The response to selection in complex mating systems

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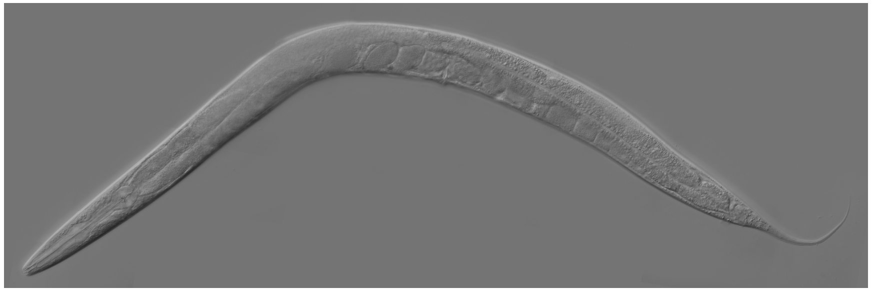
Dioecy

Bolitotherus cornutus
Vince Formica

Silene latifolia

Complex mating systems

Gynodioecy
Silene vulgaris



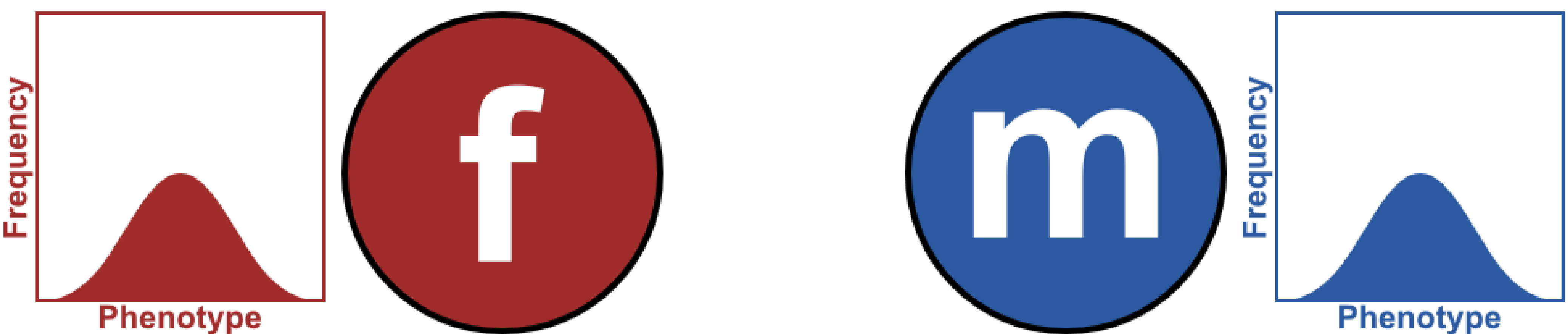
Androdioecy
Caenorhabditis elegans
Zeynep Altun

Alternative reproductive tactics
Midshipman fish
news.bbc.co.uk

Many mating types
Schizophyllum commune
Doug Bowman

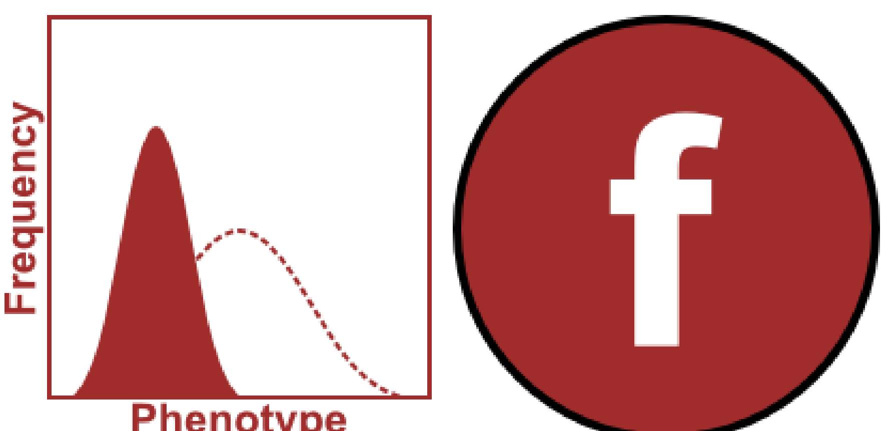
Adaptation in sexual populations

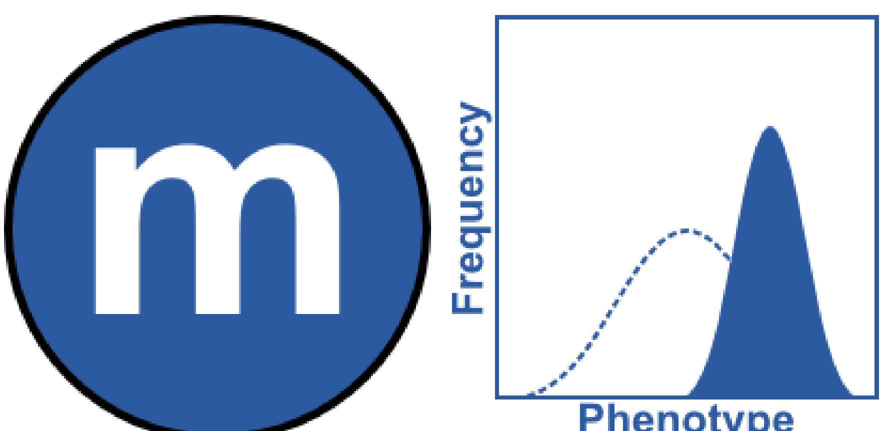
- One or more mating classes
  - Groups of individuals with different mating restrictions (e.g., sexes) or behaviors (e.g., alternative reproductive tactics)



Adaptation in sexual populations

- **Selection** (potentially different) within each mating class
- Response is mediated by **heritabilities**





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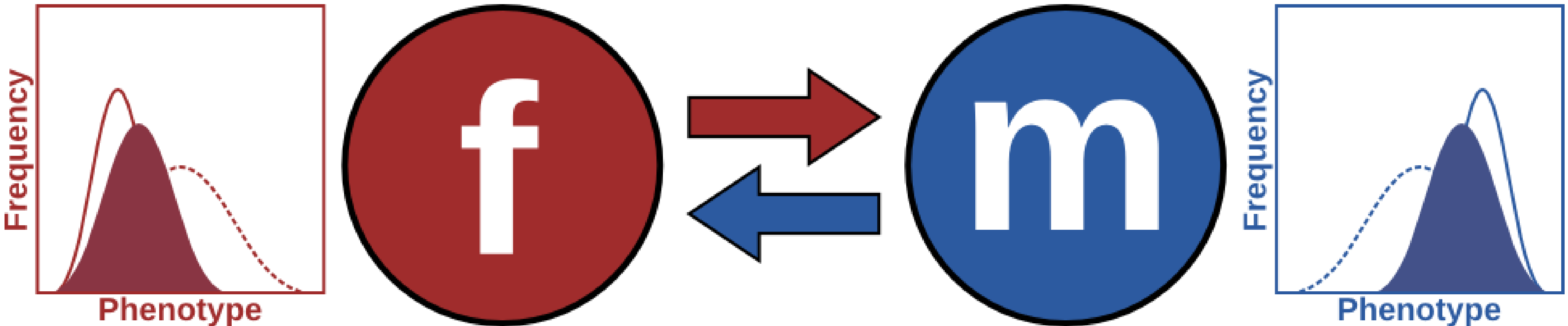
- **Allele mixing** among mating classes during fertilization



Adaptation in sexual populations

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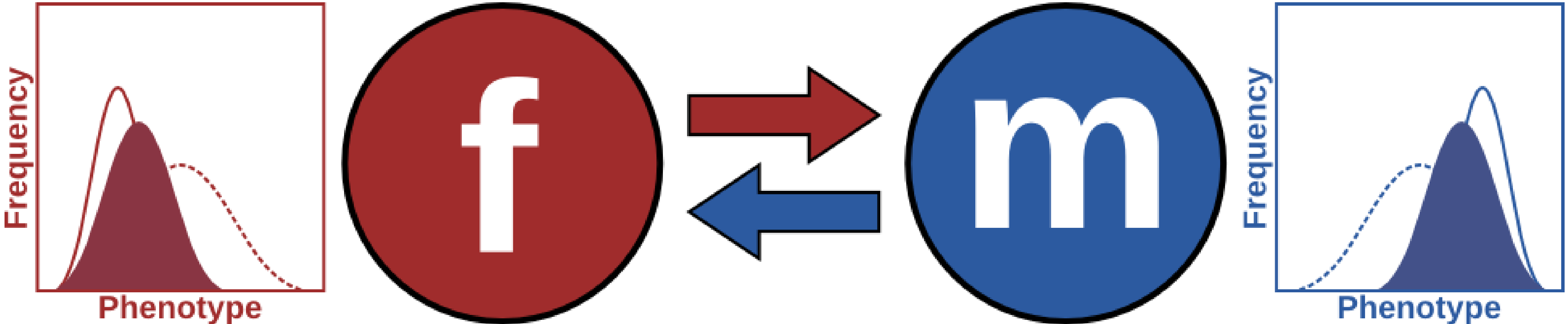
Allele mixing should constrain trait adaptation in mating classes



Questions

1. How similar are the rates of allele mixing in different mating systems?
2. Is adaptation more constrained in some mating classes due to allele mixing?

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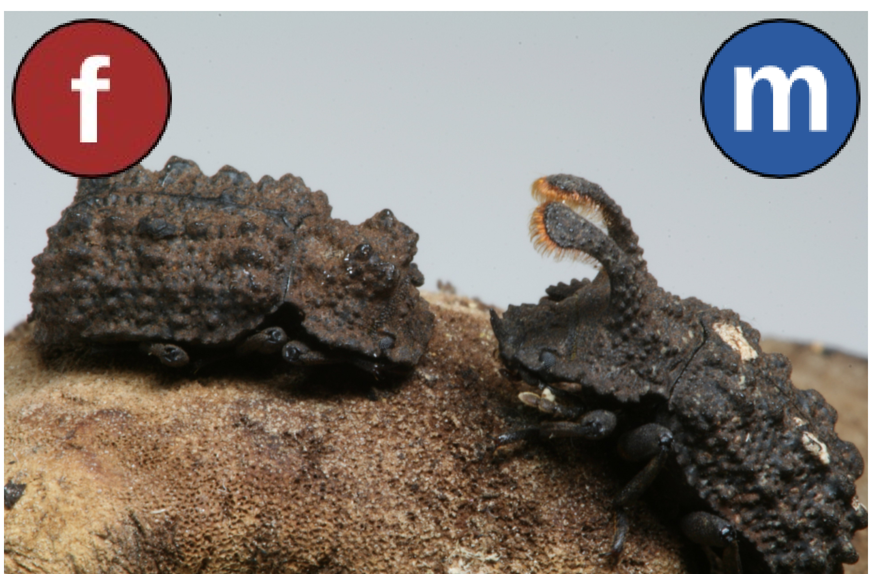
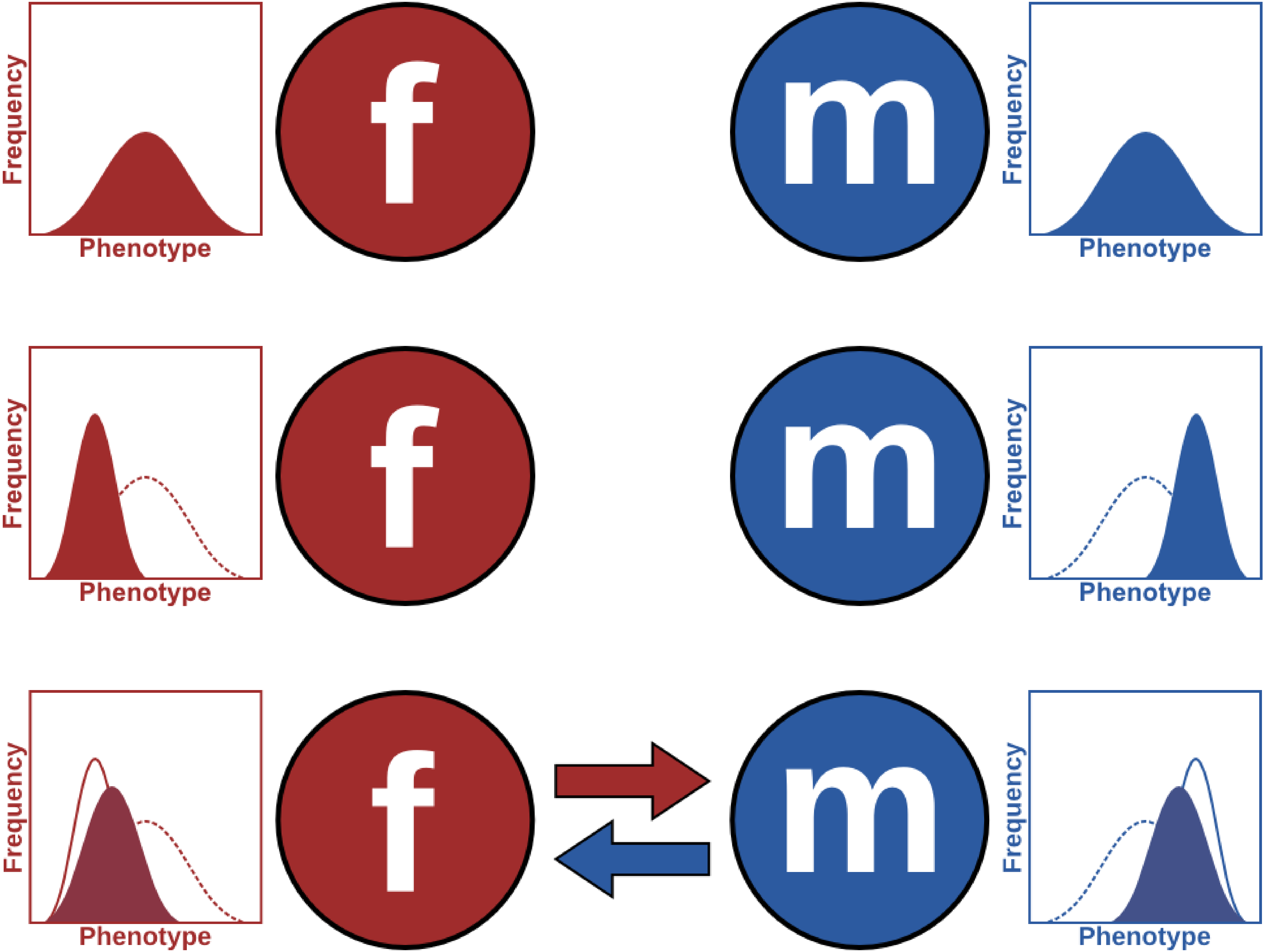
- Dioecy and gynodioecy



Dioecy

Gynodioecy


Frequency
Phenotype
f
m
Frequency
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m
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Frequency
Phenotype
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Frequency
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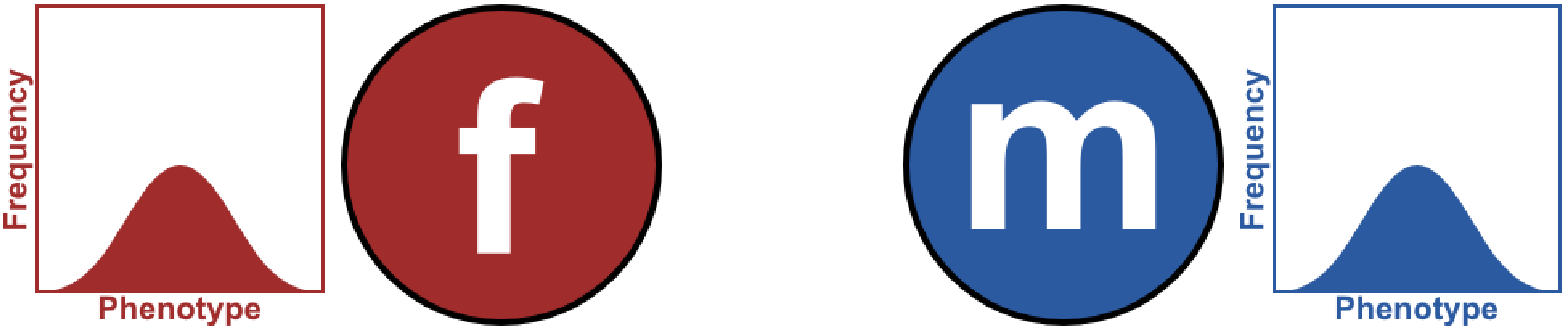
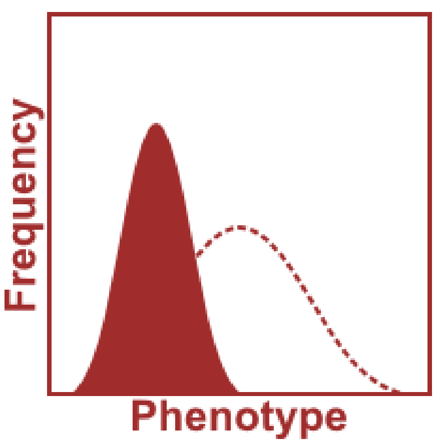
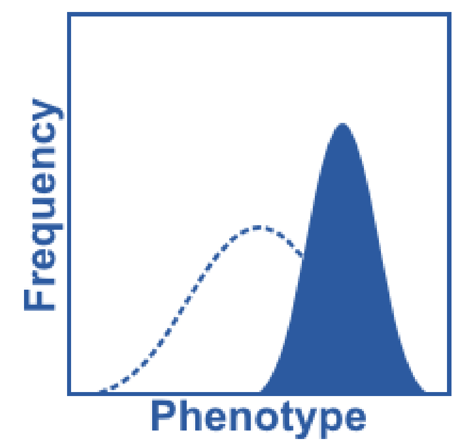
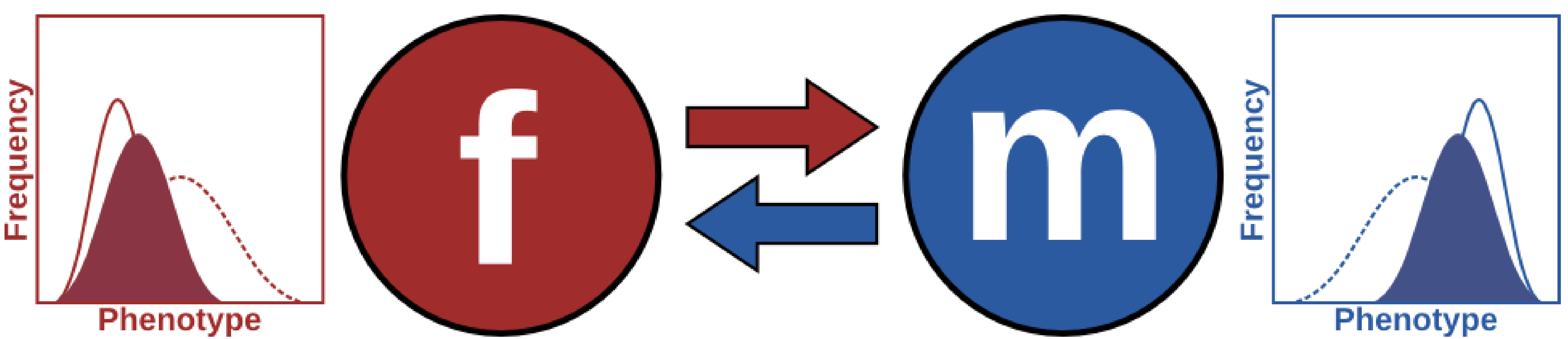




Need a common framework to describe adaptation in any mating system





Character states

- Character states: treat versions of the trait expressed in different mating classes as correlated traits
  - e.g., as though hermaphrodite body size and female body size are separate traits

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  - e.g., as though hermaphrodite body size and female body size are separate traits
- Similarity in genetic architecture is given by among-class genetic covariance, G_{hf}

$$\begin{bmatrix} G_{hh} & G_{hf} \\ G_{hf} & G_{ff} \end{bmatrix}$$

Response to selection <u>within</u> a mating class

- Breeder's equation

$$\Delta \bar{x}_h = G_{hh} \beta_h$$

- G_{hh} is the additive genetic variance of the hermaphrodite character state
- β_h is the selection on the trait in hermaphrodites

Response to selection within a mating class

- Breeder's equation

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- Selection in hermaphrodites will cause a correlated response in the female character state

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- What about allele mixing?

Between-class gene flow

- m_i the rate of gene flow <u>into</u> mating class i from other classes
- Analogous to the migration rate in spatially structured populations
- The proportion of i offspring whose parents are a different mating class

Response to selection

- m_h weights the influence of each class on the phenotypes of hermaphrodites next generation

$$\bar{x}_h^* = (1-m_h)(\bar{x}_h + \Delta\bar{x}_h) + m_h(\bar{x}_{fh} + \Delta\bar{x}_{fh})$$

Response to selection

- m_h weights the influence of each class on the phenotypes of hermaphrodites next generation

$$\begin{aligned} \bar{x}_h^* &= (1-m_h)(\bar{x}_h + \Delta\bar{x}_h) + m_h(\bar{x}_{hf} + \Delta\bar{x}_{fh}) \\ &= (1-m_h)(\bar{x}_h + G_{hh}\beta_h) + m_h(\bar{x}_{hf} + G_{hf}\beta_f) \end{aligned}$$

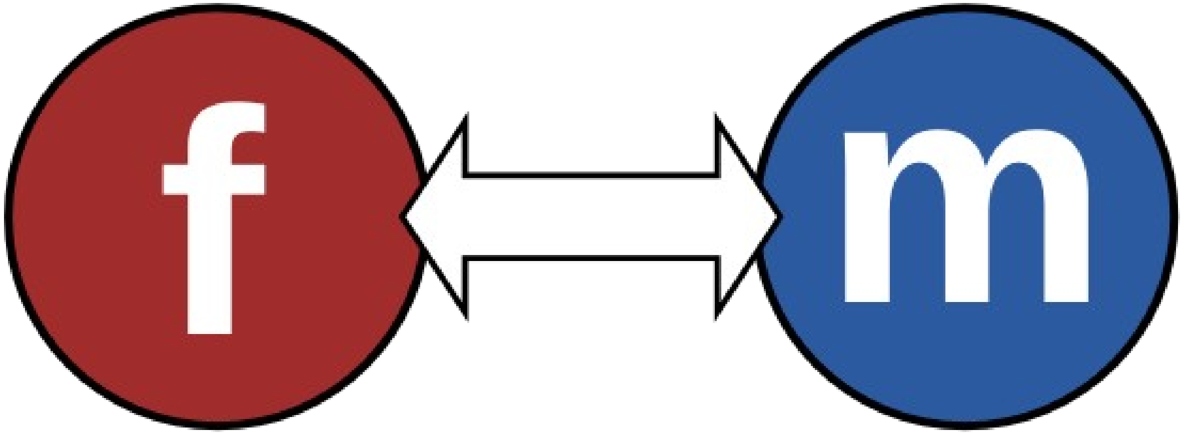
- Response depends on selection, heritabilities, and between-class gene flow

Between-class gene flow

- The proportion of i offspring whose parents are a different mating class
- Depends on:

  a = Frequency of mating among classes (demography)

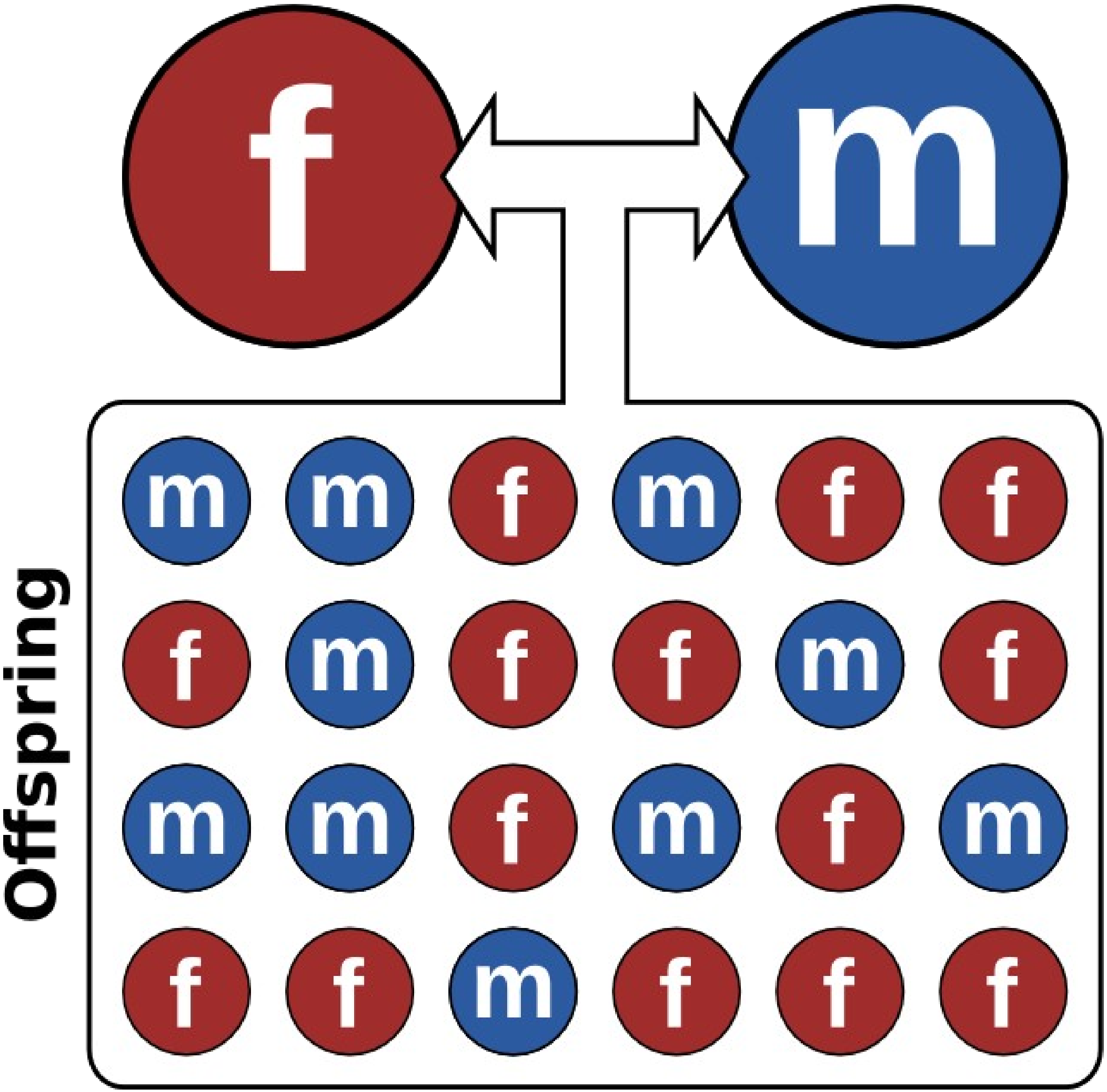
  b = Class ratio resulting from each type of mating (genetics)



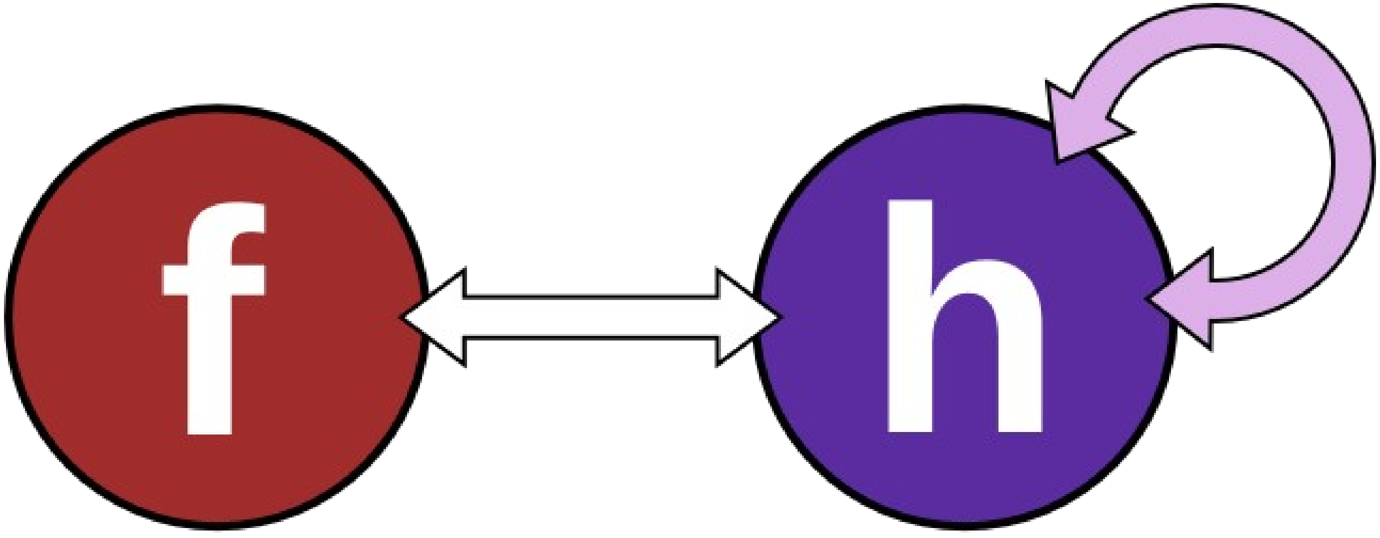
Dioecy

- Only one type of mating: male x female

Dioecy



- Only one type of mating: male x female
- Each individual has one female and one male parent, so rates of gene flow are <u>always</u> equal
- $m_m = m_f = 0.5$



Gynodioecy

- Two types of mating: h x h and h x f

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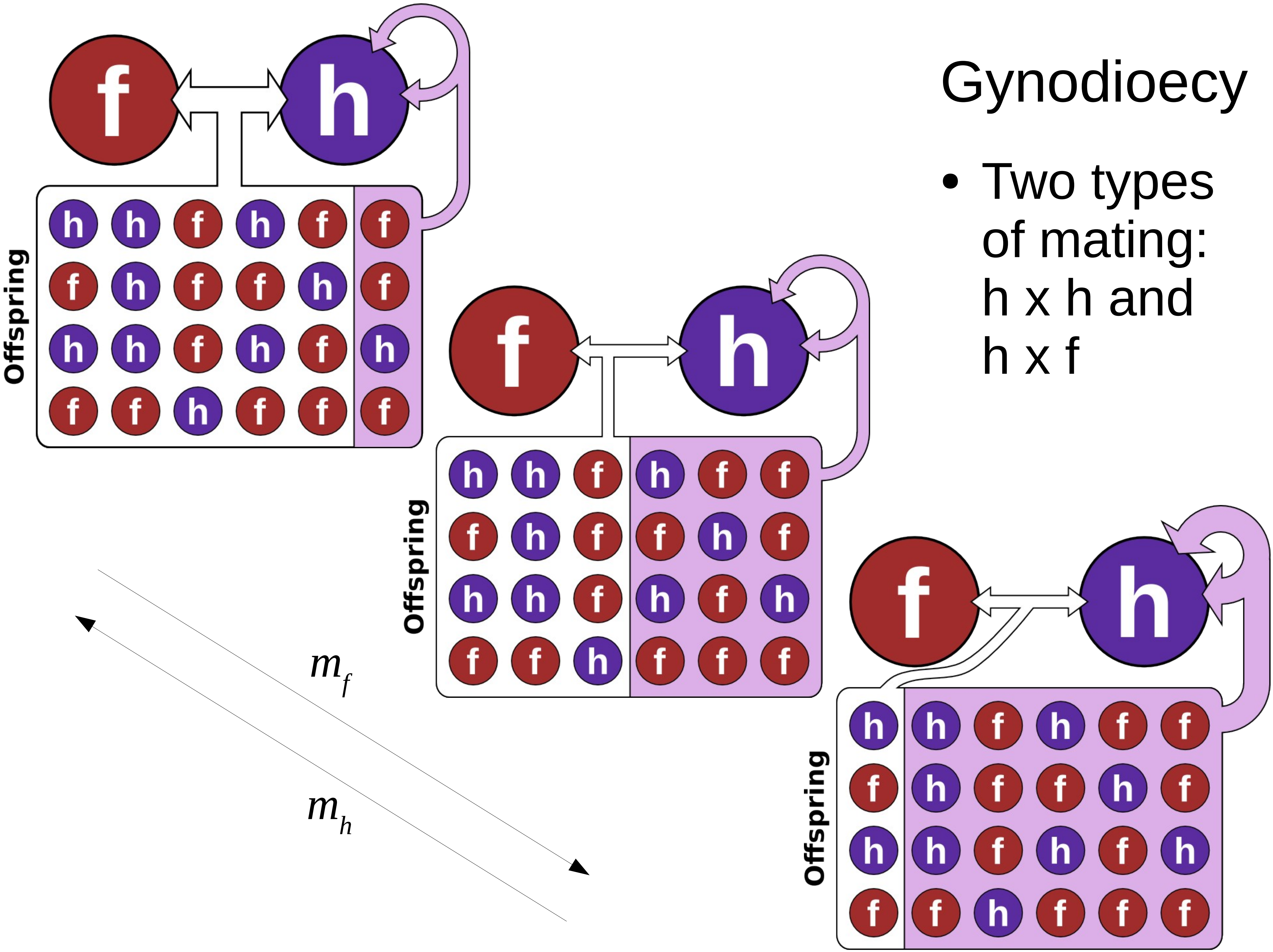

Gynodioecy

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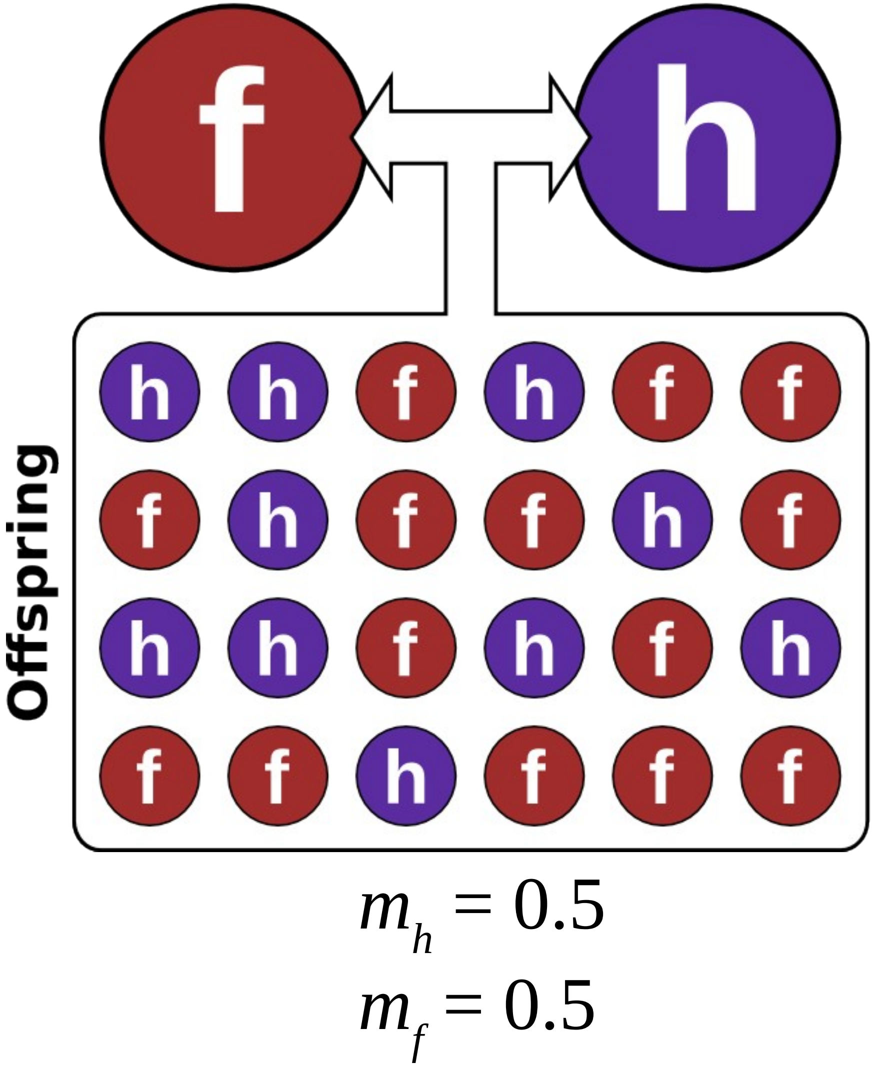
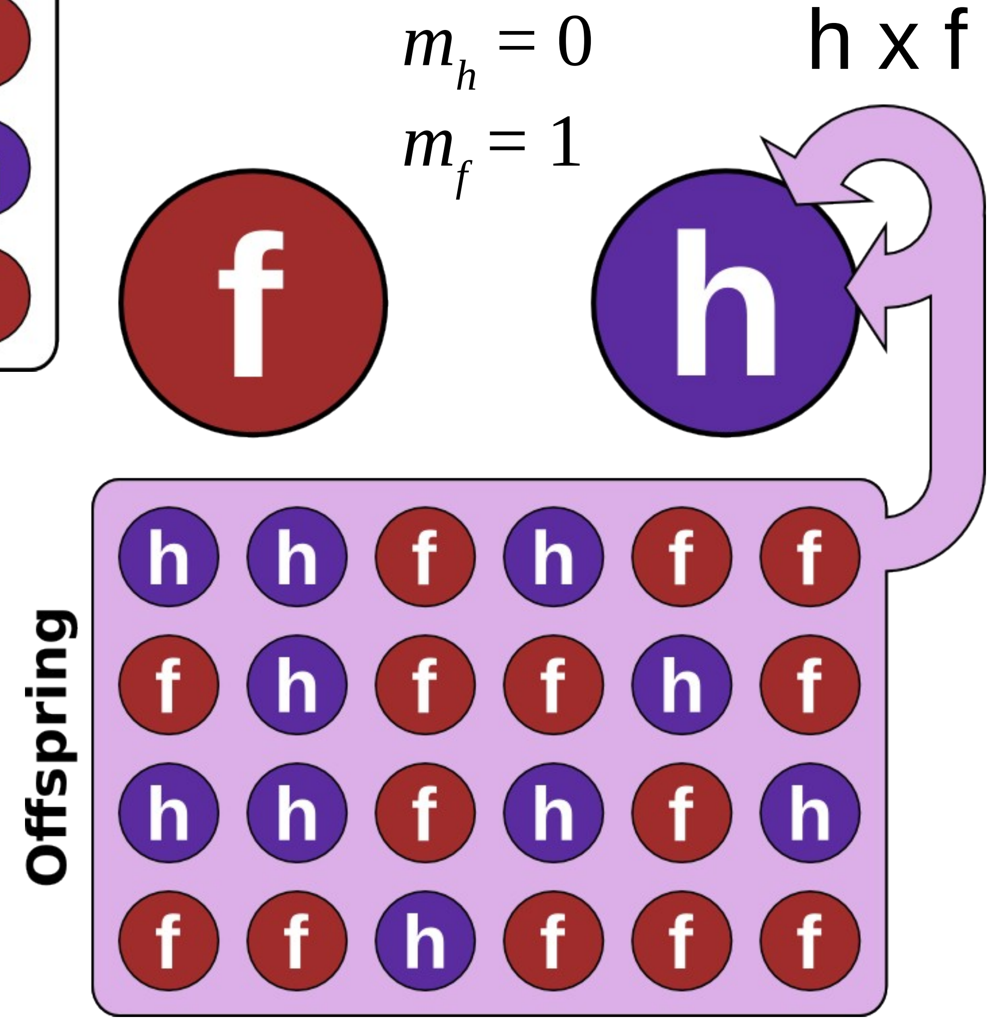
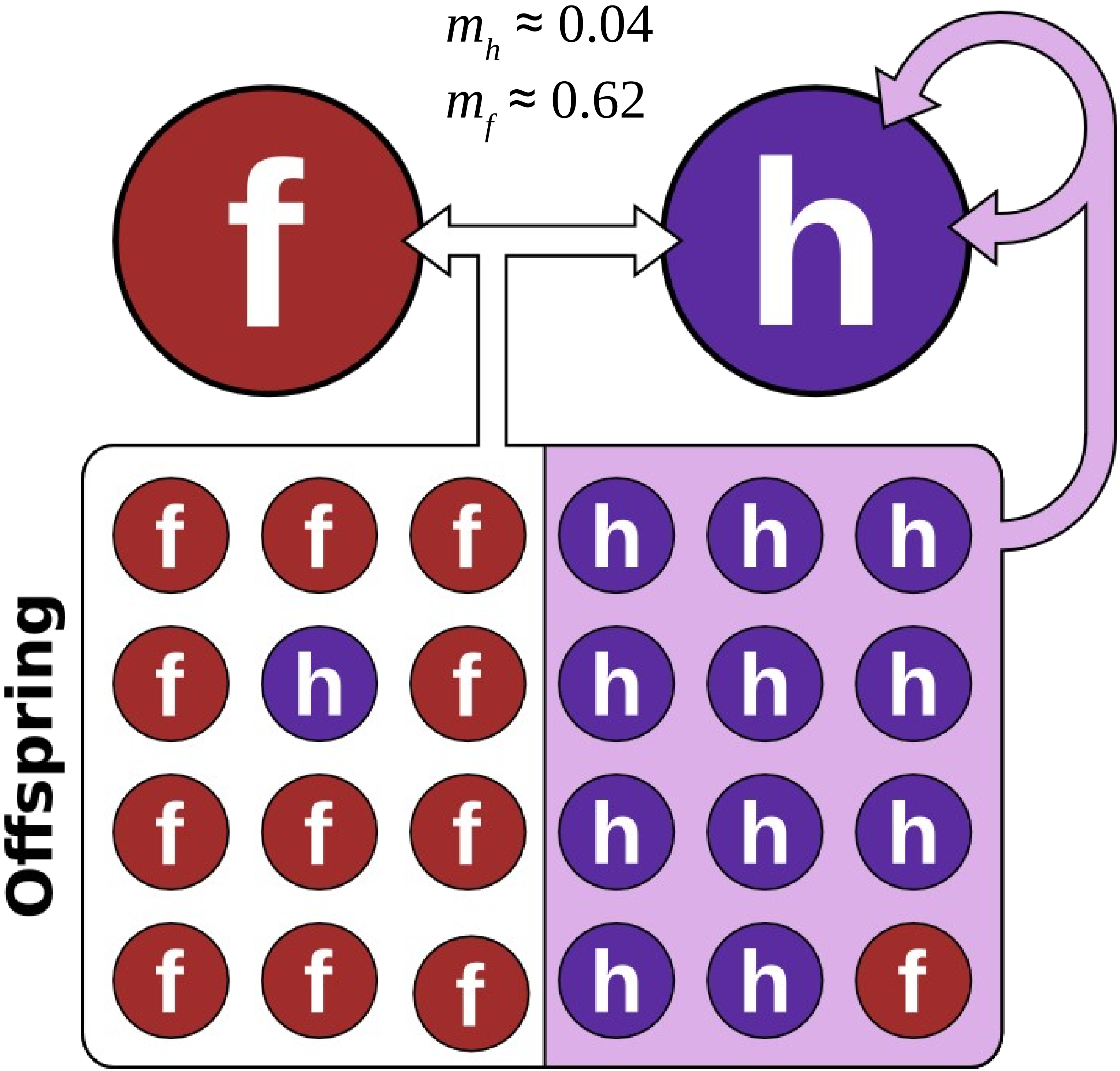






Gynodioecy

- Two types of mating: h x h and h x f

Between-class gene flow

1. How similar are the rates of allele mixing in different mating systems?

- $0 \leq m_h \leq 0.5$
- $0.5 \leq m_f \leq 1$
- But the specifics will depend on the population (a) demography and (b) genetics

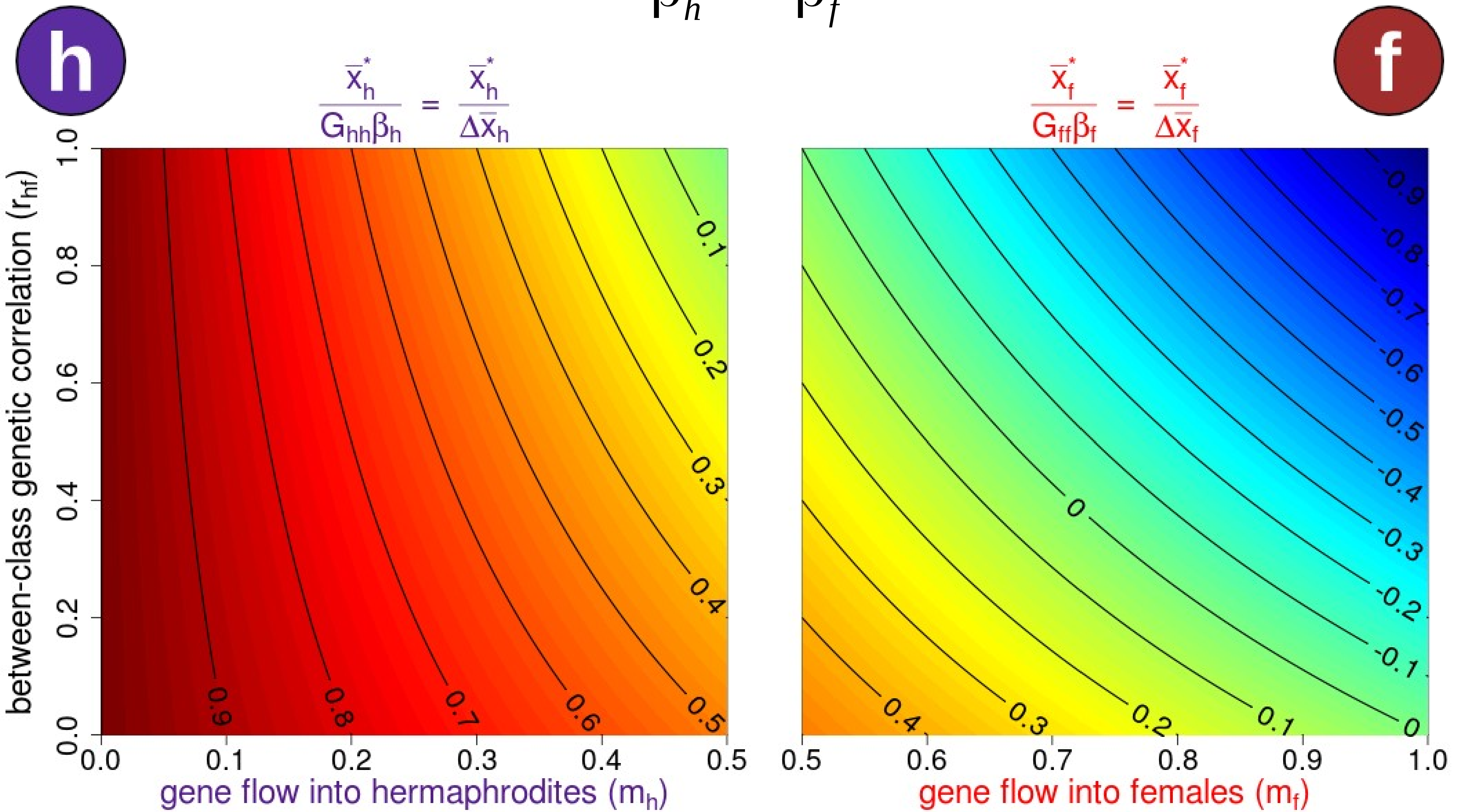
Between-class gene flow

1. How similar are the rates of allele mixing in different mating systems?

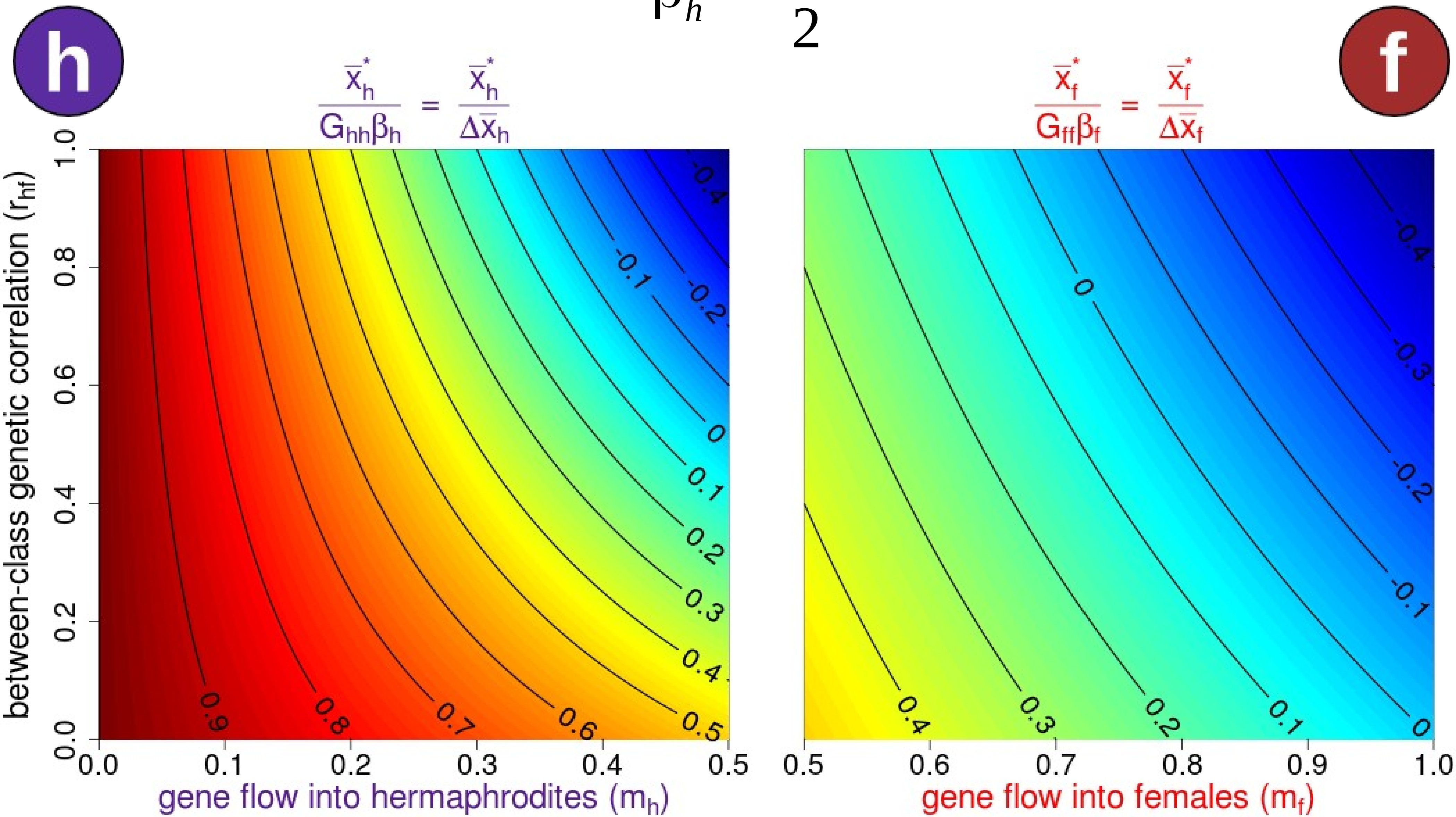
- $0 \le m_h \le 0.5$
- $0.5 \le m_f \le 1$

- How does this affect constraint for each class?

$$\beta_h = -\beta_f$$


h
f
$\frac{\bar{x}_h^*}{G_{hh}\beta_h} = \frac{\bar{x}_h^*}{\Delta\bar{x}_h}$
$\frac{\bar{x}_f^*}{G_{ff}\beta_f} = \frac{\bar{x}_f^*}{\Delta\bar{x}_f}$
between-class genetic correlation (r_{hf})
gene flow into hermaphrodites (m_h)
gene flow into females (m_f)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
-0.9
-0.8
-0.7
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0

$$\beta_h = \frac{-\beta_f}{2}$$



Constraints due to gene flow

2. Is adaptation more constrained in some mating classes due to allele mixing?

- Compared to dioecy
  - Trait evolution in females is <u>more</u> constrained by gene flow
  - Trait evolution in hermaphrodites is <u>less</u> constrained by gene flow

Implications

- Can use character state approach to compare multiple mating systems
- Adaptation in complex mating systems: rates of gene flow matter too, not just trait correlations
- The response to selection within one mating class may be a poor predictor of evolution

Acknowledgements

Laura Galloway

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Vince Formica

Brian Sanderson

Corlett Wood

Eric Wice

Between-class gene flow

$$m_i = \frac{\#\text{ "migrant" gametes into i}}{\#\text{ gametes into i}}$$

$$= \frac{\sum_{j \neq i} \bar{W}_j m_{ij}}{\bar{W}_i (1 - m_{\cdot i}) + \sum_{j \neq i} \bar{W}_j m_{ij}}$$

- m_{ji} = the proportion of gametes produced by i parents which end up in j offspring
- $m_{\cdot i}$ = the proportion of gametes produced by i parents which end up in another mating class

Between-class gene flow

- m_{ji} = the proportion of gametes produced by i parents which end up in j offspring
- $m_{\cdot i}$ = the proportion of gametes produced by i parents which end up in another mating class
- For gynodioecy:

$$
\begin{aligned}
m_{hf} &= b_{h \times f} \\
m_{fh} &= a\left(1 - b_{h \times h}\right) + \left(1 - a\right)\left(1 - b_{h \times f}\right)
\end{aligned}
$$

Gene flow into hermaphrodites

$$m_h = \frac{(1-a)b_{hxf}}{2\mathrm{b}_{hxf} + a(1+a)(b_{hxh} - b_{hxf})}$$

- If all mating is between hermaphrodites, a = 1

$$m_h = \frac{0}{2\mathrm{b}_{hxf} + 2(b_{hxh} - b_{hxf})} = 0$$

- If hermaphrodites always mate with females, a = 0

$$m_h = \frac{b_{hxf}}{2\mathrm{b}_{hxf} + 0(b_{hxh} - b_{hxf})} = \frac{b_{hxf}}{2\mathrm{b}_{hxf}} = \frac{1}{2}$$

Character states

- The version of the trait expressed in a single mating class

Locus — **Additive effects** — **Breeding value**

$$A_1 \; A_2 \Rightarrow \alpha_1 + \alpha_2 = X_m$$

Character states

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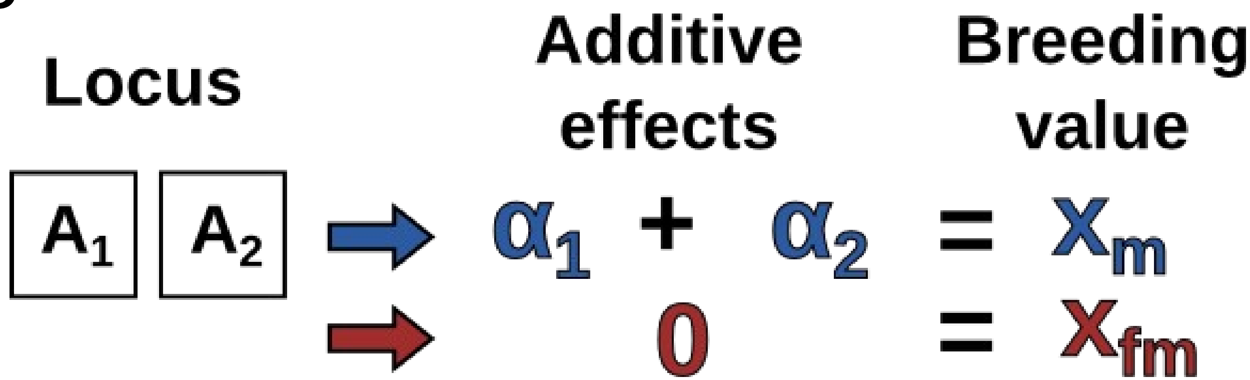

- x_{fm}: female character state carried by males

Character states

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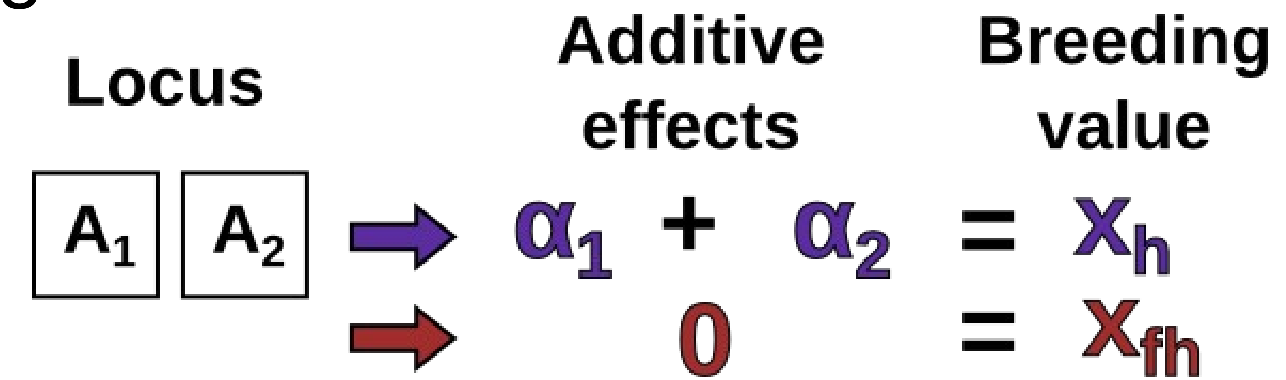

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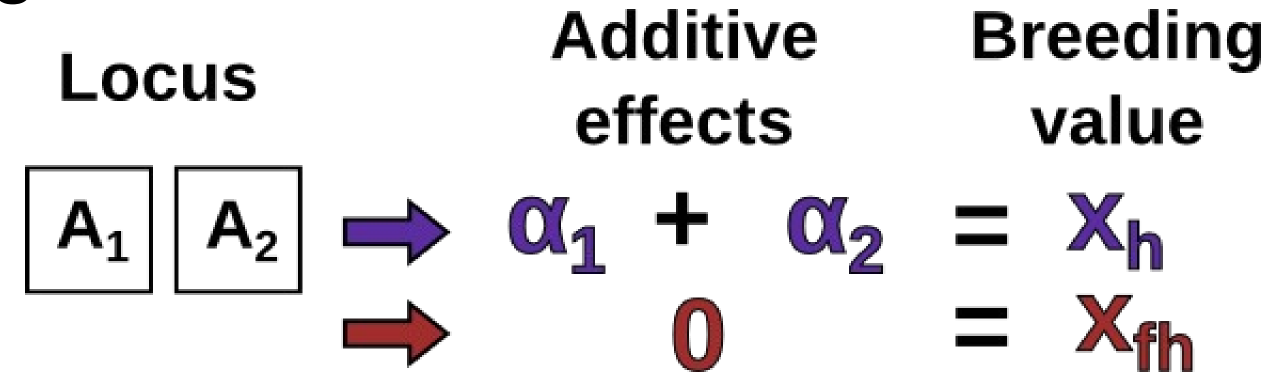

- The similarity between character states is given by G_{hf}, the additive genetic covariance

Future directions

- Other mating systems
- Assumes gene flow is independent of phenotype
- Need predictions of variance evolution to predict longer term evolution
- Are gene flow and selection related?