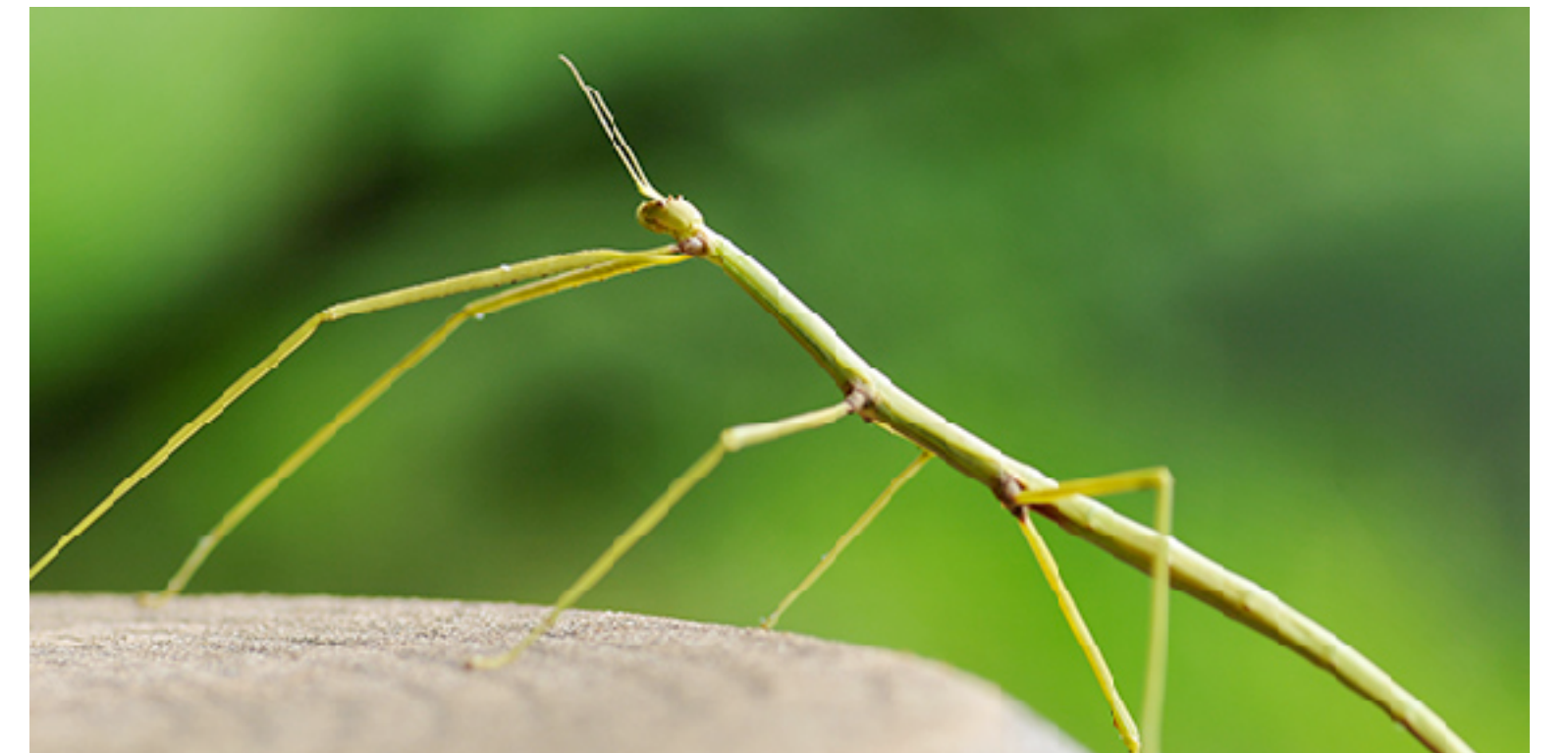


# **Part II - Sexual reproduction**

**Sex, Ageing and Foraging Theory**

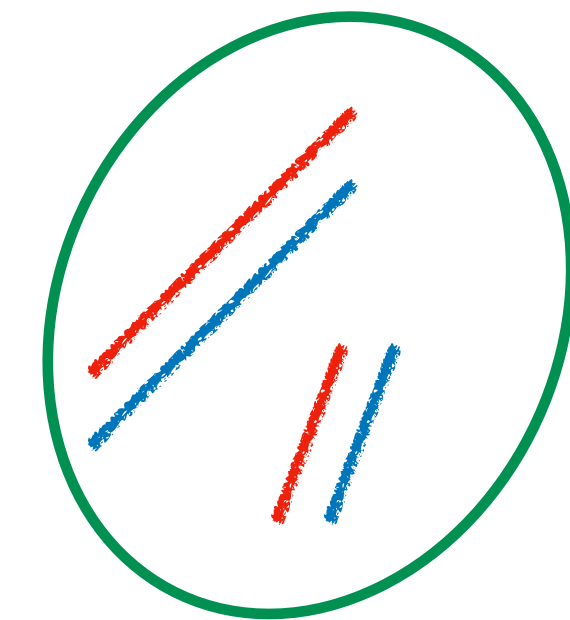
# Sexual reproduction is near universal in multicellular organisms

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.

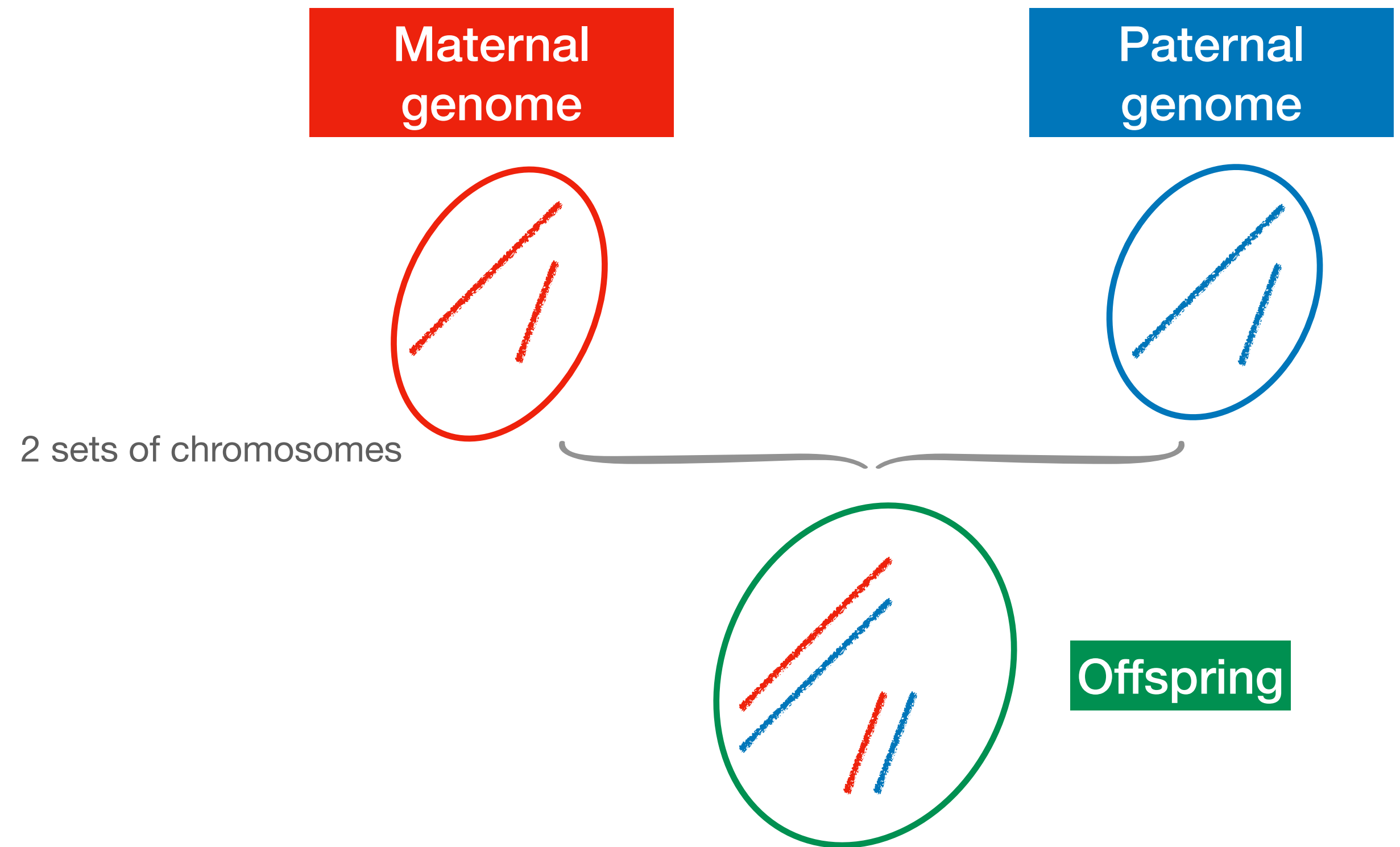


Offspring

# What is sexual reproduction?

## and what are sexes?

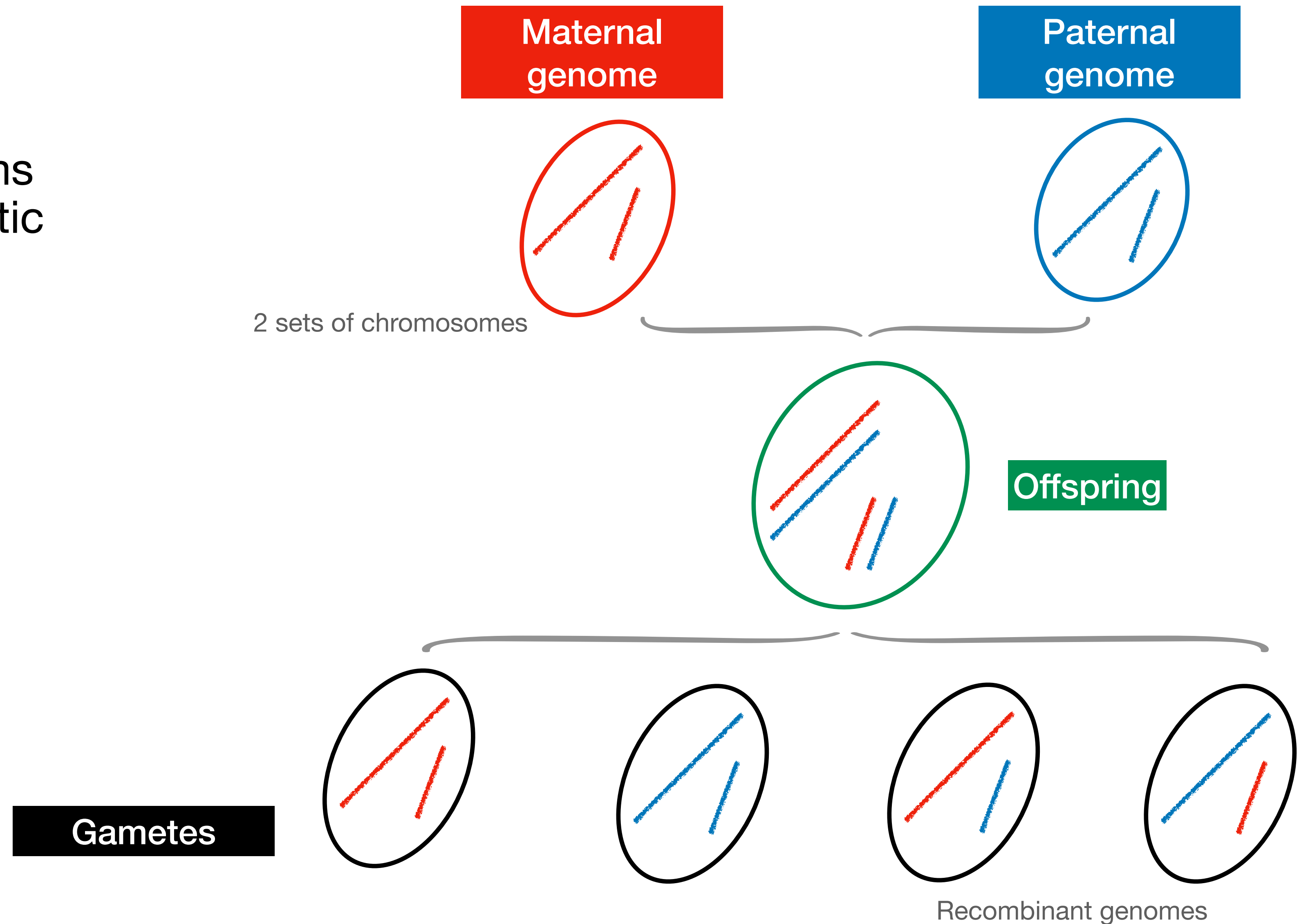
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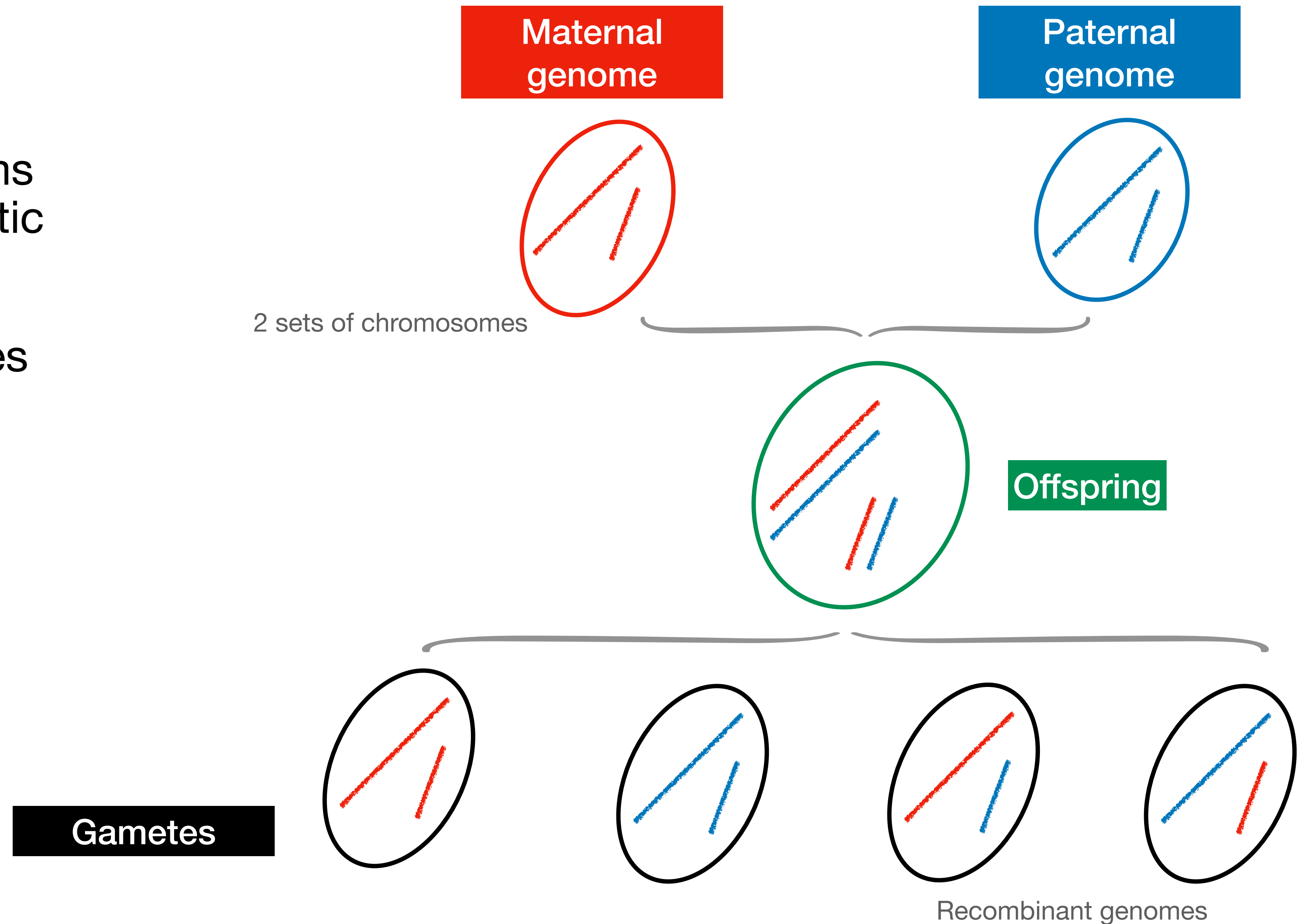
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# What is sexual reproduction?

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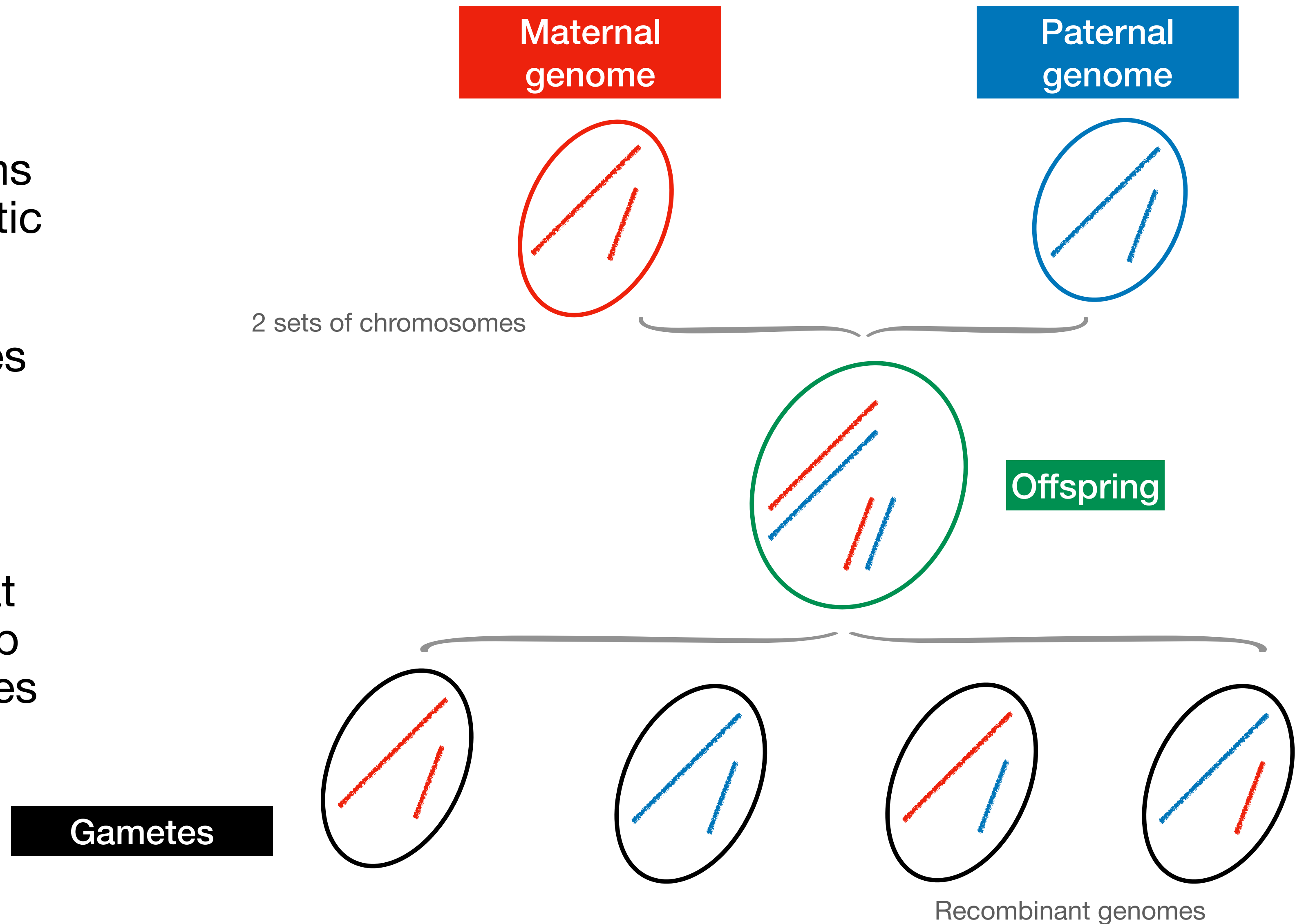
- Production of new organisms by the combination of genetic material of two individuals.
- Sexes are defined as classes of individuals that are incompatible for sexual reproduction.

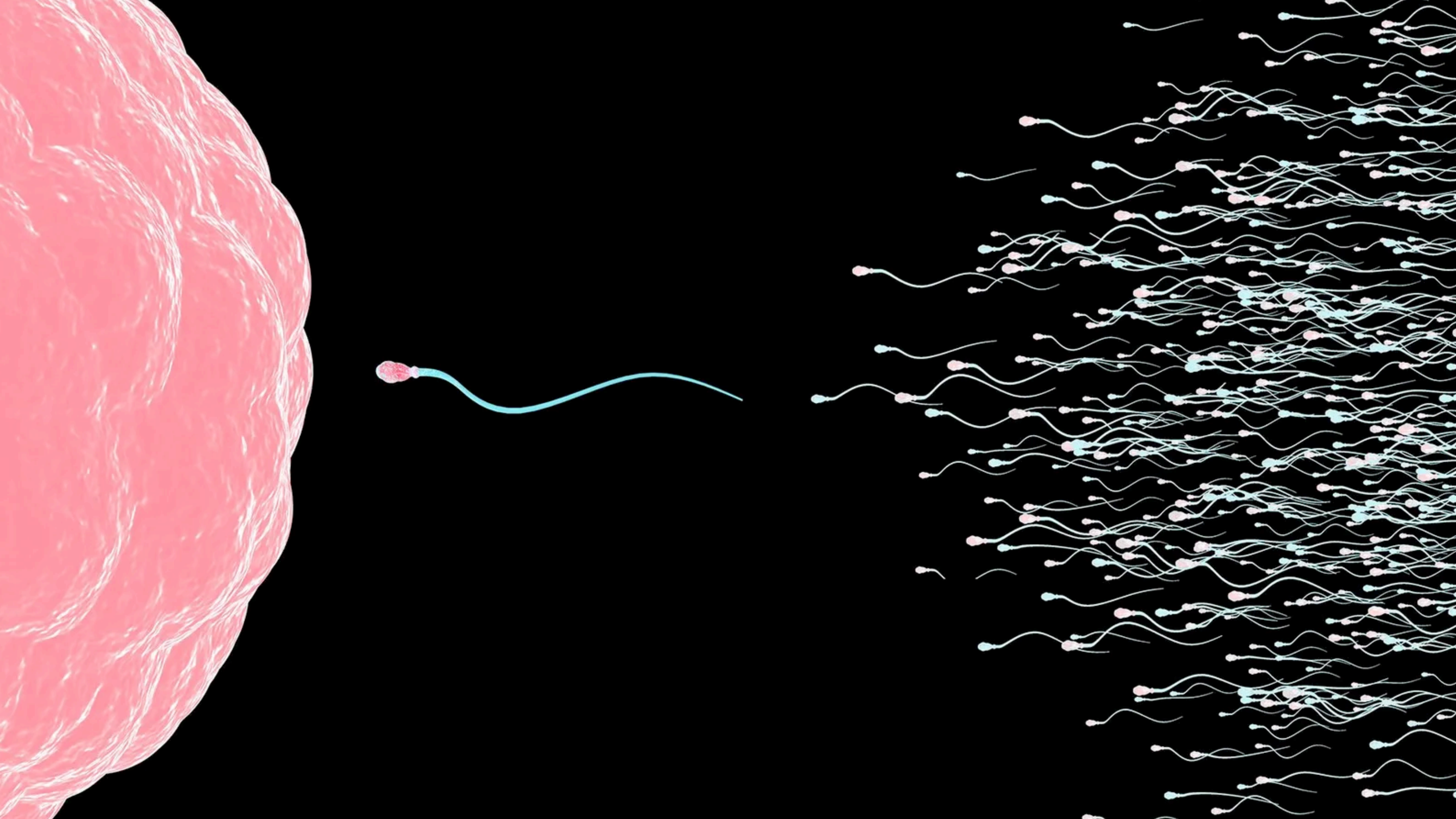


# What is sexual reproduction?

## 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: ???

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- 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)



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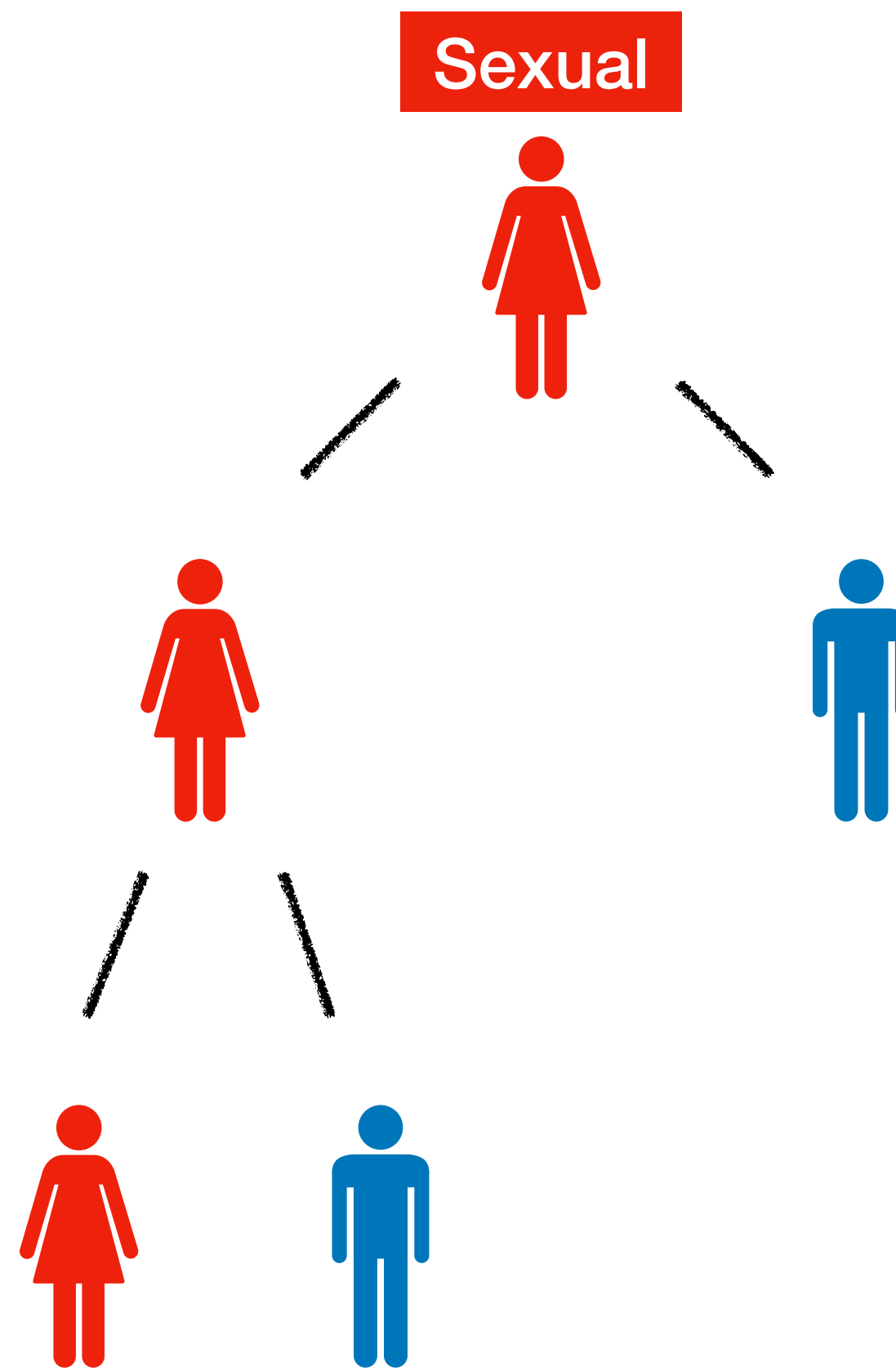
# Reproduction is female limited

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- Human man record claim: **888** offspring Ismael the Bloodthirsty, emperor of Morocco (1672-1727)



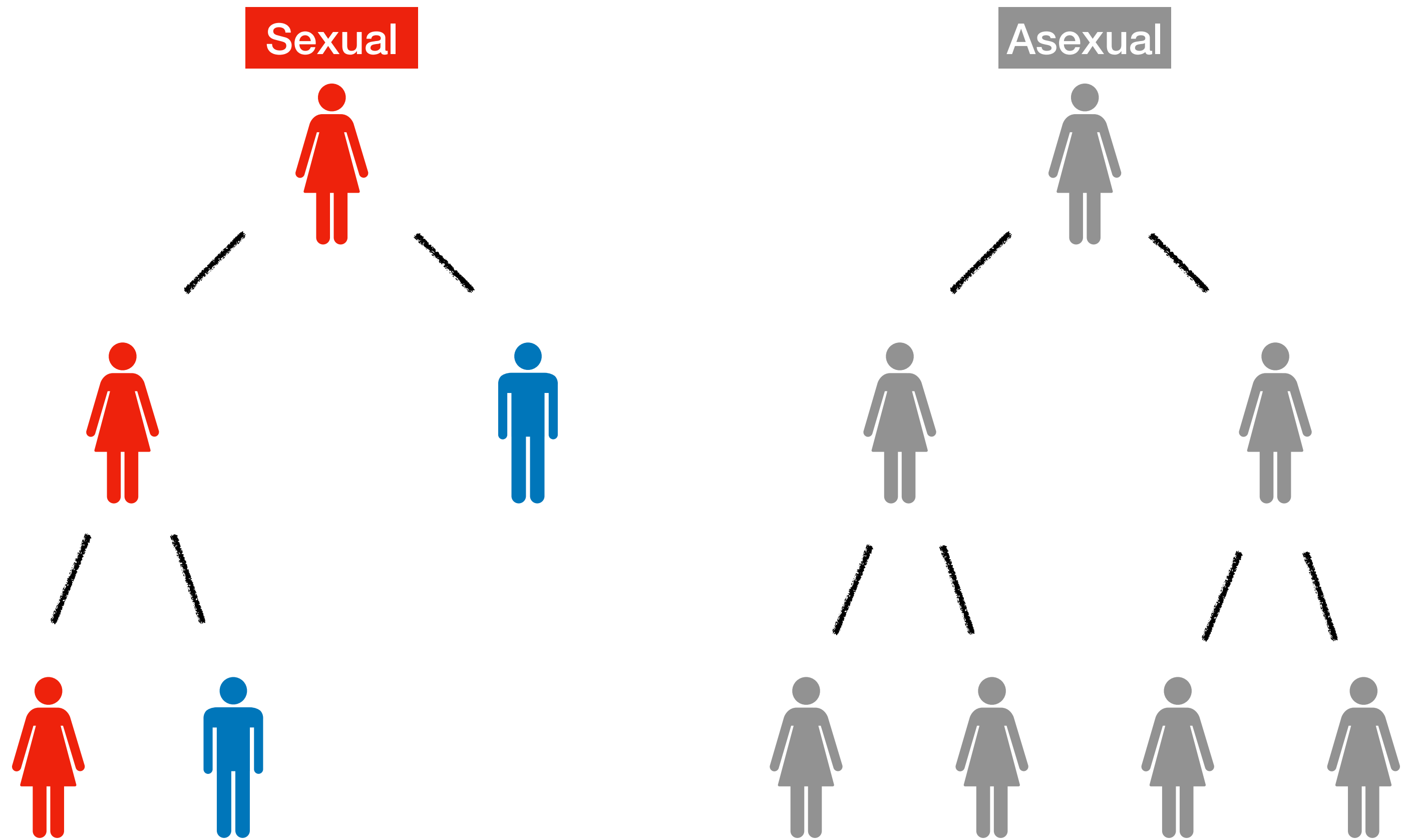
# The demographic cost of sex

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



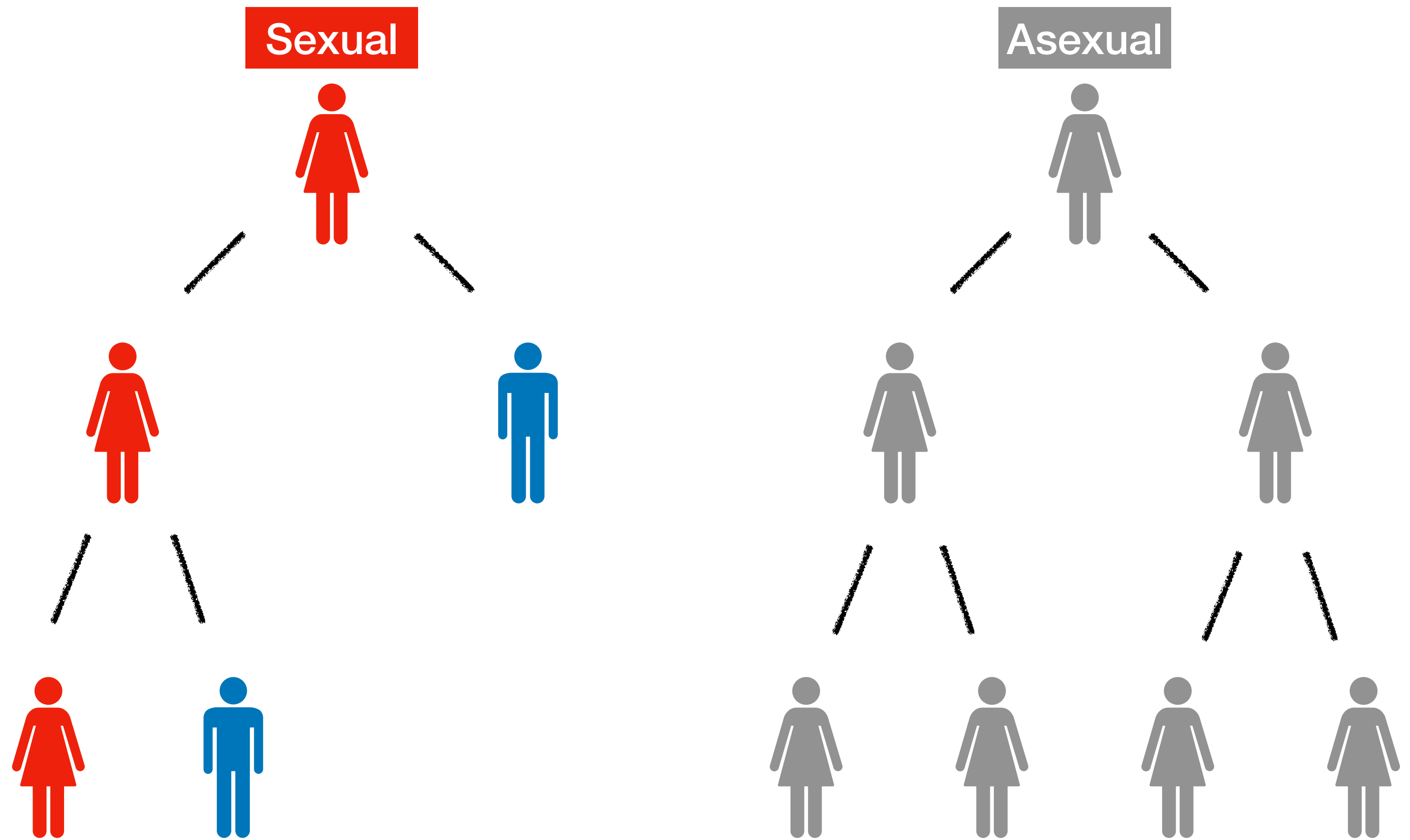
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# The demographic cost of sex

- 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

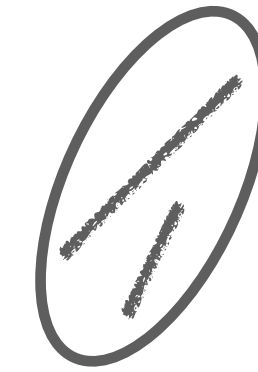
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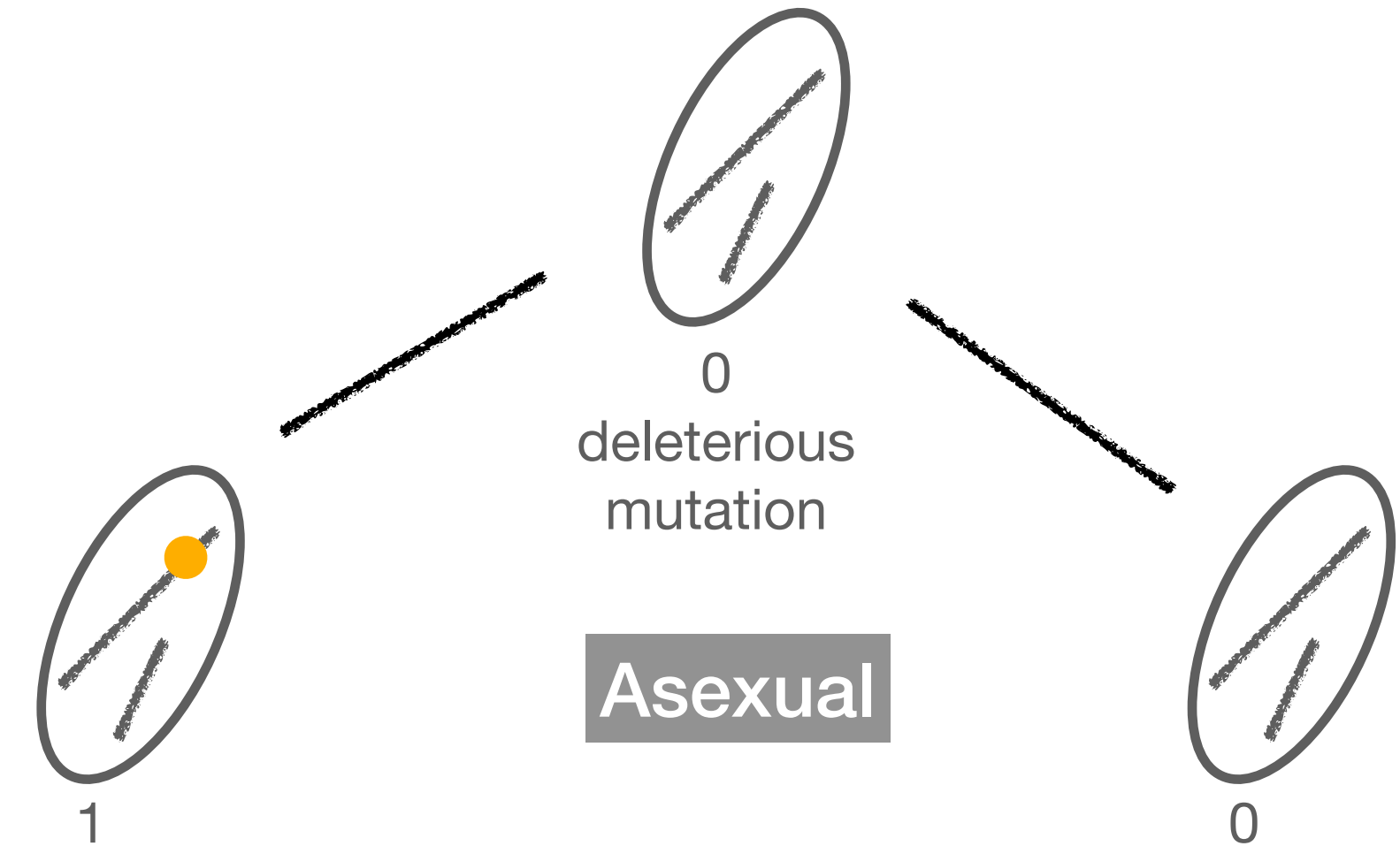
0

deleterious  
mutation

Asexual

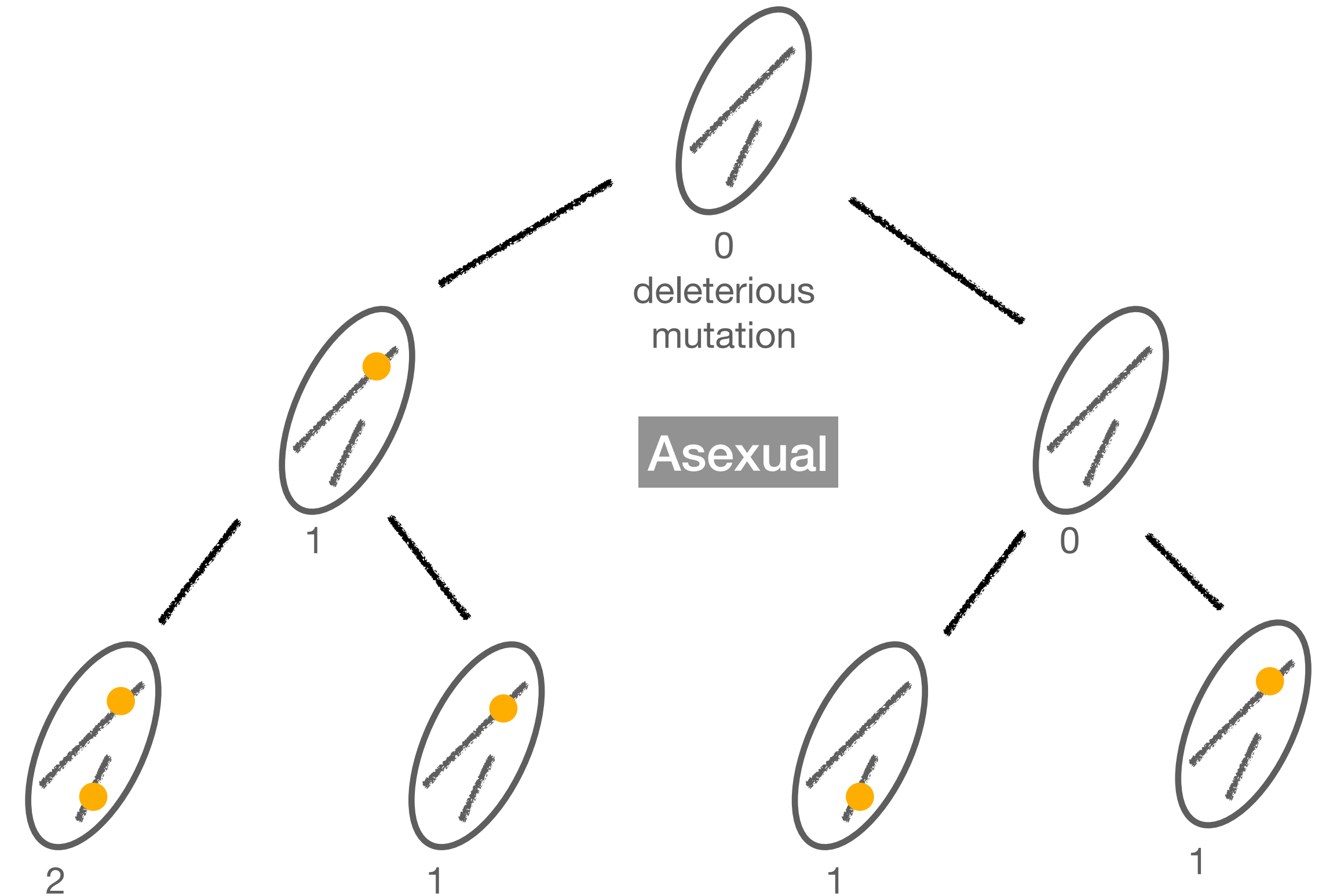
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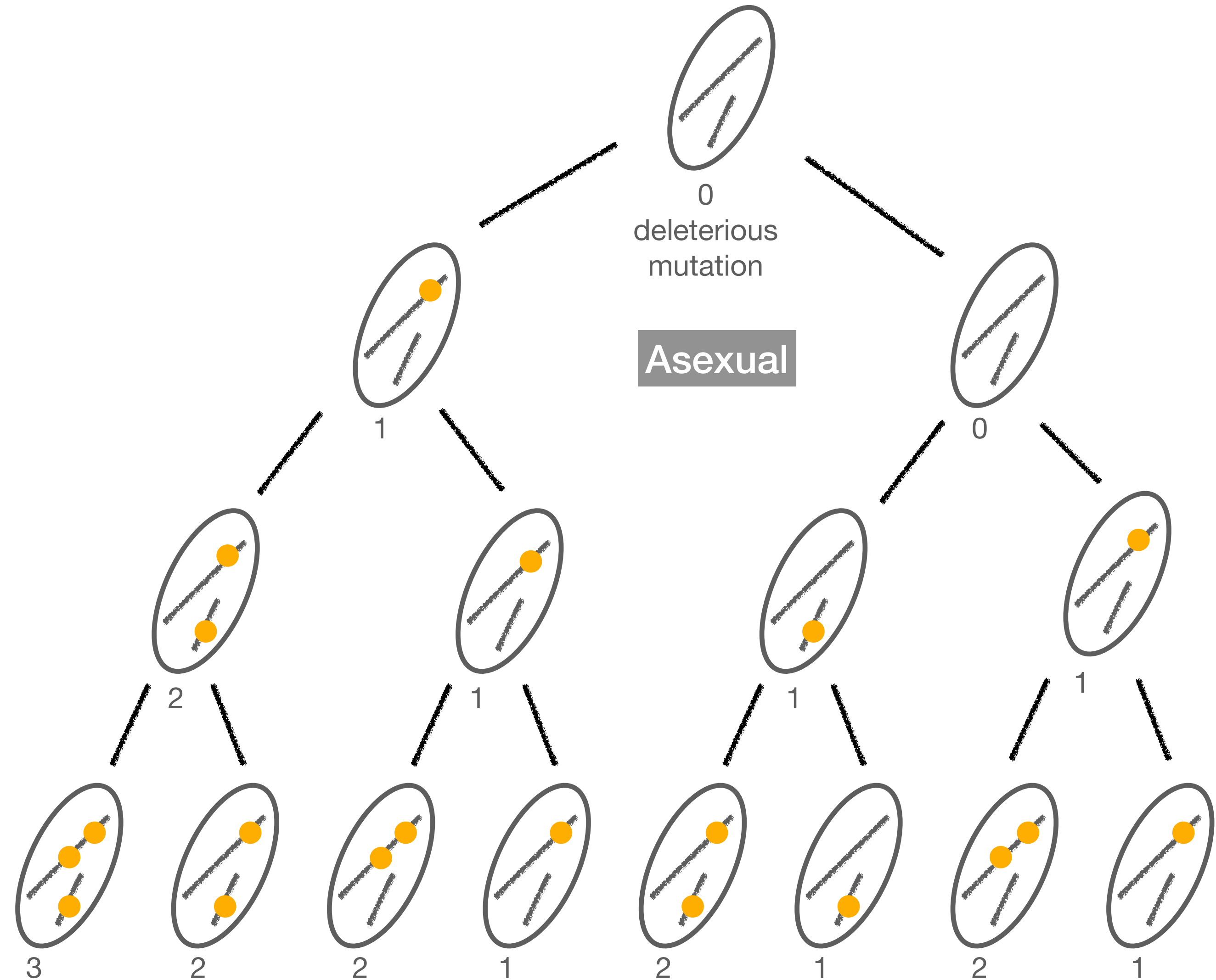
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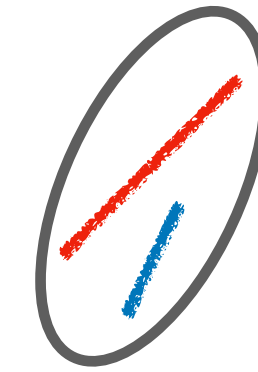
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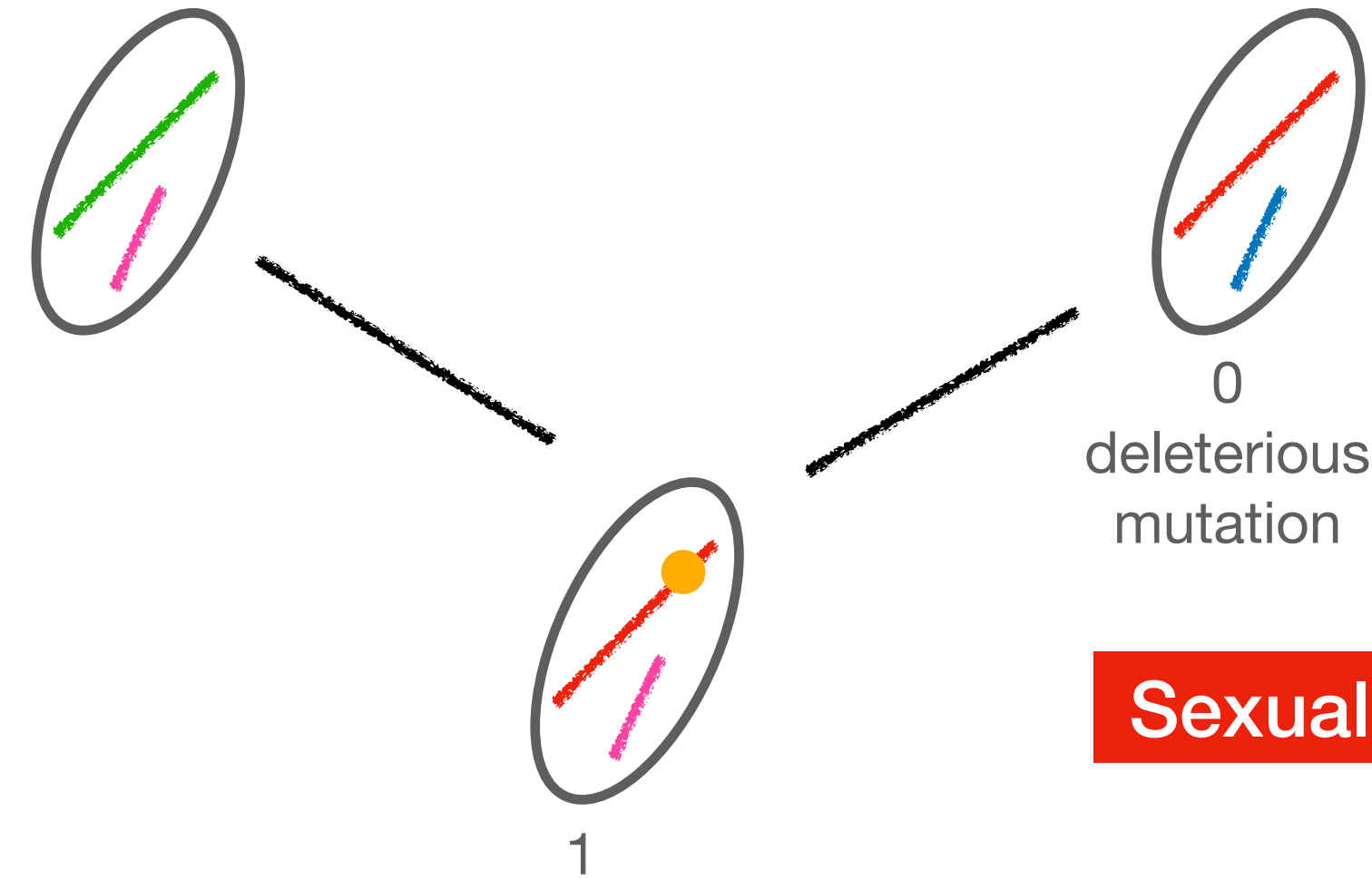


0  
deleterious  
mutation

**Sexual**

# The evolutionary cost of asexuality

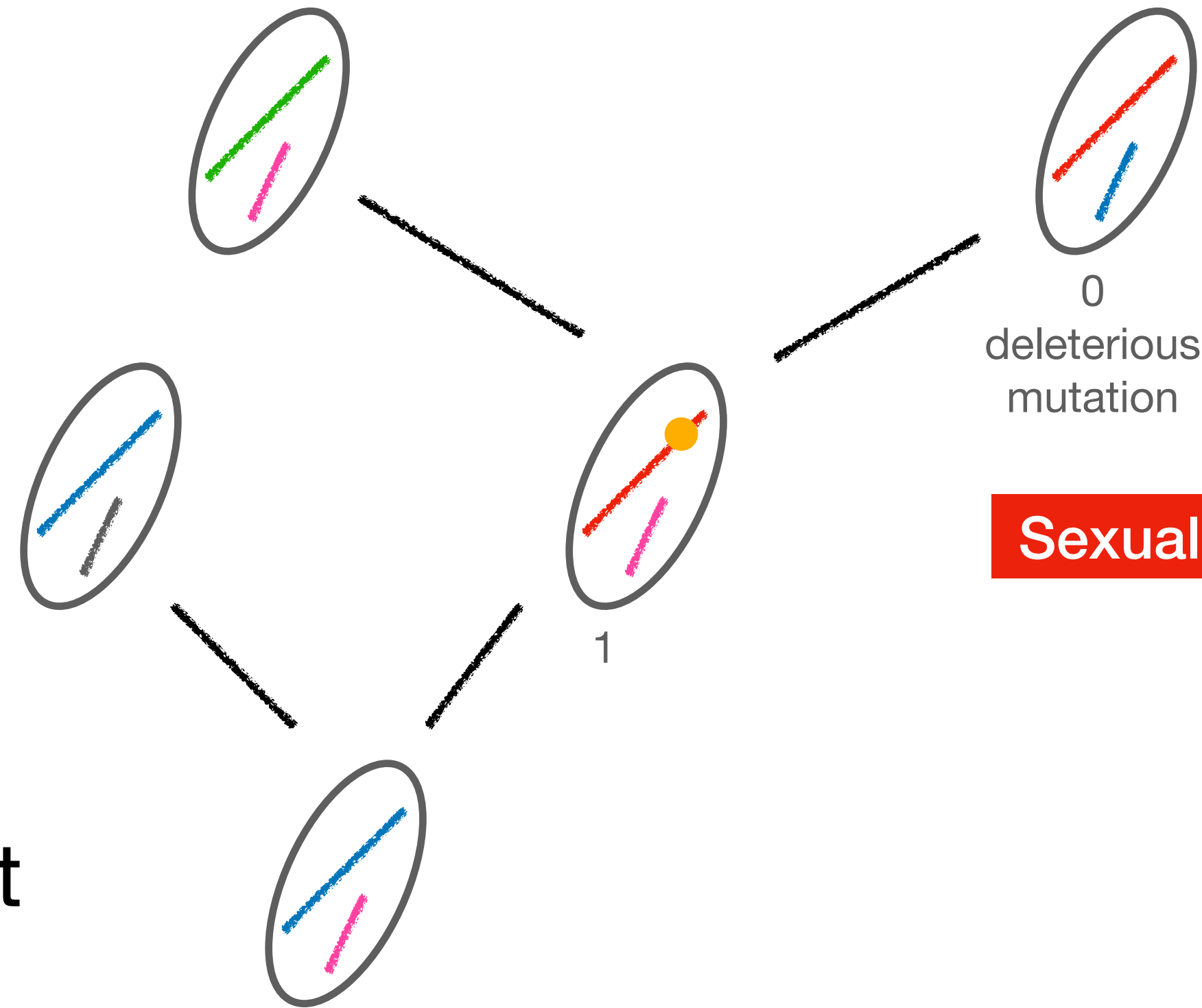
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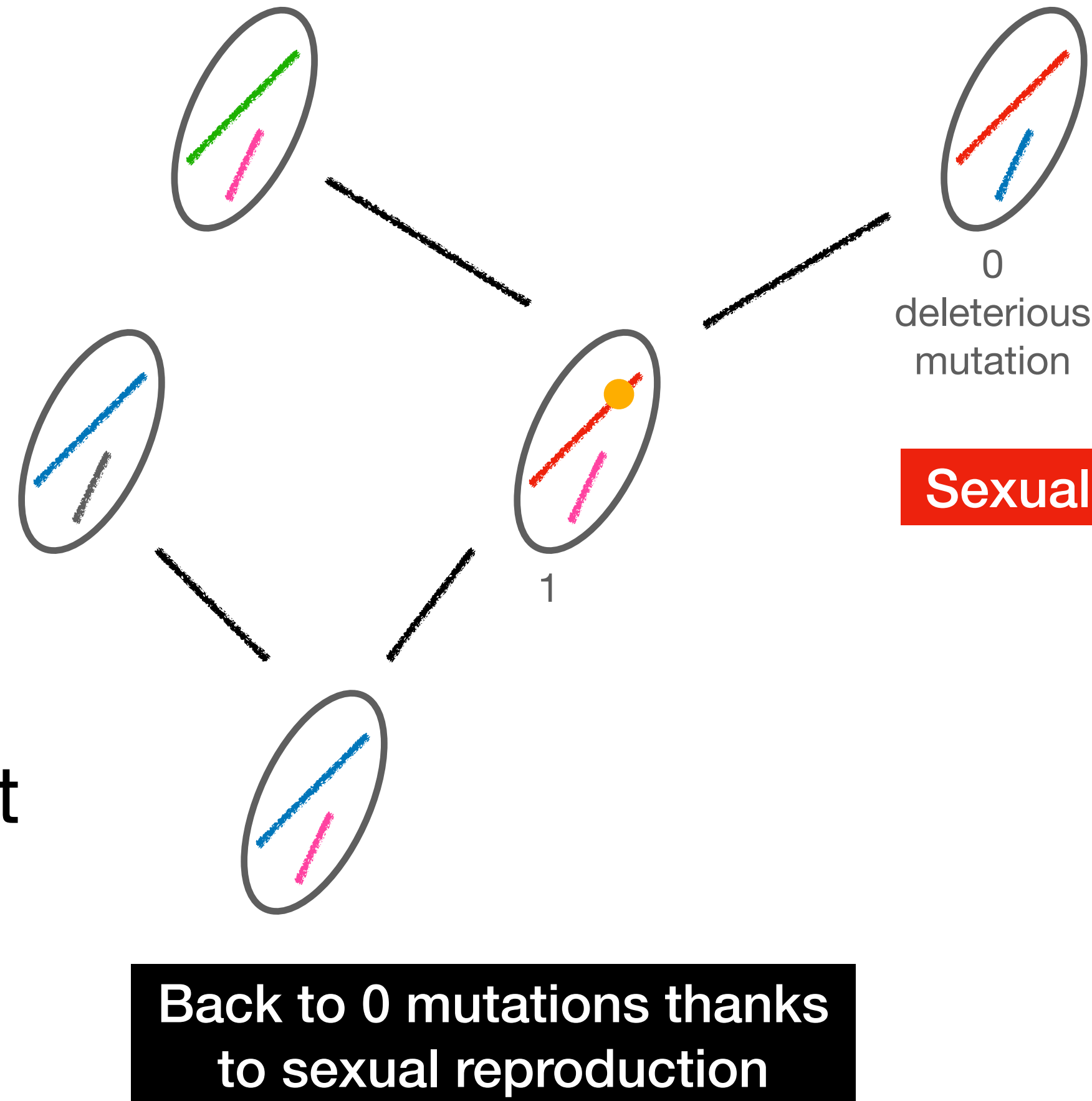
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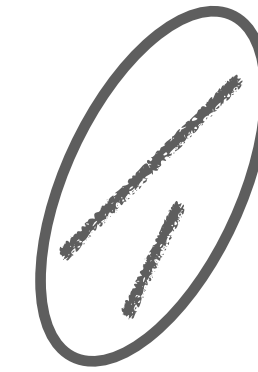


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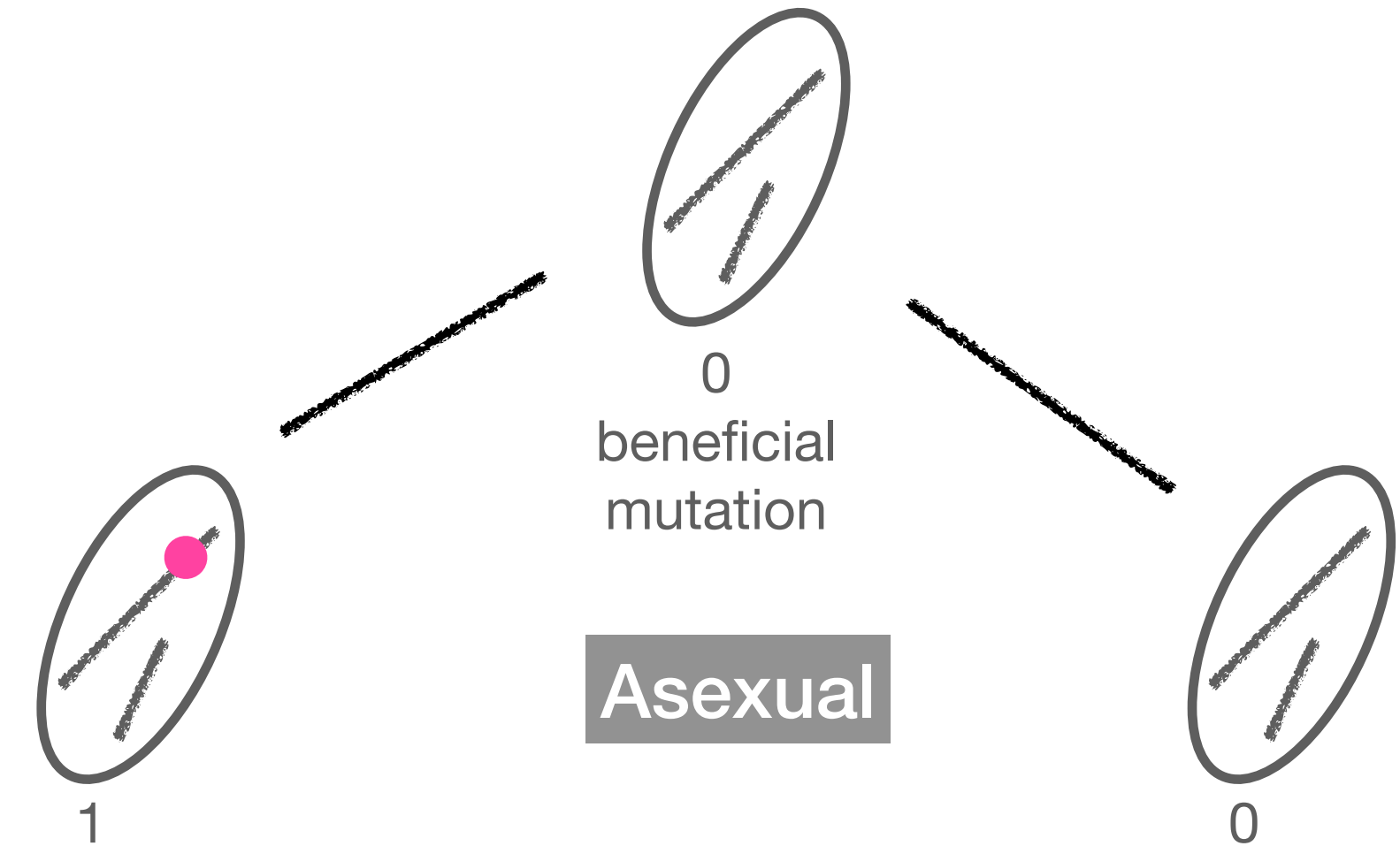


0  
beneficial  
mutation

Asexual

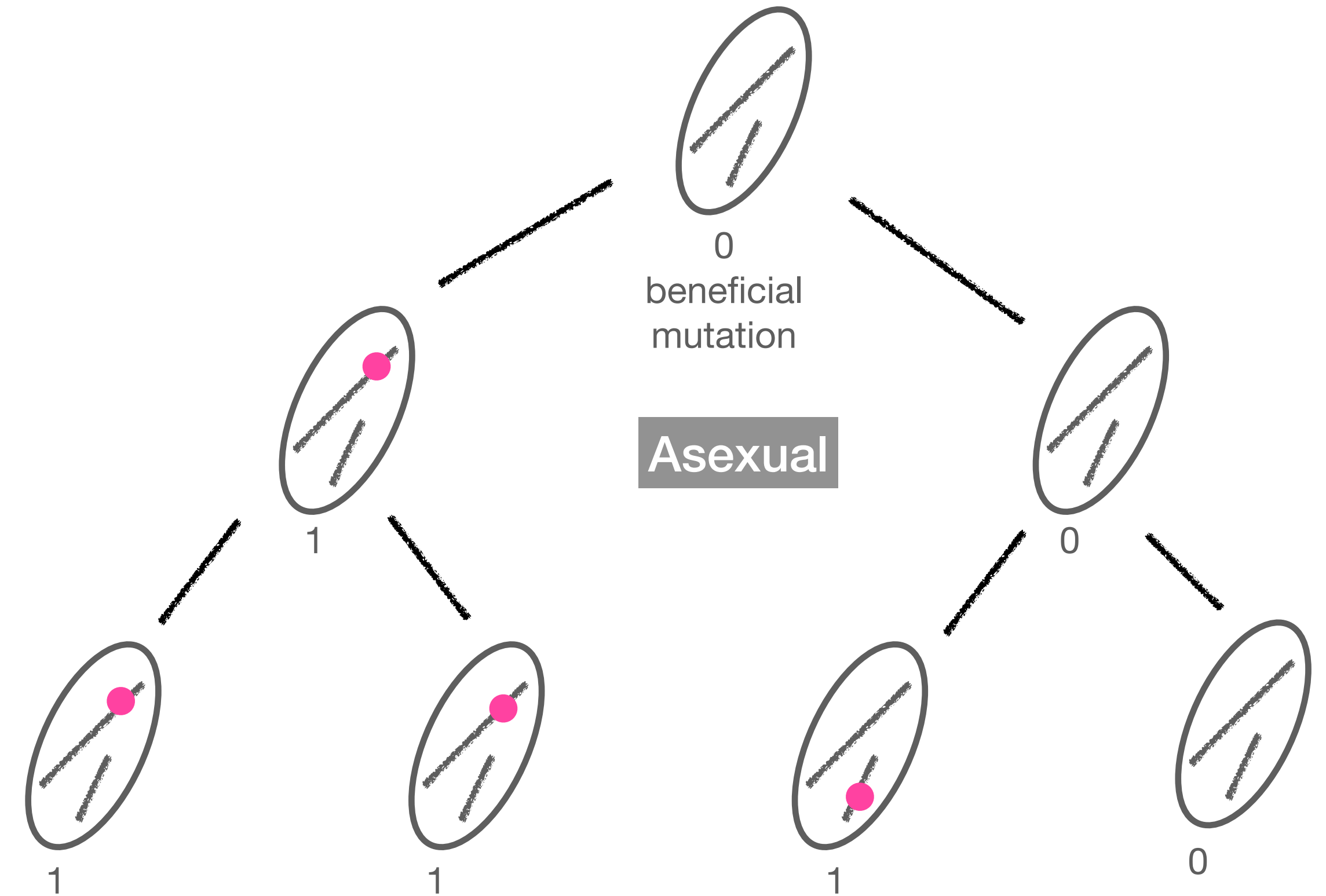
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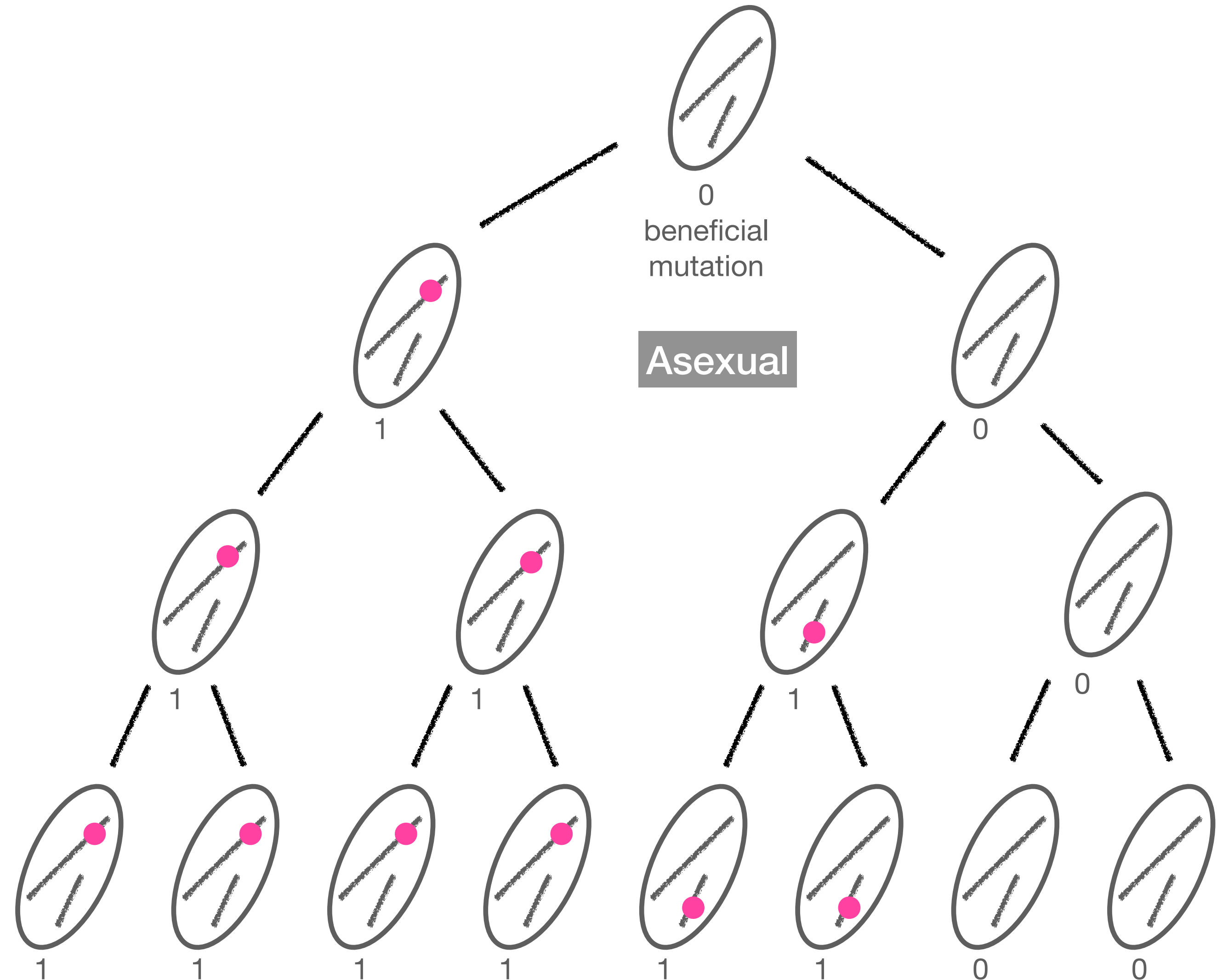
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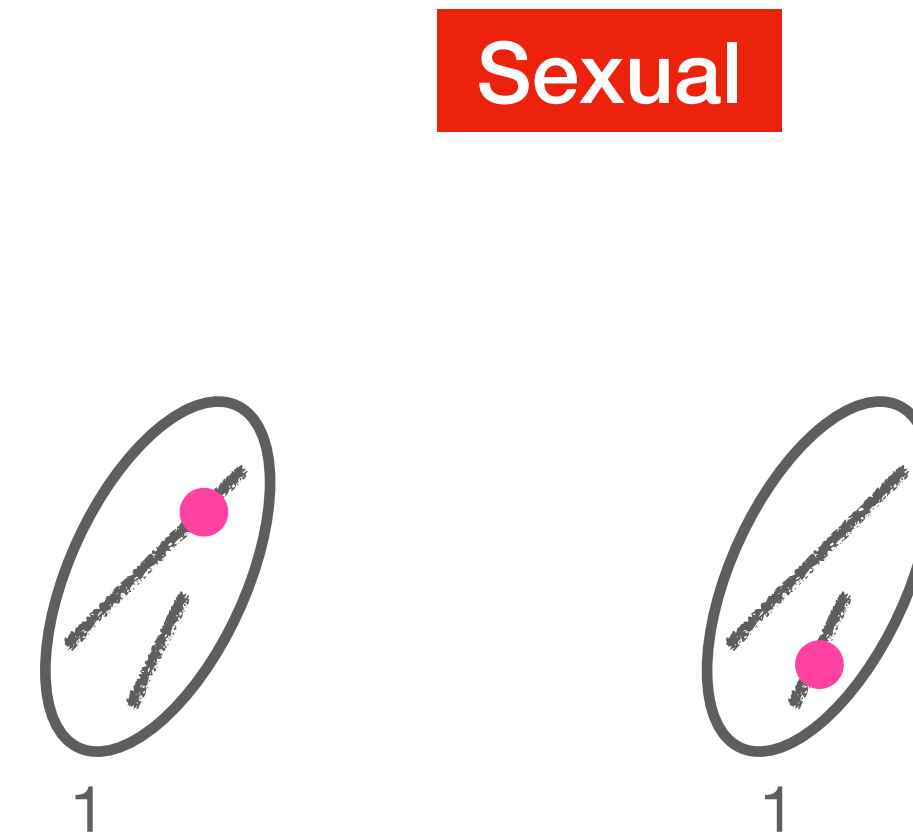
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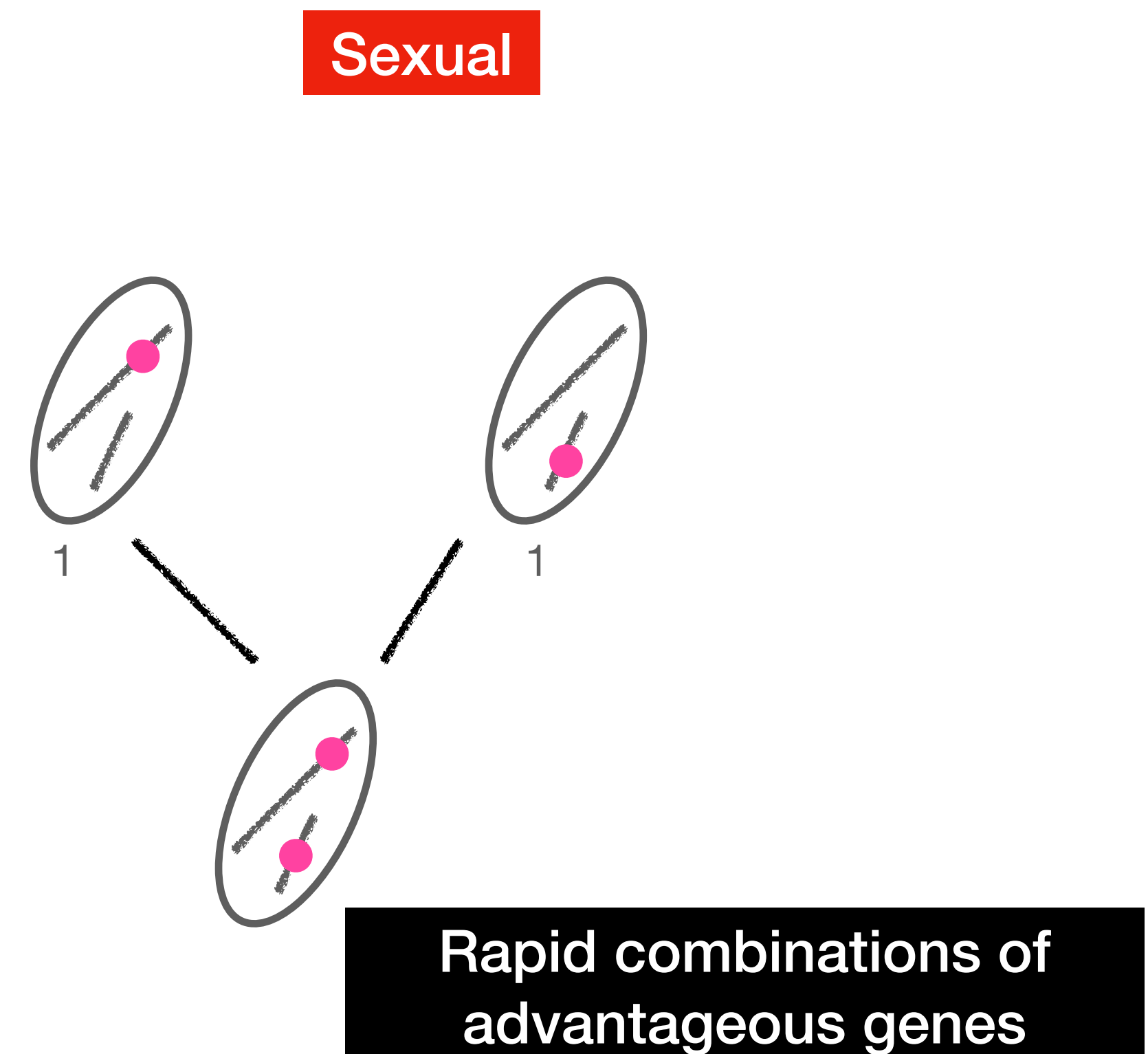
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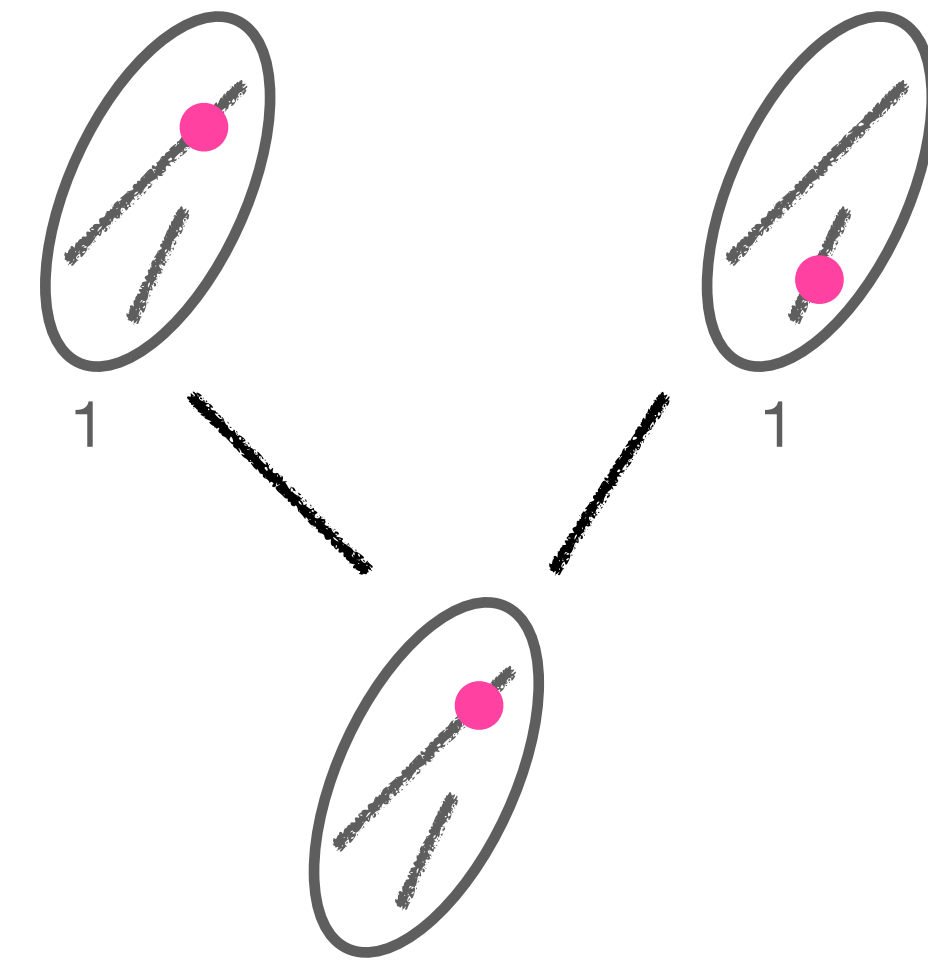
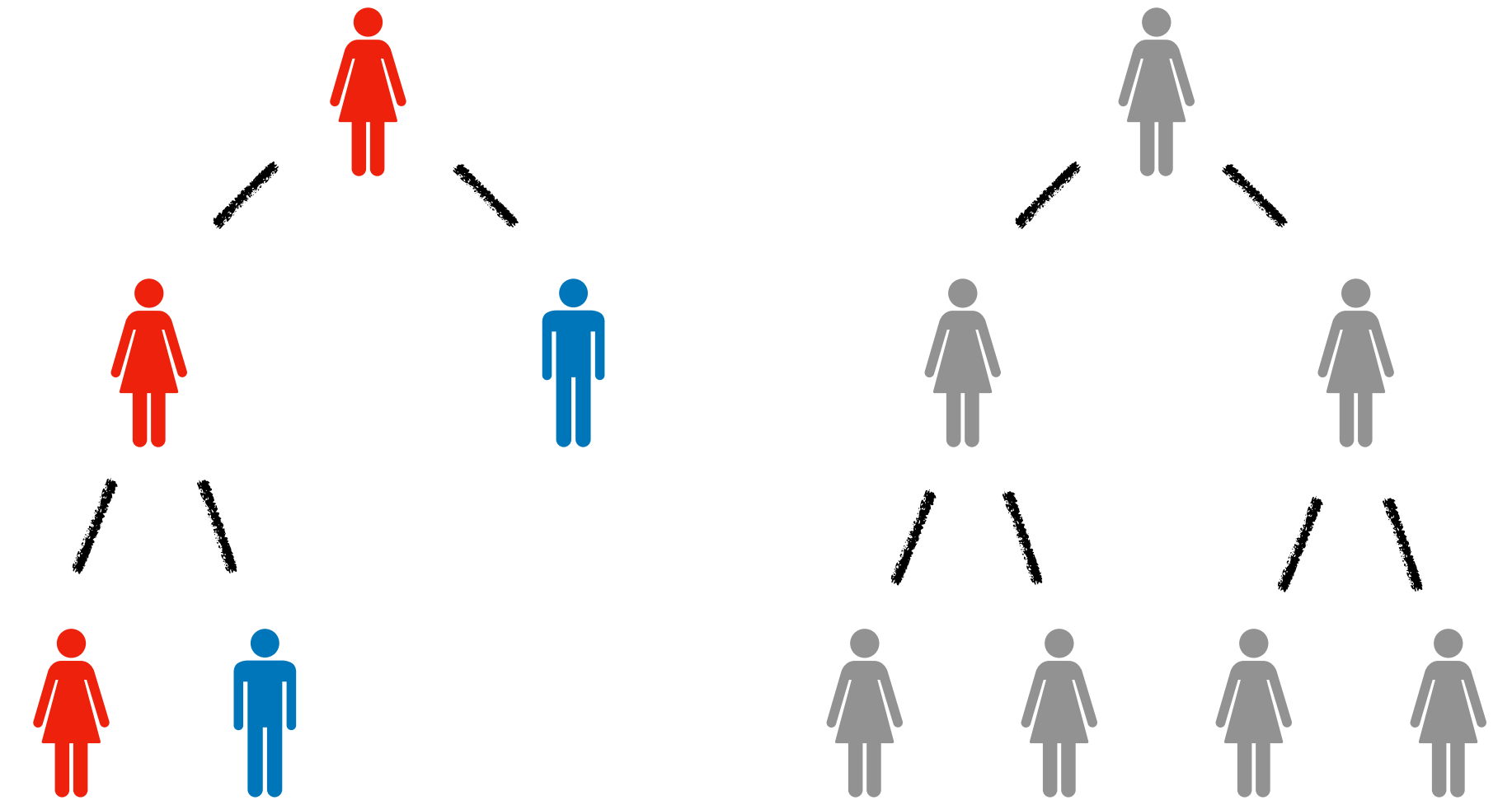
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# Summary

- 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

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Fecundity

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

Number of deleterious mutations

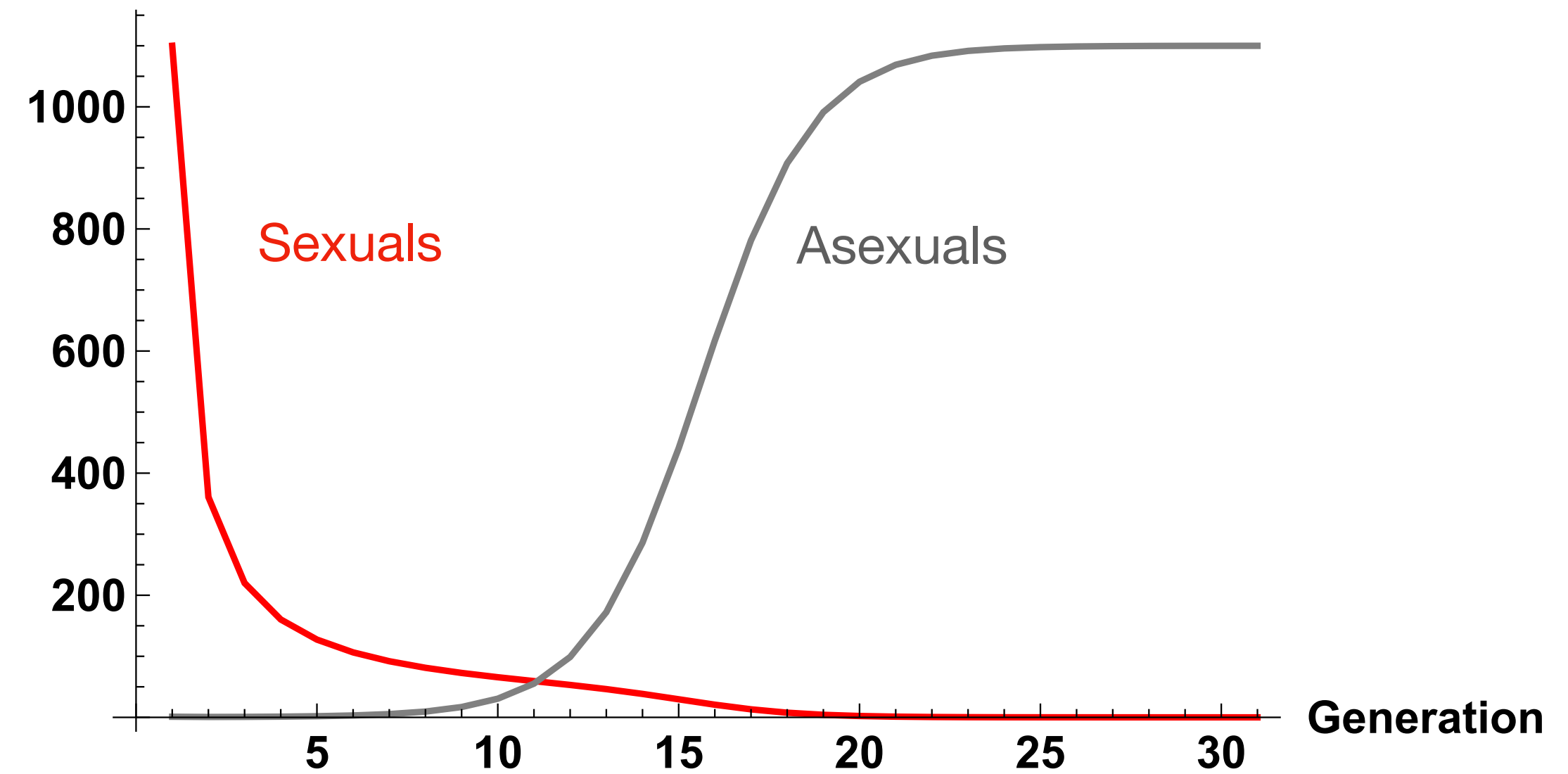
Effect of single mutation

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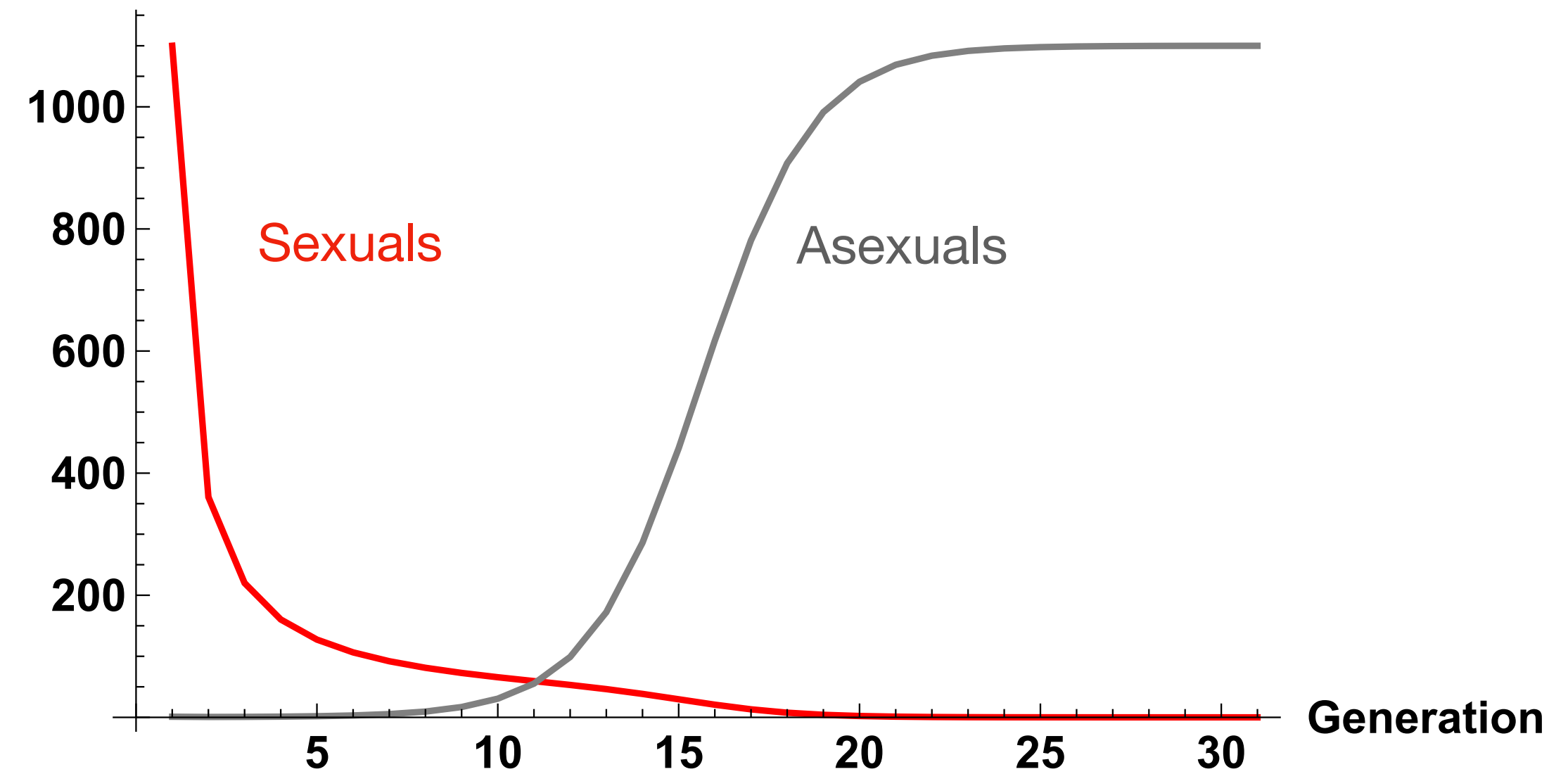
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$$f(k_A) < \frac{f(k_S)}{2}$$

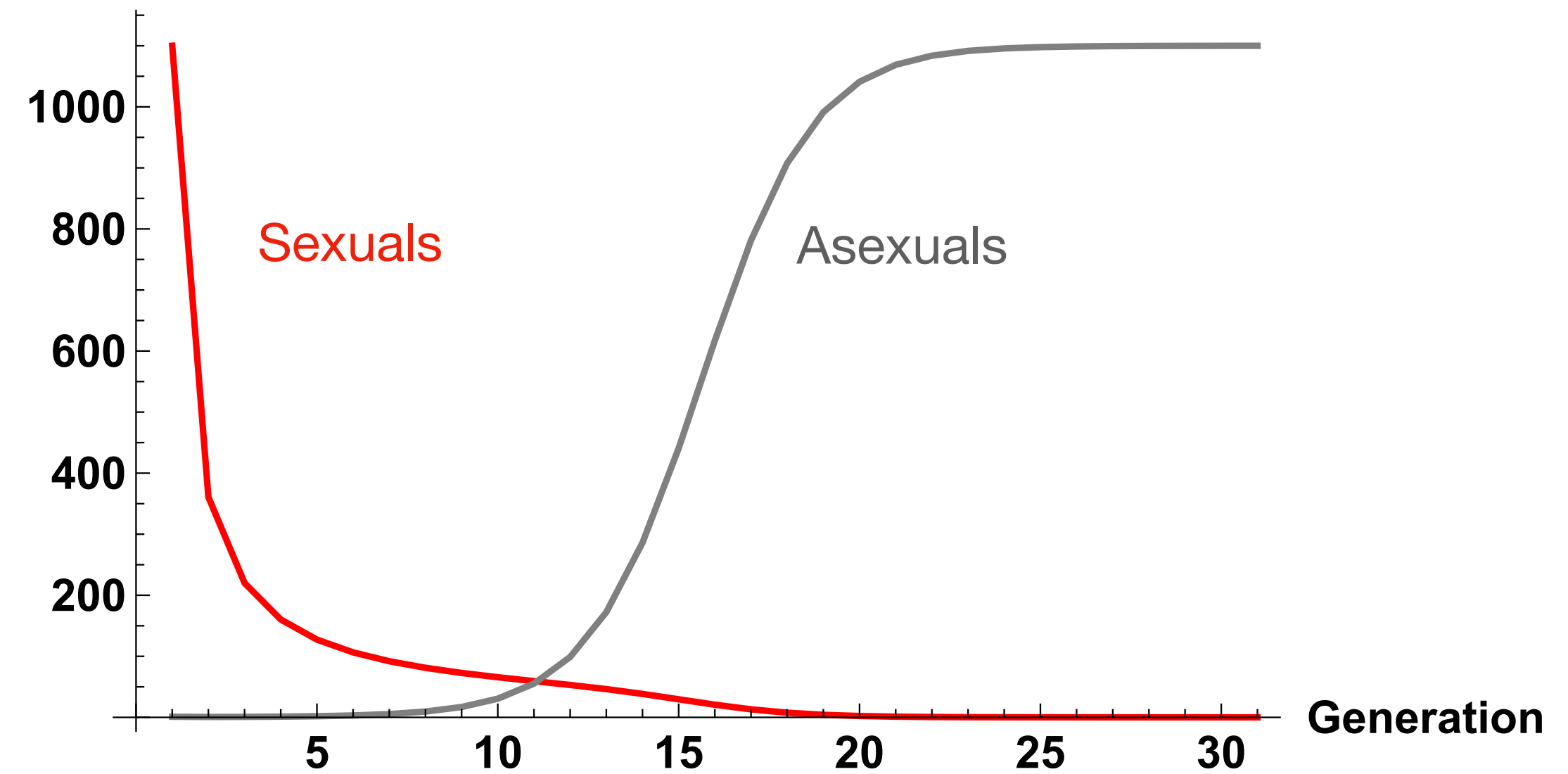
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Fecundity

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

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

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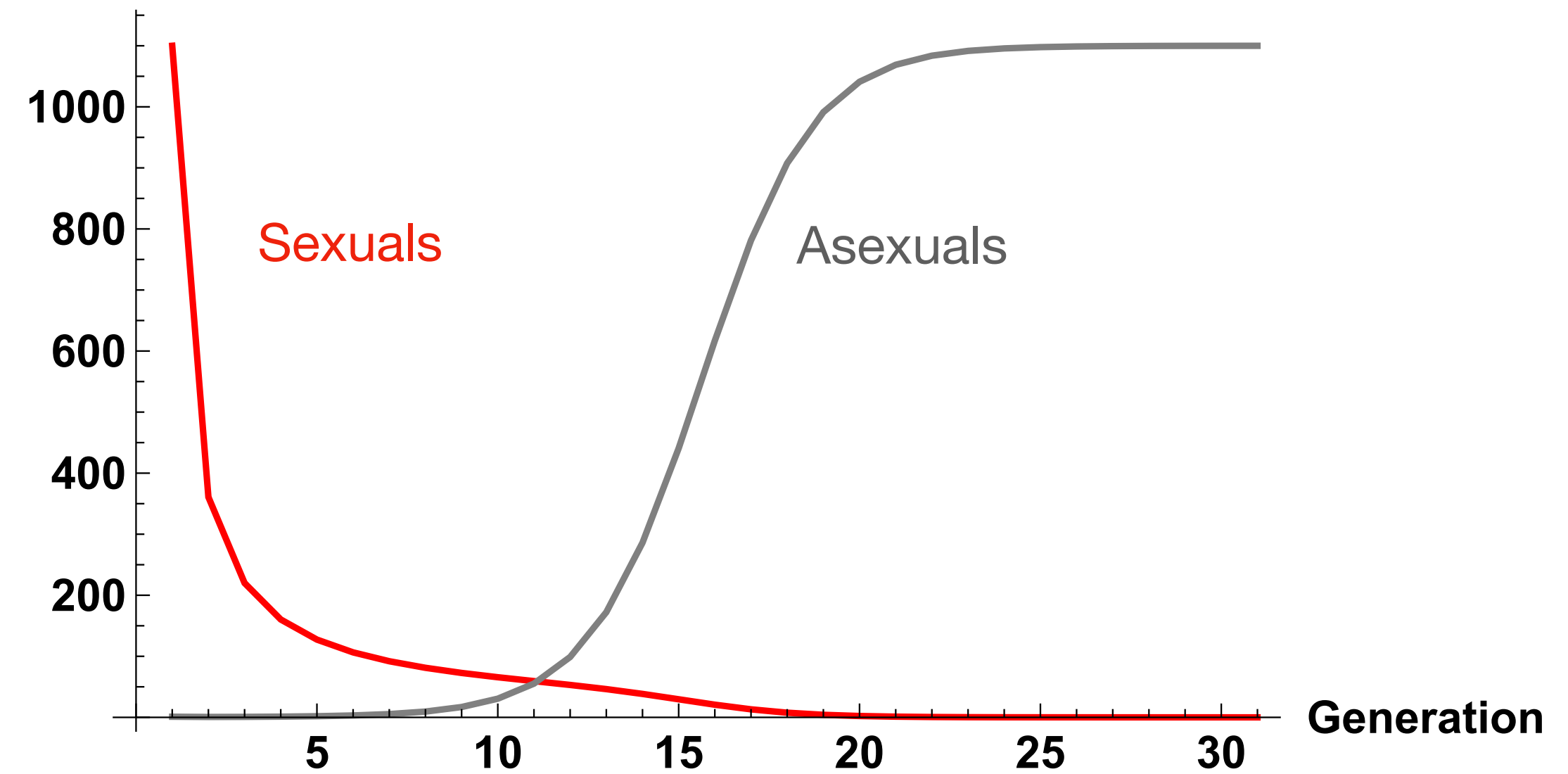


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Fecundity

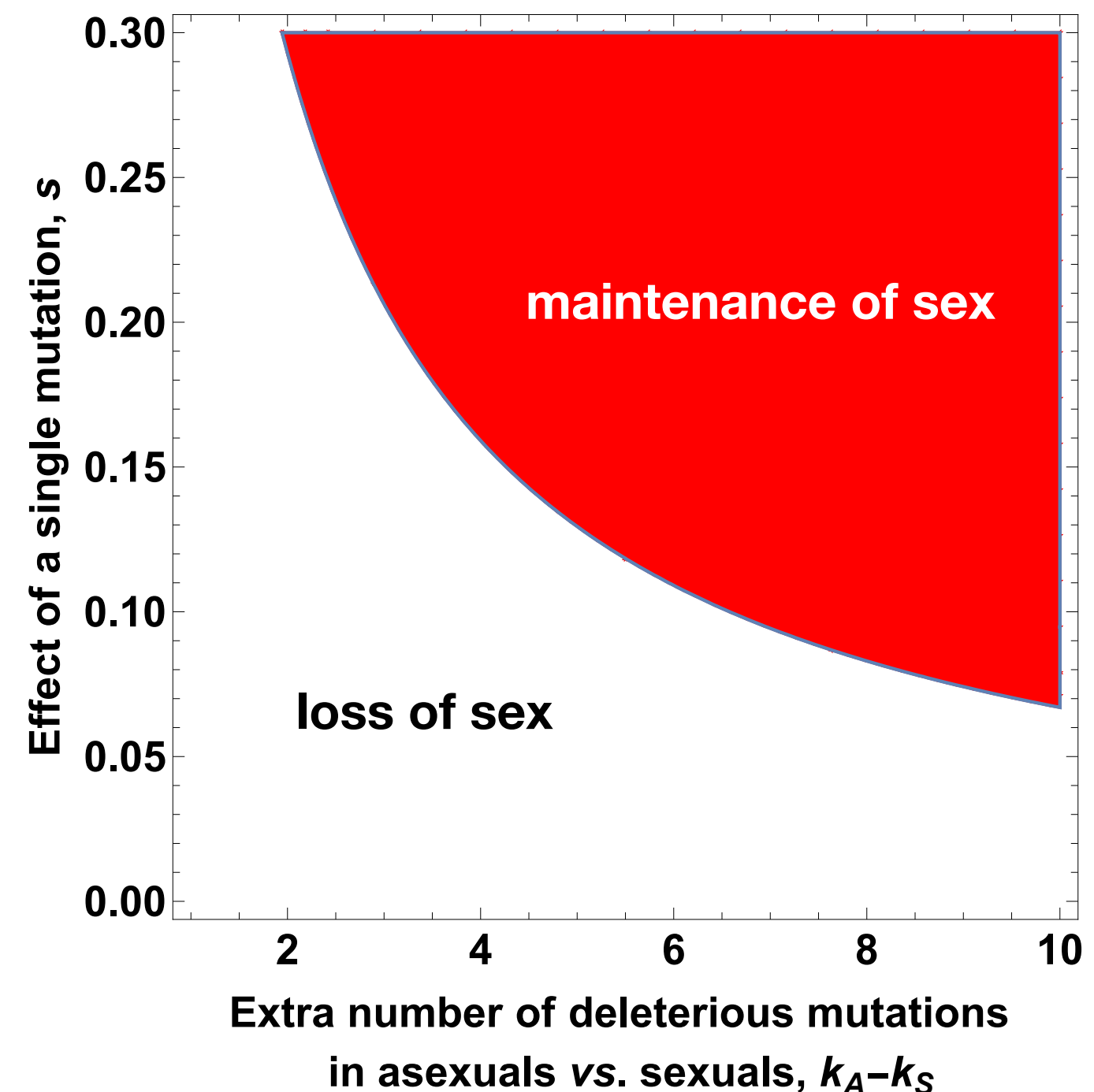
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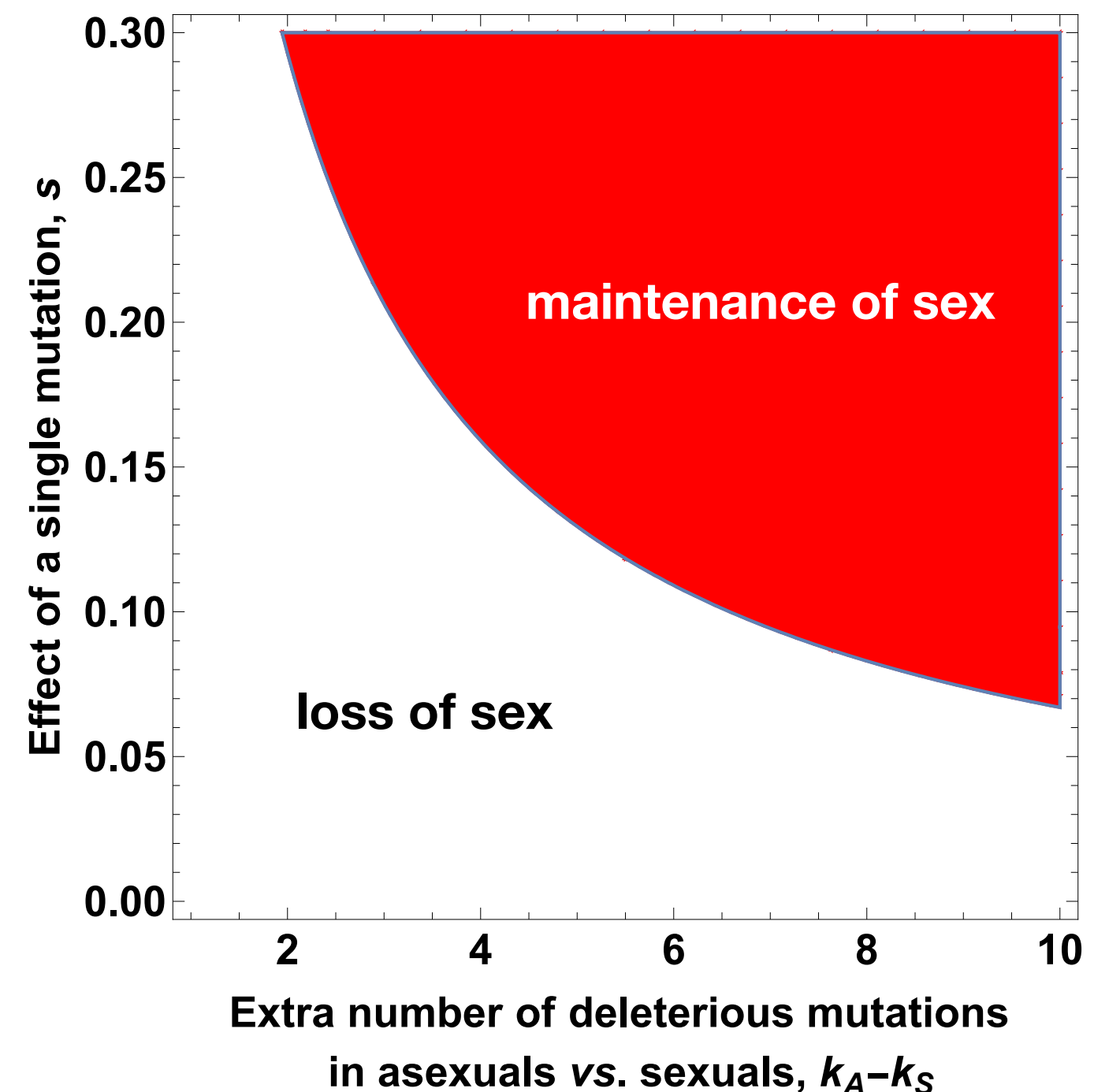
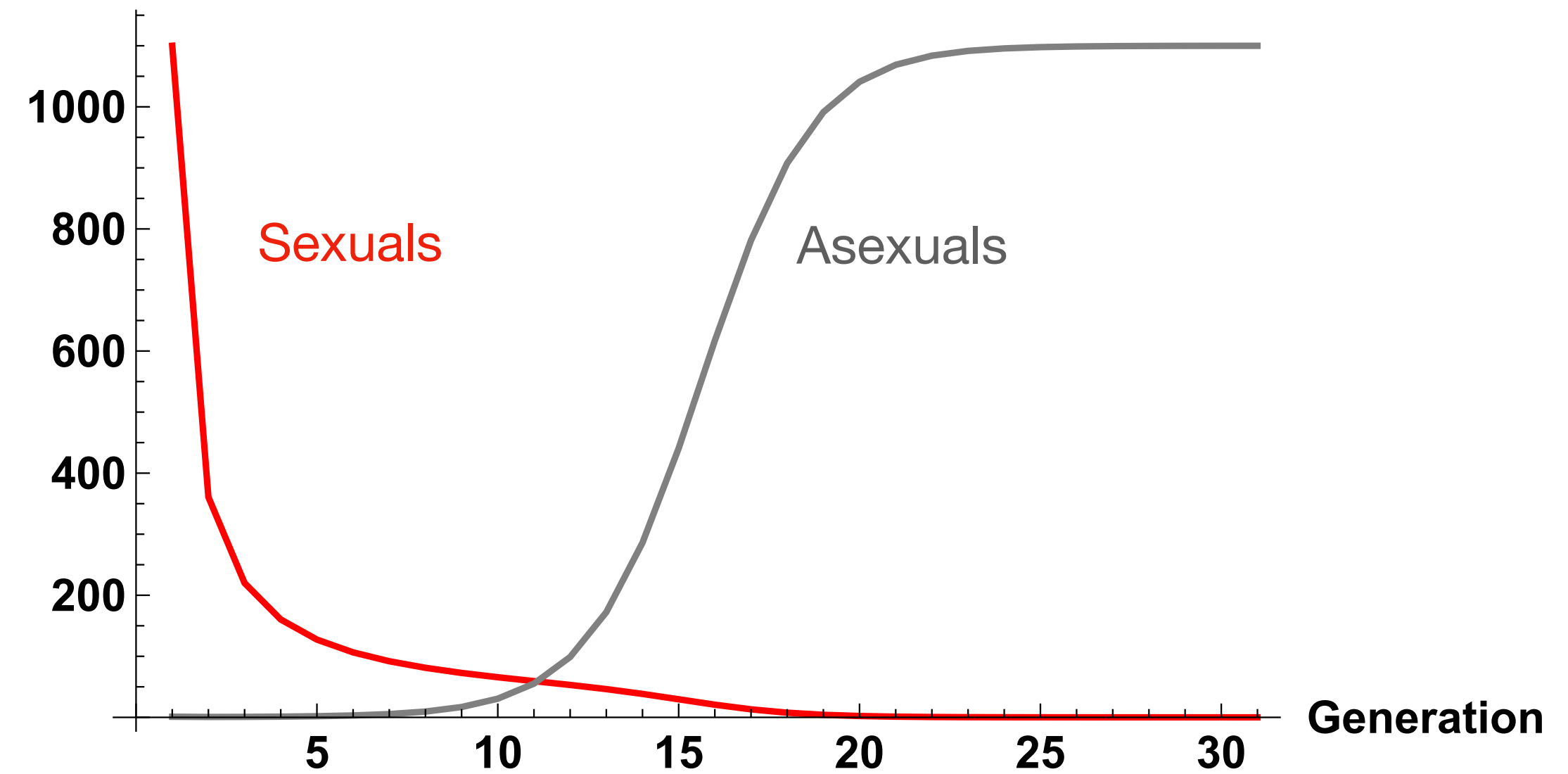
# The problem

## How to overcome the twofold cost?

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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

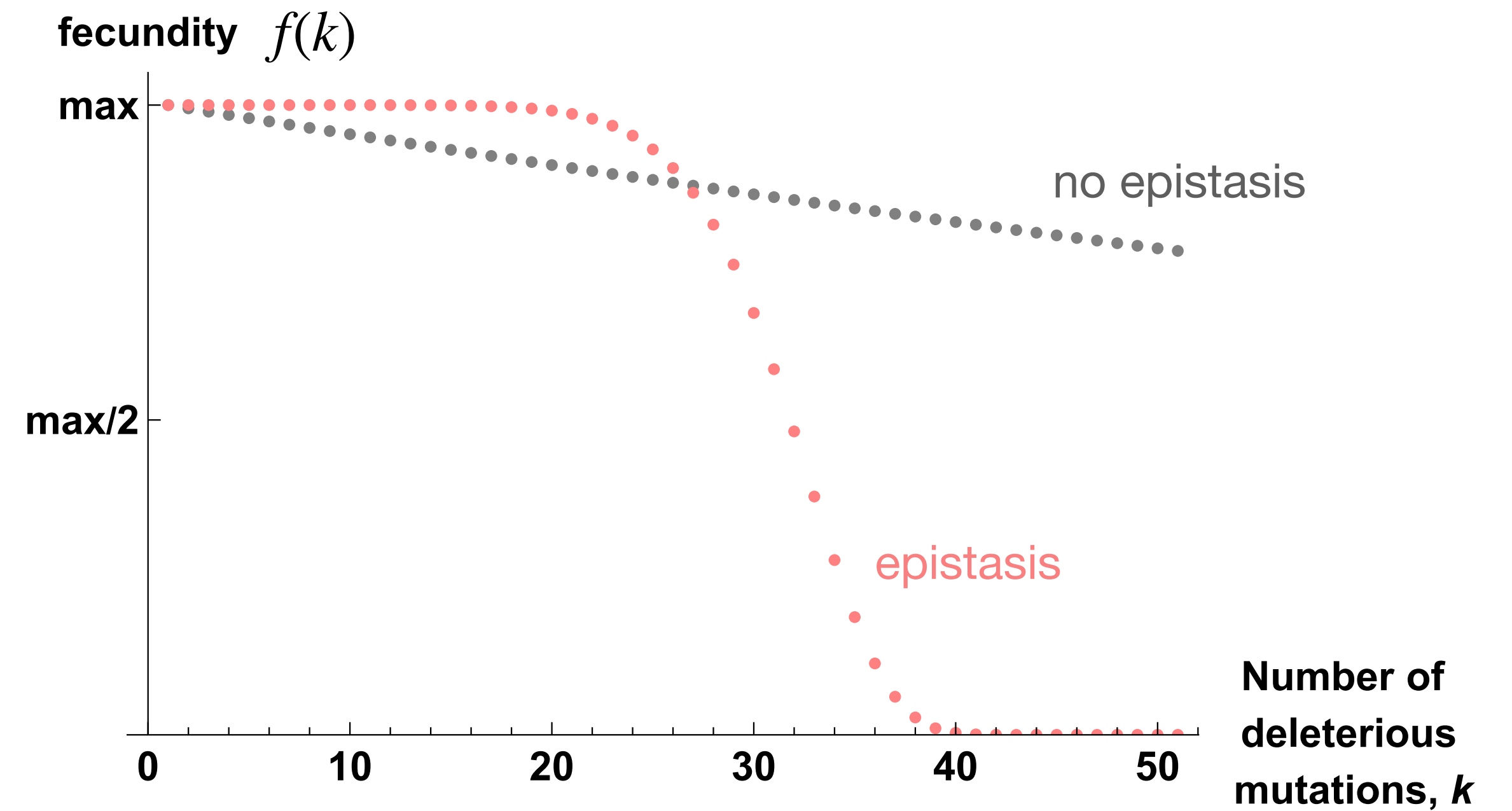


# Can strong epistasis rescue sexuals?

- Epistasis = non-additive fitness effects among loci

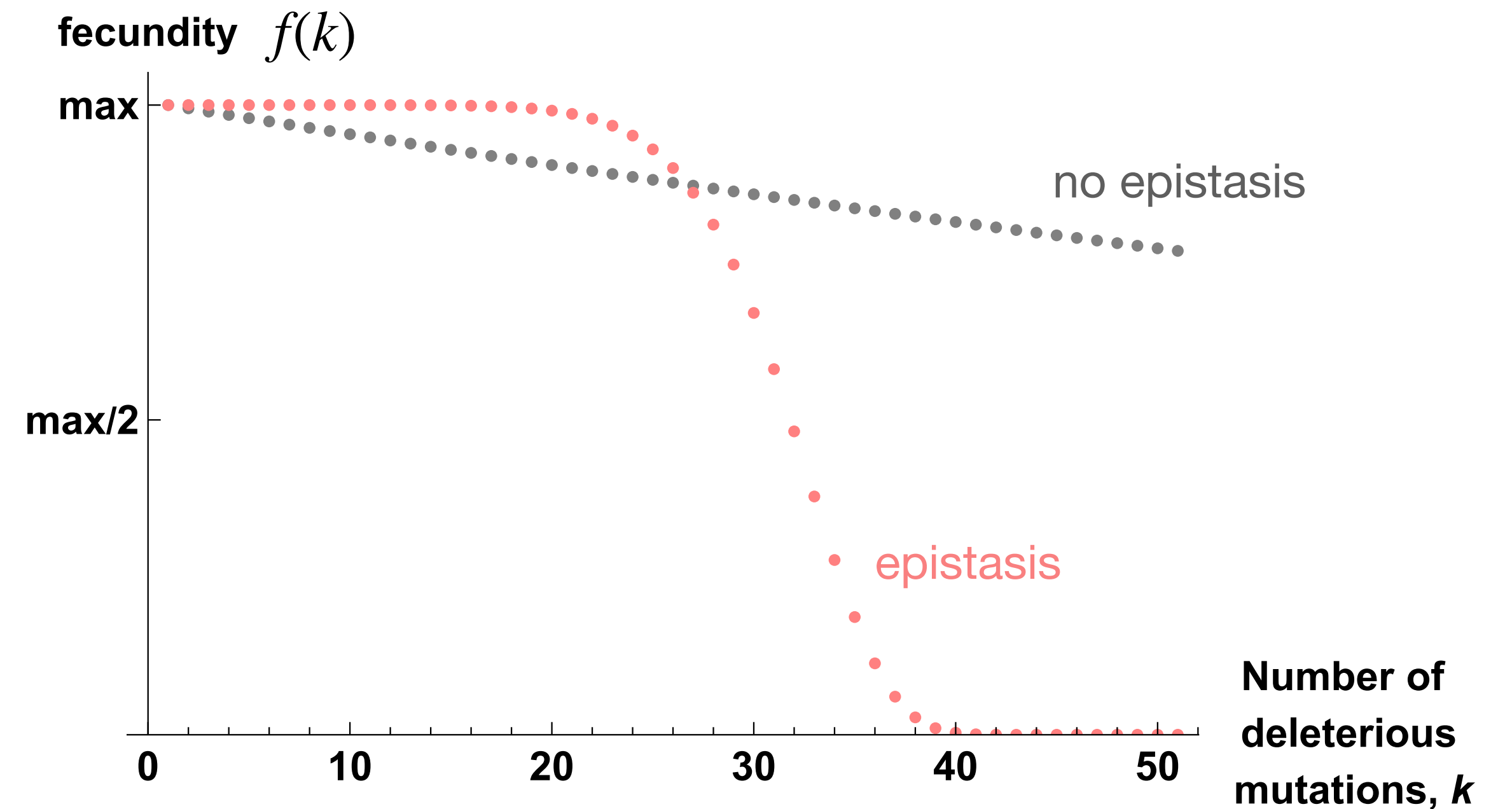
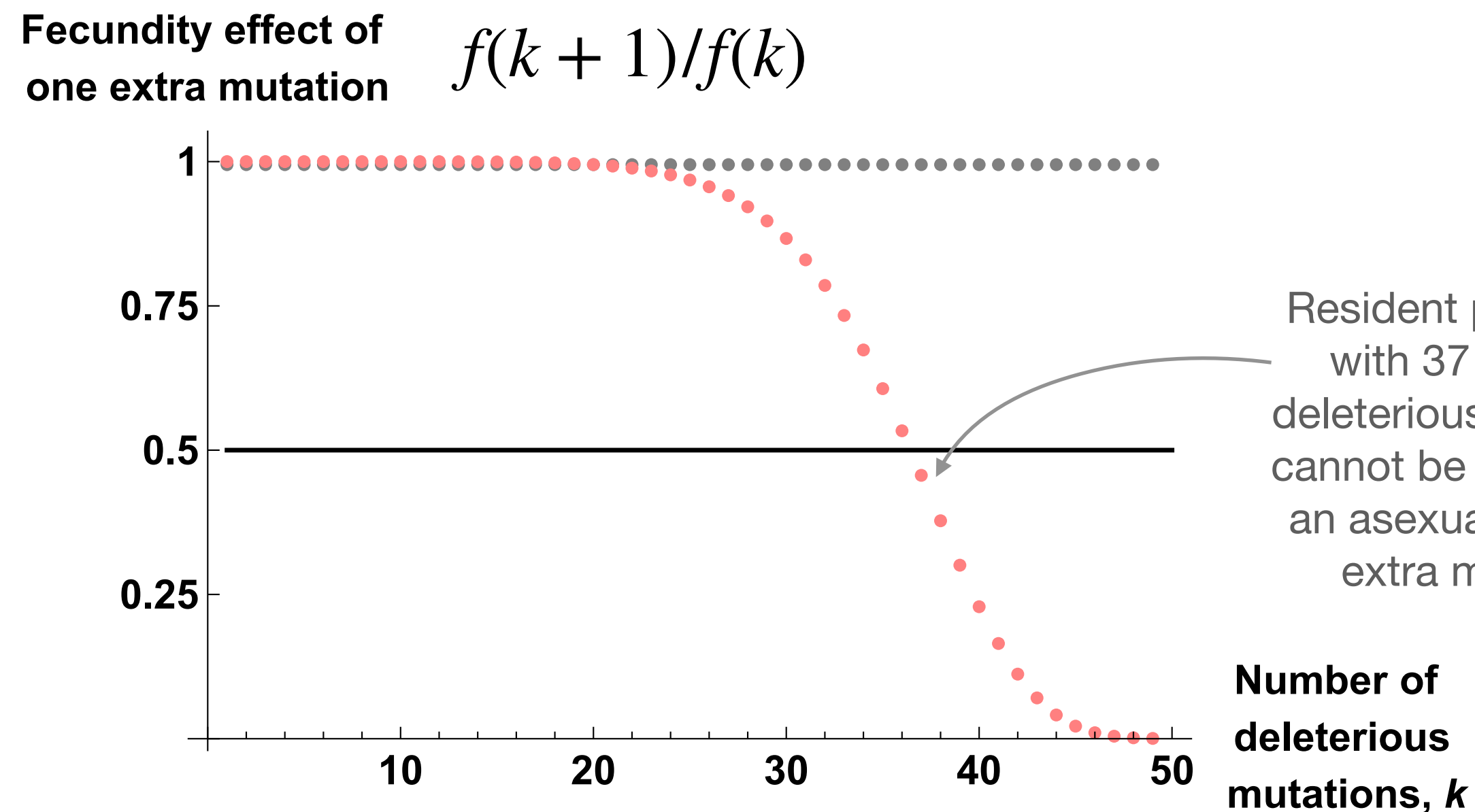
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- Epistasis = non-additive fitness effects among loci
- Allows for an abrupt decrease in fitness with number of deleterious mutations



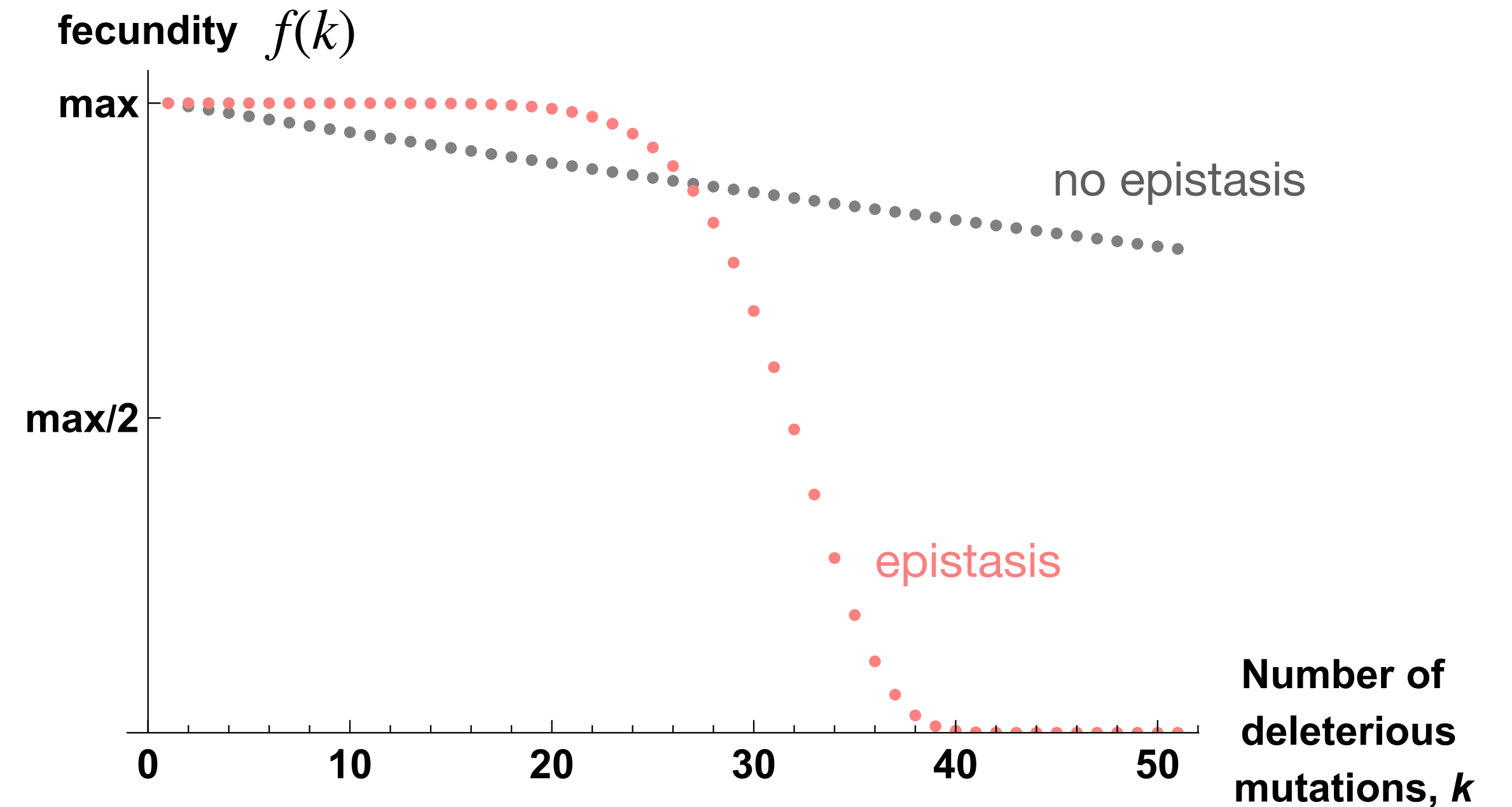
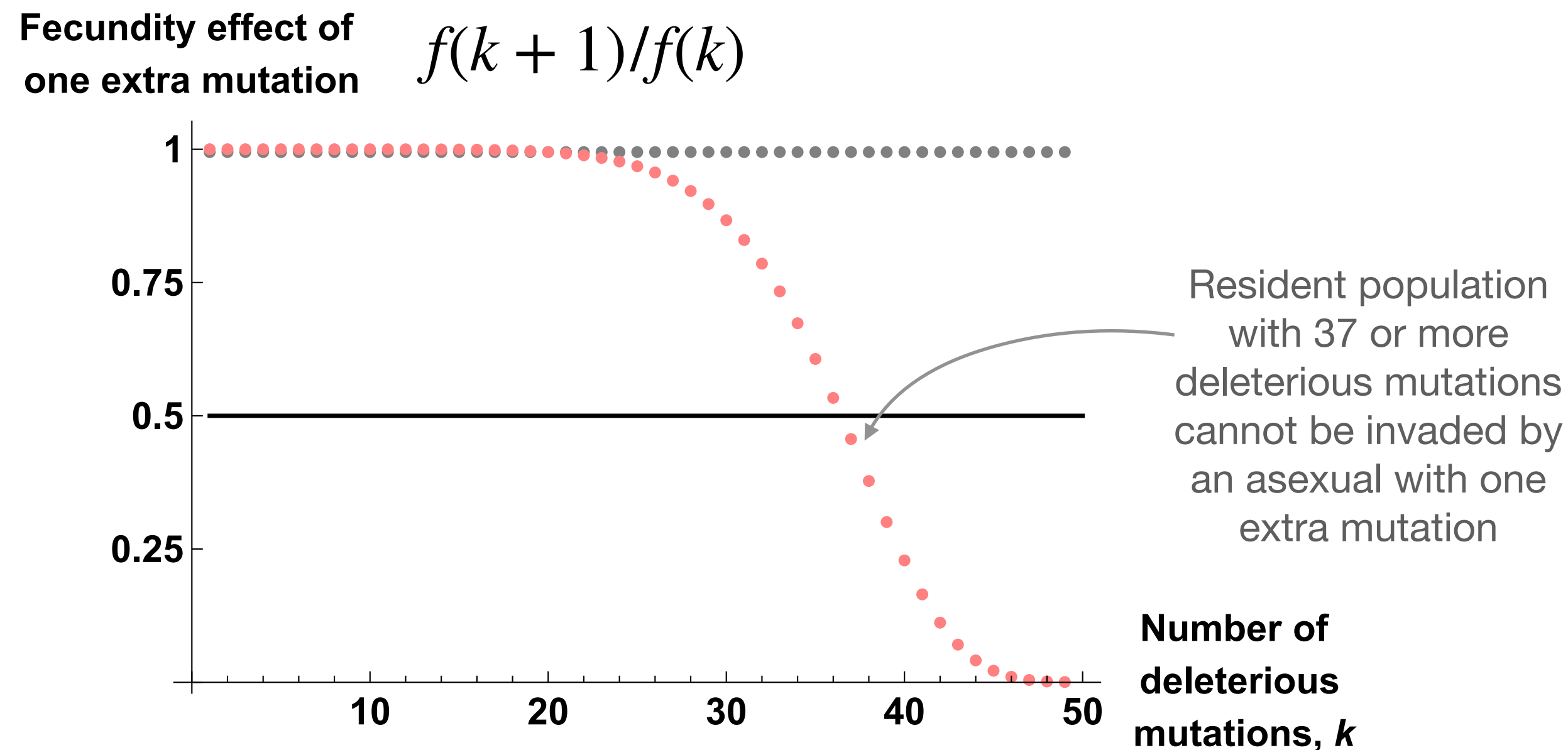
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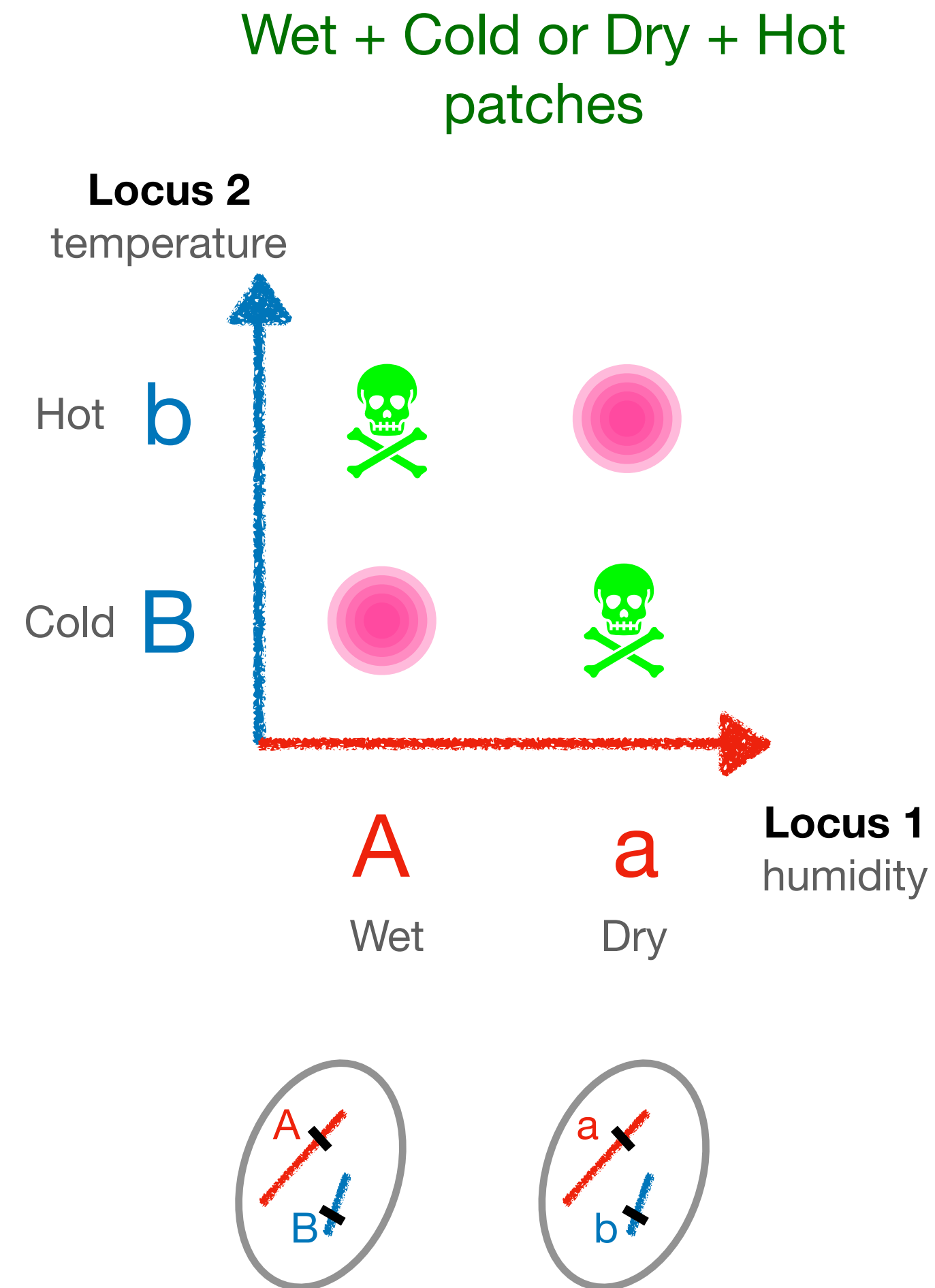


- Works if sexual population already quite loaded with mutations
- See exercise sheet 3

# Fluctuating epistasis

# Fluctuating epistasis

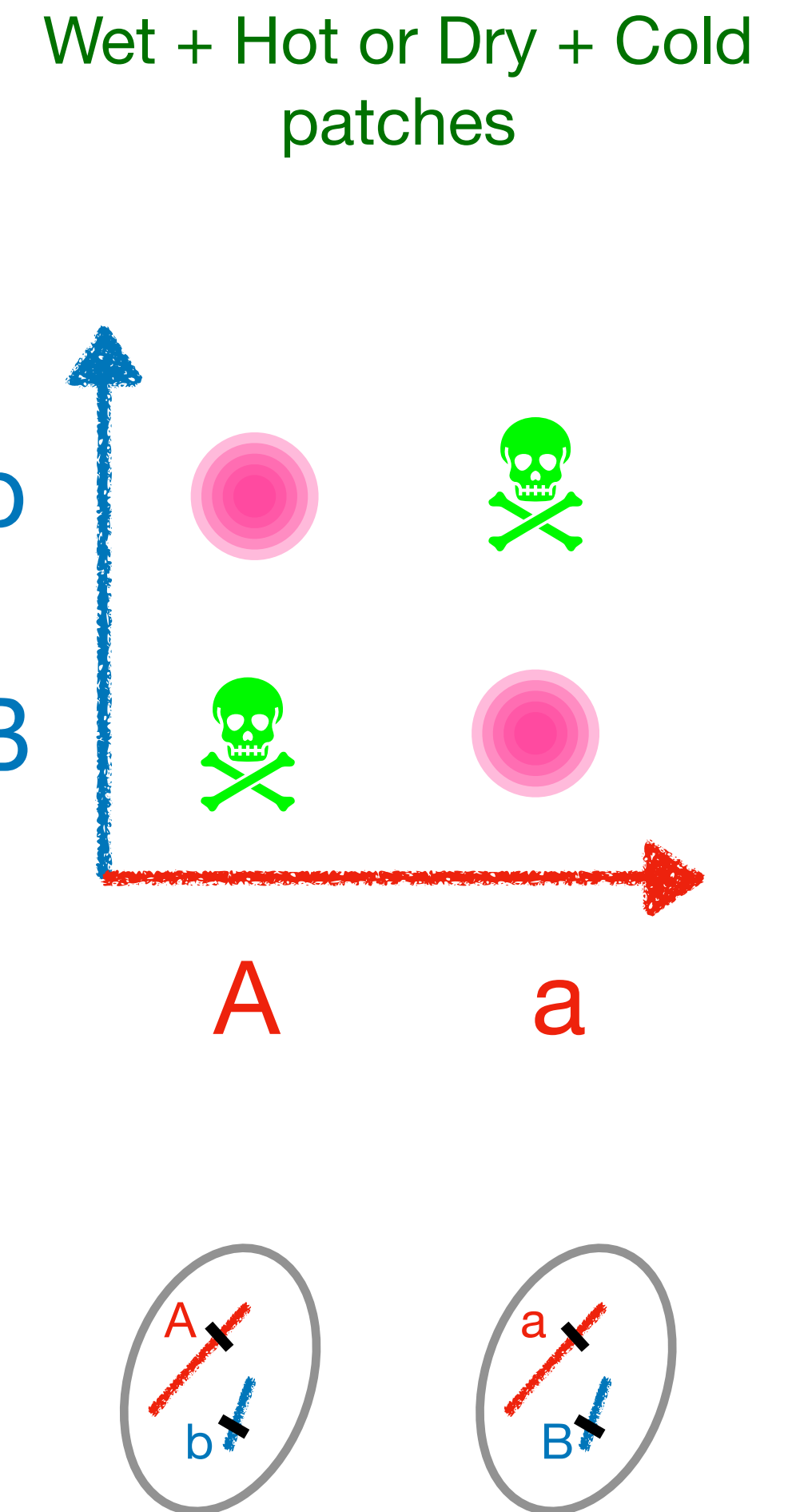
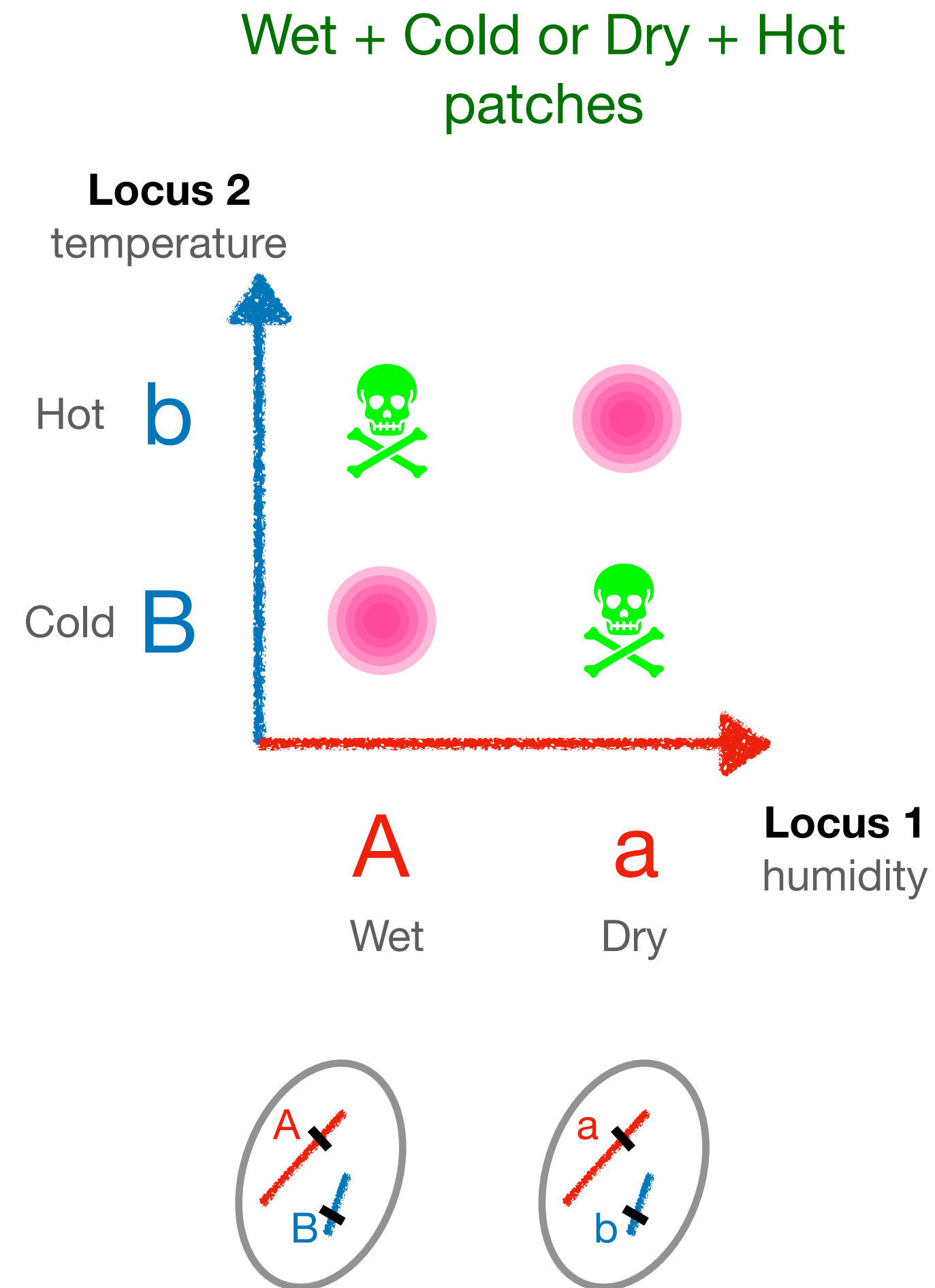
- Environment favours specific allelic associations





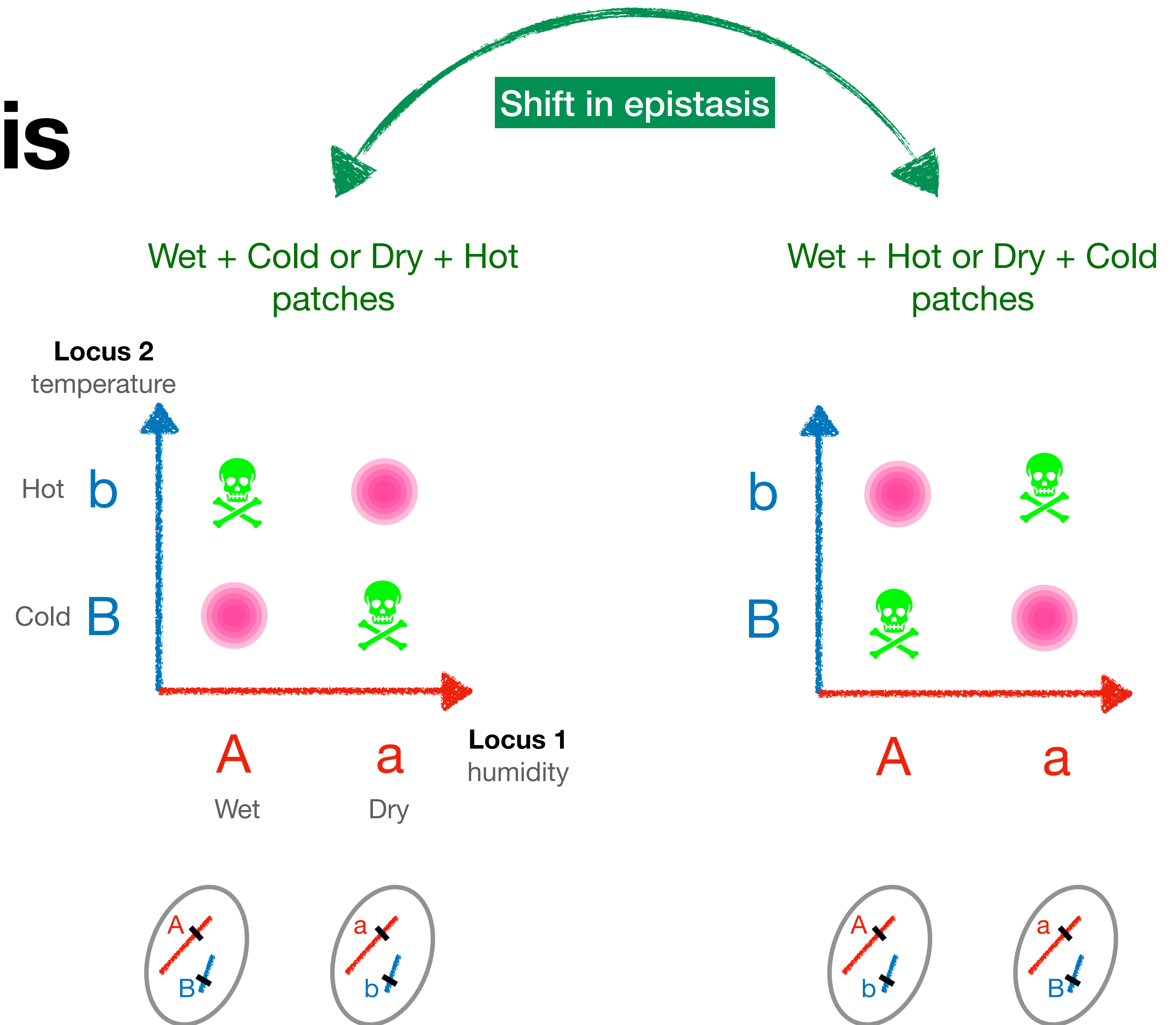
# Fluctuating epistasis

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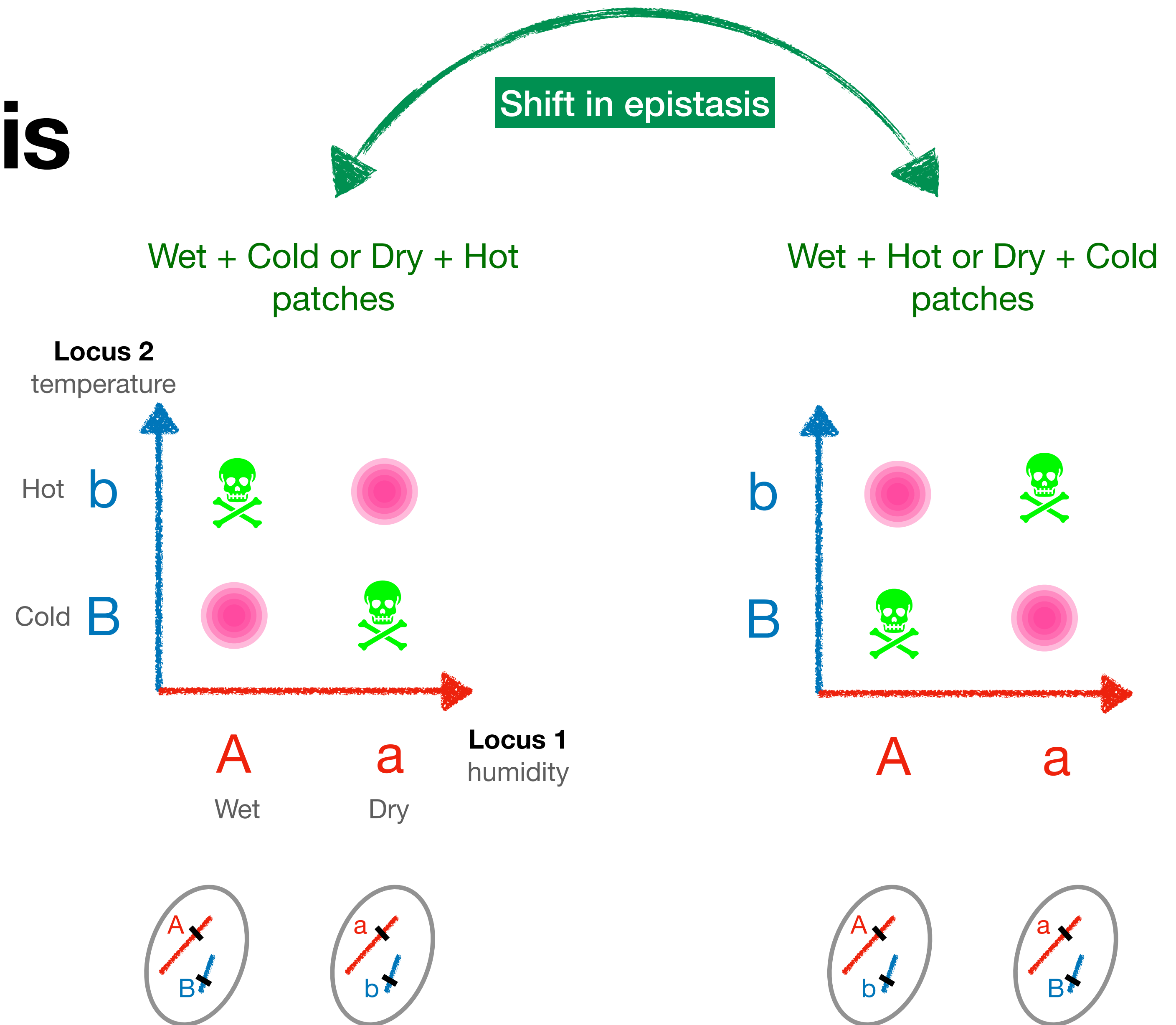
# Fluctuating epistasis

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



# Fluctuating epistasis

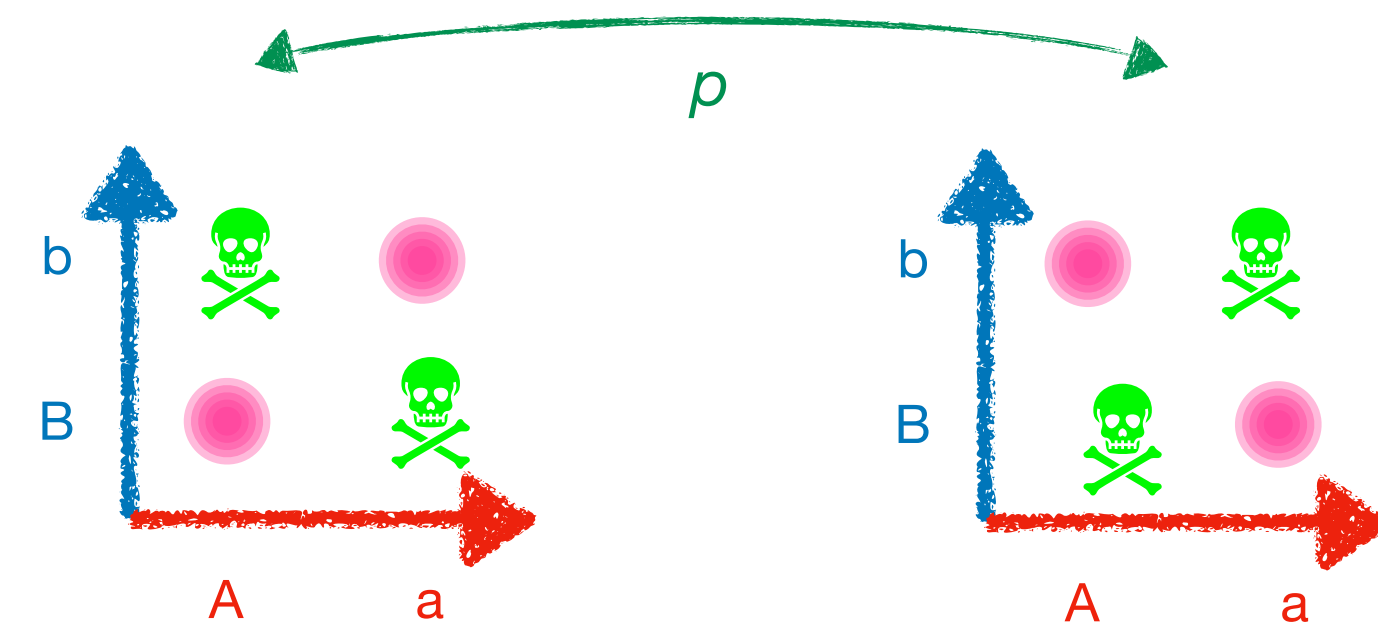
- Environment favours specific allelic associations
- The environment fluctuates in time, favouring different associations at different times
- Asexuals should lose out as the allelic associations of an asexual lineage are fixed



# Fluctuating epistasis

## Example

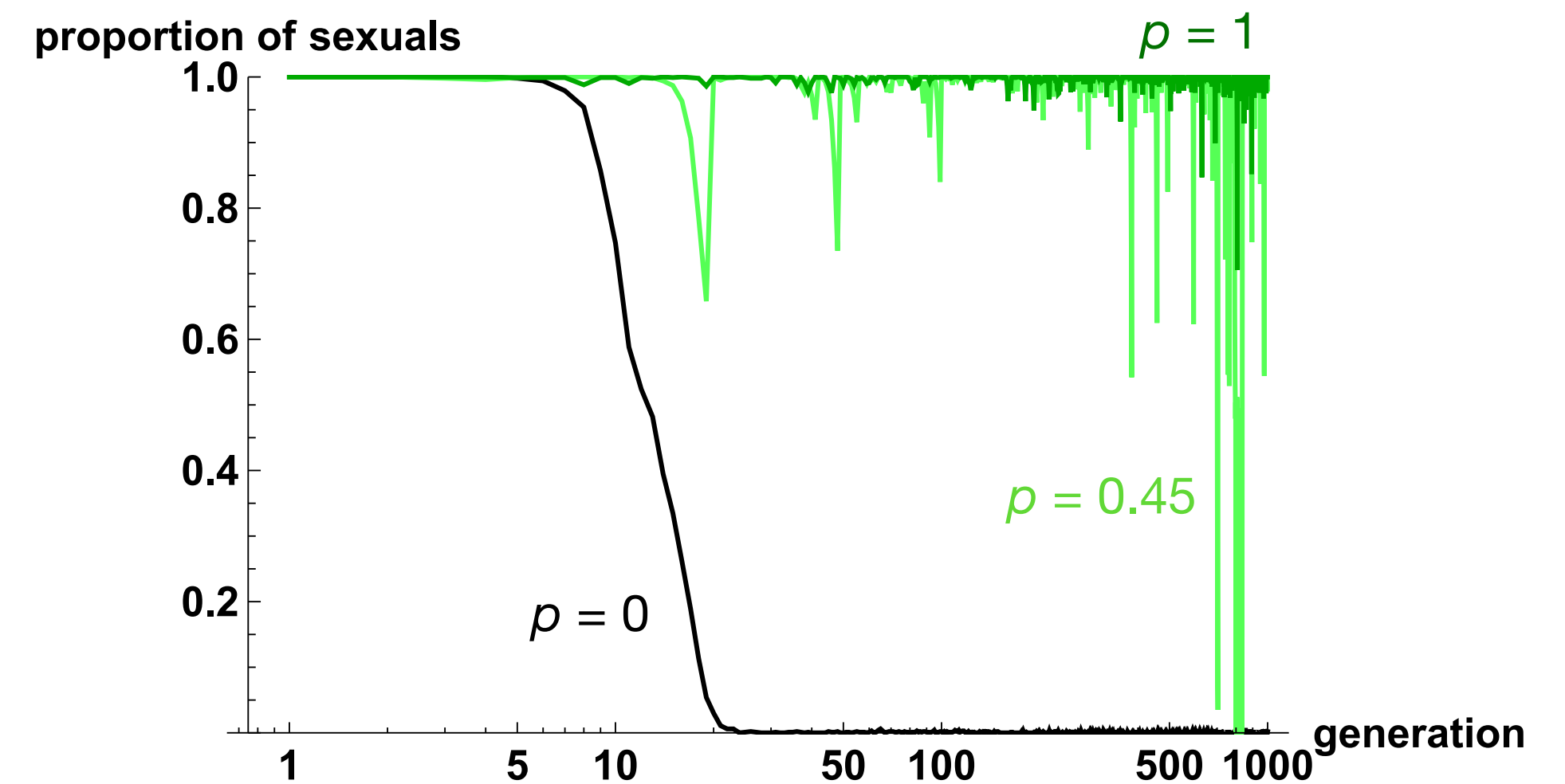
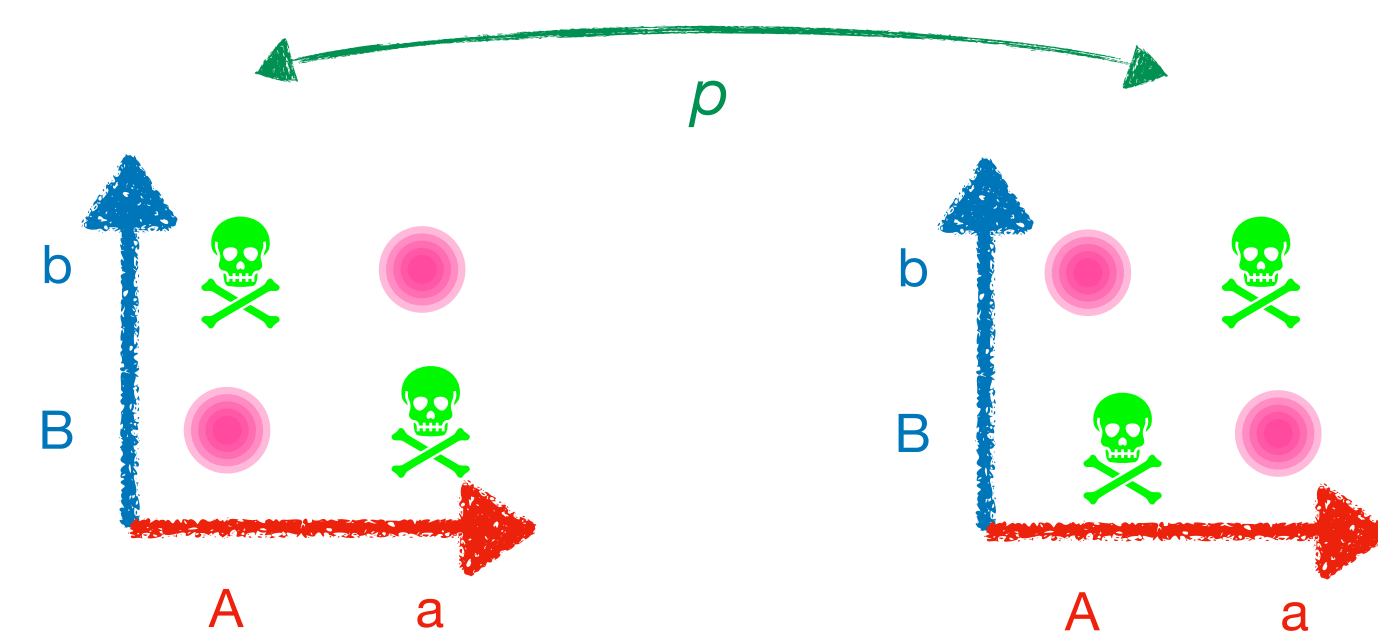
- Population with two types of habitats, each favouring a specific combination of alleles.
- Combination changes at each generation with probability  $p$ .
- Start with a population of sexuals. Introduce asexuals through mutation.



# Fluctuating epistasis

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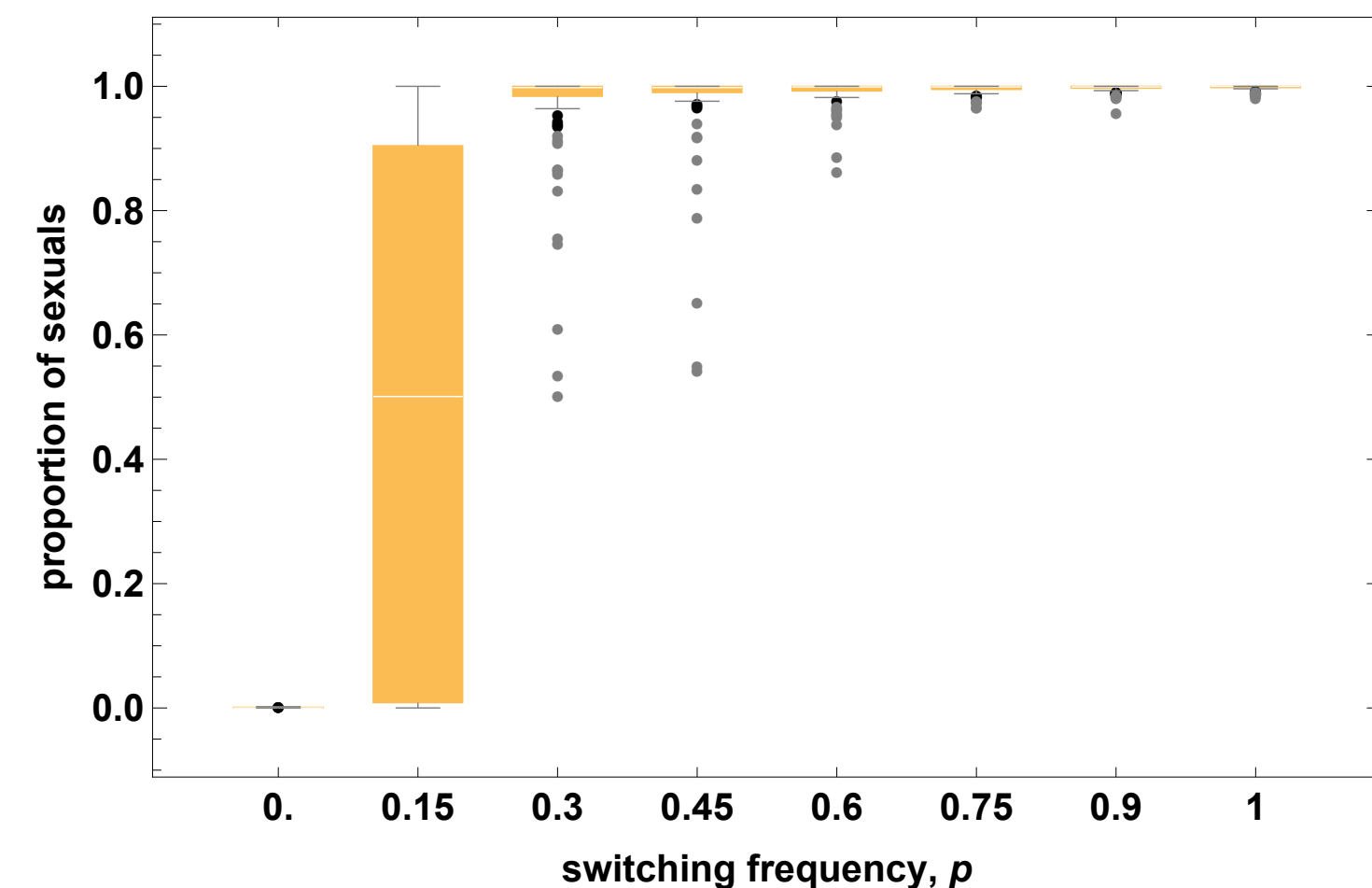
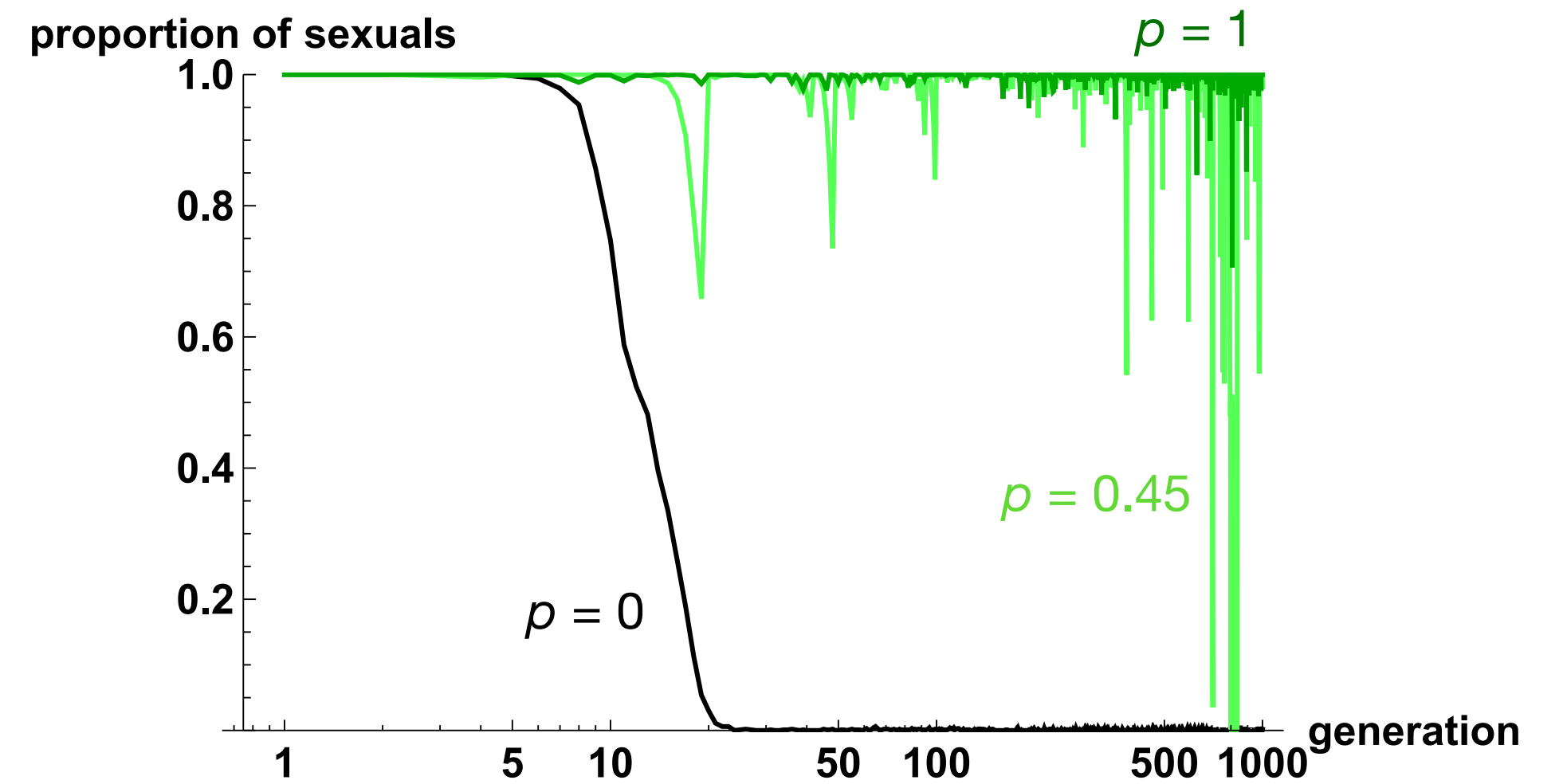
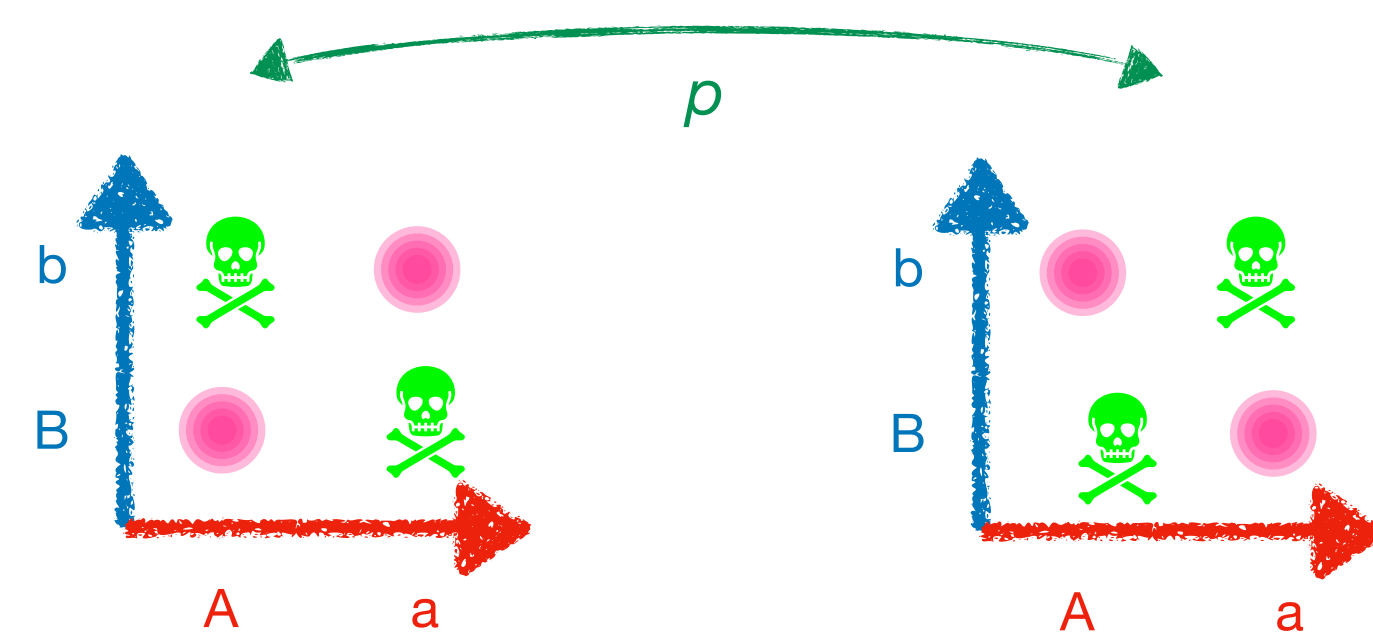
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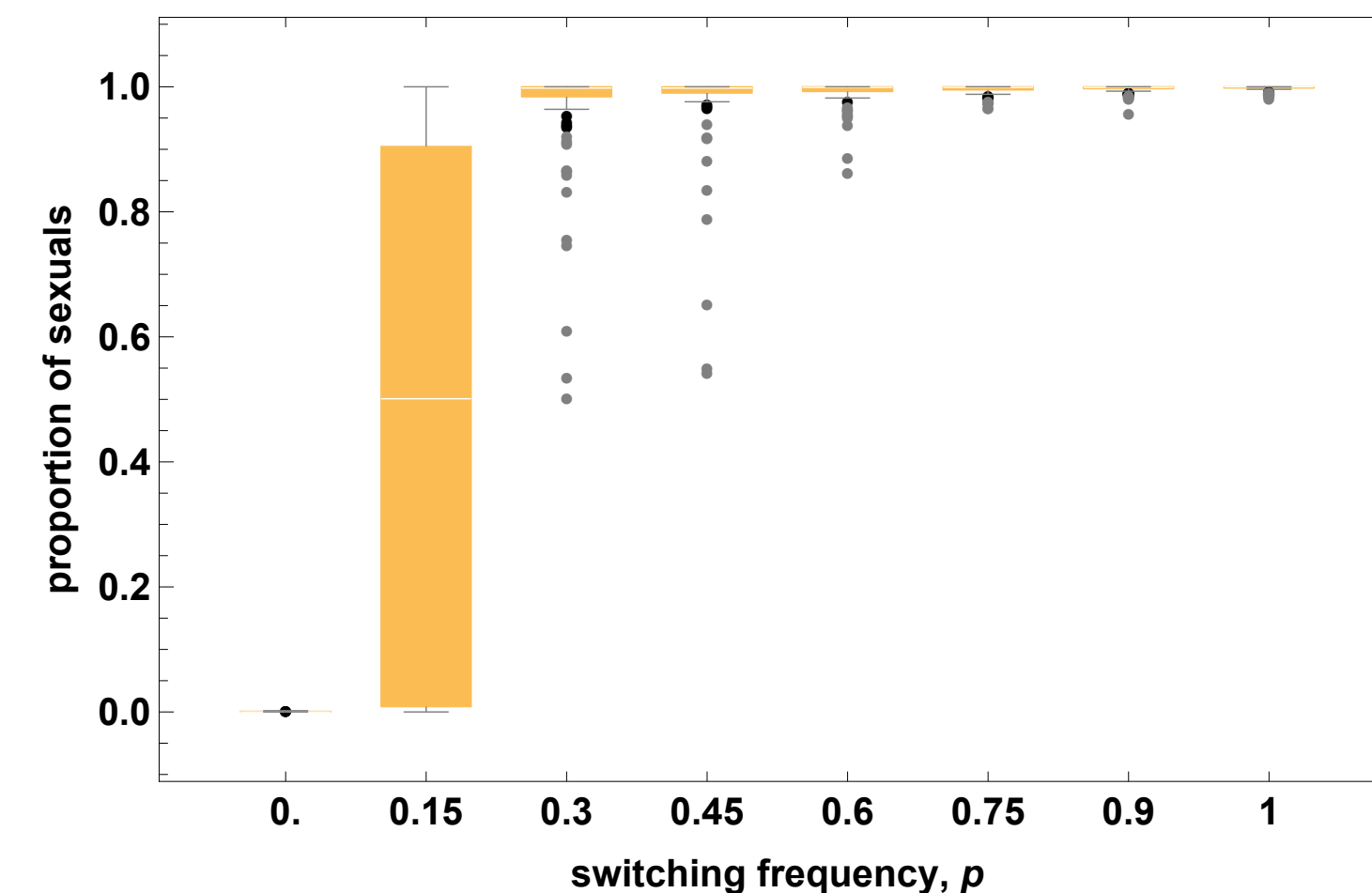
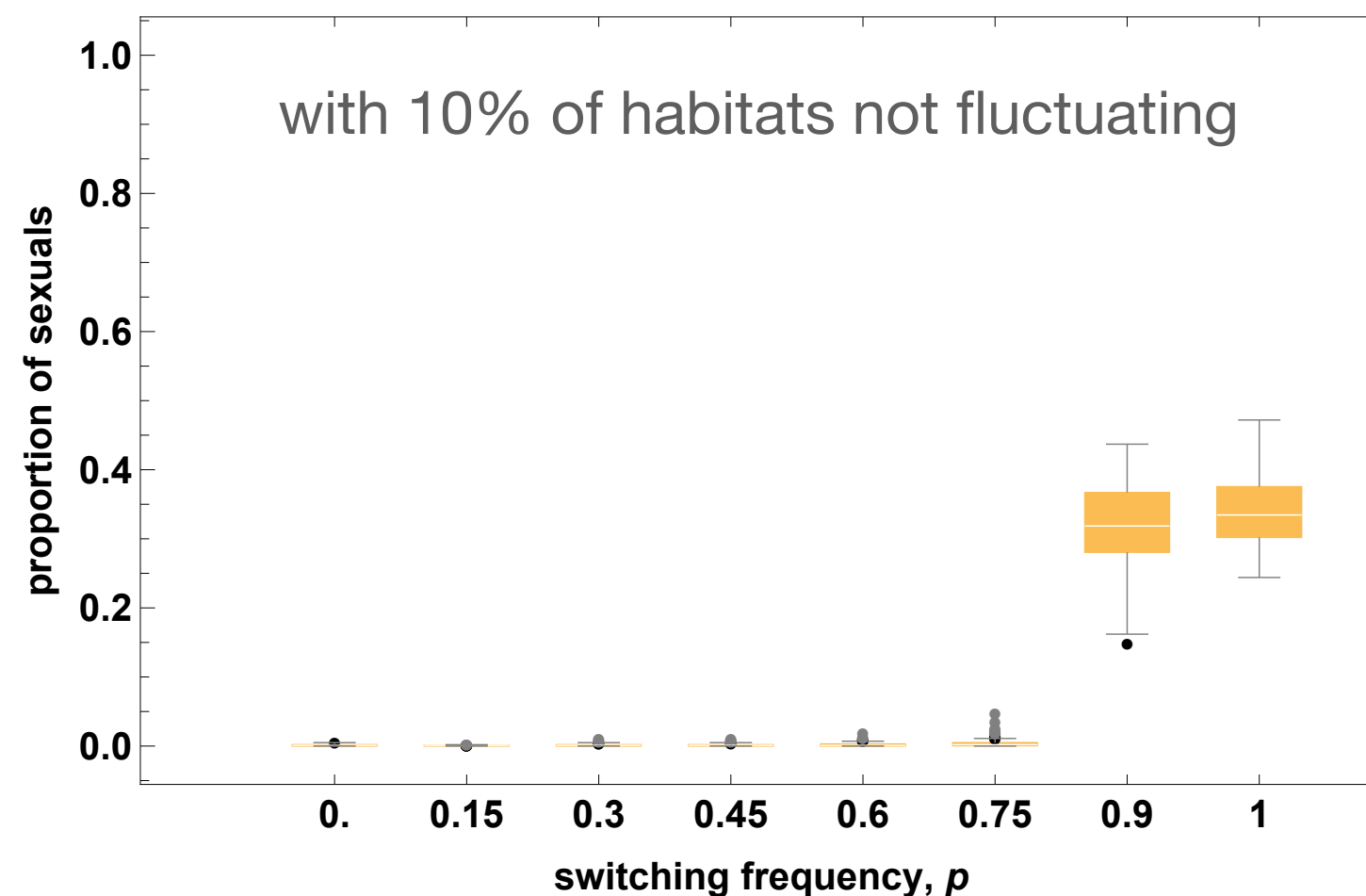
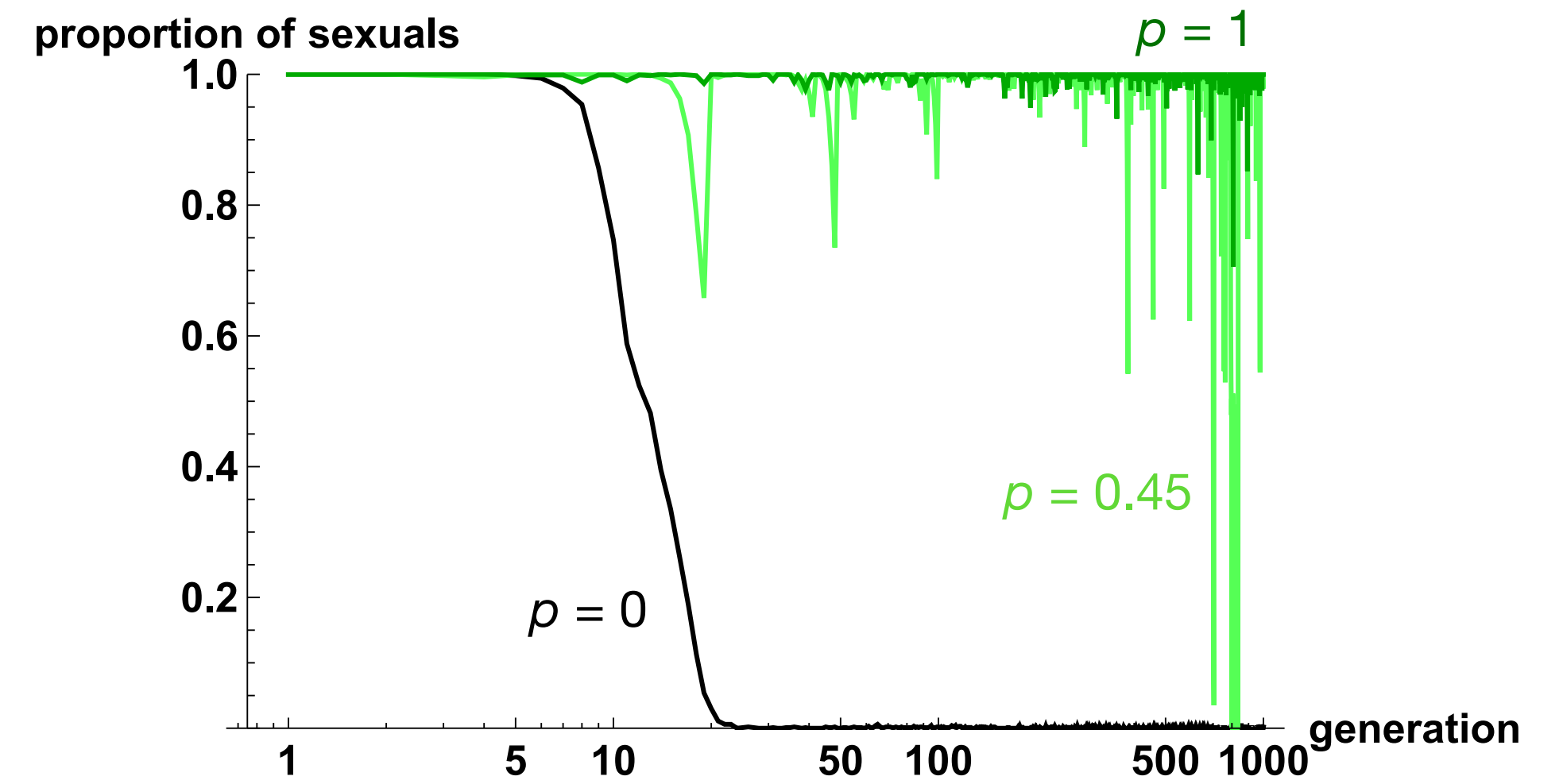
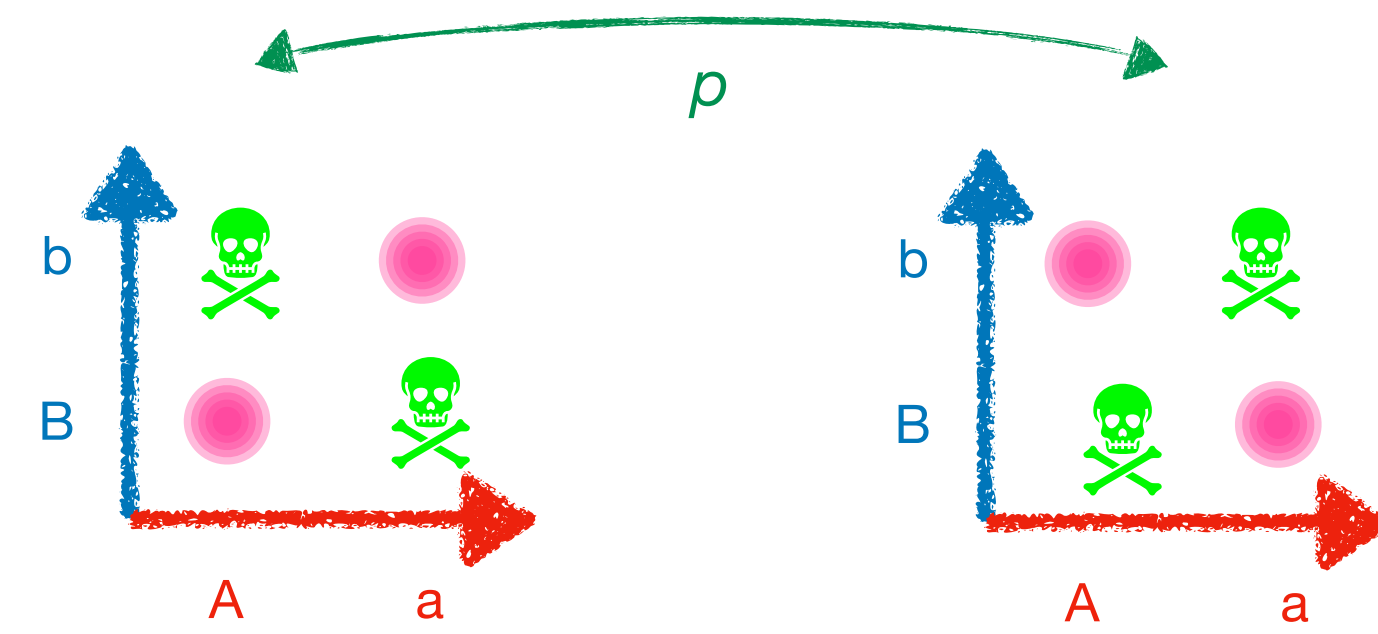
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# Fluctuating epistasis

But...

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

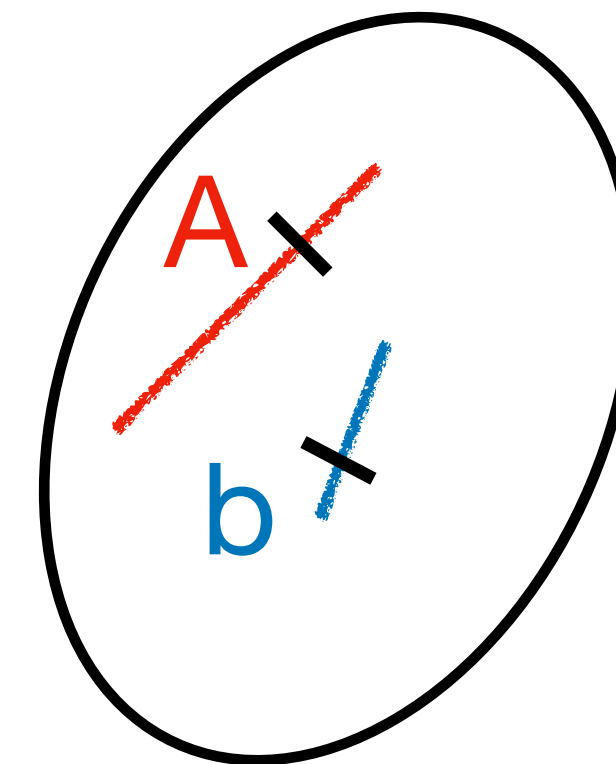
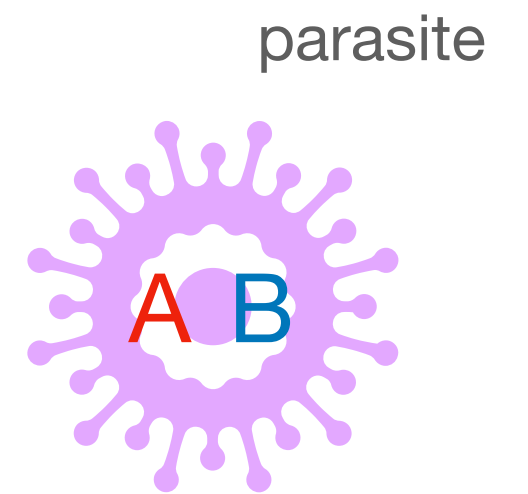
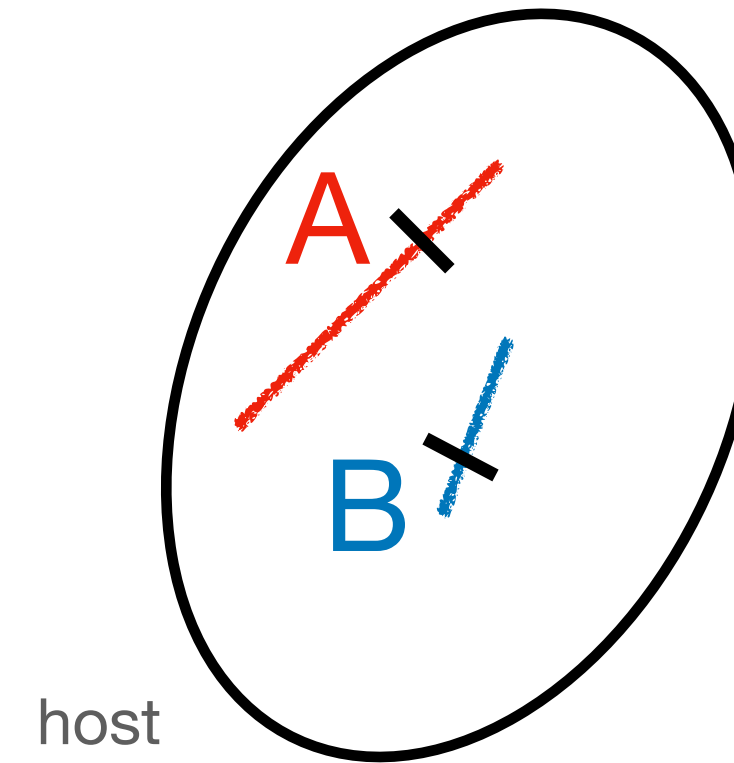


# **An ecological model of fluctuating epistasis**



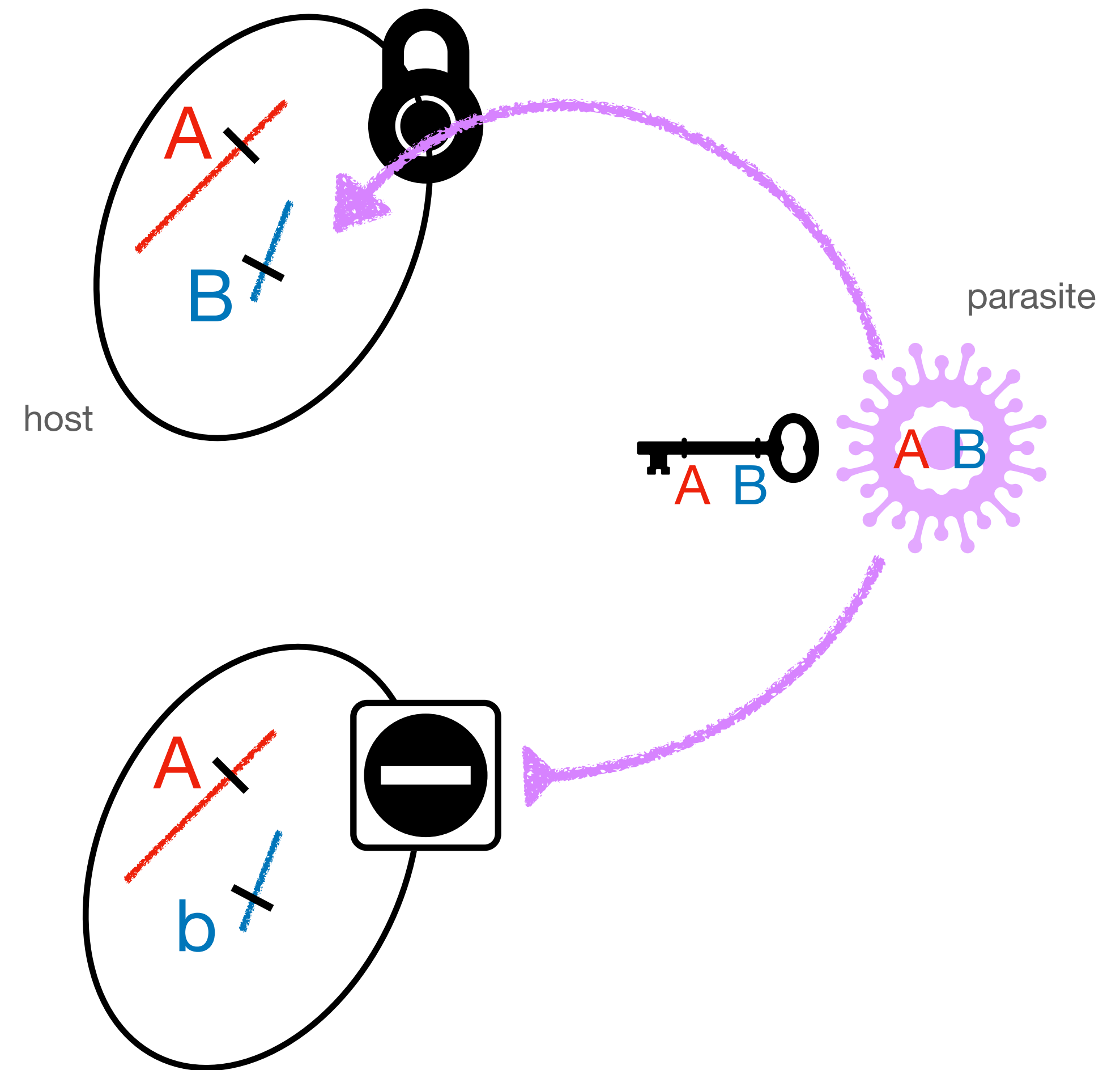
# An ecological model of fluctuating epistasis

- Coevolution of host and parasites.



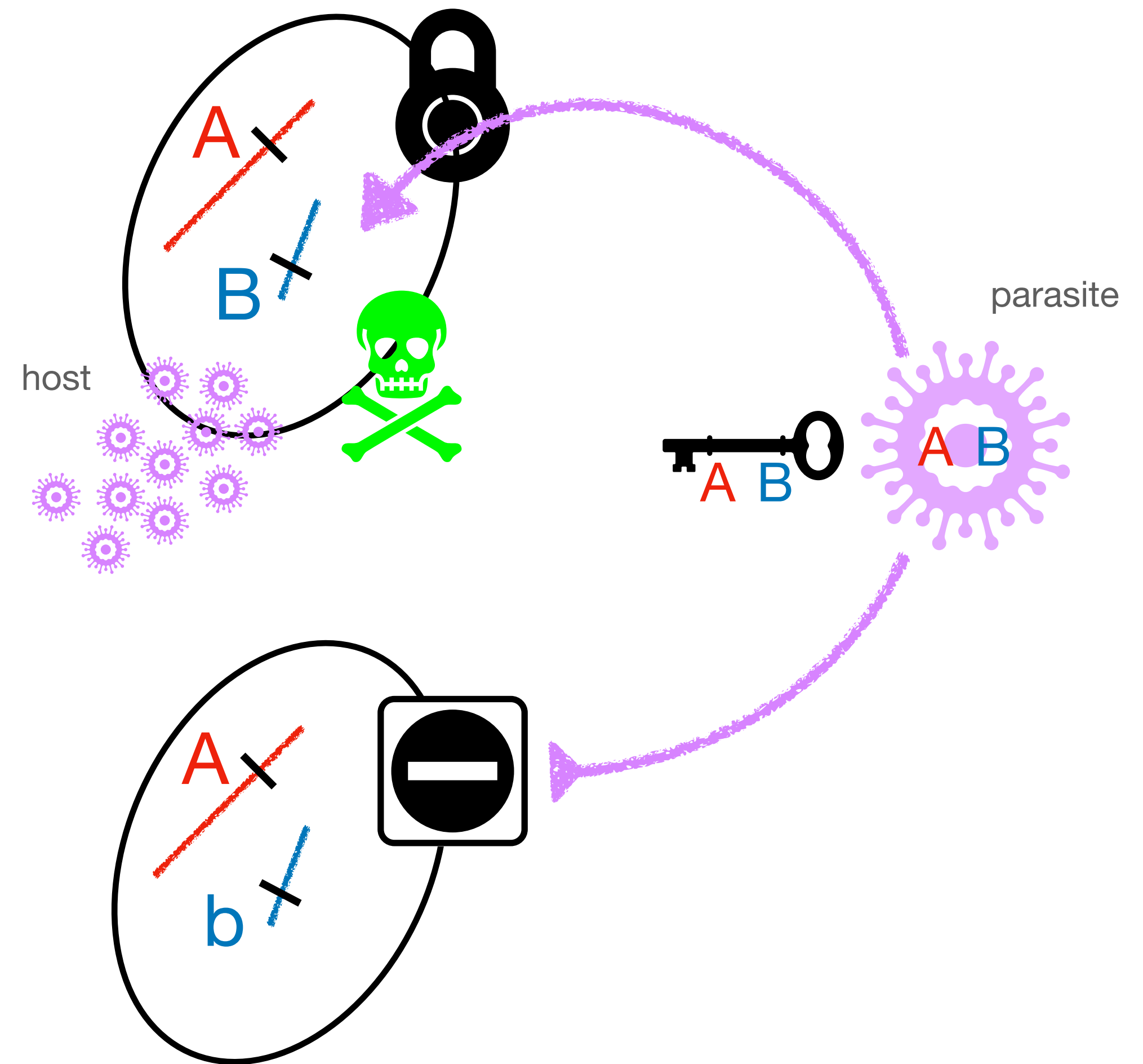
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- Coevolution of host and parasites.
- Lock and key system where parasites can only target host with matching genotype.



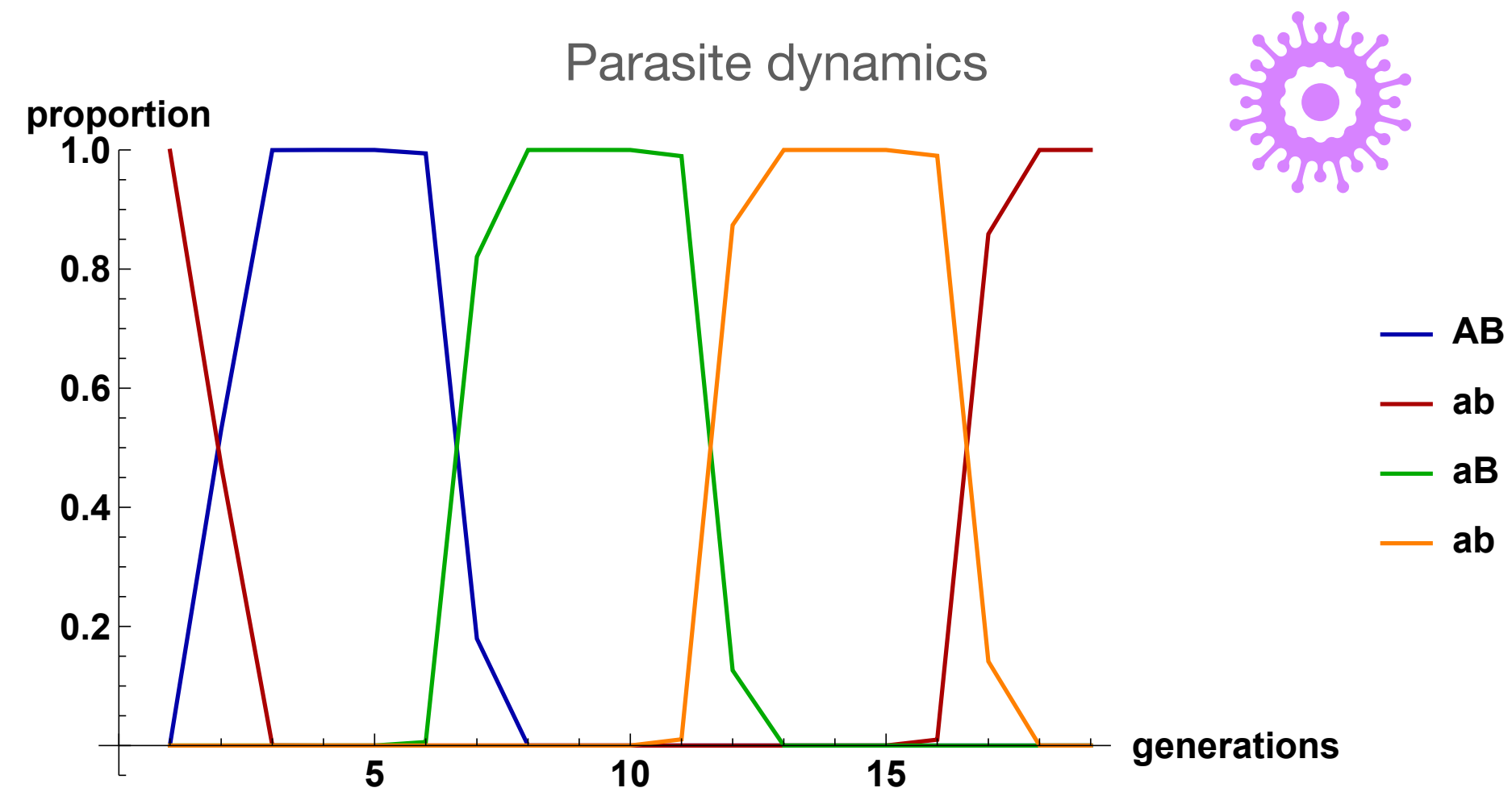
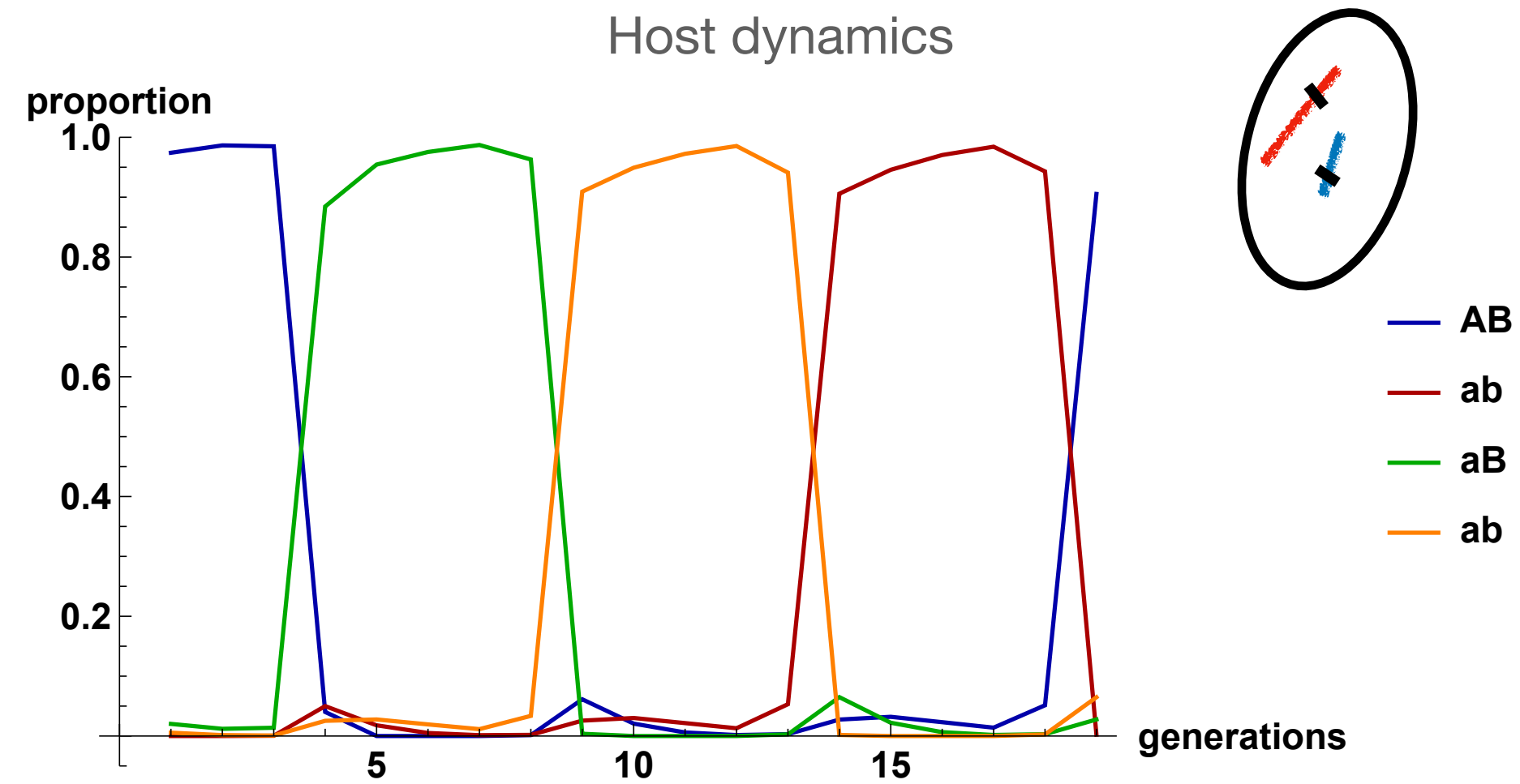
# An ecological model of fluctuating epistasis

- 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.



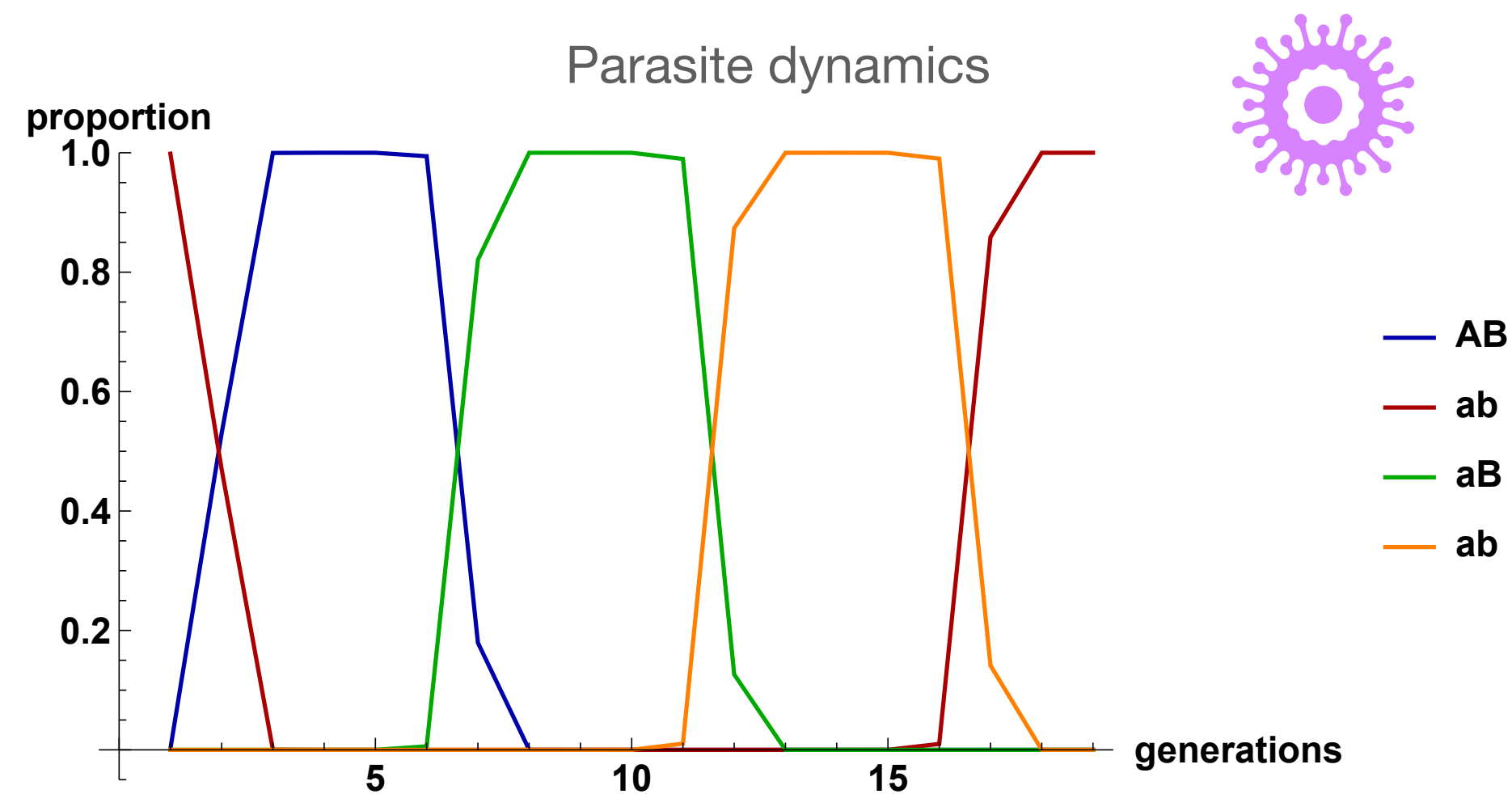
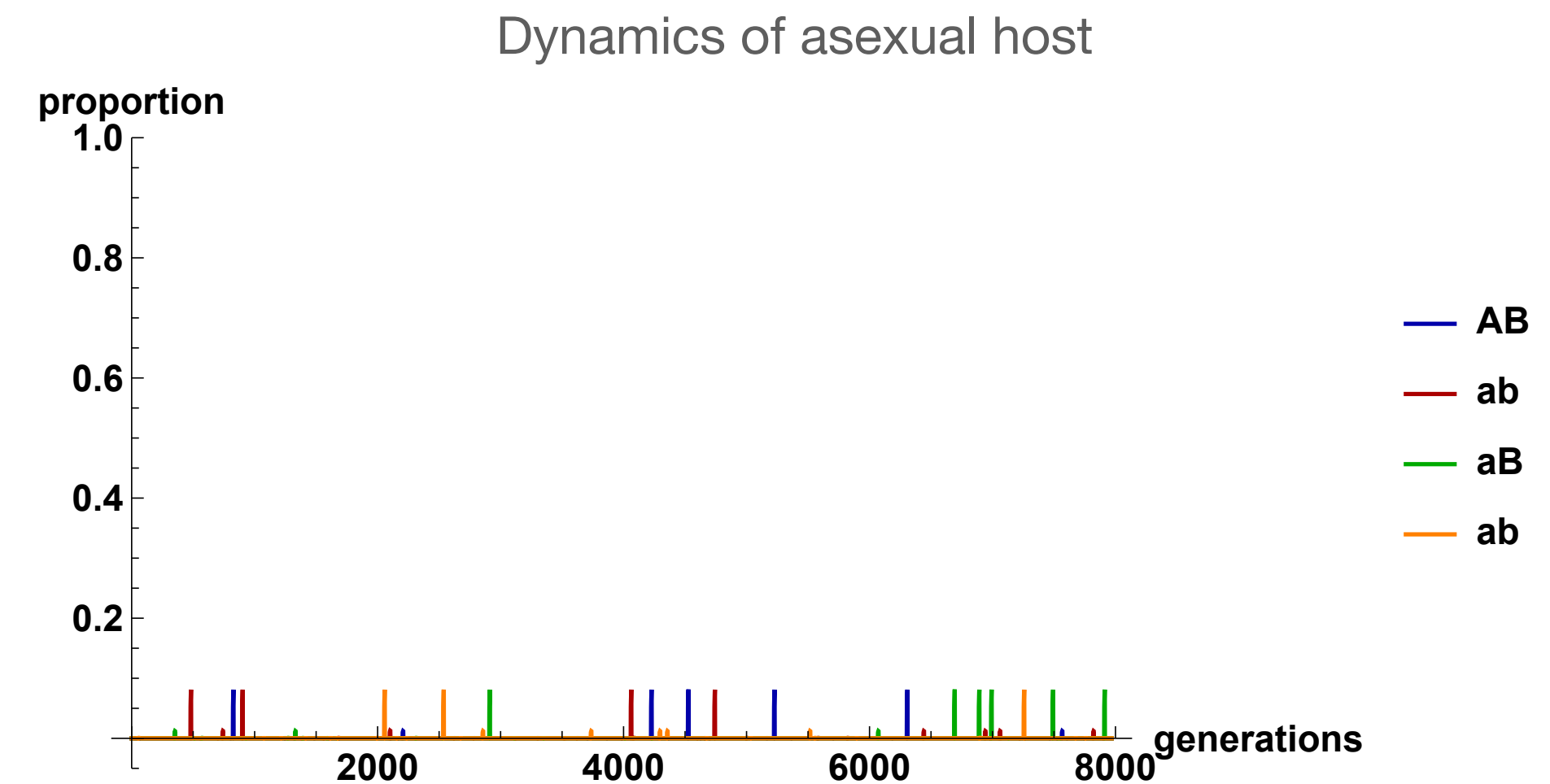
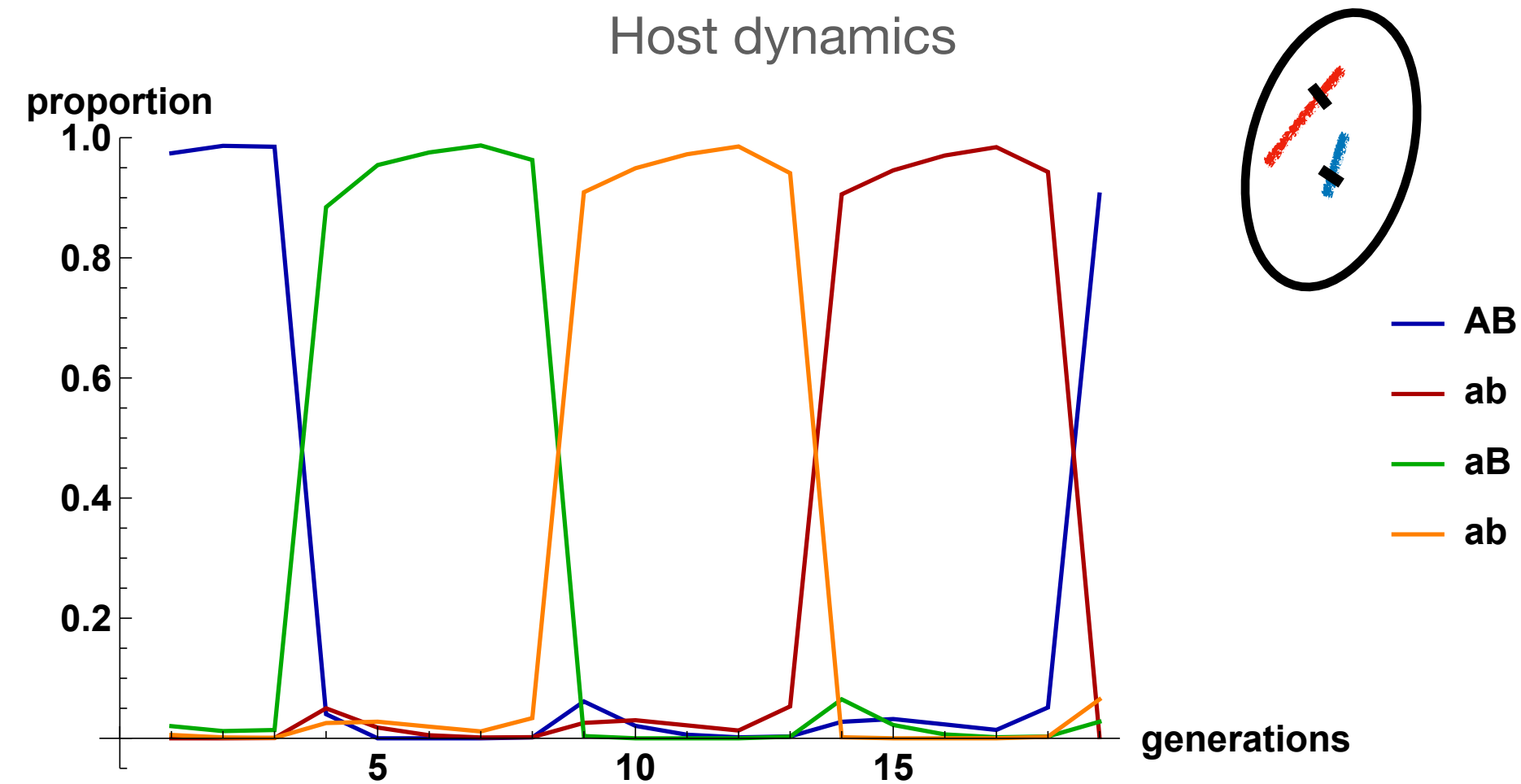
# An ecological model of fluctuating epistasis

## Red queen dynamics



# An ecological model of fluctuating epistasis

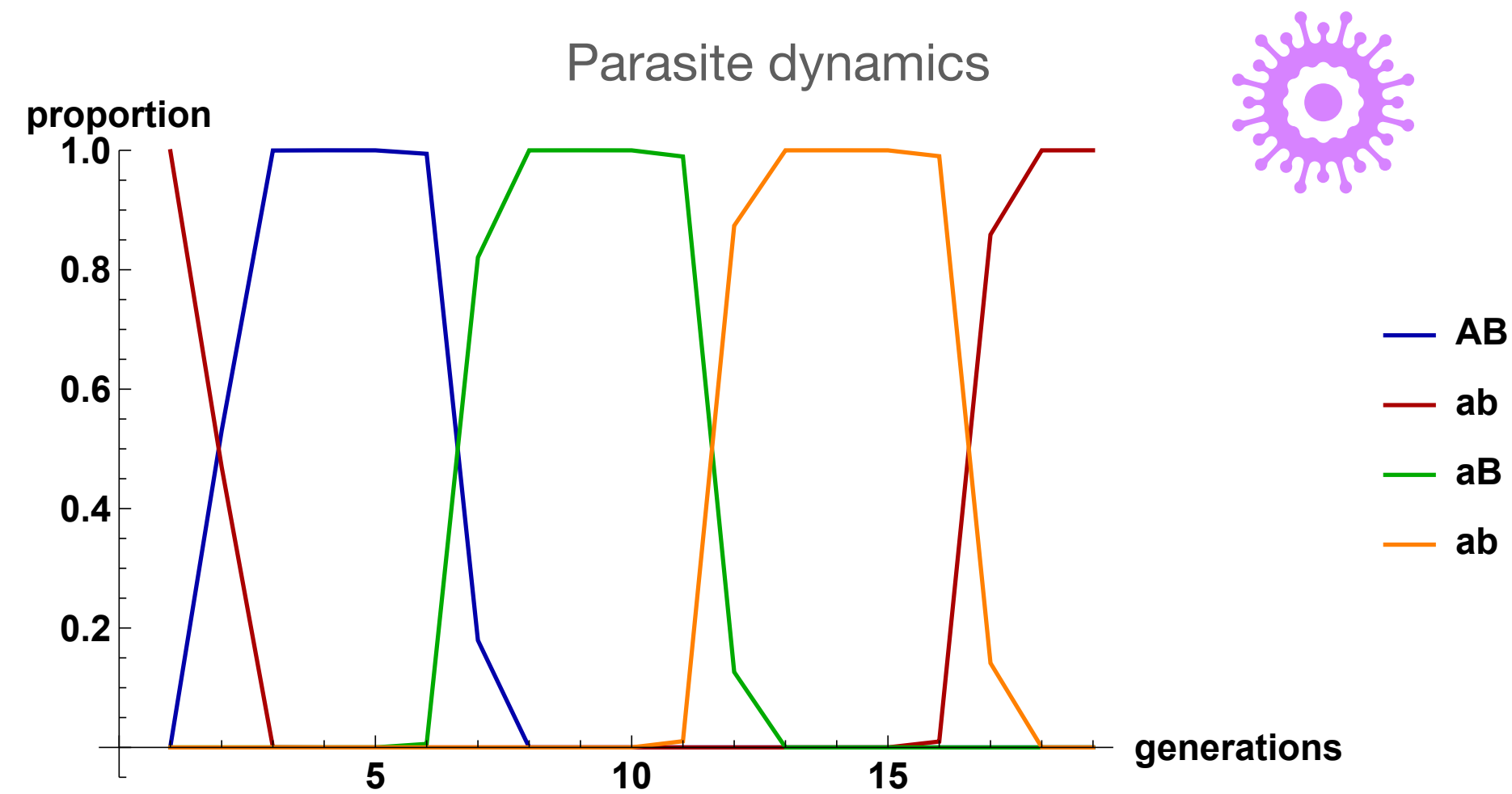
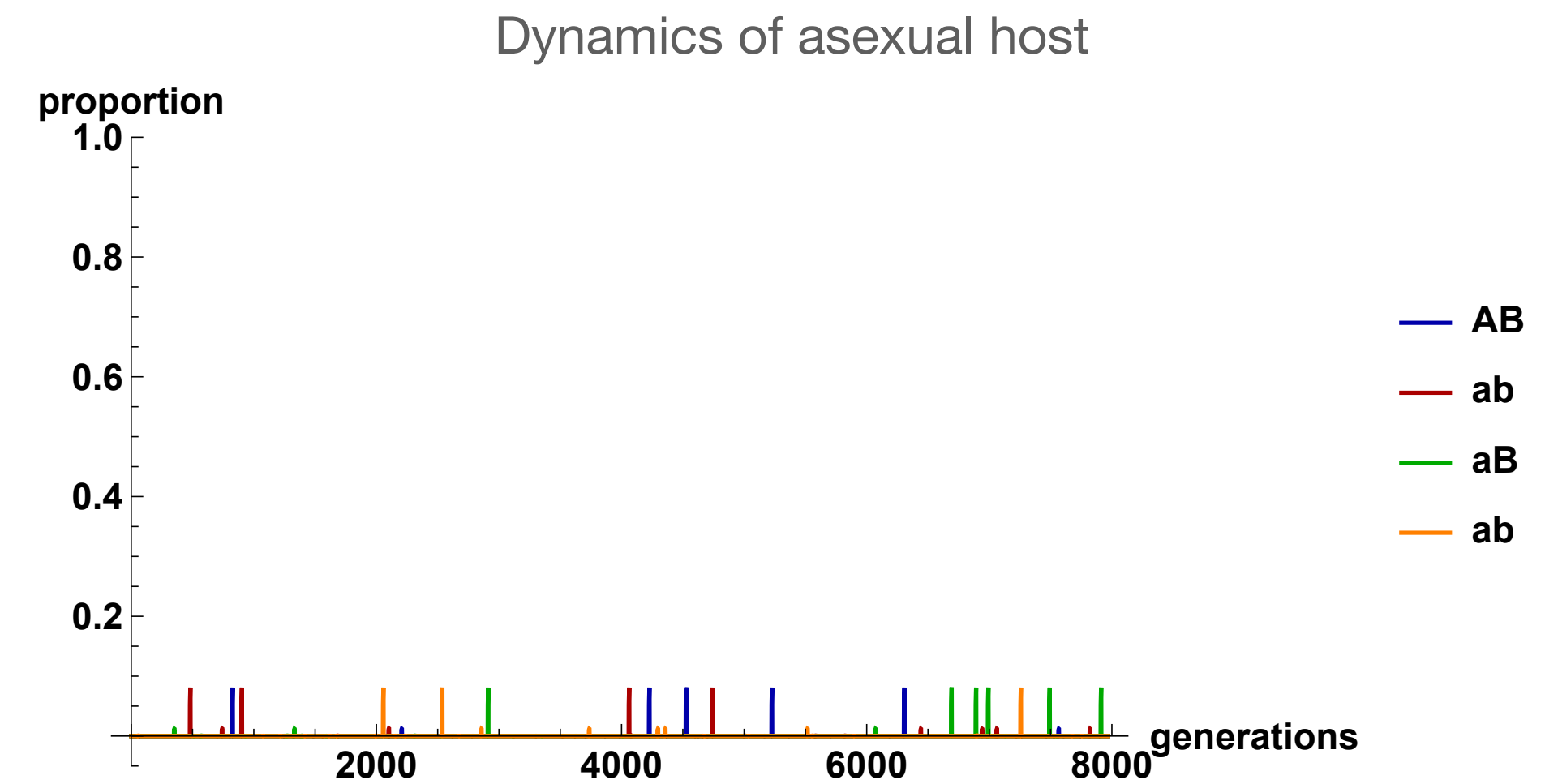
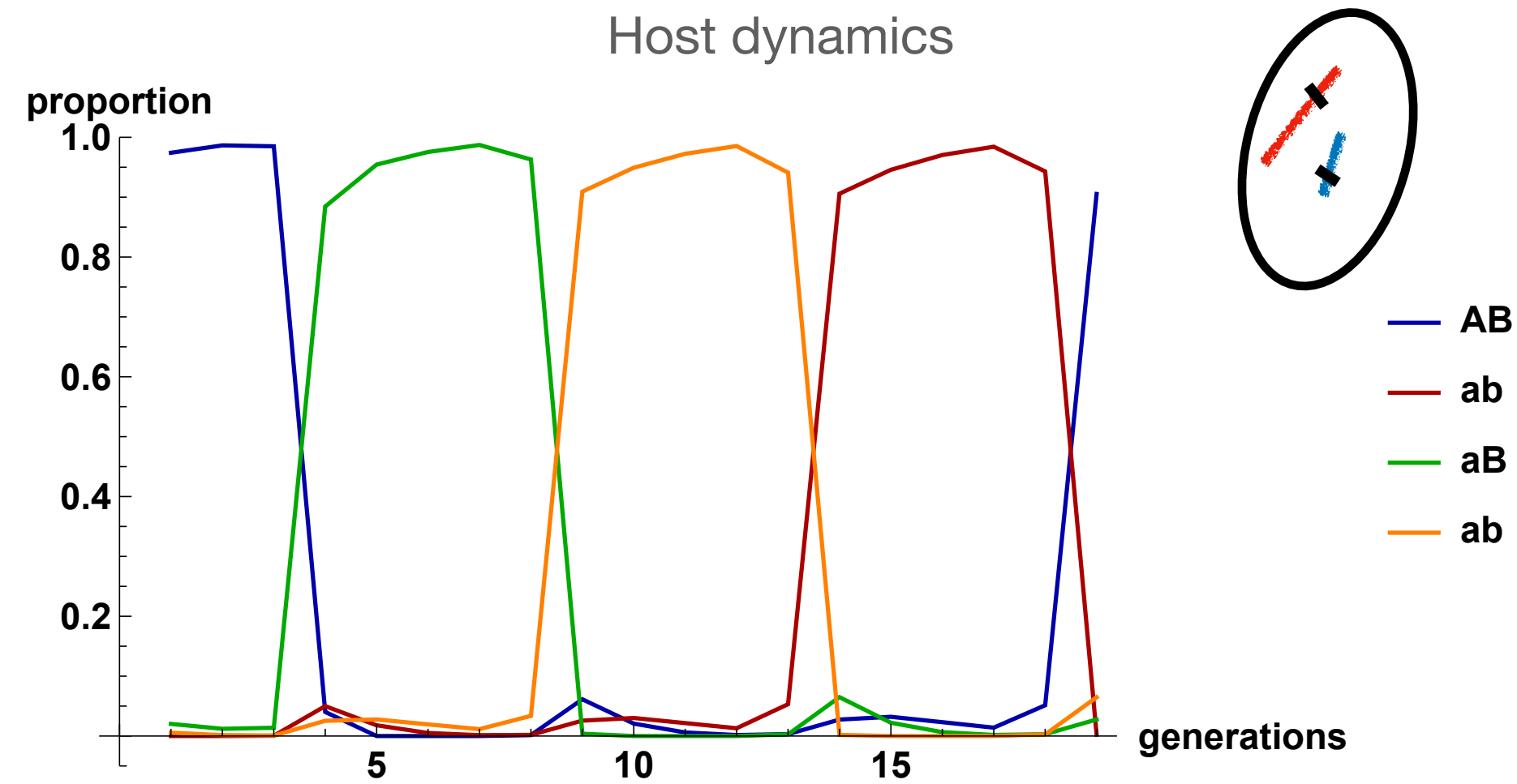
## Red queen dynamics



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

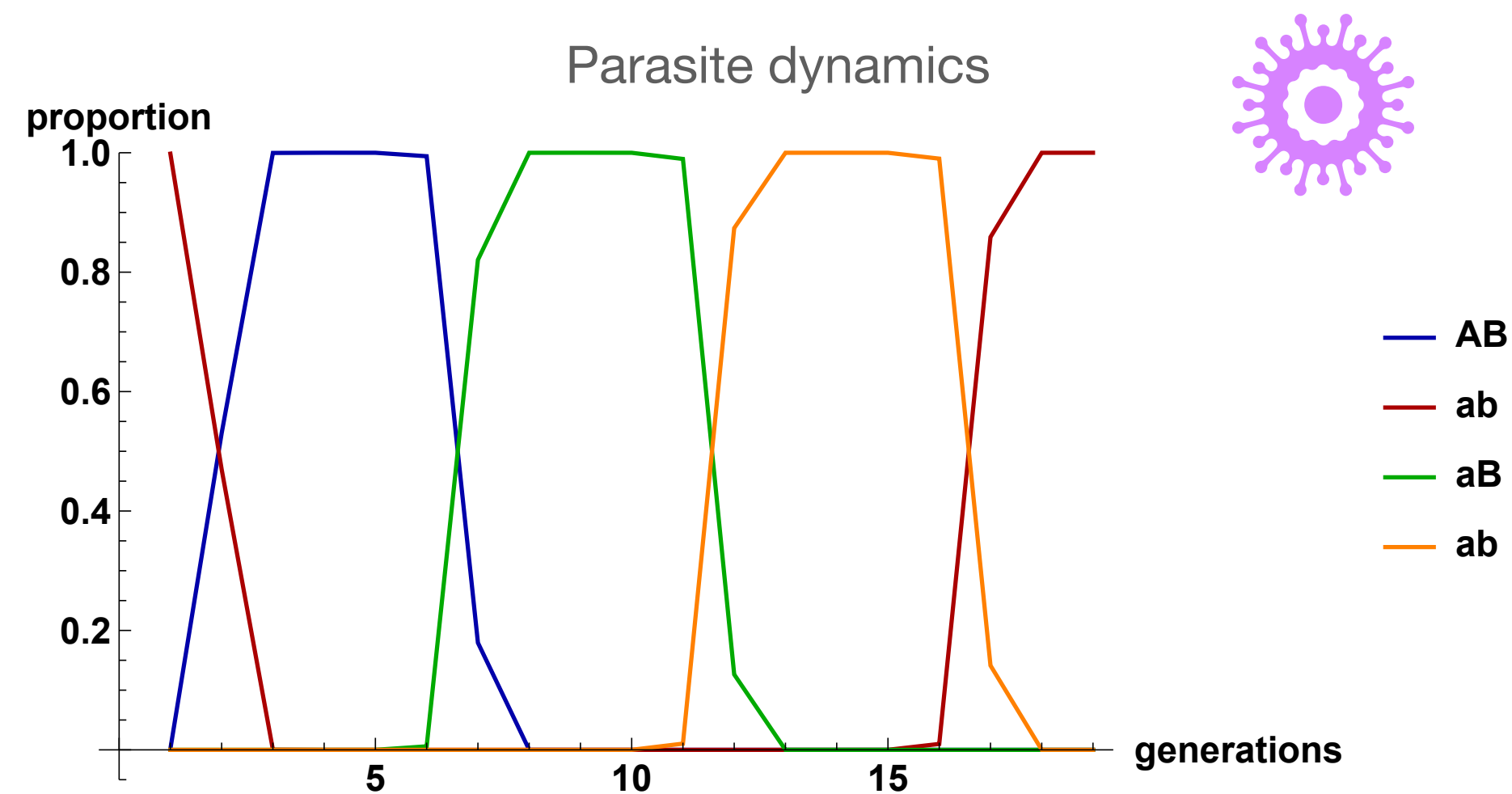
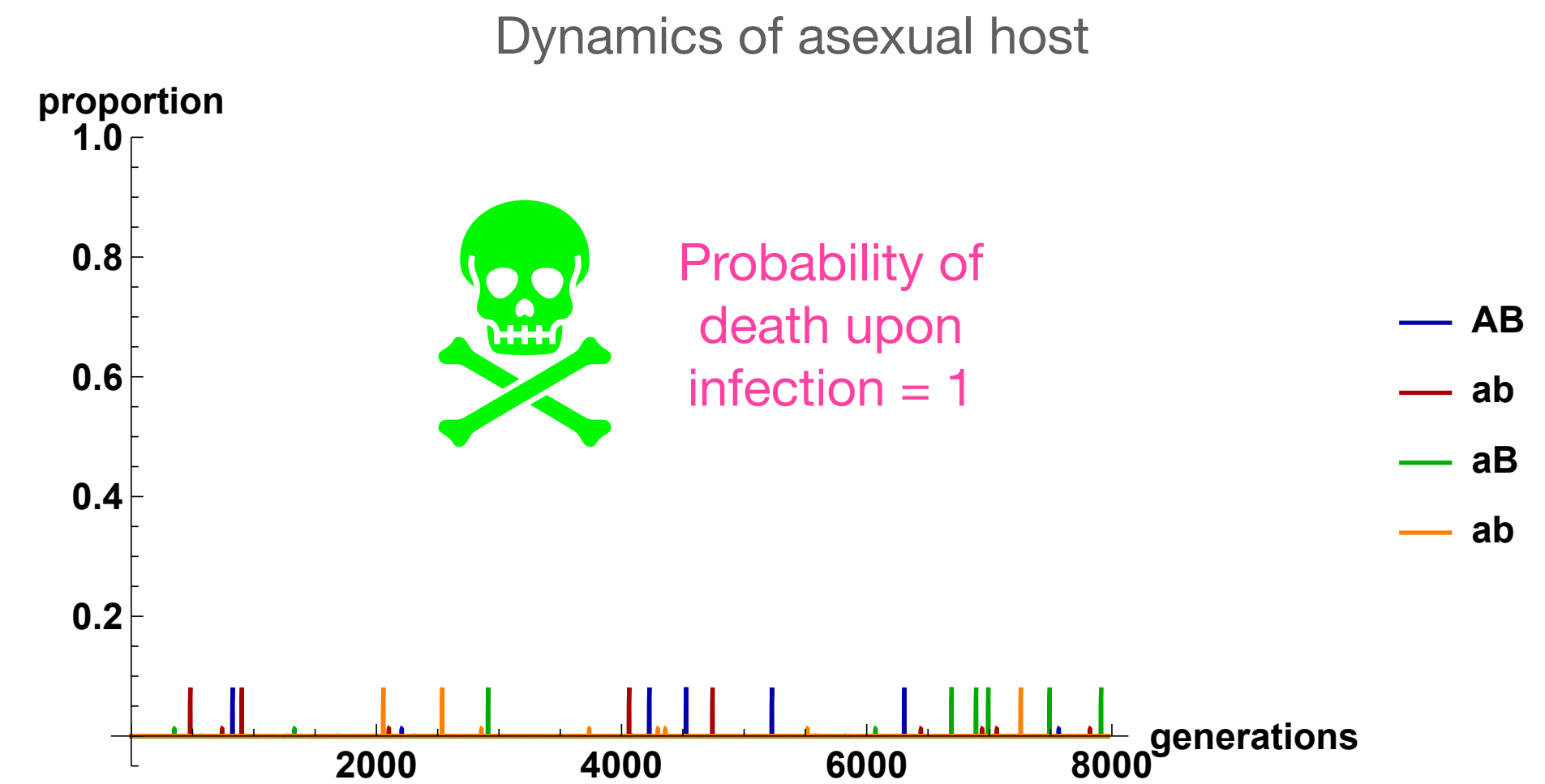
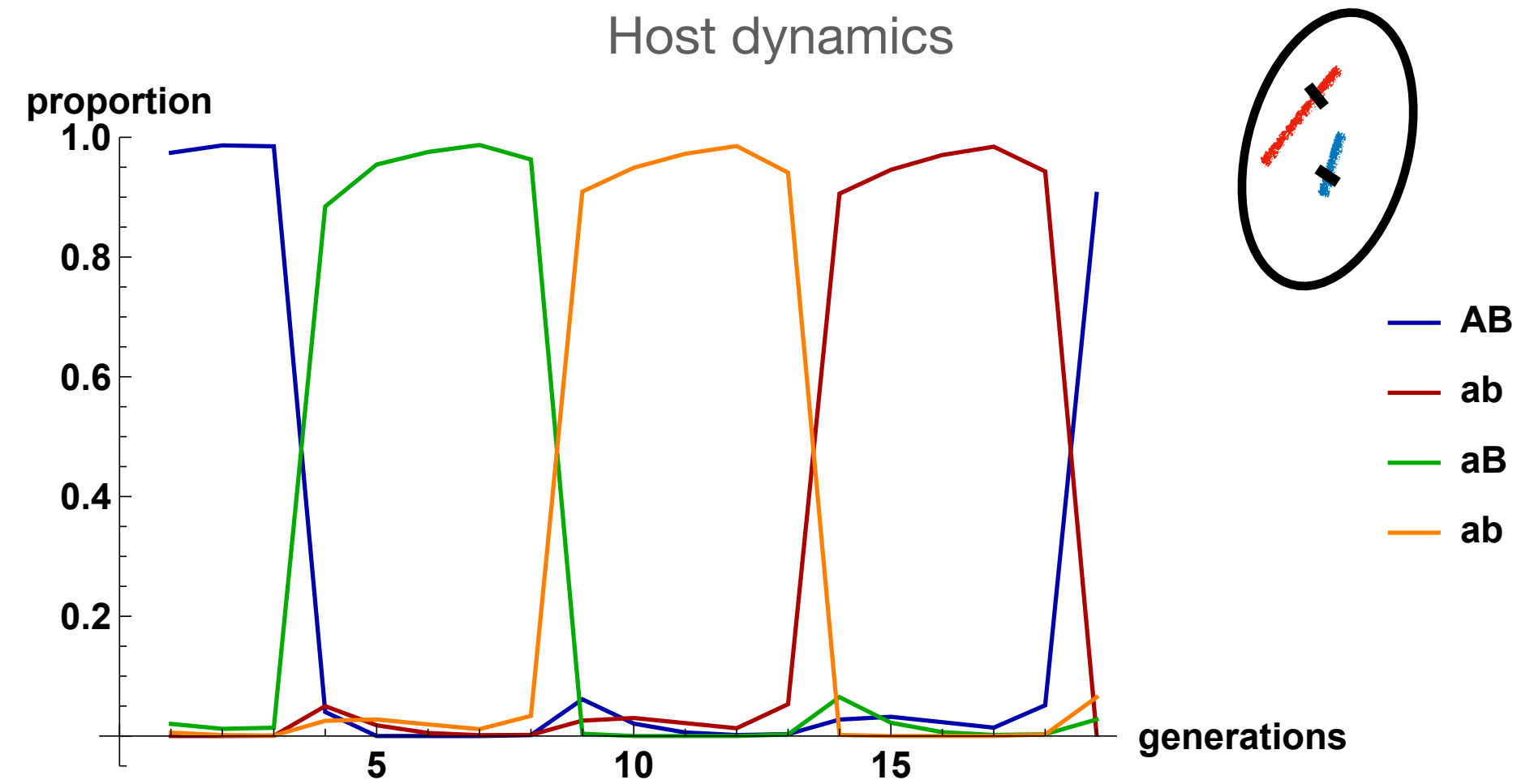
# An ecological model of fluctuating epistasis

## But...



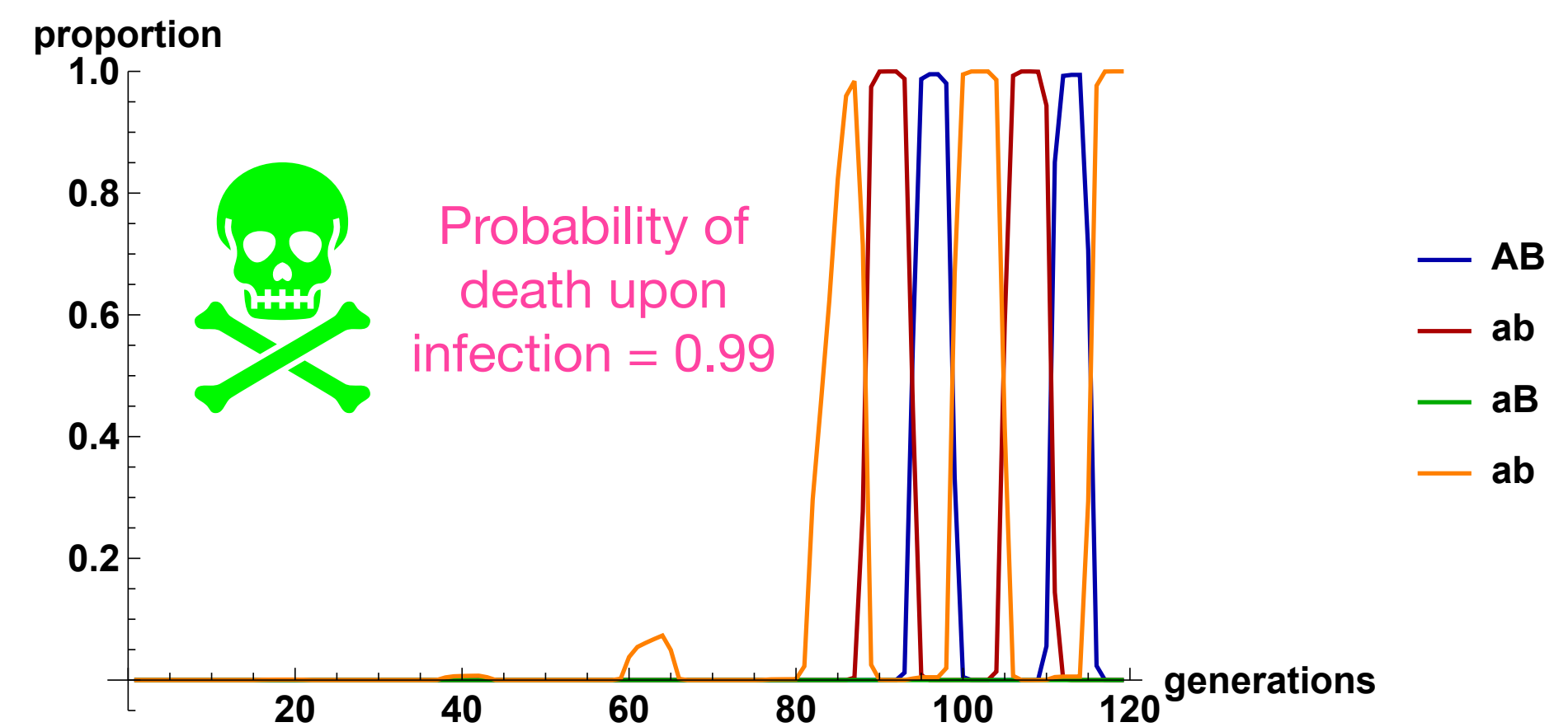
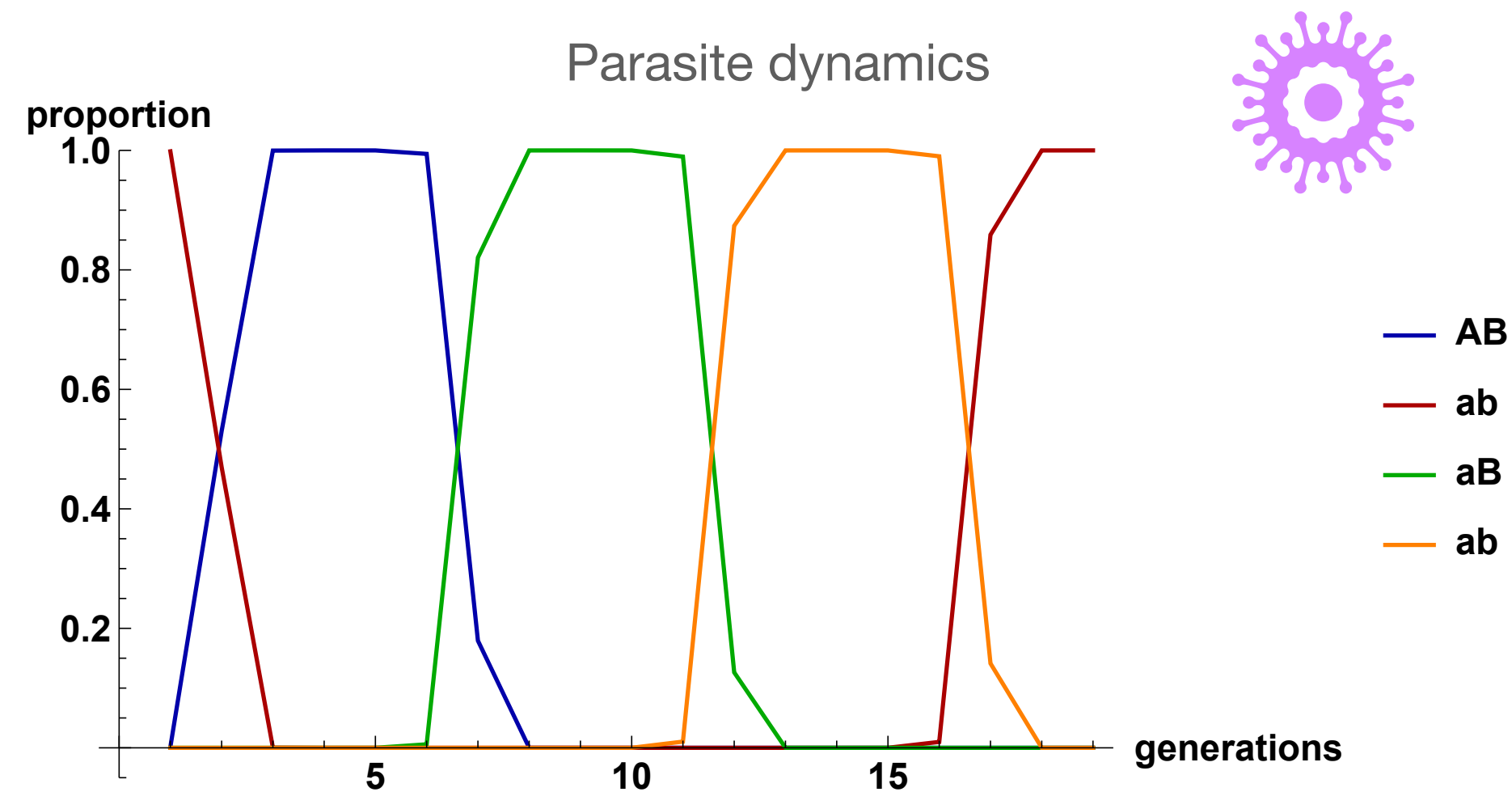
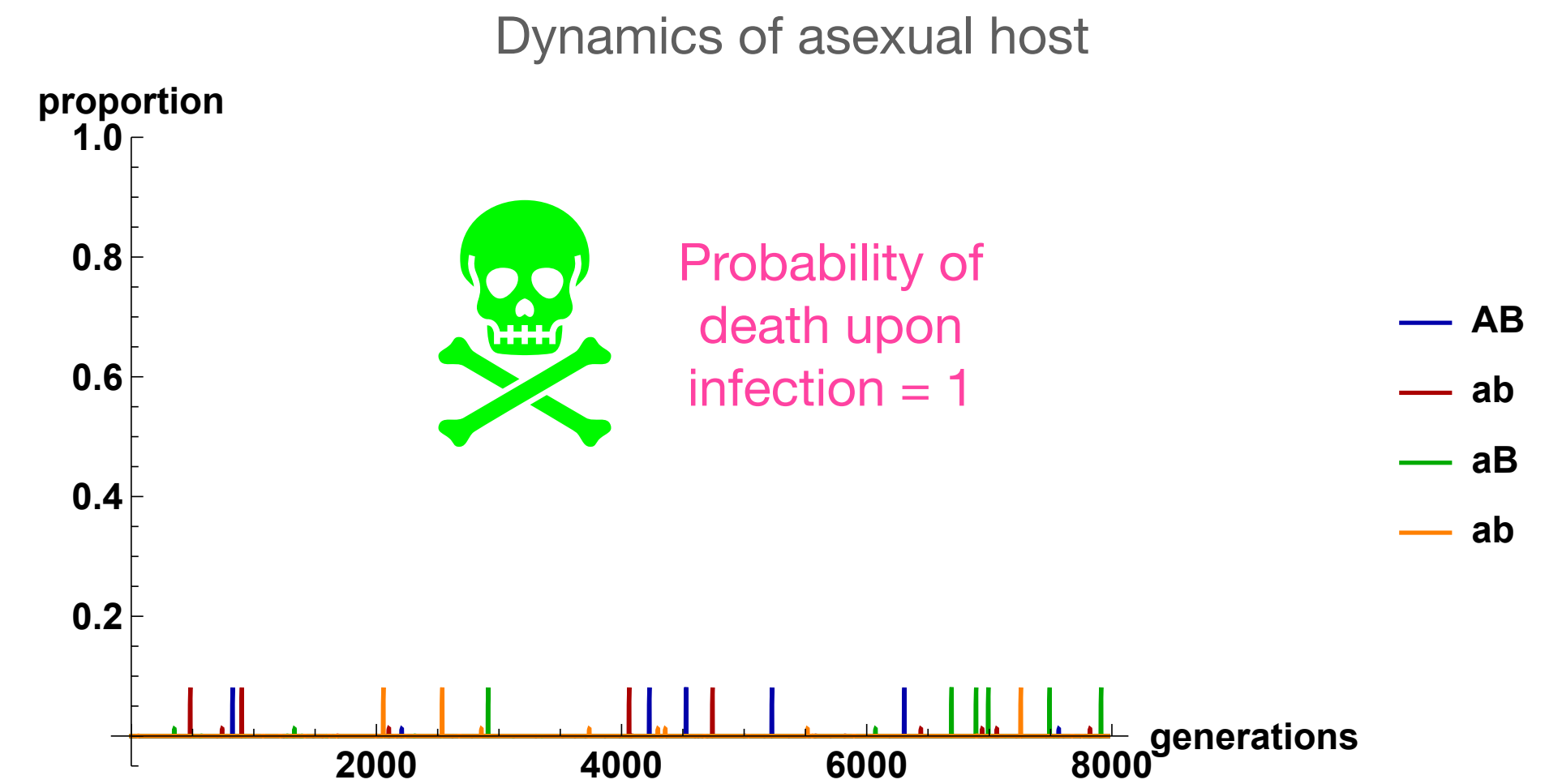
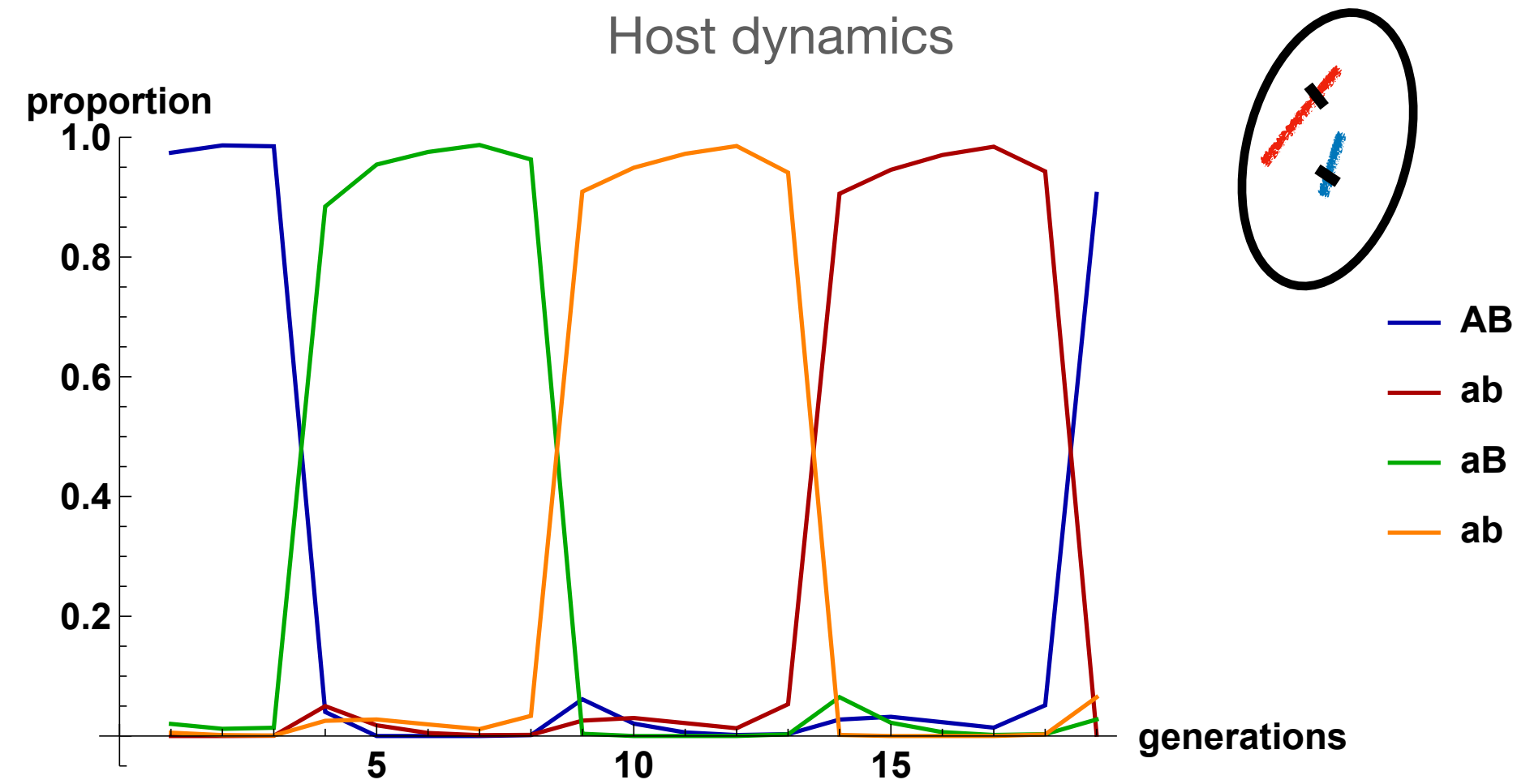
# An ecological model of fluctuating epistasis

## 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.

