PLANT OF THE DAY!

Pisonia grandis -
Devil's claws

Native to Seychelles

Lethal Zoochory!

Think plants are harmless? Think twice!

Questions

- Are species real?
- Why are there species?
- What kinds of reproductive barriers can isolate plant species?
- Which kinds of barriers are most important during speciation?

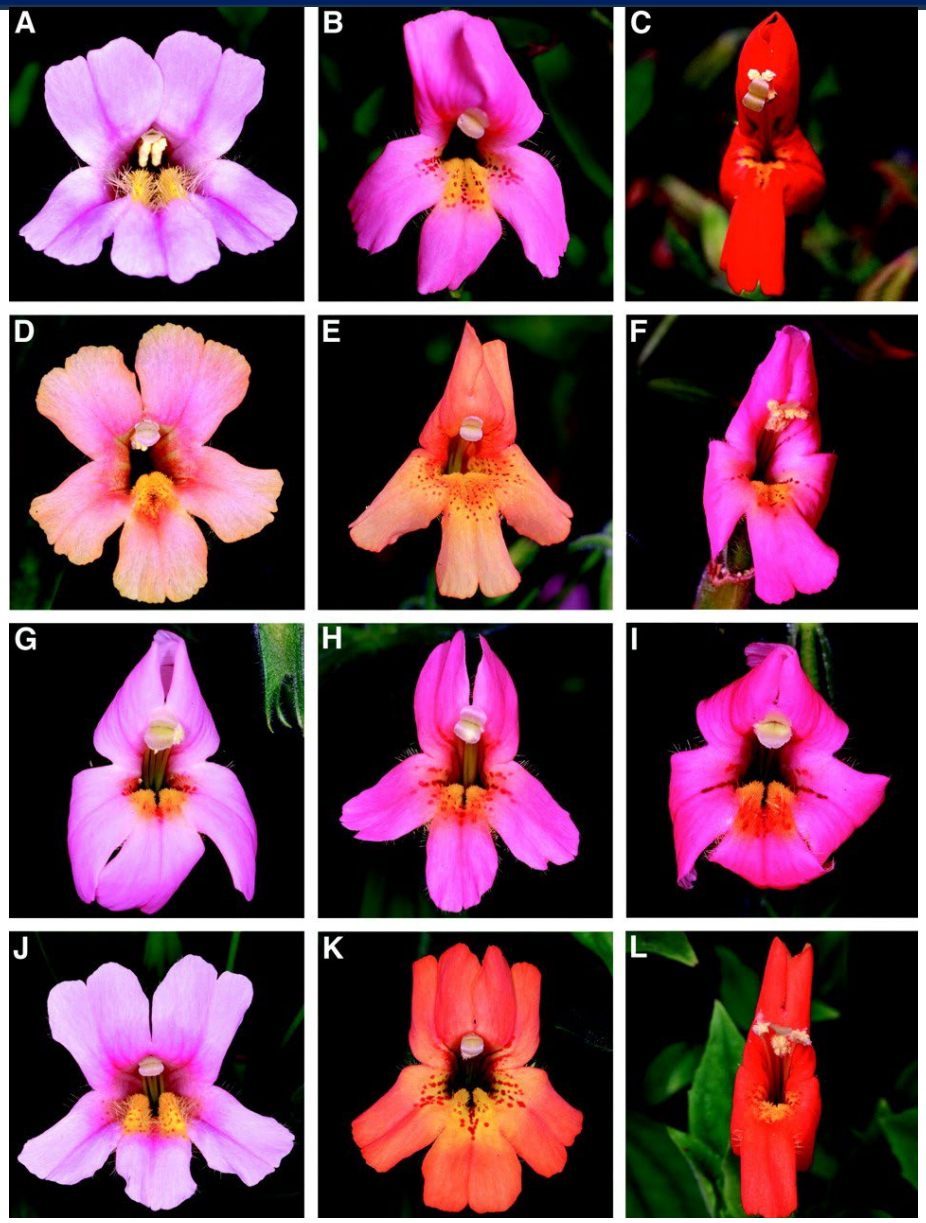
Outline

Are species real?

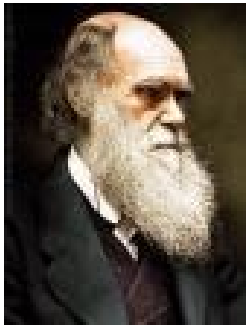
Why are there species?

Species concepts

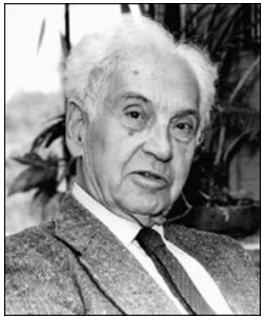
Reproductive barriers



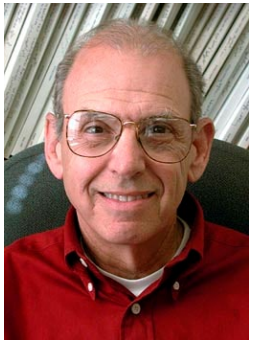
Are species real?



"From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms." (Darwin, 1859, p. 52)



"The non-arbitrariness of the biological species is the result of … the internal cohesion of the gene pool… (Mayr, 1963, p. 21)



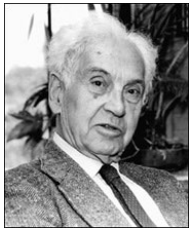
"Plant species are utilitarian mental constructs" (Levin, 1981, p.381)

Are species real?

Evidence from floras and monographs:

- 697 of 838 of named species (83.1%) in Concord Township flora were "morphologically well-defined, relatively uniform, and sharply set off against all other species"

(Mayr 1992, p. 236)



- 120 of 1,790 species (7%) from 104 botanical monographs reported as problematic.

(McDade 1995)

Criticisms: assessments are subjective
human mind adept at classification

Are species real?

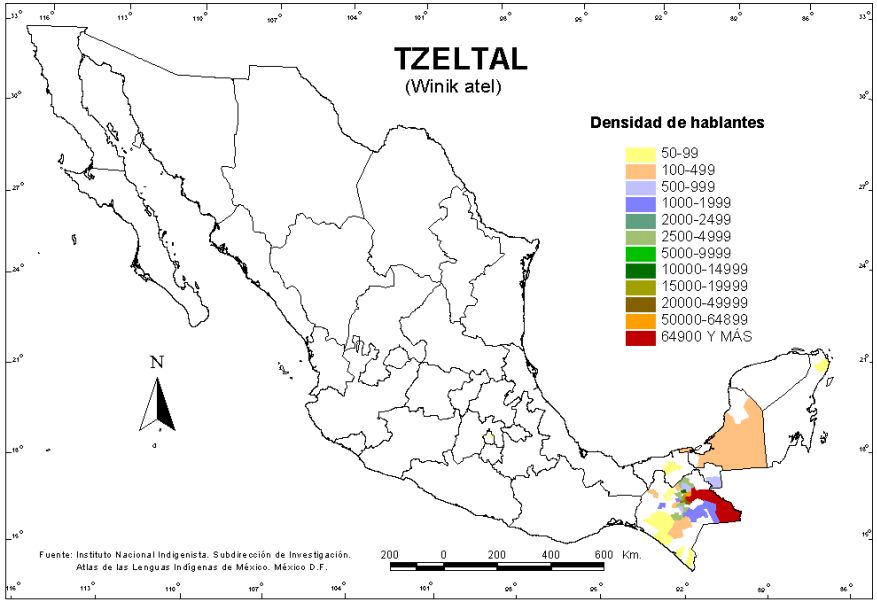
Evidence from folk taxonomies:

Animals:
Birds of New Guinea (70-90%)
Frogs of New Guinea (80%)
Reptiles of New Guinea (95%)

reviewed in Coyne & Orr (2004

Plants:
-61% of Tzeltal (S. Mexico) species correspond 1:1 with Linnaean species (Berlin et al. 1974)

-87.7% of Dai (Yunnan, China) taxa have Linnaean equivalent (Wang et al. 2004)



Criticism: all humans share similar neurological processes

Why are there species?

Statistical tests:

218 numerical taxonomy studies (*Nature* 440:524-527)

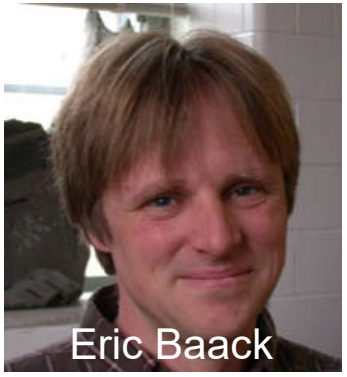
<u>Analyses:</u>
number of discrete phenotypic clusters within groups

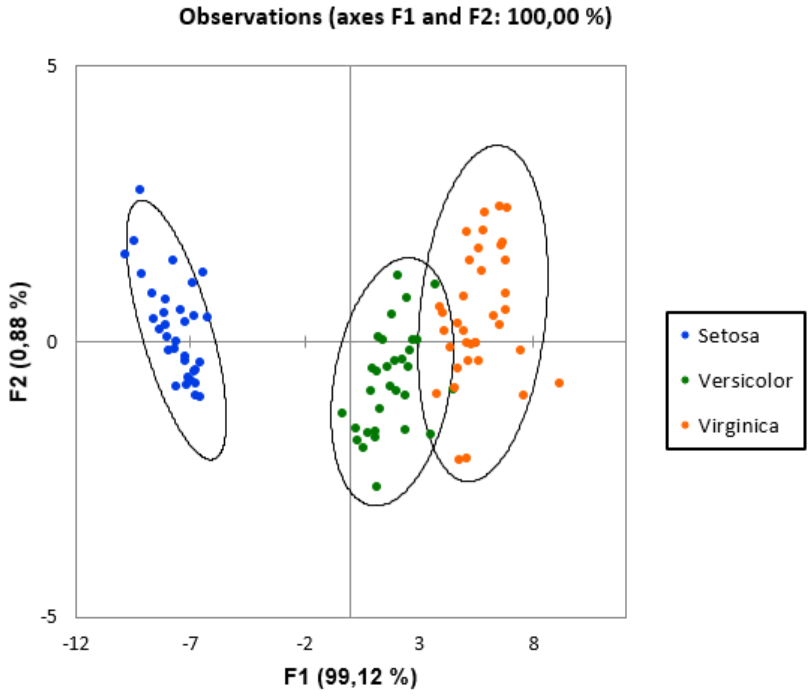
proportion of named species that correspond directly with phenetic clusters

<u>Results:</u>
discrete phenotypic clusters found in > 80% of taxa studied

correspondence between named species & phenetic clusters was low (54%)

Due to splitting by taxonomists/inadequate statistical methods





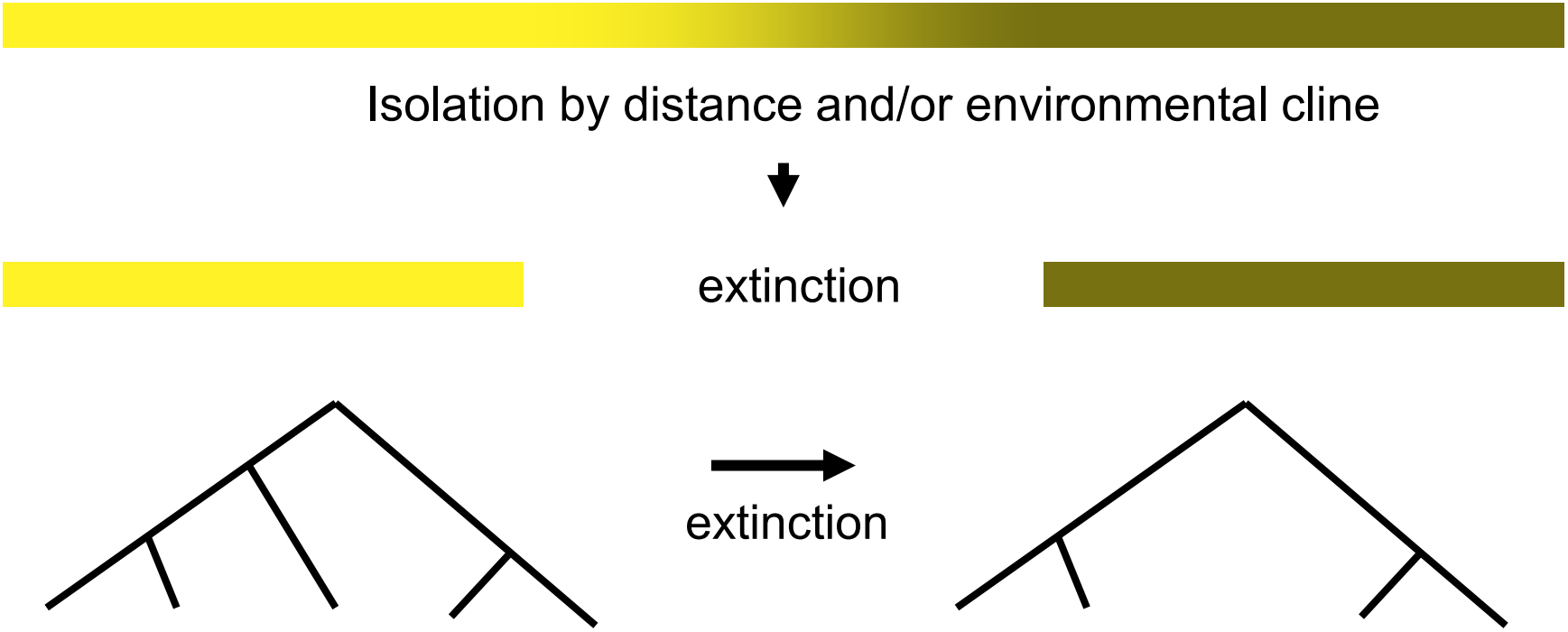
Discriminate analysis of 3 Iris species
(https://www.xlstat.com/en/solutions/features/discriminant-analysis-da)

Why are there species?

Why are organisms apportioned into clusters separated by gaps?

1) Inevitable consequence of population or lineage extinction
(allopatric speciation via the extinction of intermediate populations in a chain of races)

Population or lineage extinction:



Why are there species?

Why are organisms apportioned into clusters separated by gaps?

2) Adaptation to different niches (ecological speciation)

Clustering of adaptive phenotypic traits > in sexual than asexual species (Barraclough et al. 2004)

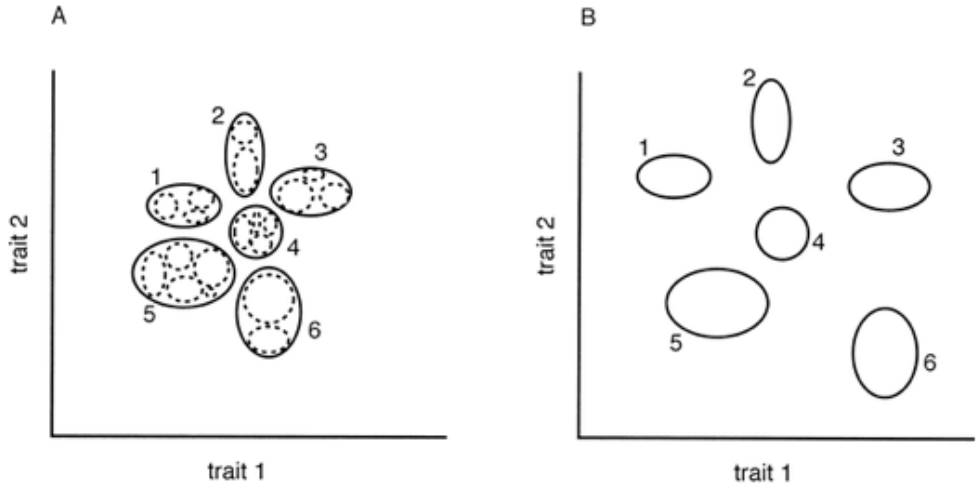


Fig. 4. Expected variation among clusters for two adaptive characters coded by multiple loci in (A) asexual and (B) sexual cases. Each ellipse represents the range of values observed within a single recognizable cluster. Note that the asexuals display further discreteness within each major cluster, due to the inherent tree structure of quantitative variation in asexual populations. The traits could be morphological measures or the first two principal components from a principal components analysis of a set of morphological characters. The number of clusters is the same in the sexual and asexual case, but the magnitude of differences among clusters (disparity) is greater in sexuals

3) Reproductive Isolation (inevitable result of mutation order divergence in finite populations that are geographically isolated)

Species Concepts

Alice explains why we name things:

"What's the use of their having names," the Gnat said, "if they don't answer to them?"
"No use to them," said Alice, "but it's useful to people that name them, I suppose. If not, why do things have names at all?"

- Lewis Carroll, Through the Looking Glass

Darwin's other view of species:

"Firstly, why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion instead of species being, as we see them, well defined?"

- Charles Darwin, The Origin of Species

Species Concepts (A-Z)

Agamospecies Concept
Biological Species Concept
Cladistic Species Concept
Cohesion Species Concept
Composite Species Concept
Ecological Species Concept
Evolutionary Significant Unit
Evolutionary Species Concept
Genealogical Concordance
Genetic Species Concept
Genotypic Cluster Concept
Hennigian Species Concept
Internodal Species Concept
Morphological Species Concept
Non-dimensional Species Concept
Phenetic Species Concept
Phylogenetic Species Concept I
Phylogenetic Species Concept II
Phylogenetic Species Concept III
Polythetic Species Concept
Recognition Species Concept
Reproductive Competition
Successional Species Concept
Taxonomic Species Concept

Mayden (1997)

Species Concepts

Biological Species Concept (BSC): "species are groups of interbreeding natural populations that are reproductively isolated from all other such groups" (Mayr 1969).

Comment: Most influential concept for sexual species

Problems: (1) Too much sex;
(2) Too little sex;
(3) difficult to apply to allopatric populations

Phylogenetic Species Concept (PSC): “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." (Cracraft, 1983).

Comment: Explicitly avoids all reference to reproductive isolation and focuses instead on phylogenetic histories of populations.

Problems: (1) confuses histories of traits with histories of organisms;
(2) classifications change with more data;
(3) creates taxonomic inflation

Species Concepts

Biological Species Concept (BSC): "species are groups of interbreeding natural populations that are reproductively isolated from all other such groups" (Mayr 1969).

Comment: Most influential concept for sexual species **(WILL BE USED IN THIS COURSE)**

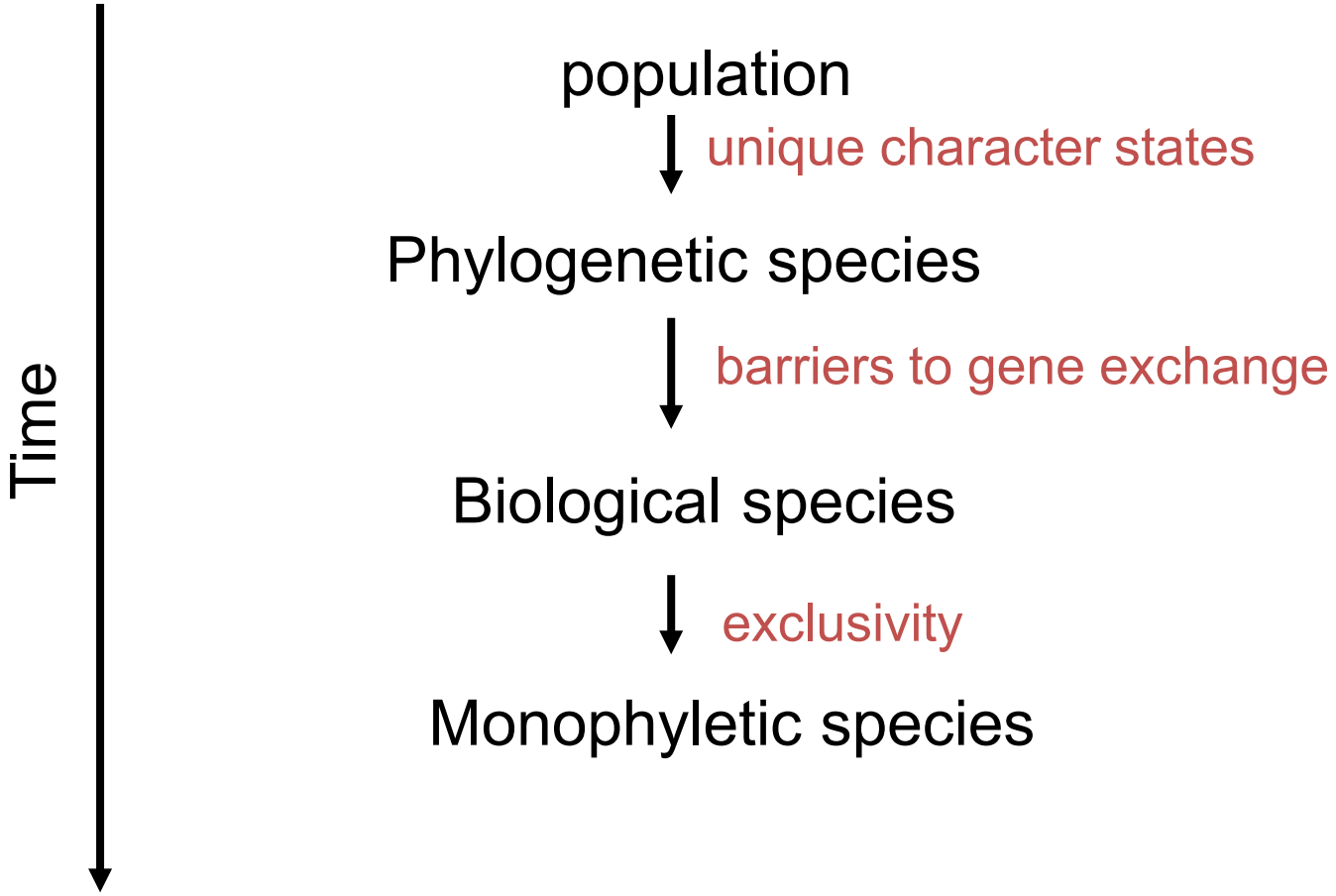
Problems:
(1) Too much sex;
(2) Too little sex;
(3) difficult to apply to allopatric populations

Phylogenetic Species Concept (PSC): “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." (Cracraft, 1983).

Comment: Explicitly avoids all reference to reproductive isolation and focuses instead on phylogenetic histories of populations (popular with taxonomists).

Problems:
(1) Confuses histories of traits with histories of organisms;
(2) Classifications change with more data;
(3) Creates taxonomic inflation

Different species concepts describe different stages of speciation



Species Life Histories (Harrison 1998)

Speciation: What is it?

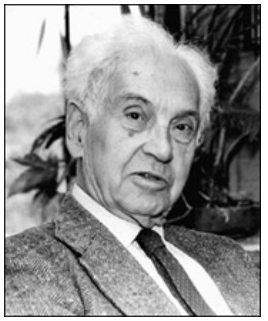
<u>For our purposes:</u>

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

“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

Reproductive Isolation

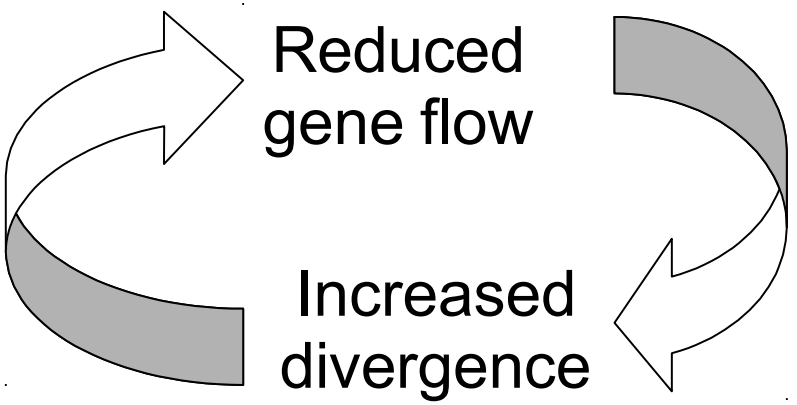


a.k.a. barriers to gene flow

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:



Barrier Components

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

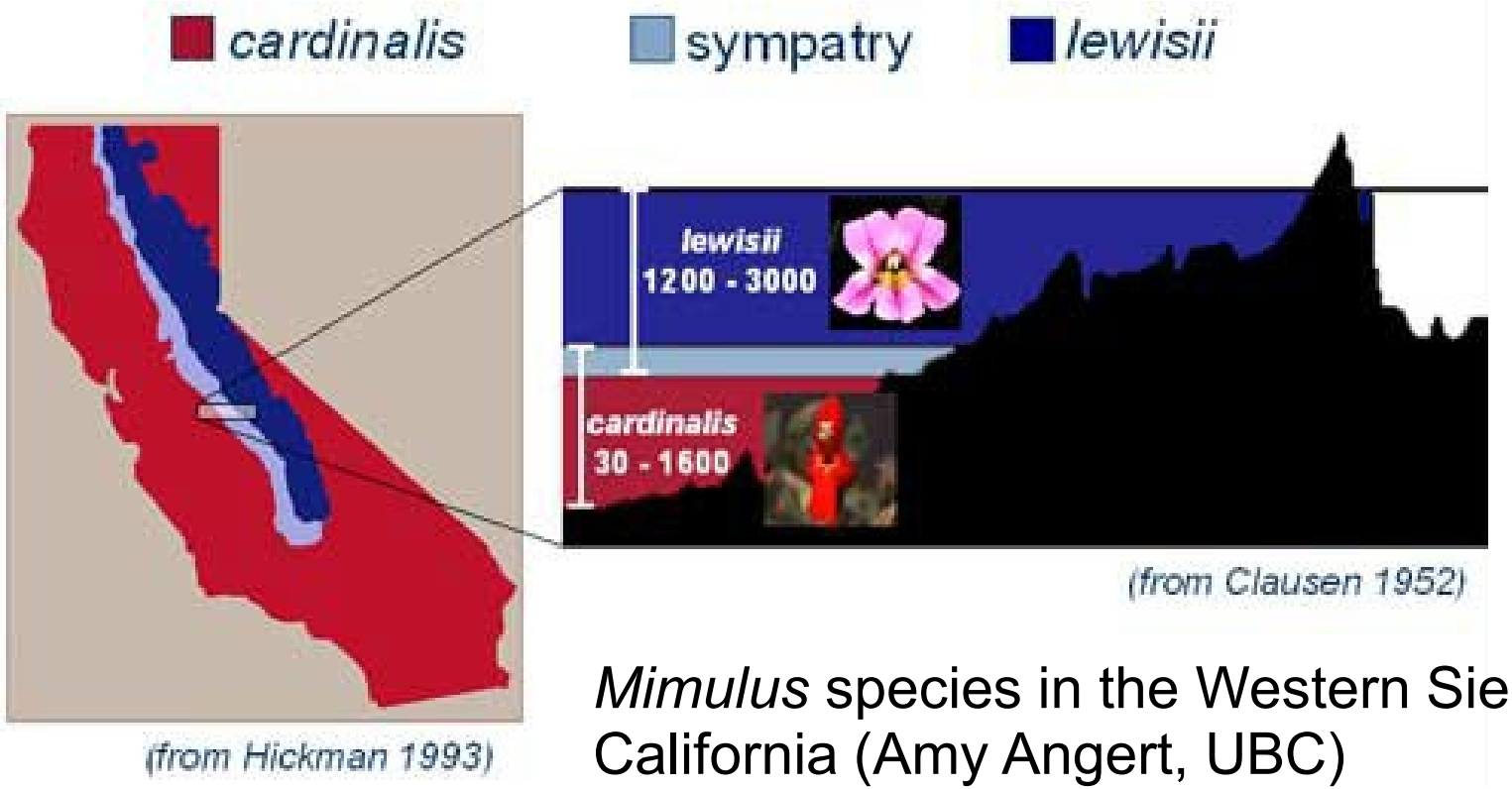
Postpollination prezygotic barriers prevent heterospecific pollen from successfully fertilizing ovules.

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).

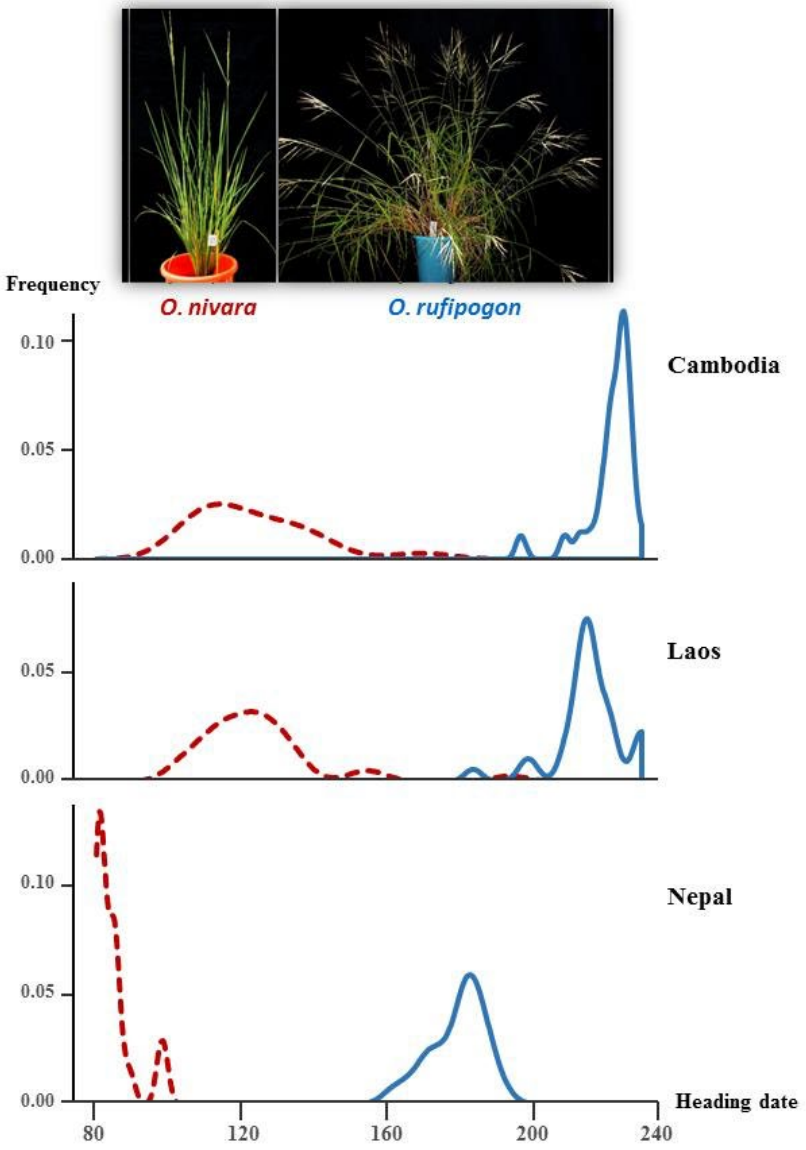
Ecogeographic Isolation/Immigrant Inviability

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



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

Temporal Isolation

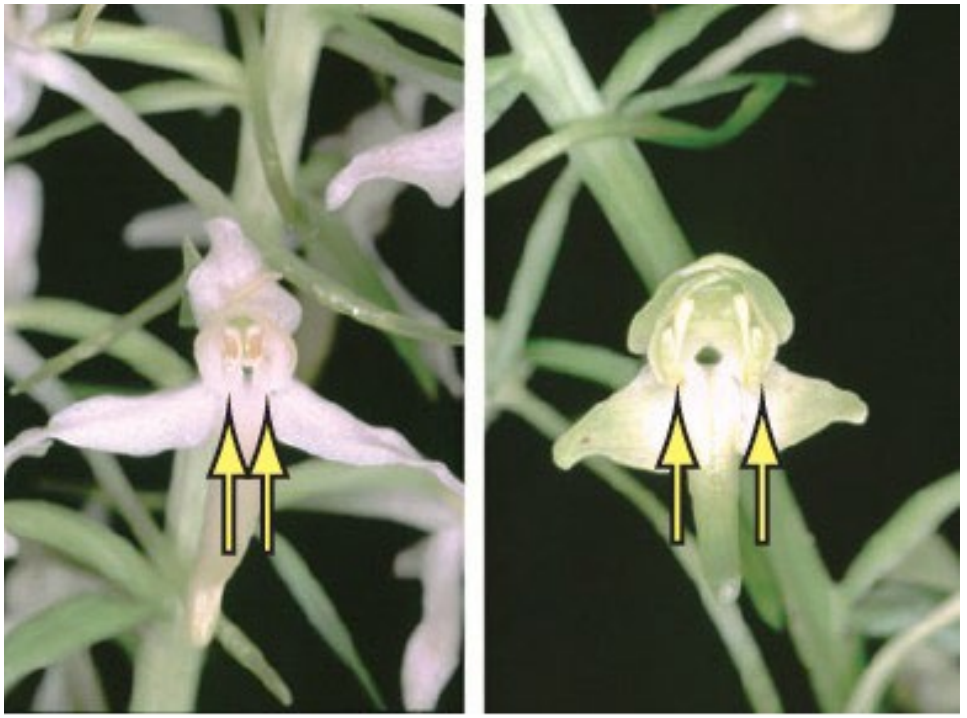


Can be seasonal, diurnal, etc.

Xu X et al. 2020. Divergence in flowering time is a major component contributing to reproductive isolation between two wild rice species (*Oryza rufipogon* and *O. nivara)*

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

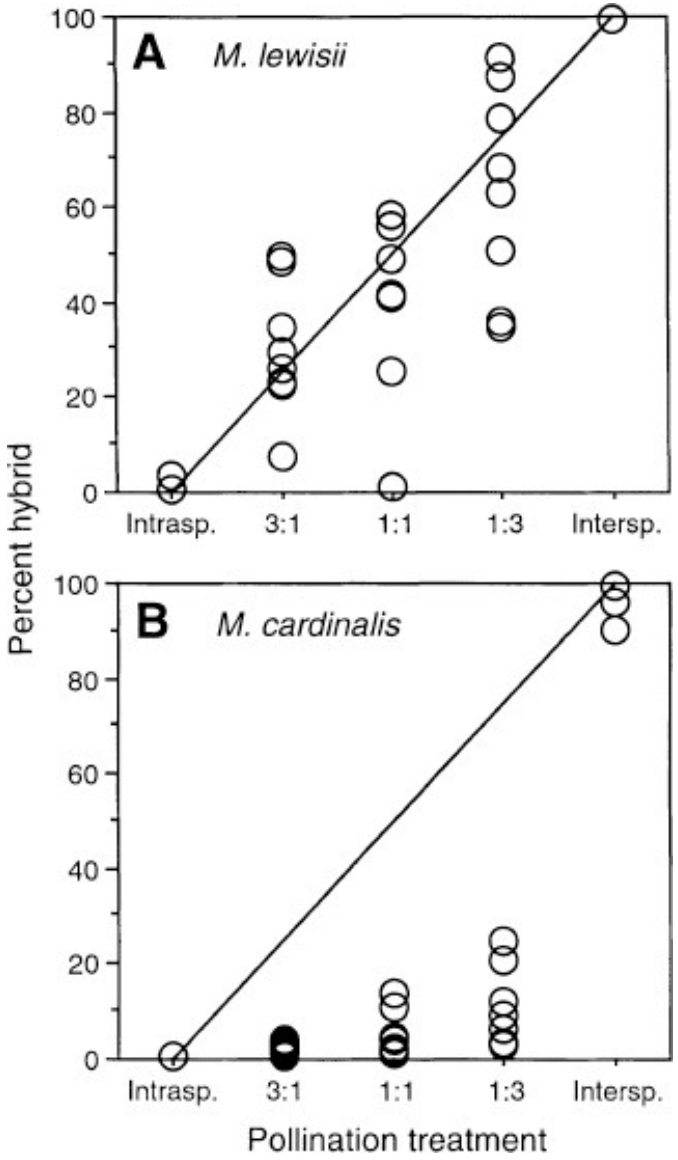
Mating System Isolation

Mimulus guttatus

Mimulus nasutus

Martin and Willis 2007

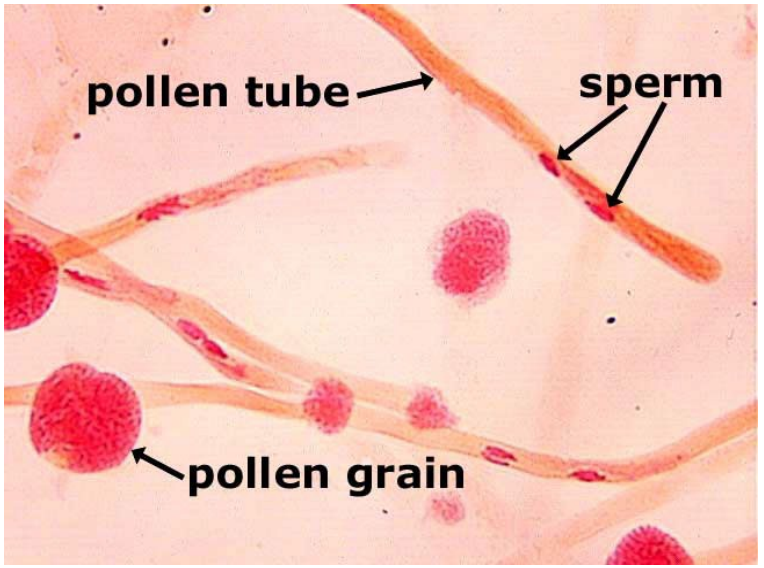
Post-pollination, Prezygotic Isolation



Ramsey et al. 2003

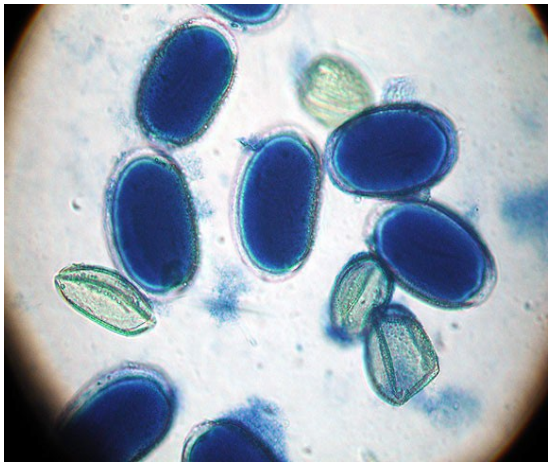
Conspecific pollen precedence
conspecific pollen often outcompetes heterospecific pollen (perhaps due to sexual selection).

Pollen-ovule incompatibilities



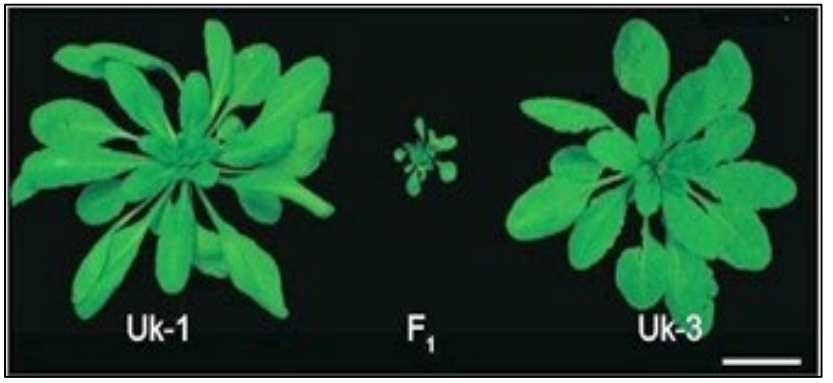
(Intrinsic) Postzygotic Isolation

Hybrid sterility: hybrids have reduced fertility



Hybrid pollen sterility

Hybrid inviability: hybrids have reduced viability



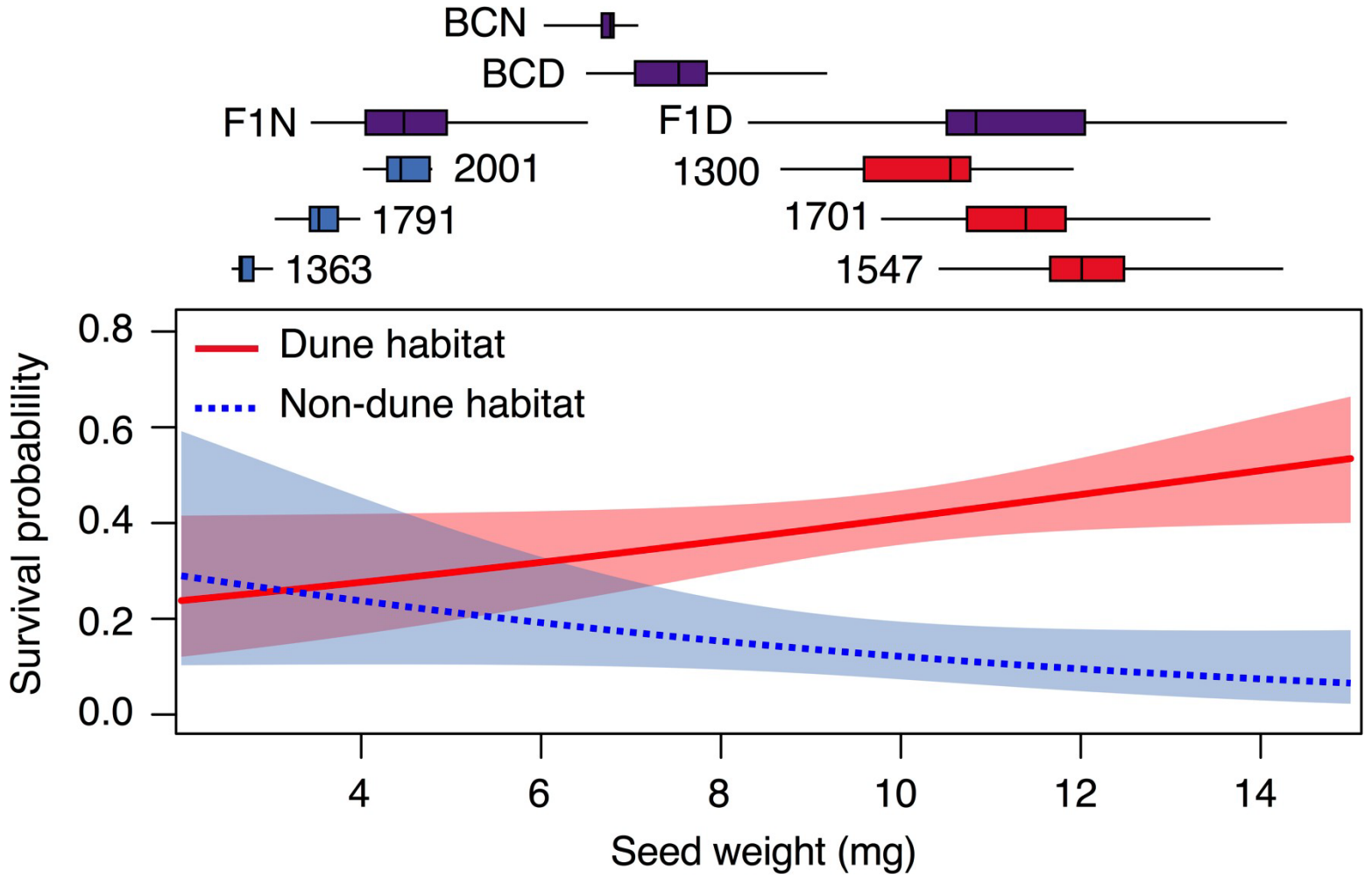
Hybrid inviability (Bomblies et al. 2007)

(Extrinsic) Postzygotic Isolation

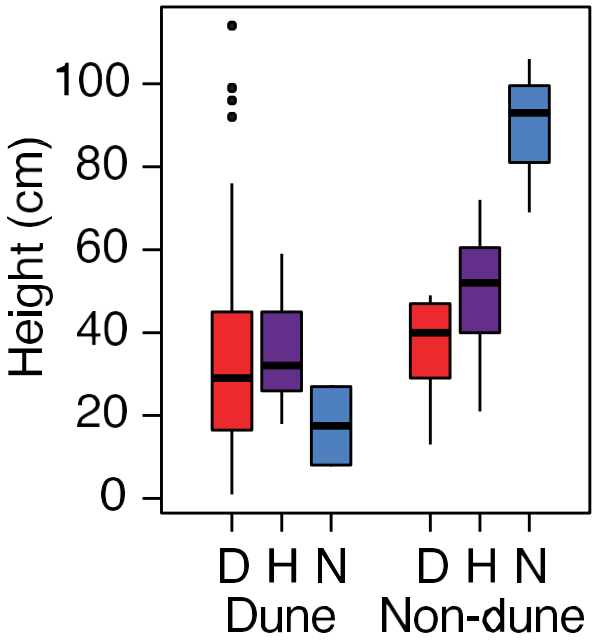
Ecological isolation: hybrids are not as fit (reduced fertility/viability) as parents in parental environments.

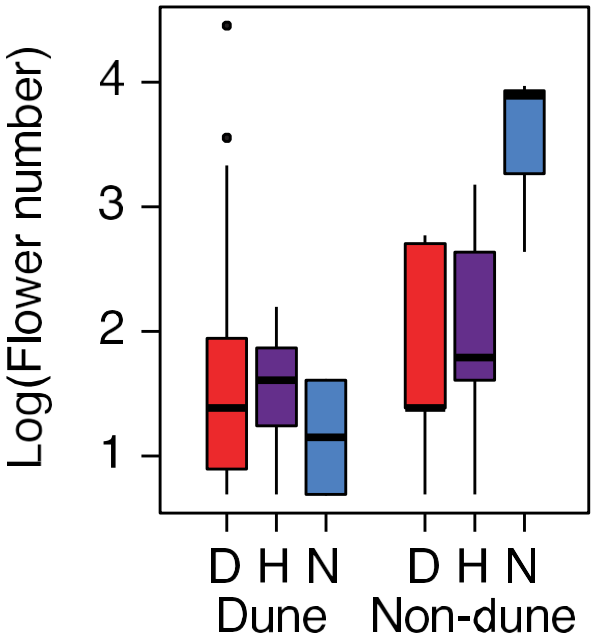
Ostevik et al. (2016)

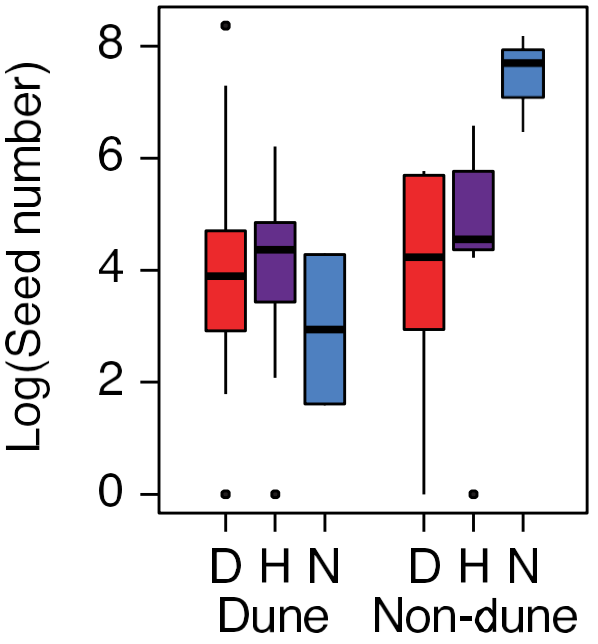
Large Seeds Favored in Dune Habitat



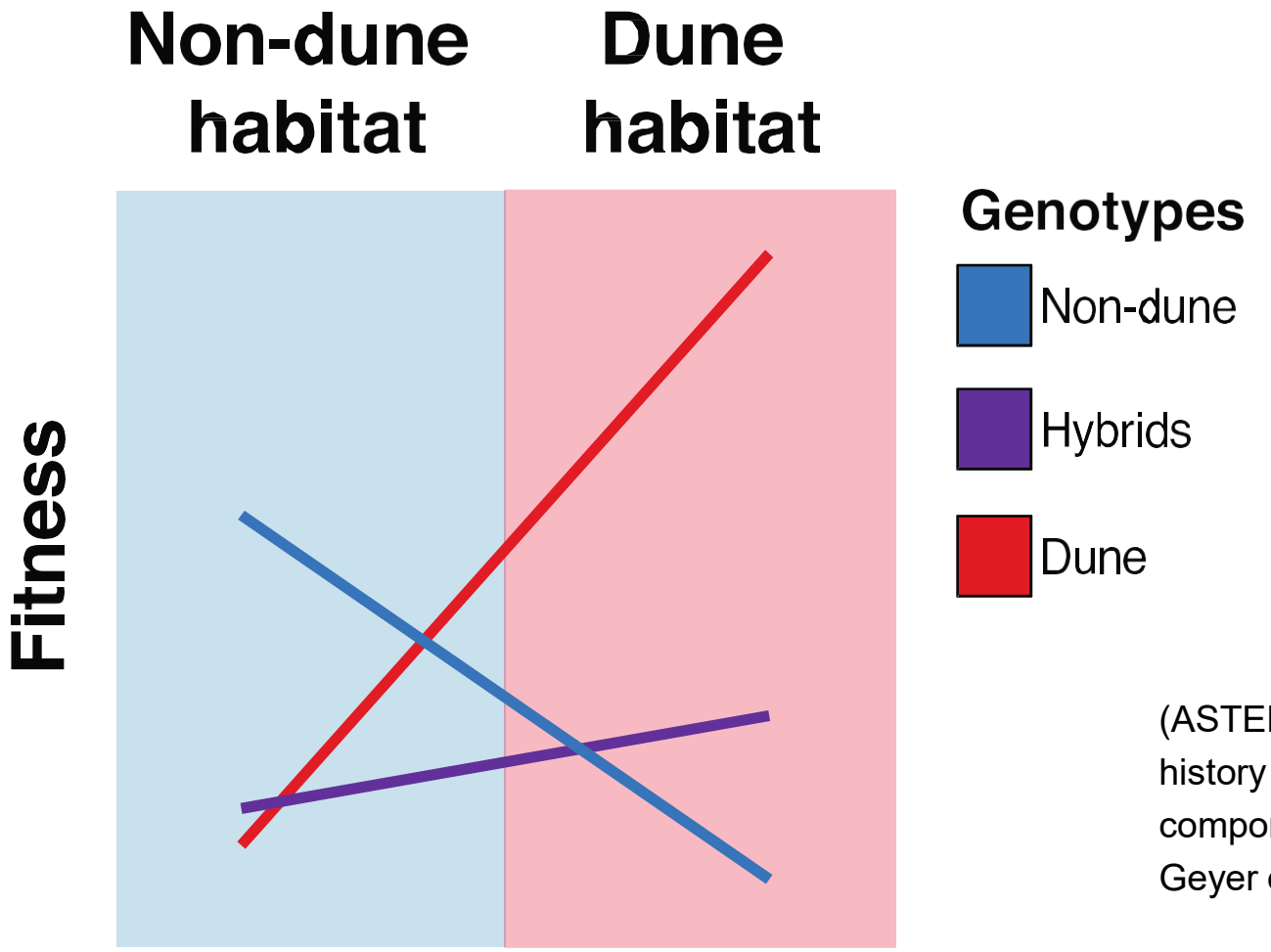
But, non-dune plants produce more flowers and seeds on sand sheet





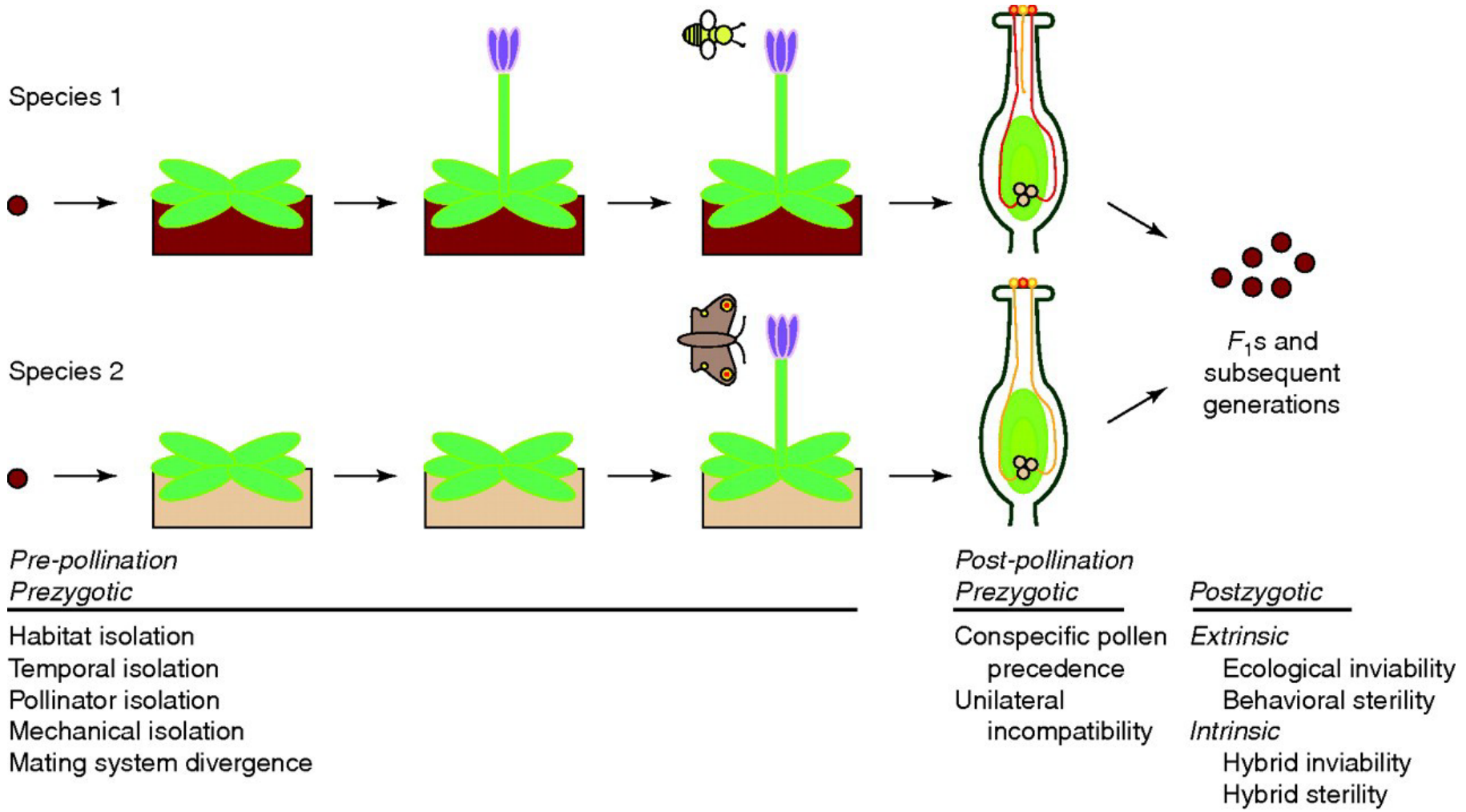


And hybrids are selected against in both parental habitats



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

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



Baack et al. (2015)

(somewhat) Unanswered Questions

- How important is reproductive isolation to the formation of discrete phenotype and genotypic clusters?
- Which reproductive barriers are most important early in speciation? Late in speciation?
- Will the answers to these questions vary with respect to taxonomic group and reproductive system?