

The Plant of the Day

Philcoxia

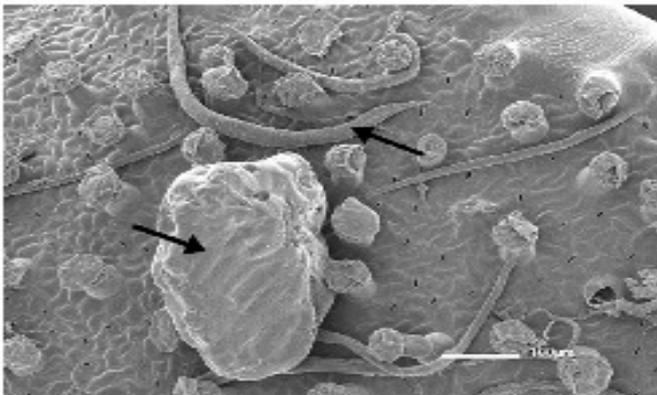
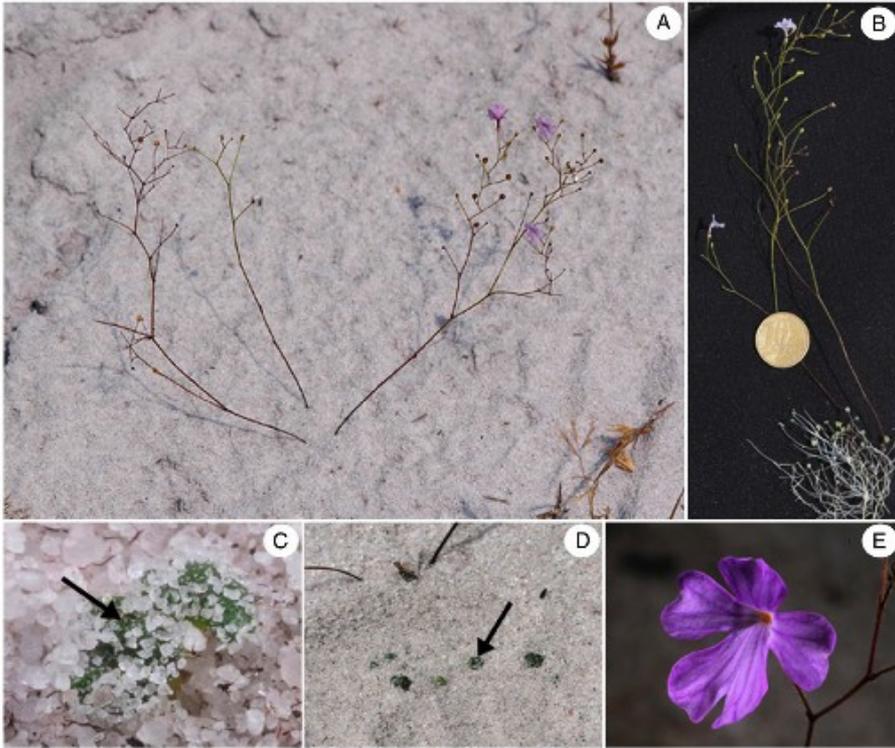
Brazil

Well lit and low-nutrient
habitat

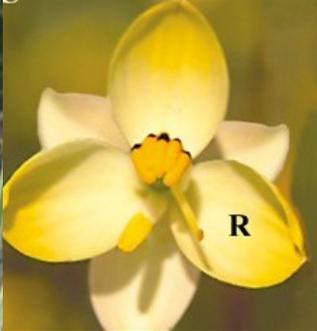
Sticky underground
leaves

Eats worms!

Pereira et al. 2012



The evolution and maintenance of plant sexual diversity





Mating Systems

What are plant mating systems?

What are the major costs and benefits of selfing?

What are the consequences of selfing on genetic variation and why?



Mating Systems

Mating system: the mode of transmission of genes from one generation to the next through sexual reproduction (e.g. maternal selfing rate)

Selfing rate (s): the proportion of seeds that are self fertilized

Outcrossing rate ($t=1-s$): the proportion of seeds that are outcrossed

The outcrossing rate of a population can be estimated from genotyping seed families



Sexual Systems

Sexual system: the particular deployment of sexual structures within and among plants and the physiological mechanisms governing mating



Why do we care about the evolution of reproductive traits?

They influence their own transmission and the transmission of all other genes

Shift in mating system can strongly influence genetic variation, speciation and evolutionary diversification

It is just really cool



The evolution of self-fertilization

20% of angiosperm species have evolved a predominantly selfing strategy

What is a major cost of self fertilization?

-inbreeding depression

What is inbreeding depression?

-inbreeding depression: the reduction in viability and fertility of inbred offspring compared with outbred offspring.

$$\delta = 1 - w_s / w_o$$

What causes inbreeding depression?

-homozygosity of recessive deleterious alleles

-overdominance (heterozygote advantage)

How would you assess inbreeding depression?

Greenhouse/field experiment

- Self and outcross plants
- Measure progeny fitness
- Calculate inbreeding depression

$$\delta = 1 - w_s / w_o$$



How would you assess inbreeding depression?

Using genetic markers compare inbreeding coefficient of parents and progeny (Ritland 1990)

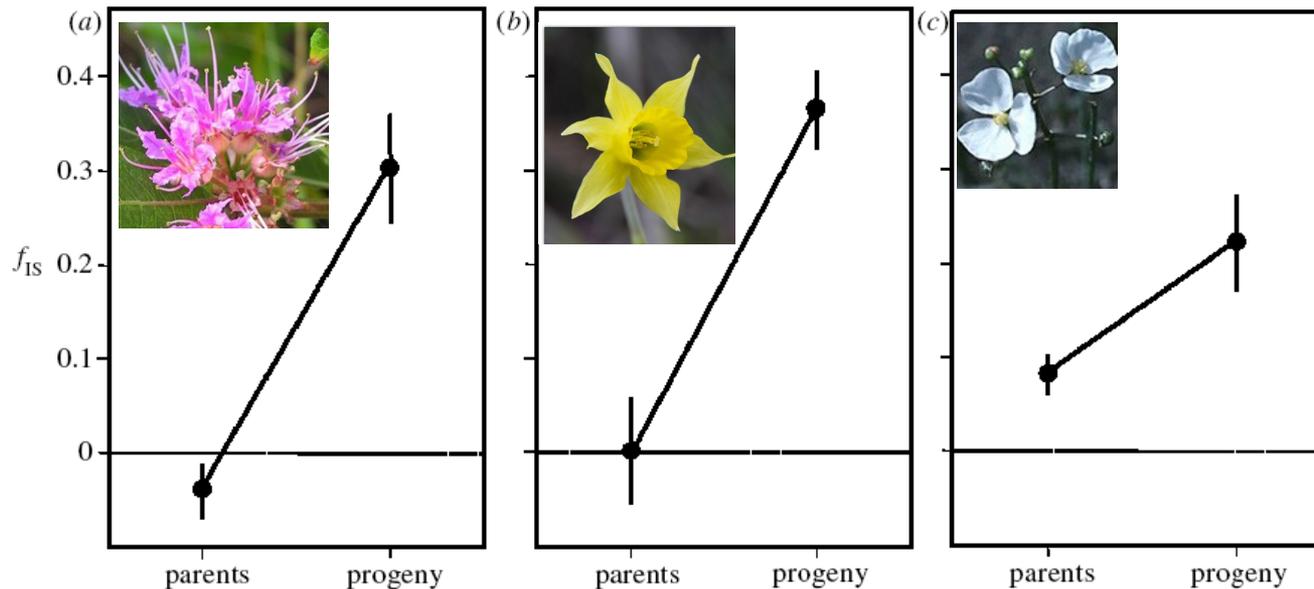


Figure 2. Selection against selfed progeny in populations of three animal-pollinated plant species with mixed mating systems. In each species there are significant changes in the mean inbreeding coefficient between parents and progeny estimated using allozyme markers. (a) *Tristylus Decodon verticillatus*: 10 populations, data in Eckert & Barrett (1994); (b) sexually monomorphic *Narcissus longispathus*: six populations, data in Barrett *et al.* (2003); and (c) monoecious *Sagittaria latifolia*: six populations, data in Dorken *et al.* (2002). Standard errors of the parental generation were estimated by bootstrapping data from Ritland's multilocus outcrossing rate program and those for progeny were the sum of the standard errors from estimates of selfing rates and parental F (see Ritland 1990).



Self fertilization

Why do so many species self despite the cost of inbreeding depression?



Self fertilization

What is a major benefit of selfing?

Transmission advantage (Fisher)

	pollen parent	seed parent	total
outcrossing	1	1	2
selfing	(1 out+1self=2)	1	3

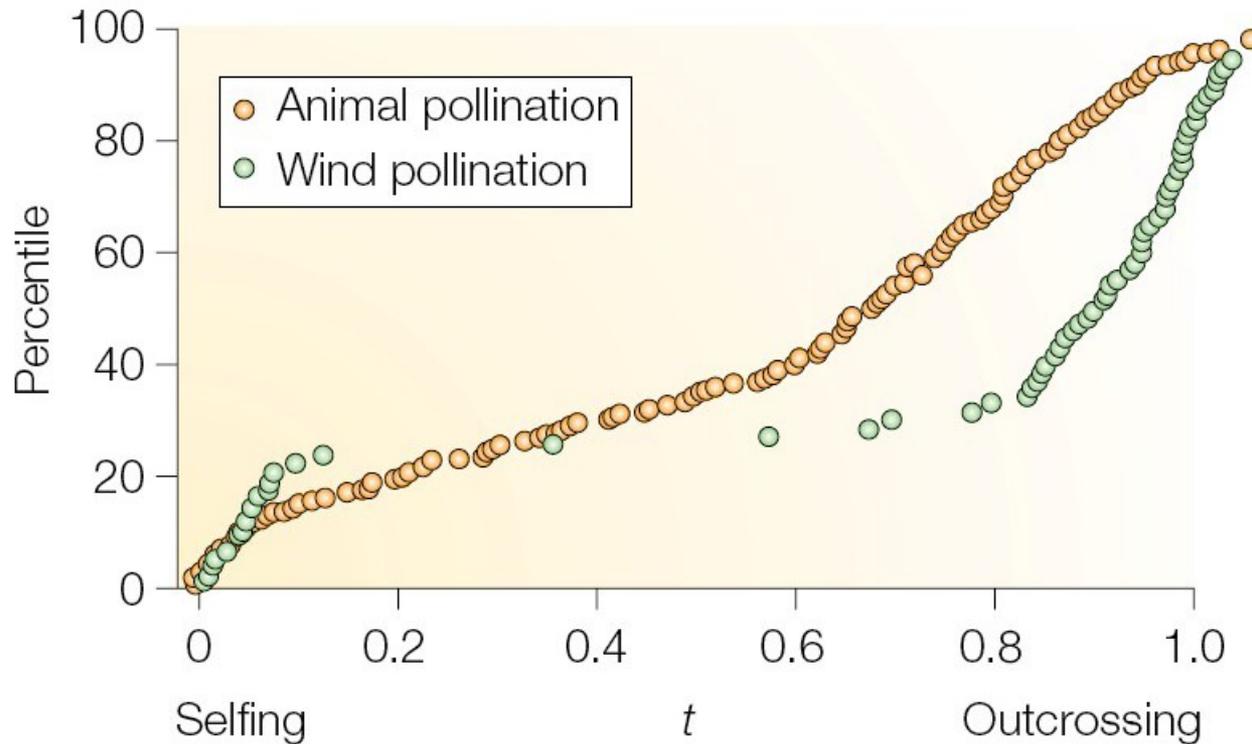
The transmission advantage lost if $\delta > 0.5$

Early models on the evolution of selfing predicted that only fully outcrossing or selfing would be evolutionary stable strategies

The evolution of self-fertilization



THINK – PAIR - SHARE



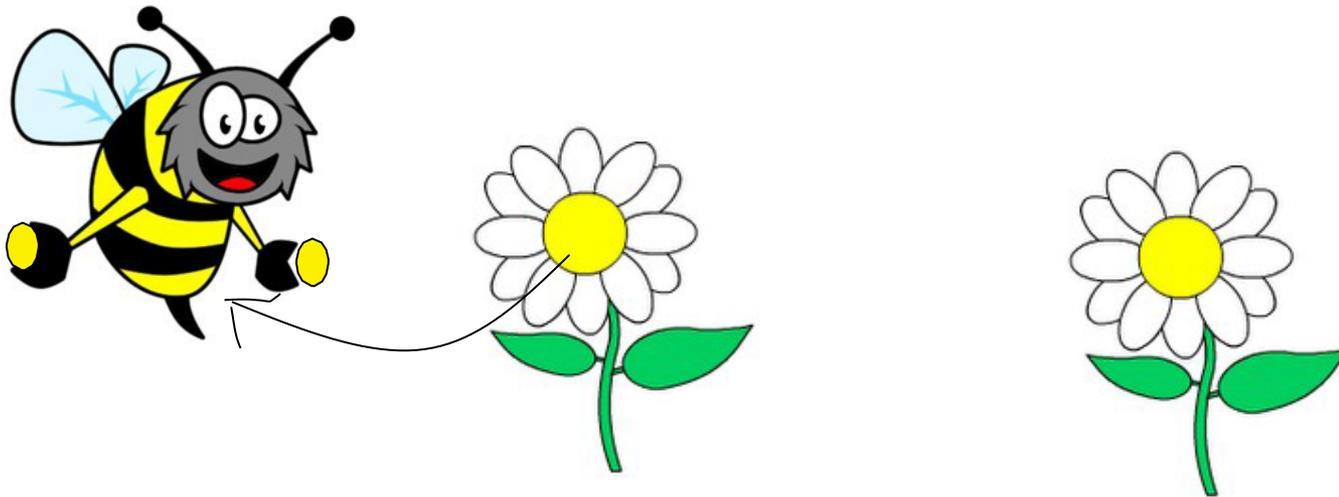
Why do so many species have a mixed mating strategy?



Self fertilization: pollen discounting

Additional costs of selfing?

i. pollen discounting: the loss in outcrossed siring success as a result of self-pollination



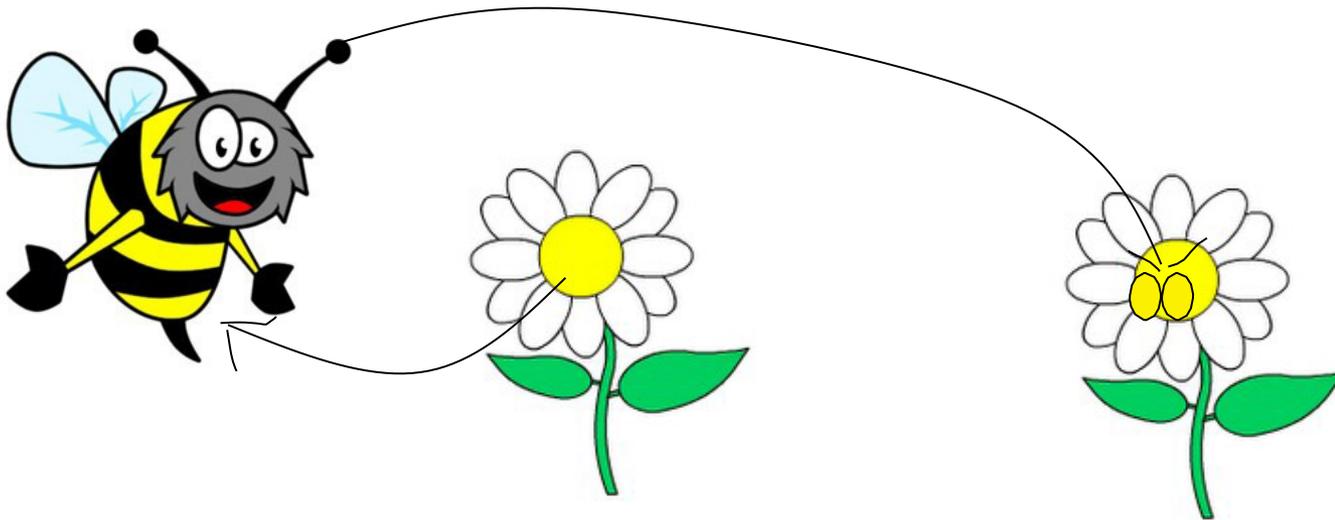
Geitonogamy: between flower self-pollination



Self fertilization: pollen discounting

Additional costs of selfing?

i. pollen discounting: the loss in outcrossed siring success as a result of self-pollination



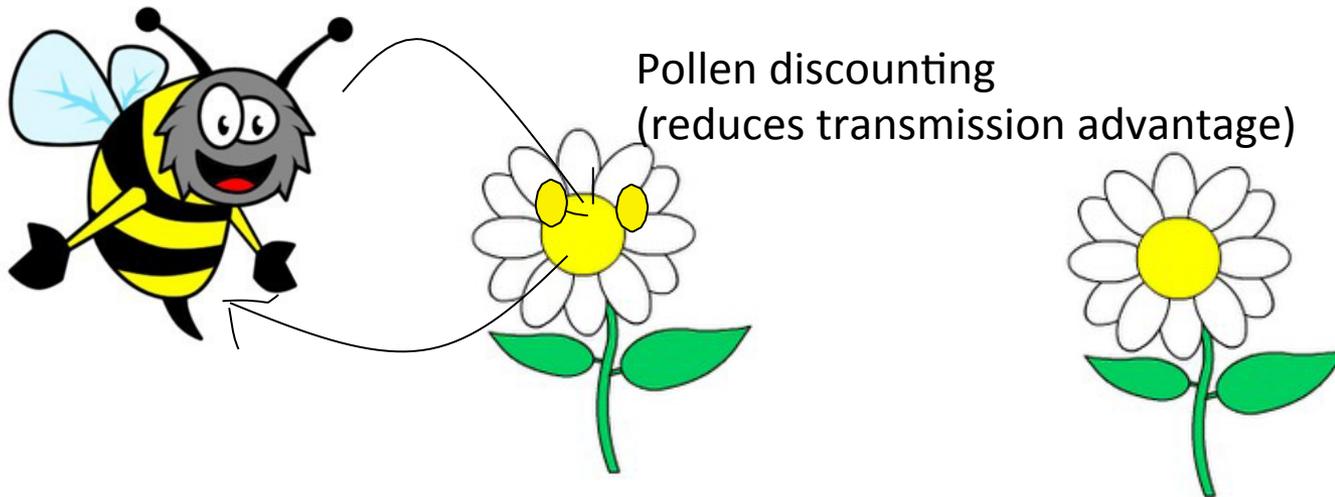
Geitonogamy: between flower self-pollination



Self fertilization: pollen discounting

Additional costs of selfing?

ii. pollen discounting: the loss in outcrossed siring success as a result of self-pollination

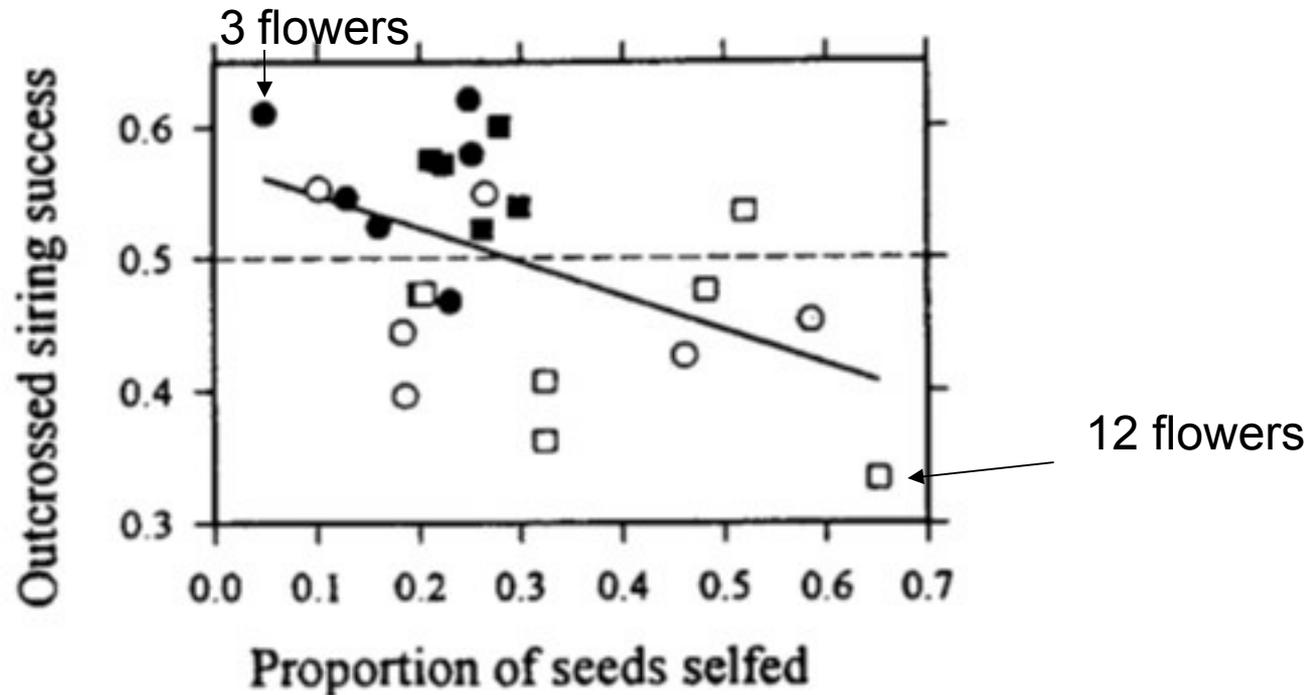


Geitonogamy: between flower self-pollination

Pollen discounting in *Eichhornia paniculata*



Spencer Barrett



Harder and Barrett 1995 Nature

Negative association between outcrossed siring success and selfing rate provides evidence for pollen discounting

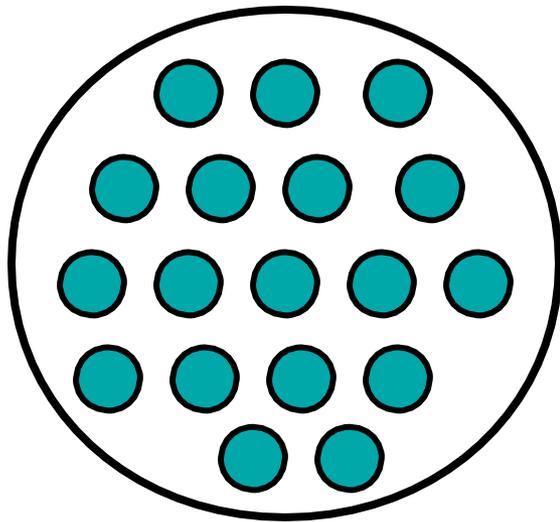
The more flowers/inflorescence the more pollen discounting



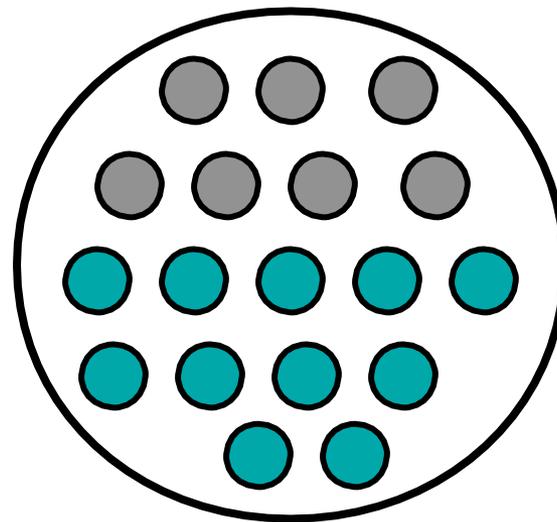
Self fertilization: seed discounting

Additional costs of selfing?

iii. seed discounting: the formation of self-fertilized seeds from ovules that, if they had not been self-fertilized, would have been cross-fertilized



Outcrossed Seed number = 18



Outcrossed Seed number = 11

If selfing had not happened there would have been 7 more outcrossed seeds



Self fertilization

Additional benefits of selfing?

ii. Reproductive assurance: assured reproduction through selfing when conditions for outcrossing are not favourable (absence of mates or pollinators)



Who can I mate with?
I guess I will mate with myself...

iii. Reduce gene flow and facilitate local adaptation (i.e., reduce outbreeding depression)



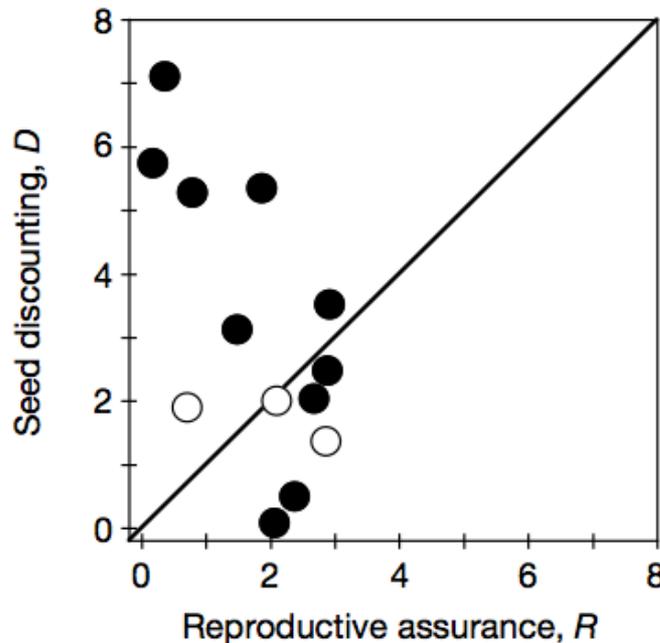
Seed discounting in *Aquilegia canadensis*

Test of reproductive assurance hypothesis:

Selfing boosts seed set by 14%

Selfing rates very high (circa 75%)

High inbreeding depression, seed discounting = costly

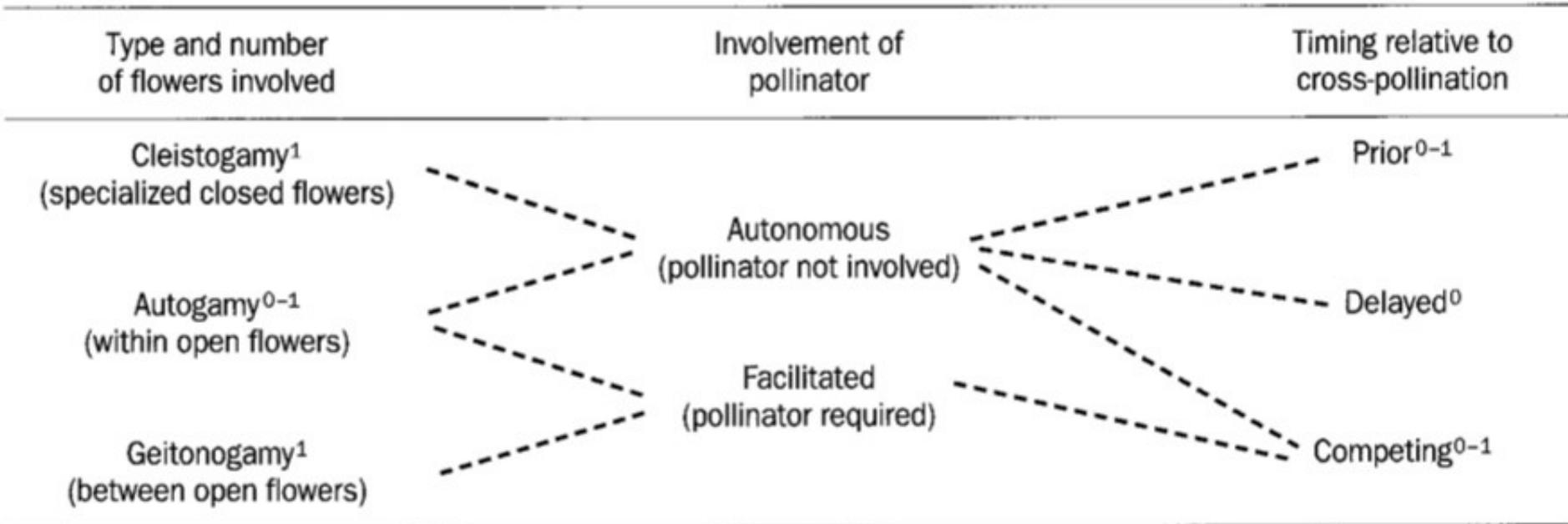


Why does this species self at such high rates?

Herlihy and Eckert 2002 Nature



Modes of self pollination



From Harder and Barrett 1996 TREE

Which type of selfing should be favored when there are no mates?

Which type of selfing should be favored when there are few pollinators?

Mating system is correlated with morphological and life history traits



What changes in floral morphology are correlated with selfing?

Eichhornia paniculata



Mimulus guttatus



M. nasutus



Amsinckia furcata *A. vernicosa*



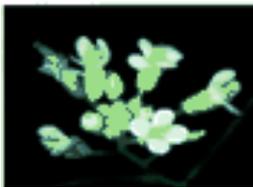
Selfing

- Smaller flowers
- Less attractive
- Fewer rewards
- Lower pollen production
- Smaller stigma-anther distance

Arabisopsis lyrata - SI



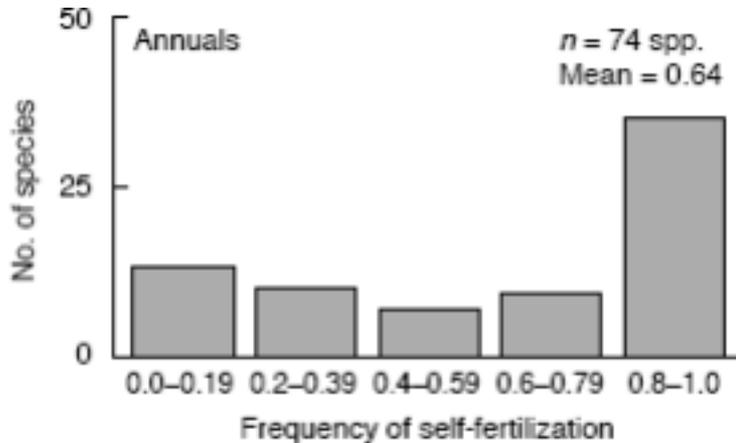
Arabisopsis thaliana - SC





Mating system is correlated with morphological and life history traits

What life history traits are associated with the evolution of selfing?

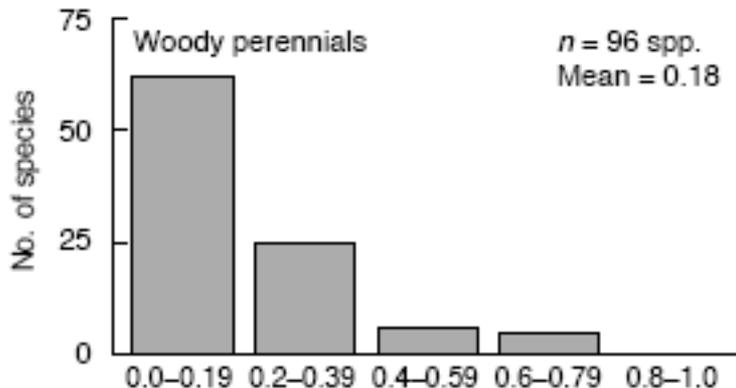


Annuals tend to be selfers

Why?

Reproductive assurance

Perennials tend to be outcrossers

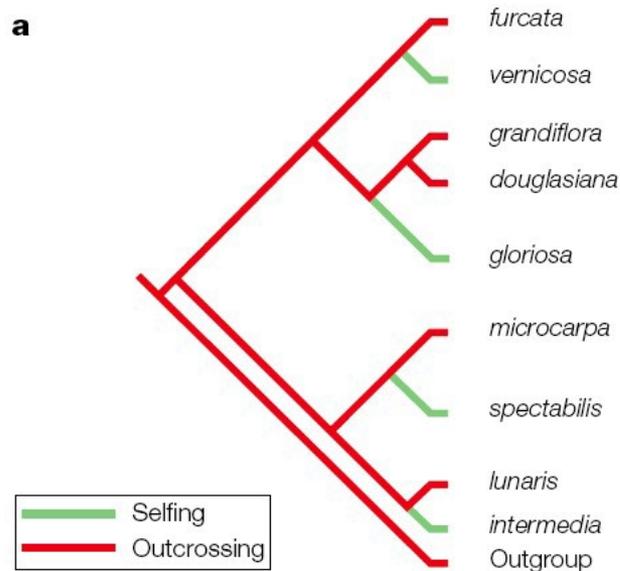


Why?

-costs to future survival and reproduction of reproductive assurance



Evolutionary transitions from outcrossing to selfing



outcrosser

selfer

Multiple origins of self-fertilization

The evolution of selfing is thought to be a unidirectional shift
Why?

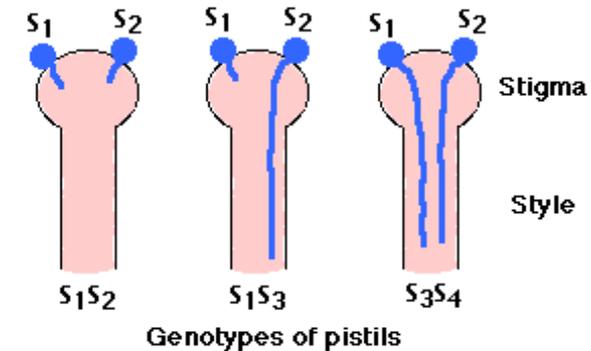


Homomorphic self incompatibility

Two main types of homomorphic incompatibility (up to 50% of angiosperms)

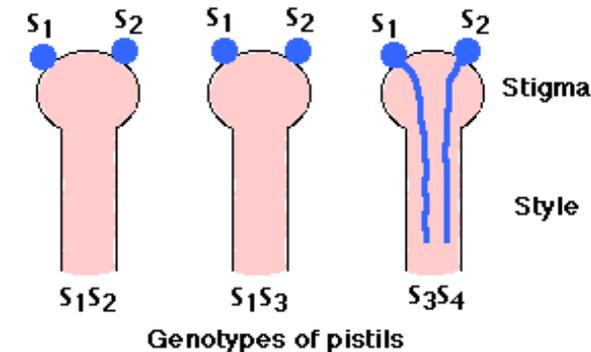
-gametophytic: incompatibility phenotype is determined by its haploid genotype
 e.g. S1 or S2 can not fertilize S1S2 plants but S3 pollen can

All pollen grains produced by an S₁S₂ plant



-sporophytic: incompatibility governed by the genotype of the pollen producing parent
 e.g. any pollen from an S1S2 plant can not fertilize an S1_ or S2_ plant

All pollen grains produced by an S₁S₂ plant



Homomorphic self incompatibility



Maintained by negative frequency dependent selection (balancing selection):

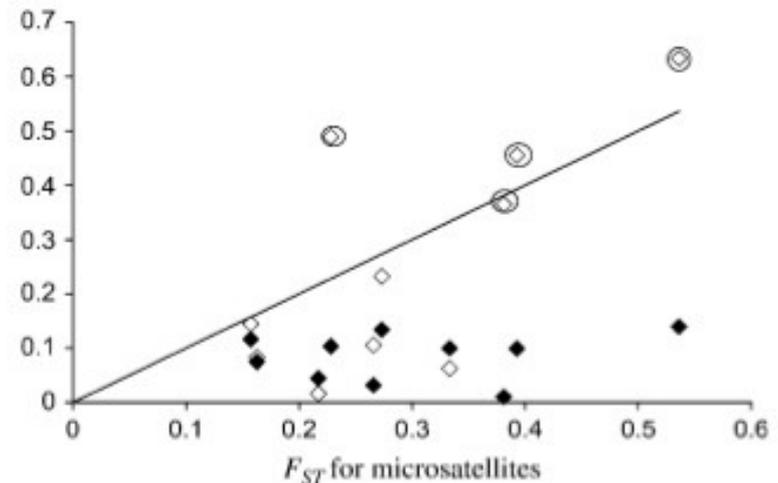
Rare SI types have a fitness advantage as they can mate with all other plants in the population

Many S alleles

Low F_{ST} compared to neutral loci (higher effective migration due to balancing selection)

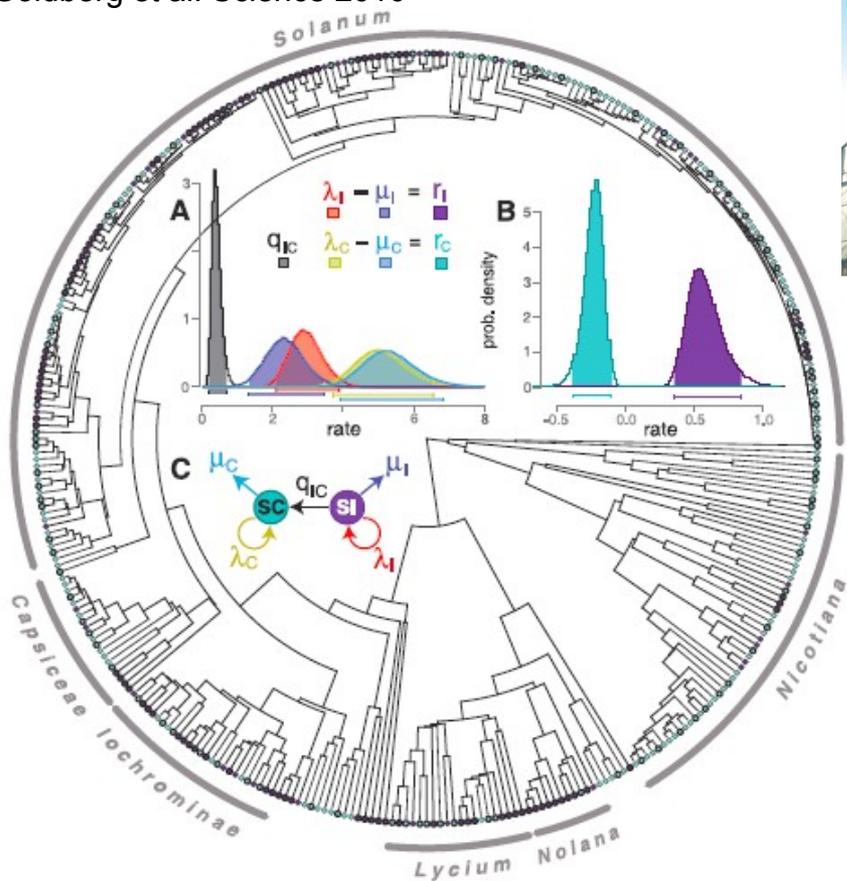
Brassica

F_{ST} at the S locus



Is selfing a dead end? Long term costs and species selection

Goldberg et al. Science 2010



Boris Igic



Emma Goldberg



Solanum dulcamara

SC species have high speciation rates but even higher extinction rates

SI species have lower speciation rates but even lower extinction rates

Long term costs to selfing?

Fig. 1. Maximum likelihood tree of phylogenetic relationships among 356 species of Solanaceae. Higher ranks are indicated around the perimeter of the tree. Purple and turquoise tip colors denote SI and SC extant species, respectively. The root age is 36 million years. Inset panels display posterior probability distributions and 95% credibility intervals of reconstructed rates of character evolution (the time unit is millions of years). (A) BiSSE estimates of transition, speciation, and extinction parameters ($q_{IC} \ll \mu_I < \lambda_I \ll \lambda_C < \mu_C$). (B) Net diversification rate—the difference between speciation and extinction rates—associated with each state. (C) Schematic summary of estimated rate parameters. For methods, species names, character states, and further results, see (19).



What are the consequences of selfing for genetic variation?

Selection and drift reduce genetic variation in inbreeding vs. outbreeding populations

Selfing and drift

- Completely selfing populations are expected to have a two-fold reduction in effective population size (N_e)
- Therefore drift is stronger in selfing vs outcrossing populations
- Reduces ability of selection to purge deleterious alleles or fix advantageous ones

Selfing demography and drift

- The capacity for uniparental reproduction gives selfers high colonizing ability
- Bottlenecks and lower census population size can further reduce N_e (thereby increasing drift)



What are the consequences of selfing for genetic variation?

definitions

Selective sweep: an advantageous variant rises to fixation eliminating polymorphism at this locus

Genetic hitchhiking: when an allele increases in frequency because it is linked to a locus under positive selection

Background selection: negative selection reduces variation at linked neutral loci



What are the consequences of selfing for genetic variation?

Selection

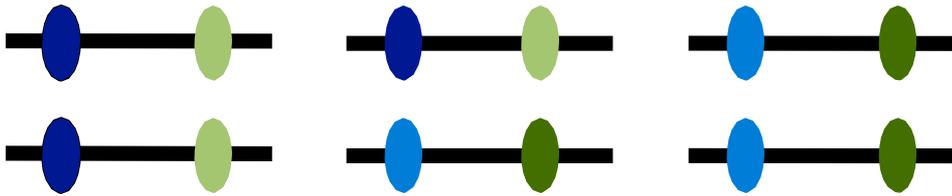
- Reduced effective recombination in selfers (due to increased homozygosity)



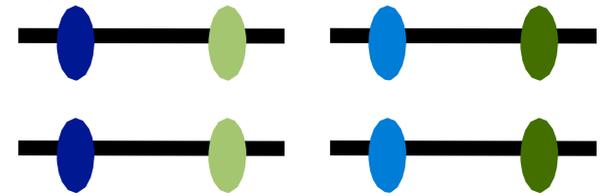
What are the consequences of selfing for genetic variation?

Reduced effective recombination

Outcrossing



Selfing

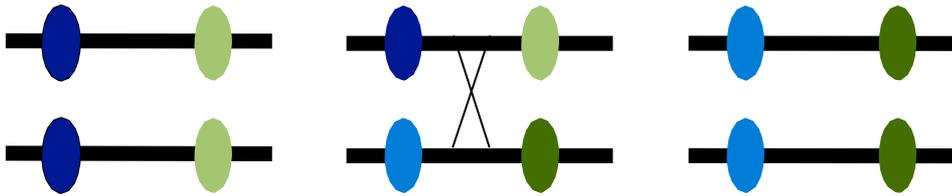




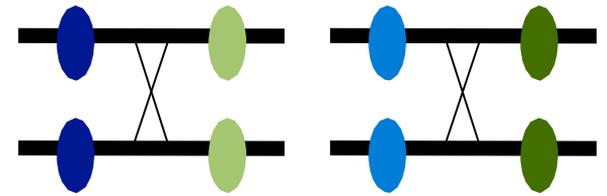
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Selfing

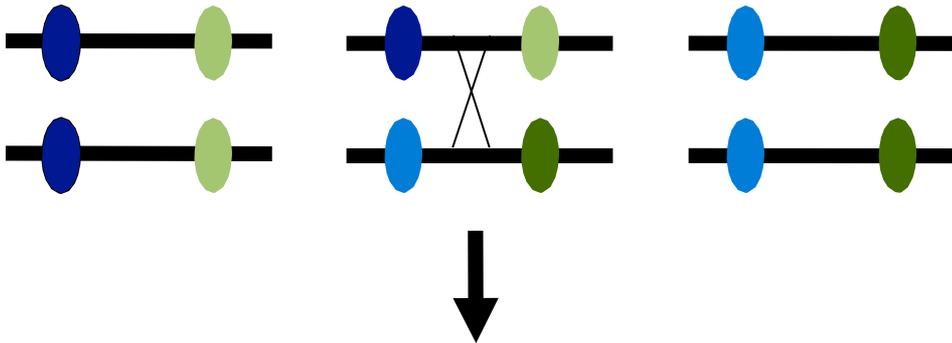




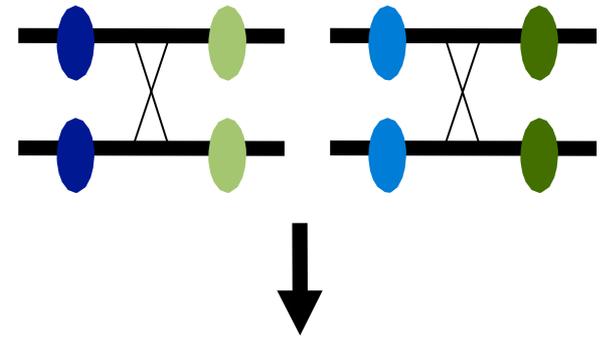
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Selfing

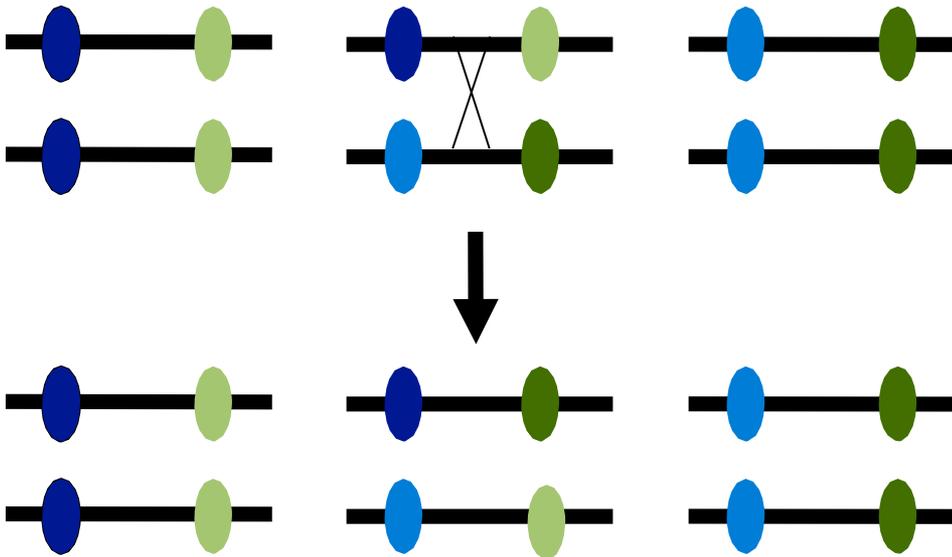




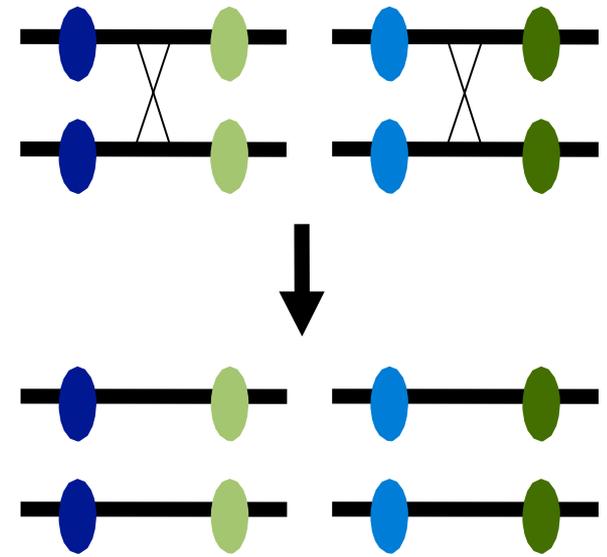
What are the consequences of selfing for genetic variation?

Reduced effective recombination

Outcrossing



Selfing





What are the consequences of selfing for genetic variation?

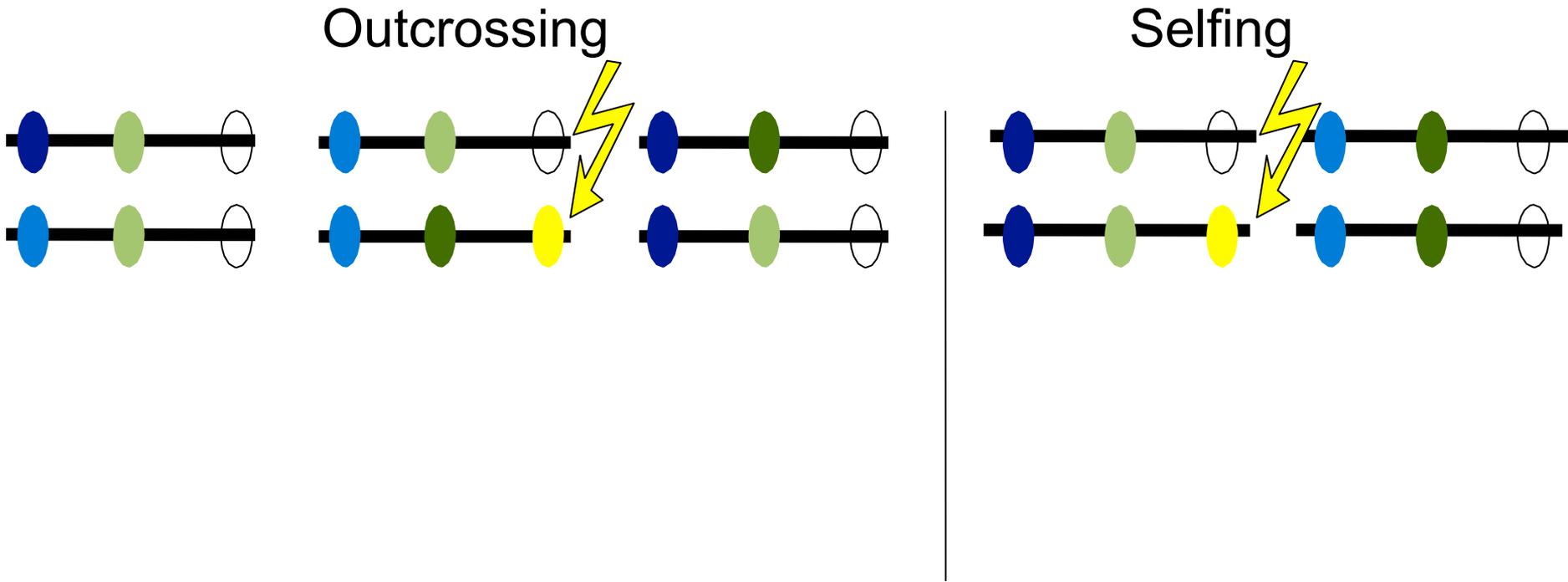
Selection

- Reduced effective recombination in selfers (due to increased homozygosity)
- Positive selection (selective sweep) or selection against deleterious mutations (background selection) reduces variation at linked loci



What are the consequences of selfing for genetic variation?

Selective sweeps and hitchhiking

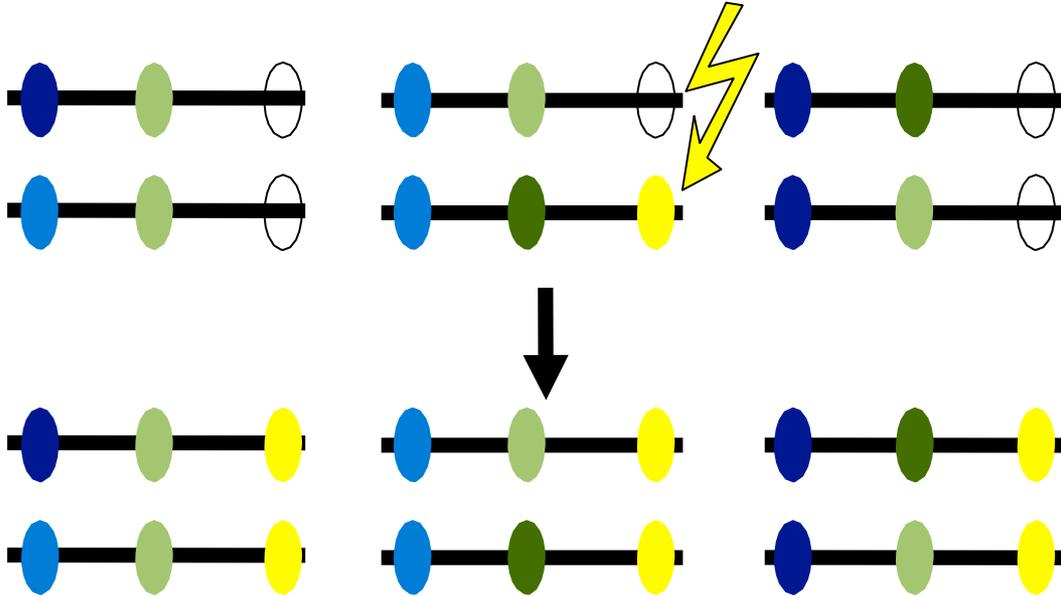




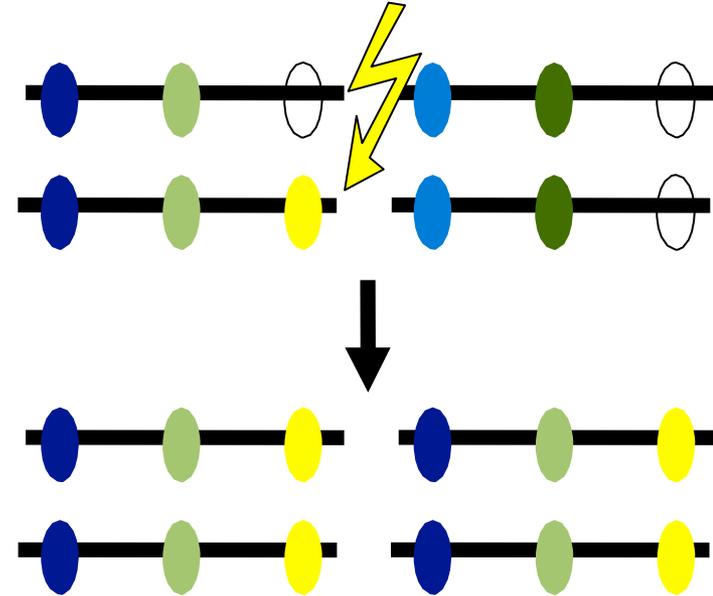
What are the consequences of selfing for genetic variation?

Selective sweeps and hitchhiking

Outcrossing



Selfing



reduced neutral diversity



What are the consequences of selfing for genetic variation?

Does genetic variation in outcrossing and selfing taxa follow these predictions?

Species	Genetic diversity (selfers vs outcrossers)
<i>Eichhornia paniculata</i>	2x
<i>Solanum SI/ SC</i>	4 to 40x
<i>Mimulus guttatus/nasutus</i>	7x
<i>Arabidopsis lyrata/thaliana</i>	4x



Mating system summary

Ecological and genetic factors influence the evolution of self fertilization from outcrossing

Selfing is associated with a number of morphological and life history traits

Mating systems and associated demographic traits have strong consequences for genetic variation, as well as speciation and extinction rates

Selfing can have many short term advantages, but appears to be an evolutionary dead end (high speciation rate and extinction rate)



Unanswered questions

What genetic changes are commonly associated with the transition to selfing?

How have transitions away from selfing occurred?

How will selfing rates affect adaptation to a changing climate?

How does the purging of inbreeding depression occur?