BIO 322

Advanced Evolutionary Ecology
(Vasanth 2016)

Ullasa Kodandaramaiah

MODULE: SPECIATION

SPECIATION

- Process of formation of new species

  i.e. Multiplication of species

- Link between microevolution and macroevolution

- Evolution of reproductive isolation

  - Prezygotic barriers

  - Postzygotic barriers

Reproductive Isolation

Prezygotic mechanisms:

Temporal isolation: Reproduce at different seasons or at different times of the day.

Behavioral isolation: Mating rituals, songs, mating calls

Mechanical isolation

Geographical (Habitat) isolation

Postzygotic Isolation

Hybrid inviability

Embryological arrest: Hybrid embryos often do not develop properly; no viable offspring is created.

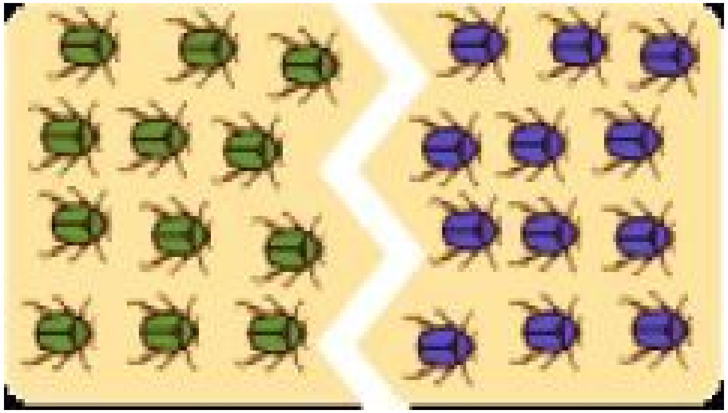
Hybrid sterility

Infertility: Hybrid offspring might grow to viable adults but these are infertile and cannot produce further offspring (Donkey + Horse = Mule; Mule is sterile).

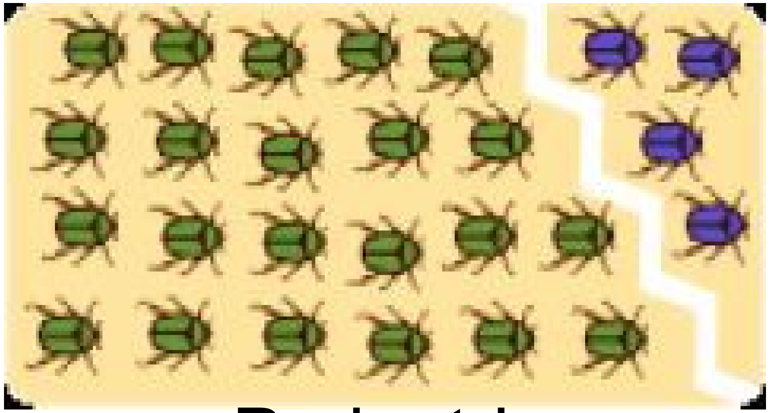
Reproductive Isolating Mechanisms

Mechanism	How It Works
Prezygotic Barriers	Prevent fertilization
Habitat isolation	Similar species reproduce in different habitats
Temporal isolation	Similar species reproduce at different times
Behavioral isolation	Similar species have distinctive courtship behaviors
Mechanical isolation	Similar species have structural differences in their reproductive organs
Gametic isolation	Gametes of similar species are chemically incompatible
Postzygotic Barriers	Reduce viability or fertility of hybrid
Hybrid inviability	Interspecific hybrid dies at early stage of embryonic development
Hybrid sterility	Interspecific hybrid survives to adulthood but is unable to reproduce successfully
Hybrid breakdown	Offspring of interspecific hybrid have problems reproducing

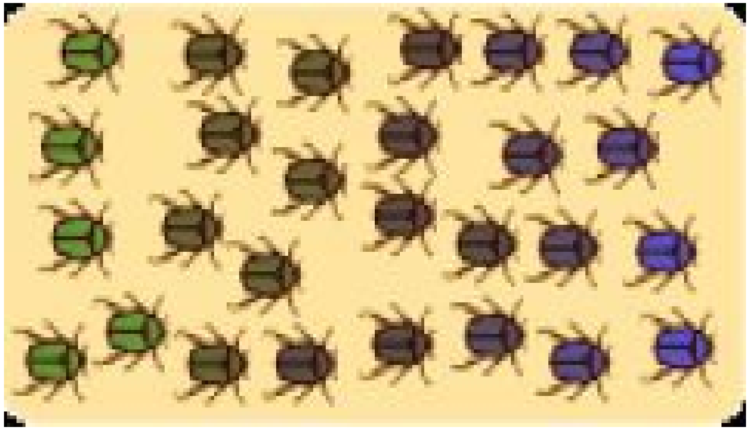
Adapted from slide by Scott Bowling



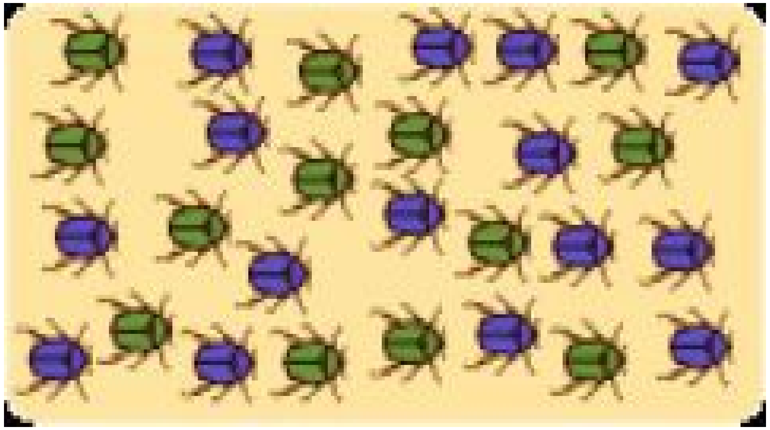
Allopatric



Peripatric



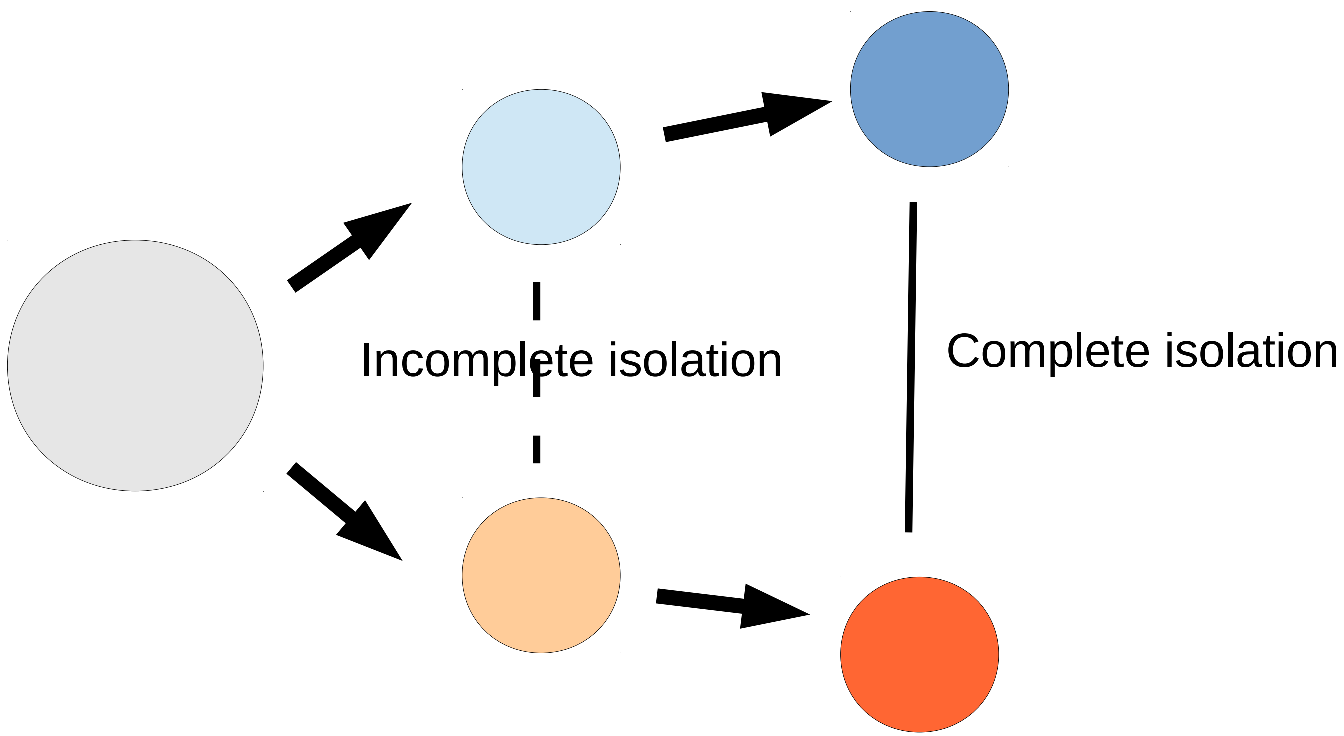
Parapatric



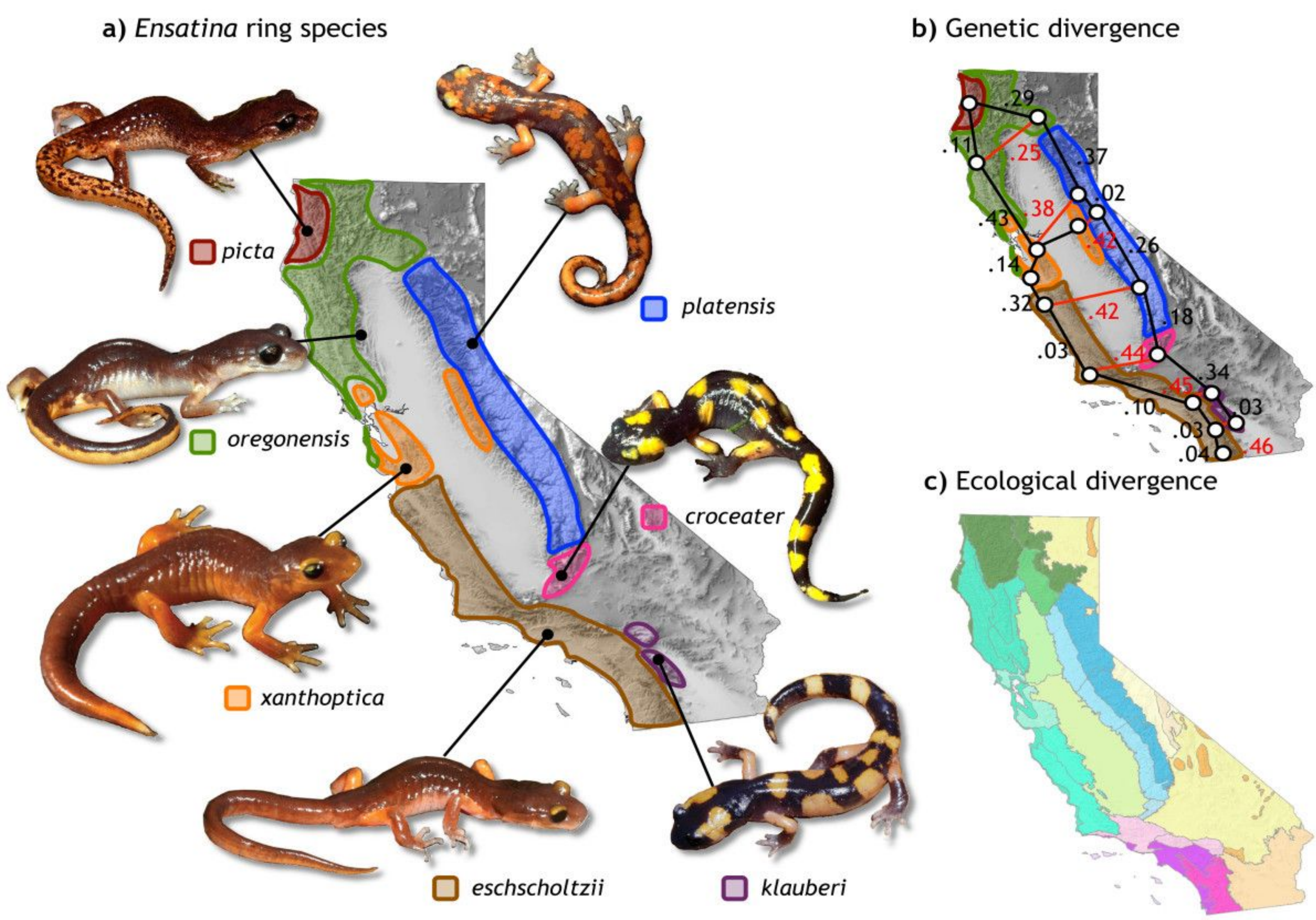
Sympatric

Images from http://evolution.berkeley.edu

Intermediate stages of speciation, ie two groups of individuals with incomplete reproductive isolation, are sometimes called *Incipient Species*



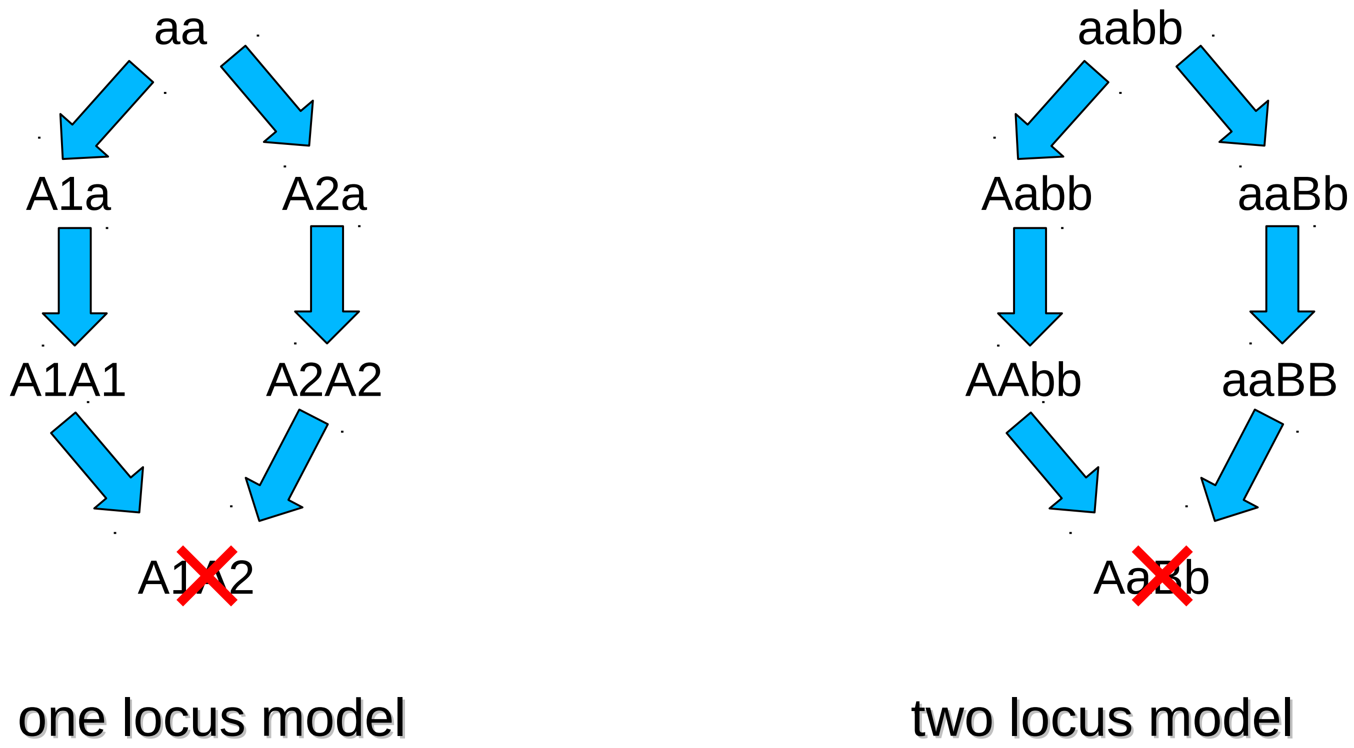
Ring species in *Ensatina* salamanders



Source: Pereira et al 2011 BMC Evol Biol

Genetics of Speciation

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



Bateson-Dobzhansky-Muller (BDM) incompatibilities

Adapted from slide by Loren. H, Riseberg

Examples of BDM incompatibilities

Species 1	Gene 1	Identity/ Function	Species 2	Gene 2	Identity/ Function	Hybrid Phenotype	Notes	Refs.
A. thaliana Columbia accession (Col)	*HPA* At5g10330	Histidine biosynthesis	*A. thaliana* Cape Verde Island accession (Cvi)	*HPA2* At5g71920	Histidine biosynthesis	Lethality	Divergent evolution of duplicate genes	Bikard (2009)
D. simulans	*Nup96*	Nucleoporin (component of NUP107 subcomplex)	*D. melanogaster*	Unknown factor(s) on X chromosome	Unknown	Lethality	Byproduct of adaptive evolution driving divergence	Presgraves et al. (2003); Tang & Presgraves (2009)
D. simulans	*Nup160*	Nucleoporin (component of NUP107 subcomplex)	*D. melanogaster*	Unknown factor(s) on X-chromosome	Unknown	Lethality	Byproduct of divergent coevolution with *Nup96*	Tang & Presgraves (2009)
India rice varieties	*Hwa1*	Unknown	India rice varieties	*Hwa2*	Unknown	Lethality		Oka (1956)
X. maculates	*Xmrk2*	Tyrosine kinase	*X. helleri*	*Regulatory gene (R)*	Tumour suppressor	Lethality		Wittbrodt et al. (1989); Coyne & Orr (2004); Schartl (2008)
D. simulans	*Maternal hybrid rescue (mhr)*	Possible suppressor of *Zhr* meiotic drive	*D. melanogaster*	*Zygotic hybrid rescue (Zhr)*	Satellite DNA involved in maintaining hetero-chromatic states (probable role in mitosis)	Lethality in F_1 females	Possible genomic conflict	Sawamura et al. (1993a, 1993c); Presgraves (2010)

From Deborah Lloyd, PhD thesis.

Mimulus guttatus (monkeyflower)

Hybrids die as embryos (hybrid inviability)

copper resistance allele (last 200 years)

Macnair, M. R., & Christie, P. (1983). Reproductive isolation as a pleiotropic effect of copper tolerance in *Mimulus guttatus.* Heredity, 50(3), 295-302.

Dodd experiments

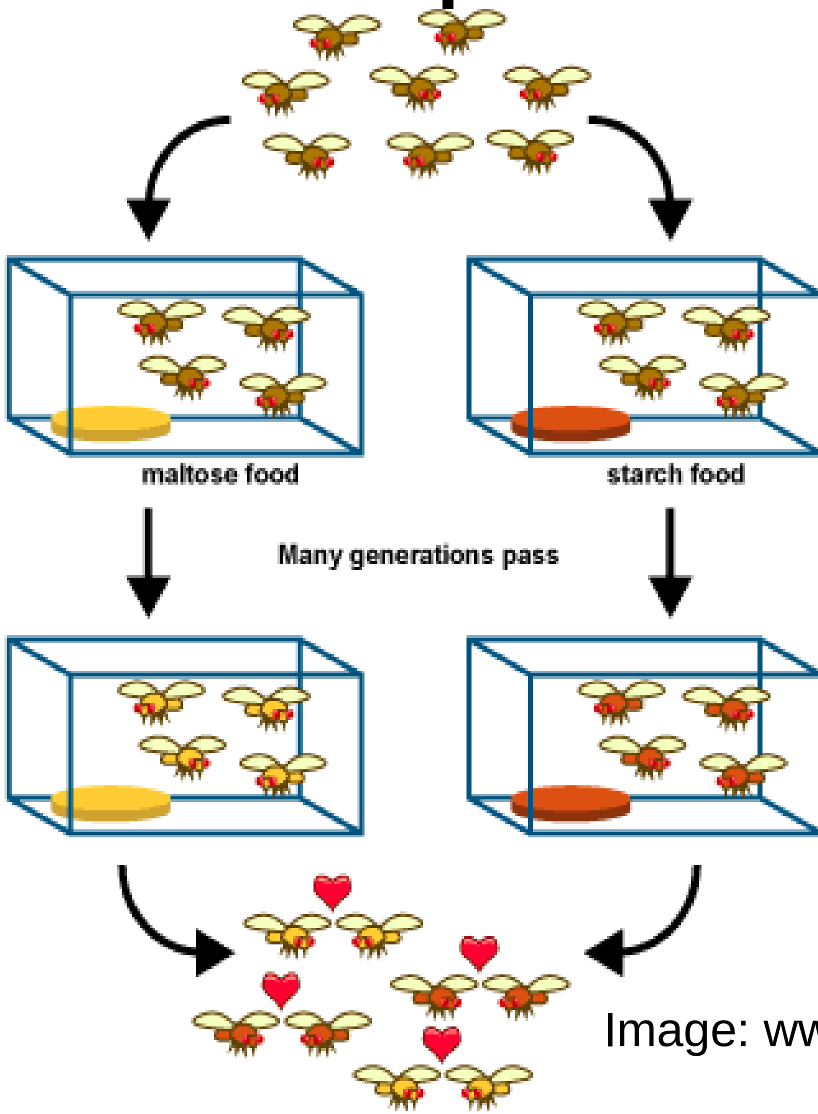


Image: www.evolution.berkeley.edu

Dodd, D.M.B. (1989) "Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*." Evolution 43:1308–1311

Testing assortative mating

- 4 maltose adapted, 4 starch adapted
- 1 year after populations started
- Reared on standard cornmeal-molasses-agar for 1 generation before experiment
- Isolation index I

  = (homogamic matings – heterogamic matings) / total matings
- 11 of 16 combinations: significant positive assortative mating. (I = 0.18 – 0.49)
- No significant assortative mating within maltose or starch (I = -0.06 to 0.14)

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.

Table from Rice and Hostert 1993

Adapted from slide by Loren. H, Riseberg

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

Table from Rice and Hostert 1993

Adapted from slide by Loren. H, Riseberg

No direct selection on mate preferences

How did reproductive isolation evolve in the flies?

Possibilities

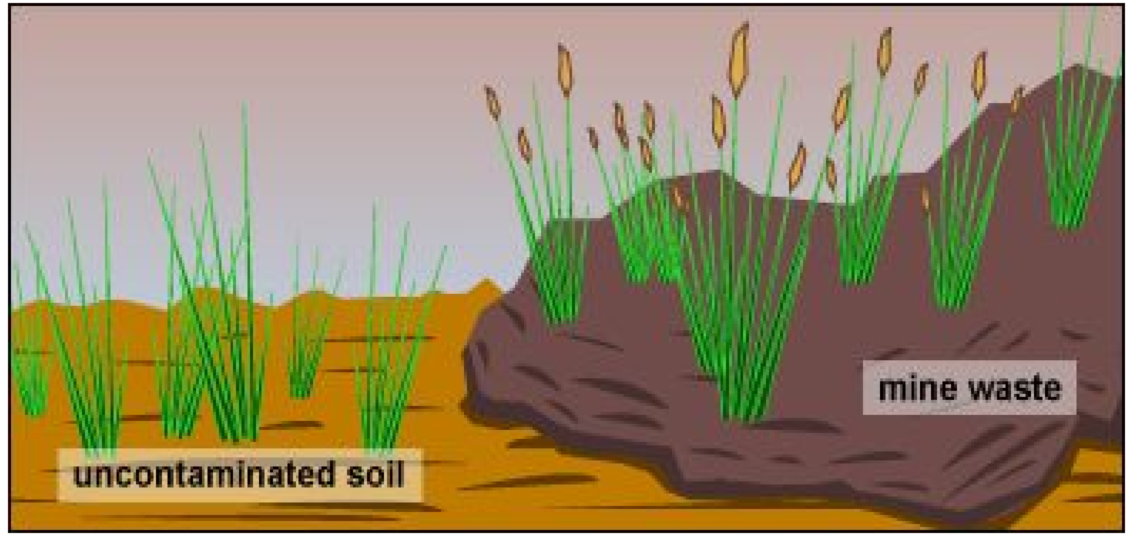
1) Pleiotropic effects
2) Linkage disequilibrium

Ecological speciation

'Evolution of barriers to gene flow between populations as a result of ecologically-based divergent selection'

- ecological source of divergent selection
- form of reproductive isolation
- genetic mechanism linking the two (ie genetic correlation between traits under disruptive selection and assortative mating)
  - Pleiotropy, linkage

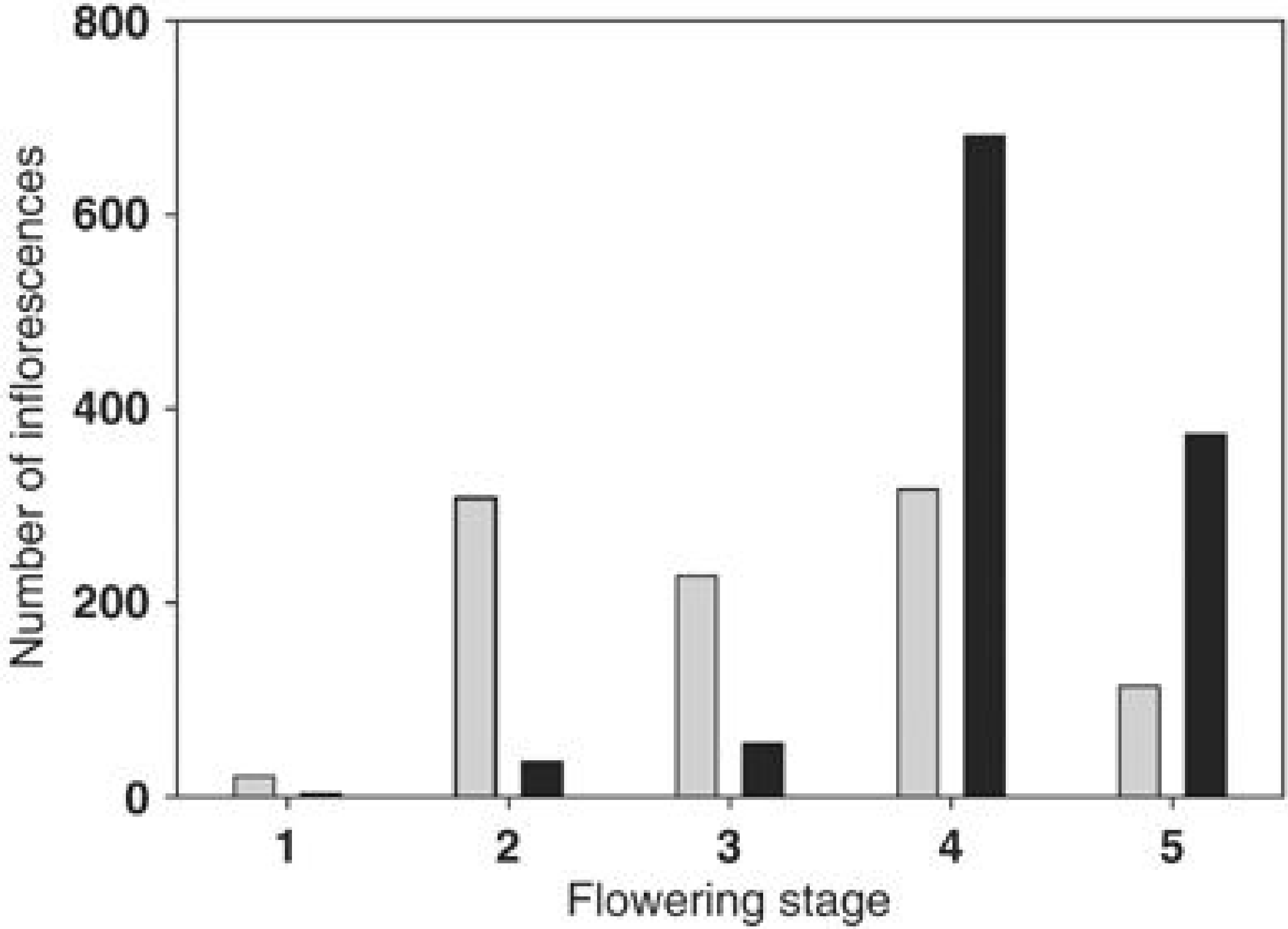
Rundle and Nosil 2005, Ecology Letters 8: 336–352



Figures: www.evolution.berkeley.edu

- Parapatric speciation in *Anthoxanthum odoratum*?
- Adaptation to heavy metal contaminated soils in many locations globally
- Divergence in flowering times (reproductive isolation) between the two populations suggests that speciation is under way

disruptive selection prevents hybridization?



Mine soils (black):
Flowering is earlier (flowers more developed in a point sample)

Antonovics, *Heredity* (2006) **97,** 33–37. doi:10.1038/sj.hdy.6800835

The apple maggot fly, *Rhagoletis pomonella*

Two incipient species specializing on two hosts (apple and hawthorn)?

Chapter 16 Opener Evolutionary Analysis, 4/e

Illustration: Pearson Prentice Inc

Illustration: www.evolution.berkeley.edu

Assortative mating via *pleiotropy*?

- mating on host fruits
- apple race flies earlier than hawthorn race