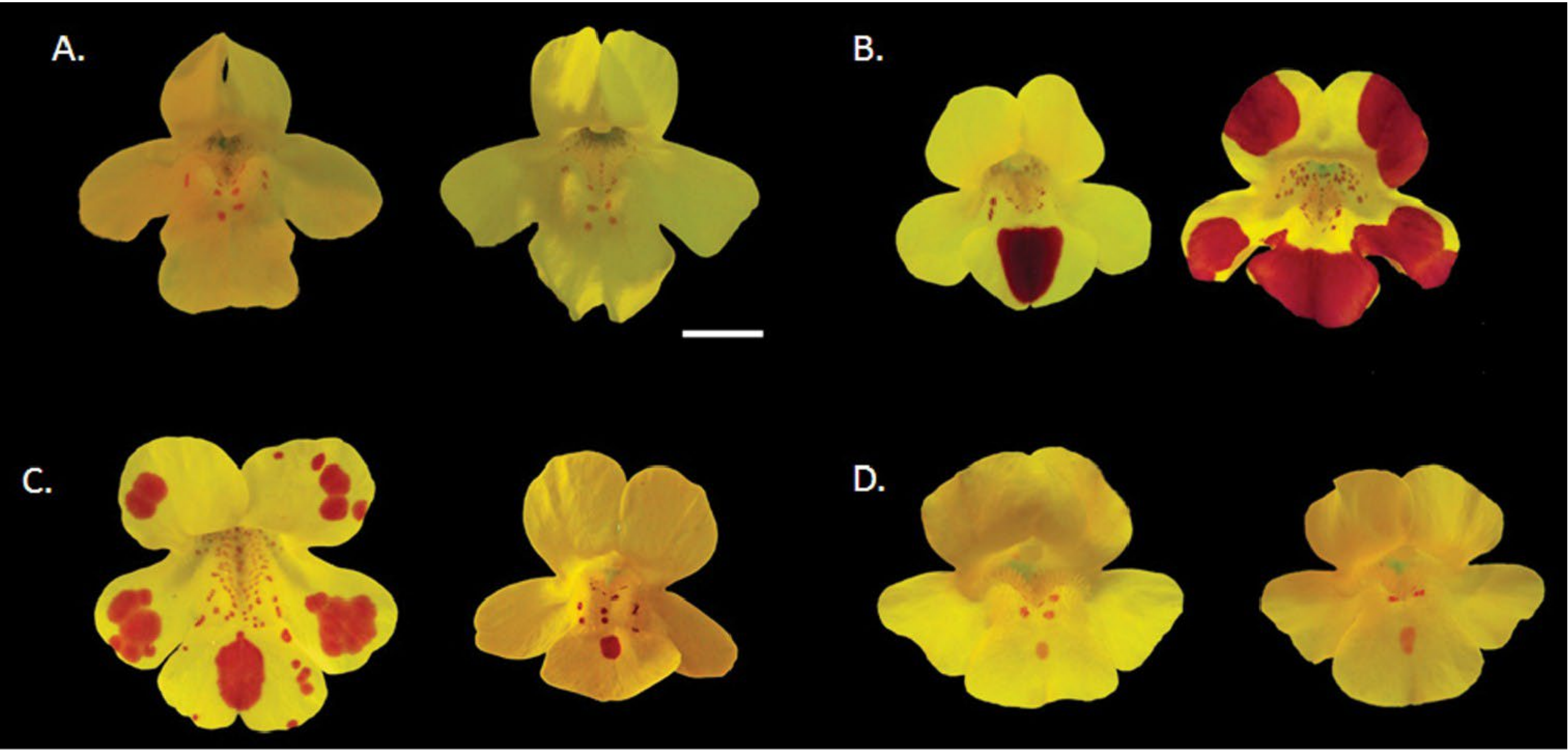
When assortative mating and disruptive selection are combined in the same trait, it is called a **magic trait.**

Such a correlation can also be achieved through the evolution of recombination suppressors such as inversions.

Sympatric Speciation- Polyploidization

M. guttatus (n= 28)

Morphs related to *M. luteus* (n= 62)



M. x robertsii (n= 44, 45)

M. peregrinus (n= 92)

(somewhat) Unanswered Questions

- 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)?
- Do hybrid incompatibilities snowball?
- Is plant speciation mostly occur via budding (peripatric/paraptric) speciation