Linking levels of selection with genetic modifiers

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SSE

SOCIETY *for the* STUDY *of* EVOLUTION

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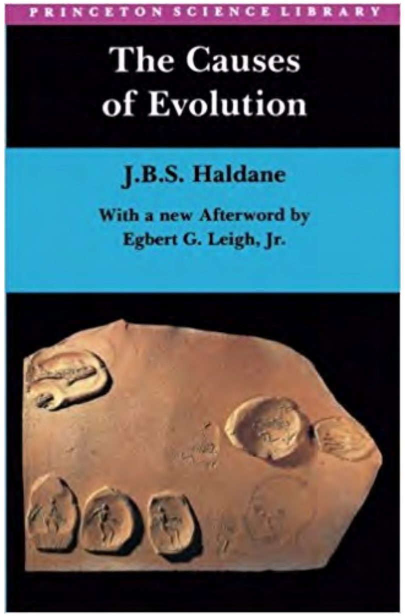
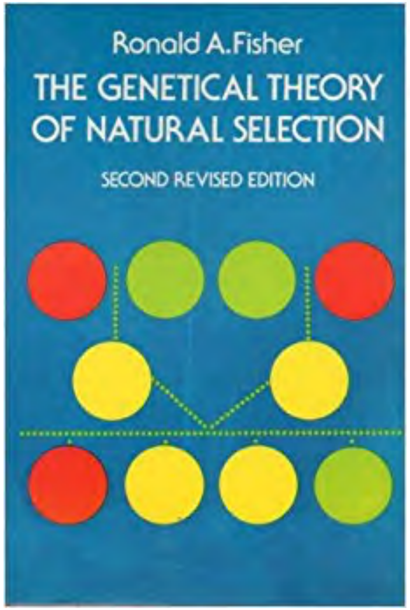
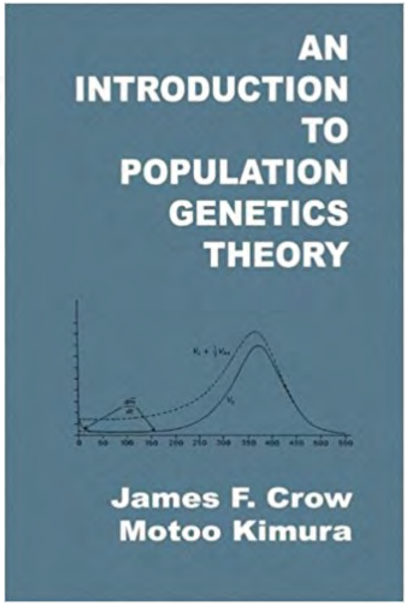
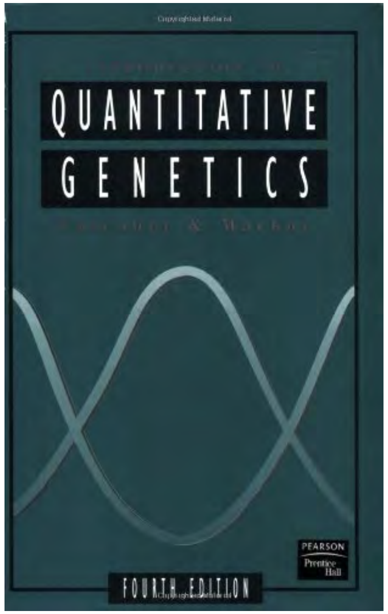
EVOLUTIONARY MODELS

Evolution is richly underpinned by mathematical theory.









EVOLUTIONARY THEORY

Classical models track **genes under selection**, given:

- Mode of reproduction
- Recombination rate
- Ploidy (haploid or diploid)
- Mutation rate
- Dominance
- Life history

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$$\frac{\mathrm{d}p}{\mathrm{d}t} = s\,p\left(1-p\right)$$

One-locus

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One-locus

$$x_1(t+1) = x_1(t)\left(\sum_{j=1}^{4} x_j(t)\left(\frac{w_{1j}+w_{j1}}{2\overline{w}}\right)\right) - r\,D^*$$

$$x_2(t+1) = x_2(t)\left(\sum_{j=1}^{4} x_j(t)\left(\frac{w_{2j}+w_{j2}}{2\overline{w}}\right)\right) + r\,D^*$$

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Two-locus

$$R = h^2 S$$

Quantitative-genetic

EVOLUTIONARY THEORY

Classical models track **genes under selection**, given:

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But how do these features evolve?

EVOLUTIONARY THEORY

Classical models track **genes under selection**, given:

- Mode of reproduction
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- Mutation rate
- Dominance
- Life history

How does an organism come to live and reproduce in the way that it does?

MODIFIER THEORY

MODIFIER THEORY

Modifiers are just genes, but

they are genes that shape the very nature of an organism

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Modifiers are just genes, but
they are genes that shape the very nature of an organism

- how it lives and reproduces
- how its genome is structured
- how its traits are inherited

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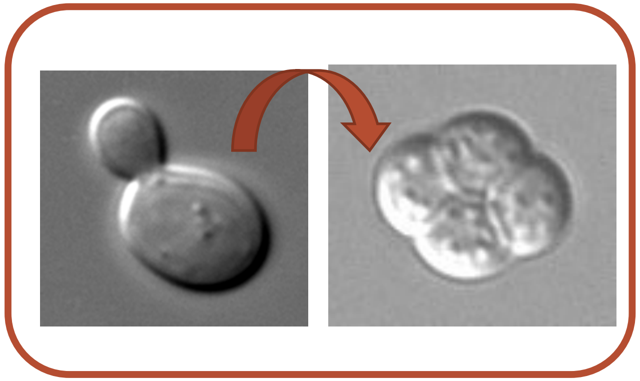

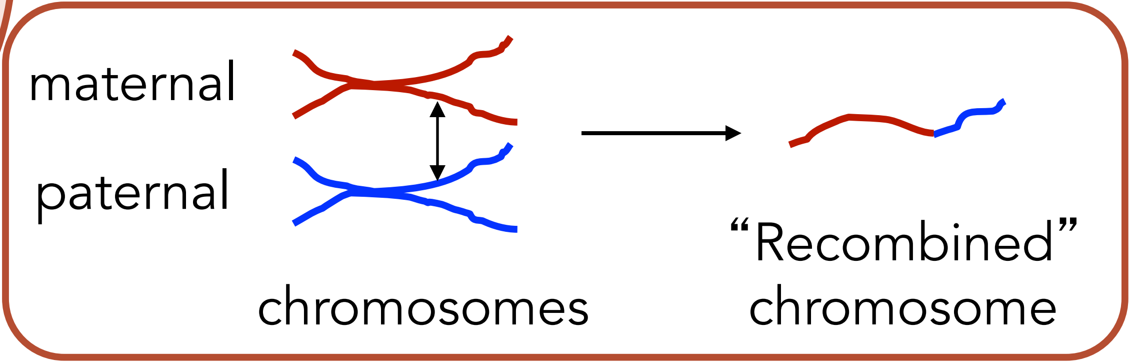

MODIFIER THEORY

Modifiers models track
the evolutionary dynamics of genes that alter

- Mode of reproduction
- Recombination rate
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- Dominance
- Life history

Helping us to answer
"Why do organisms experience evolution in the way that they do?"

MODIFIER THEORY

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Helping us to answer

"Why is the biological world so diverse?"

MODIFIER THEORY

Earliest models tracked genes modifying dominance:

- Fisher (*AmNat* 1928): "it is not the mutant gene which is modified but other hereditary factors which influence the reaction of the organism to the mutant gene"
- Wright (*AmNat* 1929): "Suppose that there is another factor, **M**, which modifies the selection against the heterozygote"

MODIFIER THEORY

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Both showed that dominance of wildtype alleles over mutant alleles could evolve, but selection was very weak (proportional to the mutation rate).

MODIFIER THEORY

Fisher and Wright calculated the average fitness of the new modifier across backgrounds, *ignoring genetic associations*.

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Nei (1967 *Genetics*) was the first to model the full dynamics of a modifier of recombination.

MODIFIER THEORY

Examples of modifier models

MODIFIER THEORY

Modifier models

Levels of selection

MODIFIER THEORY

Modifier models ⟷ Levels of selection

MODIFIER THEORY

Modifier models ⟷ Levels of selection

Evolutionary conflicts

MODIFIER THEORY

How do modifier genes evolve when there are conflicts between what is best for the individual and what is best for the group?

- Evolution of sex
- Evolution of haploidy vs diploidy
- Evolution of sex chromosomes

EVOLUTION OF SEX

Among diploids, sex allows for the segregation of alleles, e.g., *Aa* parents ➔ *AA*, *Aa*, and *aa* offspring.

Can the benefits of segregation explain the evolution of sex?

EVOLUTION OF SEX

Let’s start by considering the conflicting levels of selection, with recurrent deleterious mutations…

EVOLUTION OF SEX

Group level: Segregation can regenerate variance in fitness, making selection more efficient.

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AA *Aa* *aa*

>Expected

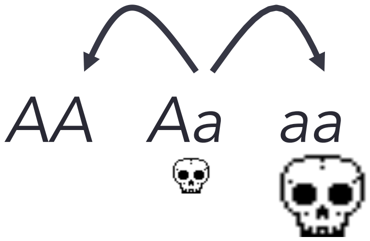
<Expected <Expected

If $W_{Aa} > \surd(W_{AA}W_{aa})$:
Variance depleted by selection

Chasnov 2000

EVOLUTION OF SEX

Group level: Segregation can regenerate variance in fitness, making selection more efficient.



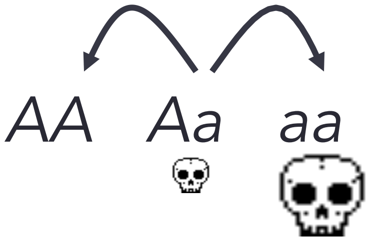
If $W_{Aa} > \sqrt{(W_{AA}W_{aa})}$:
Variance depleted by selection
Sex regenerates variance

Sex increases mean fitness if $W_{Aa} > \sqrt{(W_{AA}W_{aa})}$

Chasnov 2000

EVOLUTION OF SEX

Individual level: By breaking apart gene combinations favored by past selection, sex causes a reduction in offspring mean fitness ("segregation load").



Sex decreases offspring fitness*

Otto 2003

(*except between additive and multiplicative dominance)

EVOLUTION OF SEX

Group level:

Increase variability

Sexuality favored: $W_{Aa} > \sqrt{(W_{AA} W_{aa})}$

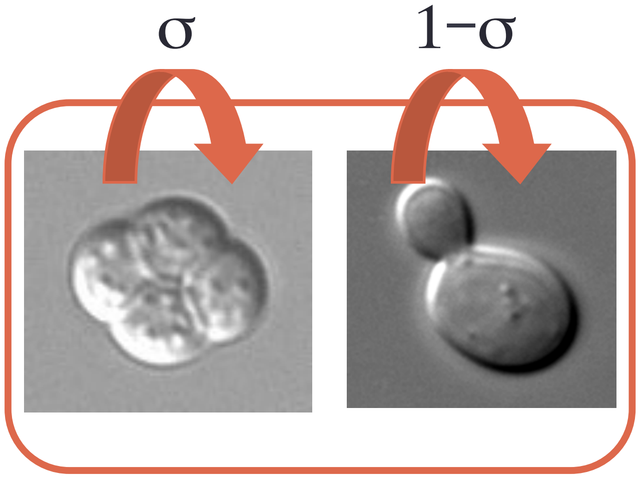
Individual level:

Avoid segregation load

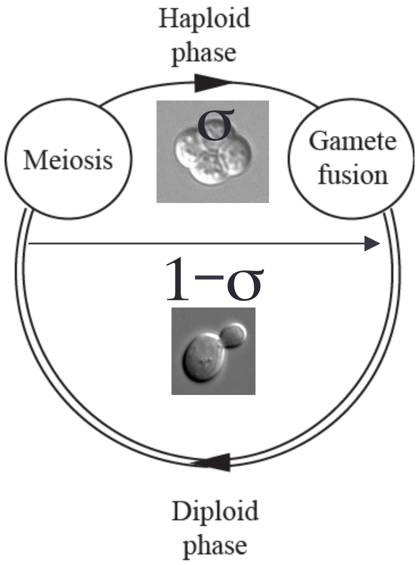
Asexuality favored

EVOLUTION OF SEX

Modifier Model: Consider a modifier that alters the probability, σ, that an individual reproduces sexually rather than asexually.



EVOLUTION OF SEX



$$x'_{11} = (1 - \sigma_1)\overset{\approx}{x}_{11} + \overline{\sigma}\,(y_1^2(1 - f) + y_1 f)$$

$$2x'_{12} = (1 - \sigma_1)2\overset{\approx}{x}_{12} + \overline{\sigma}(2y_1y_2(1 - f))$$

MAMA

MAMa

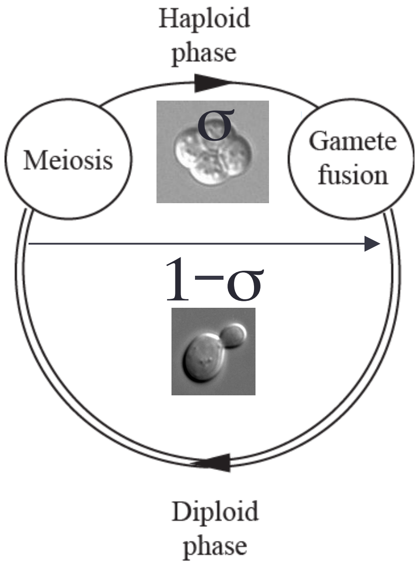
…

Diploid offspring

We track each diploid combination (*MAMA*,*MAMa*,…,*mama*)

$$(x_{11},\ x_{12},\ \dots\ x_{44})$$

EVOLUTION OF SEX



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MAMA
MAMa
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Asexual

Sexual

Diploid offspring

We track each diploid combination (*MAMA*,*MAMa*,…,*mama*)

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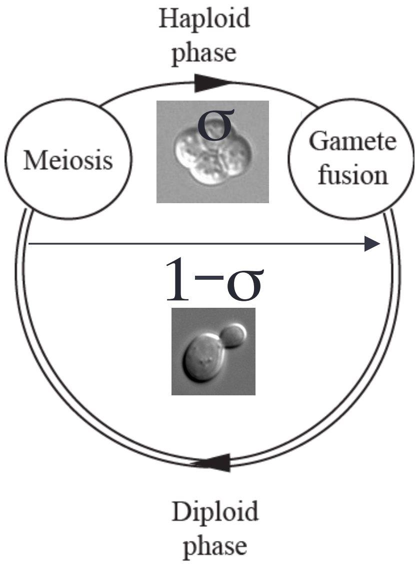
EVOLUTION OF SEX



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MAMA

MAMa

...

Asexual

Sexual

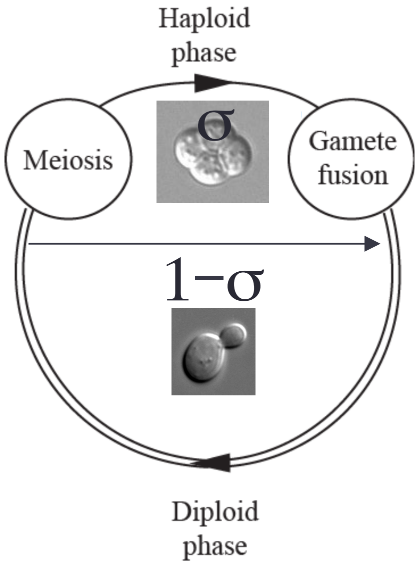
Gametes after mutation & selection

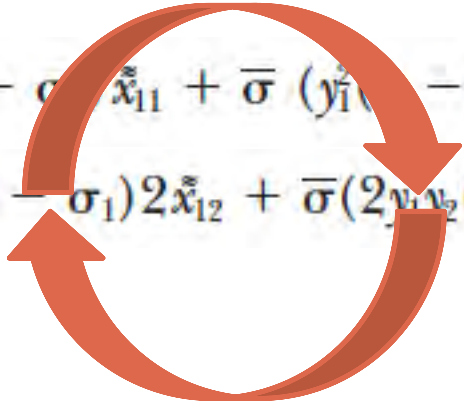
Parents after mutation & selection

We track each diploid combination (*MAMA*,*MAMa*,...,*mama*)

$(x_{11},\ x_{12},\ \ldots\ x_{44})$

EVOLUTION OF SEX





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MAMA

MAMa

…

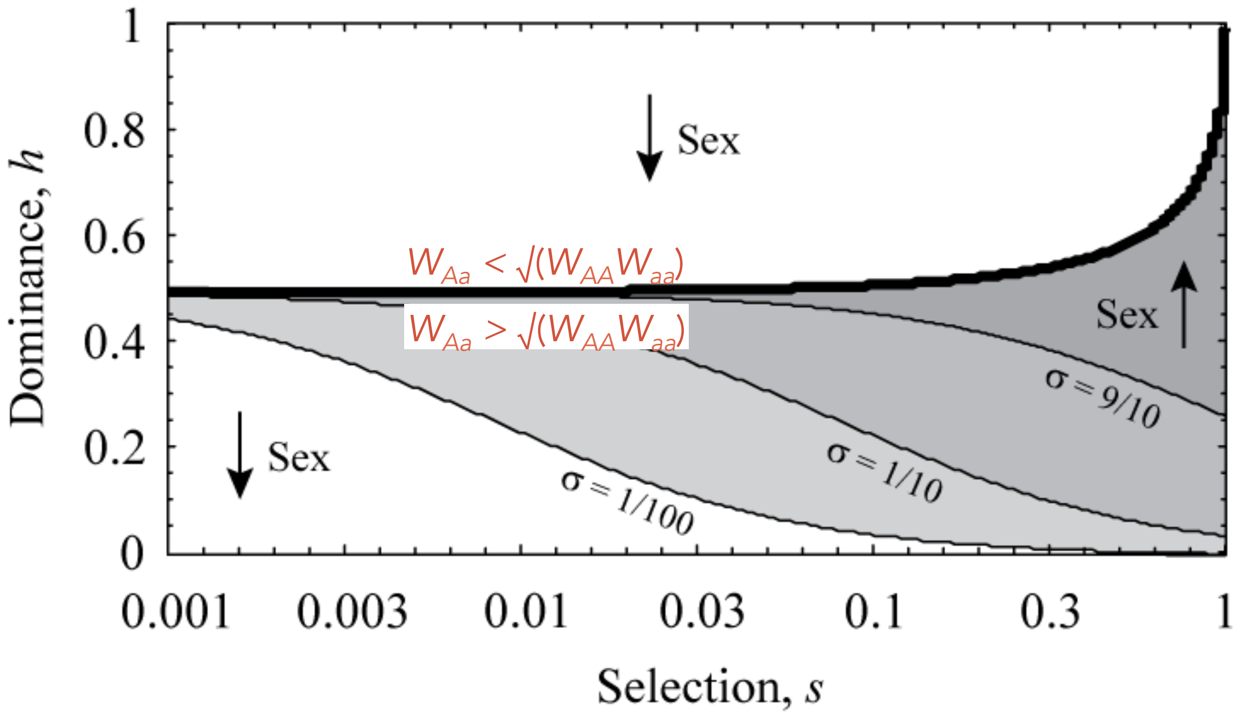
We track each diploid combination *(MAMA,MAMa,…,mama)*

$(x_{11},\ x_{12},\ \dots\ x_{44})$

➔ Determine when new modifier alleles can spread.

EVOLUTION OF SEX

Modifier promoting sexuality spreads only if $W_{Aa} > \sqrt{(W_{AA}W_{aa})}$ ***and*** sex & recombination are rare:



W_{Aa} LOW

W_{Aa} HIGH

$W_{AA} = 1$
$W_{Aa} = 1 - hs$
$W_{aa} = 1 - s$

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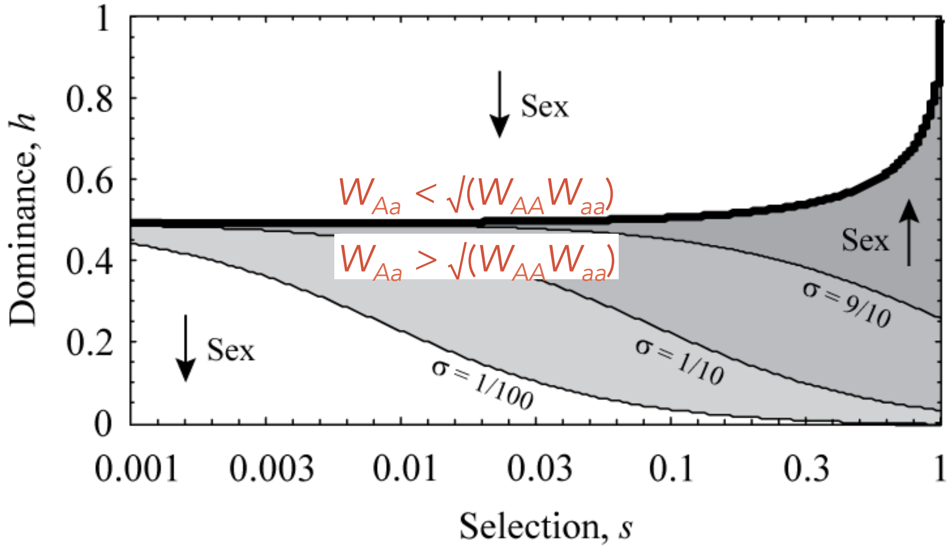
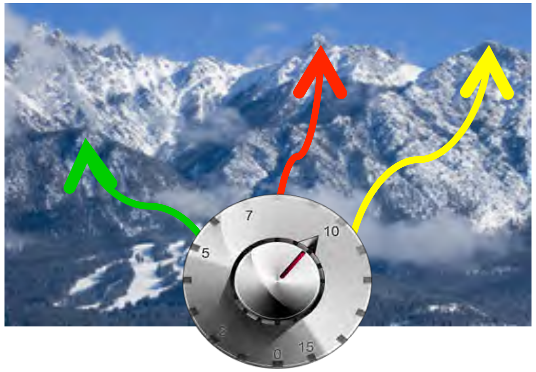
EVOLUTION OF SEX



Rate of sex/rec in population acts as a tuning parameter



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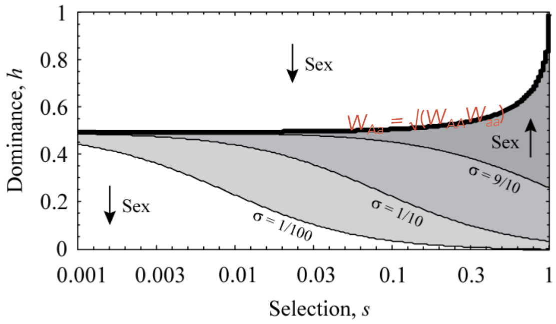
EVOLUTION OF SEX

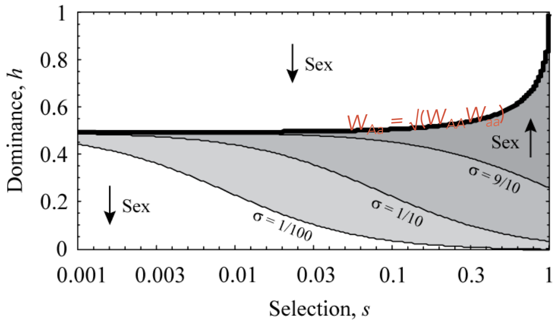
Why do the frequencies of sex and recombination matter?



EVOLUTION OF SEX

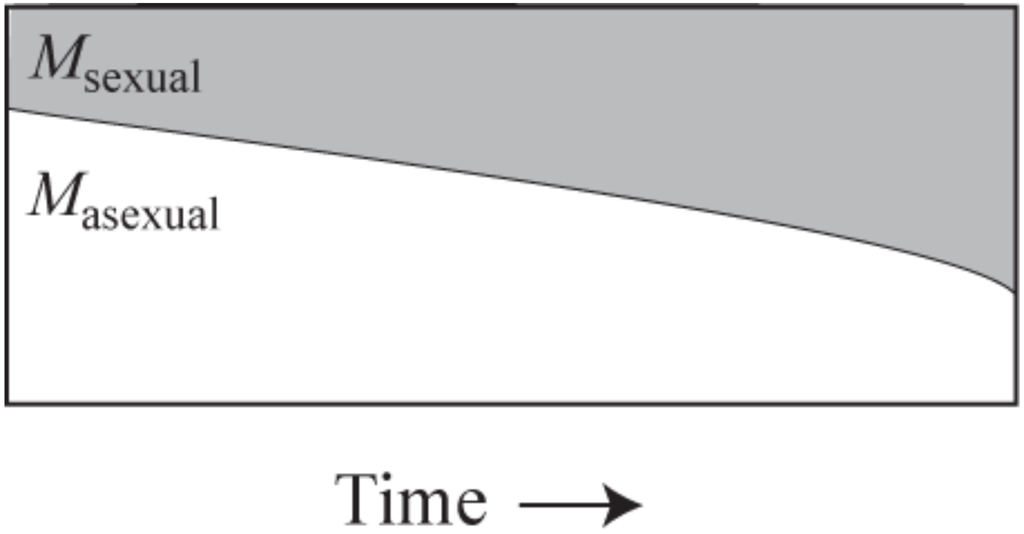
Why do the frequencies of sex and recombination matter?

The amount of genetic mixing sets
the balance between group and
individual forces acting on the modifier.

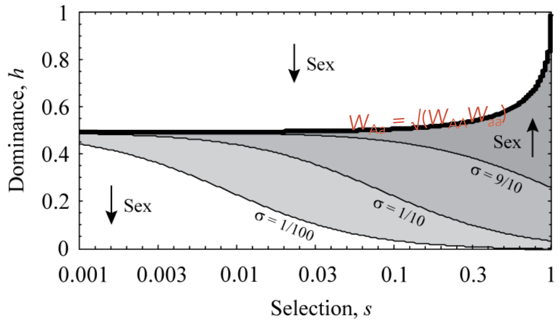


EVOLUTION OF SEX

Without much sex/rec*:



Genomes with different modifiers form almost evolutionarily separate lineages (groups).



EVOLUTION OF SEX

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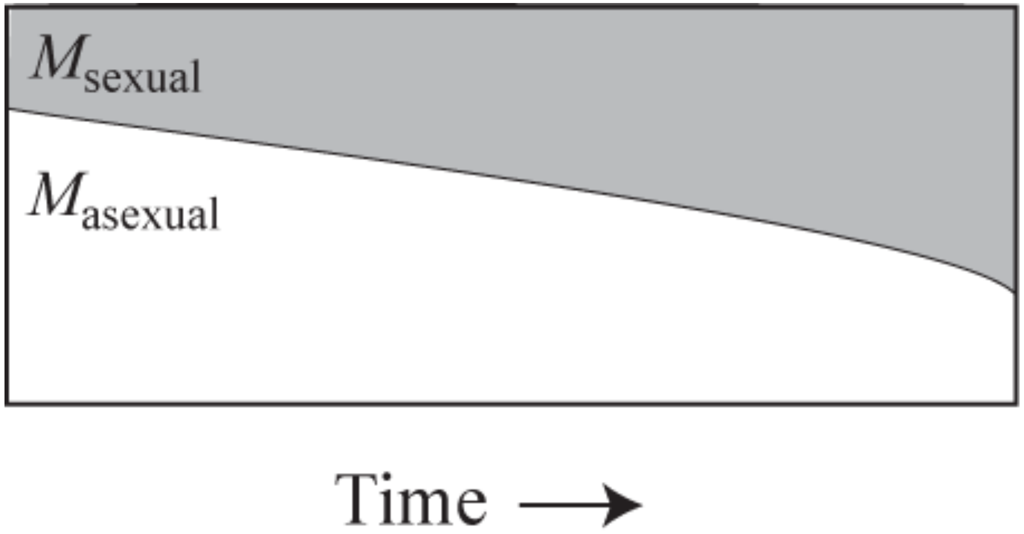
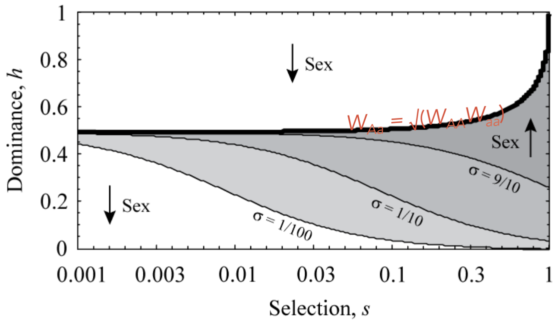


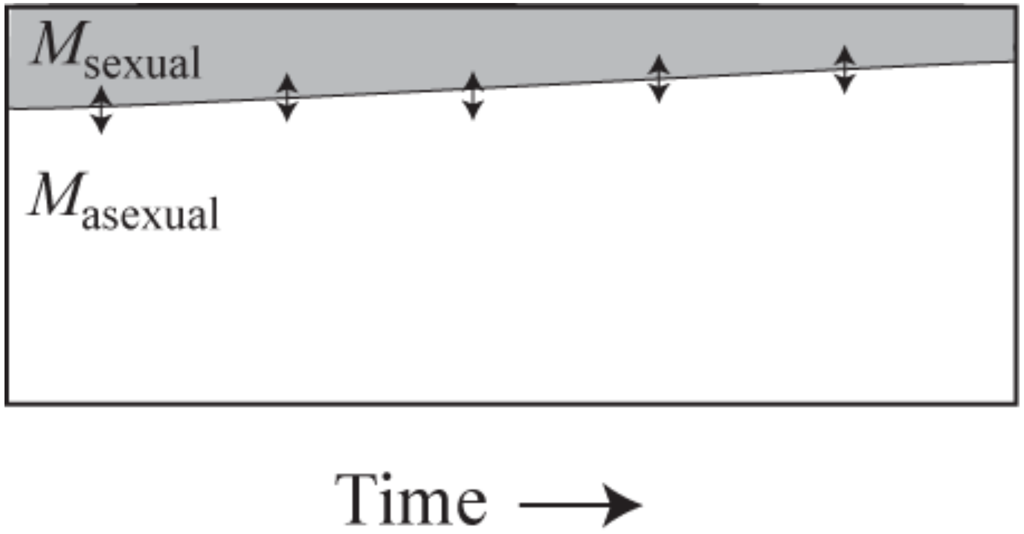
Modifiers promoting sex increase variation if $W_{Aa} > \sqrt{(W_{AA} W_{aa})}$ & become associated with a lower mutation load.

Genetic associations build & favor sex.

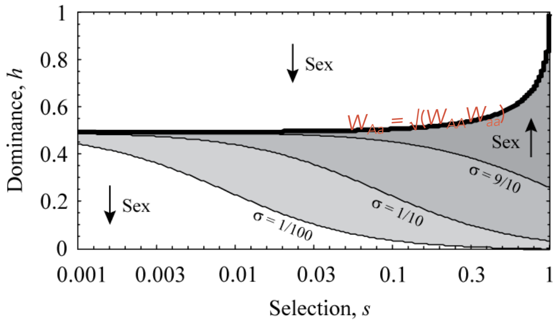


EVOLUTION OF SEX

With frequent sex/rec*:



Modifiers promoting sex share genetic variants with M_{asexual} but suffer segregation load.



EVOLUTION OF SEX

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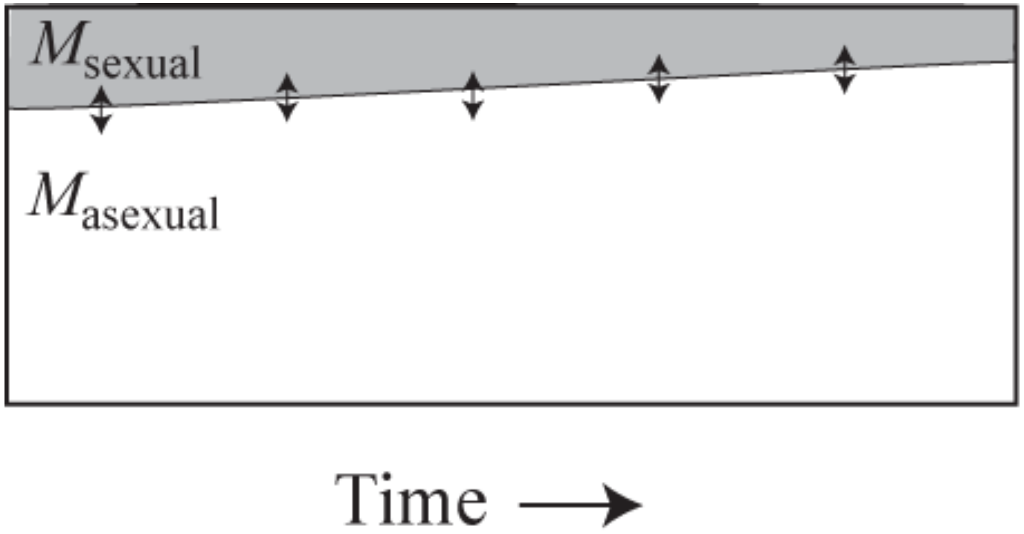
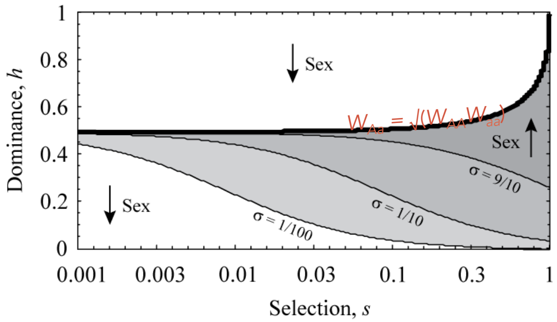


Modifiers promoting sex share genetic variants with $M_{asexual}$ but suffer segregation load.

Immediate fitness effects favor asexuality.



EVOLUTION OF SEX

Group level:

Increase variability

Individual level:

Avoid segregation

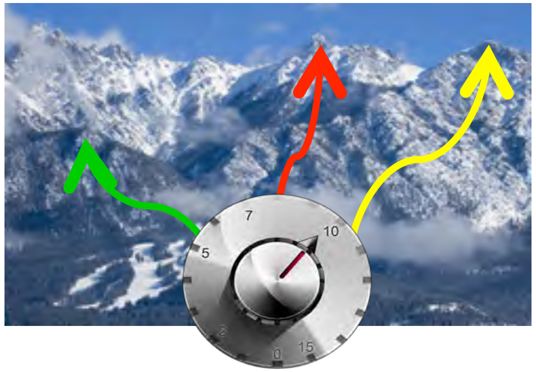
Sexuality favored: $W_{Aa}>\sqrt{(W_{AA}W_{aa})}$

Asexuality favored

Low mixing

High mixing

Genetic mixing



EVOLUTION OF SEX

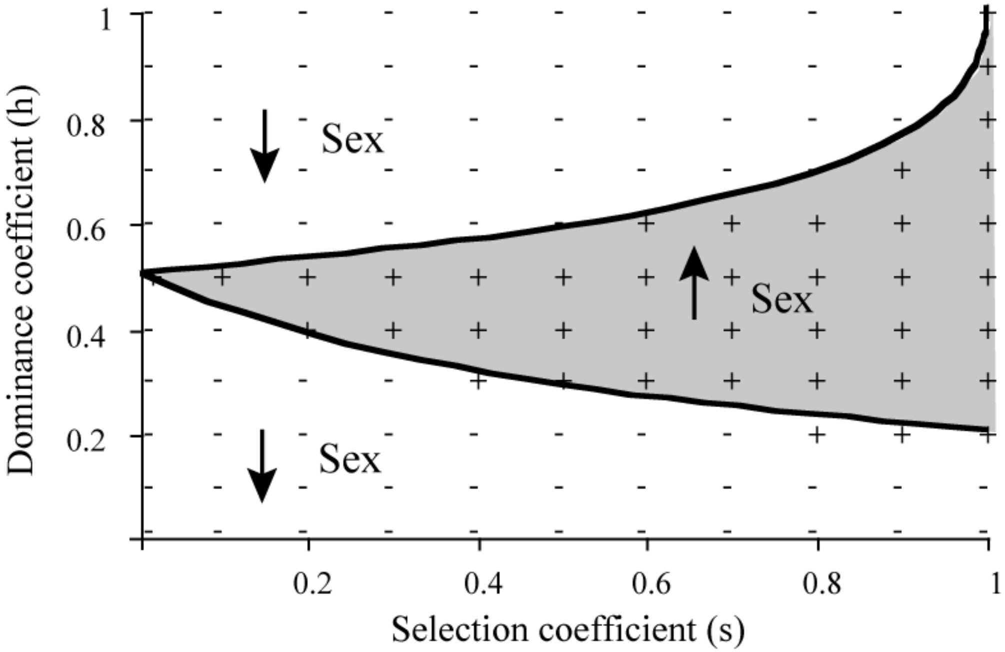
Analogous results are obtained when

- mutations are beneficial
- modifiers alter recombination rates
- drift acts (Hill-Robertson effects)

Otto 2003

Feldman et al. 1980
Barton 1995

Otto & Barton 1997
Roze & Barton 2006

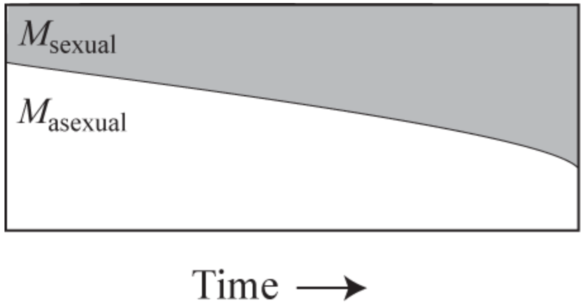


$W_{AA} = 1 + s$
$W_{Aa} = 1 + hs$
$W_{aa} = 1$

EVOLUTION OF SEX

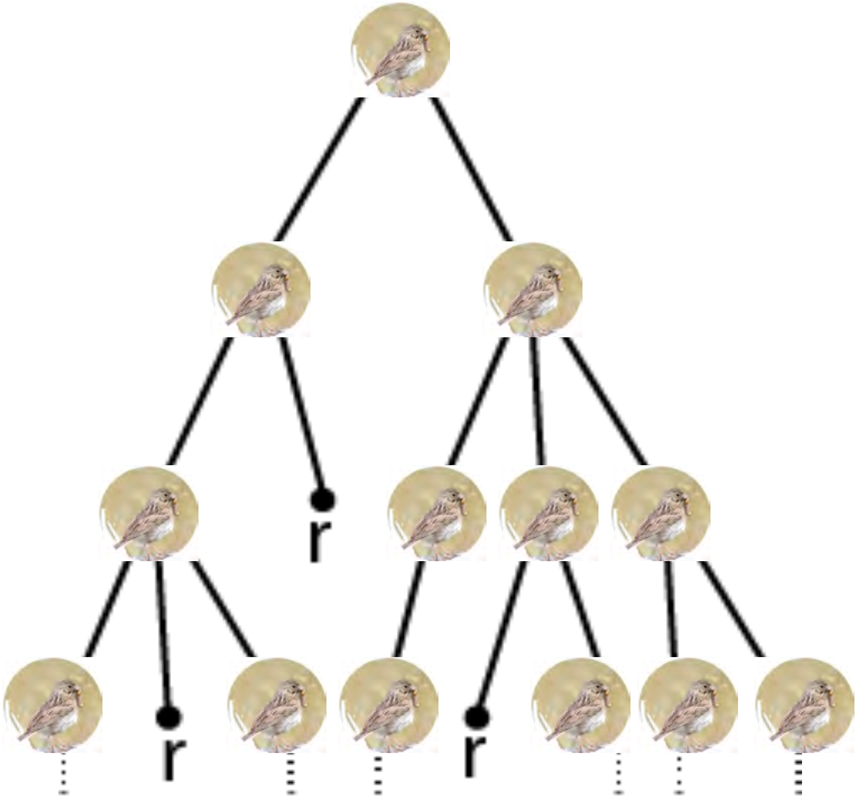
Felsenstein & Yokoyama (1976)

"in certain cases [when linkage prevents gene flow between sub-populations] there is no sharp distinction between individual selection and group selection"



EVOLUTION OF SEX

More generally, modifier models integrate **group** and **individual** selective forces.



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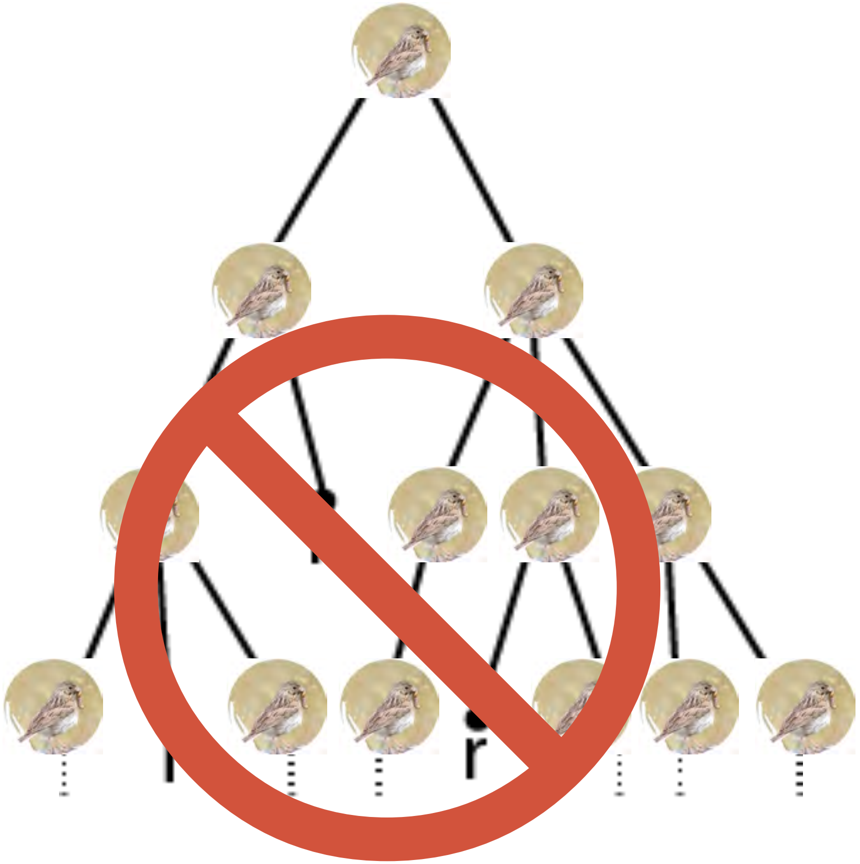


Fisher (1930)

EVOLUTION OF SEX

More generally, modifier models integrate **group** and **individual** selective forces.

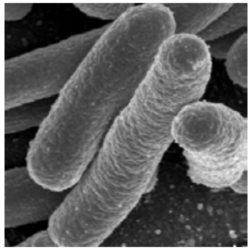
> It may be doubted if it would be possible to point to any such character, **with the possible exception…of sexuality itself**, which could be interpreted as evolved for the specific rather than for the individual advantage.
>
> Fisher (1930, p. 50)

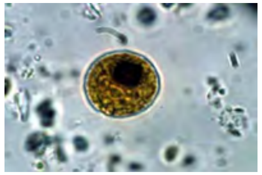
MODIFIER APPROACH

How do modifier genes evolve when there is conflict between what is best for the individual and what is best for the group?

- Evolution of sex
- Evolution of haploidy vs diploidy
- Evolution of sex chromosomes

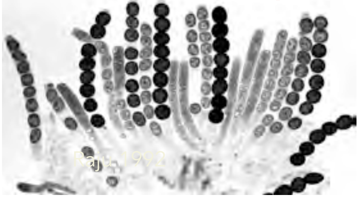
EVOLUTION OF PLOIDY





Haploid

One copy of each gene

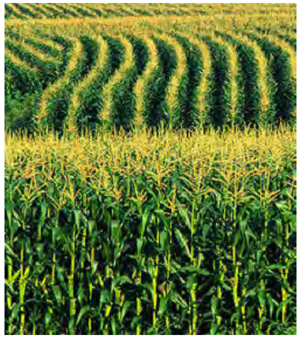


Diploid

Two copies of each gene

Polyploid

Multiple copies of each gene



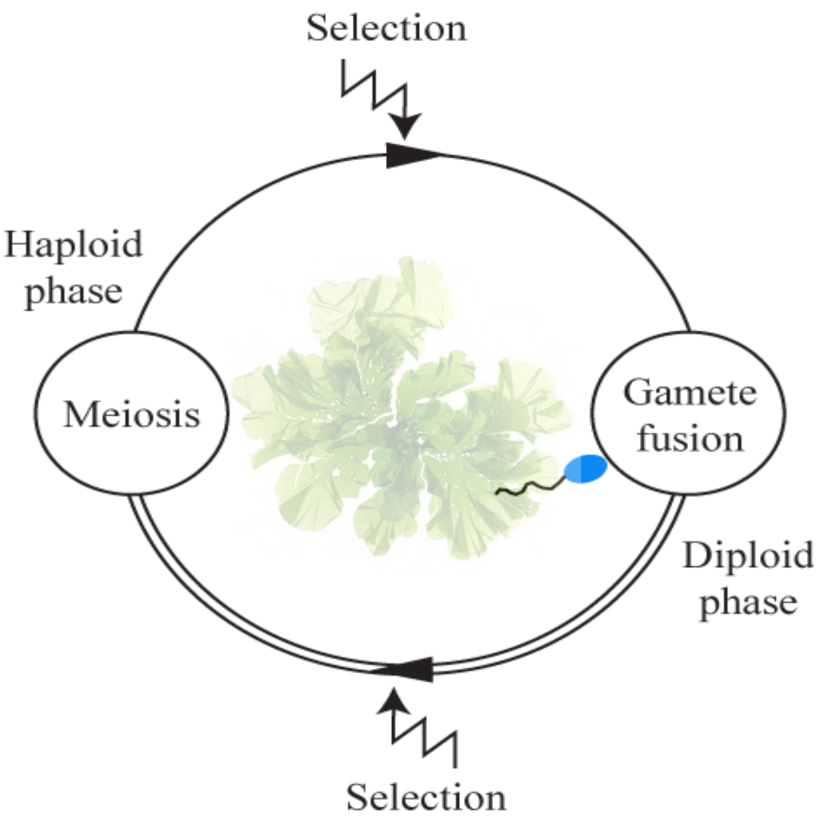
EVOLUTION OF PLOIDY

Deleterious mutations are often recessive or partially so ($h < ½$).

Can the costs & benefits of expressing mutations help explain ploidy diversity?

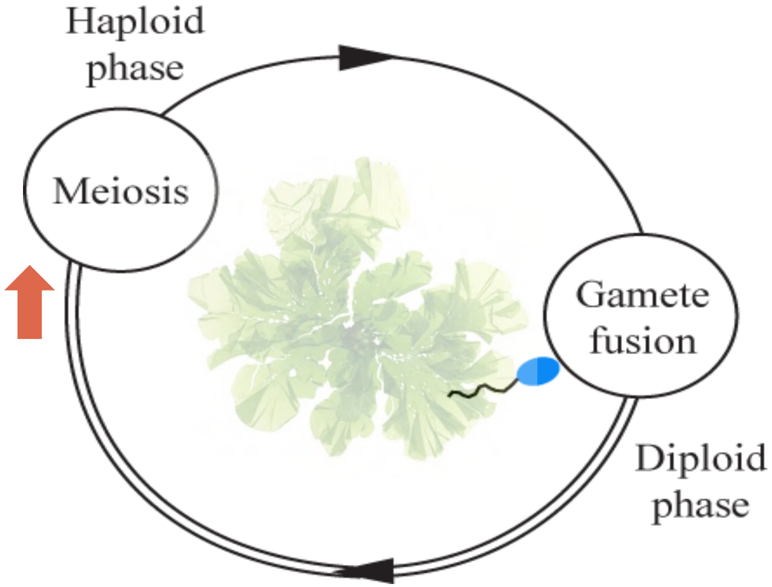
EVOLUTION OF PLOIDY

We now consider genes ("modifiers") that alter the life cycle.



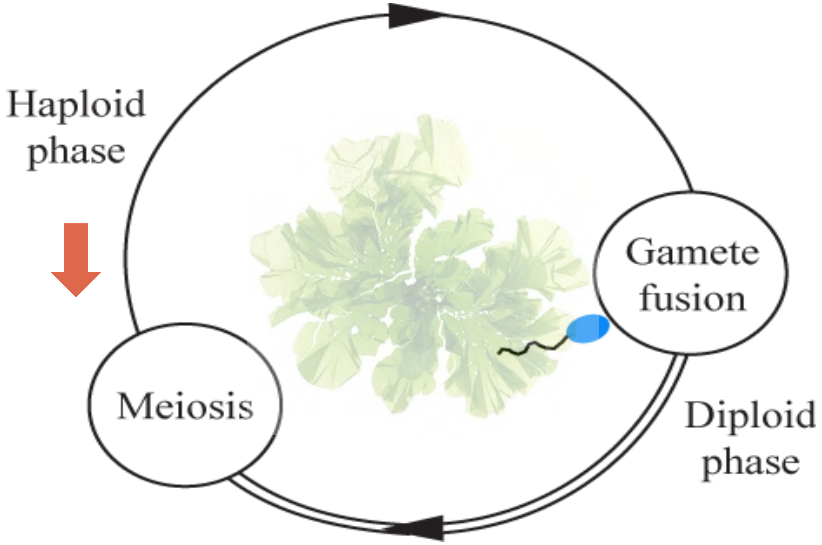
EVOLUTION OF PLOIDY

We now consider genes ("modifiers") that alter the life cycle.



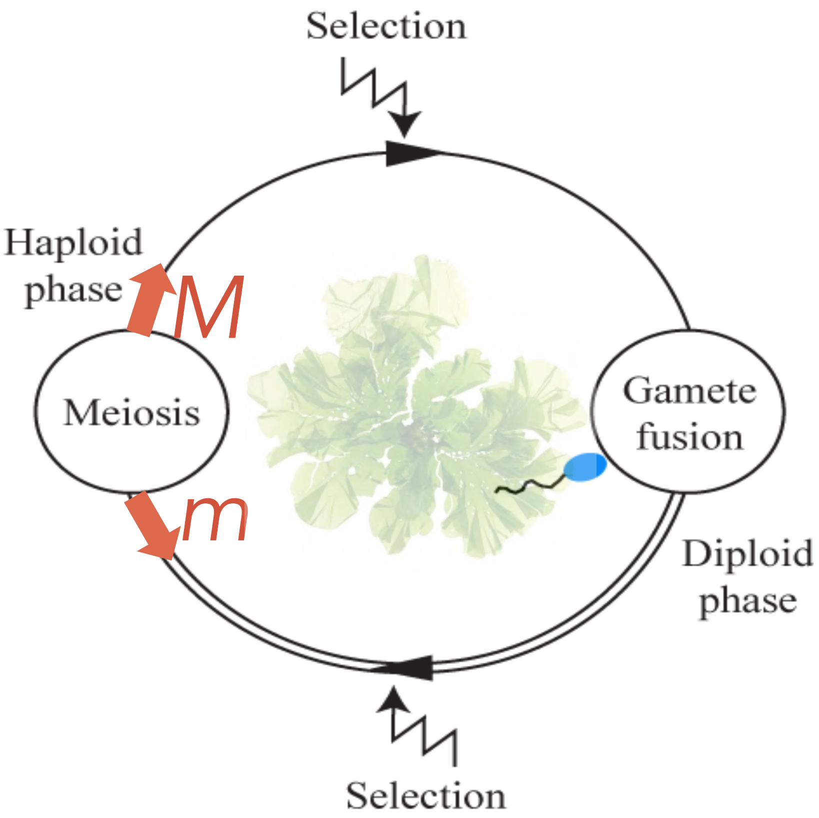
EVOLUTION OF PLOIDY

We now consider genes ("modifiers") that alter the life cycle.



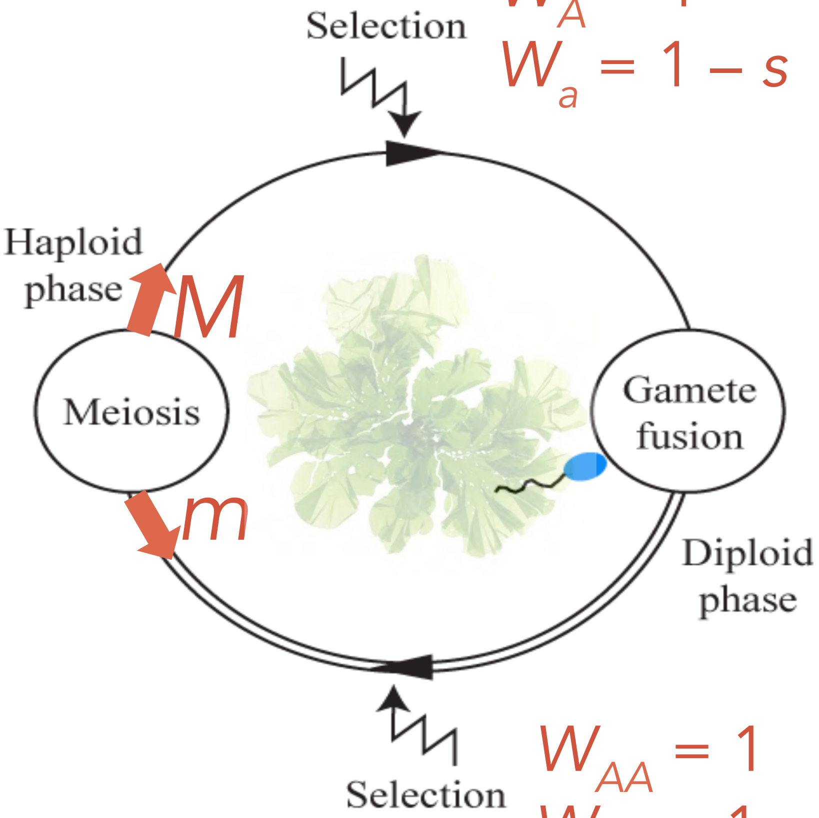
EVOLUTION OF PLOIDY

When does *M* or *m* spread?



EVOLUTION OF PLOIDY

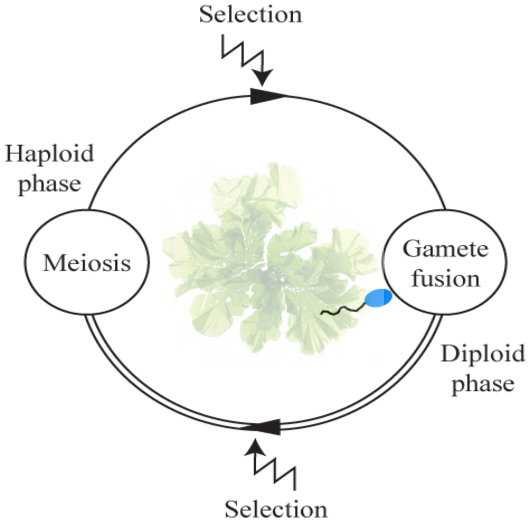
We track each chromosome combination (*MA*,*Ma*,*mA*,*ma*)



$W_A = 1$
$W_a = 1 – s$

$W_{AA} = 1$
$W_{Aa} = 1 – hs$
$W_{aa} = 1 – s$

EVOLUTION OF PLOIDY



$$
\begin{aligned}
Tx'_1 &= (1-\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1 + (1\pm hs)^{d_{11}}x_1x_2 + x_1x_3 \\
&\qquad +(1\pm hs)^{d_{12}}(1-r)x_1x_4 + (1\pm hs)^{d_{12}}rx_2x_3]
\end{aligned}
$$

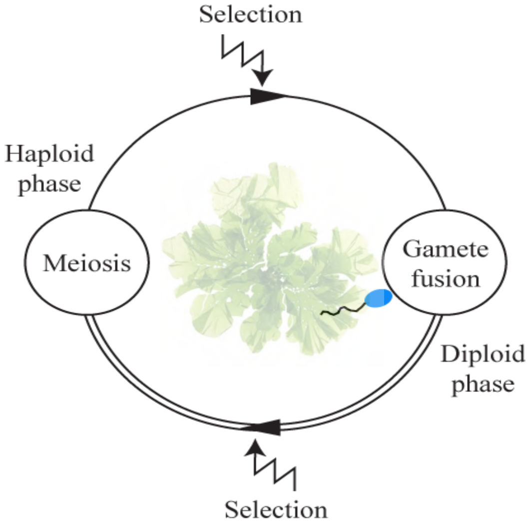
$$
\begin{aligned}
Tx'_2 &= (\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1 + (1\pm hs)^{d_{11}}x_1x_2 + x_1x_3 \\
&\qquad +(1\pm hs)^{d_{12}}(1-r)x_1x_4 + (1\pm hs)^{d_{12}}rx_2x_3] \\
&\quad +(\frac{\mu_1}{2})[(1\pm s)^{(1-d_{11})}x_1x_1 + (1\pm hs)^{d_{11}}(1\pm s)^{(1-d_{11})}x_1x_2 \\
&\qquad +(1\pm s)^{(1-d_{12})}x_1x_3 + (1\pm hs)^{d_{12}}(1\pm s)^{(1-d_{12})}(1-r)x_1x_4 \\
&\qquad +(1\pm hs)^{d_{12}}(1\pm s)^{(1-d_{12})}x x \; x]
\end{aligned}
$$

We track each chromosome combination (*MA*,*Ma*,*mA*,*ma*)

(x_1, x_2, x_3, x_4)

Haploid selection

EVOLUTION OF PLOIDY



$$
\begin{aligned}
Tx_1' &= (1-\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1 + (1\pm hs)^{d_{11}}x_1x_2 + x_1x_3 \\
&\qquad +(1\pm hs)^{d_{12}}(1-r)x_1x_4 + (1\pm hs)^{d_{12}}rx_2x_3]
\end{aligned}
$$

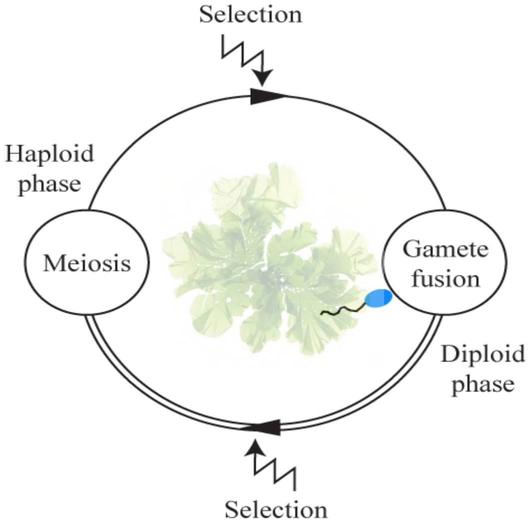
$$
\begin{aligned}
Tx_2' &= (\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1 + (1\pm hs)^{d_{11}}x_1x_2 + x_1x_3 \\
&\qquad +(1\pm hs)^{d_{12}}(1-r)x_1x_4 + (1\pm hs)^{d_{12}}rx_2x_3] \\
&\quad +(\frac{\mu_1}{2})[(1\pm s)^{(1-d_{11})}x_1x_1 + (1\pm hs)^{d_{11}}(1\pm s)^{(1-d_{11})}x_1x_2 \\
&\qquad +(1\pm s)^{(1-d_{12})}x_1x_3 + (1\pm hs)^{d_{12}}(1\pm s)^{(1-d_{12})}(1-r)x_1x_4 \\
&\qquad +(1\pm hs)^{d_{12}}(1\pm s)^{(1-d_{12})}
\end{aligned}
$$

We track each chromosome combination (*MA*,*Ma*,*mA*,*ma*)

(x_1, x_2, x_3, x_4)

Gamete fusion

EVOLUTION OF PLOIDY



$$
\begin{aligned}
Tx_1' \quad &= \quad (1-\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1 + (1 \pm hs)^{d_{11}} x_1x_2 + x_1x_3 \\
&\qquad +(1 \pm hs)^{d_{12}}(1-r)x_1x_4 + (1 \pm hs)^{d_{12}} r x_2x_3]
\end{aligned}
$$

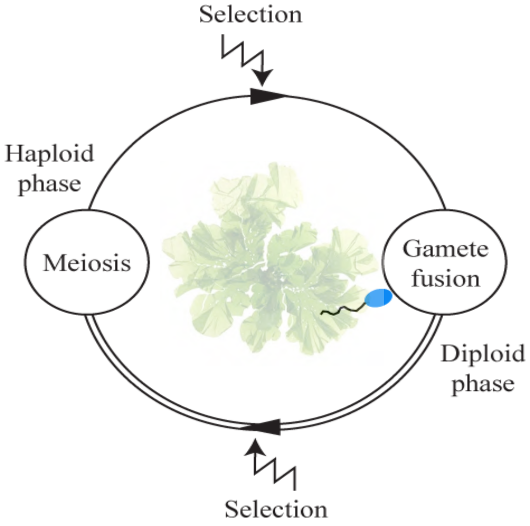
$$
\begin{aligned}
Tx_2' \quad &= \quad (\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1 + (1 \pm hs)^{d_{11}} x_1x_2 + x_1x_3 \\
&\qquad +(1 \pm hs)^{d_{12}}(1-r)x_1x_4 + (1 \pm hs)^{d_{12}} r x_2x_3] \\
&\quad +(\frac{\mu_1}{2})[(1 \pm s)^{(1-d_{11})} x_1x_1 + (1 \pm hs)^{d_{11}}(1 \pm s)^{(1-d_{11})} x_1x_2 \\
&\qquad +(1 \pm s)^{(1-d_{12})} x_1x_3 + (1 \pm hs)^{d_{12}}(1 \pm s)^{(1-d_{12})}(1-r)x_1x_4 \\
&\qquad +(1 \pm hs)^{d_{12}}(1 \pm s)^{(1-d_{12})} r x_2x_3]
\end{aligned}
$$

Diploid selection

We track each chromosome combination (*MA*,*Ma*,*mA*,*ma*)

$(x_1, \; x_2, \; x_3, \; x_4)$

EVOLUTION OF PLOIDY



$$\begin{aligned}
Tx_1' &= (1-\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1+(1\pm hs)^{d_{11}}x_1x_2+x_1x_3\\
&\qquad +(1\pm hs)^{d_{12}}(1-r)x_1x_4+(1\pm hs)^{d_{12}}rx_2x_3]
\end{aligned}$$

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Tx_2' &= (\frac{\mu_2}{2})(1-\frac{\mu_1}{2})[x_1x_1+(1\pm hs)^{d_{11}}x_1x_2+x_1x_3\\
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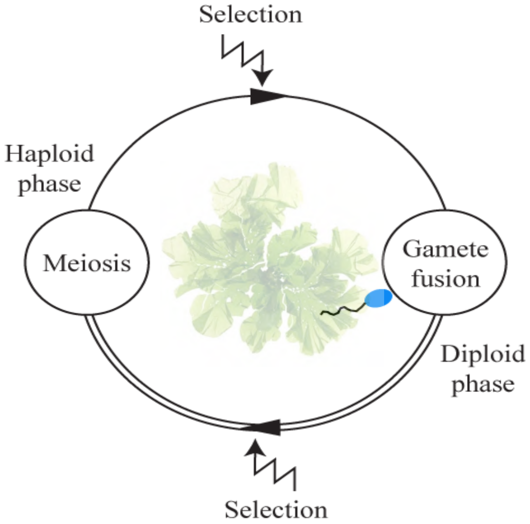
&\qquad +(1\pm s)^{(1-d_{12})}x_1x_3+(1\pm hs)^{d_{12}}(1\pm s)^{(1-d_{12})}(1-r)x_1x_4\\
&\qquad +(1\pm hs)^{d_{12}}(1\pm s)^{(1-d_{12})}
\end{aligned}$$

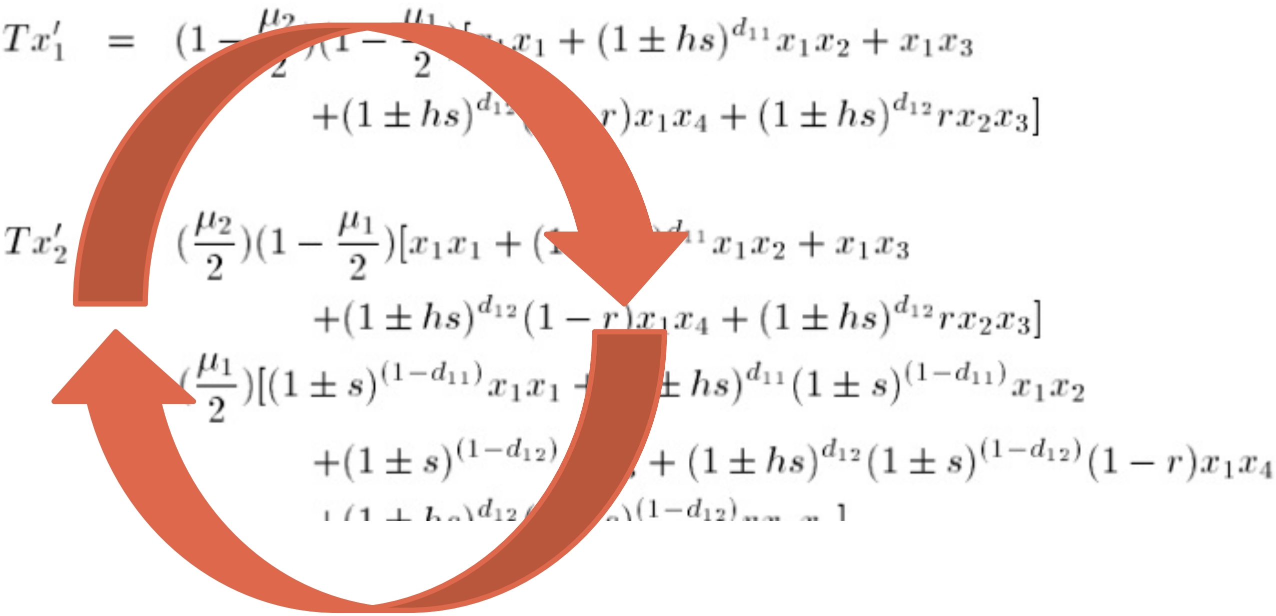
We track each chromosome combination (*MA*,*Ma*,*mA*,*ma*)

(x_1, x_2, x_3, x_4)

Meiosis

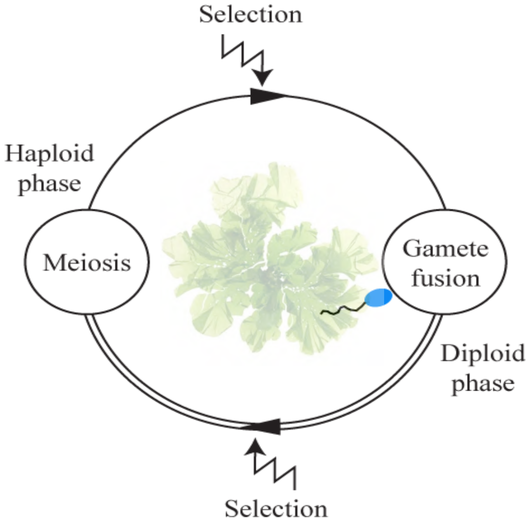
EVOLUTION OF PLOIDY

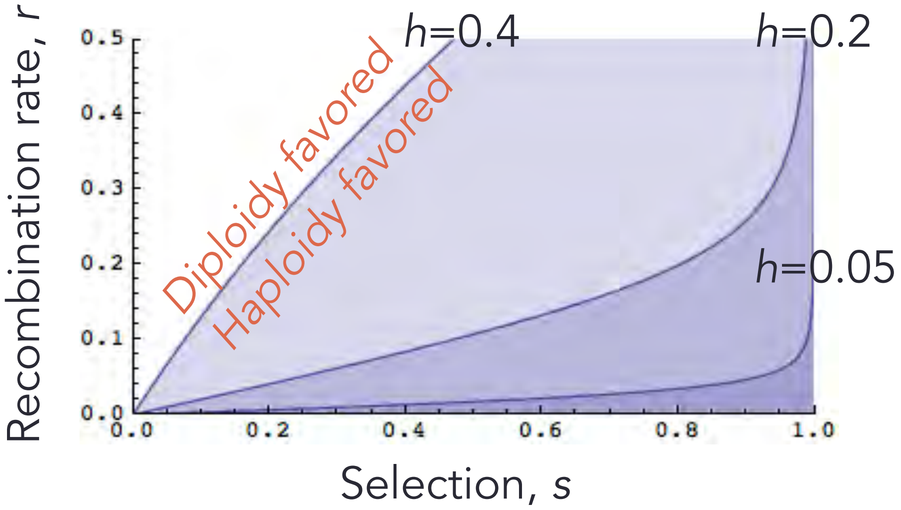




- ➔ Determine when new modifier alleles can spread.

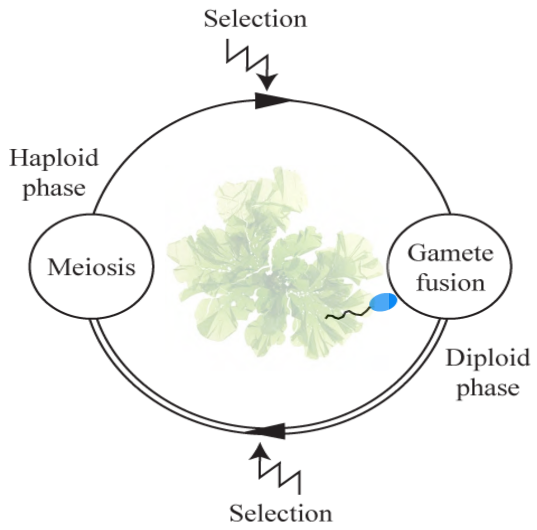
EVOLUTION OF PLOIDY

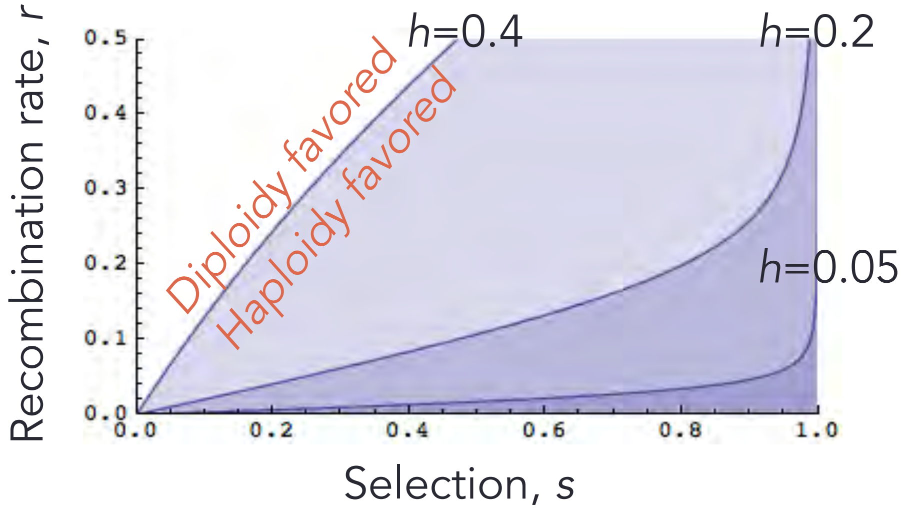




Otto & Goldstein (1992)
Otto & Marks (1996)
Otto & Gerstein (2008)

EVOLUTION OF PLOIDY



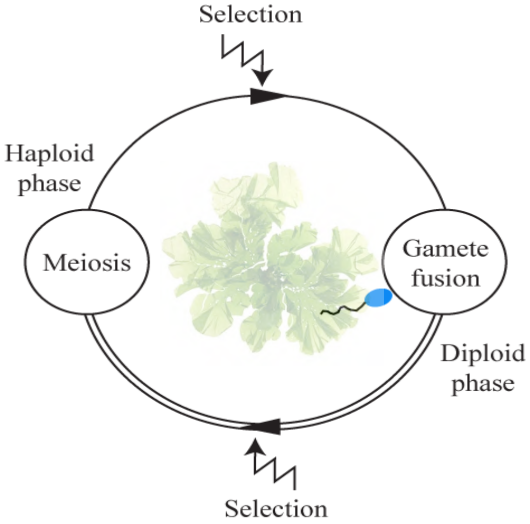


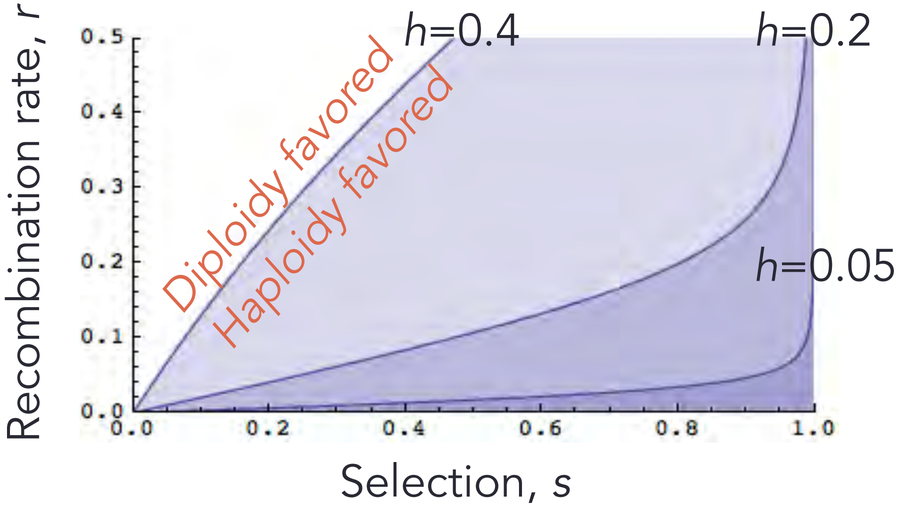
Haploid life cycles favored when organisms are primarily asexual, tend to mate with relatives, or have low rates of recombination.

Diploid life cycles favored when exchange is common.

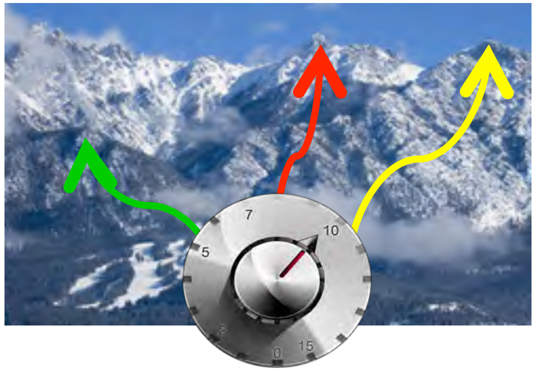
Otto & Goldstein (1992)
Otto & Marks (1996)
Otto & Gerstein (2008)

EVOLUTION OF PLOIDY





Rate of sex/rec in population again acts as a tuning parameter



Otto & Goldstein (1992)
Otto & Marks (1996)
Otto & Gerstein (2008)

EVOLUTION OF PLOIDY

The amount of genetic mixing sets the balance between group and individual forces acting on the modifier.

EVOLUTION OF PLOIDY

Group level: Selection is more efficient when mutations are fully revealed in haploids.

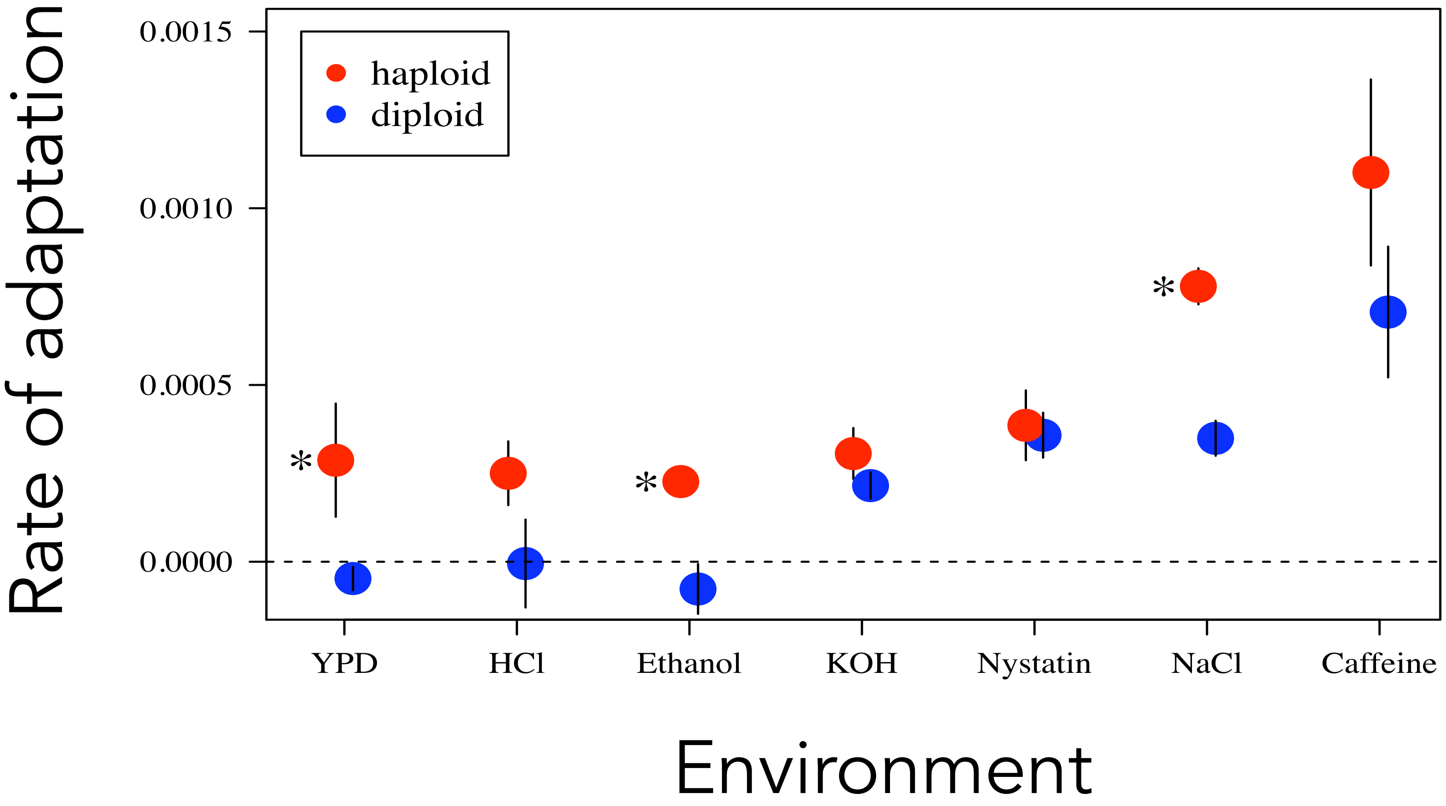
Misako Inaoka, *Green-pin Bird*

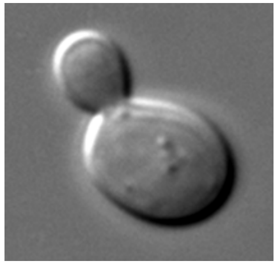
Haploidy always favored

Haploid load = μ Diploid load = 2μ

EVOLUTION OF PLOIDY

Example: Selection purges deleterious alleles and hastens the spread of beneficial alleles more rapidly in haploid yeast





Gerstein et al. (2011)

EVOLUTION OF PLOIDY

Individual level: Any individual is better off as a diploid if it can mask deleterious mutations.

Diploidy favored if $h < 1/2$

EVOLUTION OF PLOIDY

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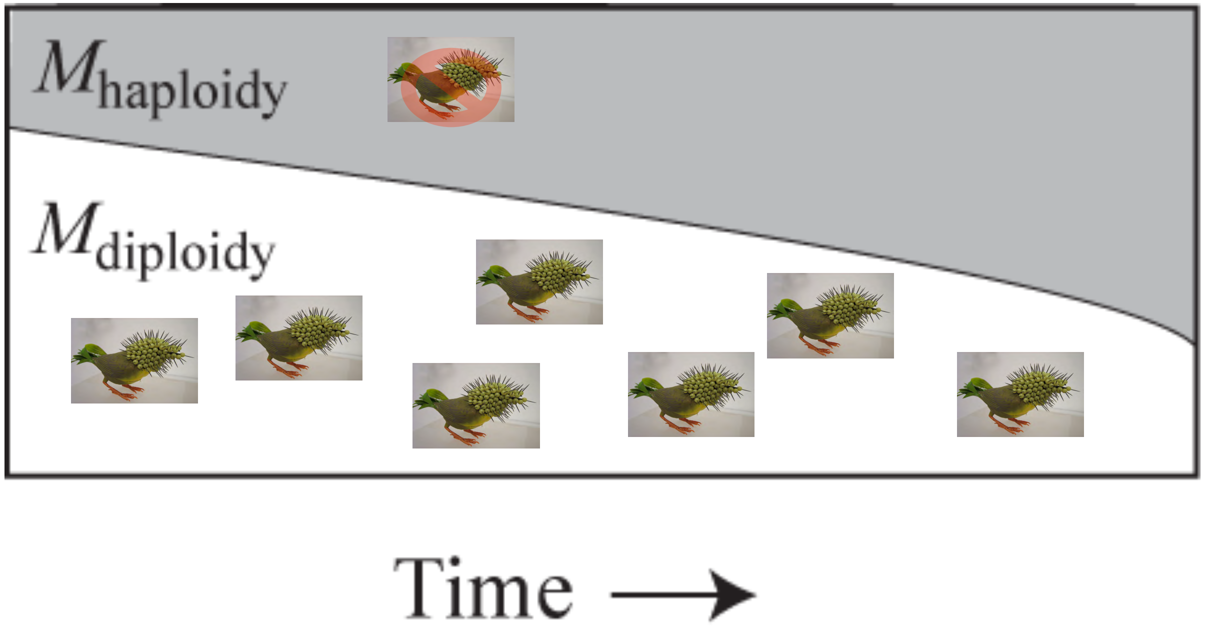
Diploidy favored if $h < 1/2$

EVOLUTION OF PLOIDY

With little genetic mixing:

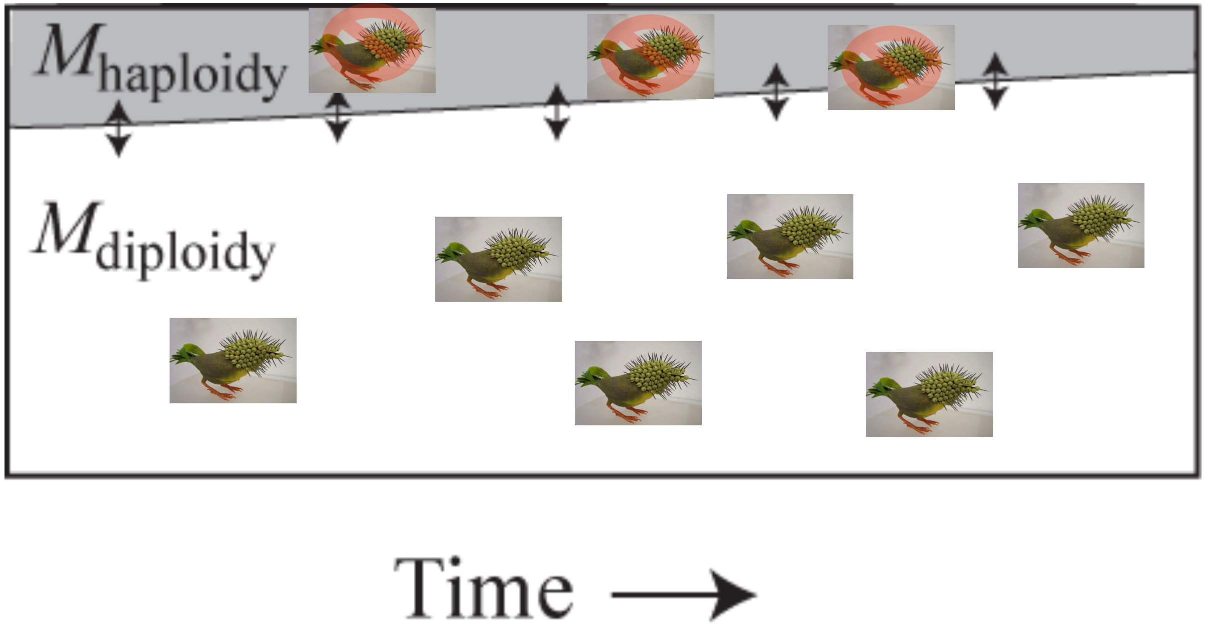


Genes promoting haploidy purge deleterious mutations, producing more fit lineages.

Haploidy favored

EVOLUTION OF PLOIDY

With frequent genetic mixing:



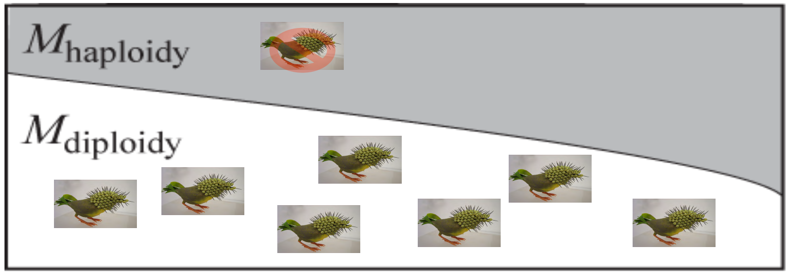
Mutations are largely masked in diploids but passed onto and exposed in haploids.

Diploidy favored

EVOLUTION OF PLOIDY

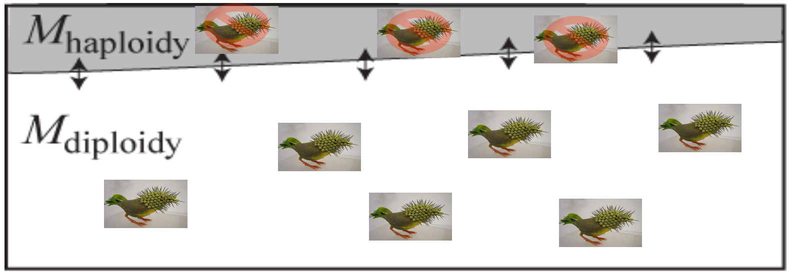
Group level: Purging

Low mixing ➔ *Haploidy*



Individual level: Masking

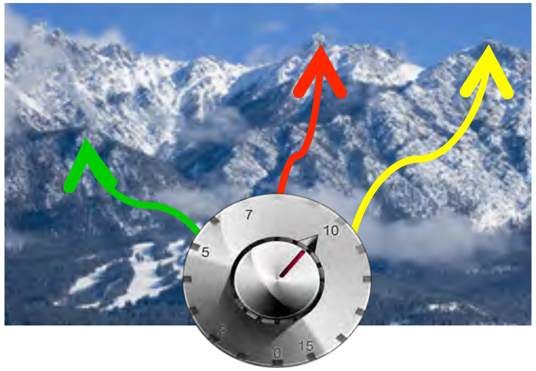
High mixing ➔ *Diploidy*



Low mixing

High mixing

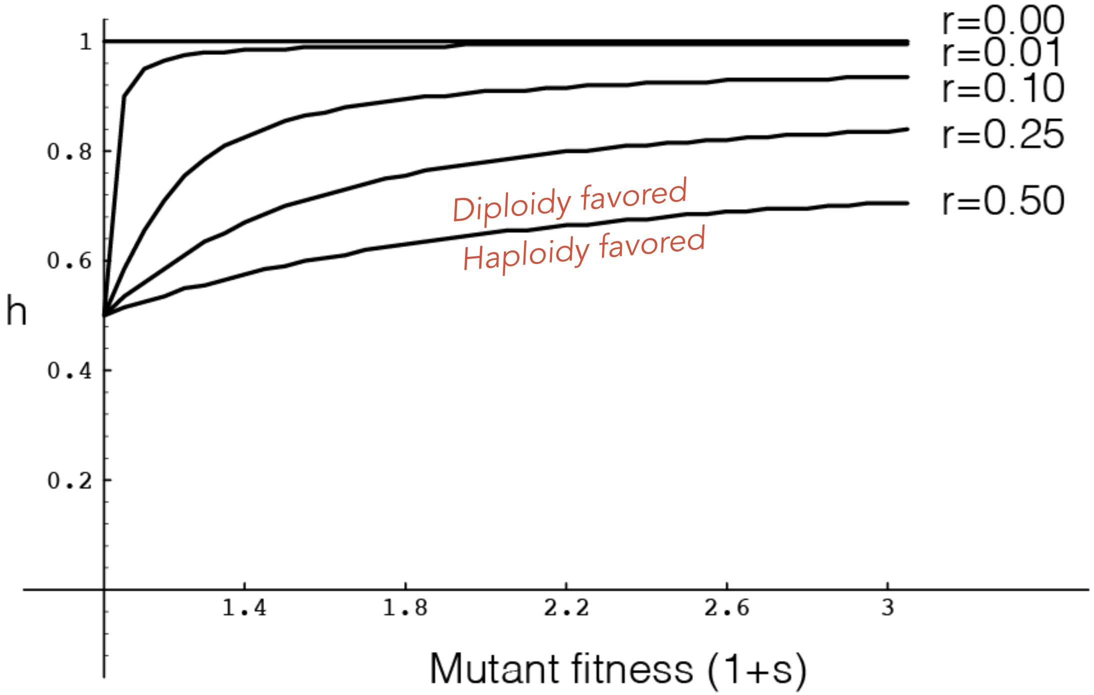
Genetic mixing



EVOLUTION OF PLOIDY

Analogous results are obtained when

- mutations are beneficial — Otto 1994
- haploids & diploids have intrinsic differences — Scott & Rescan 2017



$$W_{AA} = 1 + s$$
$$W_{Aa} = 1 + hs$$
$$W_{aa} = 1$$

MODIFIER APPROACH

How do modifier genes evolve when there is conflict between what is best for the individual and what is best for the group?

- Evolution of sex
- Evolution of haploidy vs diploidy
- Evolution of sex chromosomes

EVOLUTION OF SEX CHROMOSOMES

One of the first modifier models explored the tendency for recombination to decrease between two sex determining genes on a sex chromosome.

- Nei 1969

EVOLUTION OF SEX CHROMOSOMES

The force favoring linkage – selection against intersexes – is an example of *epistasis* creating a strong **recombination load**.

EVOLUTION OF SEX CHROMOSOMES

More generally, when different alleles benefit males and females ("sexually antagonistic selection"), tighter linkage is favored between that locus and the sex determining region.

Fisher 1931, Rice 1987,
Charlesworth & Charlesworth 1980,
Lenormand 2003

EVOLUTION OF SEX CHROMOSOMES

Group level: Tight linkage keeps alleles that work well together in male and female descendants.

Tighter linkage favored

EVOLUTION OF SEX CHROMOSOMES

Group level: Tight linkage keeps alleles that work well together in male and female descendants.

Tighter linkage favored

Individual level: Tight linkage keeps alleles that work well together in offspring.

Tighter linkage favored

EVOLUTION OF SEX CHROMOSOMES

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EVOLUTION OF SEX CHROMOSOMES

But is the loss of recombination on sex chromosomes inevitable?

EVOLUTION OF SEX CHROMOSOMES

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Theoretically: No

Modifier models indicate that increased recombination can sometimes be favored.

Otto 2014
Scott et al. (in prep)

EVOLUTION OF SEX CHROMOSOMES

But is the loss of recombination on sex chromosomes inevitable?

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Modifier models indicate that increased recombination can sometimes be favored.

What??

Otto 2014
Scott et al. (in prep)

EVOLUTION OF SEX CHROMOSOMES

Step back:

While we focus on male and female individuals, these do not breed true.

EVOLUTION OF SEX CHROMOSOMES

Step back:

While we focus on male and female individuals, these do not breed true.

Consider instead the chromosomes:

- X in females
- X in males
- Y

The sexual three-some

EVOLUTION OF SEX CHROMOSOMES

With some forms of selection, the allele that is beneficial in females ("a") can also be favored on the Y.

- X in females: a↑
- X in males: a↓
- Y in males: a↑

(Overdominance in males or sexually antagonistic selection with the female-beneficial allele also favored in pollen/sperm.)

EVOLUTION OF SEX CHROMOSOMES

With some forms of selection, the allele that is beneficial in females ("a") can also be favored on the Y.

- X in females: a↑
- X in males: a↓
- Y in males: a↑

When the same allele is favored in females and on the Y, fathers that recombine produce fitter daughters.

Unlinked modifier

$F_{AA} = 0.75$

$F_{Aa} = 1$

$F_{aa} = 0.75$

1

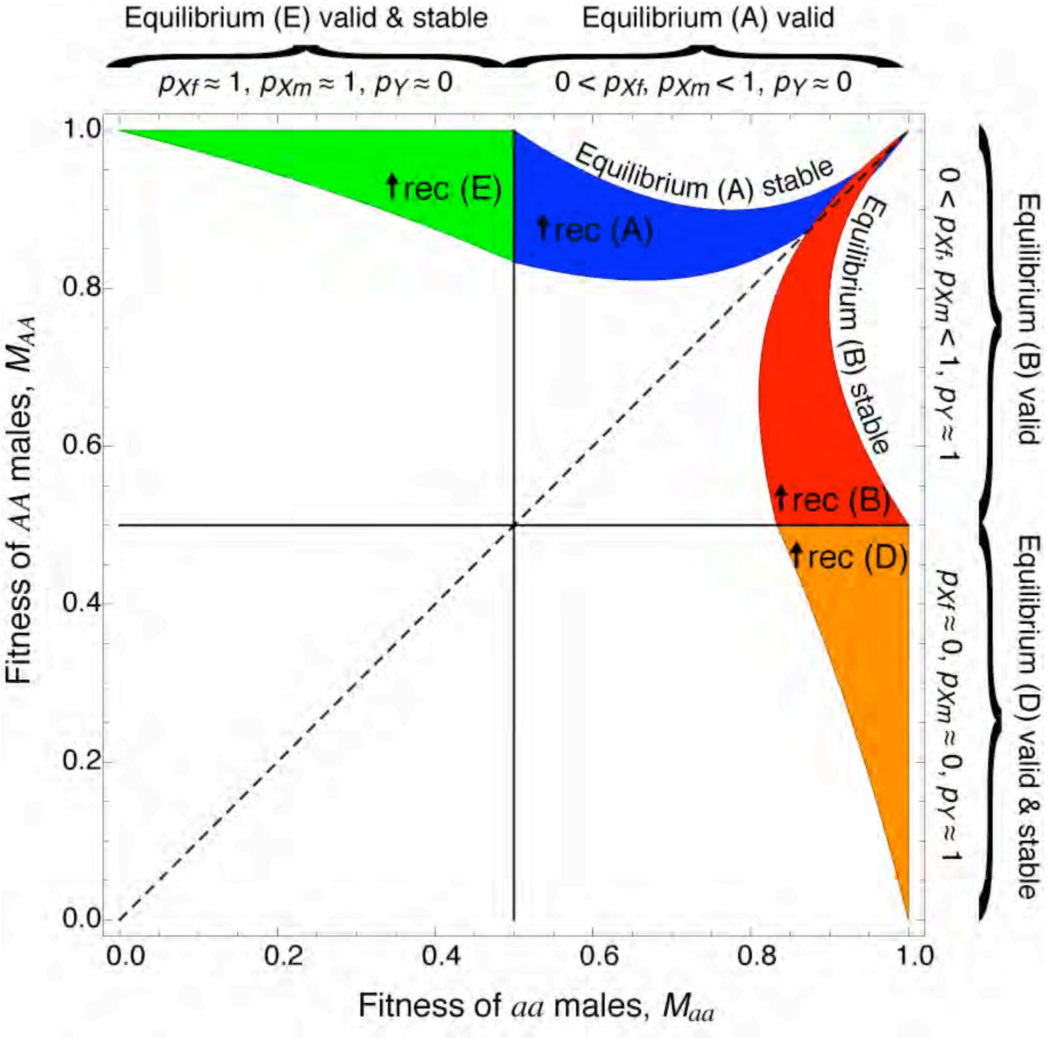
1

0

$$\frac{1+M_{aa}-2F_{aa}M_{aa}}{2\left(1+M_{aa}-F_{AA}-F_{aa}M_{aa}\right)}$$

$$\frac{1+M_{aa}-2F_{aa}M_{aa}}{\left(1+M_{aa}\right)^2-2\left(F_{aa}+F_{AA}\right)M_{aa}}$$

0



$$\frac{1+M_{AA}-2F_{aa}}{2\left(1+M_{AA}-F_{aa}-F_{AA}M_{AA}\right)}$$

$$\frac{M_{AA}+M_{AA}^2-2F_{aa}M_{AA}}{\left(1+M_{AA}\right)^2-2\left(F_{aa}+F_{AA}\right)M_{AA}}$$

1

0

0

1

Unlinked modifier

$F_{AA} = 0.75$

$F_{Aa} = 1$

$F_{aa} = 0.75$

1

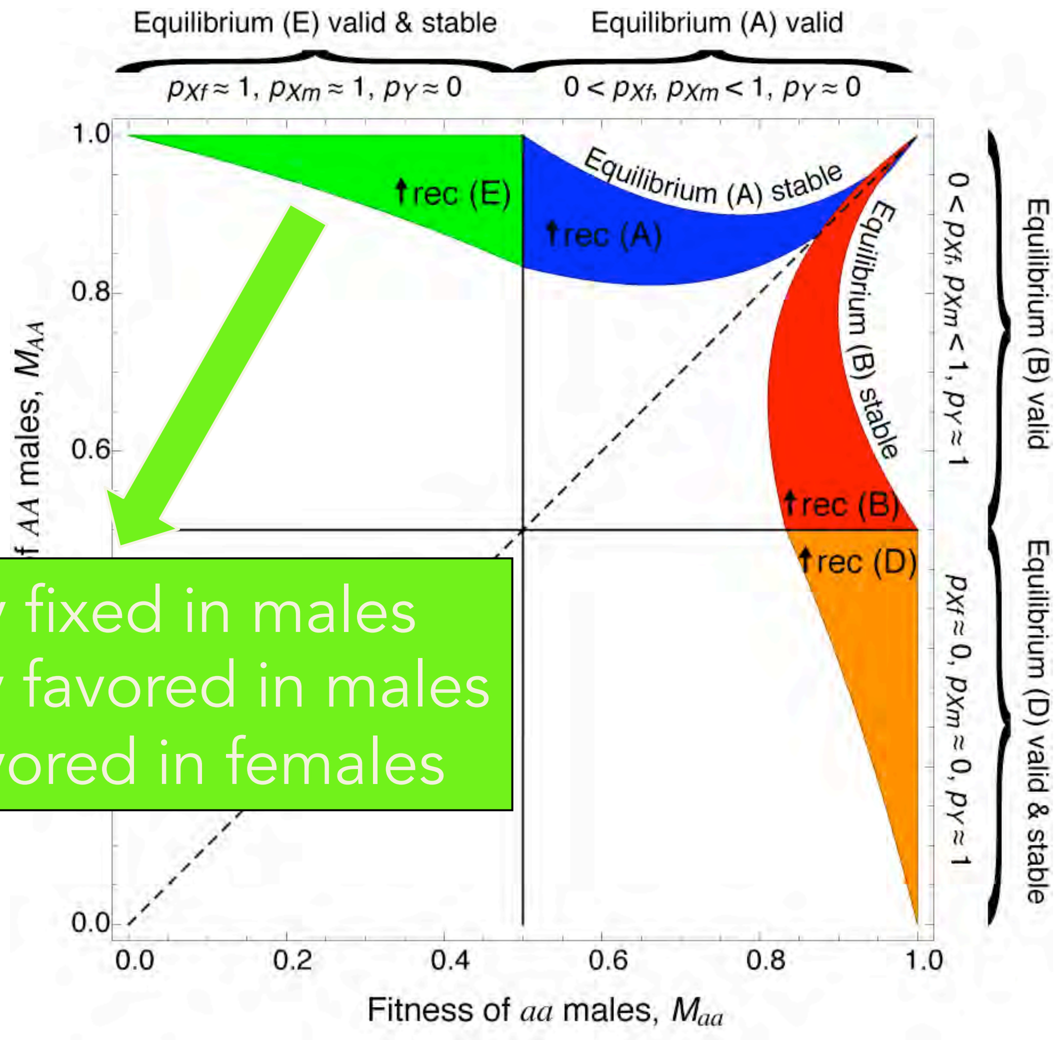
1

0

$$\frac{1+M_{aa}-2F_{aa}M_{aa}}{2\left(1+M_{aa}-F_{AA}-F_{aa}M_{aa}\right)}$$

$$\frac{1+M_{aa}-2F_{aa}M_{aa}}{\left(1+M_{aa}\right)^2-2\left(F_{aa}+F_{AA}\right)M_{aa}}$$

$$0$$



$$\frac{1+M_{AA}-2F_{aa}}{2\left(1+M_{AA}-F_{aa}-F_{AA}M_{AA}\right)}$$

$$\frac{M_{AA}+M_{AA}^2-2F_{aa}M_{AA}}{\left(1+M_{AA}\right)^2-2\left(F_{aa}+F_{AA}\right)M_{AA}}$$

$$1$$

0

0

1

*Y*a nearly fixed in males
X*A* strongly favored in males
but X*a* favored in females

EVOLUTION OF SEX CHROMOSOMES

Group level: Tight linkage keeps alleles that work well together in male and female descendants.

Individual level: Tight linkage keeps alleles that work well together in offspring.

Tighter linkage favored

Tighter linkage favored

EVOLUTION OF SEX CHROMOSOMES

Group level: Tight linkage keeps alleles that work well together in male and female descendants.

Individual level: Looser linkage allows fathers to produce fitter daughters.

Tighter linkage favored

Looser linkage favored

EVOLUTION OF SEX CHROMOSOMES

Group level: Specialization

♀ beneficial alleles with X
♂ beneficial alleles with Y

Tight linkage favored

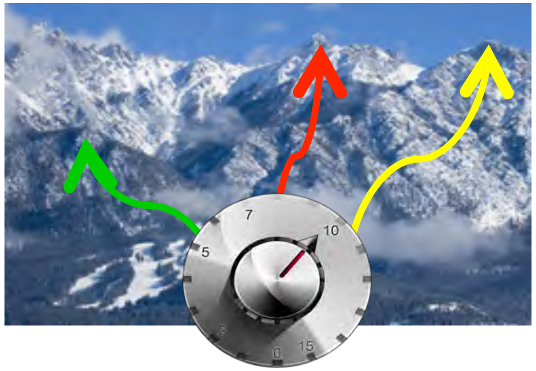
Chromosome level: Sharing

♀ beneficial alleles from Y to X

Recombination favored

Tightly
Linked
modifier

Loosely
Linked
modifier



EVOLUTION OF SEX CHROMOSOMES

<u>Group level</u>: Specialization

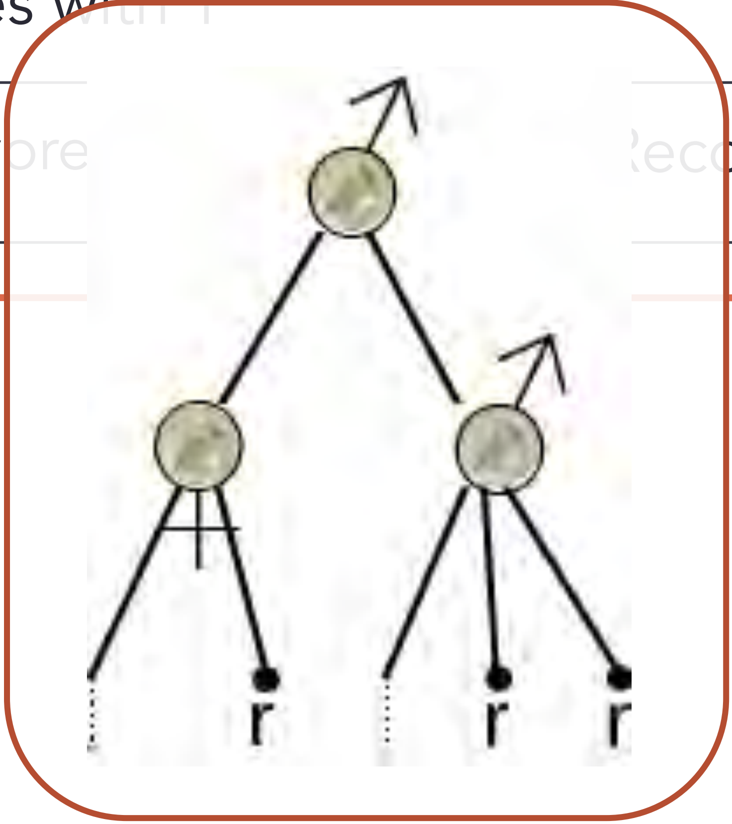
♀ beneficial alleles with X
♂ beneficial alleles with Y

<u>Chromosome level</u>: Sharing

♀ beneficial alleles from Y to X

Tight linkage favore

Recombination favored



Tightly Linked modifier

Loosely Linked modifier

MODIFIER THEORY

Modifier models ⟷ Levels of selection

Balance

Insight

Inspiration

Simplification

MODIFIER THEORY

SOCIETY *for the* STUDY *of* EVOLUTION

Mutation rate: Fidelity vs responsiveness [Gillespie 1981]

Epigenetics: Mutability vs stability [Furrow & Feldman 2005]

Migration: Local adaptation vs kin competition [Billiard & Lenormand 2005]

Mating system: Inbreeding vs outbreeding depression [Epinat & Lenormand 2009]

Phenotypic canalization: Responsiveness vs stability [Kawecki 2000]

Mating preferences: Natural vs sexual selection [Kirkpatrick 1982]

Species boundaries: Conspecific vs heterospecific matings [Banks et al. 2012]

Summary

Modifier models shift our perspective…

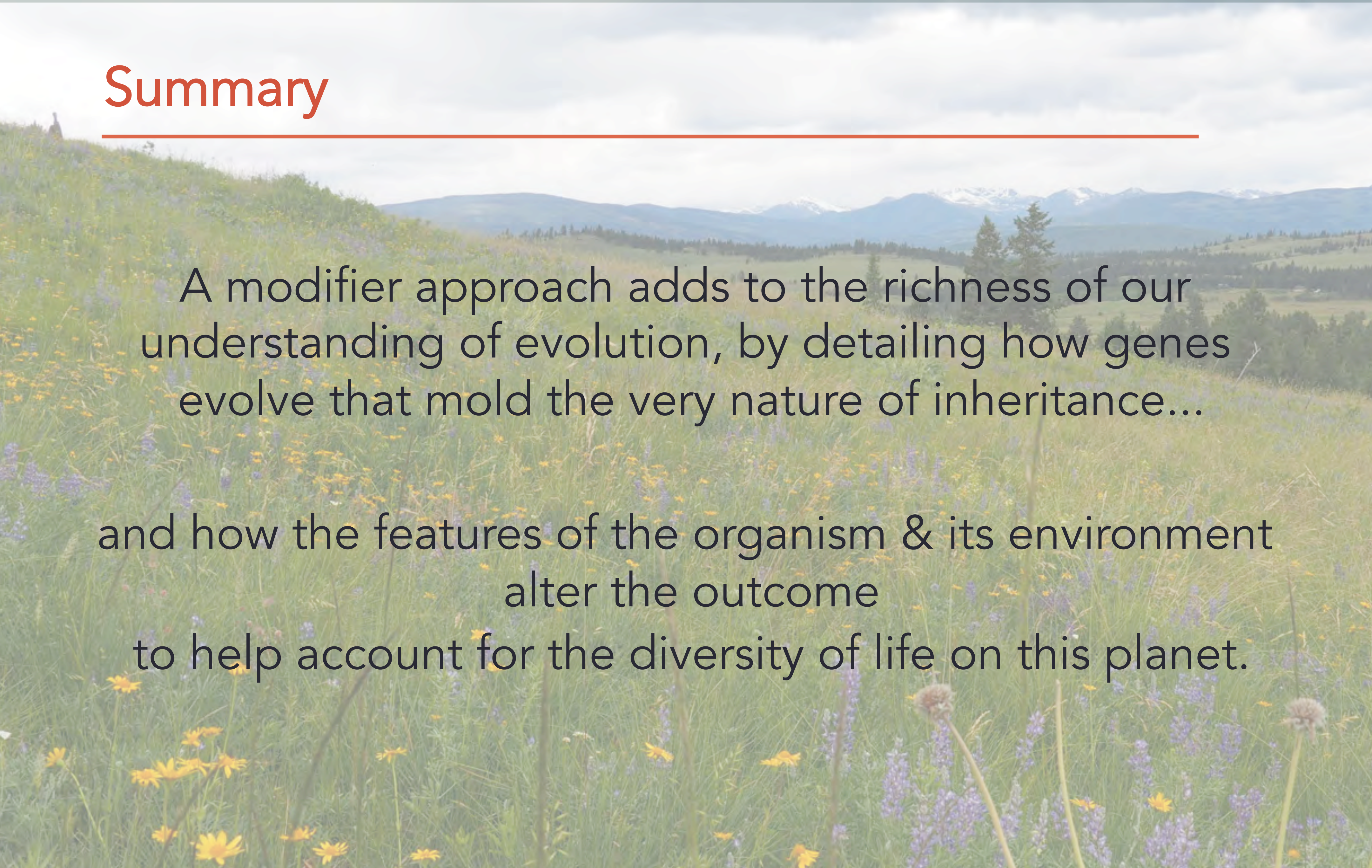
- from “what is best” to “what can evolve”
- from genes that affect fitness to genes that mold how an organisms lives and reproduces

Summary

- Group-level (long-term) evolutionary forces most important with tight linkage and low levels of sex

- Individual-level (short-term) evolutionary forces more important with frequent genetic mixing

➔ Modifier models find the balance



Summary

A modifier approach adds to the richness of our understanding of evolution, by detailing how genes evolve that mold the very nature of inheritance…

and how the features of the organism & its environment
alter the outcome
to help account for the diversity of life on this planet.

Acknowledgments

Marc Feldman

Nick Barton **Joe Felsenstein**

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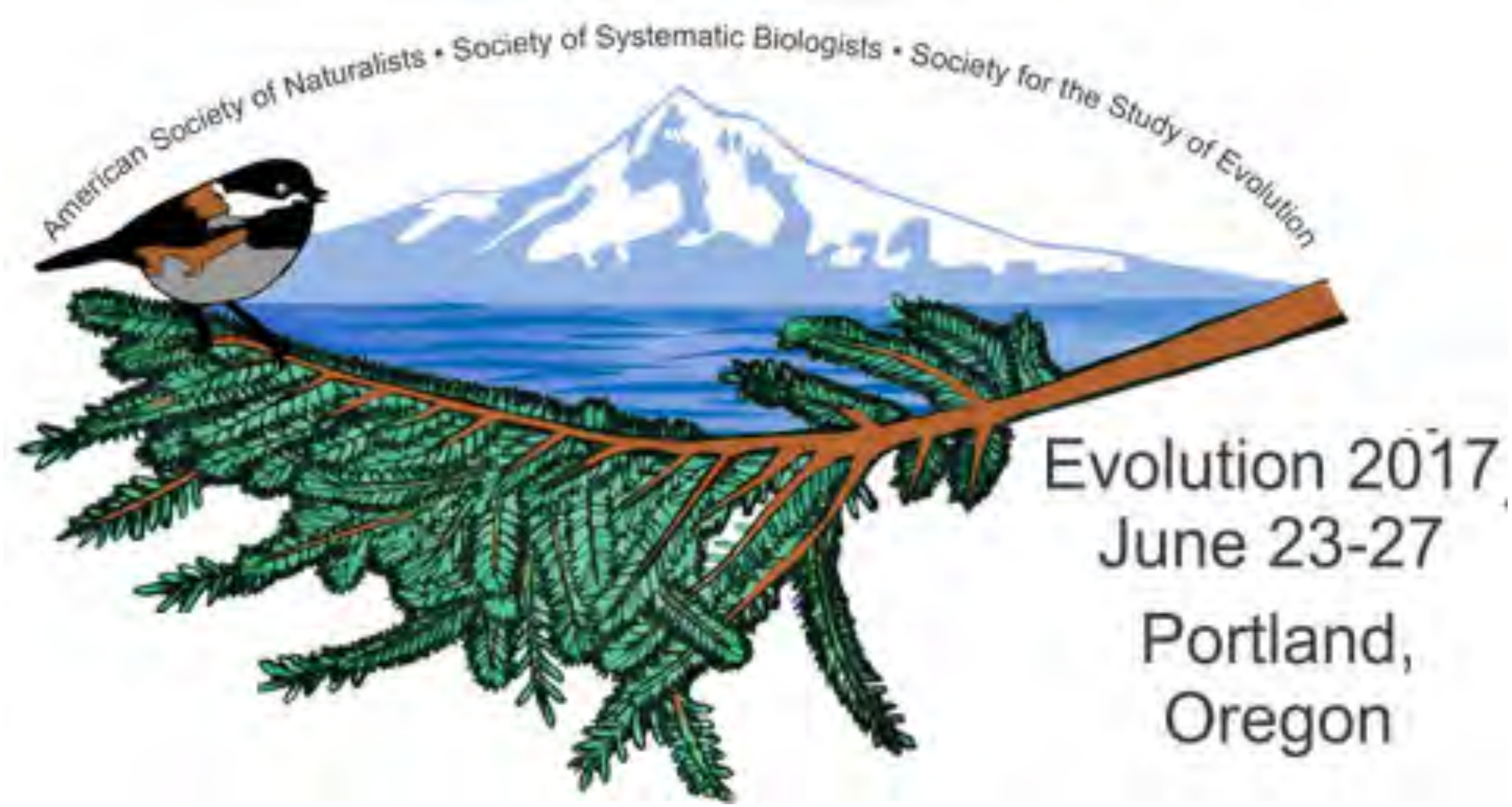
CRSNG

Aleeza
Gerstein

Michael
Scott

Alirio
Rosales



Howard Rundle

Mitch Cruzan

Meeting Organizing Committee