PLANT OF THE DAY!

Yacón (*Smallanthus sonchifolius*) - relative of sunflower.

Grown in Andes for its crisp, sweet-tasting tuberous roots.

Roots contain inulin, an indigestible sugar, which means that although they have a sweet flavour, the roots contain fewer calories than would be expected.

Photos from : https://en.wikipedia.org/wiki/Yac%C3%B3n




Recombination and Speciation

Questions

- Does speciation occur in the presence of gene flow?
- If so, how?
- How do recombination suppressors such as chromosomal rearrangements become established in natural populations?

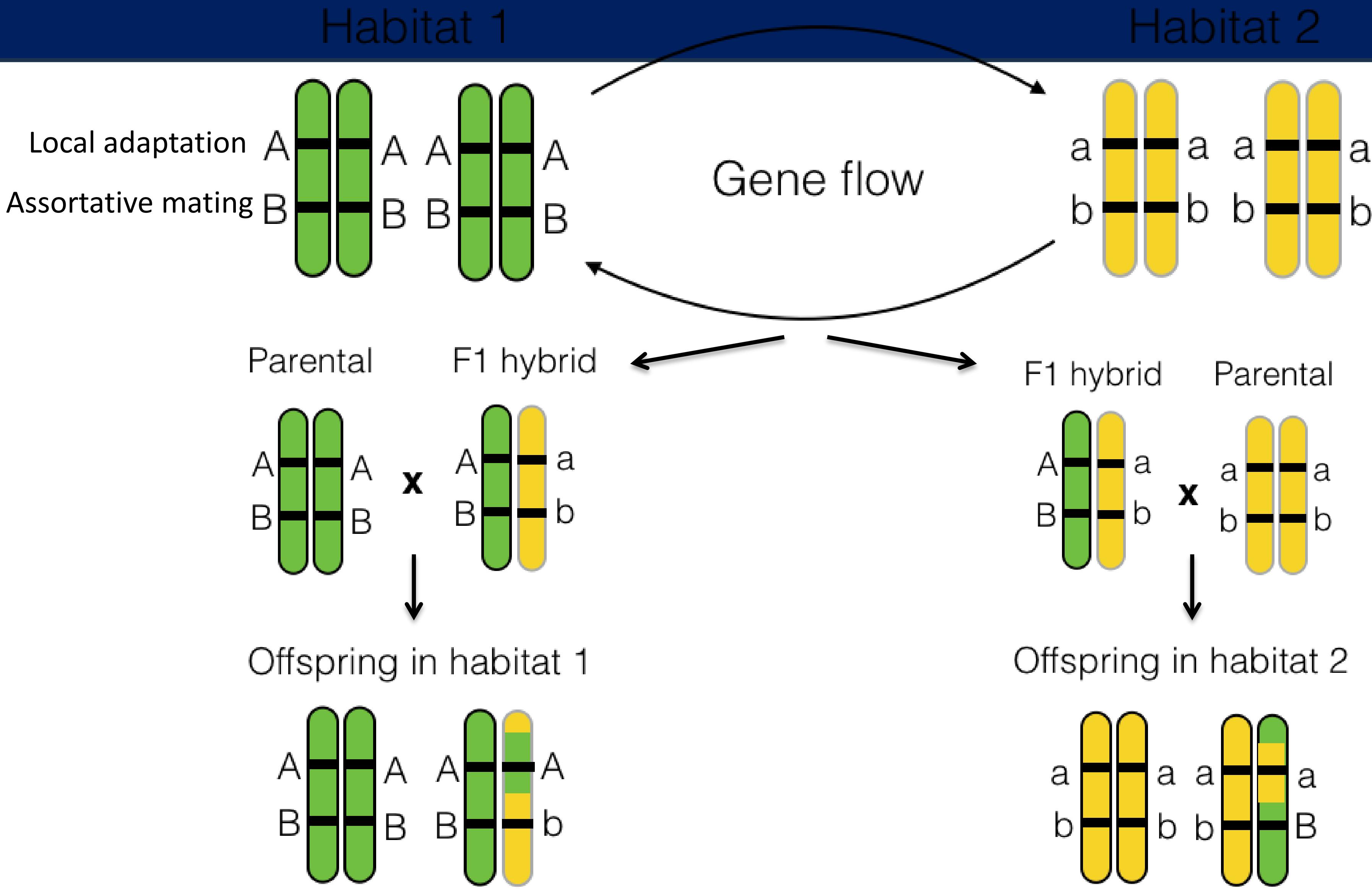
Role of recombination in speciation

- Recombination considered to be main impediment to speciation in sexual species.
- Divergent selection drives populations apart, whereas gene flow and recombination hold them together.
- One Solution: geographic isolation
  – prominent evolutionists have argued that speciation is improbable in the absence of geographic isolation.

Ernst Mayr

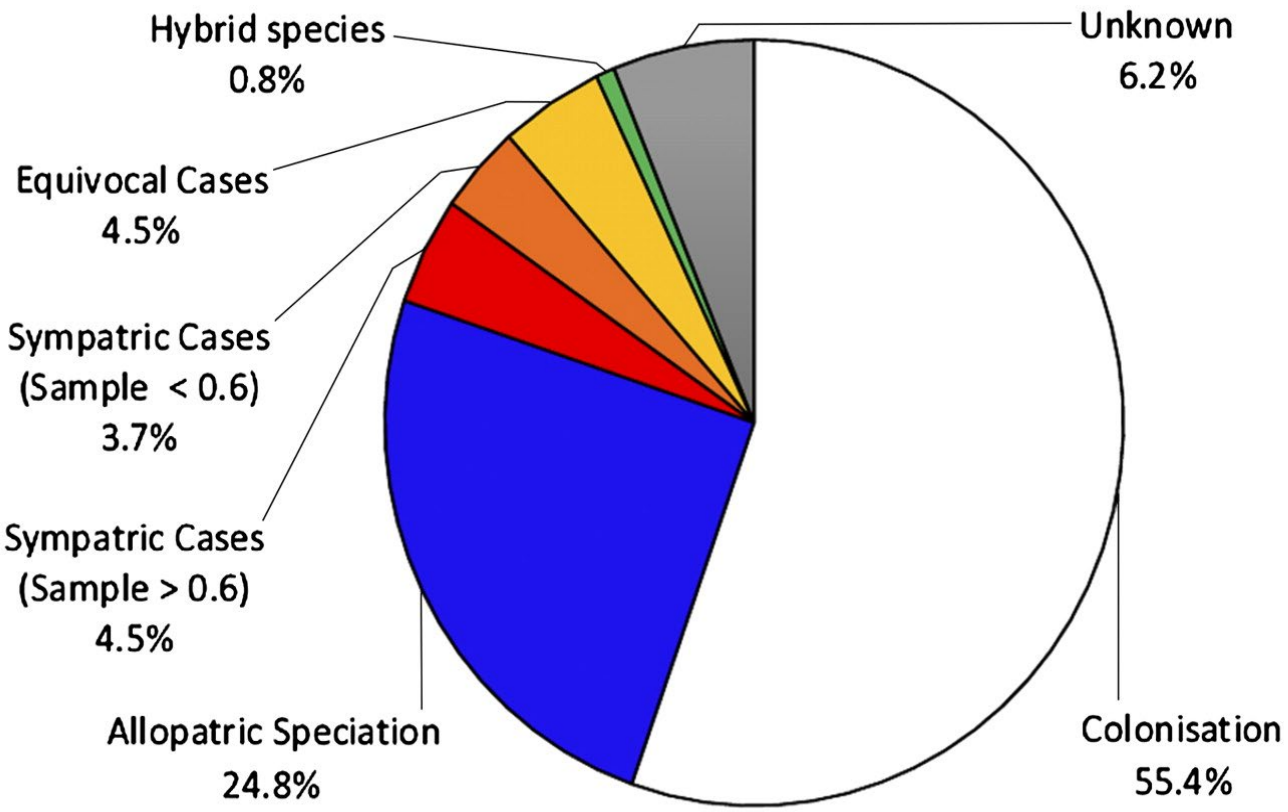
Doug Futuyma

Gene flow and recombination impede speciation



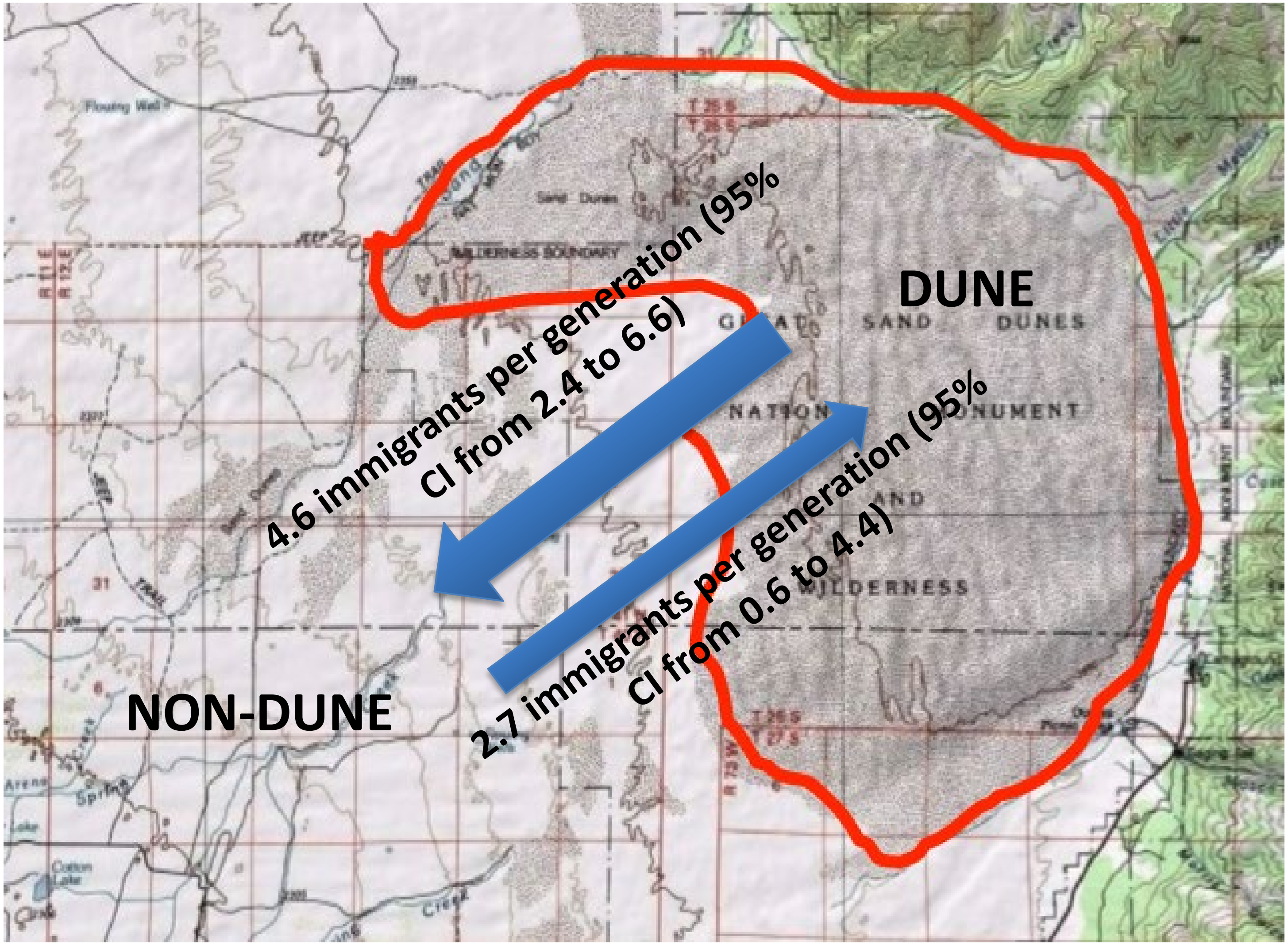
Speciation with Gene Flow is Common

Origins of the Lord Howe Island flora.



Alexander S. T. Papadopulos et al. PNAS 2011;108:32:13188-13193

Speciation with Gene Flow is Common



Total Reproductive Isolation (RI) = 0.993 to 0.996

(Andrew et al. 2013)

Dune and non-dune sunflower ecotypes have strong reproductive barriers despite gene flow

Resolving Antagonism between Selection and Recombination

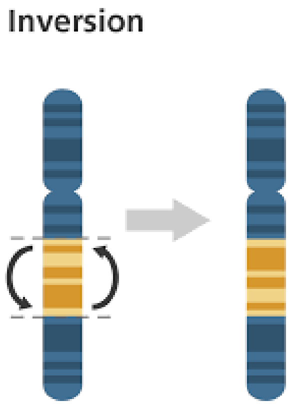
- Magic traits, in which a trait under divergent selection also contributes to reproductive isolation (e.g., soil preference and flowering time in Lord Howe Island Palms).

- Genetic linkage, in which genes/traits under divergent selection are tightly linked to genes/traits causing reproductive isolation.

  – Many examples of speciation with gene flow appear to involve recombination suppressors, such as chromosomal inversions.

Recombination Modifiers

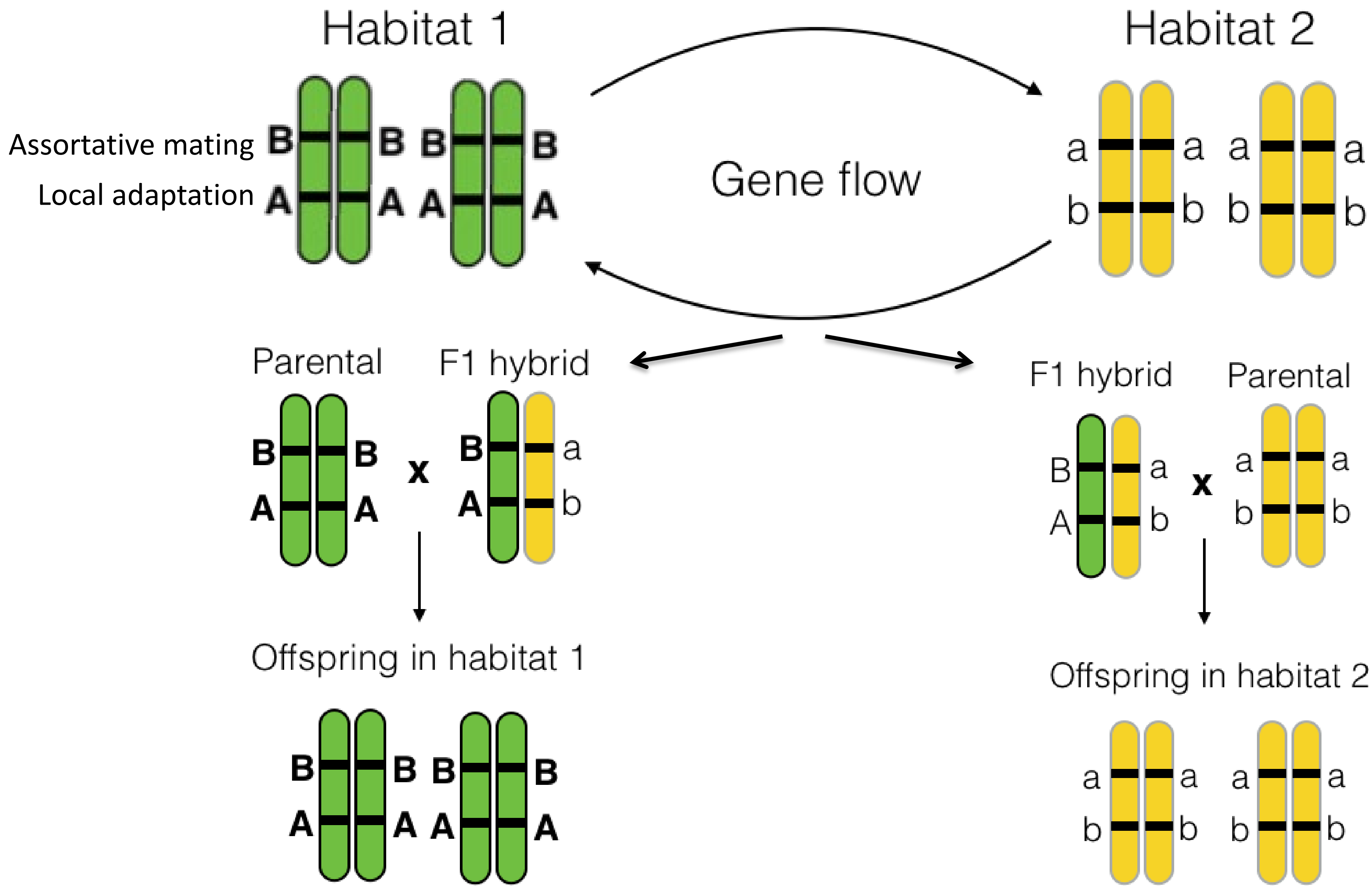
- Chromosomal rearrangements
  - inversions
  - chromosomal fissions and fusions
  - translocations



- Genic modifiers

- Epigenetic changes

Inversion facilitates speciation by impeding recombination



Chromosomal rearrangements may also contribute to speciation by causing hybrid sterility

Differ by a reciprocal translocation and two paracentric Inversions. Hybrids are readily made, but have near-complete sterility.

Types of Rearrangements

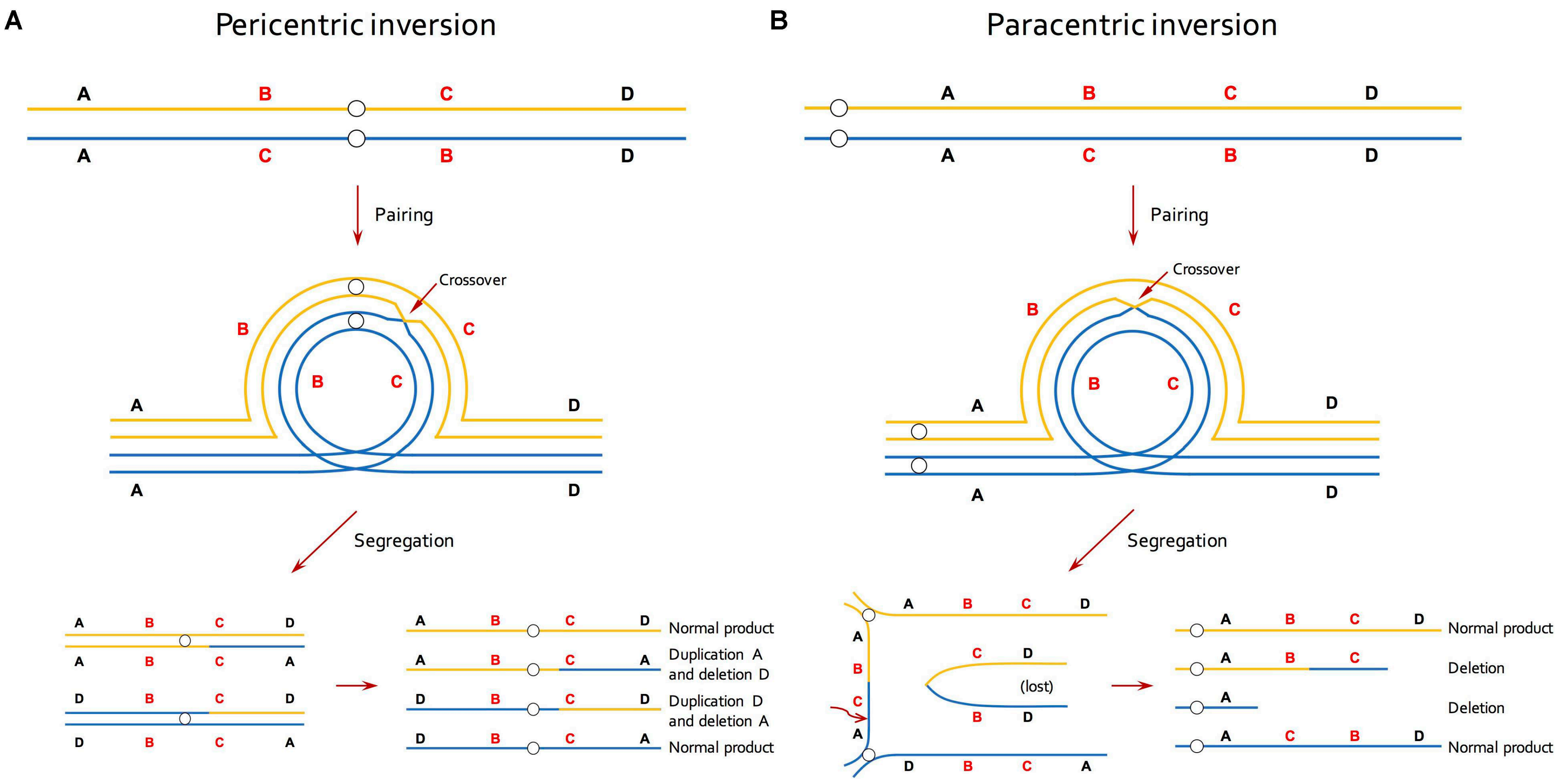
1. Inversions
   - paracentric (centromere outside inversion)
   - pericentric (centromere inside inversion)

A B C D E o F G H → A D C B E o F G H

or

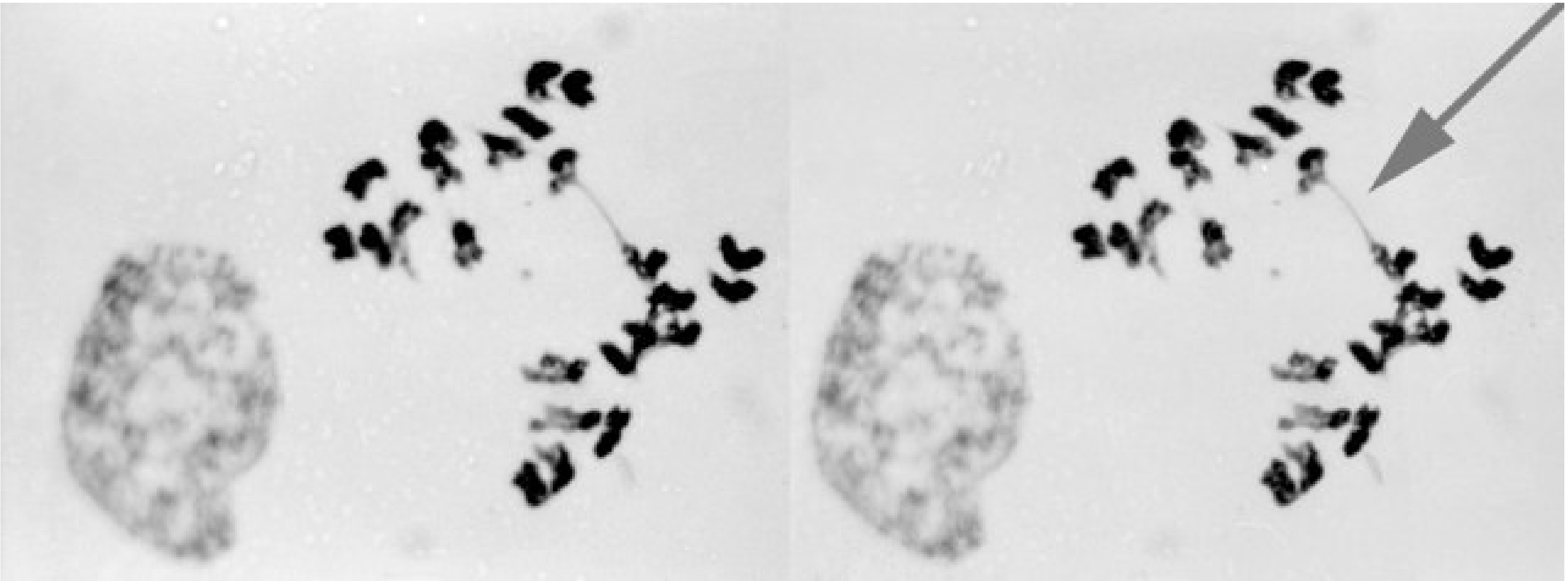
A B C o D E F → A E D o C B F

Predicted meiotic configurations for inversions illustrating effective reduction of recombination



Huang and Rieseberg (2020)

What kind of rearrangement is responsible for meiotic abnormality seen below?



Heslop-Harrison 2013

Types of Rearrangements

1. Inversions (continued)

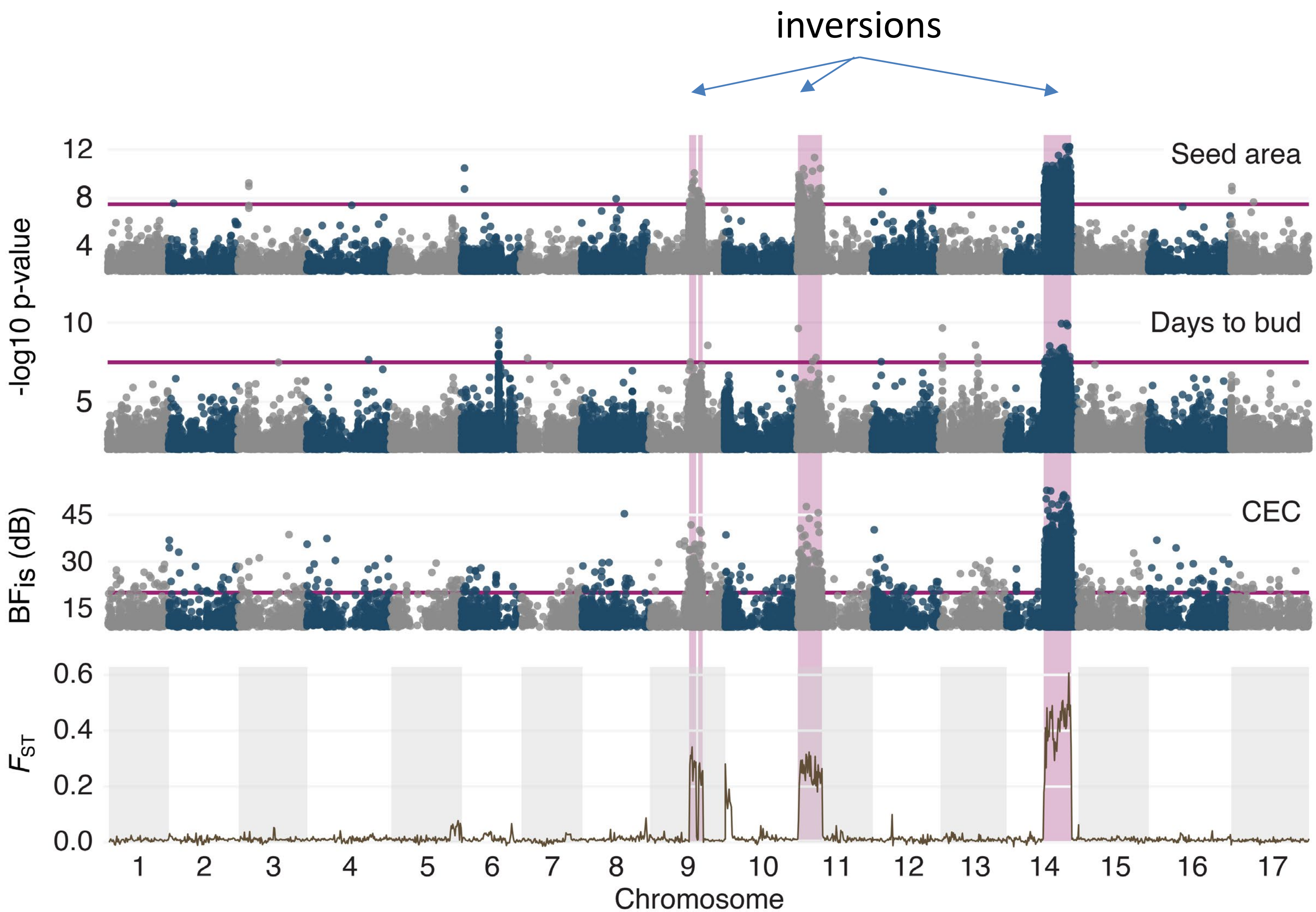
Fertility effects

- up to 50% of gametes can carry duplications or deficiencies
- but most do not affect fertility because inviable gametes do not develop

Recombination effects

- recombination suppressed near chromosomal breakpoints and within inverted region

Example of inversion impacts in dune vs non-dune sunflower ecotypes



Todesco et al. (2020)

Types of Rearrangements

2. Chromosome fusions / fissions

Fertility effects

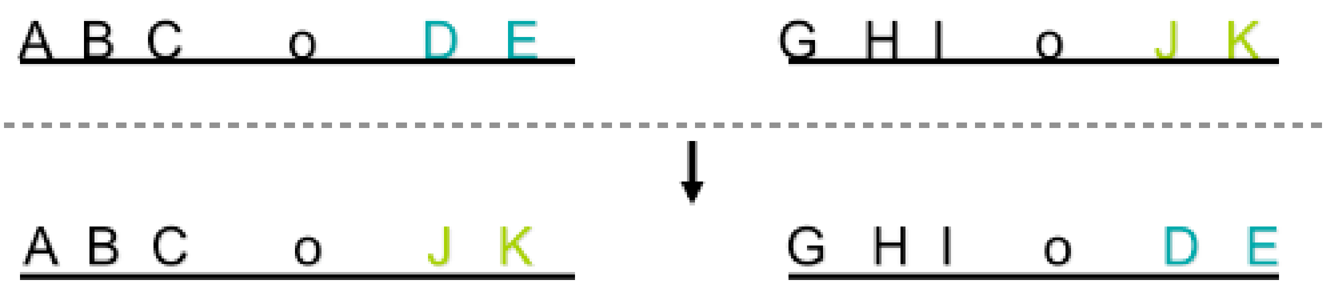
- none to mild

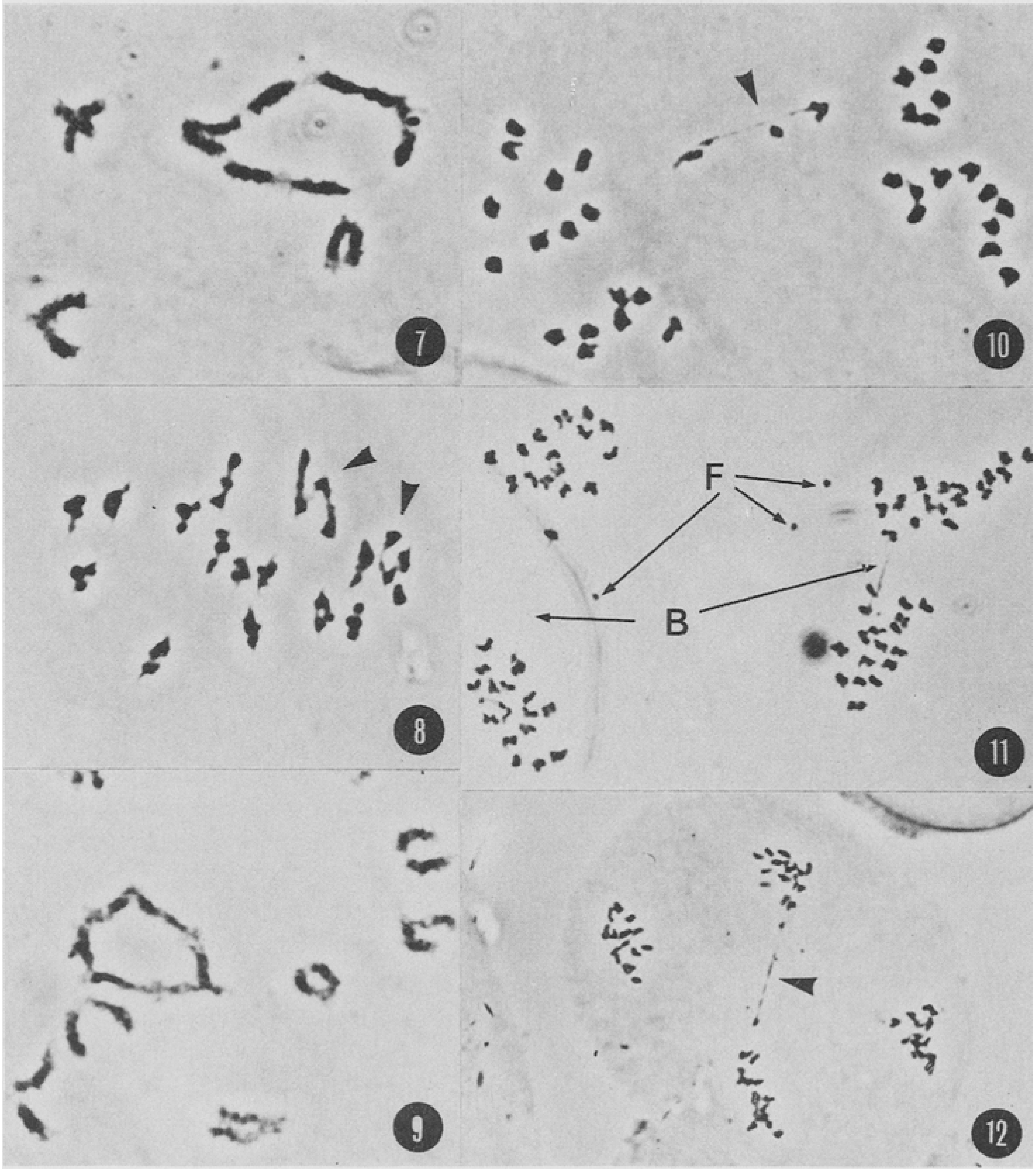
Recombination effects

- Fusions reduce recombination rates, whereas fissions increase them.

Types of Rearrangements

3. Translocations
   - reciprocal
   - nonreciprocal





Meiotic abnormalities in hybrids between *Helianthus* species. First generation hybrids typically exhibit >90% inviable pollen

(Chandler et al. 1986)

Types of Rearrangements

3. Translocations (continued)

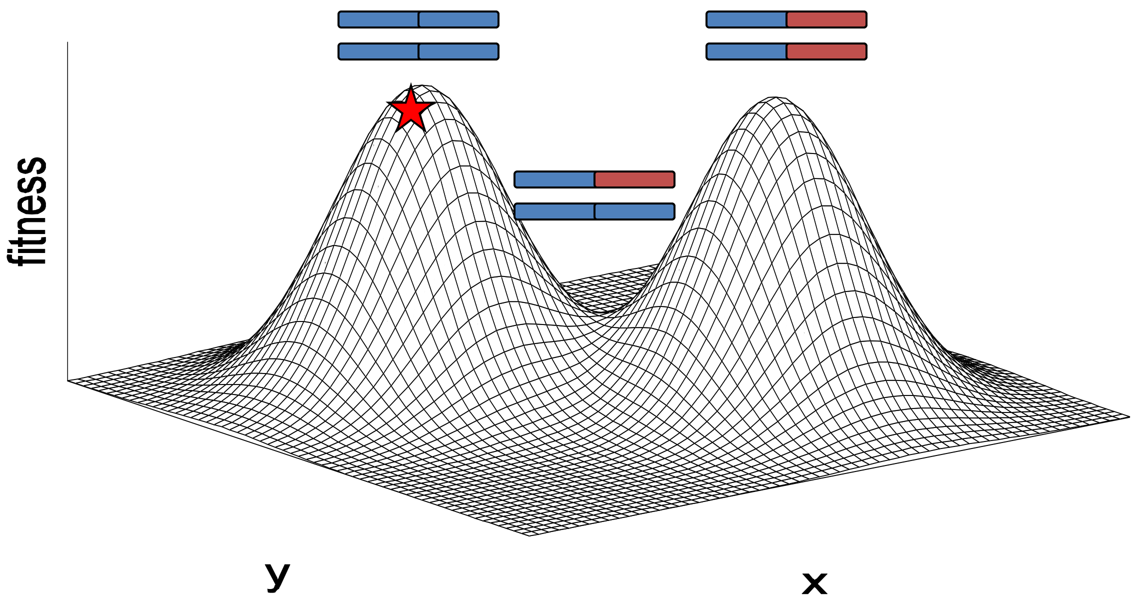
Fertility effects

- up to 2/3 of gametes will carry duplications or deficiencies
- fertility effects slightly mitigated in some plant species by non-random meiotic configurations

Recombination effects

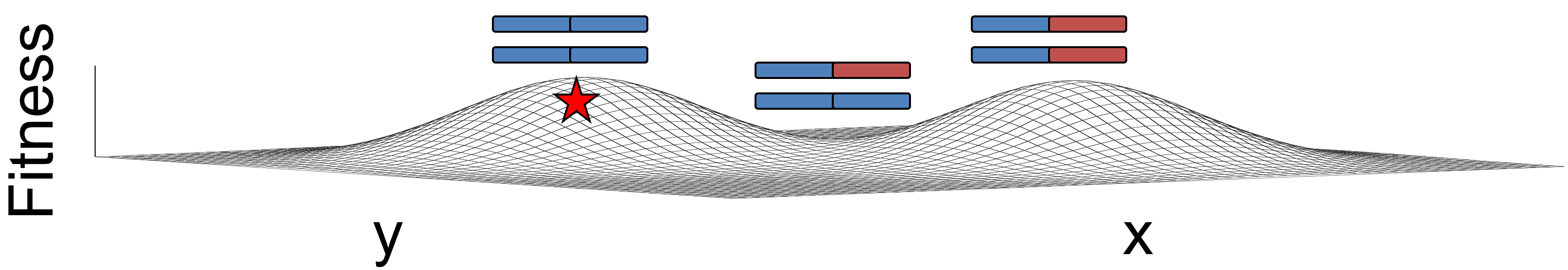
- recombination suppressed near centromere
- considerable recombination in distal regions of chromosomes

How are chromosomal rearrangements established?



-Strong underdominance (heterozygotes < fit than homozygotes)
-Establishment difficult
-Strong reproductive barrier

How are chromosomal rearrangements established?



Weak underdominance
-Establishment easier
-Weak reproductive barrier

How are chromosomal rearrangements established?

paradox: strong underdominance - establishment unlikely
weak underdominance - weak reproductive barrier

1. Drift (small population size, founder effects, kin founding)
   - Unlikely in outcrossers: fastest rates of chromosomal evolution recorded in taxa with very large populations (**Strasburg and Rieseberg 2008**)

2. Selection for rearrangements that limit recombination between co-selected alleles

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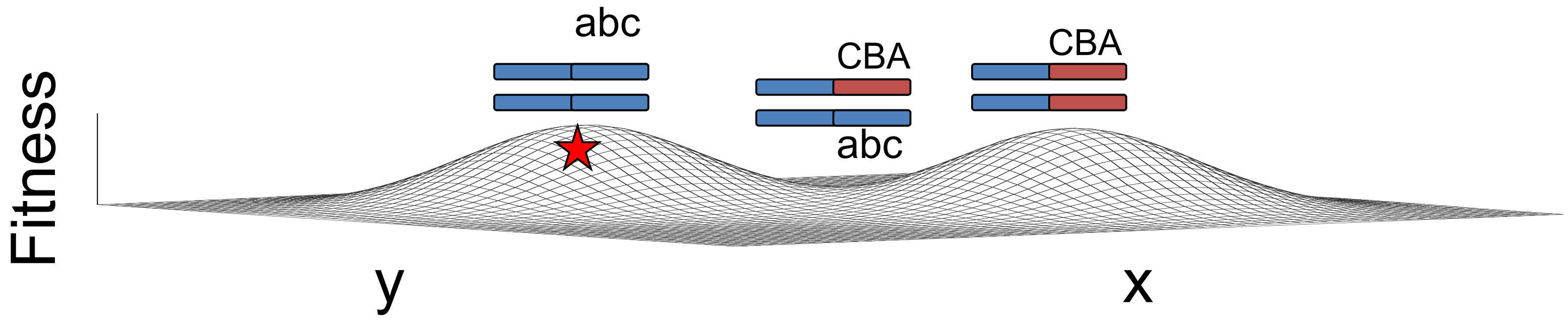
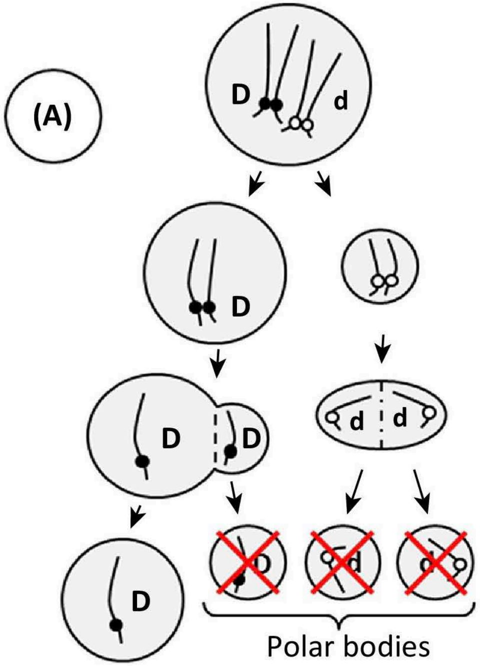


How are chromosomal rearrangements established?

3. Meiotic Drivers - genetic variants that selfishly manipulate the production of gametes to increase their own rate of transmission



Female meiotic drive in *Mimulus* (from Lindholm et al. 2016)

Summary

1. Recombination modifiers such as chromosomal rearrangements facilitate speciation with gene flow by preventing recombination between alleles under divergent natural selection and those causing reproductive isolation.

2. Many inversions are likely established by selection to prevent recombination between locally adapted alleles.

3. Establishment of underdominant translocations probably occurs via female meiotic drive, but evidence for this remains scant.

4. Chromosomal evolution in selfing taxa may be driven (in part) by drift.

Unanswered Questions

- Do genic or epigenetic recombination modifiers contribute importantly to speciation?
- What fraction of the differences mapping to inversions arise before versus after inversion establishment?
- Does female meiotic drive account for the establishment of underdominant rearrangements?