Ecole de la chaire MMB – Aussois – 7 au 10 avril 2015

Evolution of plant mating systems: the interplay of ecology and genetics

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CESCO - Muséum national d'Histoire naturelle

Mating system

- Characteristics influencing the choice of mating partner(s) for sexual reproduction
  - **Animals**

Monogamy

Polygamy

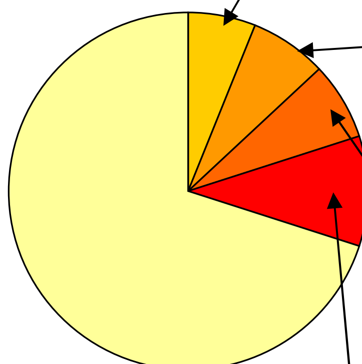
  - **Flowering plants**
    - Many reproductive organs
      - With ♀/♂ functions
      - ⇨ Distribution of genders (♀/♂)
        - among flowers and individuals
      - Self-fertilization
        - And mechanisms to avoid it
    - Reliance on pollen vectors

Wide diversity of plant mating systems ⇨ wide diversity of floral morphology

Many plant species can self-fertilize

Ornithogalum dubium

Hermaphroditism
≈ 70 %



Silene dioica

Dioecy
≈ 5 %

Sagittaria cuneata

Monoecy
≈ 7 %

Thymus vulgaris

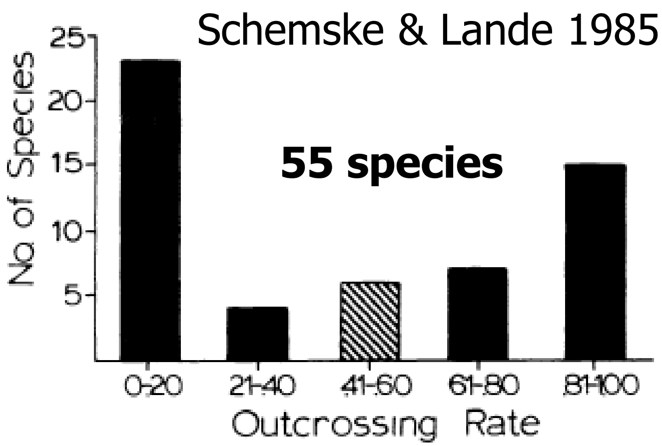
Gyno/Andro-dioecy
≈ 7 %

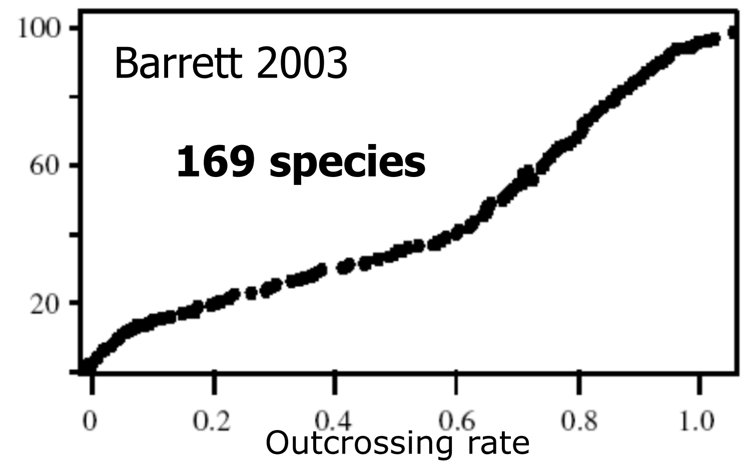
Dianthus sylvestris

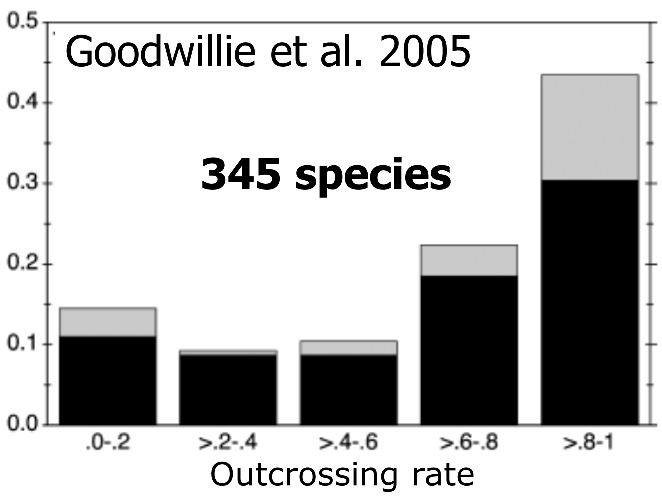
Others
≈ 10 %

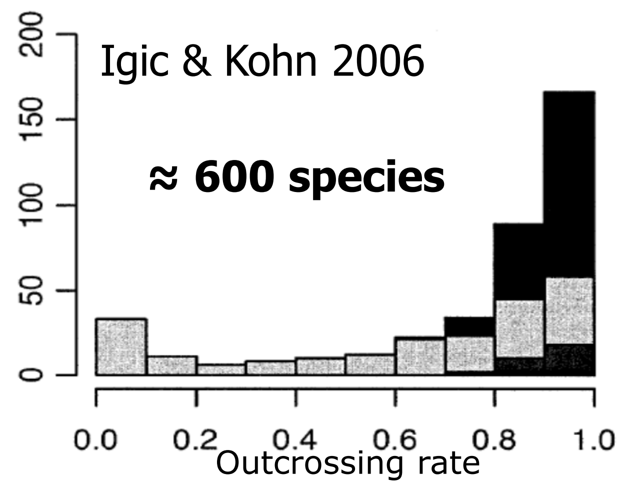
- What forces drive the evolution of selfing and selfing rates?

Distribution of outcrossing rates in natural populations of hermaphroditic plants





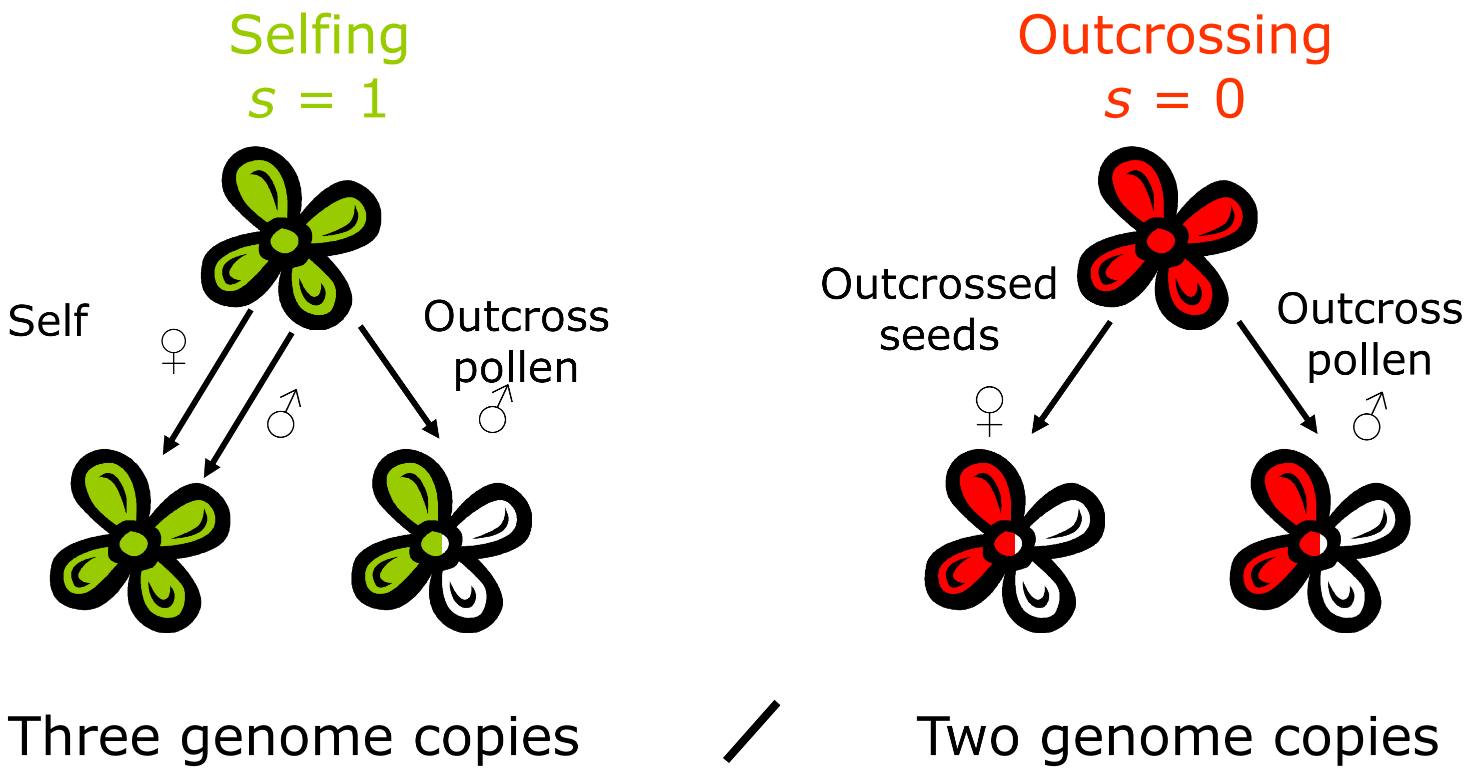




Which mechanisms drive the evolution of selfing rates ?

Genetic mechanisms controlling the evolution of selfing

- Automatic advantage of selfing



- **50 %** advantage of selfing for complete selfers (s=1)

Genetic mechanisms controlling the evolution of selfing

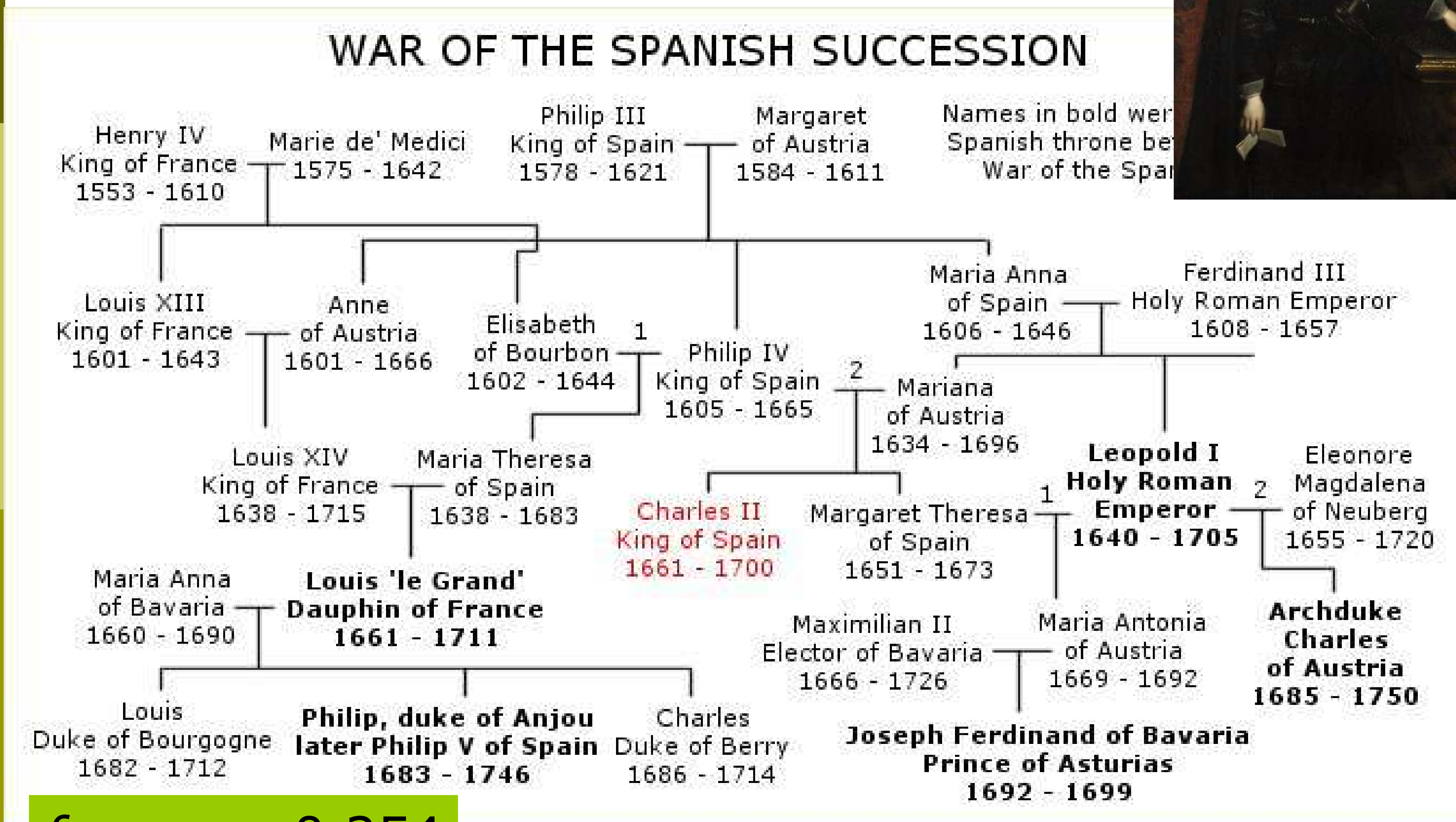
- Inbreeding depression
  - Reduction in fitness of individuals produced by selfing vs. outcrossing

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

Outcrossed Selfed

Outcrossed Selfed

An example of inbreeding depression in human populations



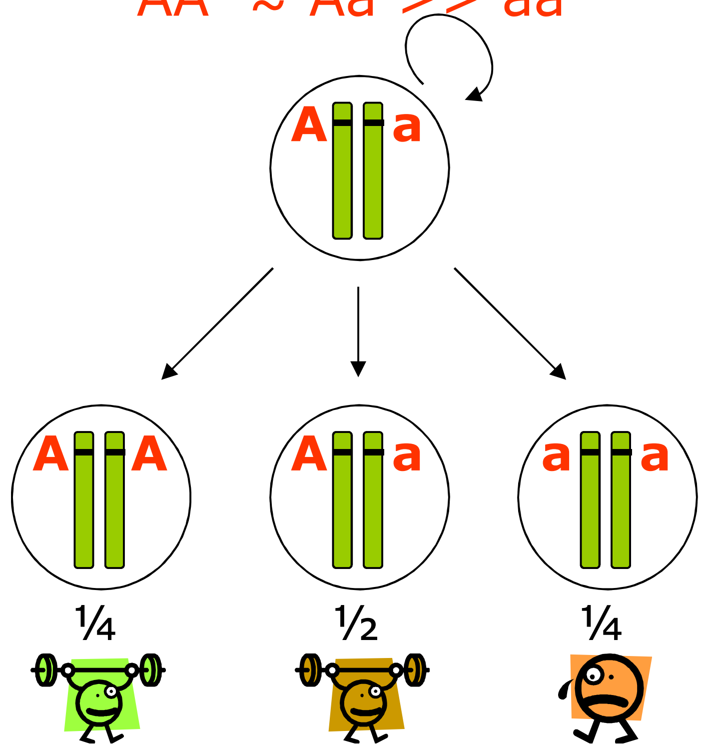
$f_{CharlesII} = 0.254$

Alvarez et al. 2009, PLOS One

Inbreeding depression

- Caused mostly be recessive, highly deleterious mutations

AA ≈ Aa >> aa

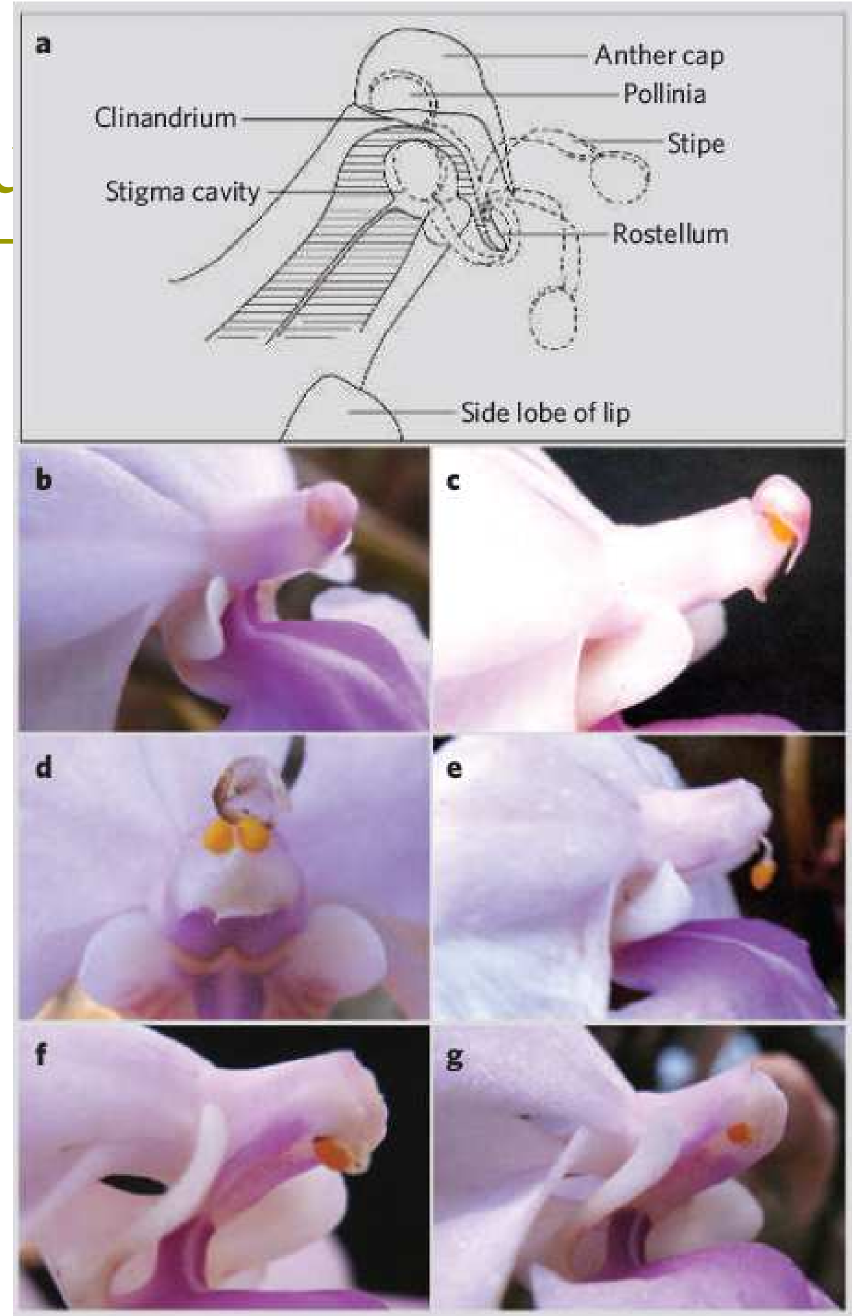


- ⇨Purging is possible

Models for the evolu

- The selfing rate is the trait under selection

- Major assumptions :
  - The selfing rate is under the plant control
  - The selfing rate can evolve freely between 0 and 1



Holcoglossum amesianum, Liu et al. 2006

How plants control their selfing rate

- Traits favoring increased selfing

Viola sp.

Cleistogamy

Arabidopsis thaliana

Herkogamy

How plants control their selfing rate

- Traits favoring decreased selfing ⇨ Separation of male and female functions
  - Within a flower

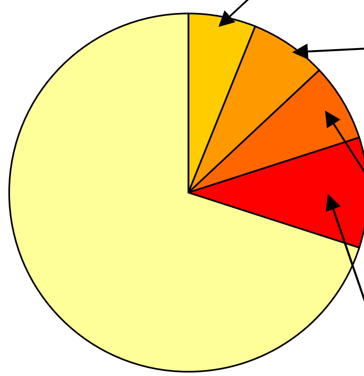
Temporal separation
Dichogamy

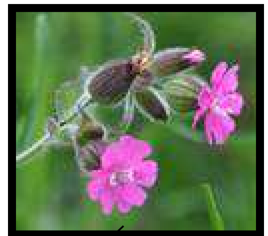
Spatial separation
Herkogamy

  - Between flowers or individuals ⇨ Diversity of gender distribution within / among individuals

Diversity of gender distribution within and among individuals

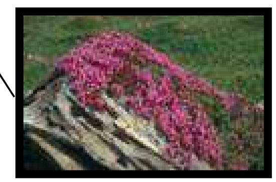
Hermaphroditism
≈ 70 %



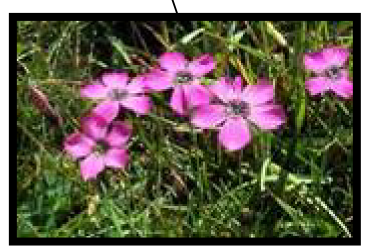


Dioecy
≈ 5 %

Monoecy
≈ 7 %



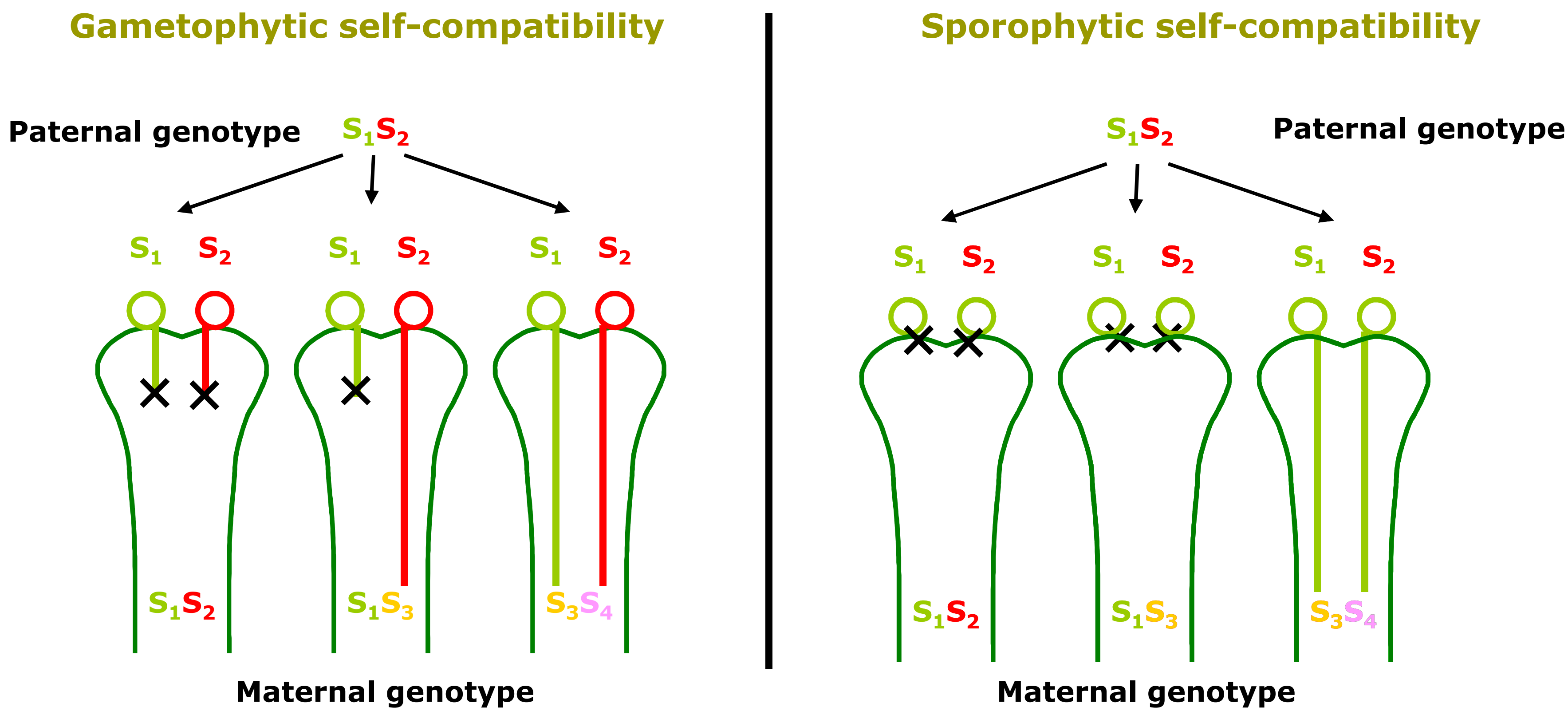
Gyno/Andro-dioecy
≈ 7 %



Others
≈ 10 %

How plants control their selfing rate

- Traits to avoid selfing ⇨ self-incompatibility
  - Ability of a plant to recognize and reject its own pollen

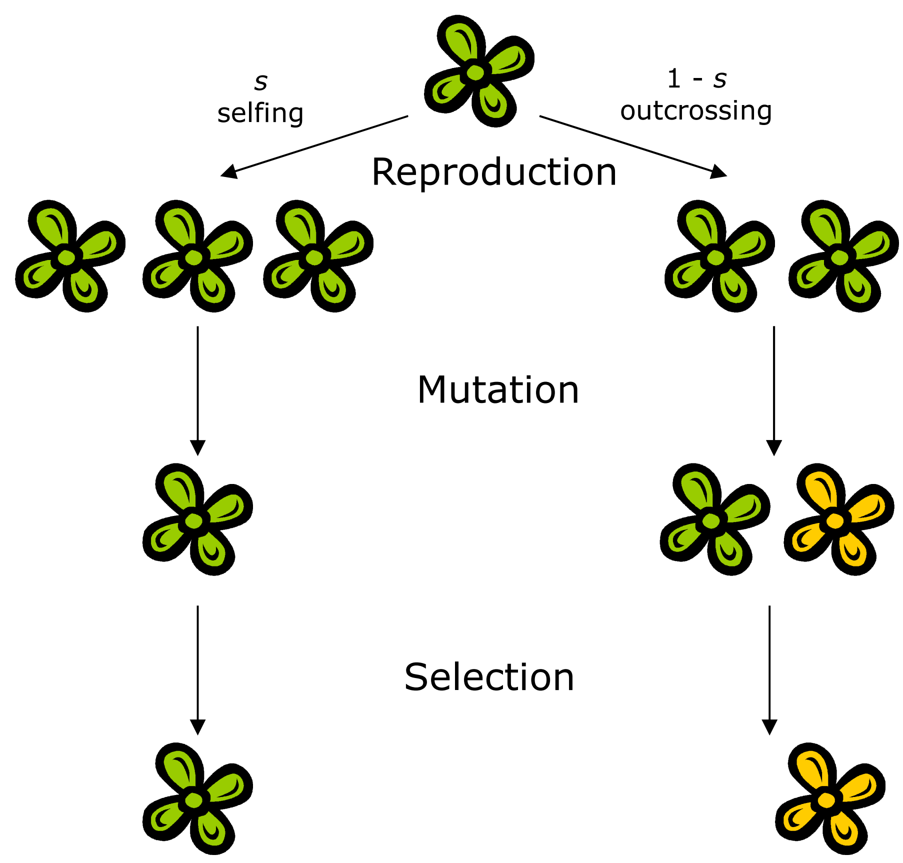


A genetic model for inbreeding depression (Kondrashov 1985)

- Infinite populations
- Inbreeding depression caused by mutation to nearly recessive lethals at an infinite number of loci

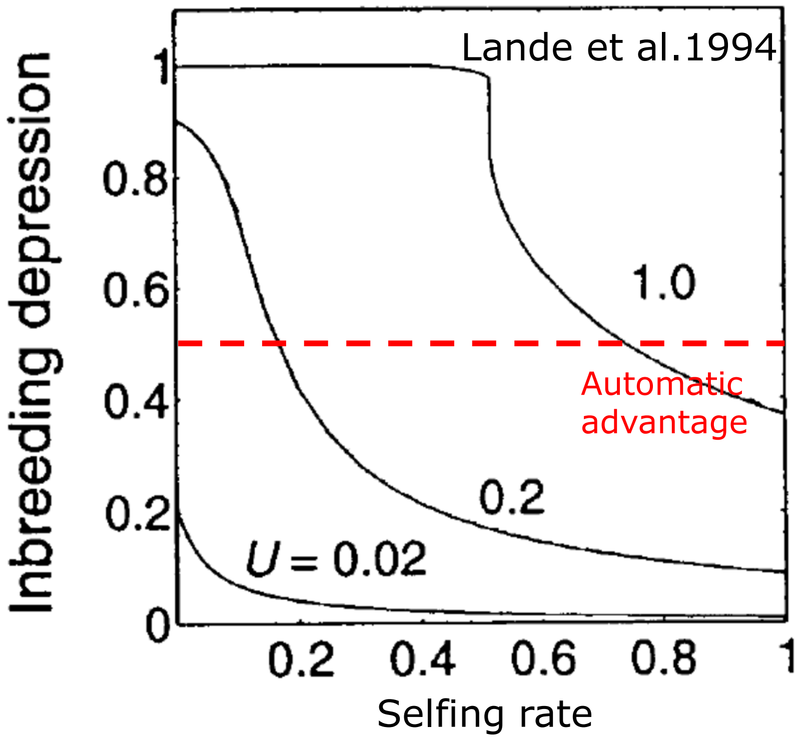
AA	Aa	aa
1	1 - *h*	0

- Each mutation is individually rare
  - Homozygous individuals are only produced by selfing

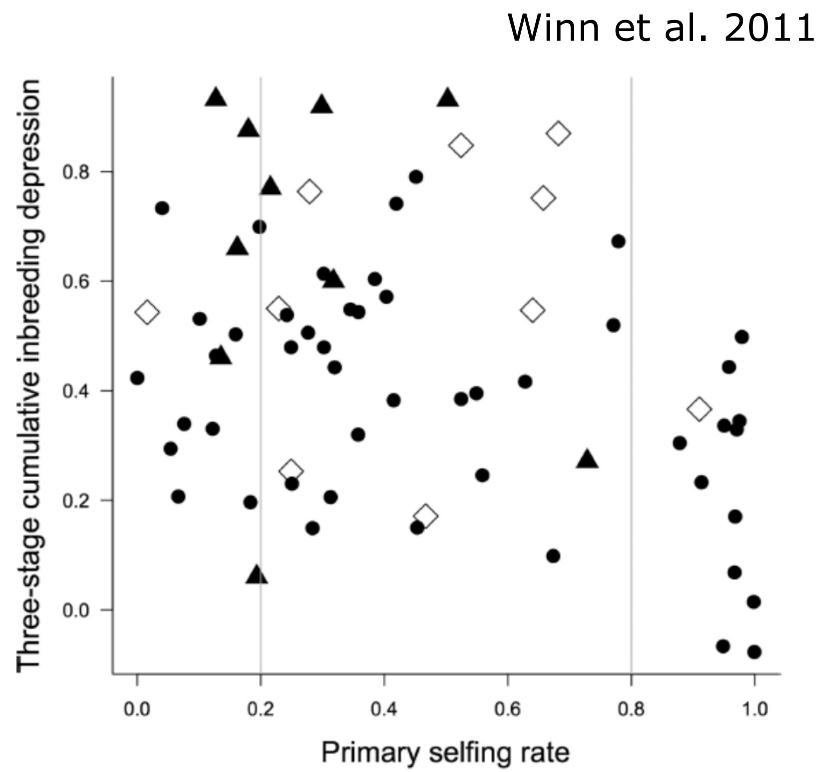


Inbreeding depression evolves with the mating system

- Theory



- Data



Evolutionarily stable selfing rates = complete outcrossing or complete selfing
The “paradox” or the “enigma” of mixed mating

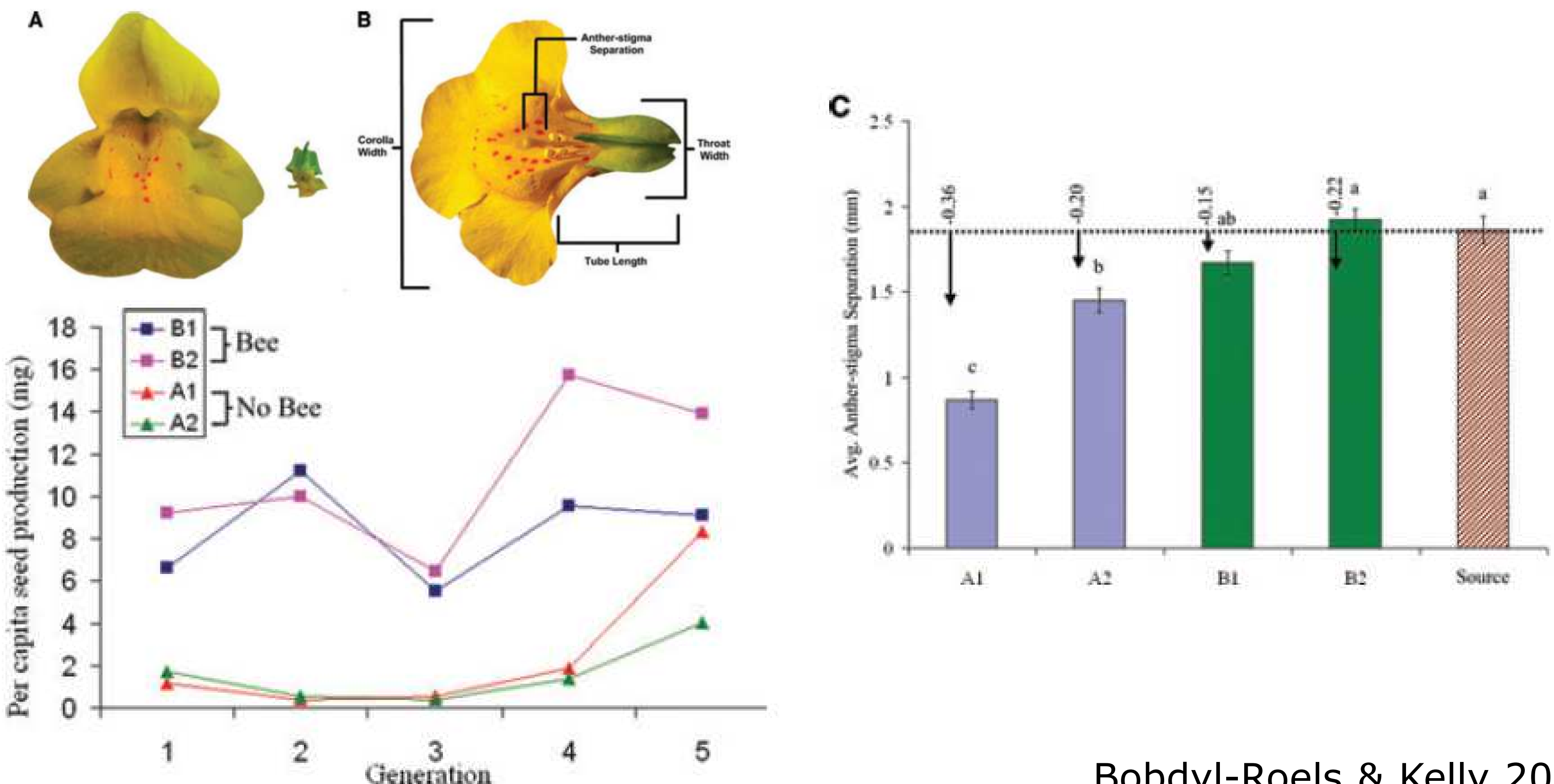
What else influences the evolution of selfing rates?

- Ecology!
  - Pollination ecology

- Pollen limitation
- Pollen discounting
- Constraints imposed by pollinators

An example of the impact of pollinators on evolution of selfing

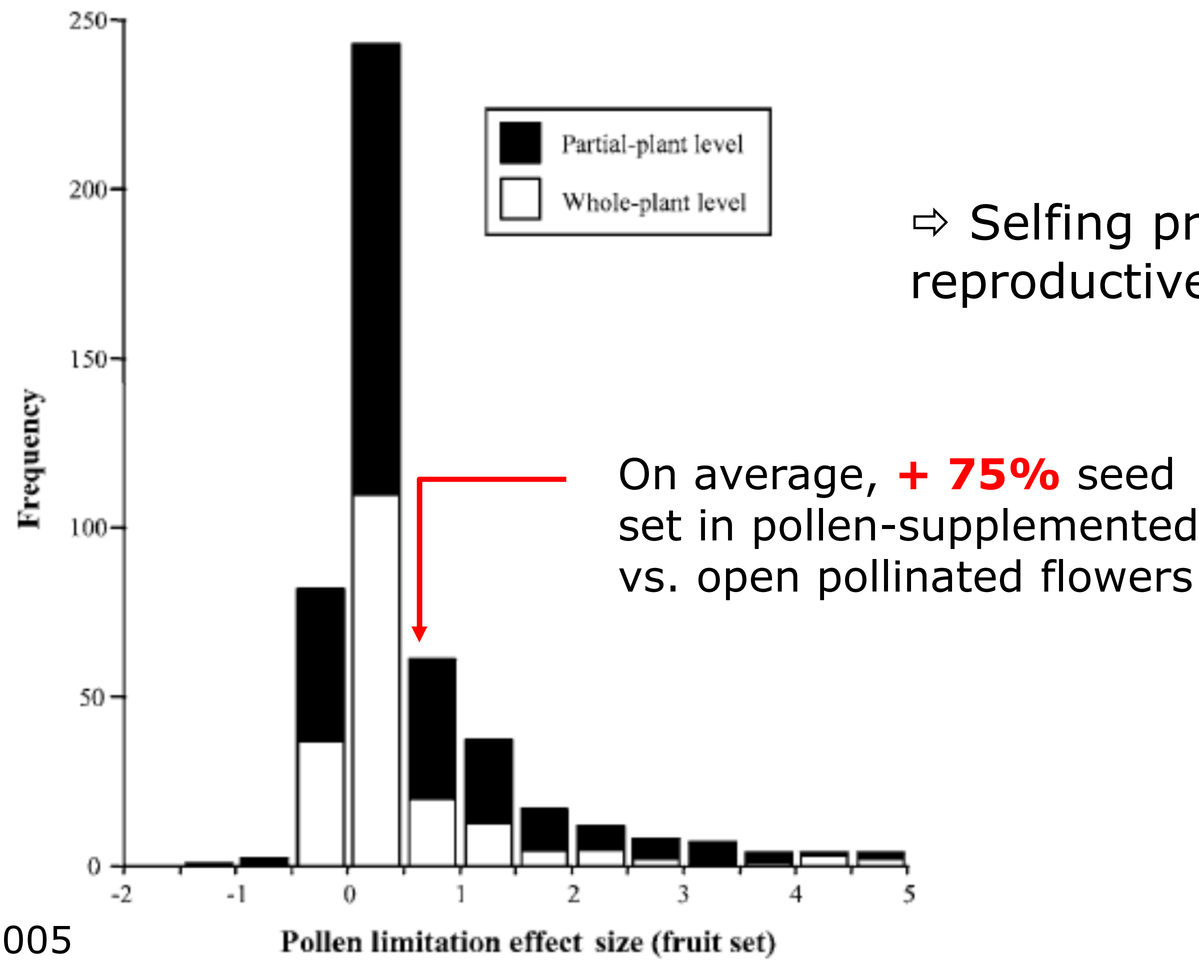
- Experimental removal of pollinators in *Mimulus guttatus*



Bobdyl-Roels & Kelly 2011

Pollen limitation

- Limitation of seed set by pollen availability



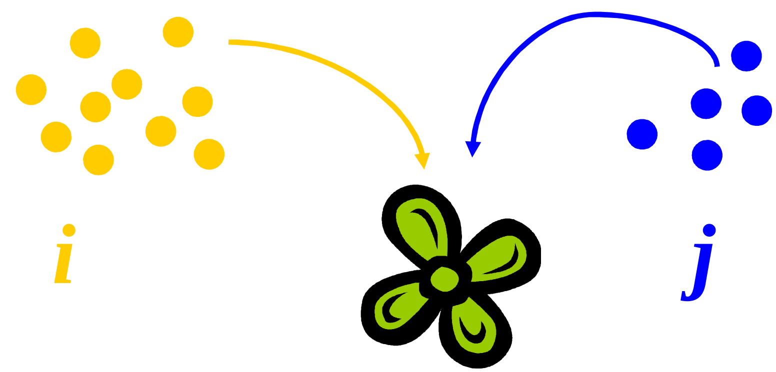
⇨ Selfing provides reproductive assurance

Knight et al. 2005

Pollen discounting

- In many species, self and outcross pollen compete

- Mass-action model
  - The probability that a given pollen type fertilizes ovules is proportional to its frequency on the stigma



$$p_i = i / (i + j)$$

Holsinger 1991

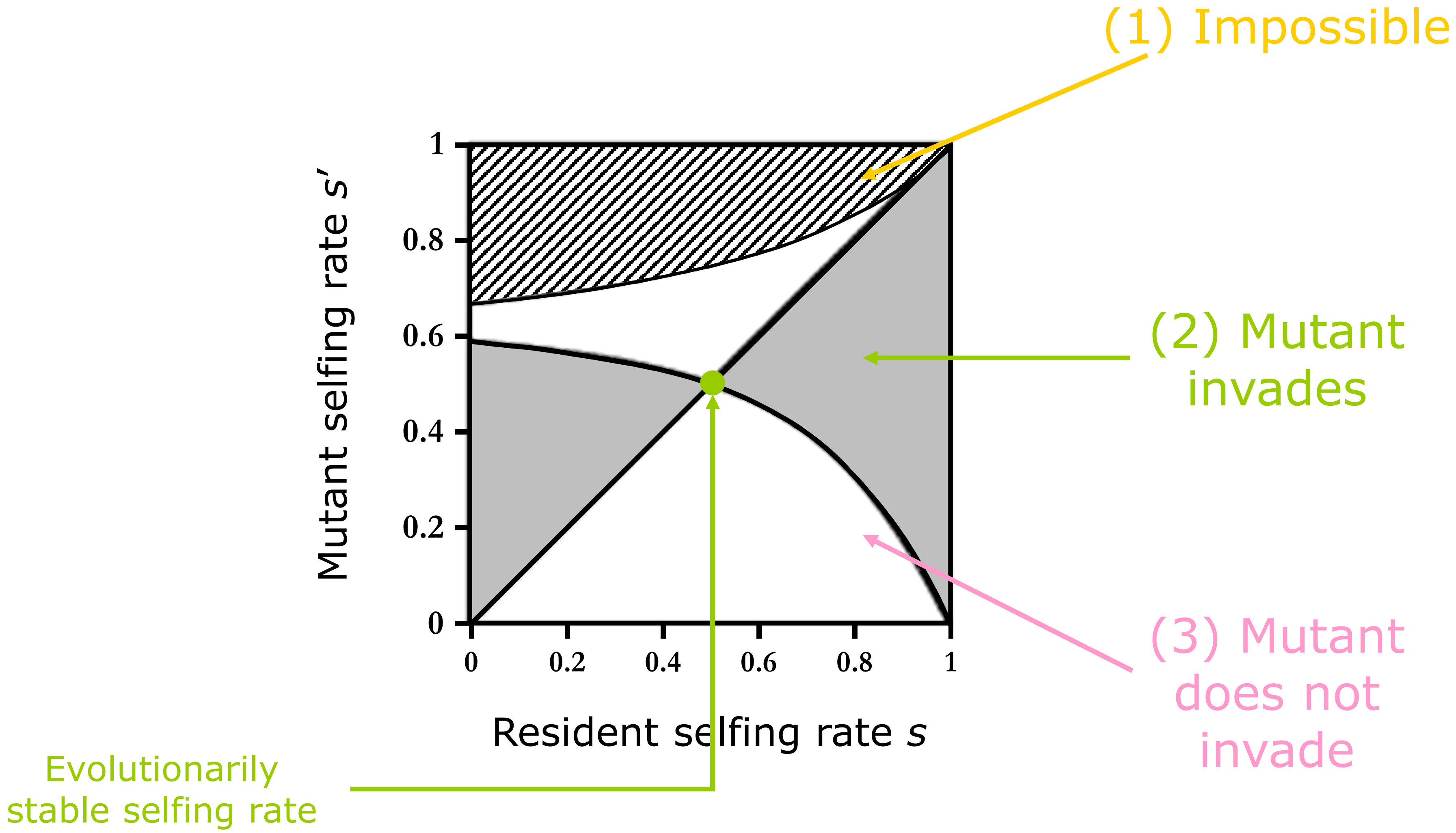
Pollen discounting

- Mass-action model of selfing, under competing pollination

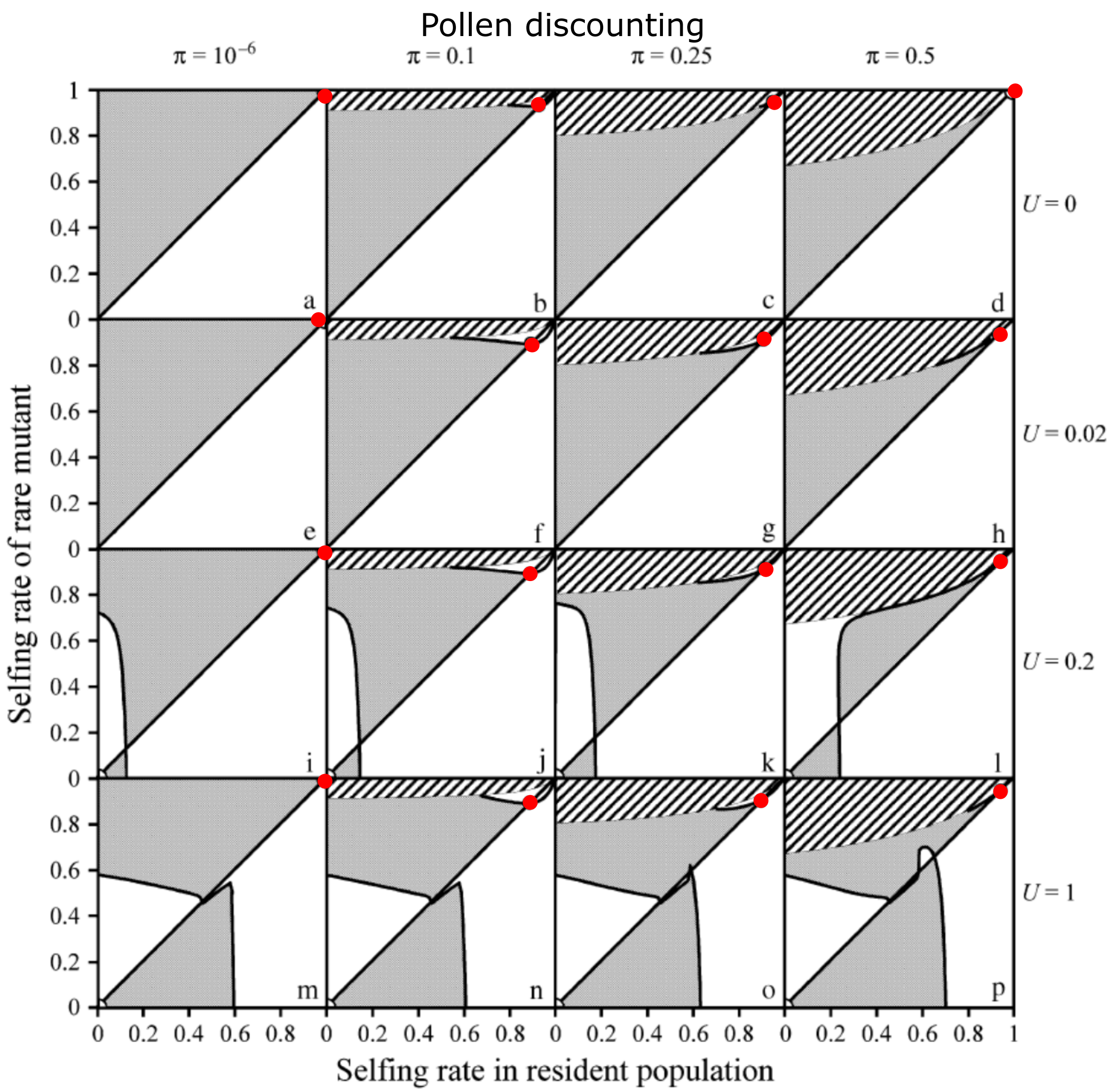
- Using pollen to self-fertilize decreases outcross male reproductive success

- Model of the evolution of the selfing rate incorporating:
  - Evolving inbreeding depression (due to nearly recessive lethals)
  - Pollen discounting
  - Pollen limitation ⇨ Reproductive assurance
- Evolving trait = selfing rate

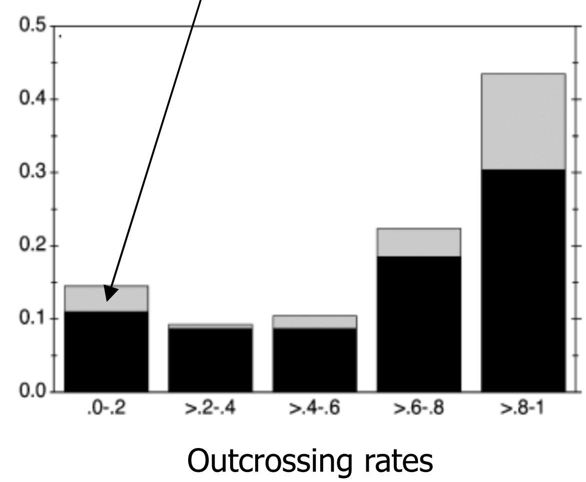
Results: Pairwise Invasibility Plots



Evolutionarily stable selfing rates under pollen limitation and pollen discounting



- Only large (but <1) selfing rates are evolutionarily stable



Porcher & Lande 2005

Pollinators constrain plant selfing rates

- In many models, trait under selection = selfing rate
  - Free to evolve between 0 and 1

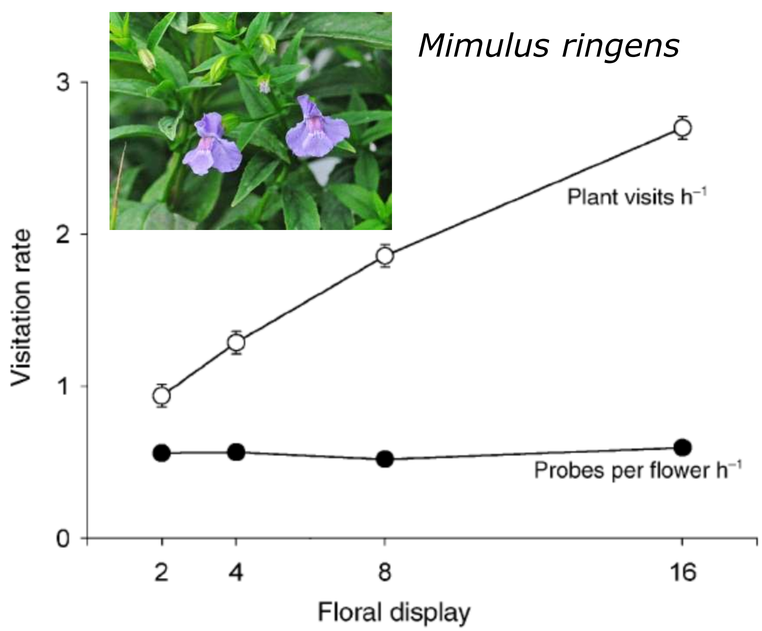
- But pollinators can constrain selfing rates

$$s = \frac{\text{self pollen}}{\text{self pollen} + \text{outcross pollen}}$$

- Models of plant (and pollinator) traits influencing pollinator behavior and pollen transport

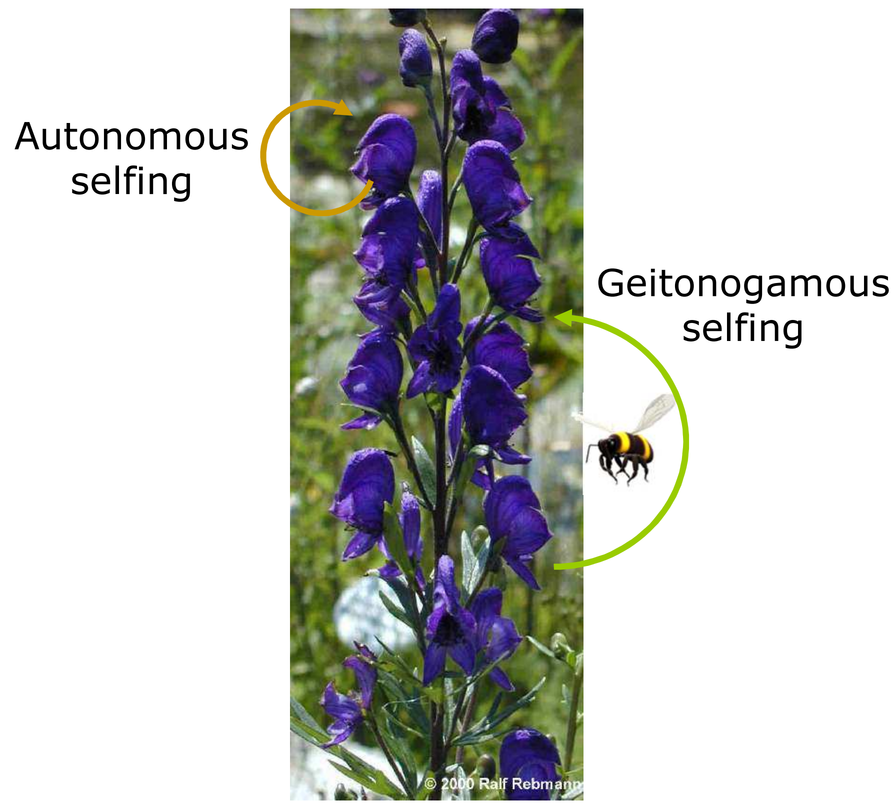
Floral display influences pollinator behavior and selfing rates

- Pollen limitation
  - Widespread in natural populations
  - Selection for increased pollinator attraction

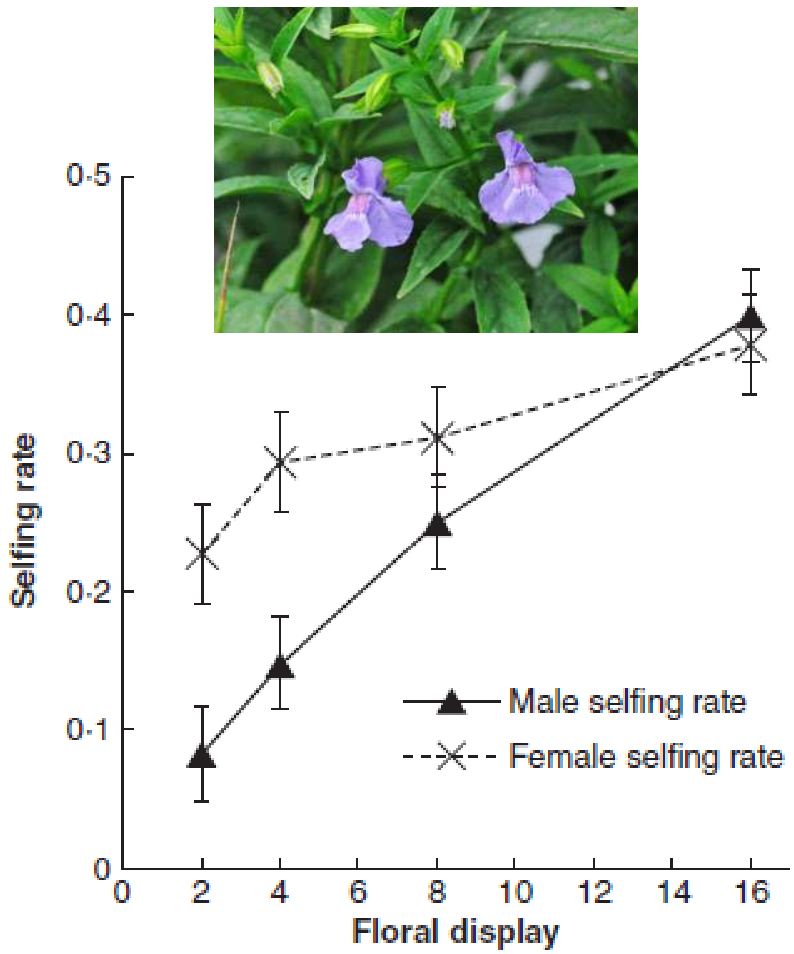


Mitchell et al. 2004

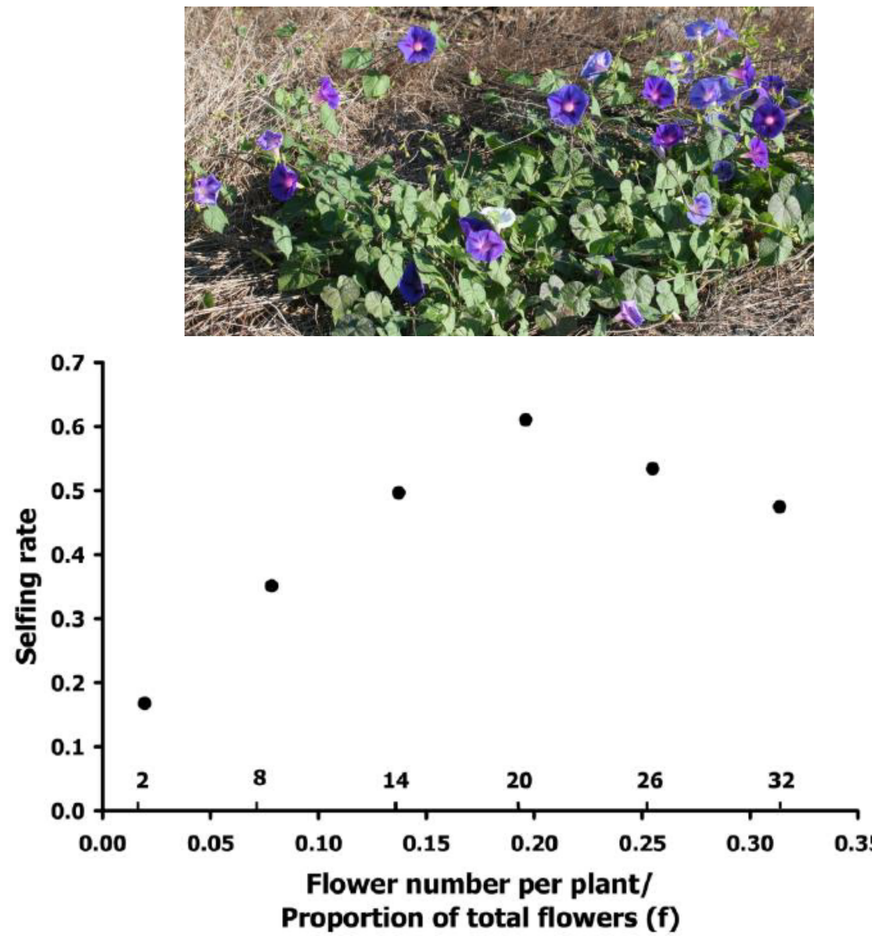
- Geitonogamous selfing
  - Fertilization among flowers on the same plant



Flower number influences geitonogamous selfing rates



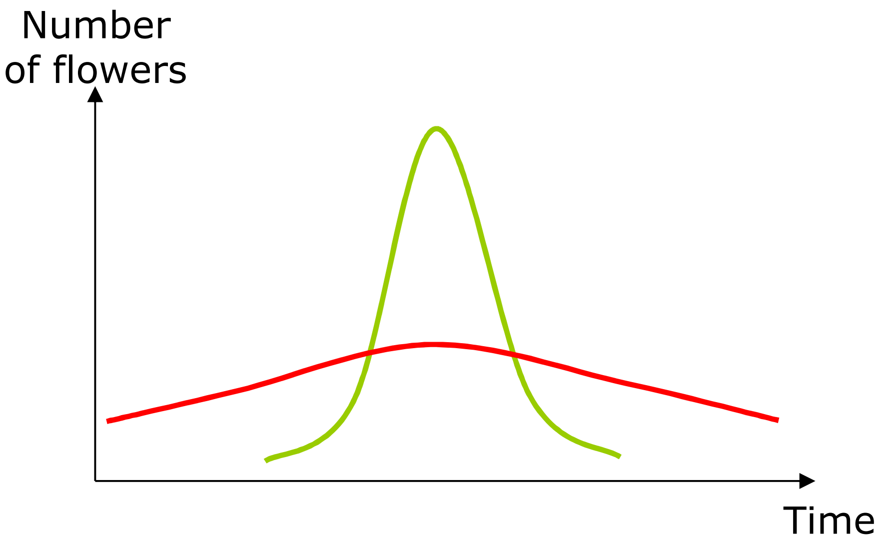
Karron et al. 2012
Mimulus ringens



Lau et al. 2008
Ipomoea purpurea

Flowering phenology and the evolution of selfing rates

- With a constant total number of flowers



- What conditions favor mass blooming vs. extended flowering?
- Consequences for the evolution of selfing?

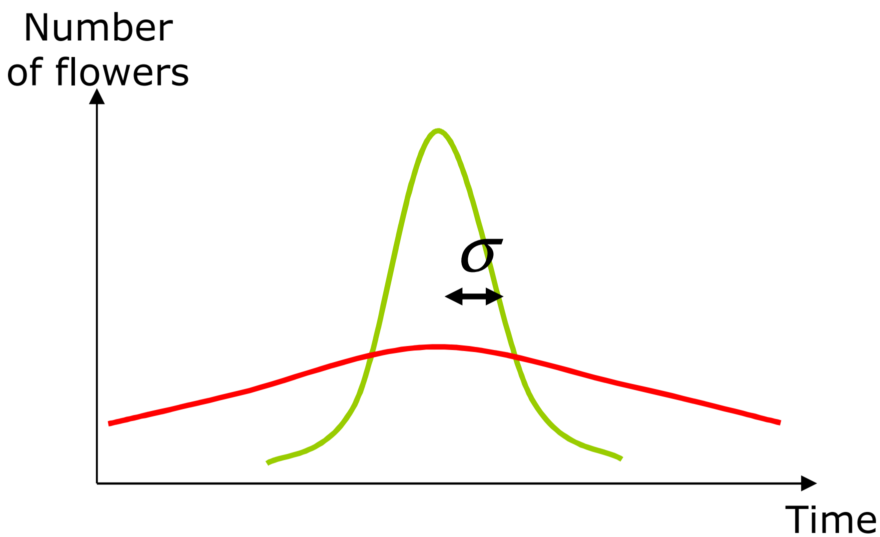
In the *Aphelandra* genus (Acanthaceae):

Aphelandra storkii

Aphelandra saintclairiana

Pollinator behaviour and the evolution of flowering phenology

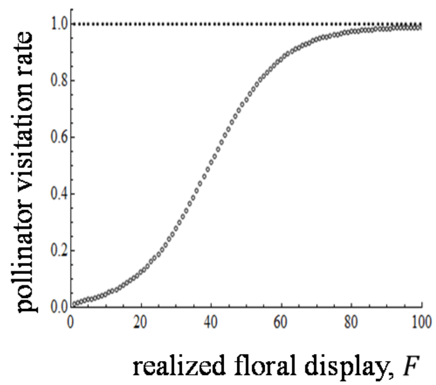
- Evolving trait = standard deviation in flowering time σ



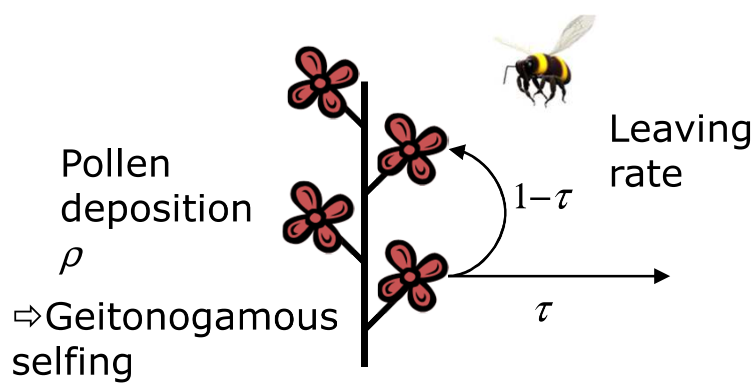
  - Genetic model of inbreeding depression
  - Selection gradient

$$\left.\frac{\partial w^*}{\partial \sigma^*}\right|_{\sigma=\sigma^*} = 0$$

- Pollinator behavior
  - Attracted by large numbers of flowers

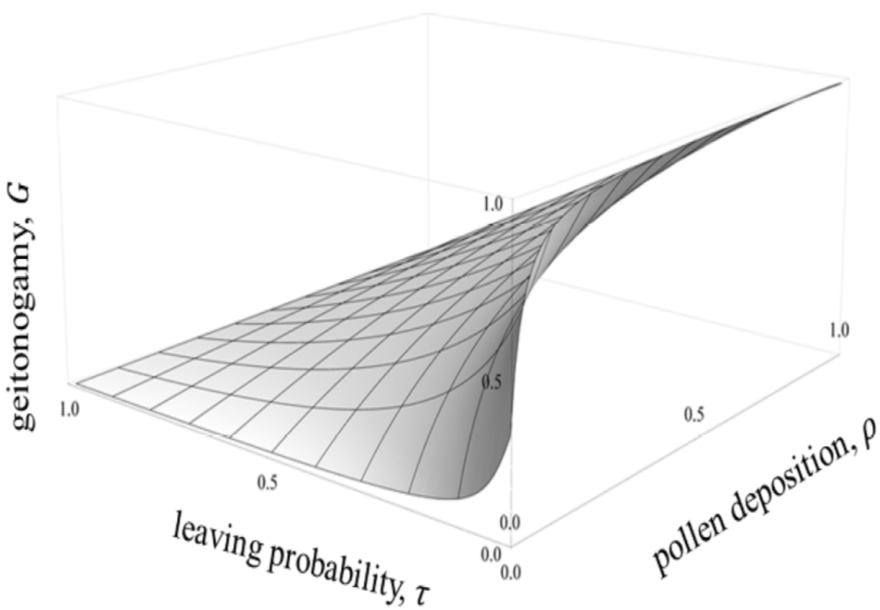


  - Within-inflorescence behavior

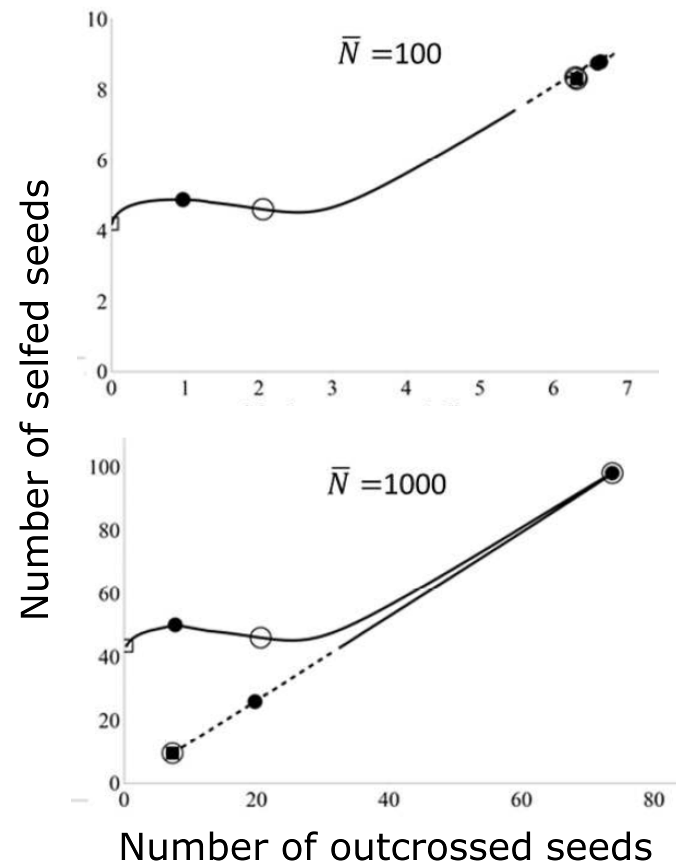


Impact of pollinator behavior on fitness components

- Maximum geitonogamous selfing rates (in a mass-blooming plant, $\sigma = 0$)

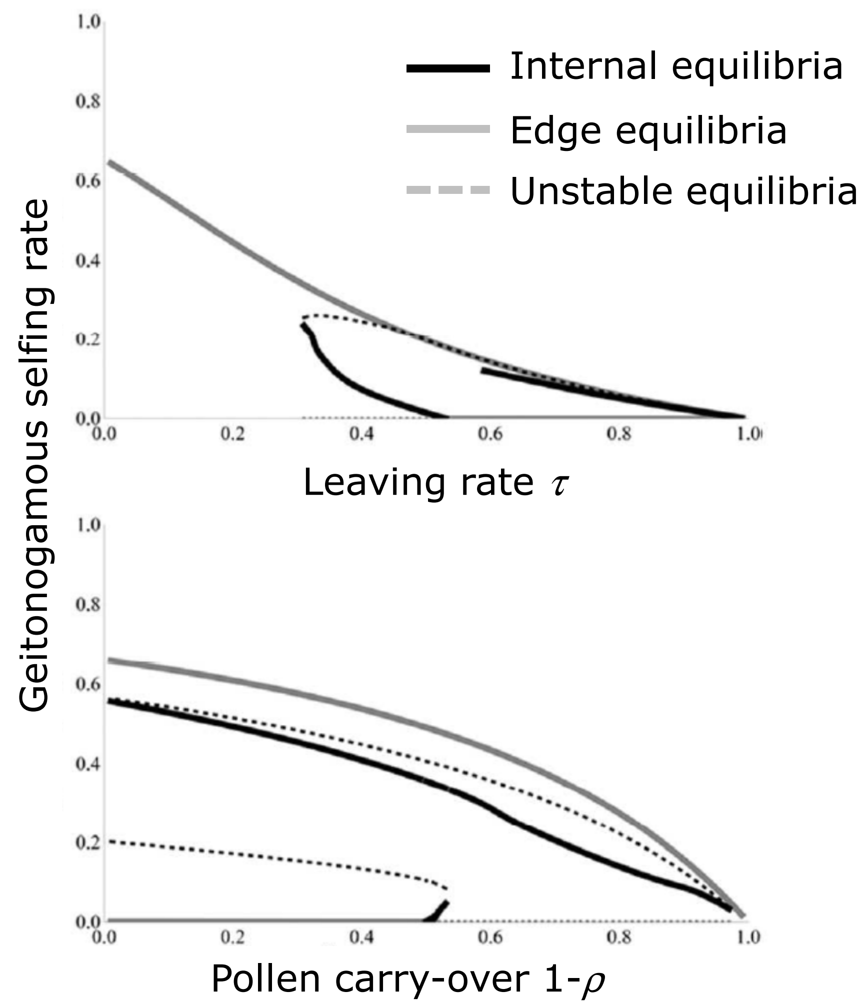


- Functional relationships among fitness components



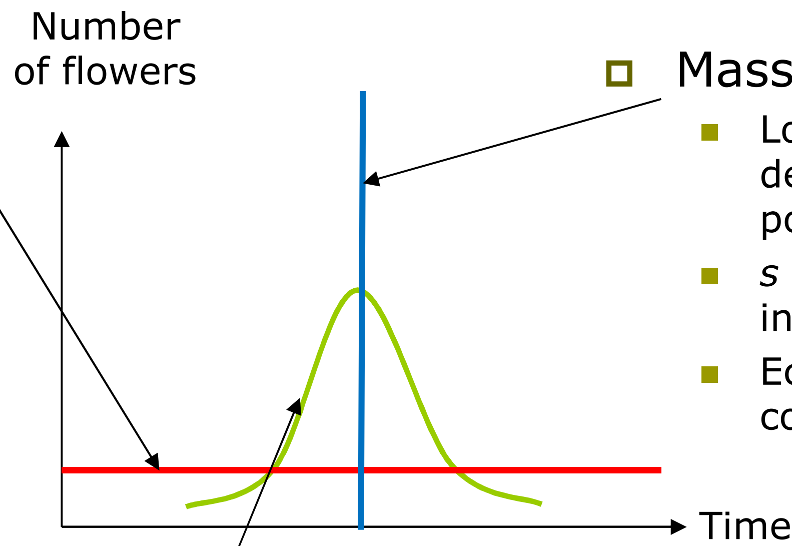
Equilibrium (phenology and) selfing rates

- Two types of stable equilibria
  - Edge equilibria: constrained by pollinator behavior
  - Internal equilibria: evolutionarily stable eq., resulting from a trade-off between pollinator attraction and inbreeding depression
  - Internal equilibria occur at intermediate values of ρ and τ, comparable with experimental estimates



Three major types of outcomes

- Extended blooming
  - High inbreeding depression + no pollinator limitation
  - *s* = 0
  - Infrequent & unlikely in a seasonal env.

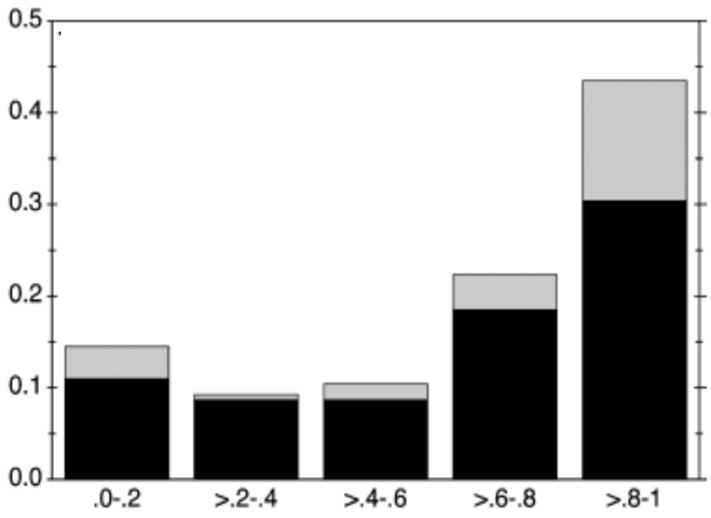


- Mass blooming
  - Low inbreeding depression + pollinator limitation
  - *s* small to intermediate
  - Ecological constraints

- Intermediate duration of flowering
  - High inbreeding depression + pollinator limitation
  - *s* small (<0.5)
  - ESS, trade-off between pollinator attraction and avoidance of inbreeding depression

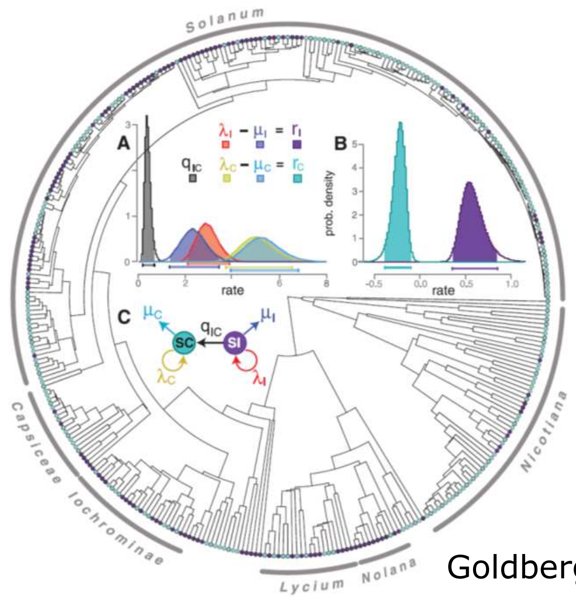
Conclusions: the paradox of mixed mating?

- Combination of ecological and genetic models
  - ⇨ Stable intermediate selfing rates



- Overall, selfing is favored in many situations

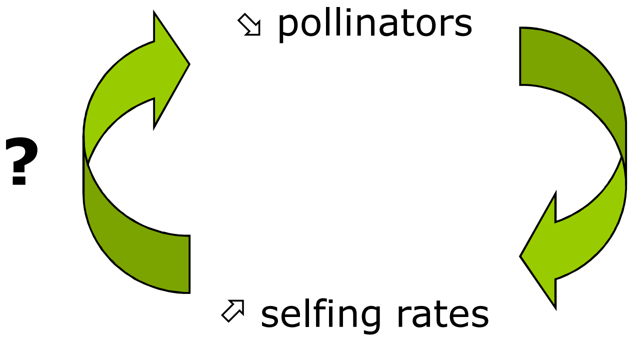
- ⇨ Longer-term evolution and species selection?
  - Impact of selfing on extinction / speciation

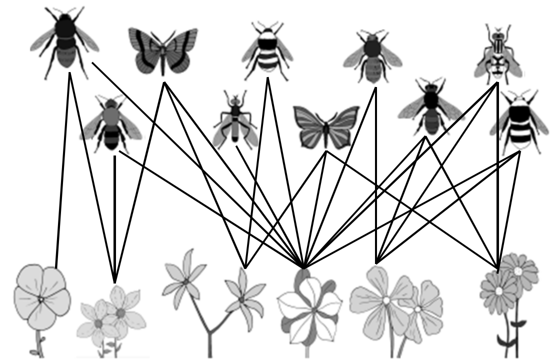


Goldberg et al. 2010

Interplay between plant mating systems and their pollinators

- So far, one plant / one pollinator
  - Joint plant/pollinator dynamics?
  - Dynamics of plant/pollinator networks?





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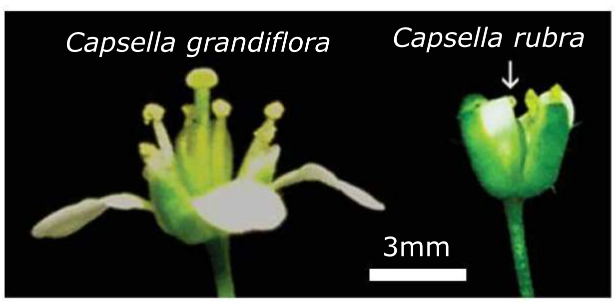
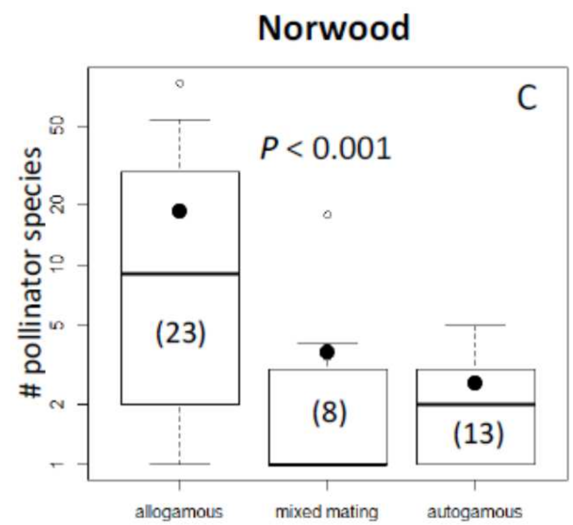


Sicard & Lenhard 2011



Devaux et al., JEB 2014