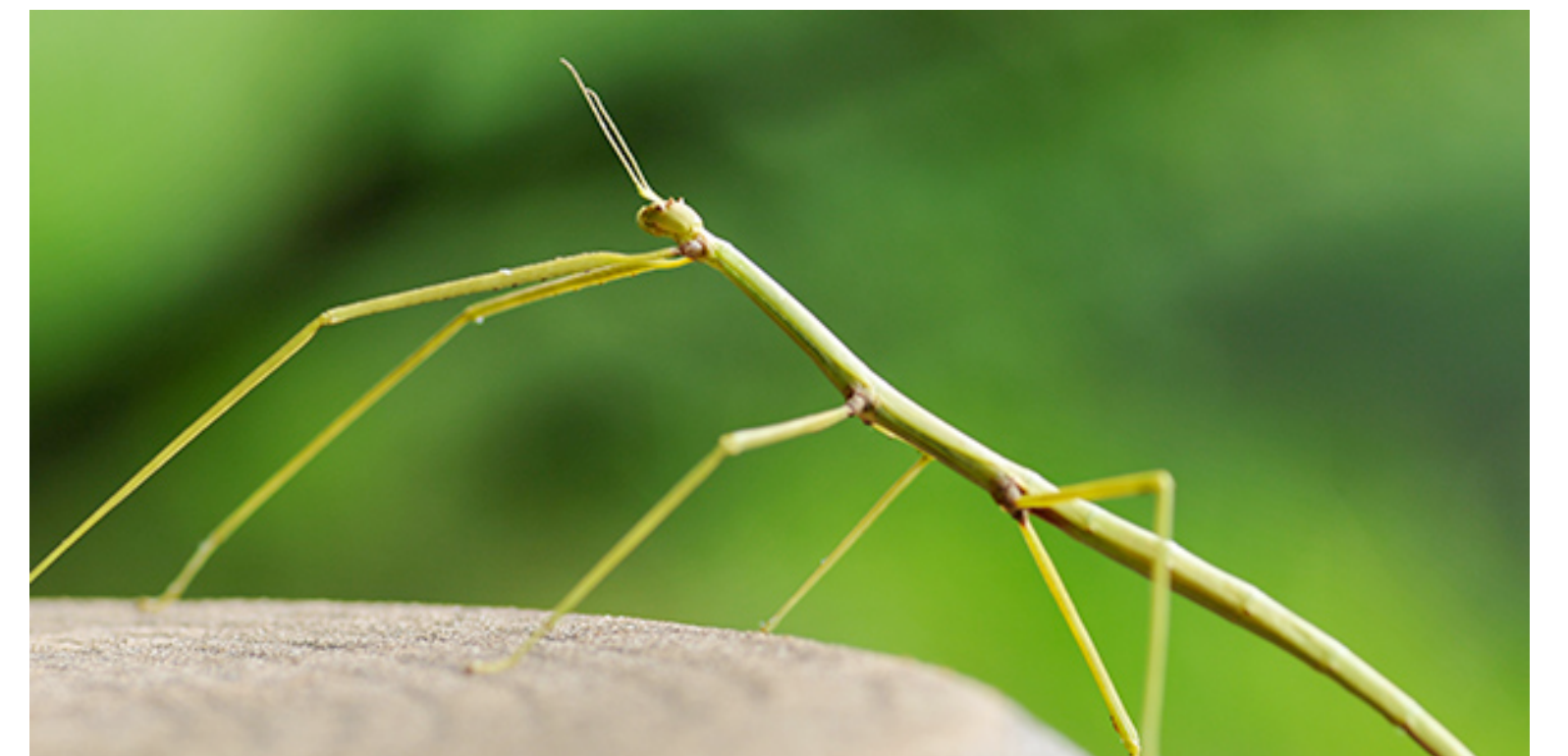


Part II - Sexual reproduction

Sex, Ageing and Foraging Theory

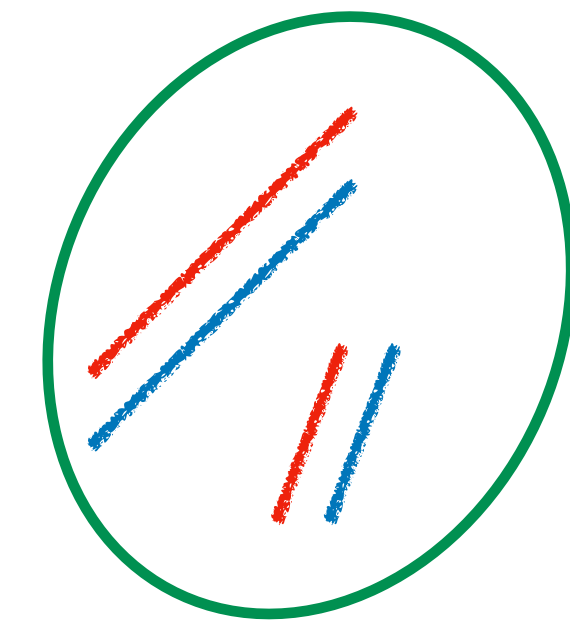
Sexual reproduction is near universal in multi- cellular organisms

Very few ancestral asexual lineages



What is sexual reproduction? and what are sexes?

- Production of new organisms by the combination of genetic material of two individuals.

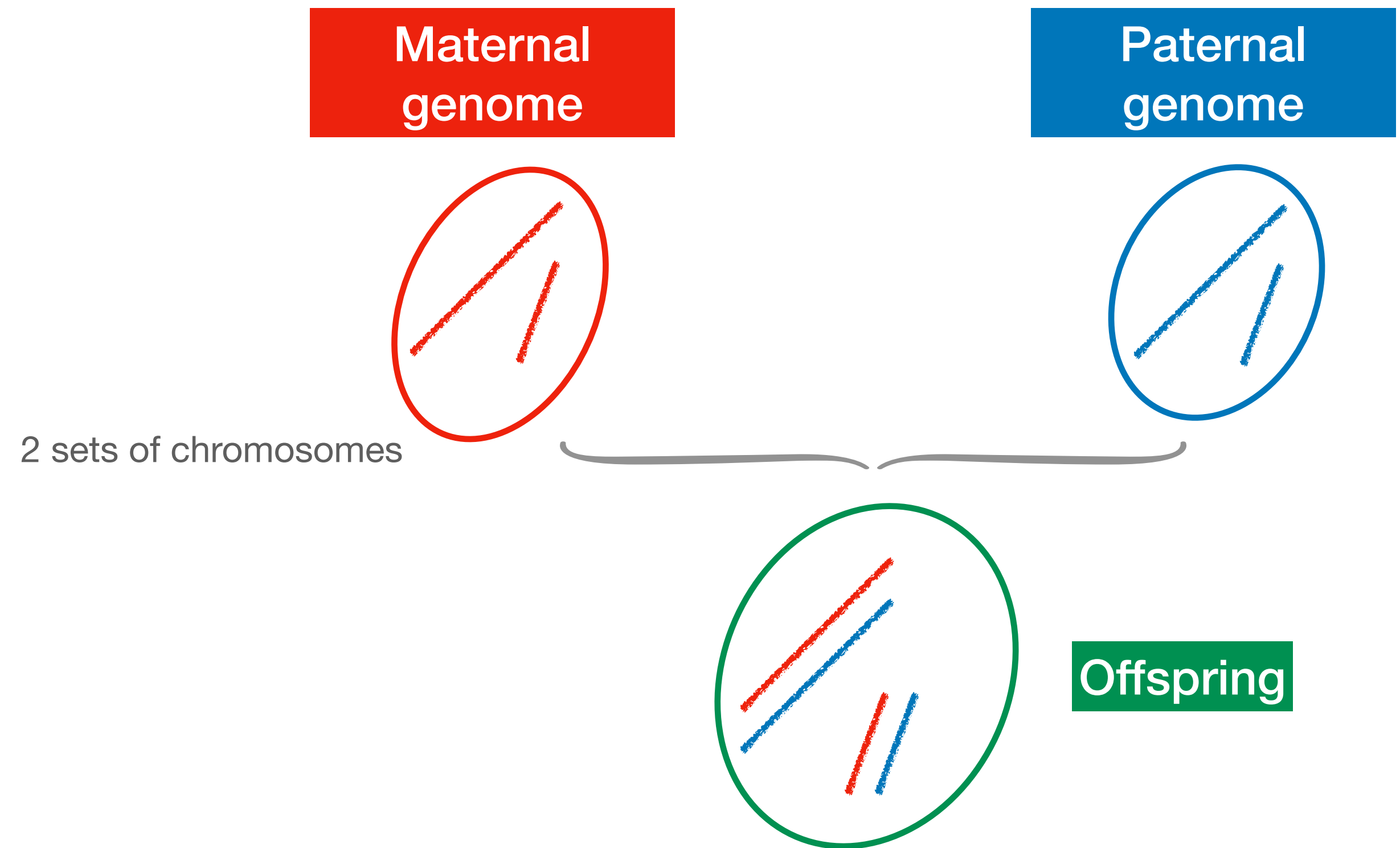


Offspring

What is sexual reproduction?

and what are sexes?

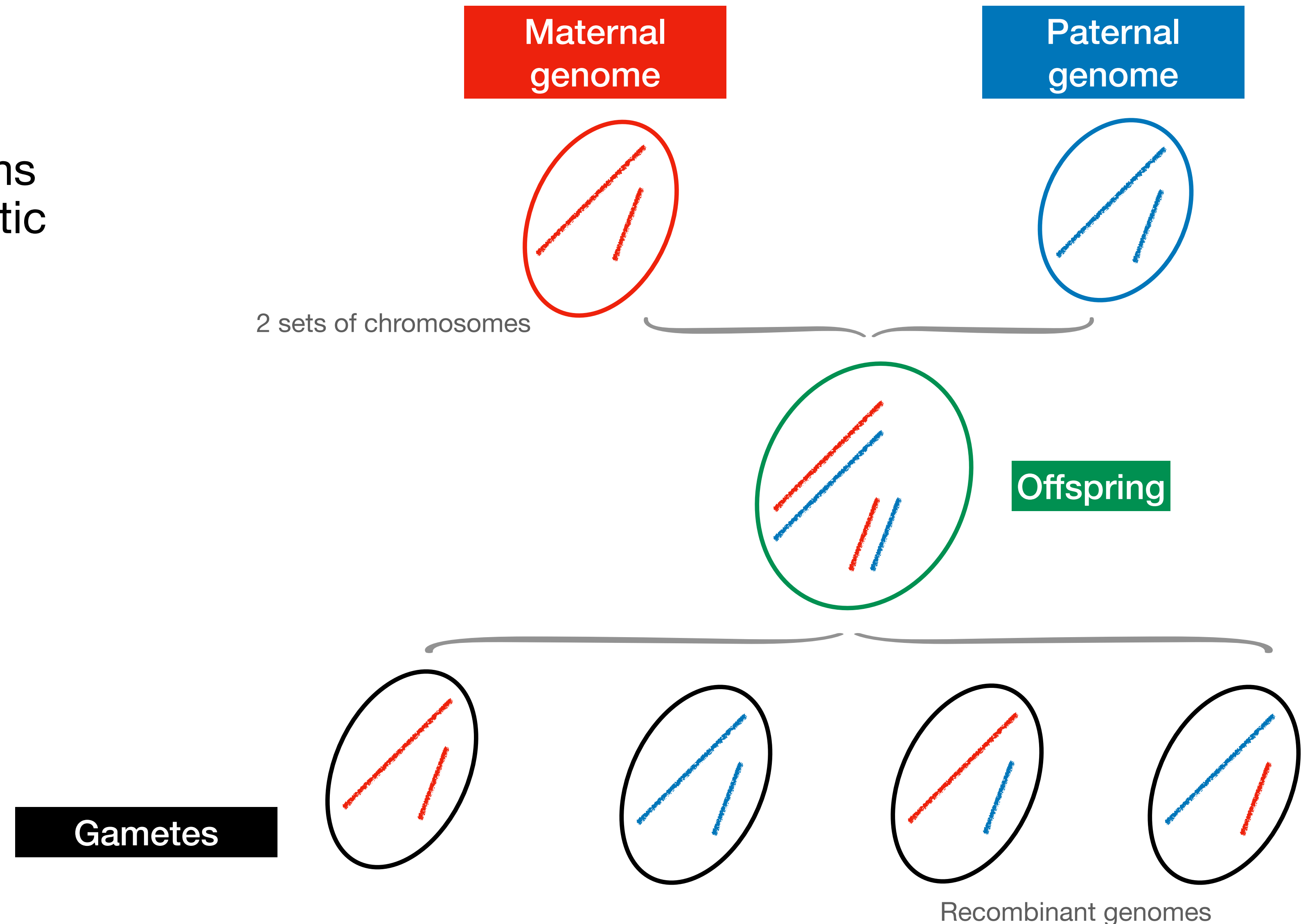
- Production of new organisms by the combination of genetic material of two individuals.



What is sexual reproduction?

and what are sexes?

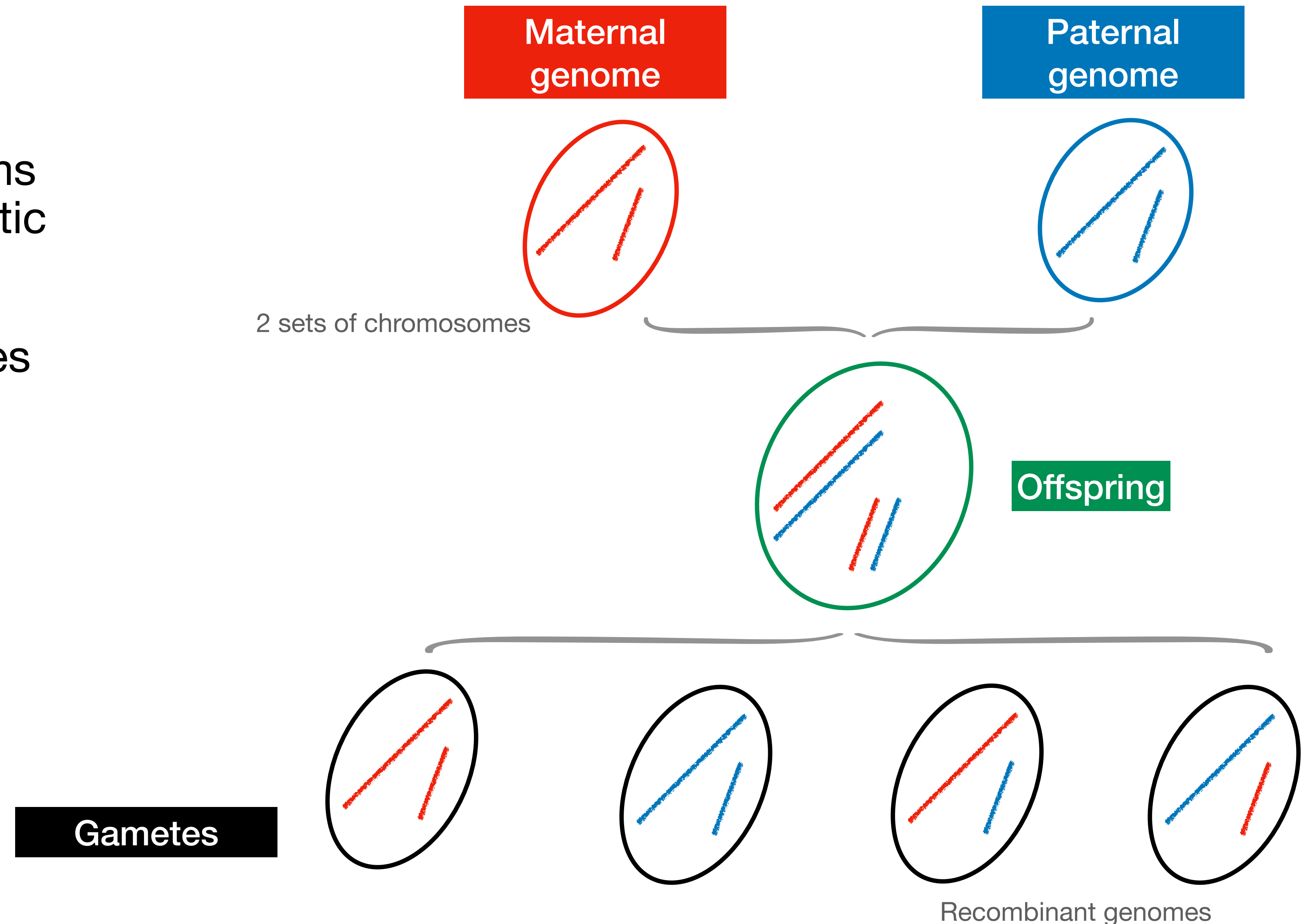
- Production of new organisms by the combination of genetic material of two individuals.



What is sexual reproduction?

and what are sexes?

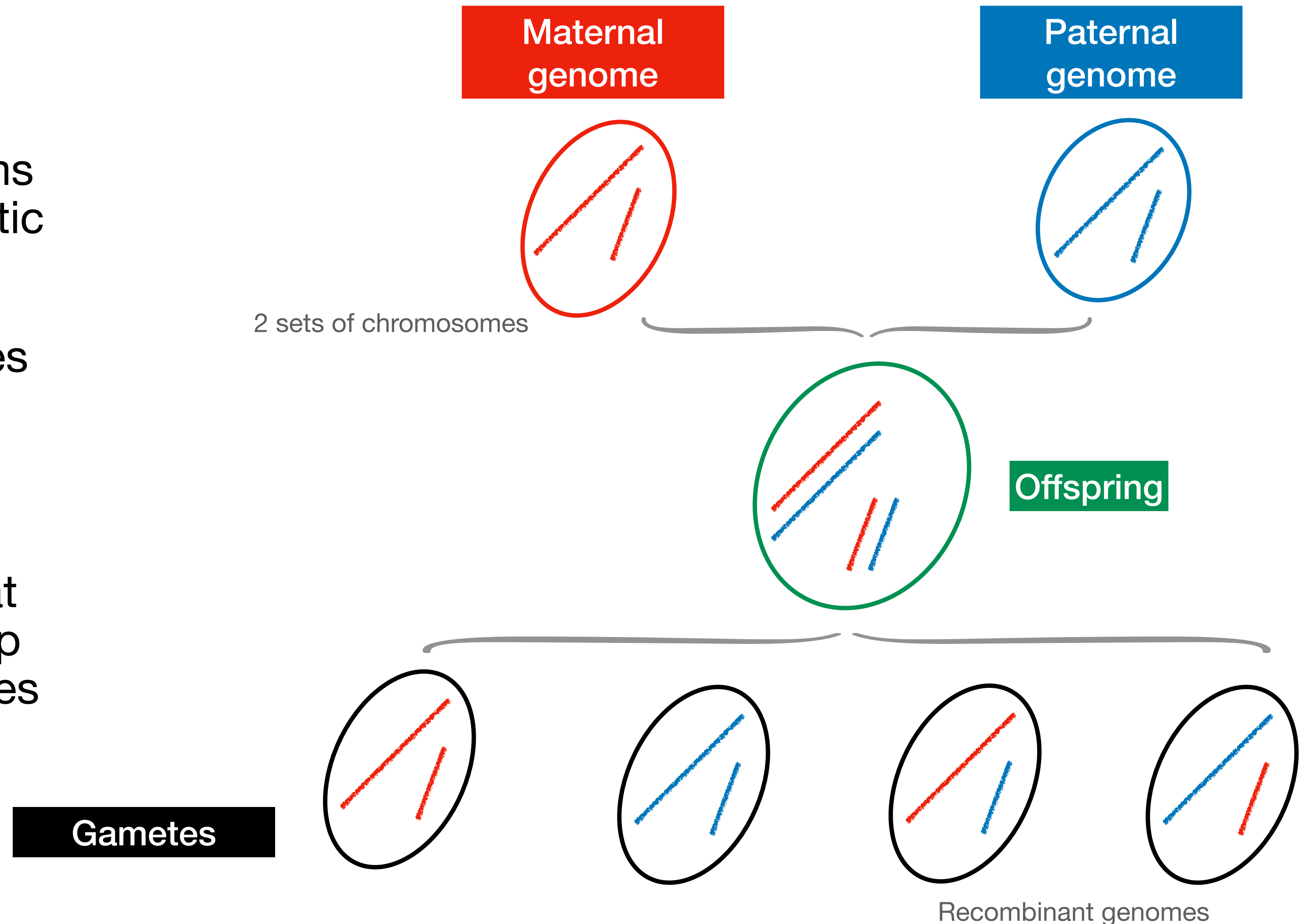
- Production of new organisms by the combination of genetic material of two individuals.
- Sexes are defined as classes of individuals that are incompatible for sexual reproduction.

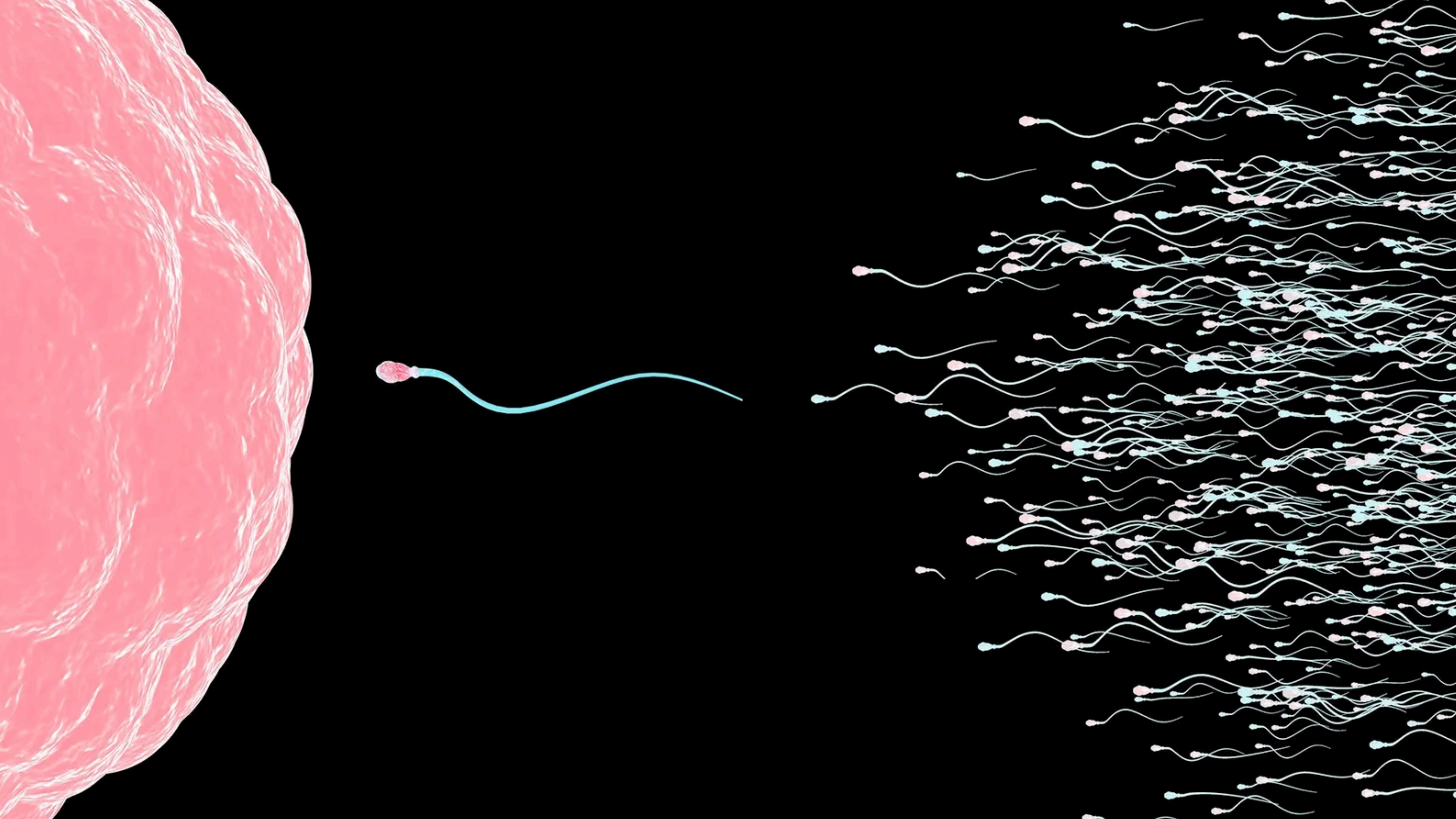


What is sexual reproduction?

and what are sexes?

- Production of new organisms by the combination of genetic material of two individuals.
- Sexes are defined as classes of individuals that are incompatible for sexual reproduction.
- Typically 2 sexes: males that produce many minute cheap gametes (sperm) and females that produce fewer large expensive ones (eggs).





Reproduction is female limited

Reproduction is female limited

- Human female record claim: ???

Reproduction is female limited

- Human female record claim: **69** offspring! (First wife of 18th century Russian peasant Fyodor Vassilyev with 16 pairs of twin, 7 sets of triplets and 4 sets of quadruplets)



Reproduction is female limited

- Human female record claim: **69** offspring! (First wife of 18th century Russian peasant Fyodor Vassilyev with 16 pairs of twin, 7 sets of triplets and 4 sets of quadruplets)
- Human man record claim: ???



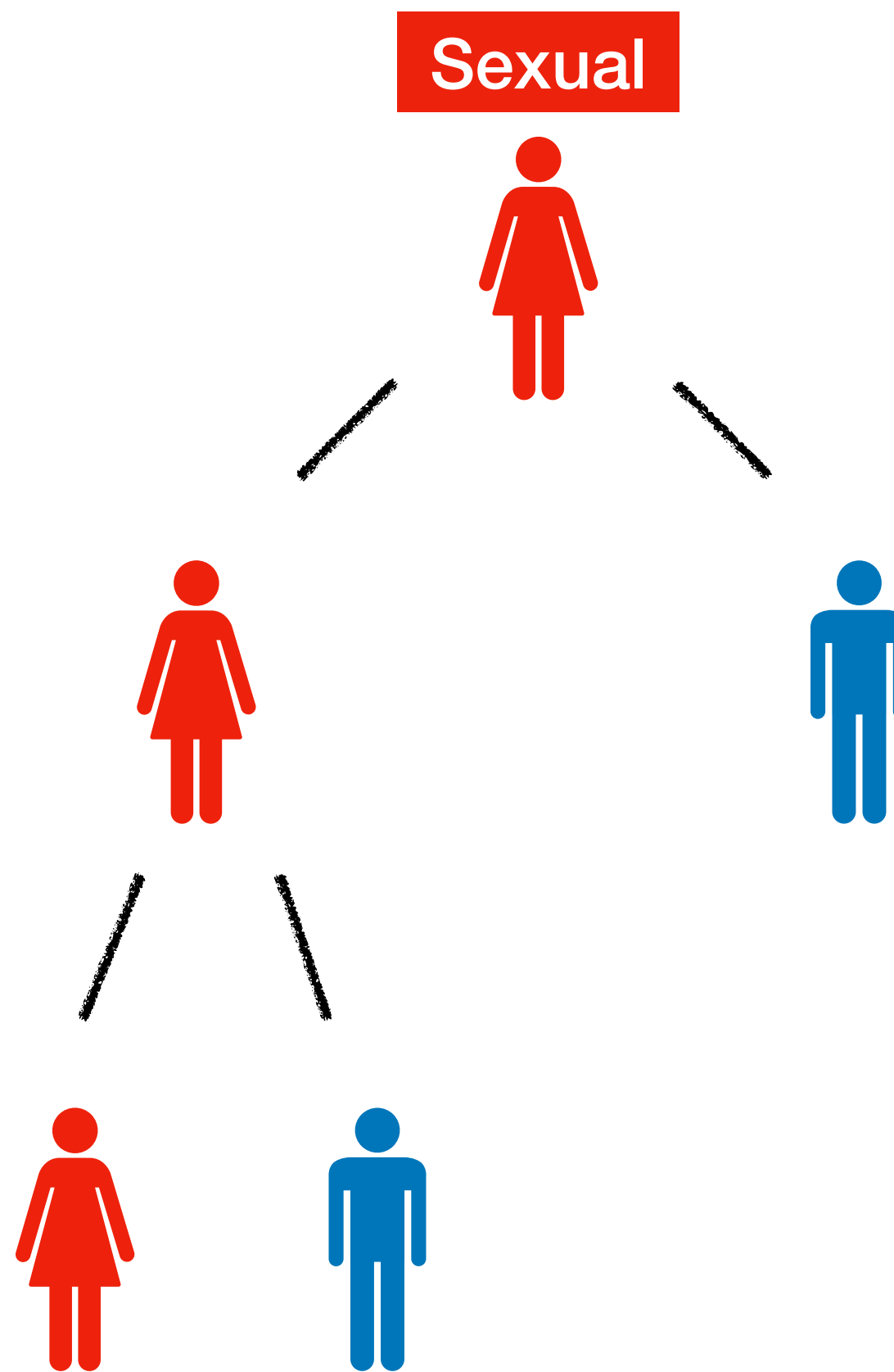
Reproduction is female limited

- Human female record claim: **69** offspring! (First wife of 18th century Russian peasant Fyodor Vassilyev with 16 pairs of twin, 7 sets of triplets and 4 sets of quadruplets)
- Human man record claim: **888** offspring Ismael the Bloodthirsty, emperor of Morocco (1672-1727)



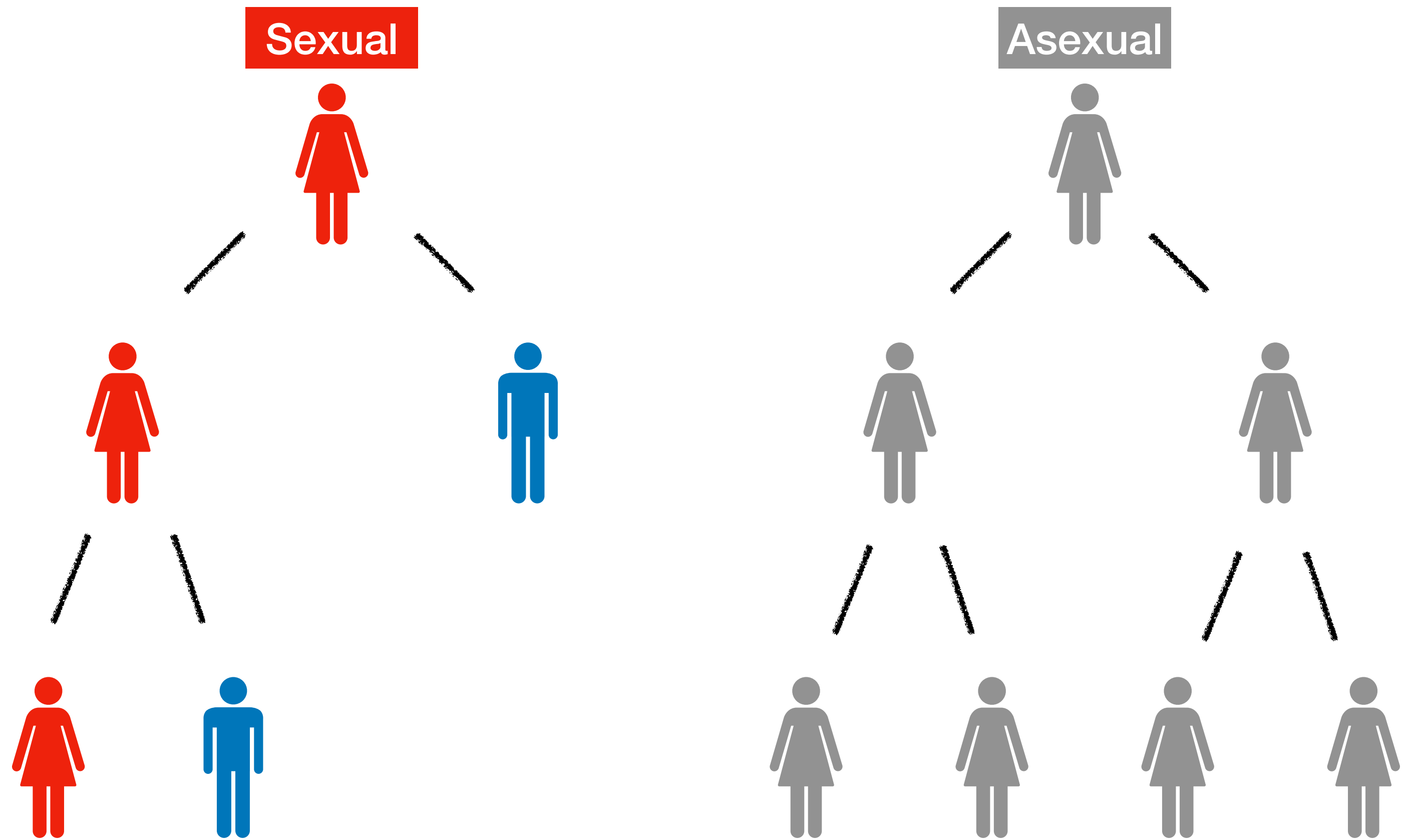
The demographic cost of sex

- For every daughter a sexual female makes, an asexual makes two.



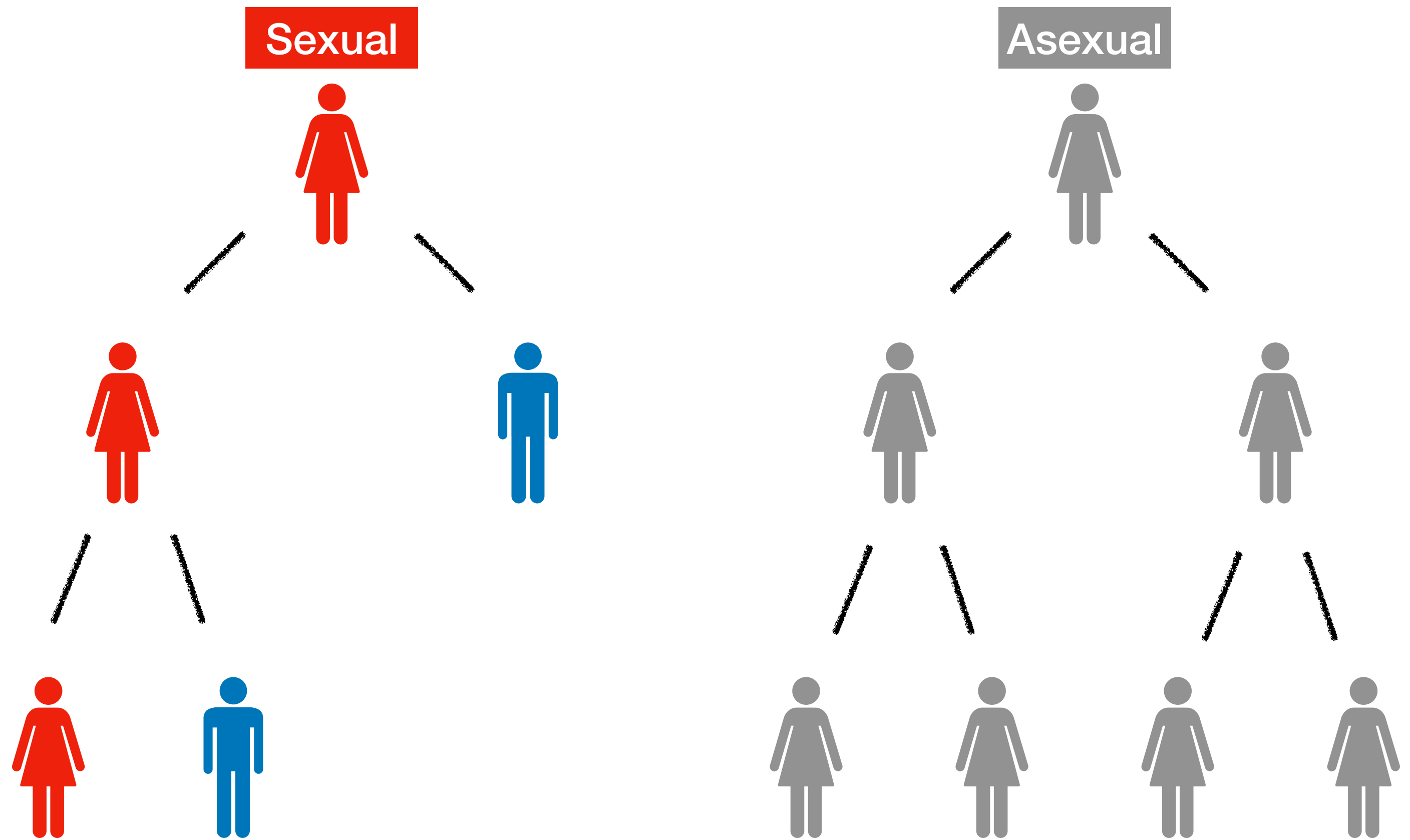
The demographic cost of sex

- For every daughter a sexual female makes, an asexual makes two.



The demographic cost of sex

- For every daughter a sexual female makes, an asexual makes two.
- Asexuals have a huge demographic advantage and should easily outcompete sexual.



The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems

The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet

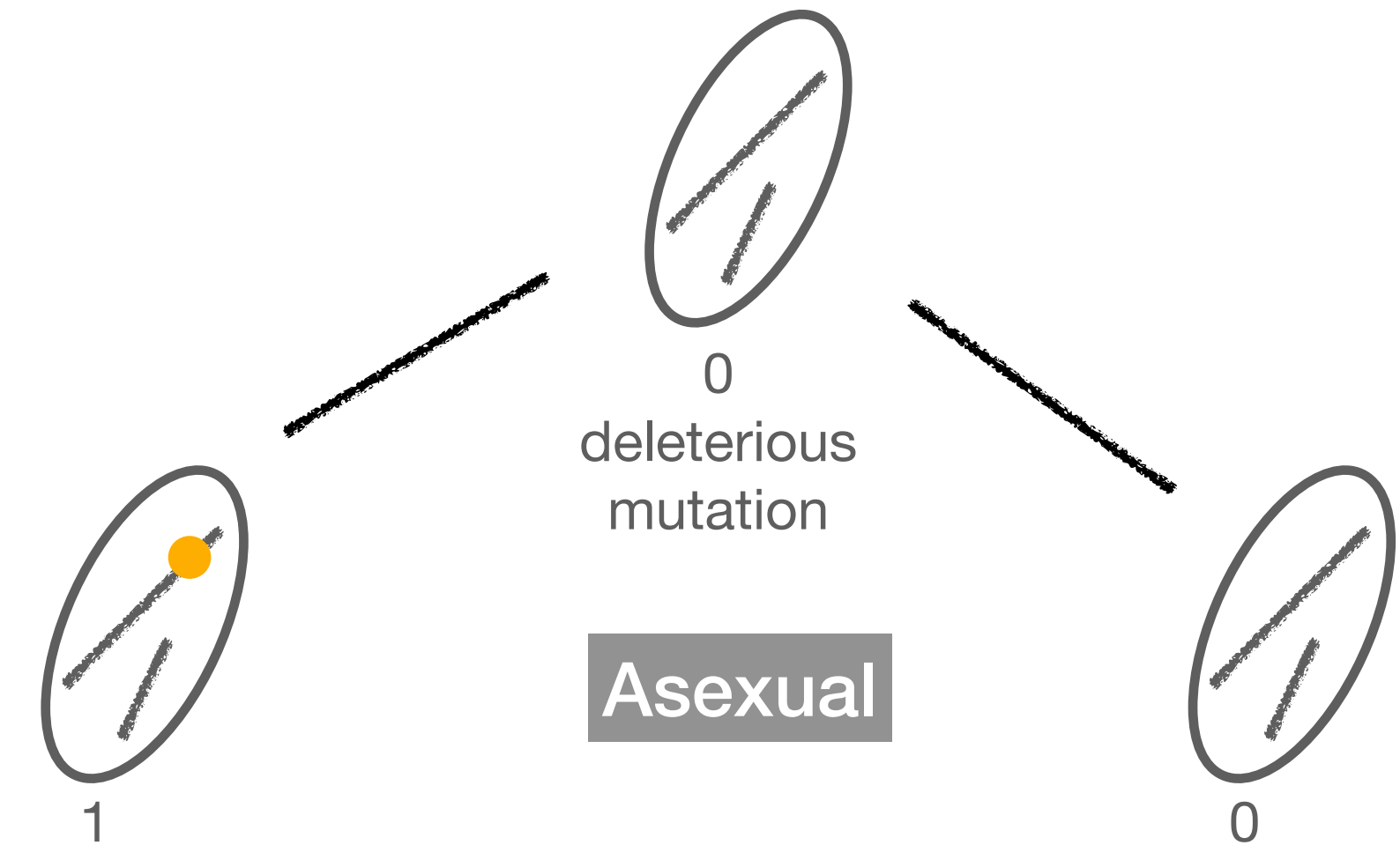
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
- Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet



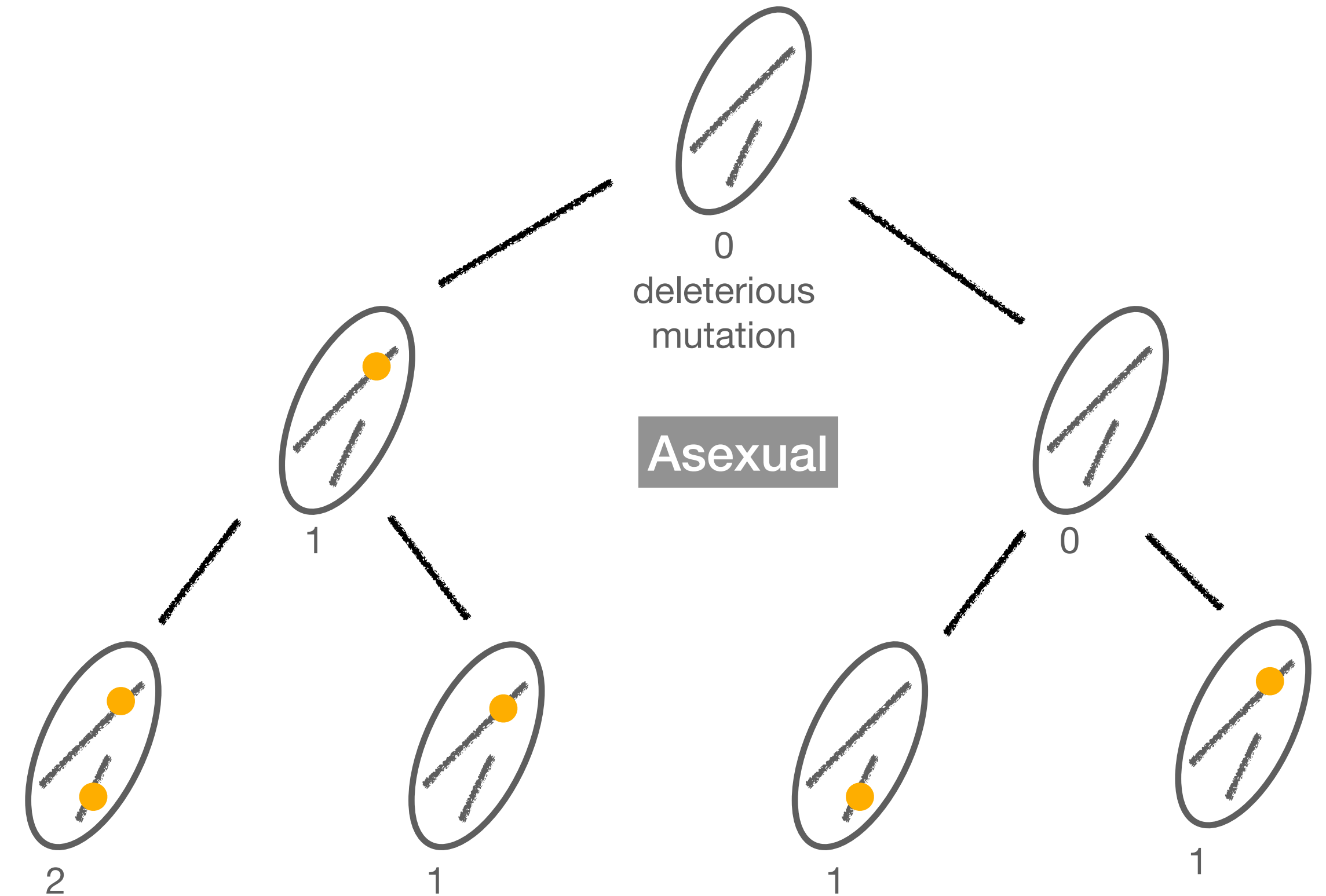
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet



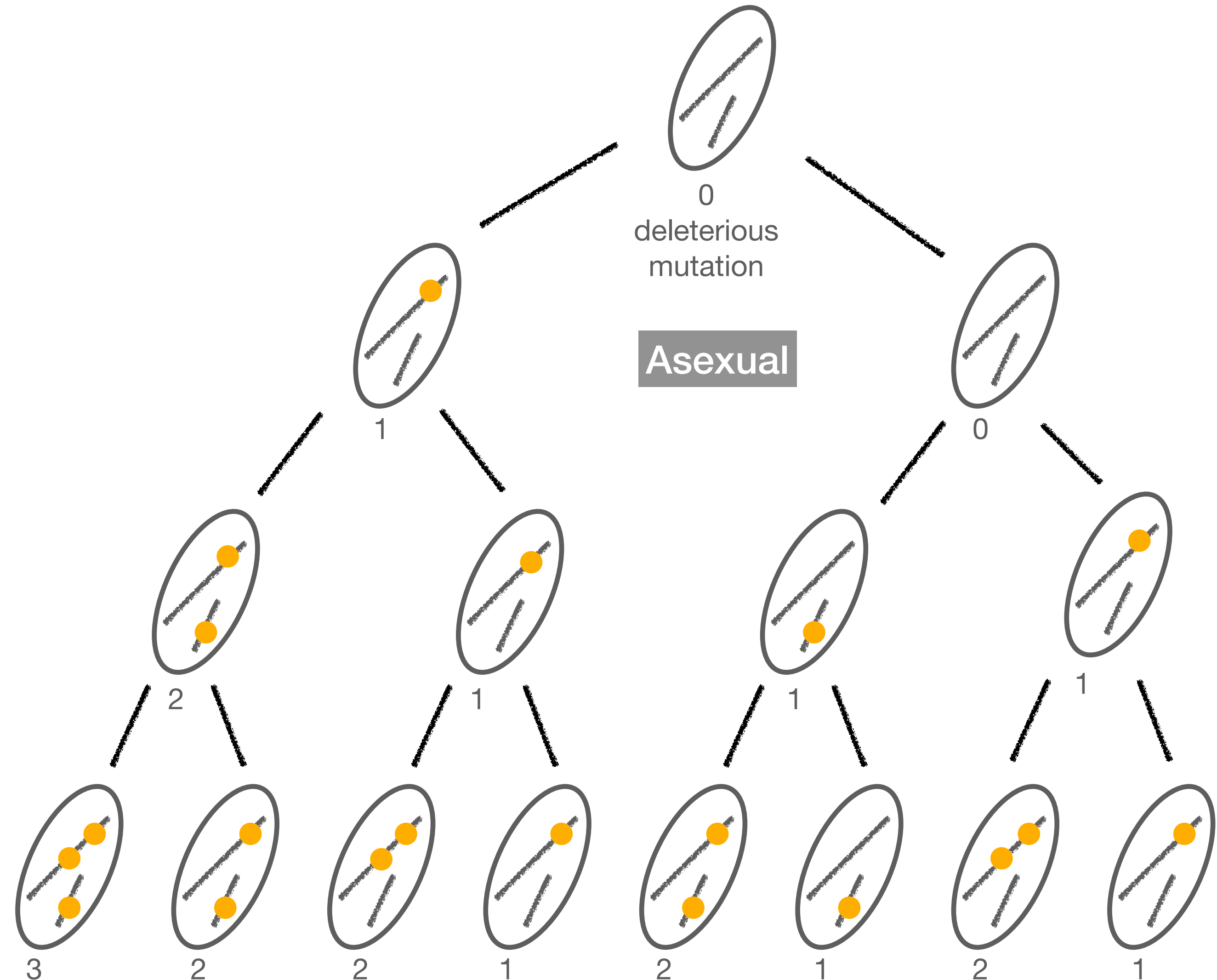
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
- Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet



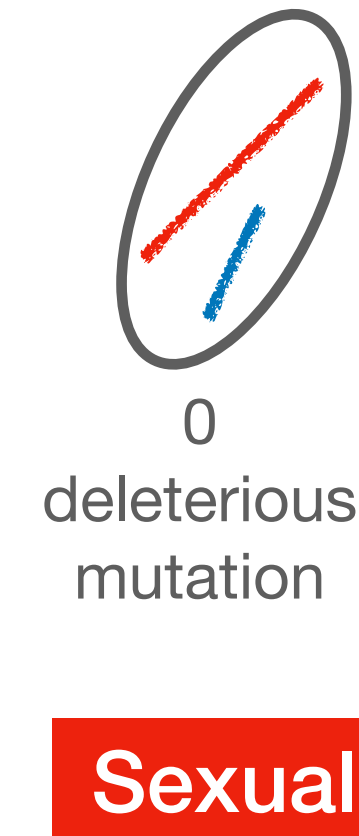
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
- Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet



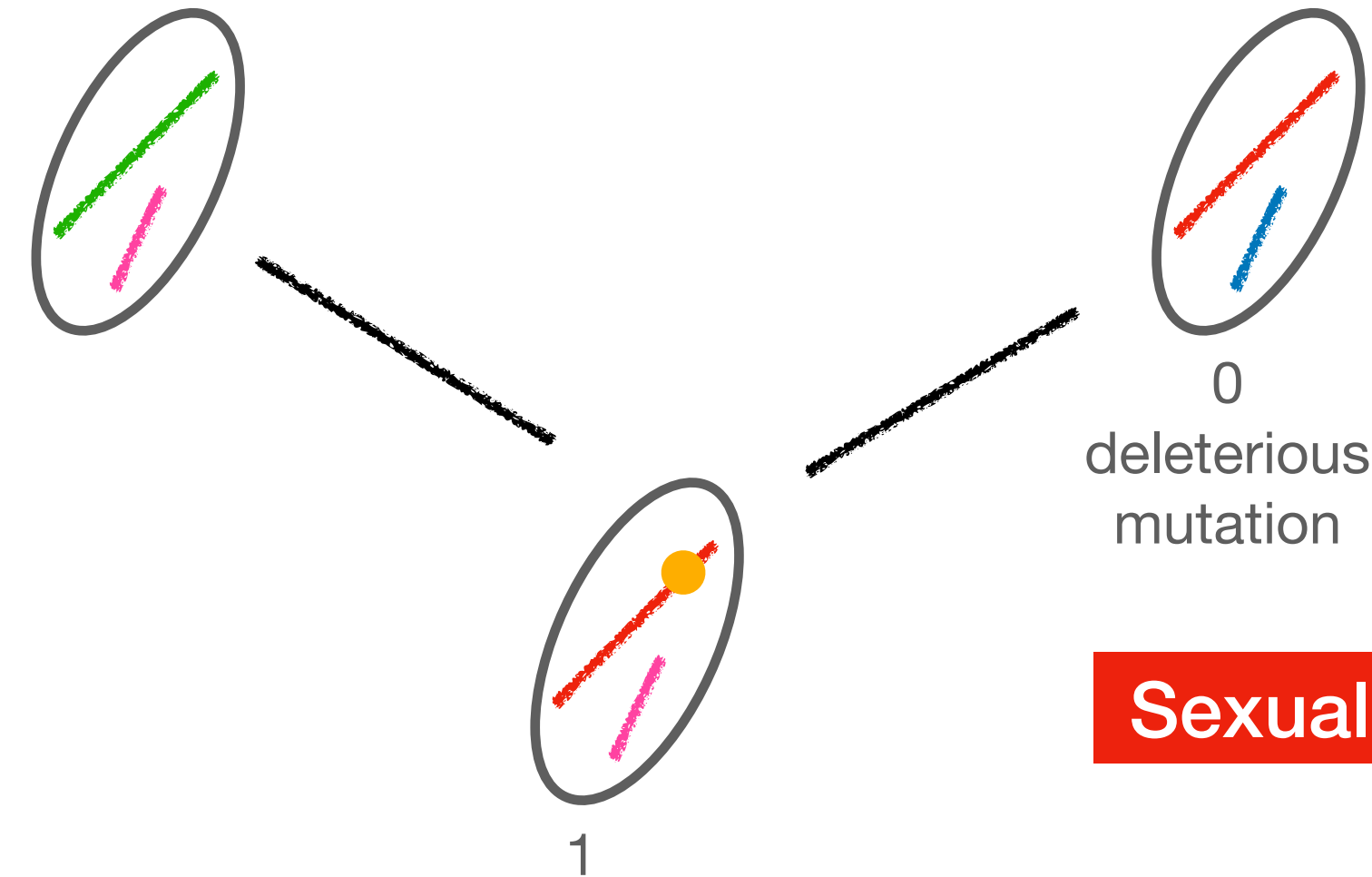
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
- Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet



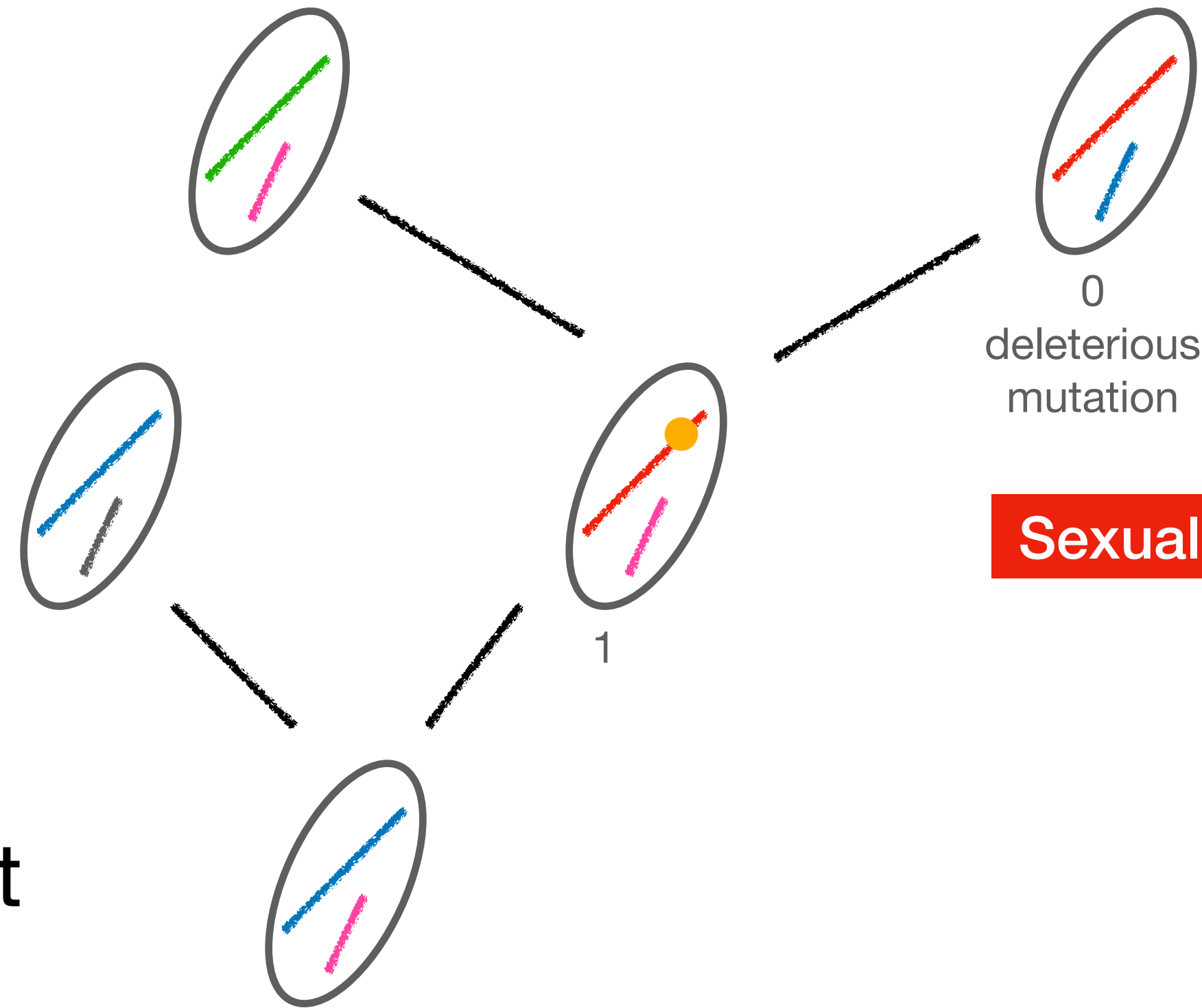
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet



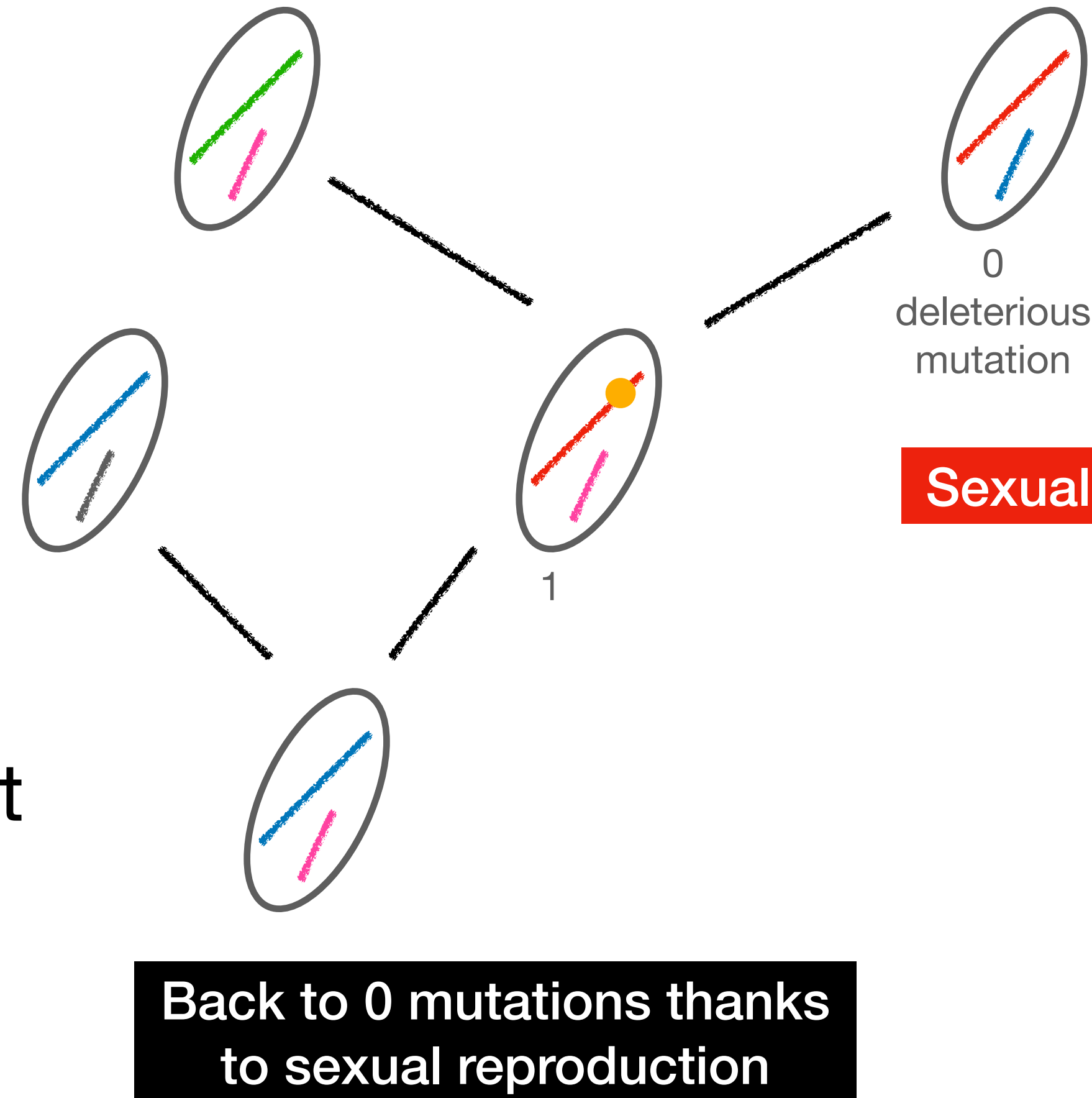
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
- Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet



The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
- Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet

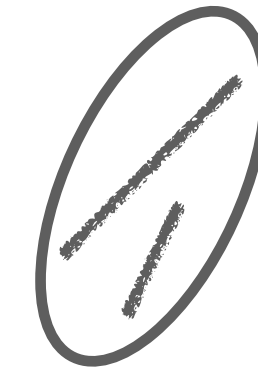


The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet
 - Difficulty to combine advantageous mutations in different parts of the genomes, i.e. difficult to adapt

The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet
 - Difficulty to combine advantageous mutations in different parts of the genomes, i.e. difficult to adapt

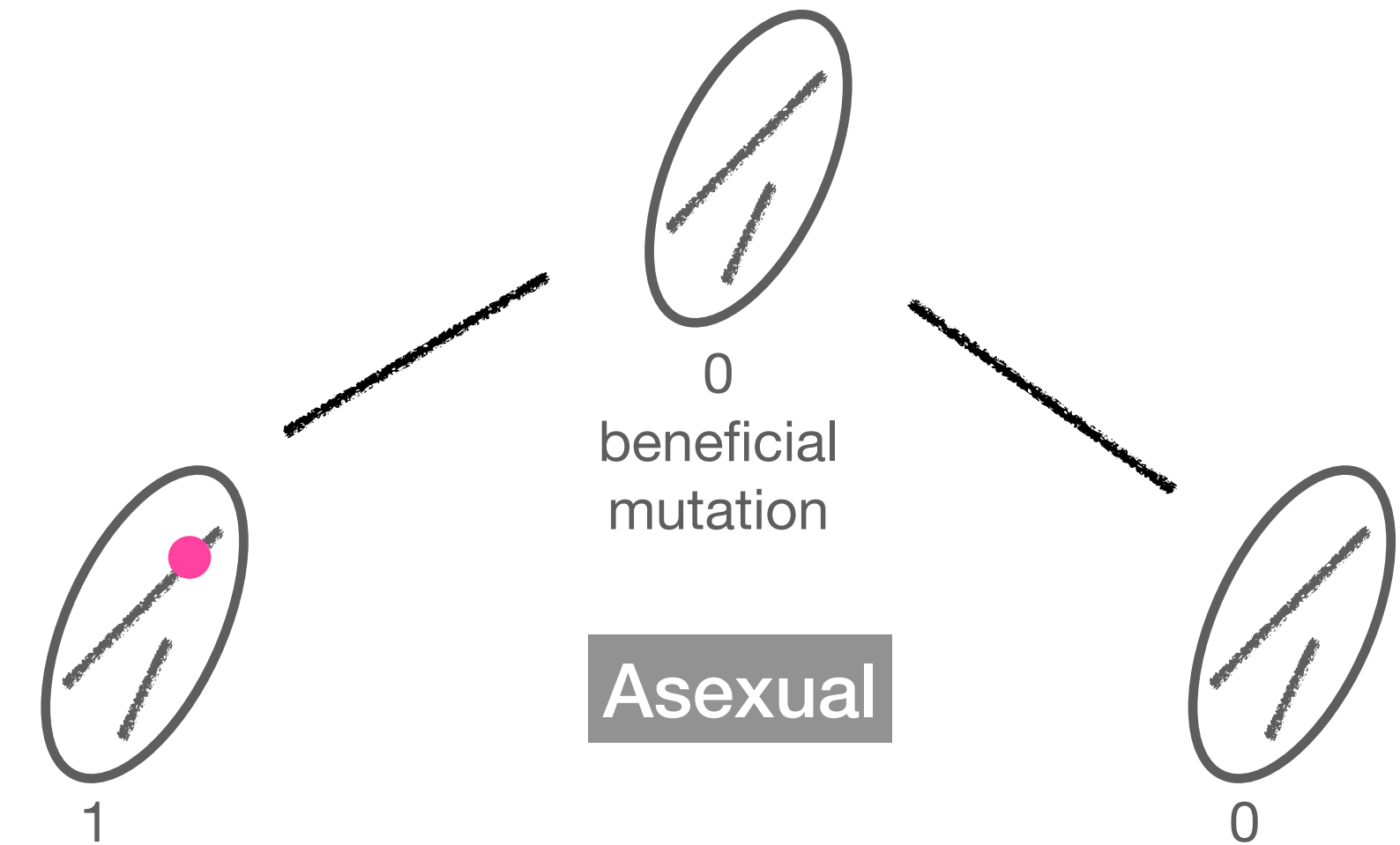


0
beneficial
mutation

Asexual

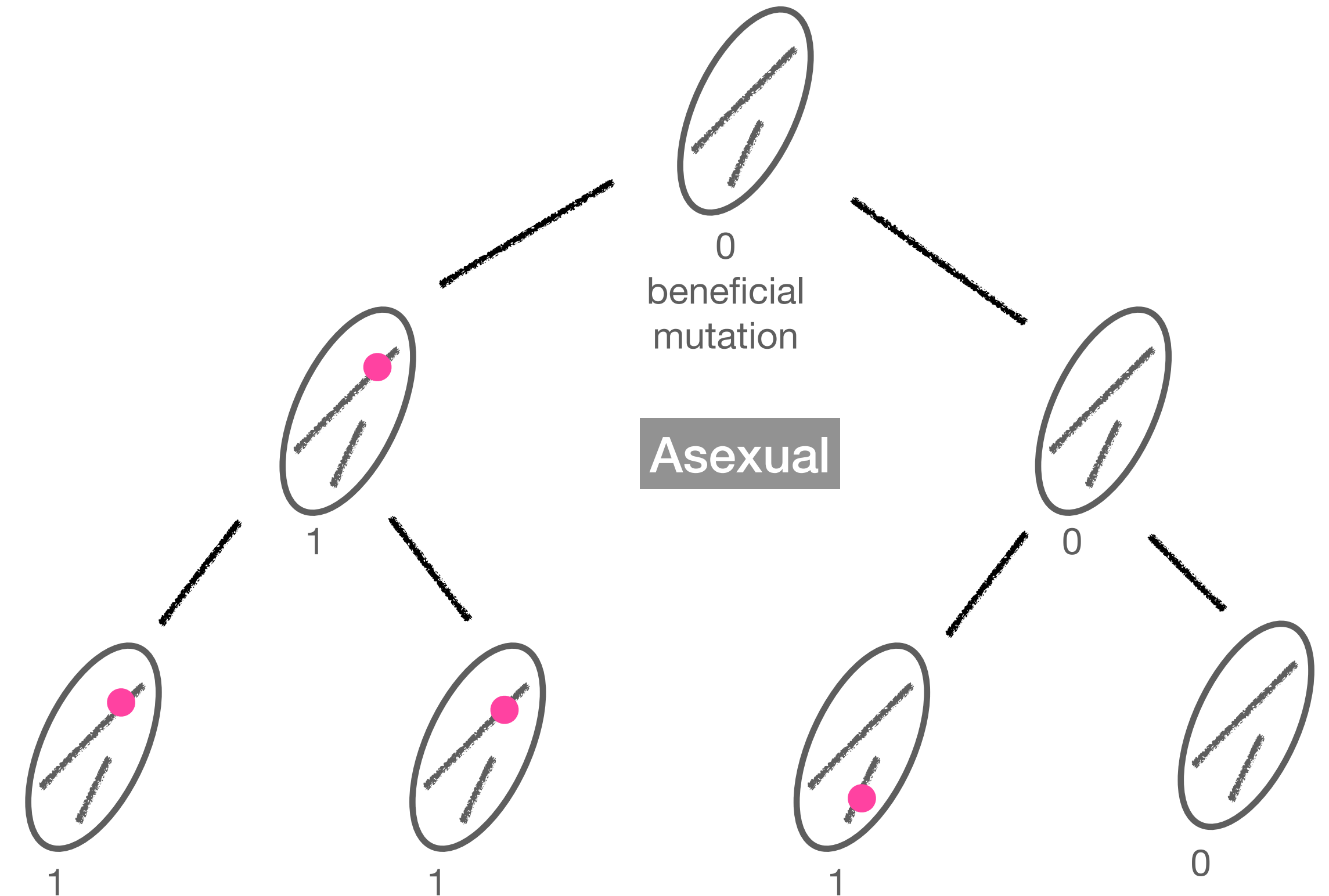
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet
 - Difficulty to combine advantageous mutations in different parts of the genomes, i.e. difficult to adapt



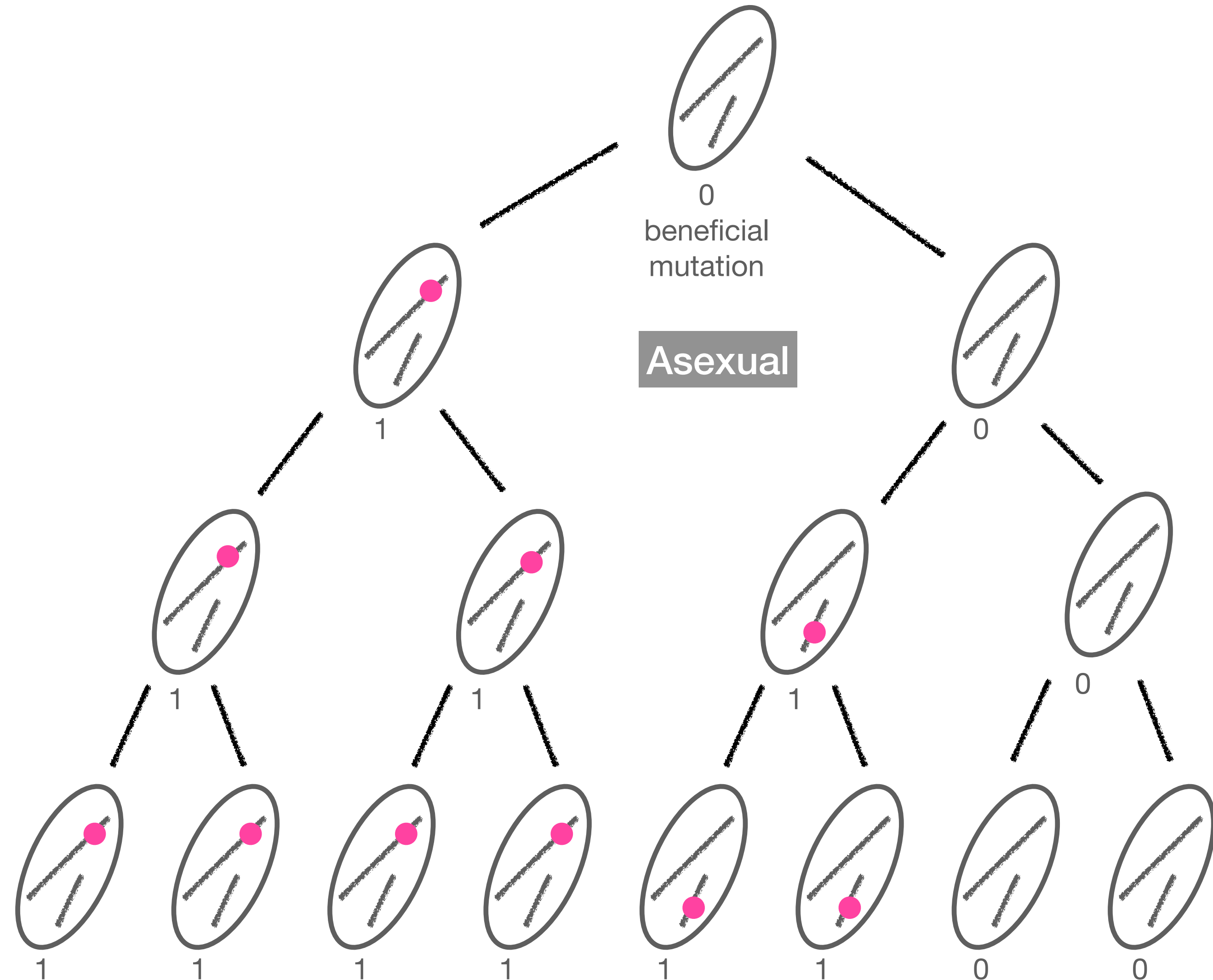
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet
 - Difficulty to combine advantageous mutations in different parts of the genomes, i.e. difficult to adapt



The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet
 - Difficulty to combine advantageous mutations in different parts of the genomes, i.e. difficult to adapt



The evolutionary cost of asexuality

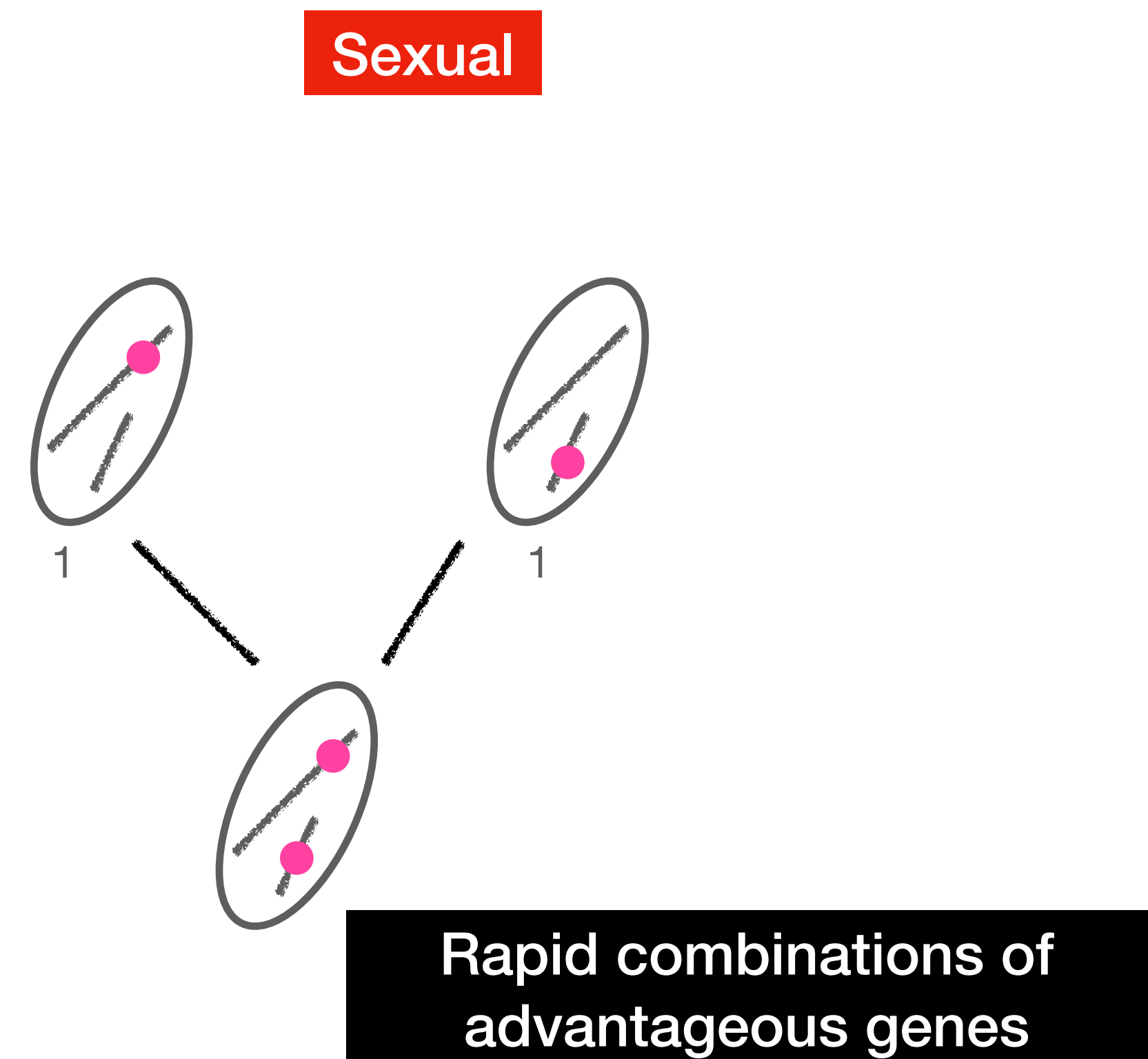
- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet
 - Difficulty to combine advantageous mutations in different parts of the genomes, i.e. difficult to adapt

Sexual



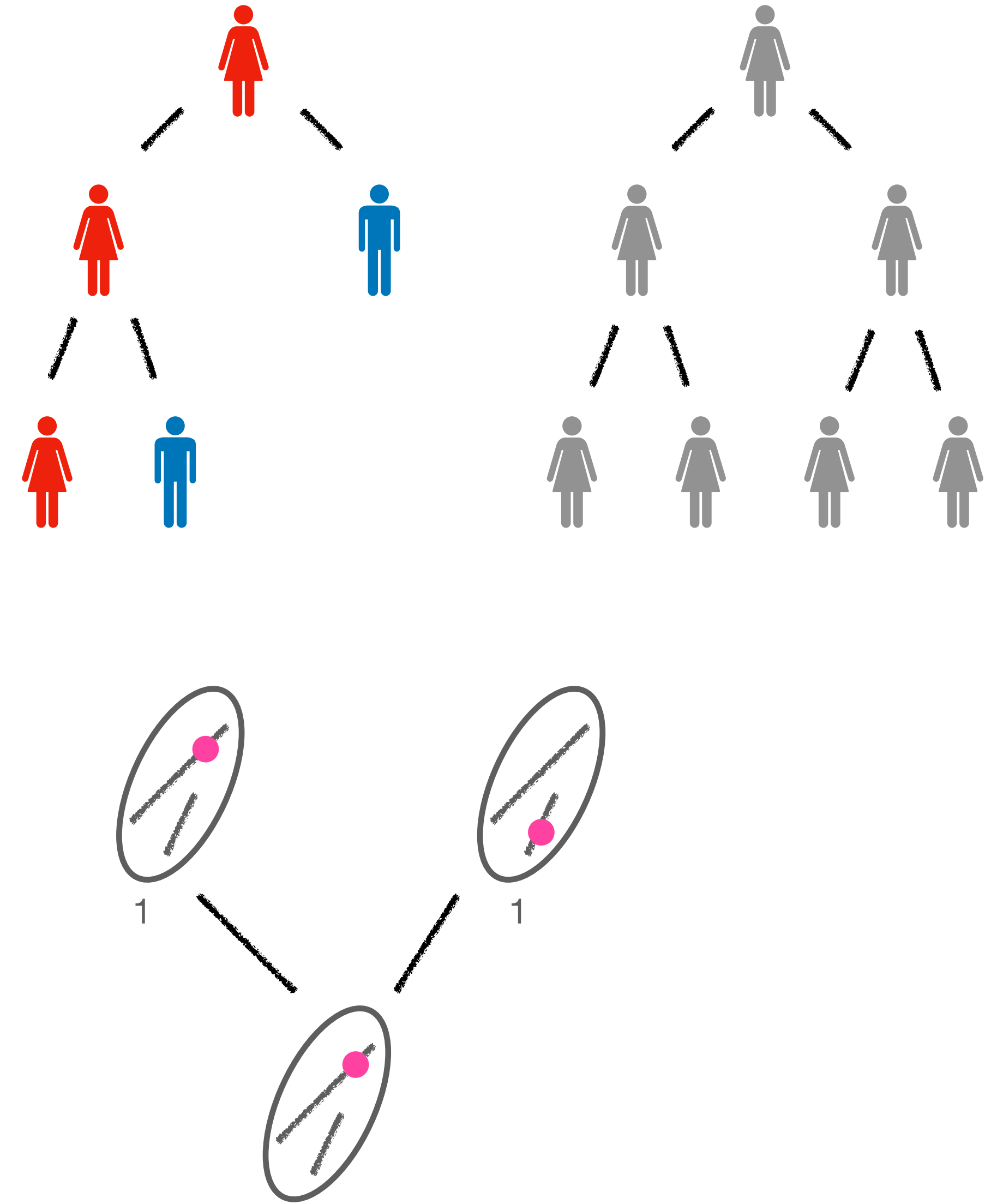
The evolutionary cost of asexuality

- By not allowing their genomes to mix, asexuals face two potential problems
 - Accumulation of deleterious mutations (especially in small populations) aka Muller's ratchet
 - Difficulty to combine advantageous mutations in different parts of the genomes, i.e. difficult to adapt



Summary

- Sex = production of new organisms by the combination of genetic information of two individuals.
- Males = many small gametes (sperm). Females = fewer larger gametes (egg).
- Population growth is female limited.
- Two-fold demographic cost of sex.
- Asexuals accumulate more deleterious mutations and adapt less efficiently than sexual.



The maintenance of sex

The problem

How to overcome the twofold cost?

- Rapid demographic advantage versus slow evolutionary cost of asexuality

The problem

How to overcome the twofold cost?

- Rapid demographic advantage versus slow evolutionary cost of asexuality

Fecundity

$$f(k) \propto (1 - s)^k$$

Number of deleterious mutations

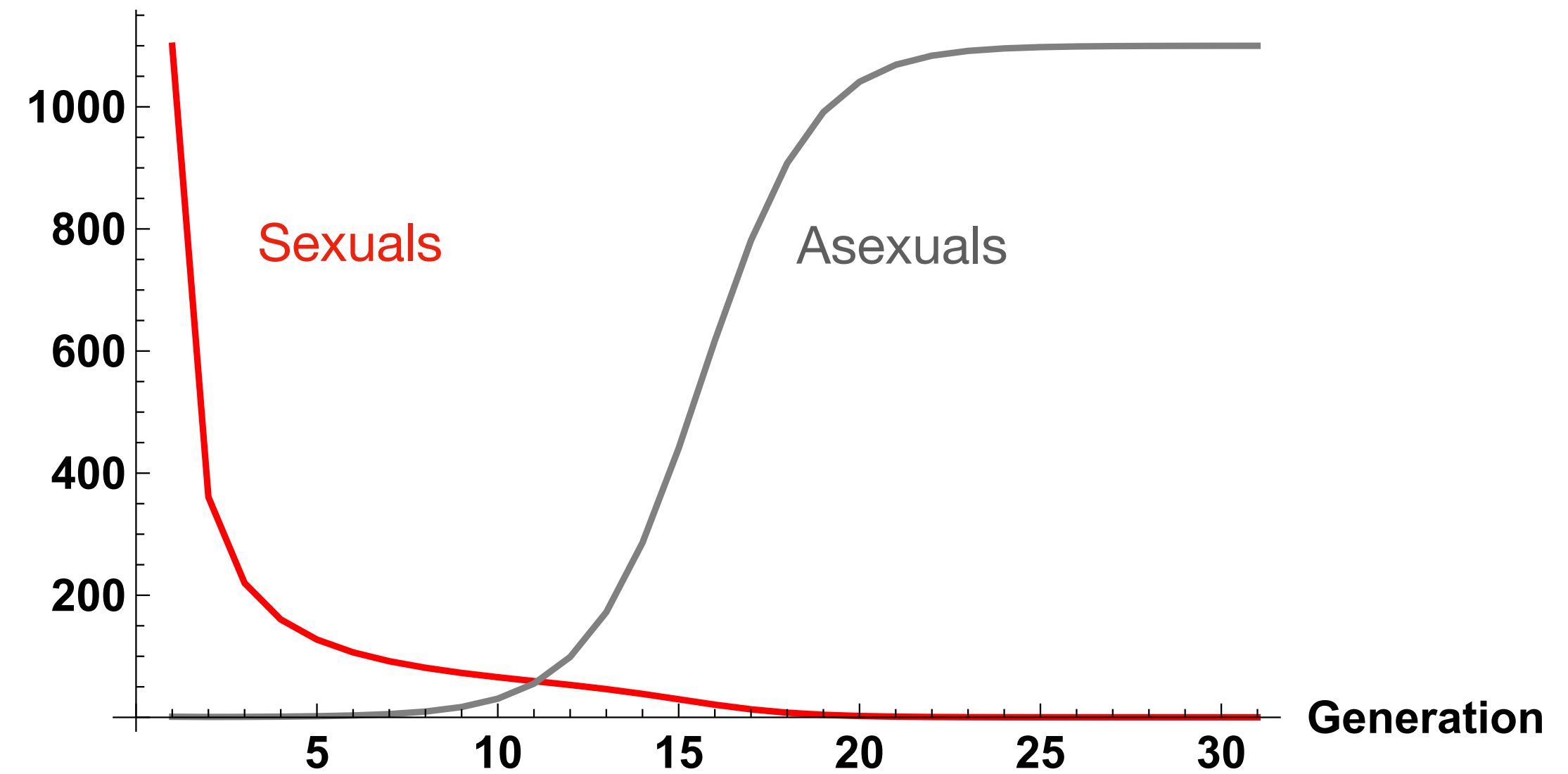
Effect of single mutation

The problem

How to overcome the twofold cost?

- Rapid demographic advantage versus slow evolutionary cost of asexuality

Number of females



Fecundity

$$f(k) \propto (1 - s)^k$$

Number of deleterious mutations

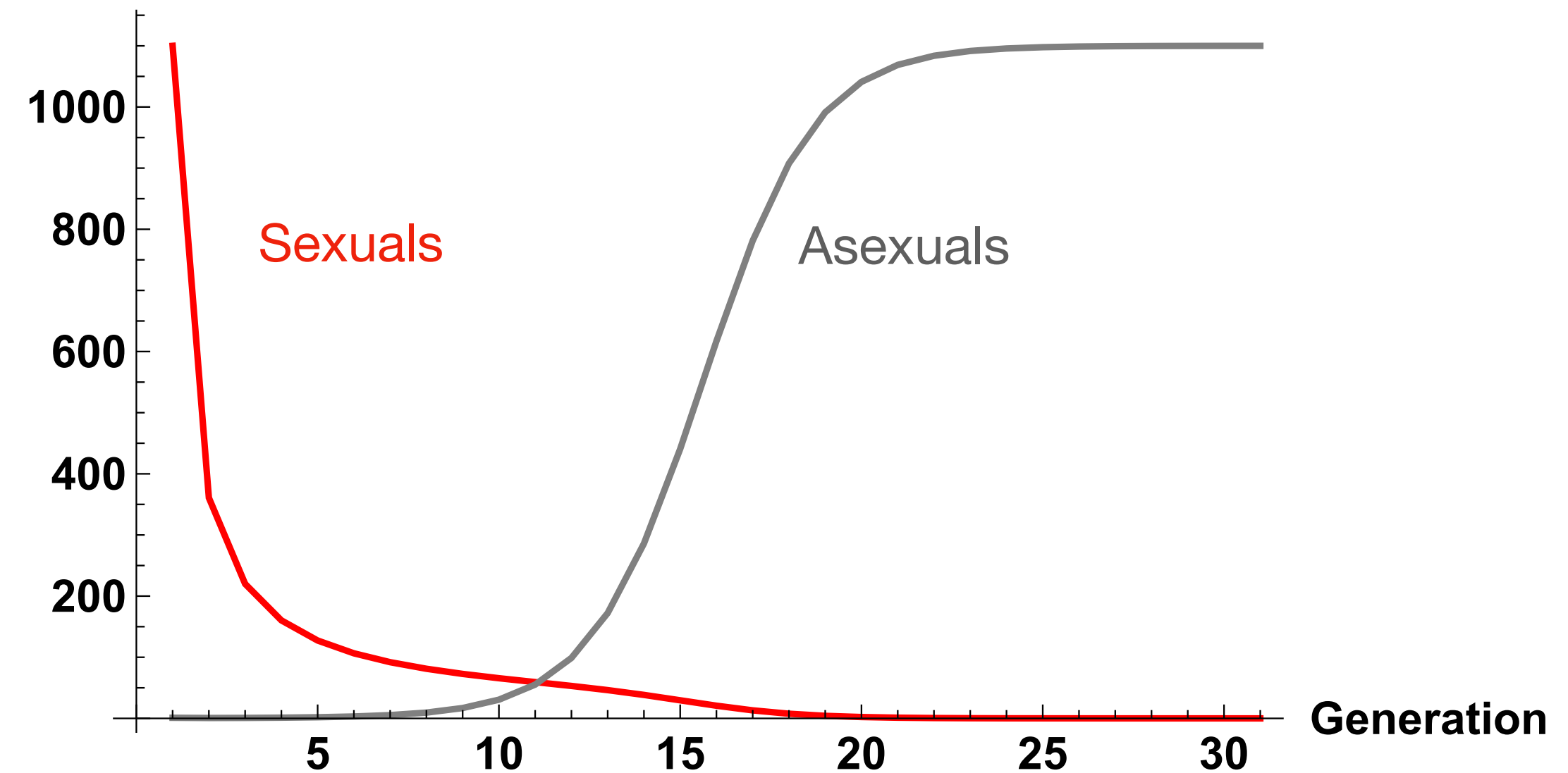
Effect of single mutation

The problem

How to overcome the twofold cost?

- Rapid demographic advantage versus slow evolutionary cost of asexuality

Number of females



Fecundity

$$f(k) \propto (1 - s)^k$$

Number of deleterious mutations

Effect of single mutation

$$f(k_A) < \frac{f(k_S)}{2}$$

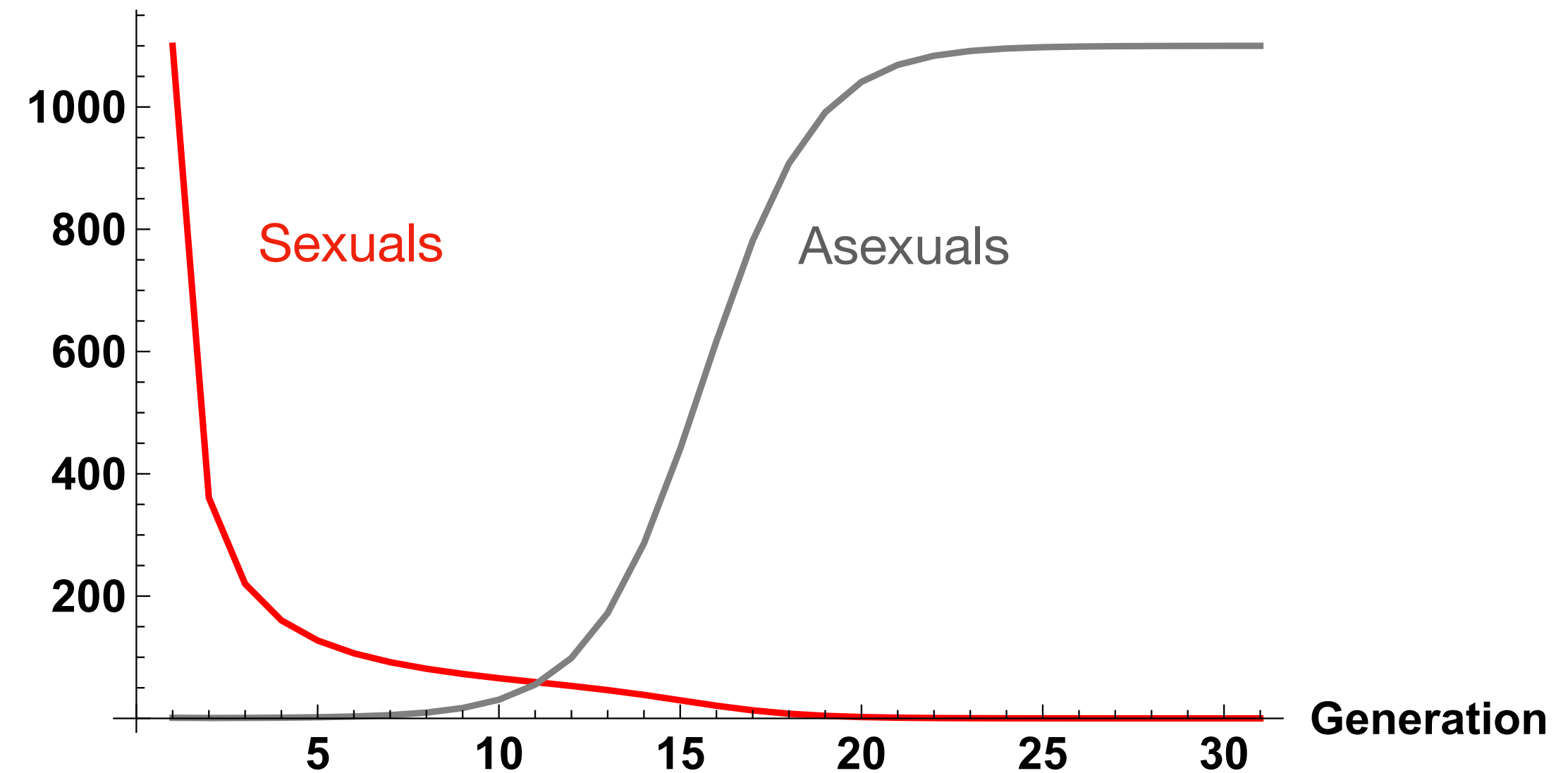
condition for maintenance of sex due to deleterious mutations

The problem

How to overcome the twofold cost?

- Rapid demographic advantage versus slow evolutionary cost of asexuality

Number of females



Fecundity

$$f(k) \propto (1 - s)^k$$

Number of deleterious mutations

Effect of single mutation

$$f(k_A) < \frac{f(k_S)}{2} \iff (1 - s)^{k_A - k_S} < \frac{1}{2}$$

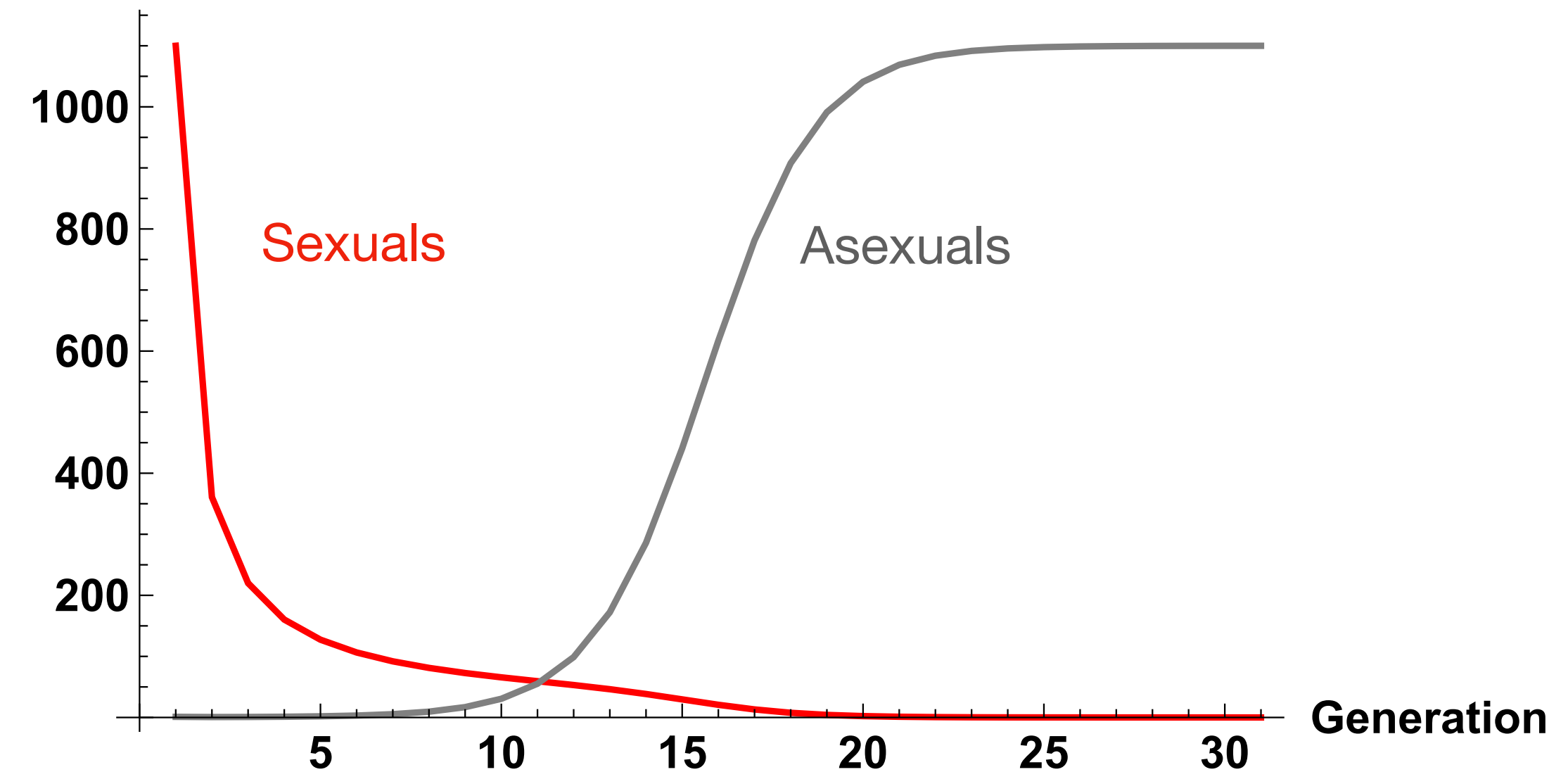
condition for maintenance of sex due to deleterious mutations

The problem

How to overcome the twofold cost?

- Rapid demographic advantage versus slow evolutionary cost of asexuality

Number of females



Fecundity

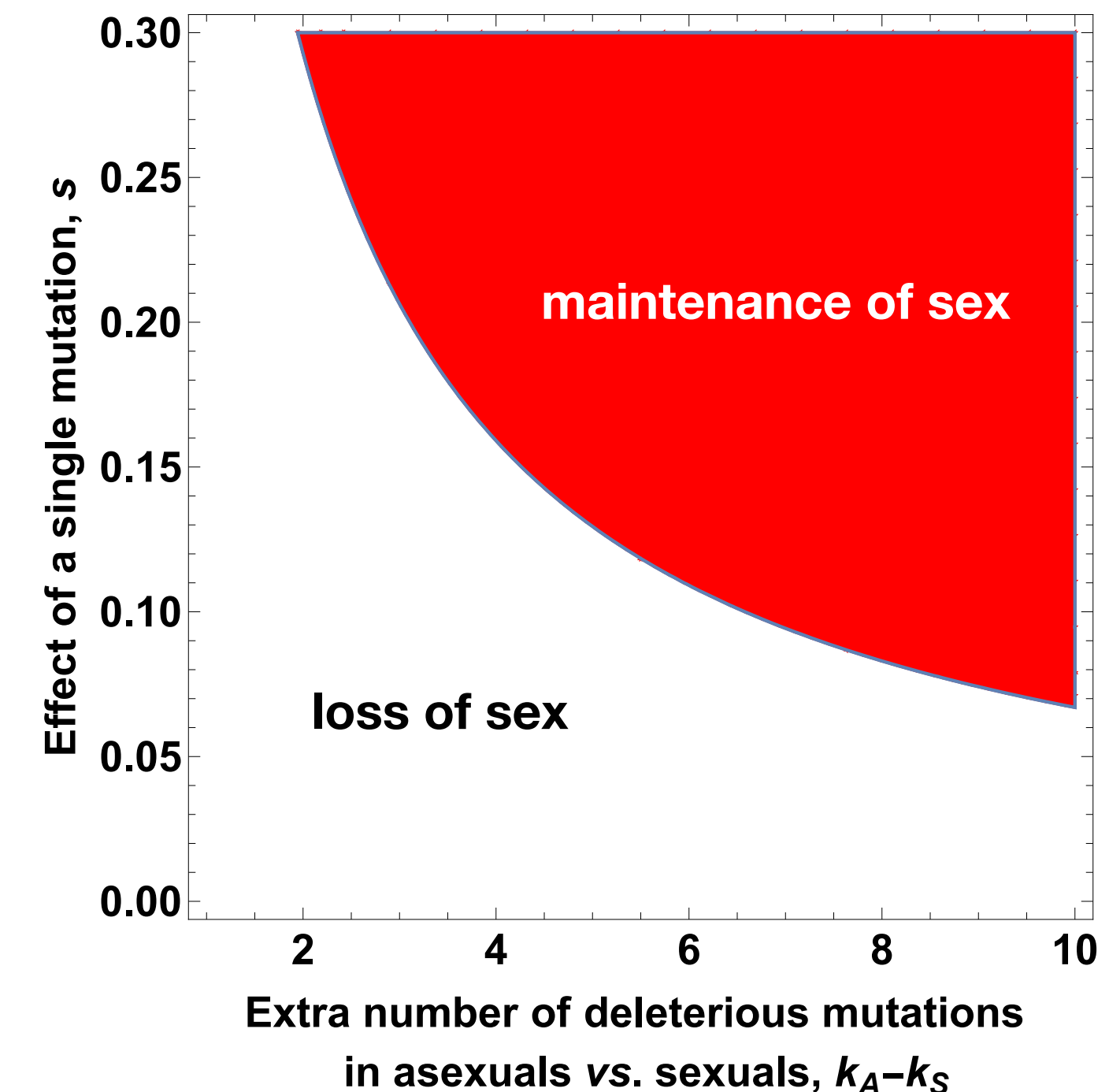
$$f(k) \propto (1 - s)^k$$

Number of deleterious mutations

Effect of single mutation

$$f(k_A) < \frac{f(k_S)}{2} \iff (1 - s)^{k_A - k_S} < \frac{1}{2}$$

condition for maintenance of sex due to deleterious mutations



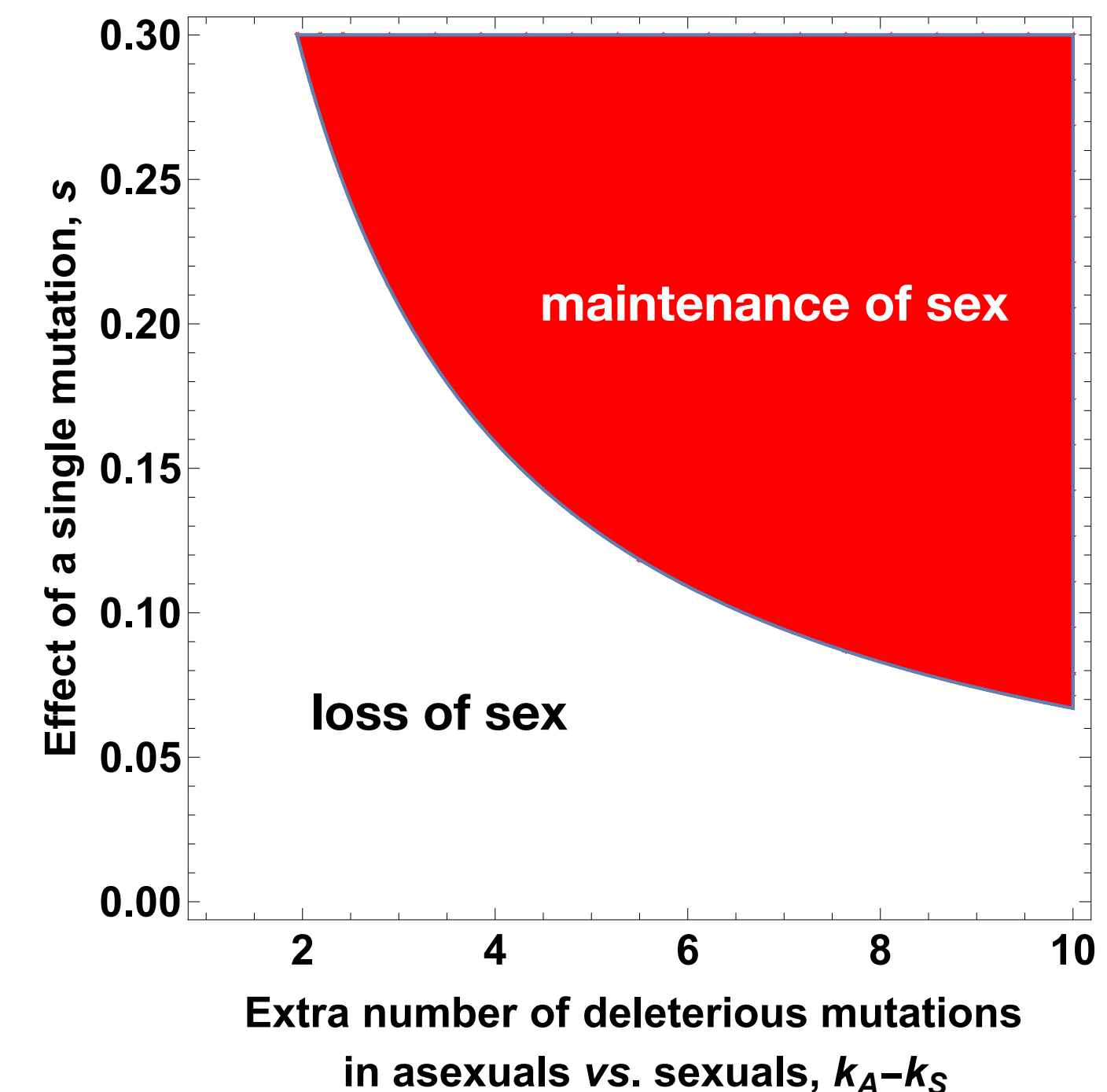
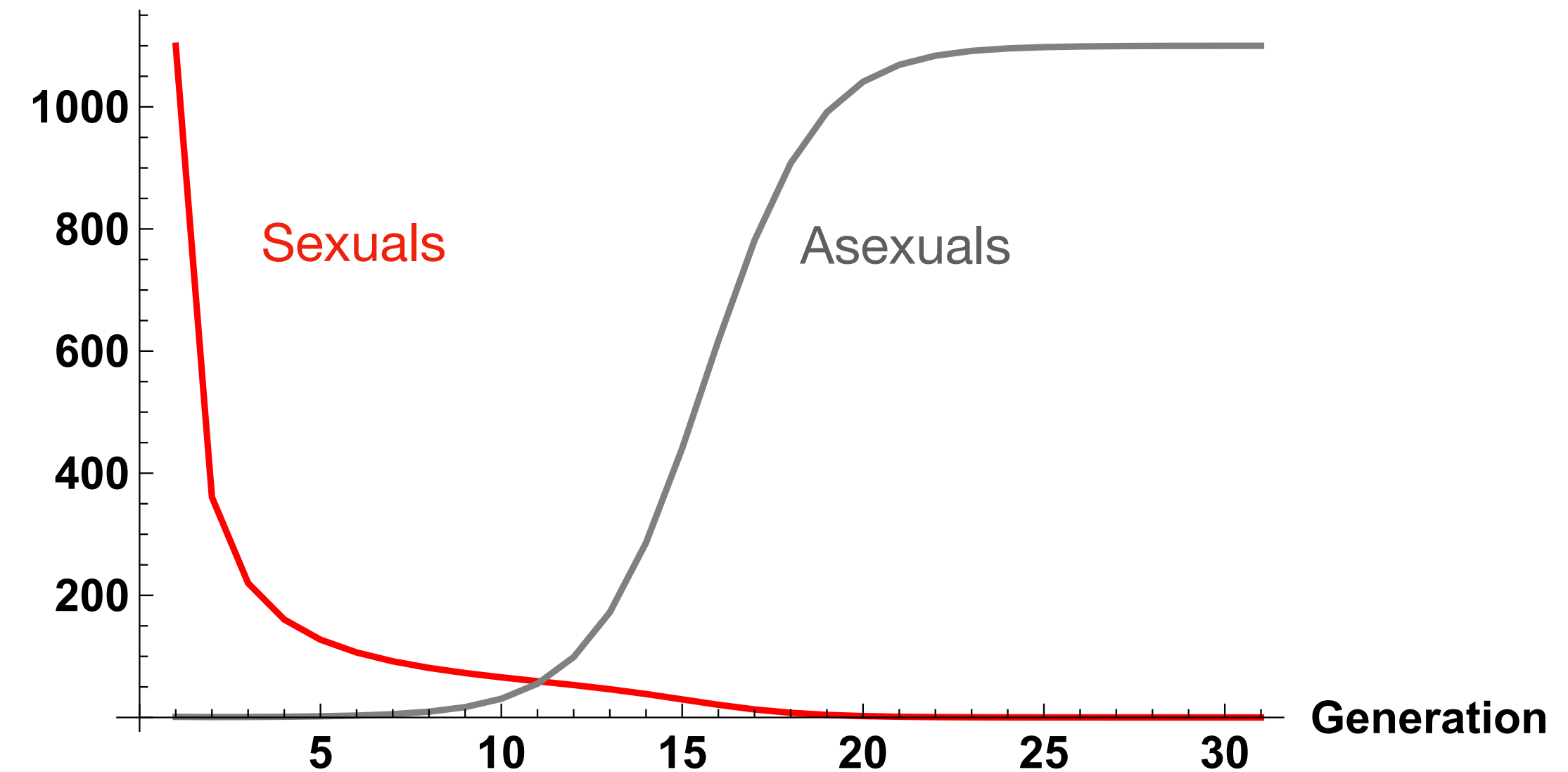
The problem

How to overcome the twofold cost?

- Rapid demographic advantage versus slow evolutionary cost of asexuality

Assuming an asexual is initially equivalent to a sexual, deleterious mutations must accumulate impossibly fast or have unrealistically large fitness effects for sexuality to be maintained.

Number of females

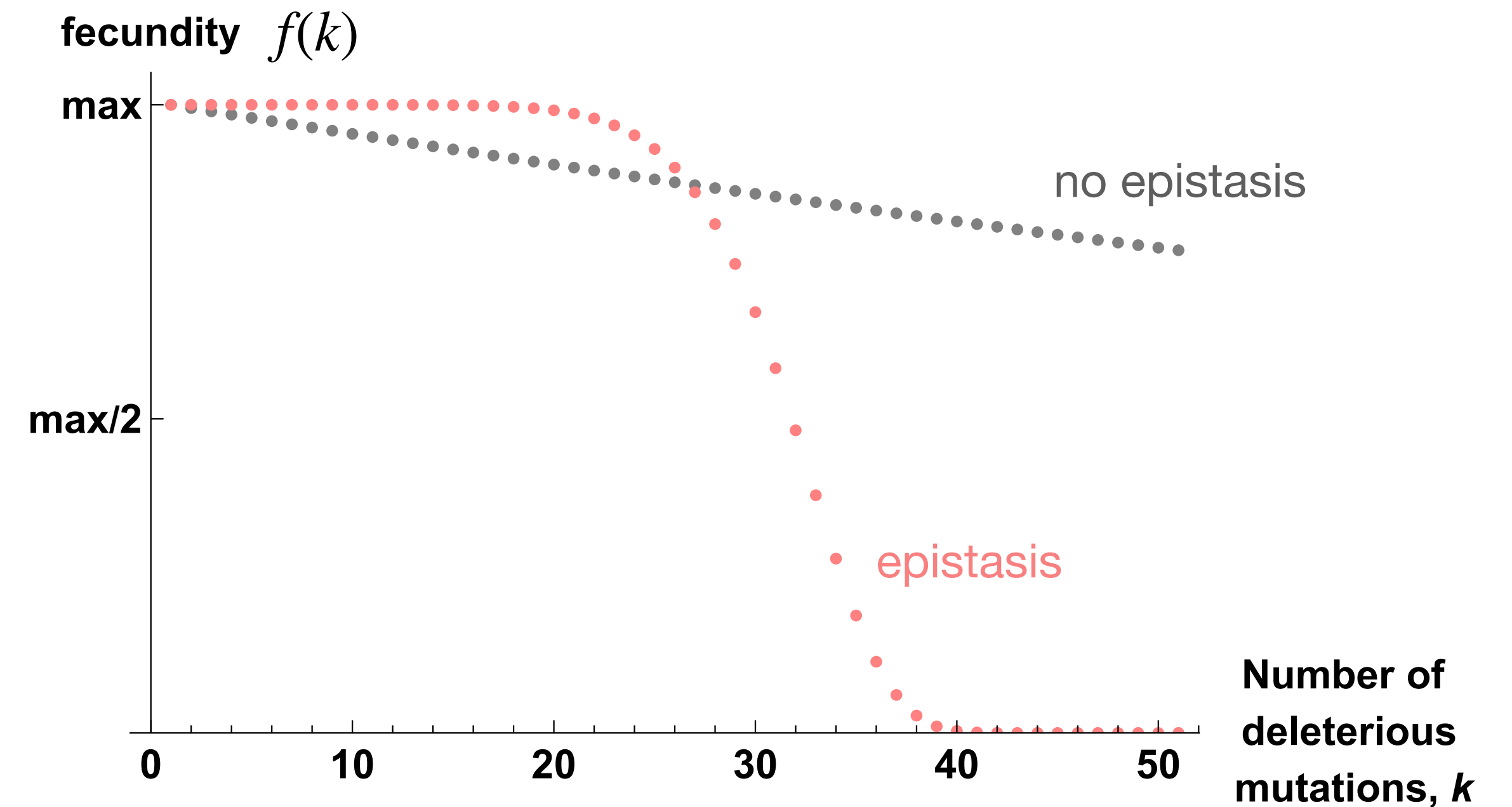


Can strong epistasis rescue sexuals?

- Epistasis = non-additive fitness effects among loci

Can strong epistasis rescue sexuals?

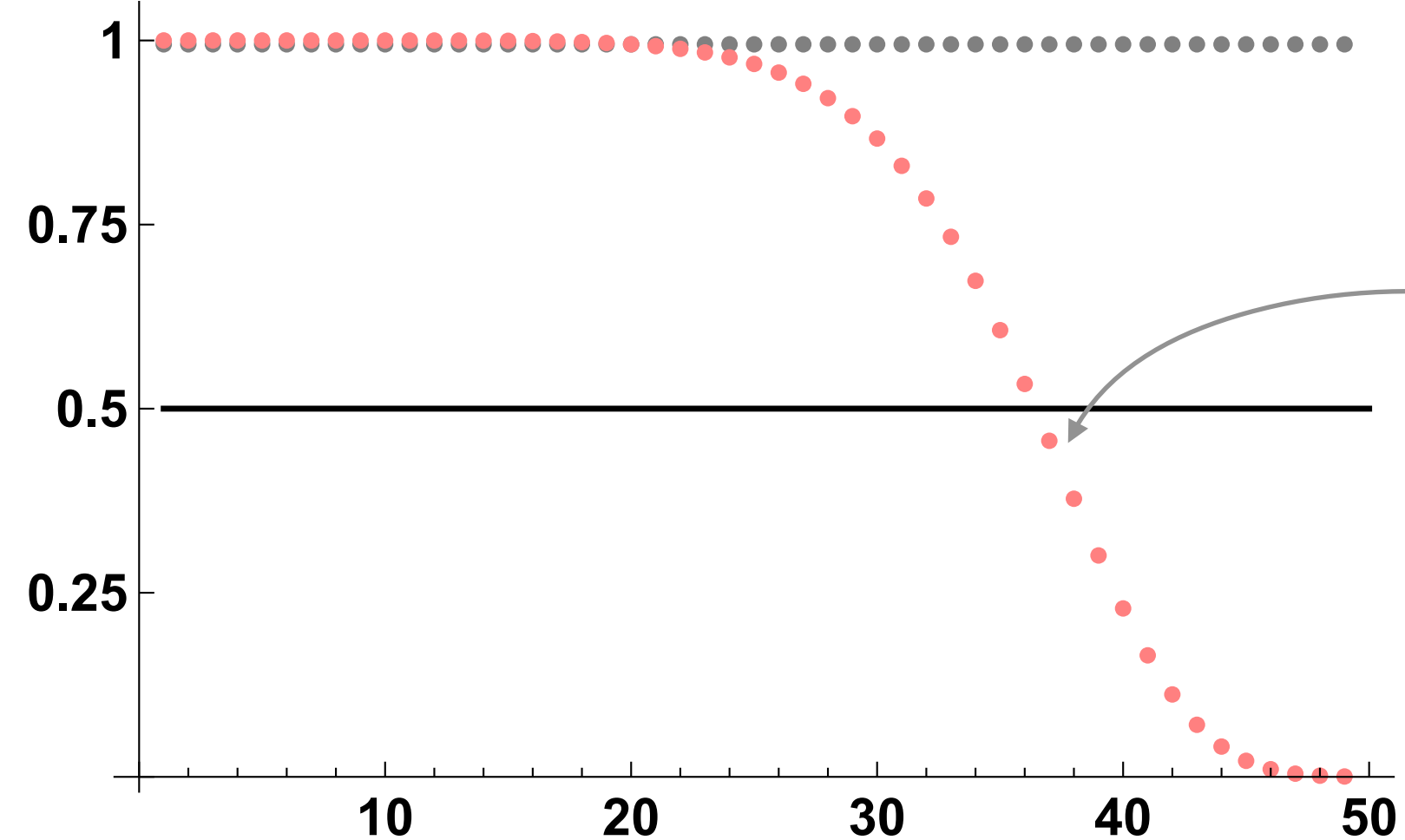
- Epistasis = non-additive fitness effects among loci
- Allows for an abrupt decrease in fitness with number of deleterious mutations



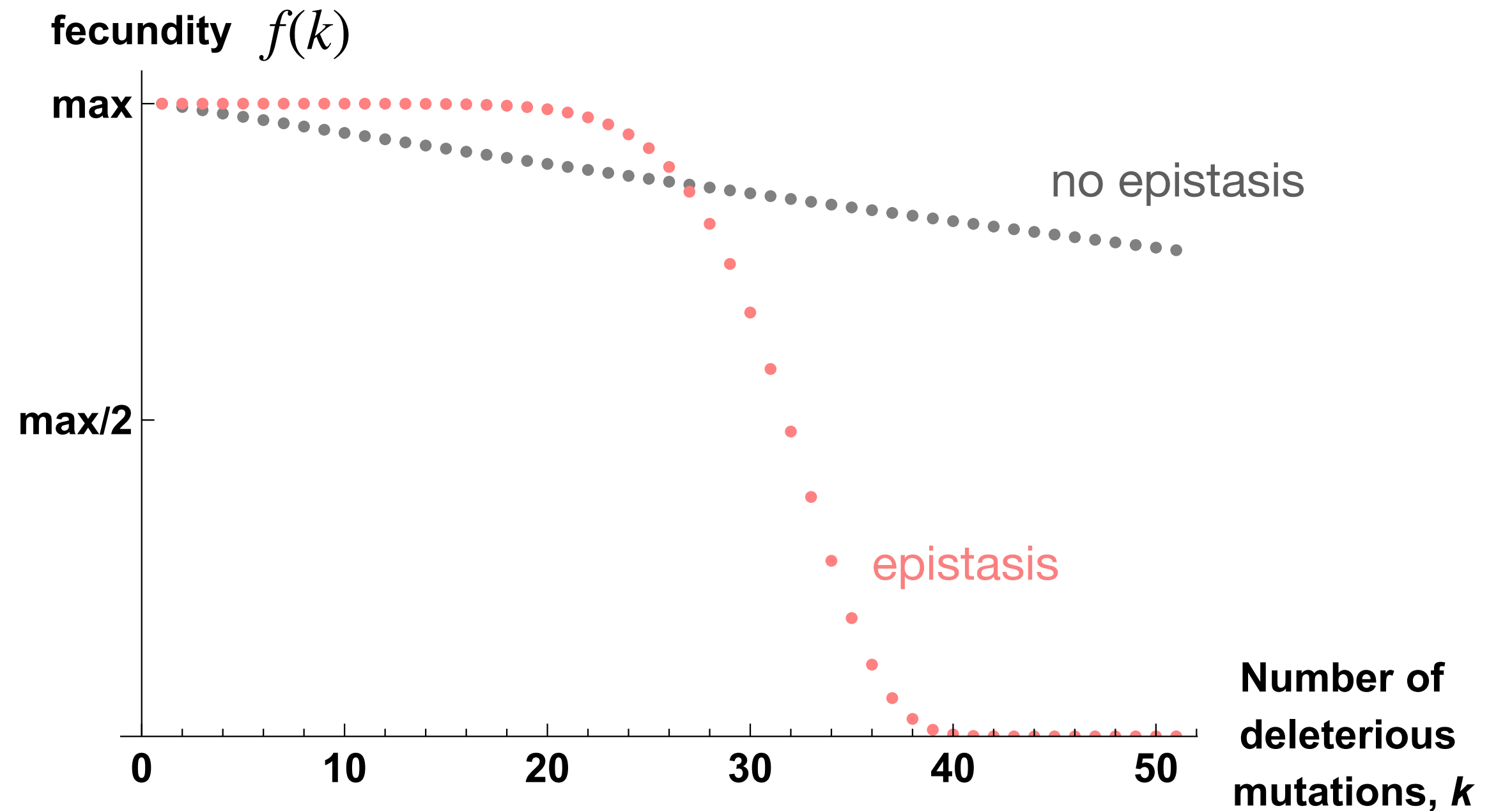
Can strong epistasis rescue sexuals?

- Epistasis = non-additive fitness effects among loci
- Allows for an abrupt decrease in fitness with number of deleterious mutations

Fecundity effect of one extra mutation $f(k+1)/f(k)$

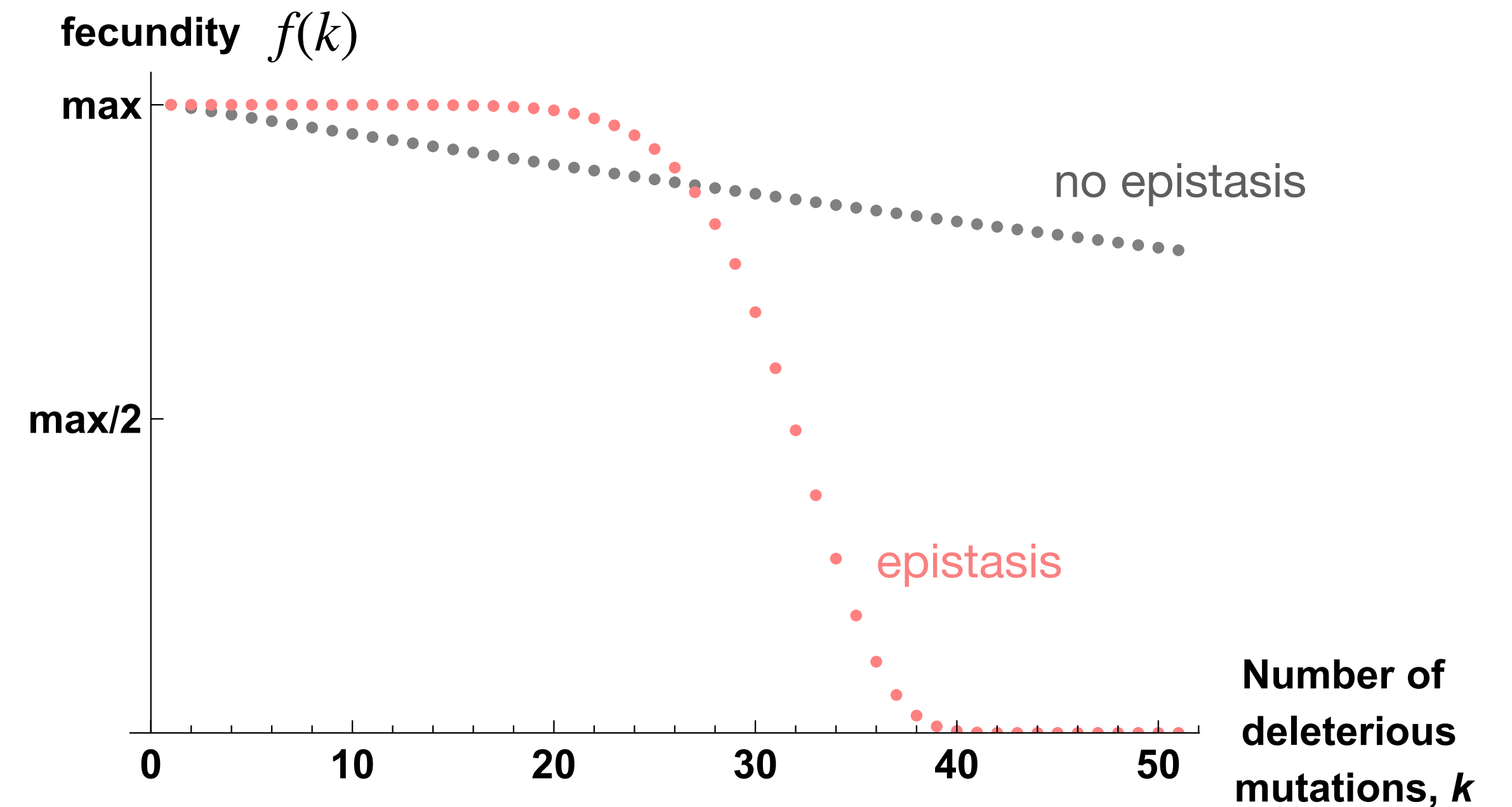
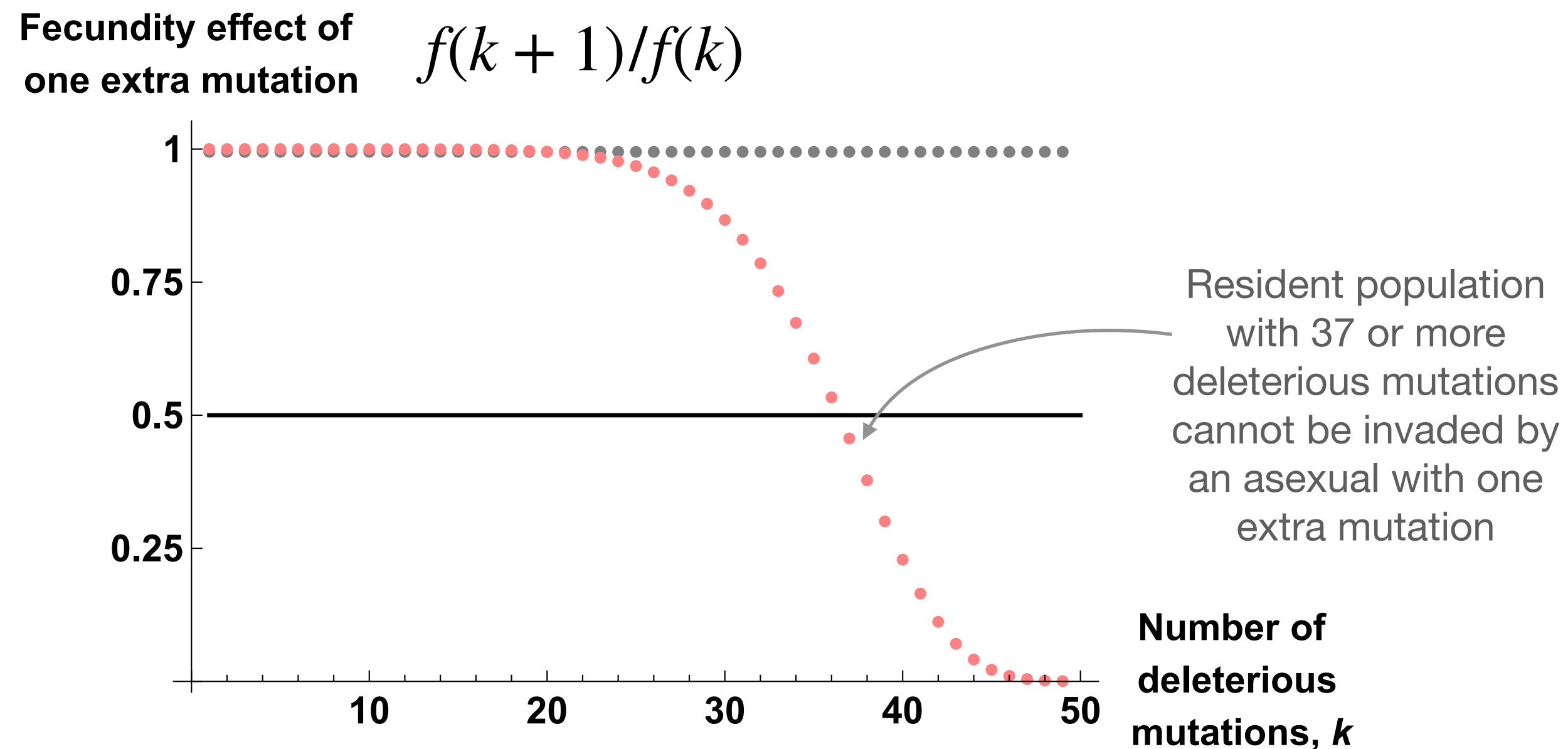


Resident population with 37 or more deleterious mutations cannot be invaded by an asexual with one extra mutation



Can strong epistasis rescue sexuals?

- Epistasis = non-additive fitness effects among loci
- Allows for an abrupt decrease in fitness with number of deleterious mutations

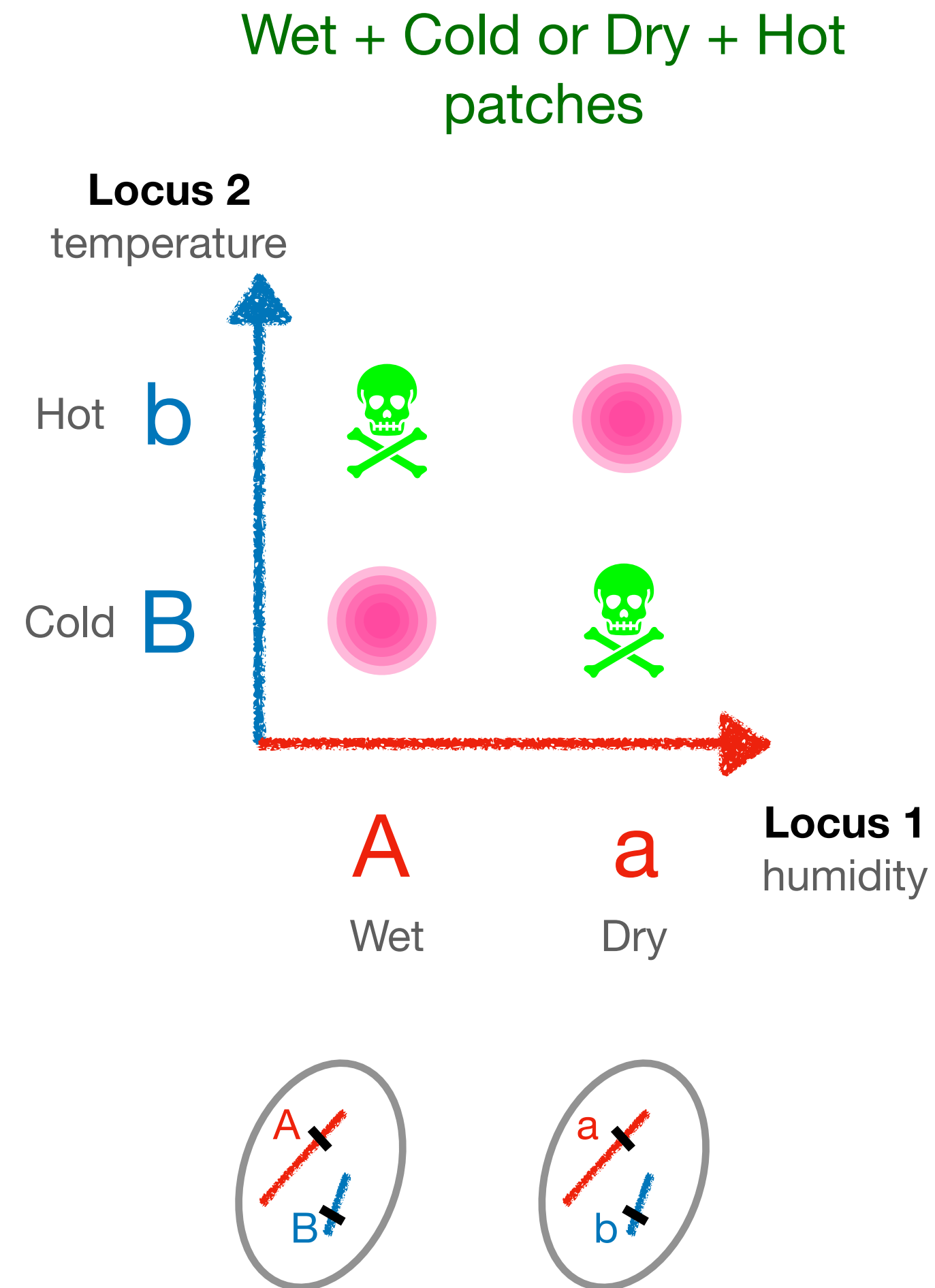


- Works if sexual population already quite loaded with mutations
- See exercise sheet 3

Fluctuating epistasis

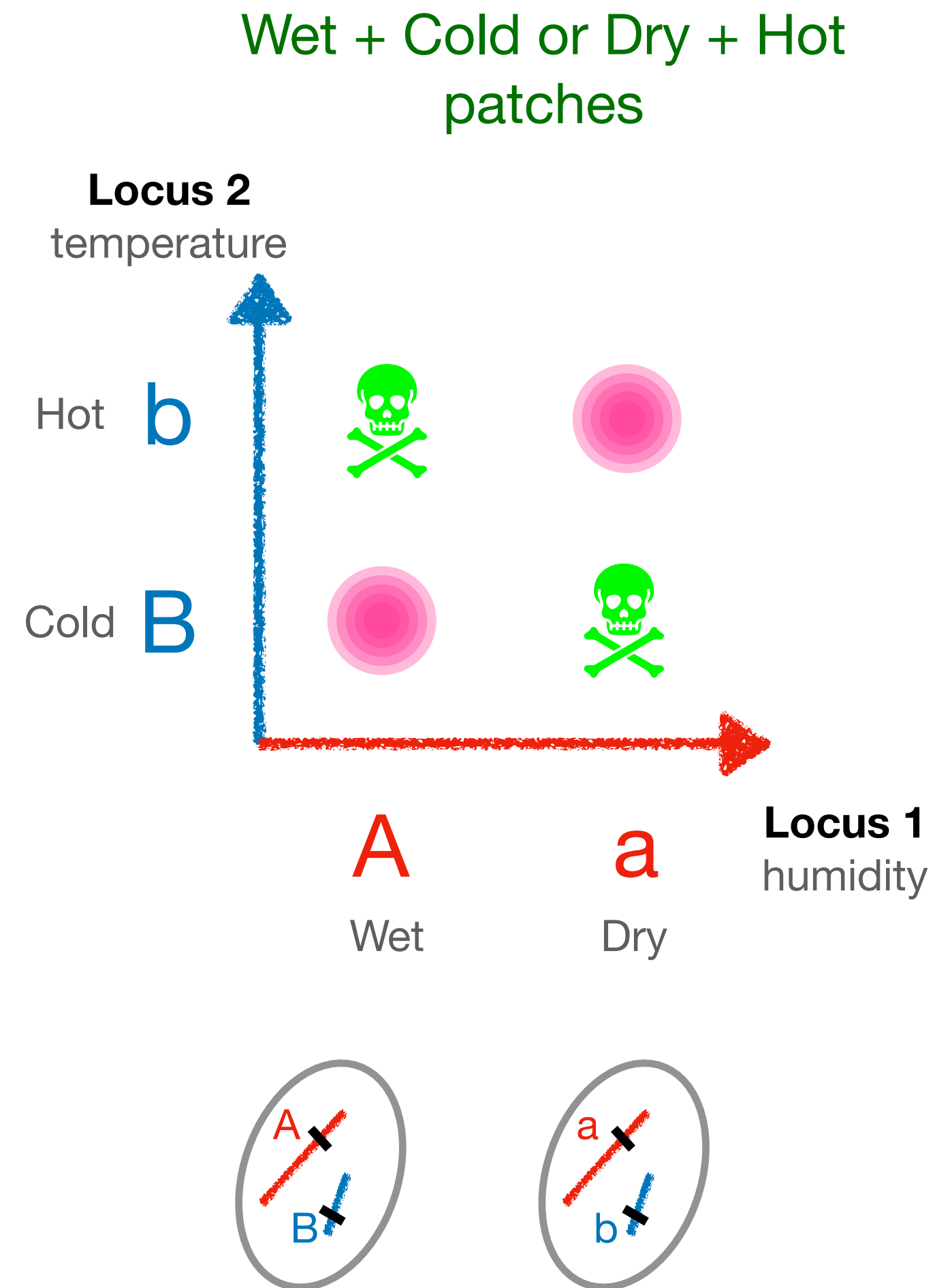
Fluctuating epistasis

- Environment favours specific allelic associations

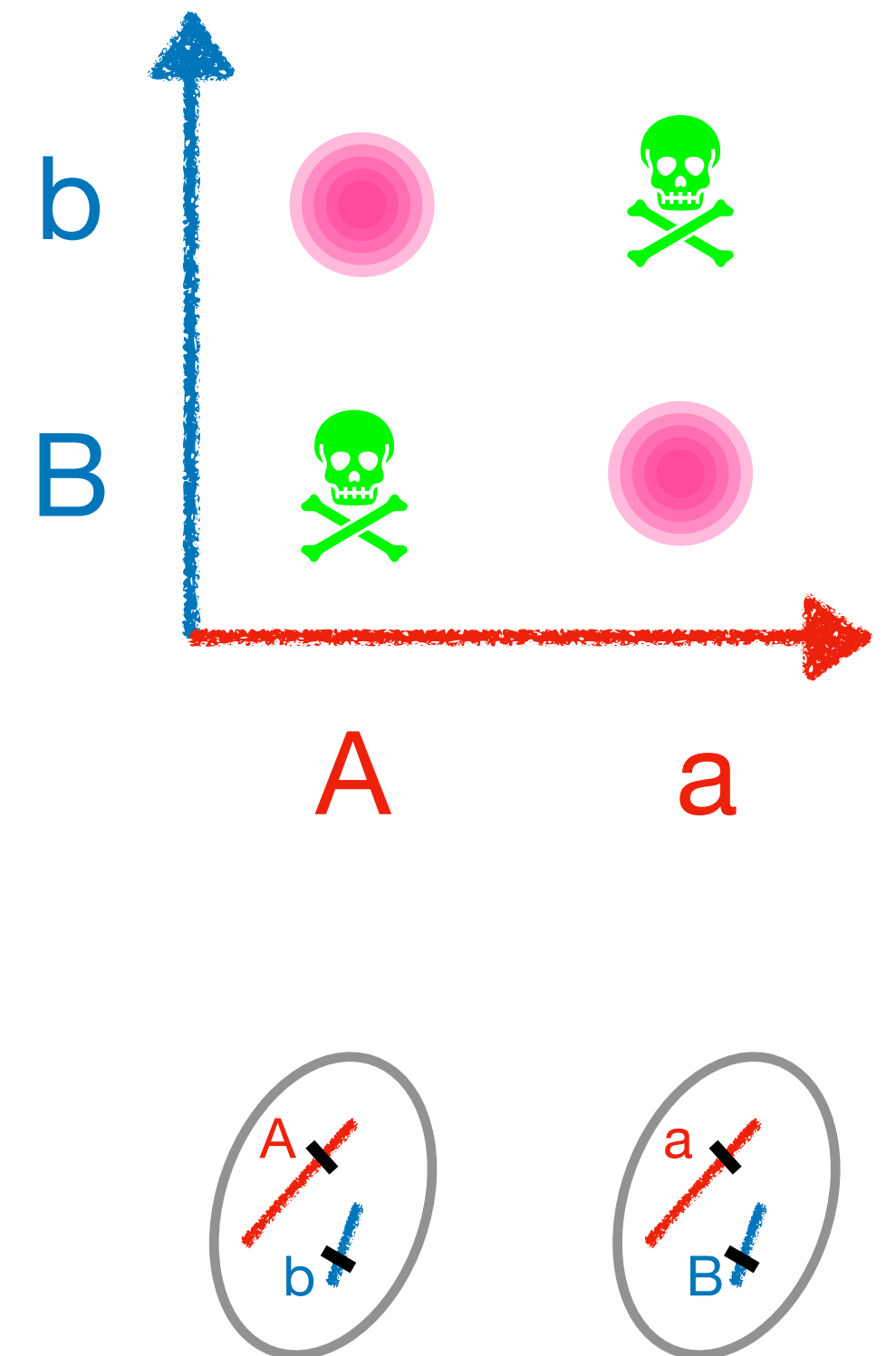


Fluctuating epistasis

- Environment favours specific allelic associations

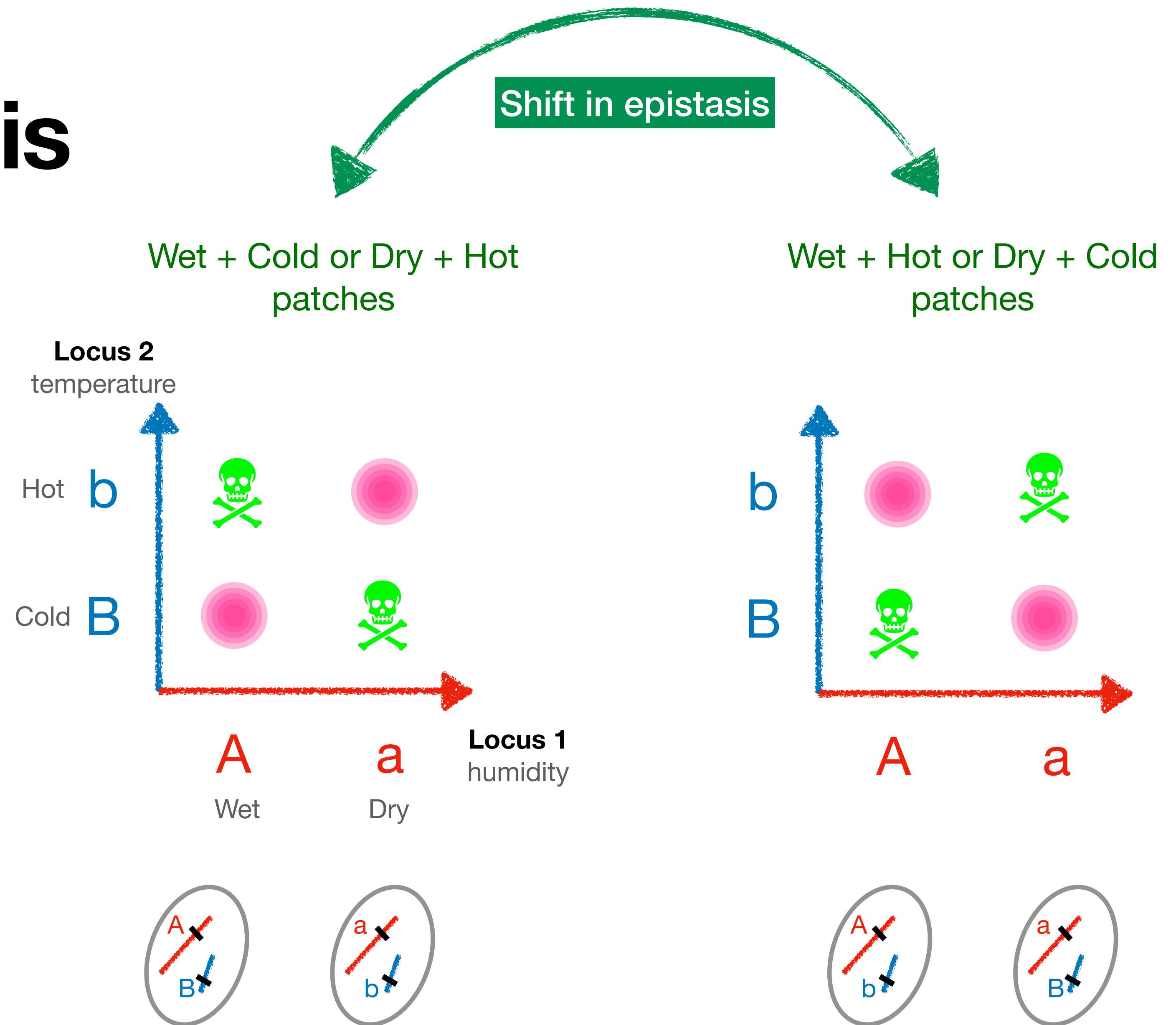


Wet + Hot or Dry + Cold patches



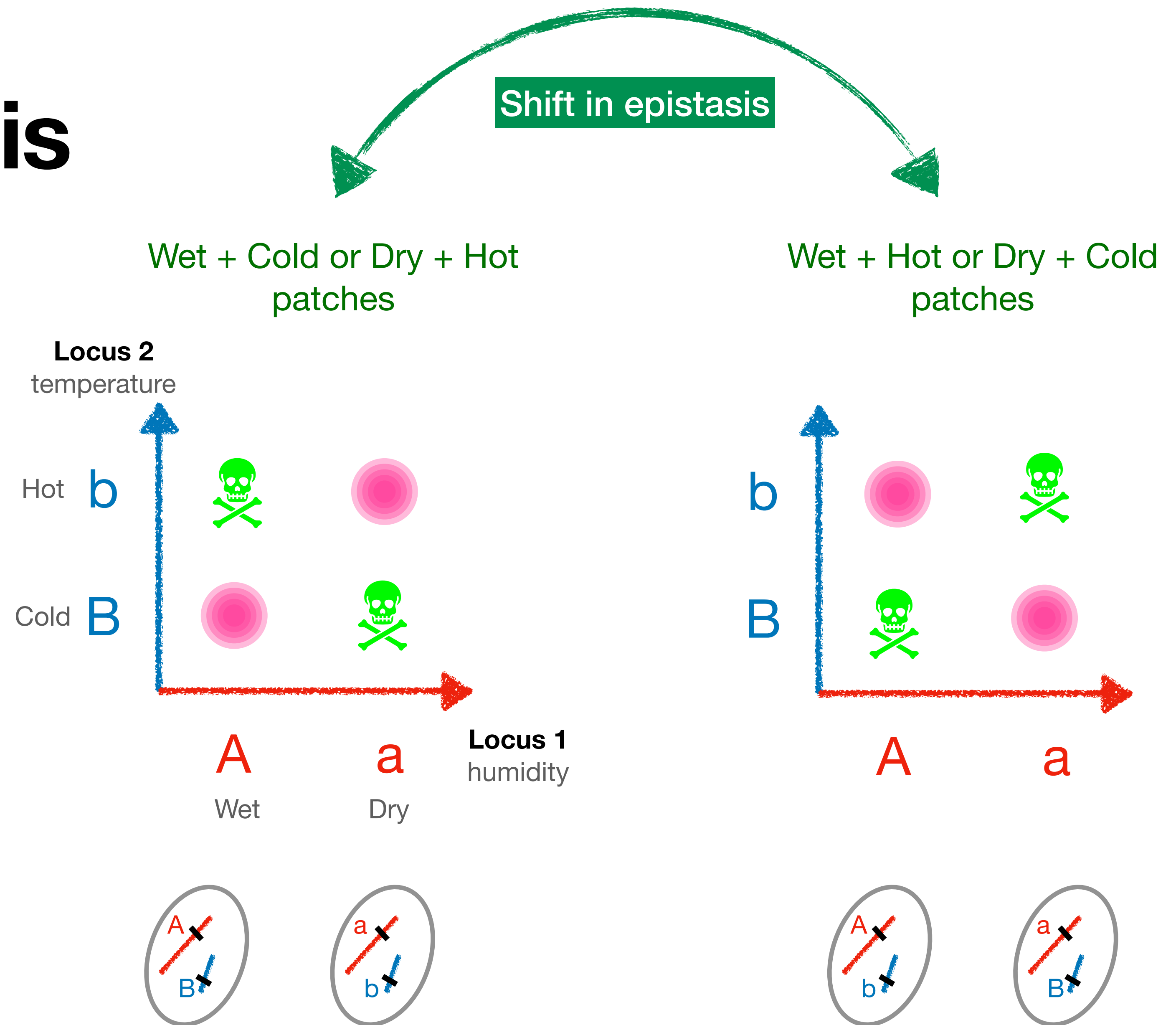
Fluctuating epistasis

- Environment favours specific allelic associations
- The environment fluctuates in time, favouring different associations at different times



Fluctuating epistasis

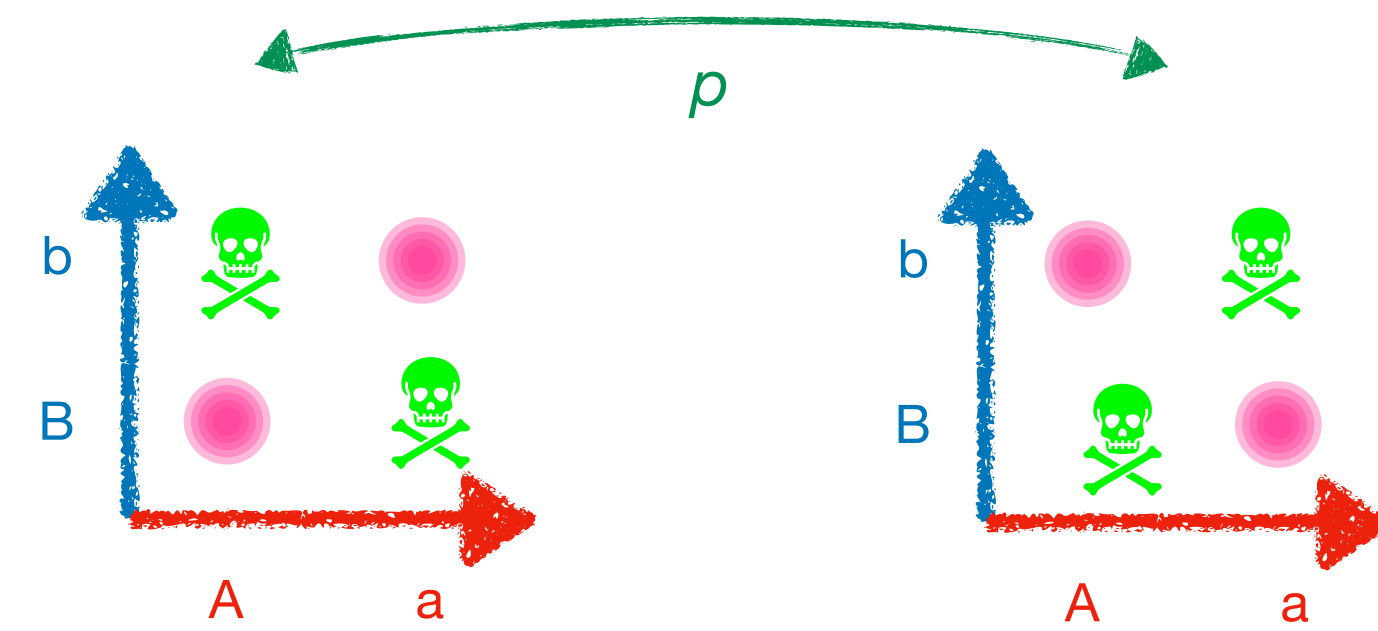
- Environment favours specific allelic associations
- The environment fluctuates in time, favouring different associations at different times
- Asexuals should lose out as the allelic associations of an asexual lineage are fixed



Fluctuating epistasis

Example

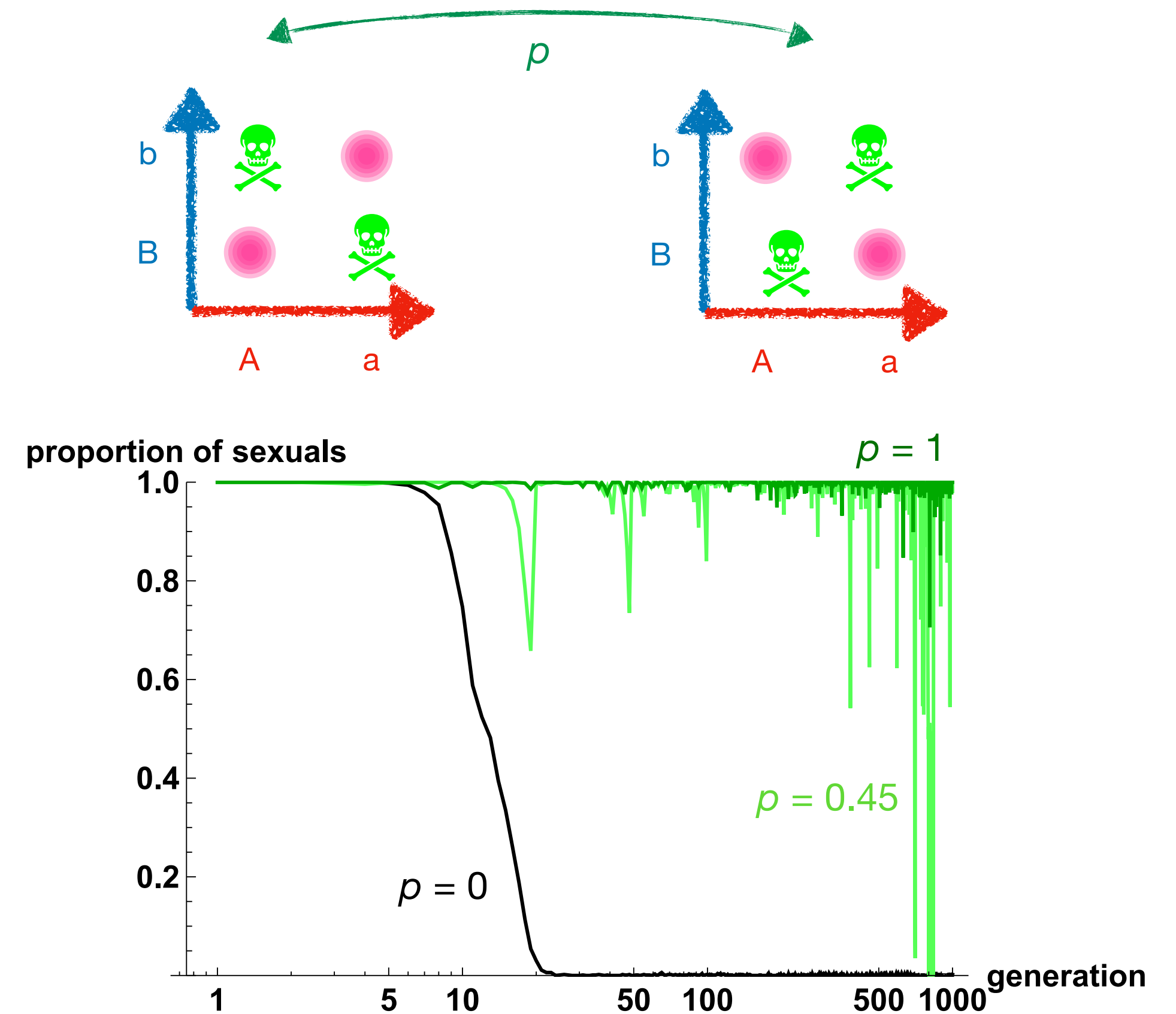
- Population with two types of habitats, each favouring a specific combination of alleles.
- Combination changes at each generation with probability p .
- Start with a population of sexuals. Introduce asexuals through mutation.



Fluctuating epistasis

Example

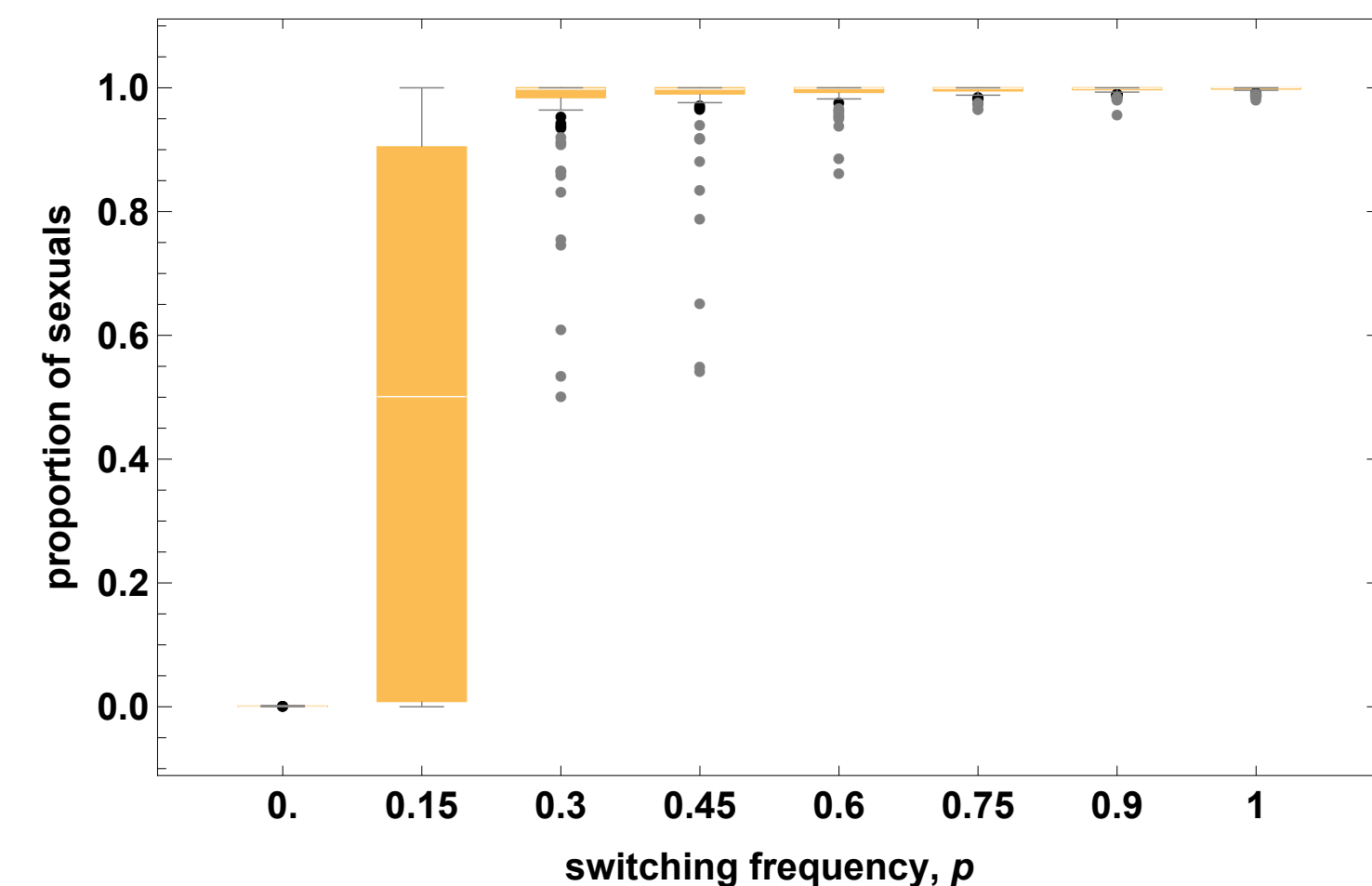
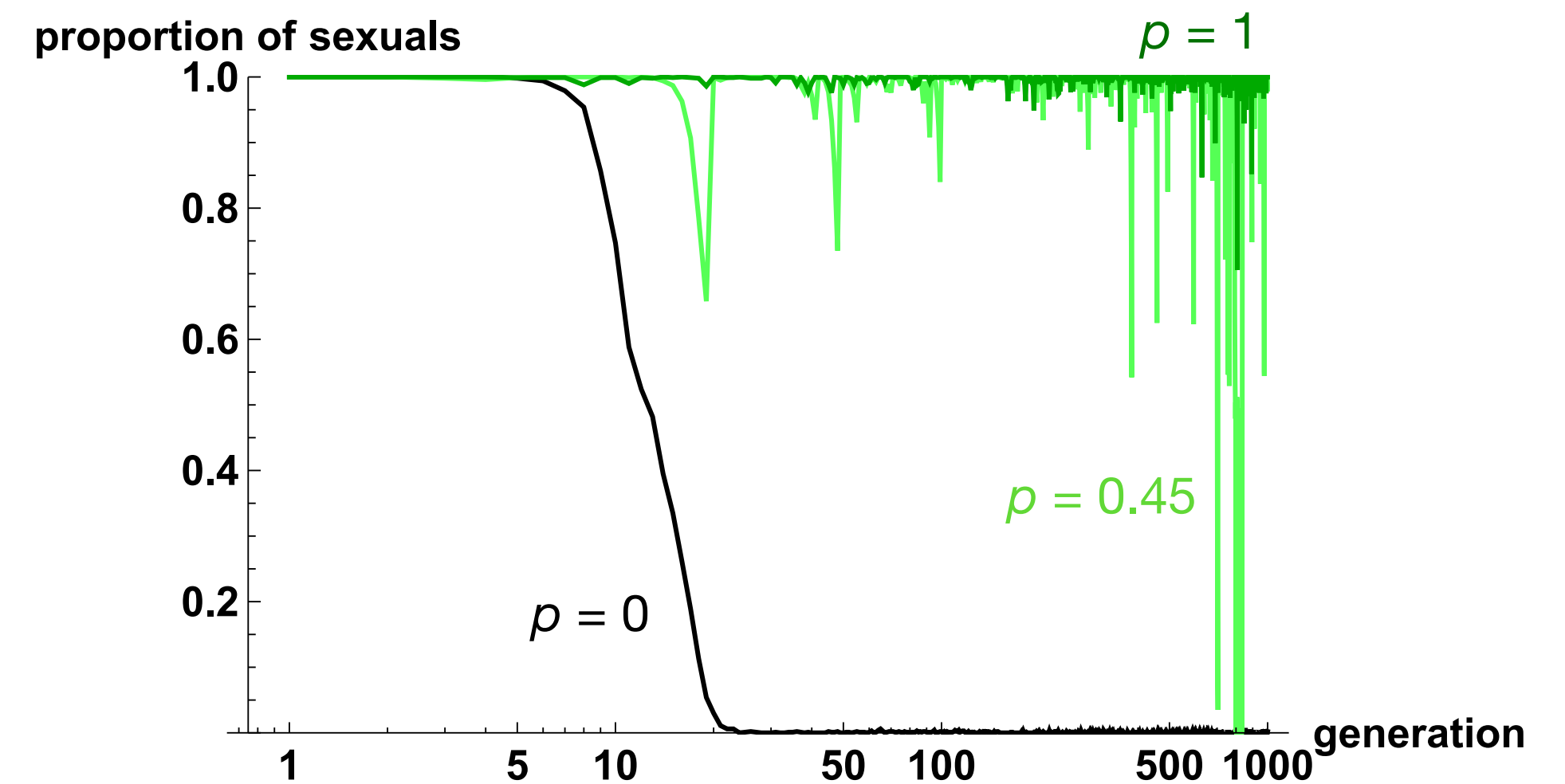
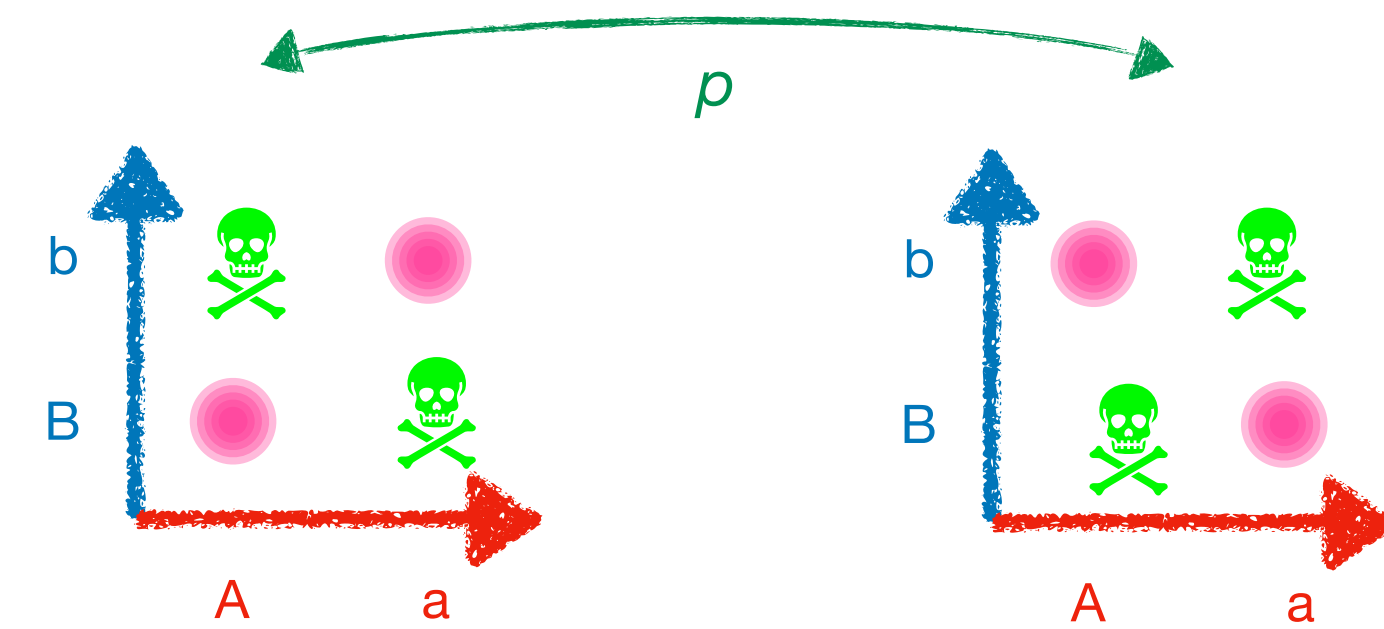
- Population with two types of habitats, each favouring a specific combination of alleles.
- Combination changes at each generation with probability p .
- Start with a population of sexuals. Introduce asexuals through mutation.



Fluctuating epistasis

Example

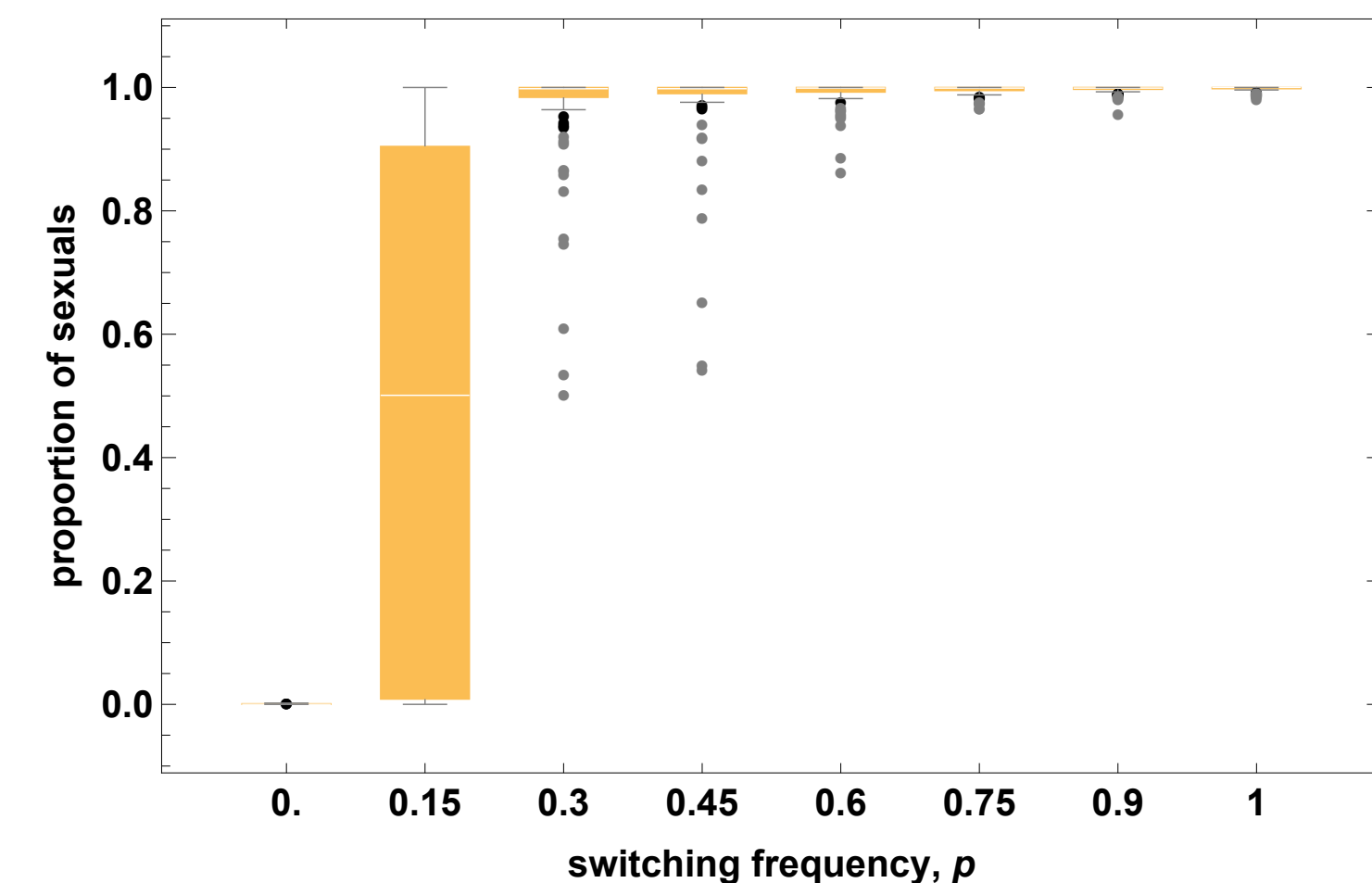
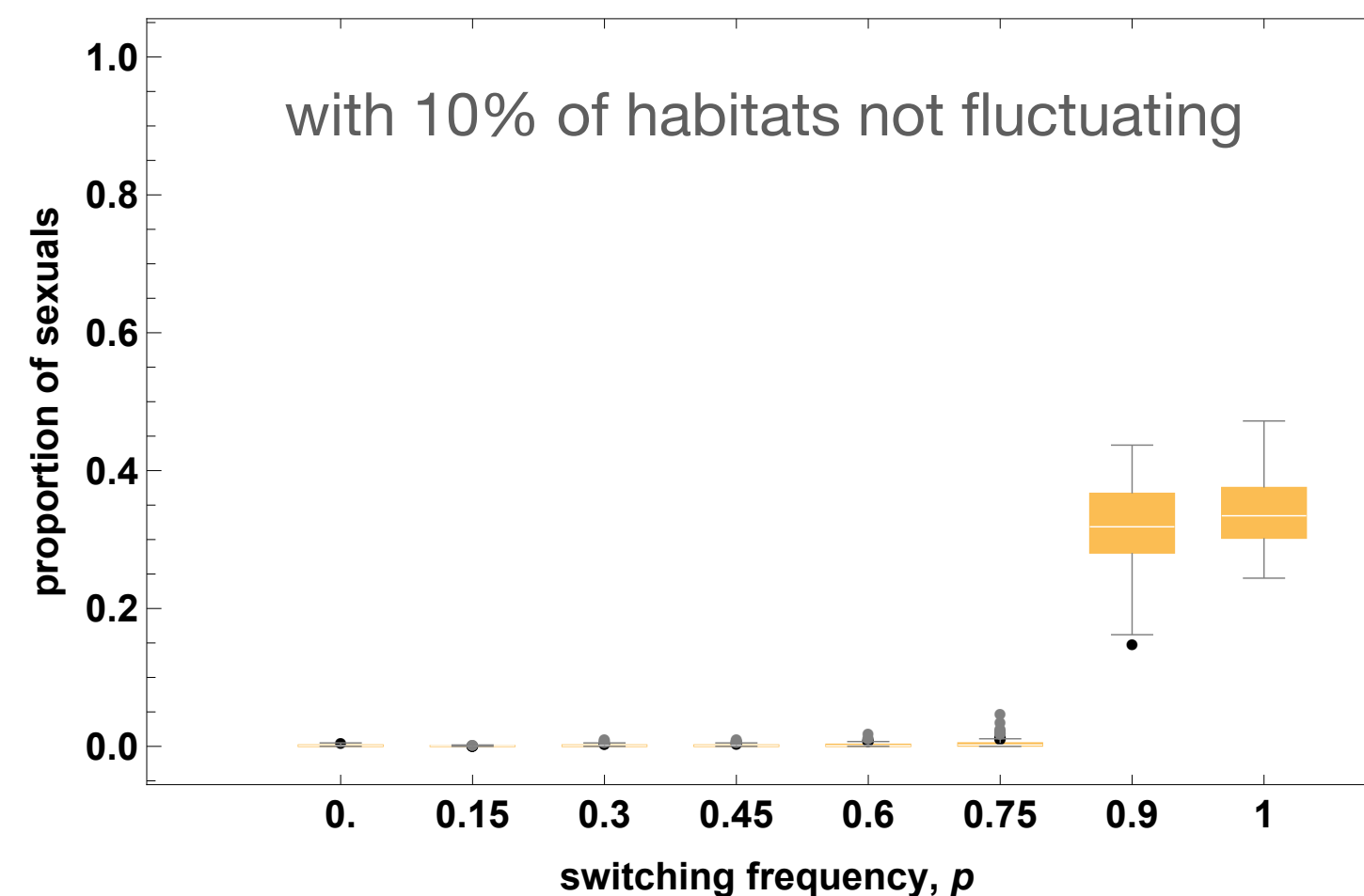
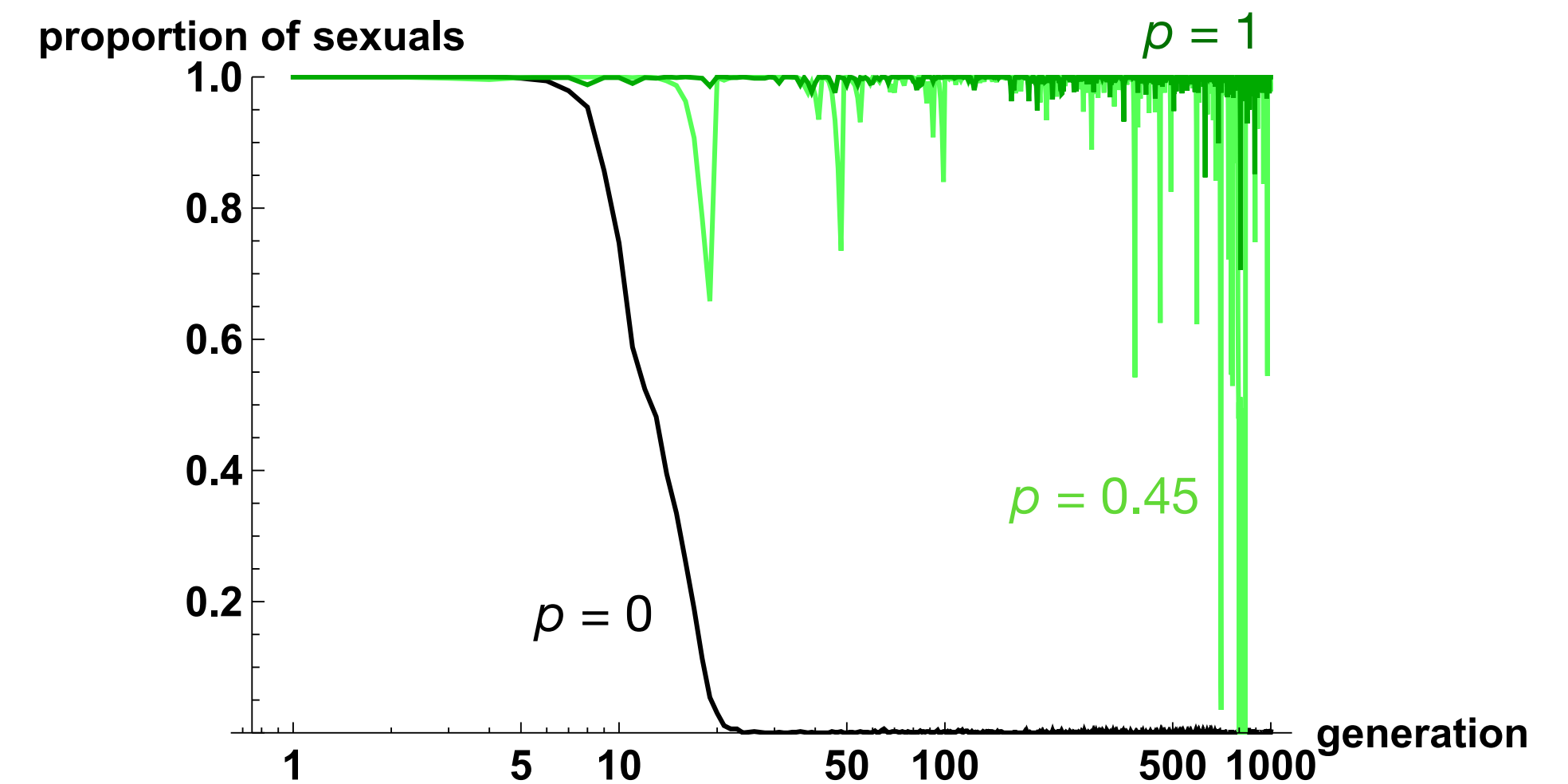
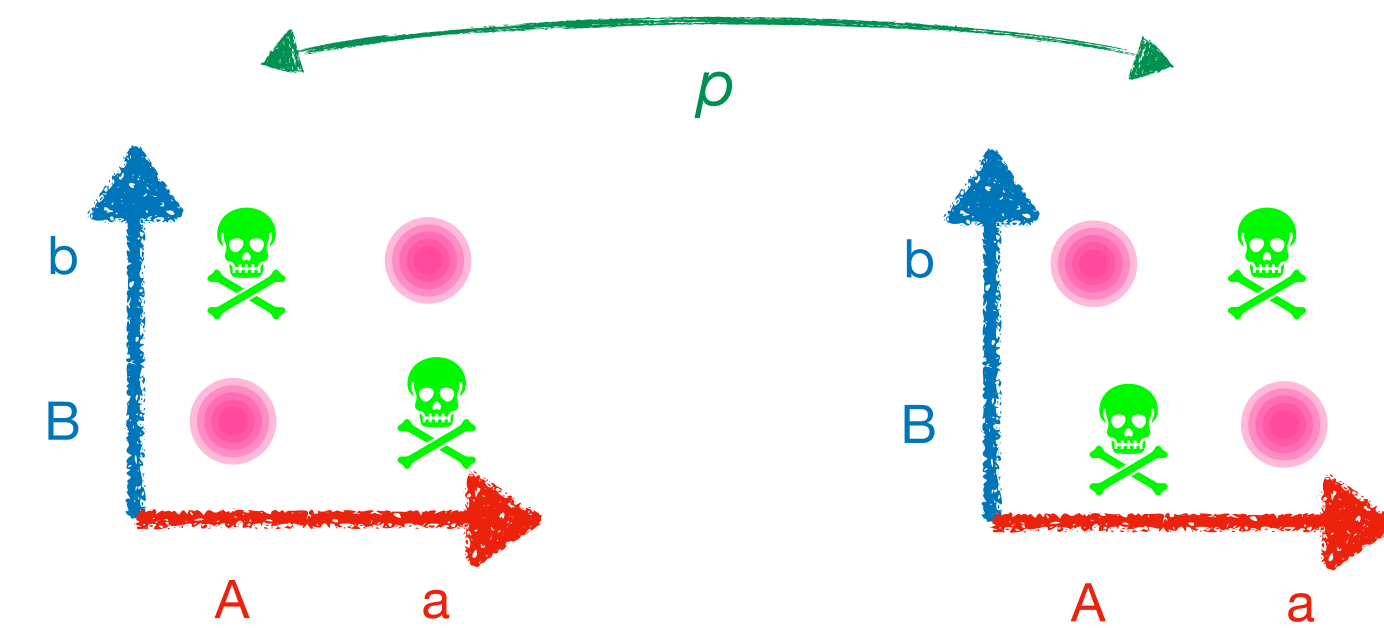
- Population with two types of habitats, each favouring a specific combination of alleles.
- Combination changes at each generation with probability p .
- Start with a population of sexuals. Introduce asexuals through mutation.



Fluctuating epistasis

But...

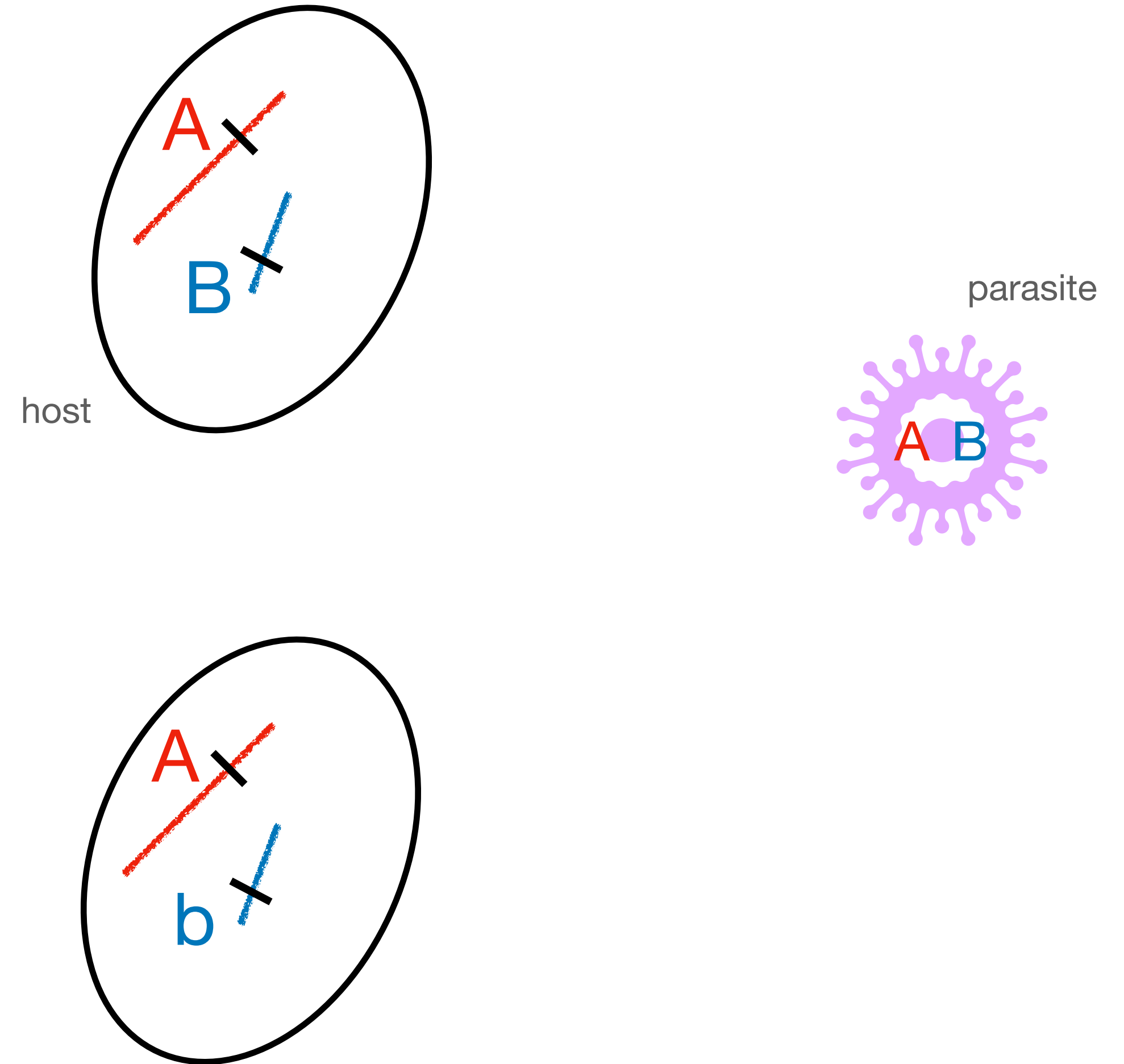
- Environmental and genetic assumptions seem unrealistic.
- Allowing for refugia makes it much more difficult to maintain sexual reproduction:



An ecological model of fluctuating epistasis

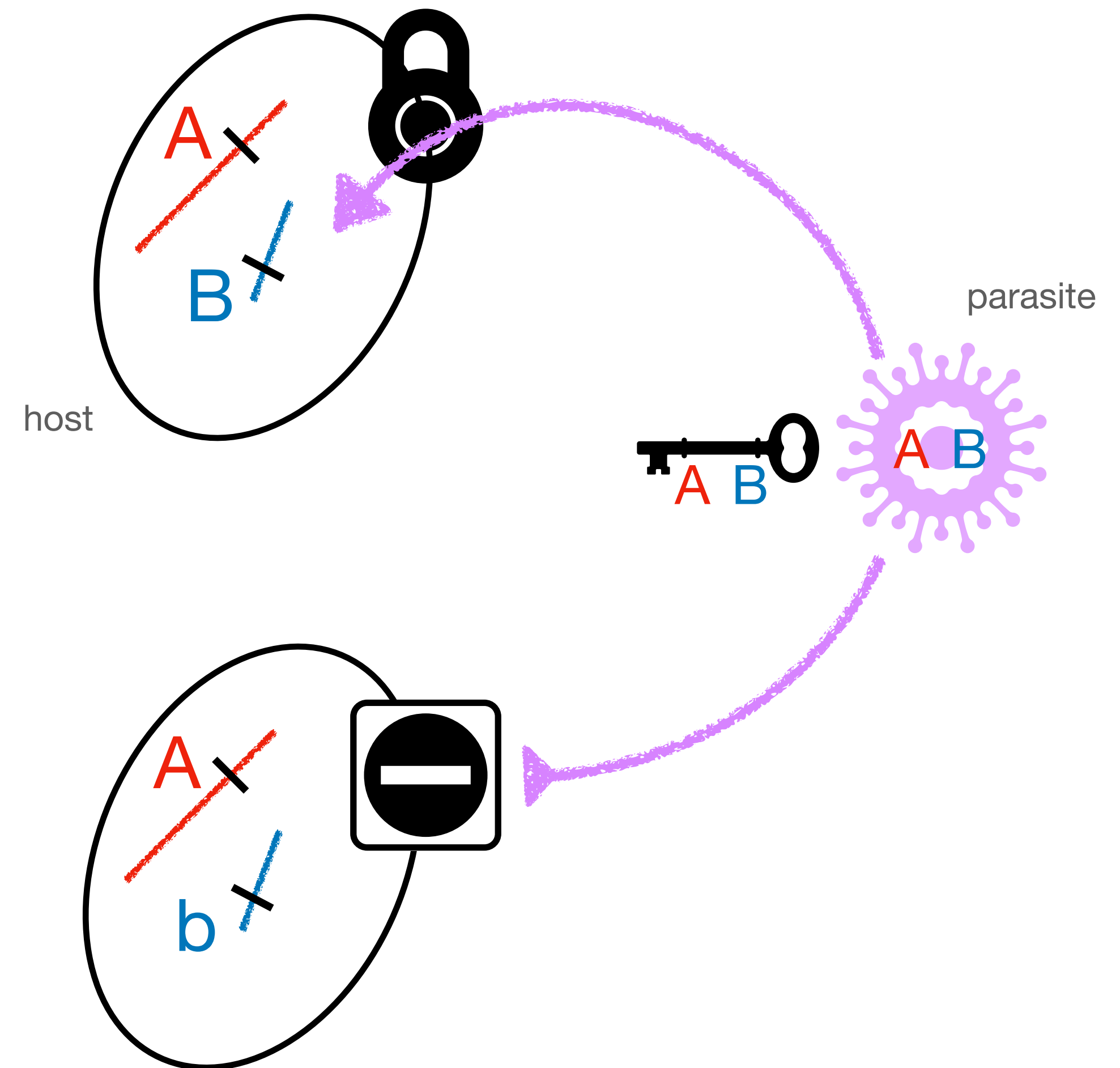
An ecological model of fluctuating epistasis

- Coevolution of host and parasites.



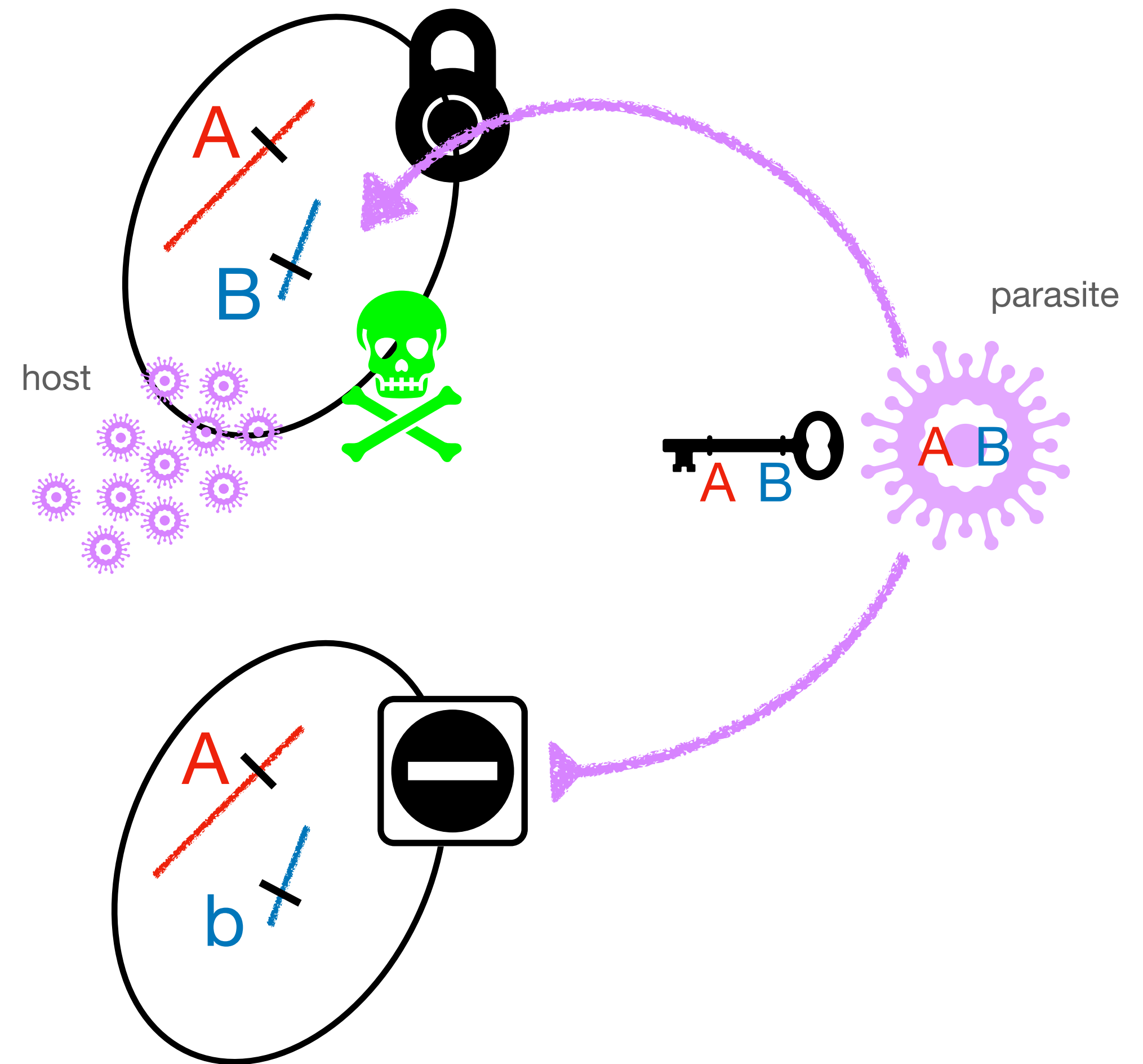
An ecological model of fluctuating epistasis

- Coevolution of host and parasites.
- Lock and key system where parasites can only target host with matching genotype.



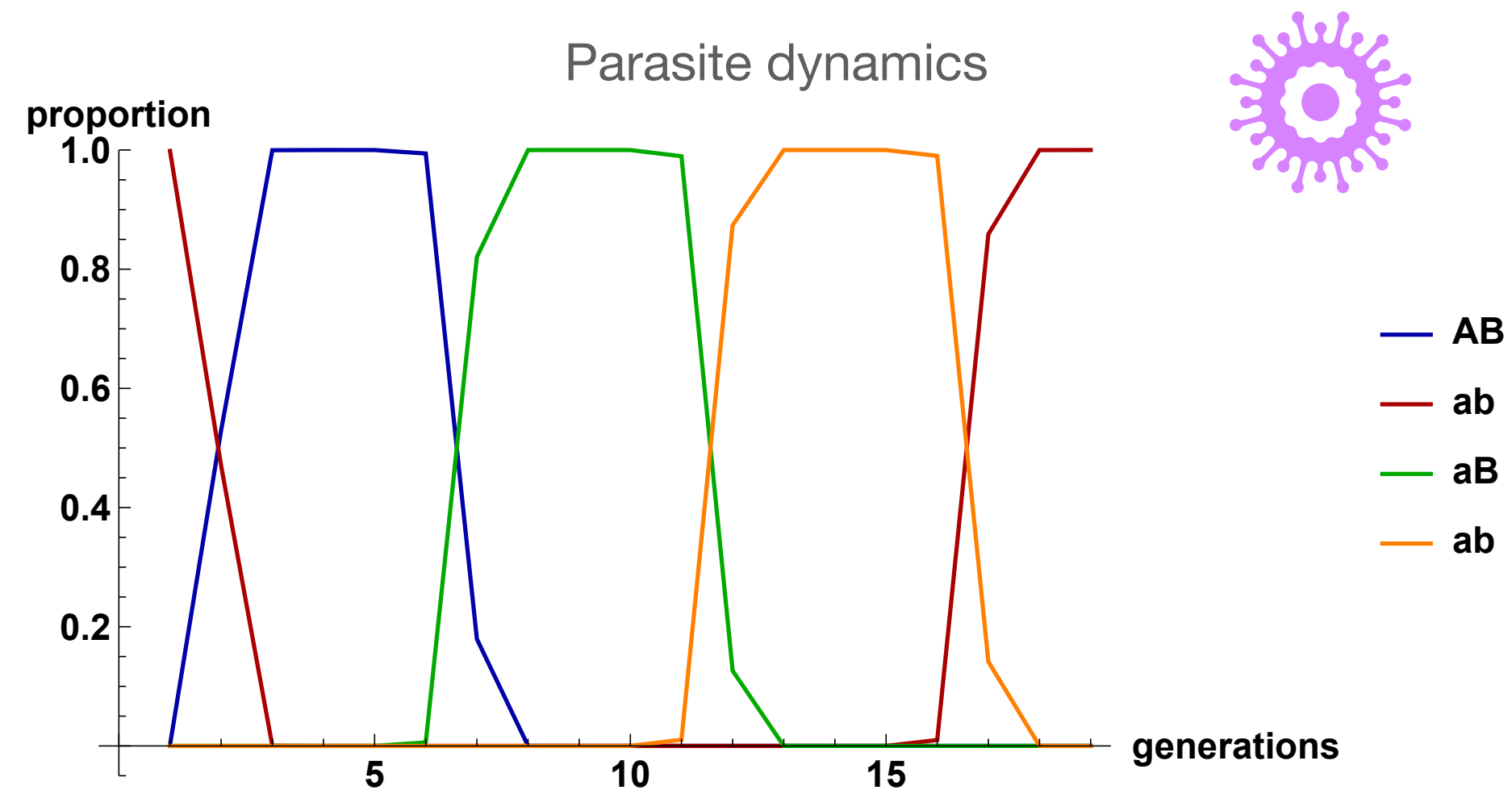
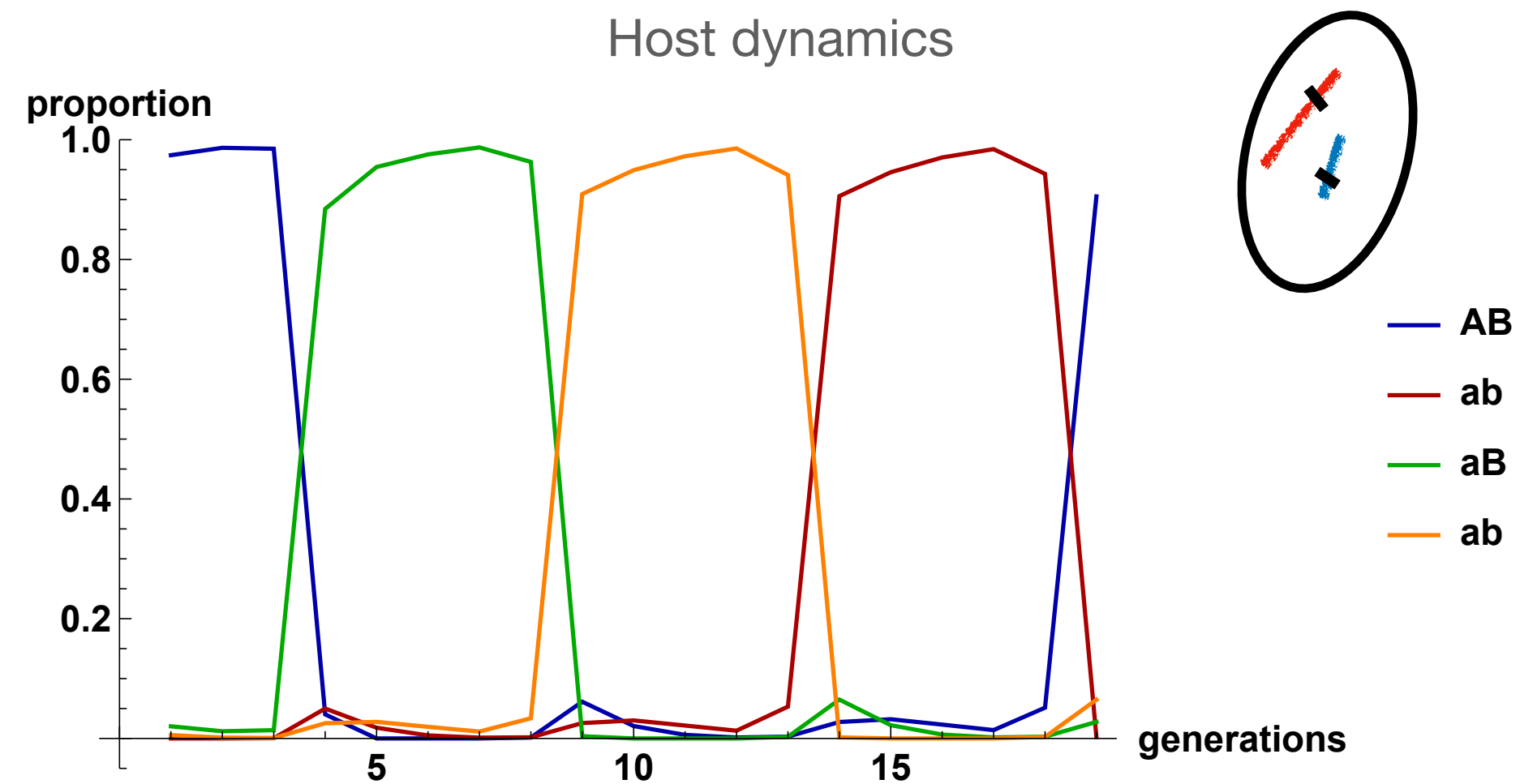
An ecological model of fluctuating epistasis

- Coevolution of host and parasites.
- Lock and key system where parasites can only target host with matching genotype.
- Selection on parasites to match most common host, selection on host to evade most common parasite.
- Creates fluctuating epistasis in host.



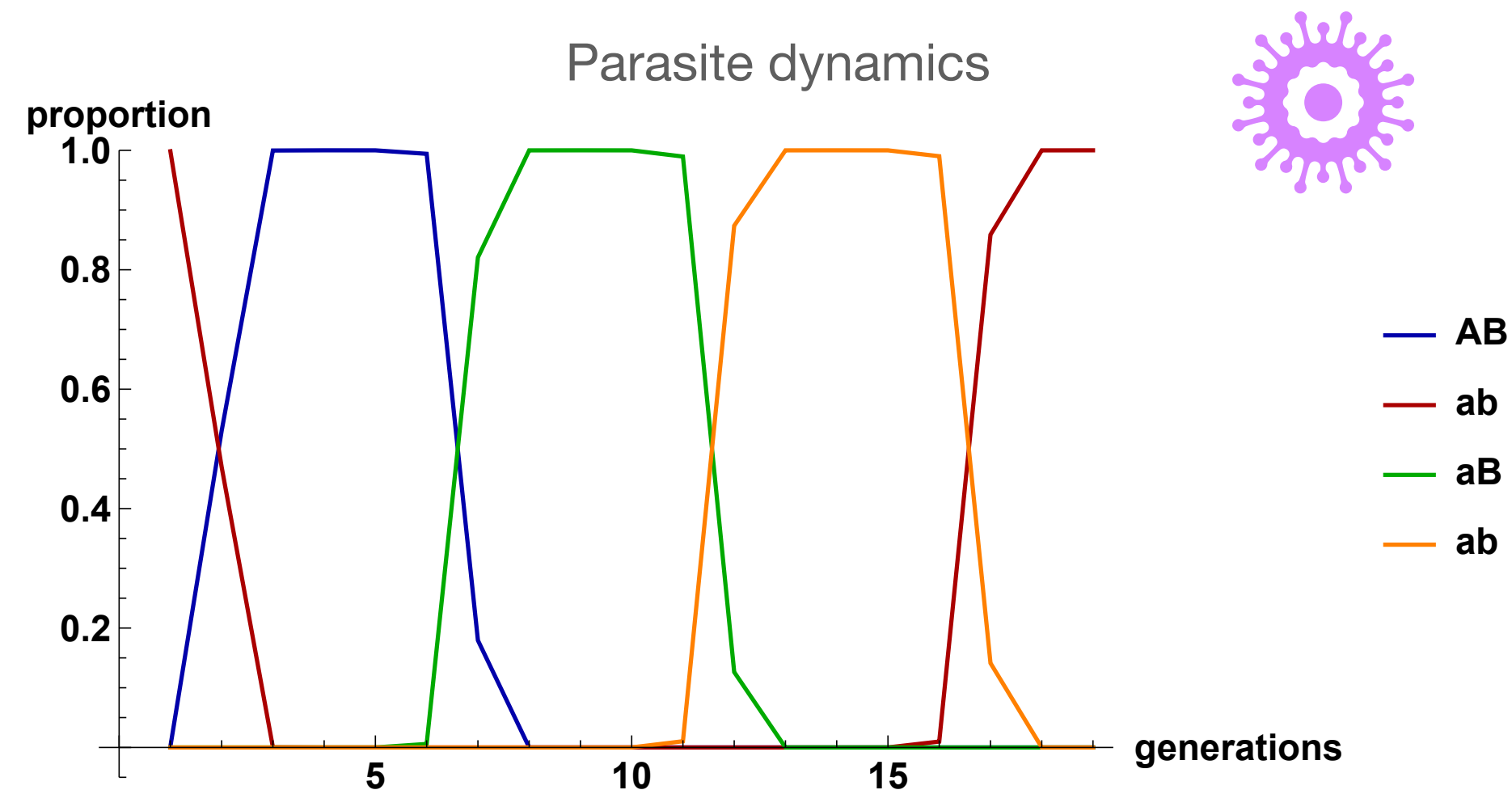
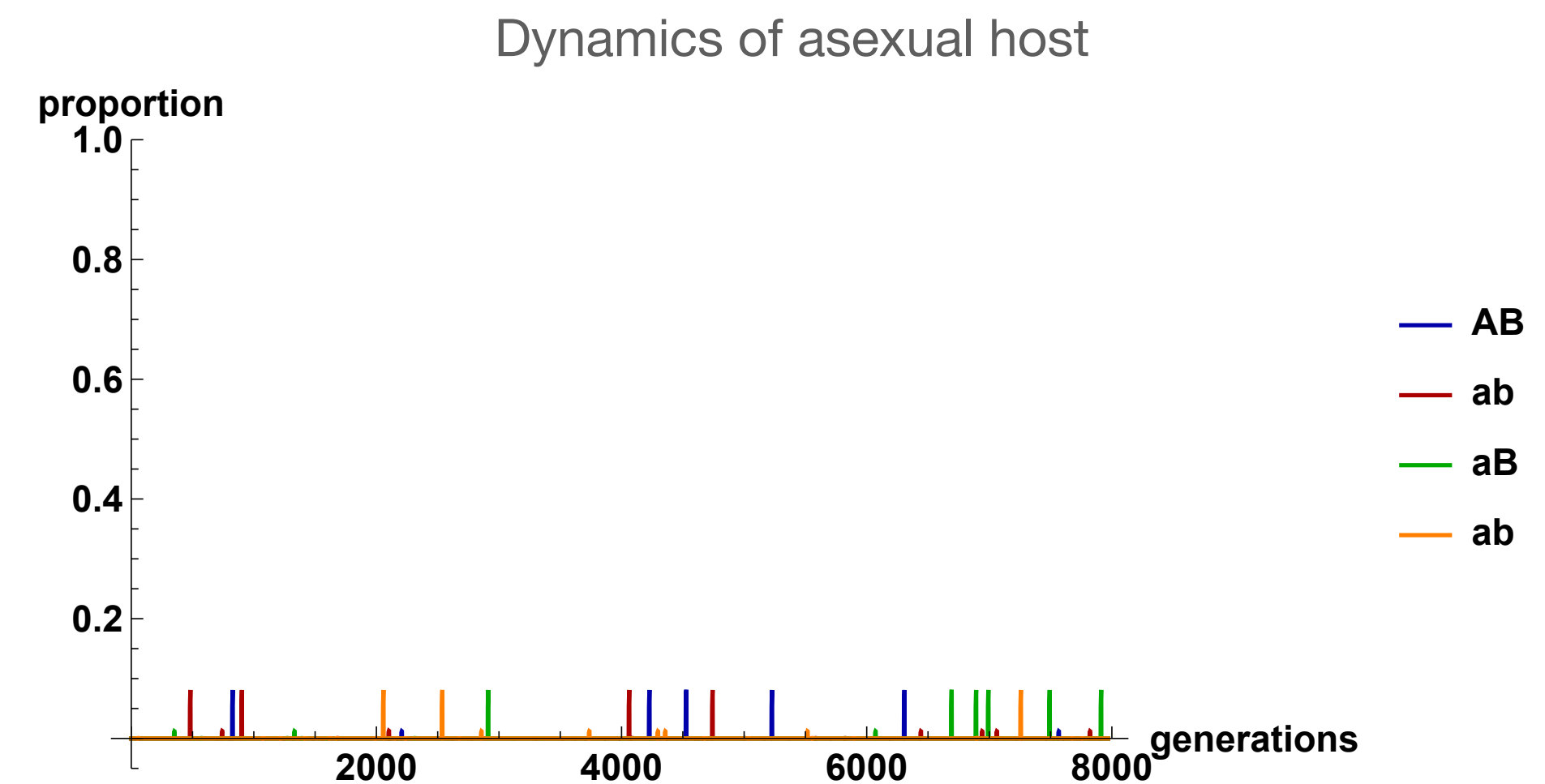
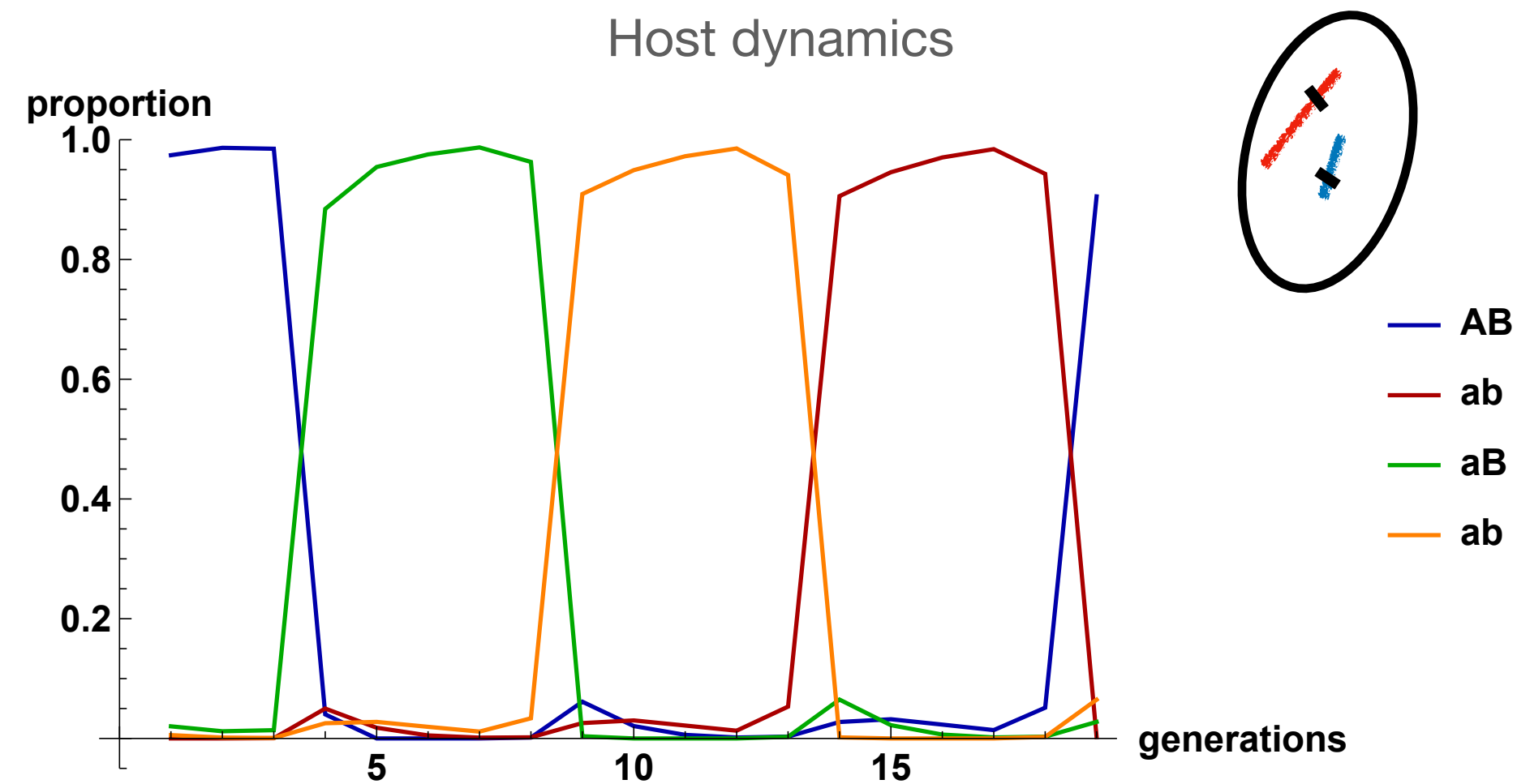
An ecological model of fluctuating epistasis

Red queen dynamics



An ecological model of fluctuating epistasis

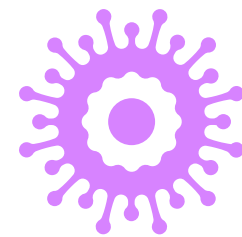
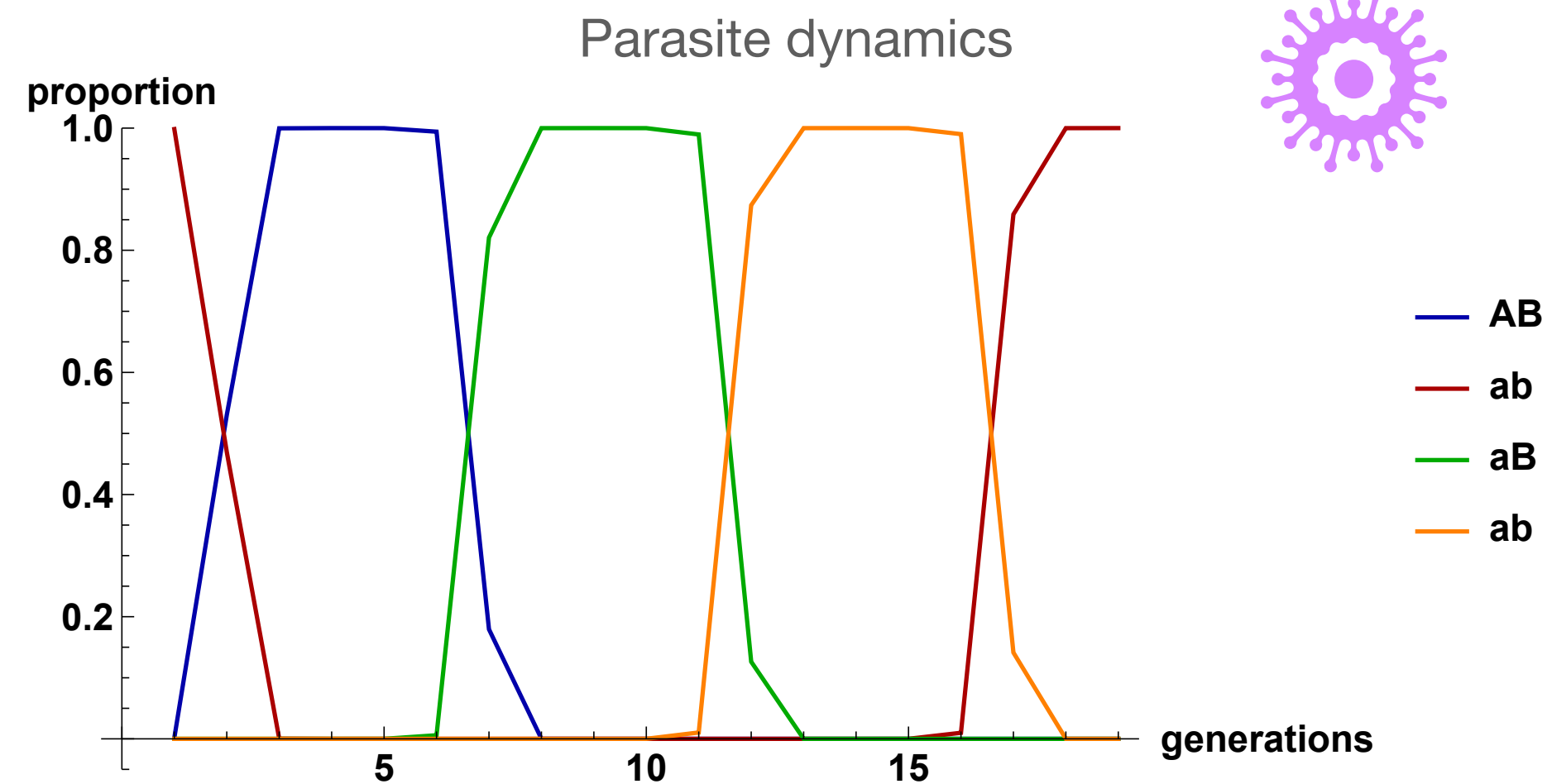
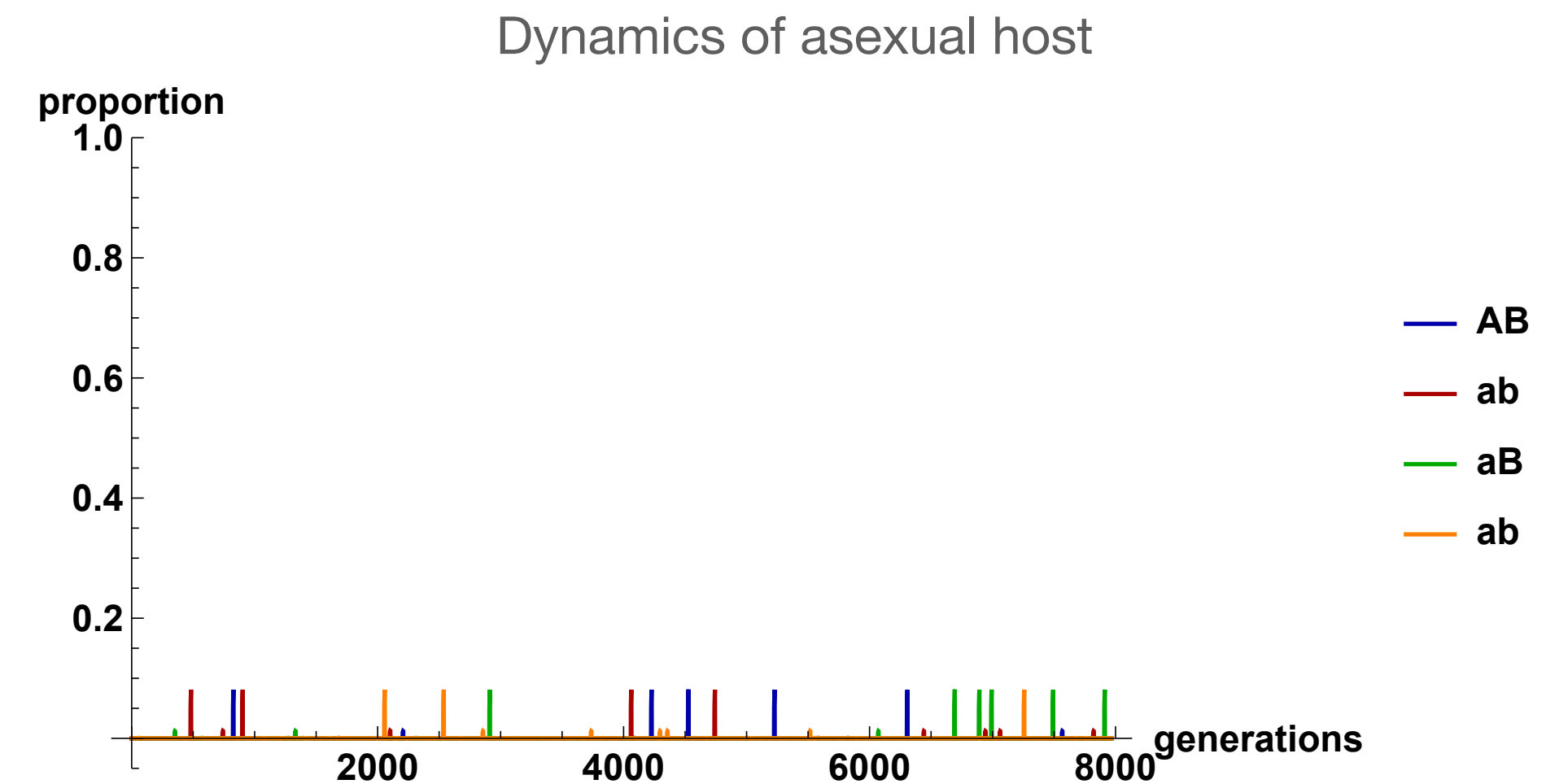
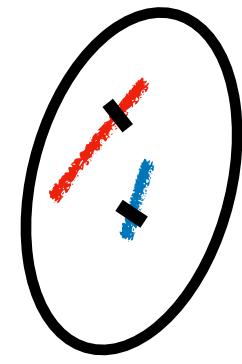
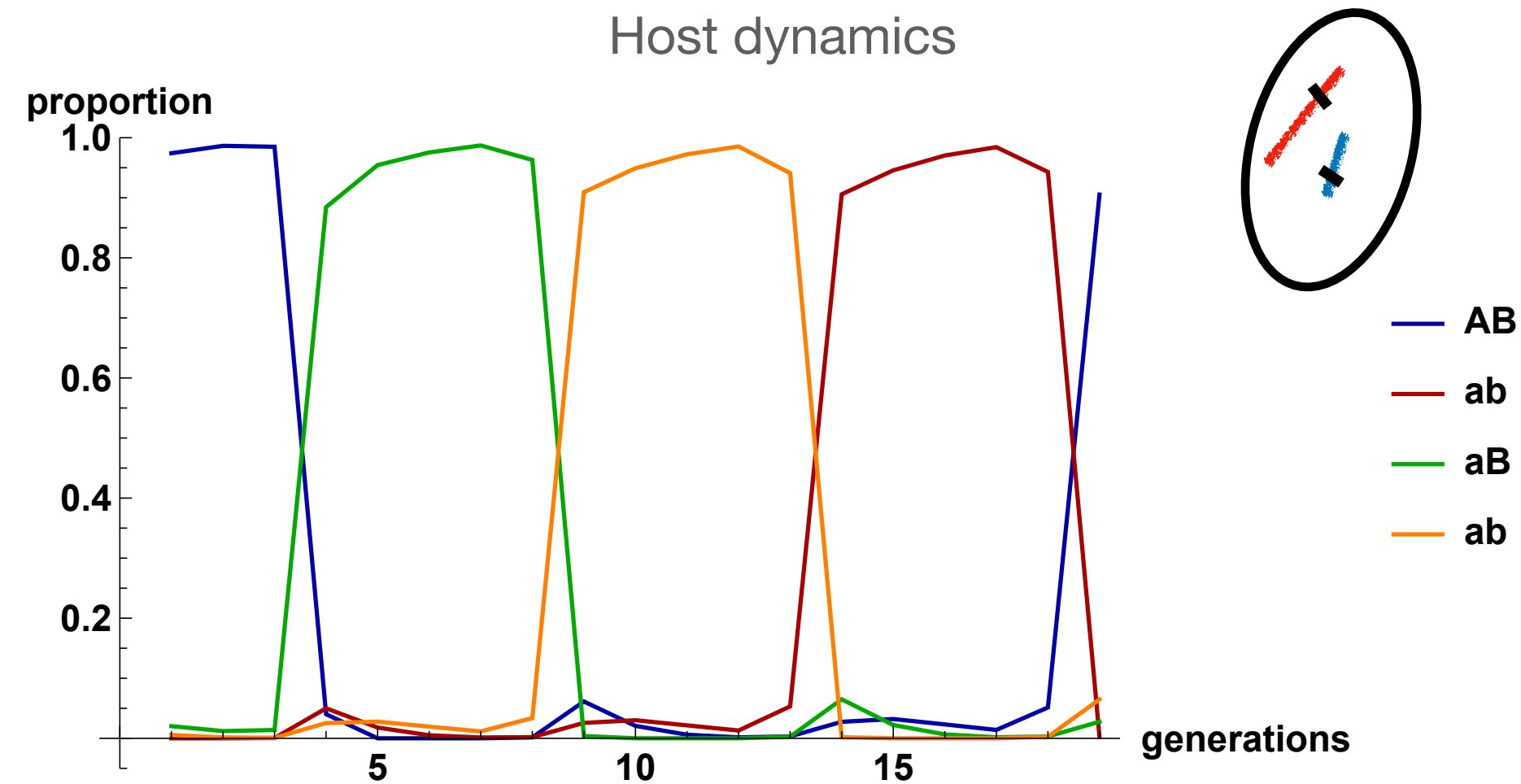
Red queen dynamics



Red queen dynamics can trigger fluctuating epistasis, favouring sexual reproduction.

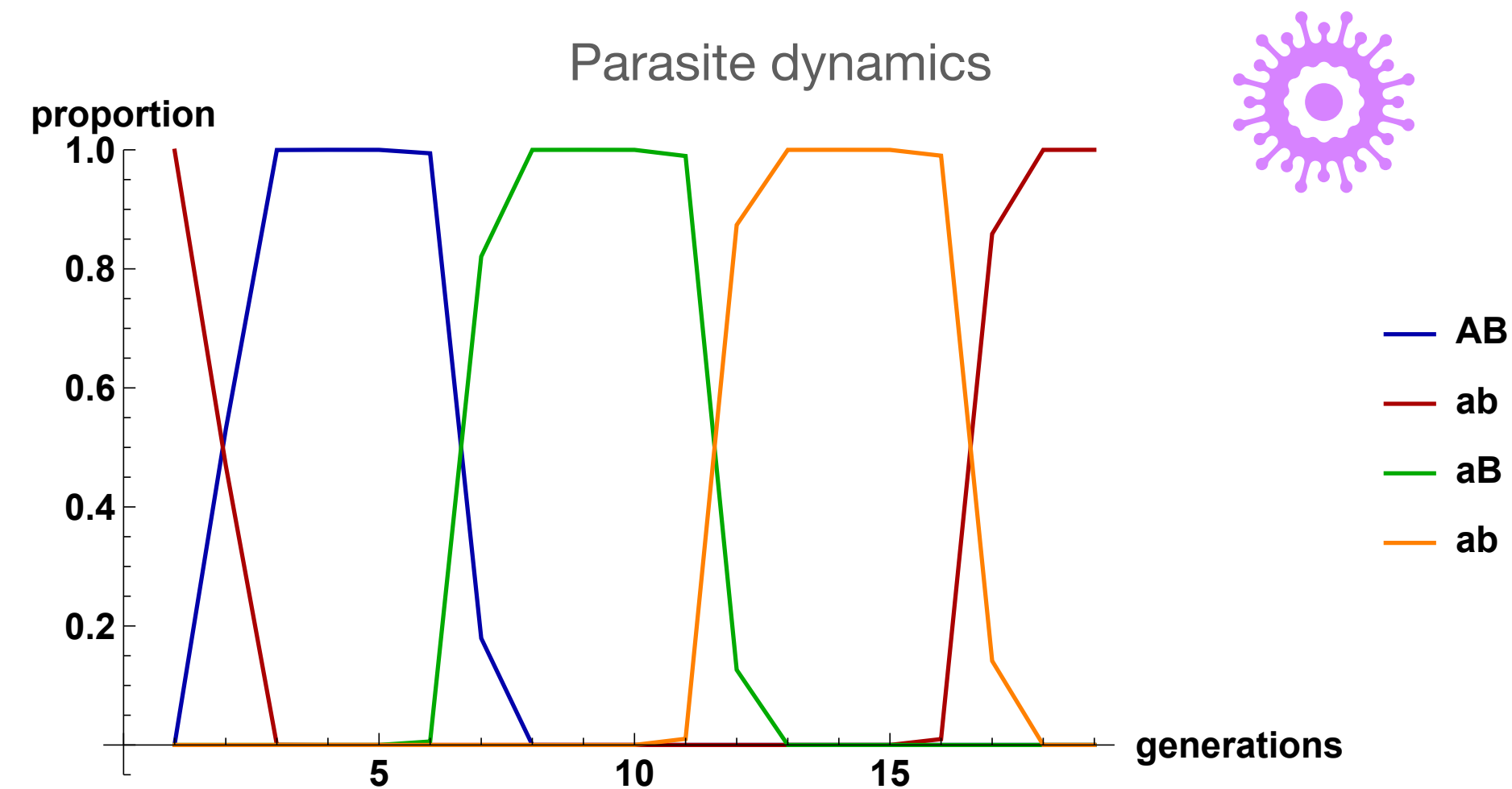
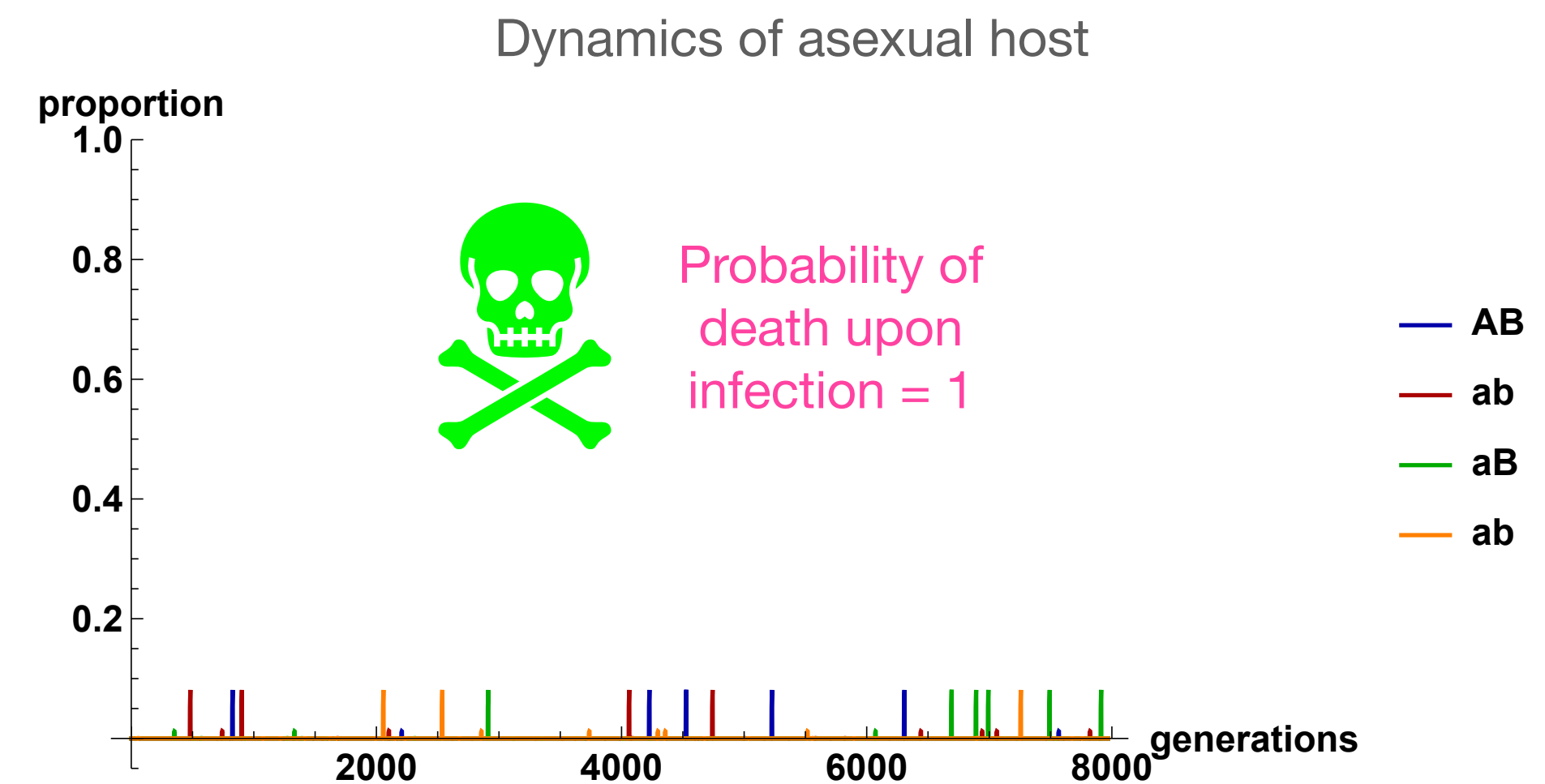
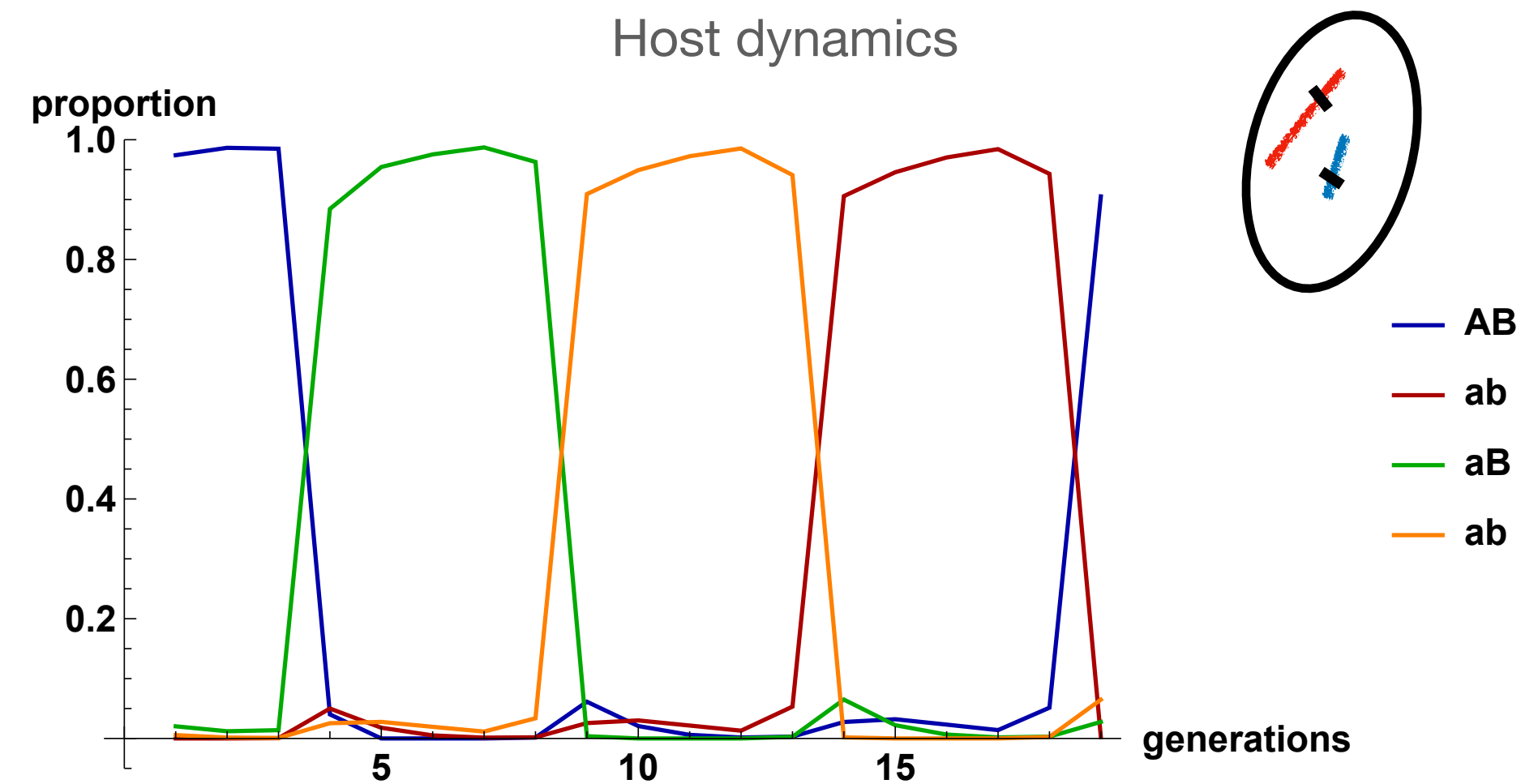
An ecological model of fluctuating epistasis

But...



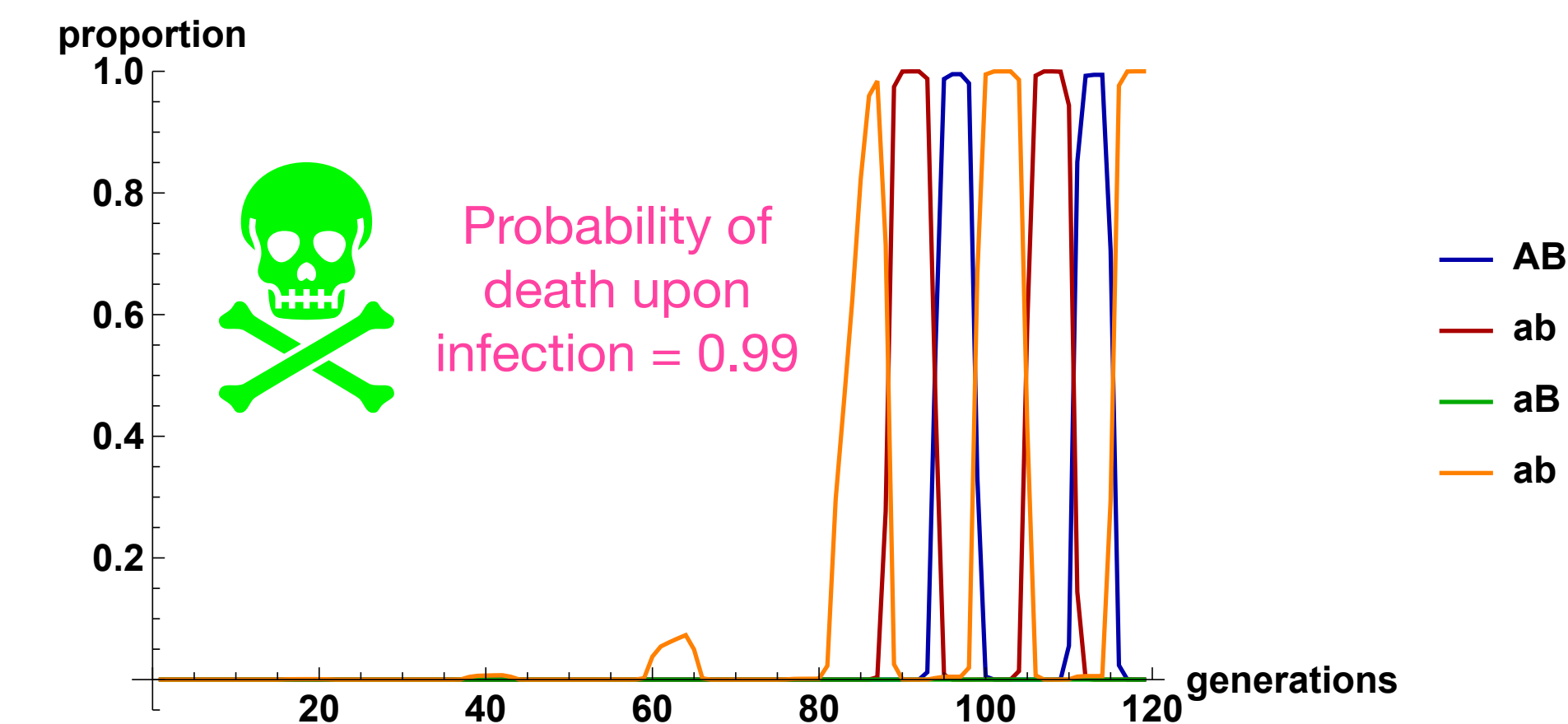
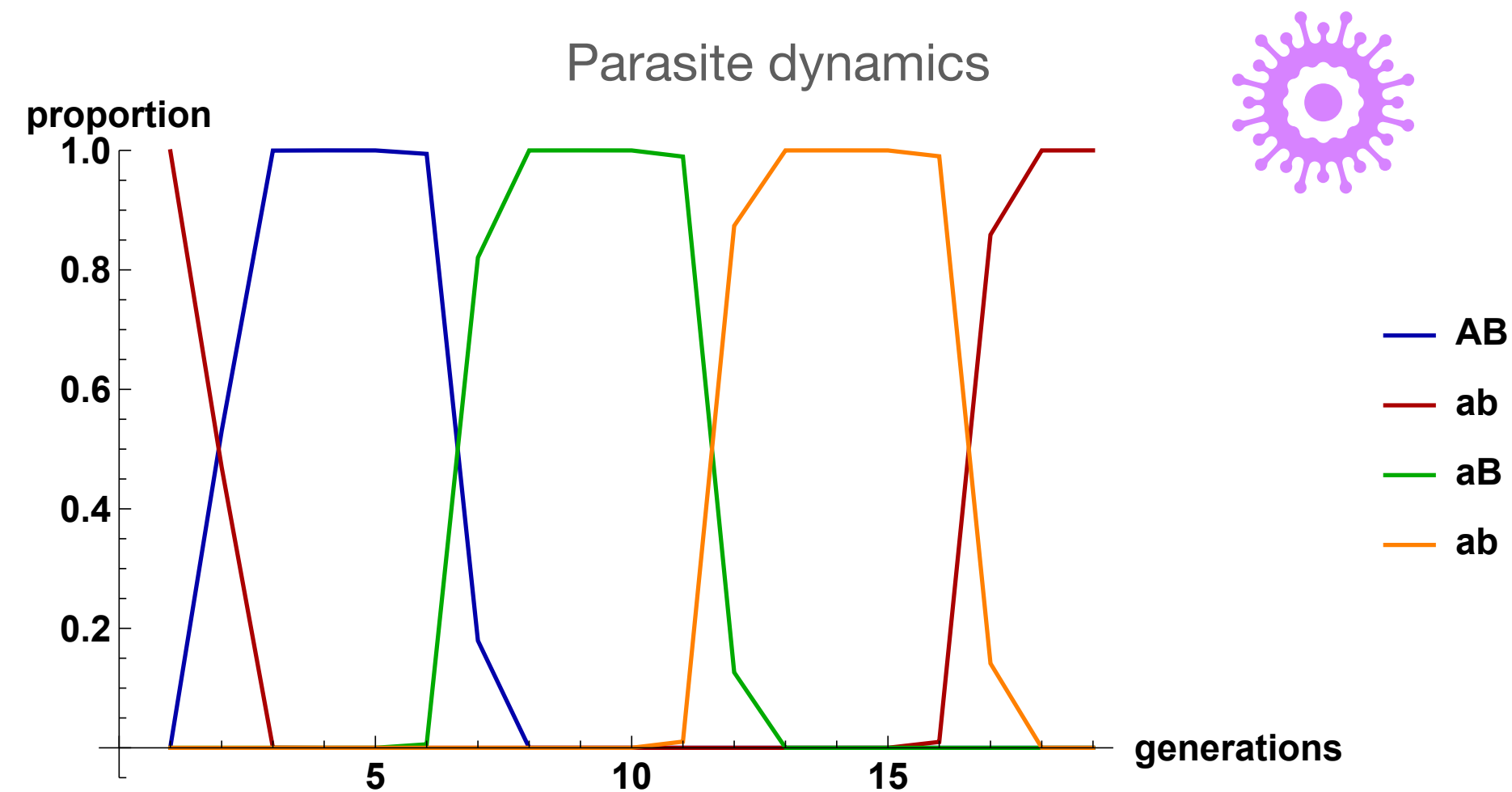
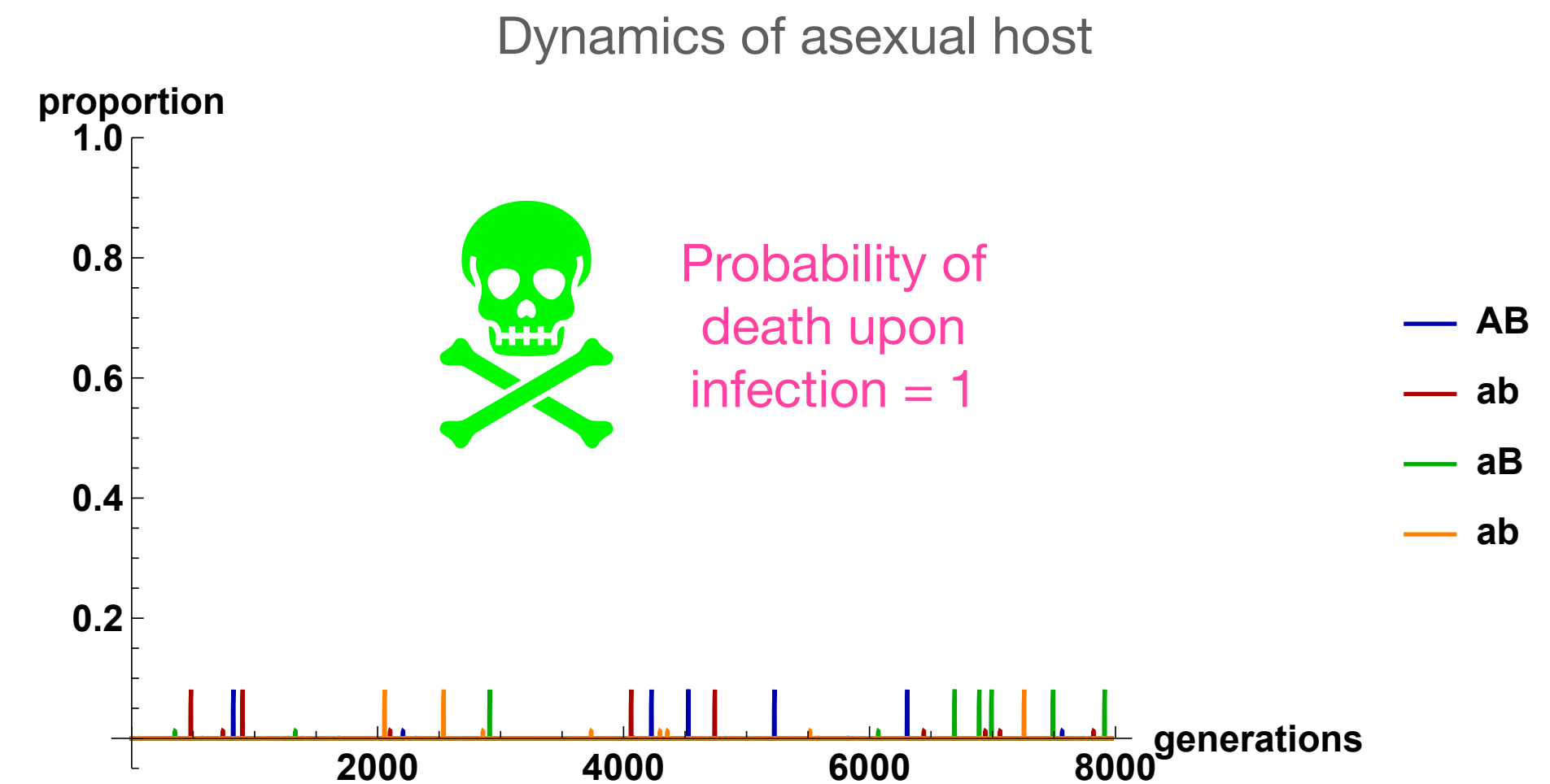
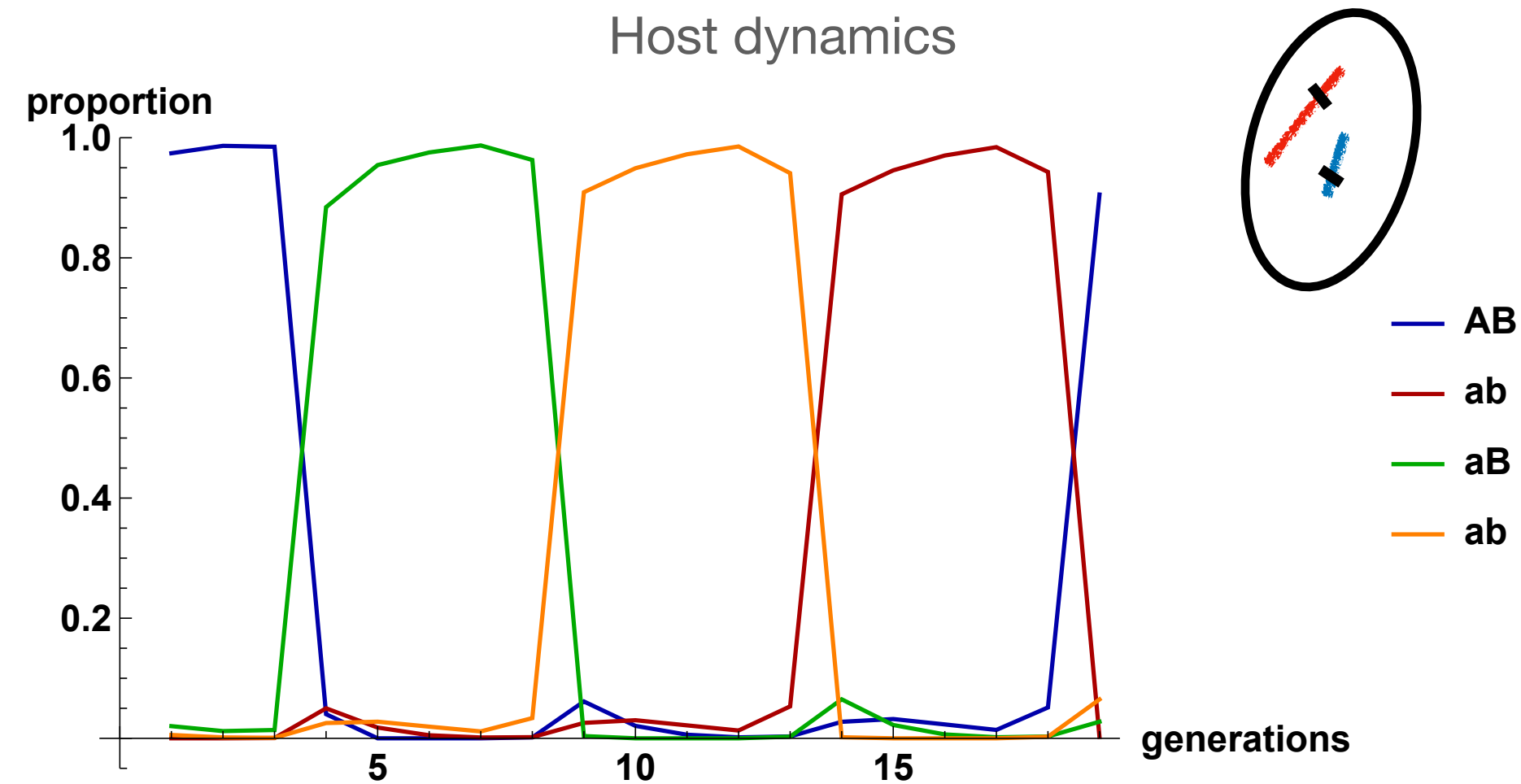
An ecological model of fluctuating epistasis

But...



An ecological model of fluctuating epistasis

But...



Summary

- Maintenance of sex is not straightforward: rapid demographic advantage versus slow evolutionary cost of asexuality.
- Strong epistasis can mitigate demographic advantage as fitness decreases rapidly with new mutations.
- Fluctuating epistasis also disadvantages asexuals who cannot easily create novel allelic combinations.
- Ecological interactions can lead to red queen dynamics and fluctuating epistasis, favouring sexual reproduction.
- But existing models do not fully answer the question.

