

Dobzhansky-Muller Incompatibilities in Parapatry

Joachim Hermisson, Claudia Bank & Reinhard Bürger

Mathematics & Biology, University of Vienna

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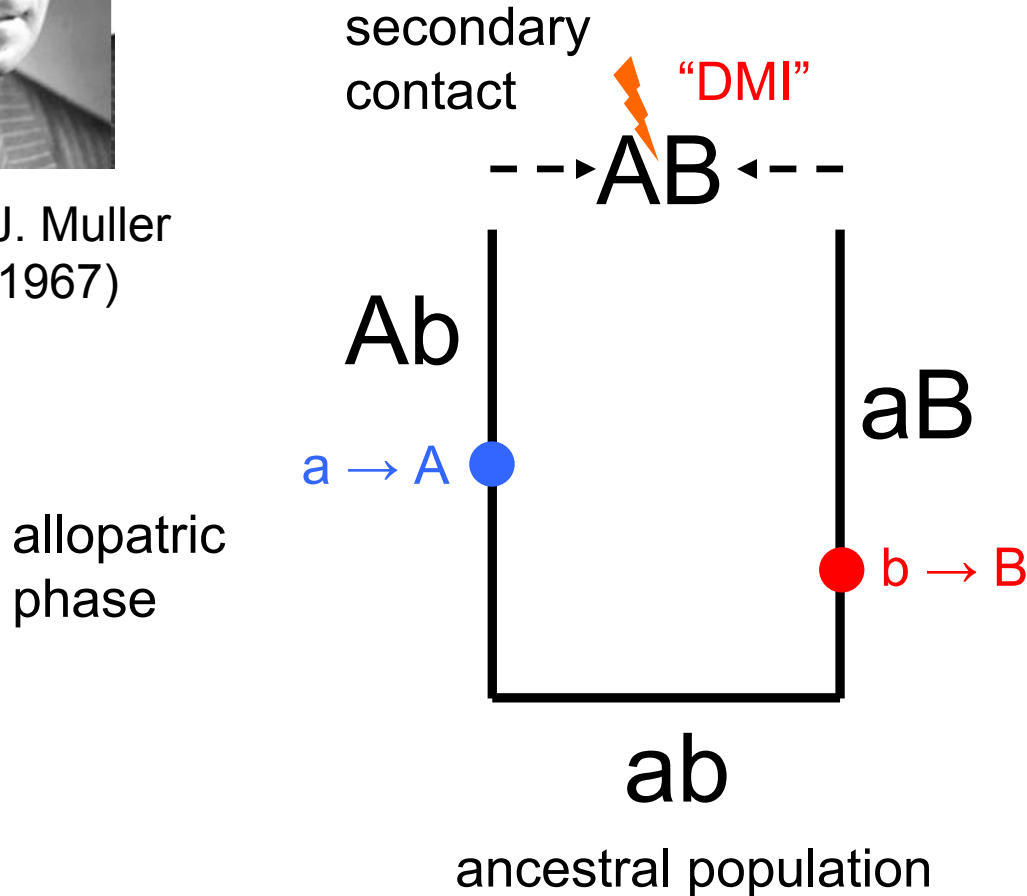


Hermann J. Muller
(1890 - 1967)

Speciation due to genetic incompatibilities: **allopatry**



Theodosius Dobzhansky
(1900-1975)



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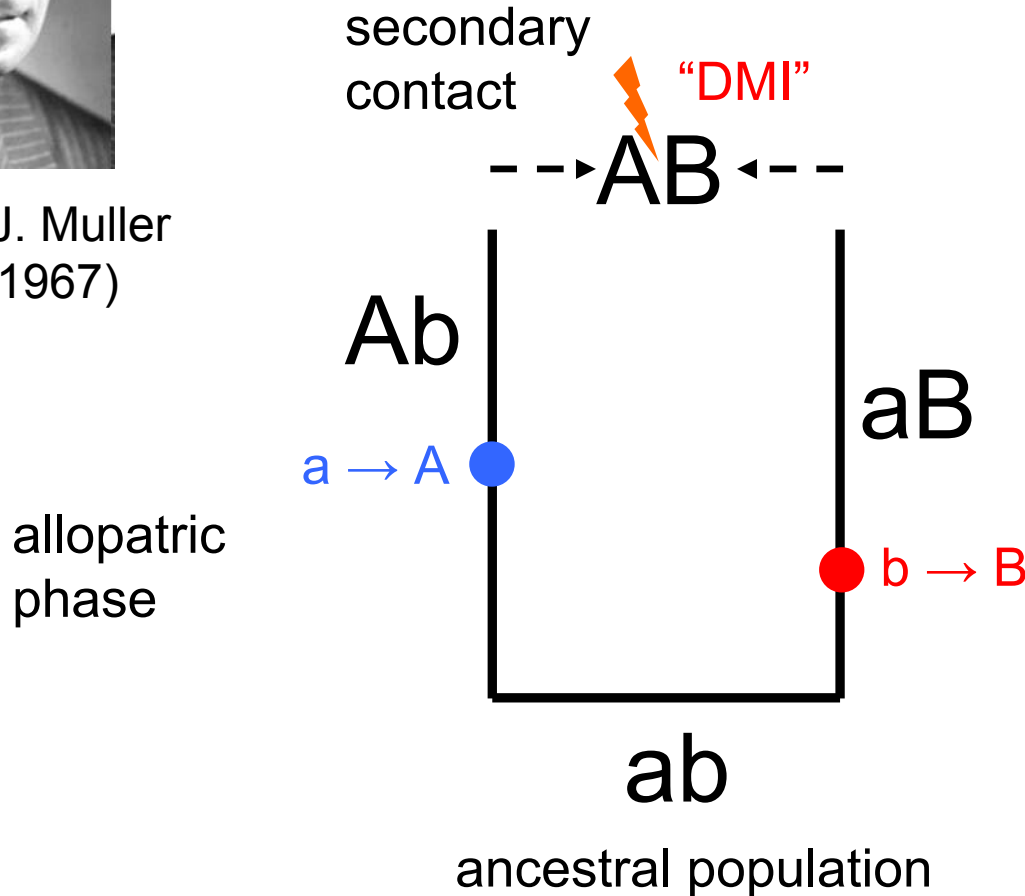


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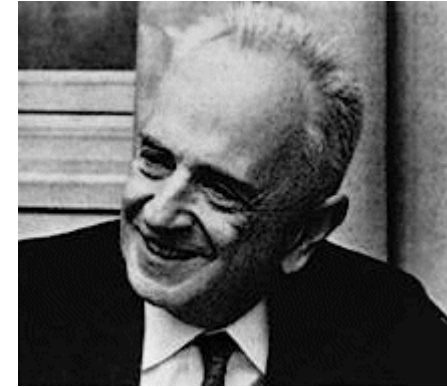
- theory by Orr, Turelli, *et al.*
- standard allopatric speciation model

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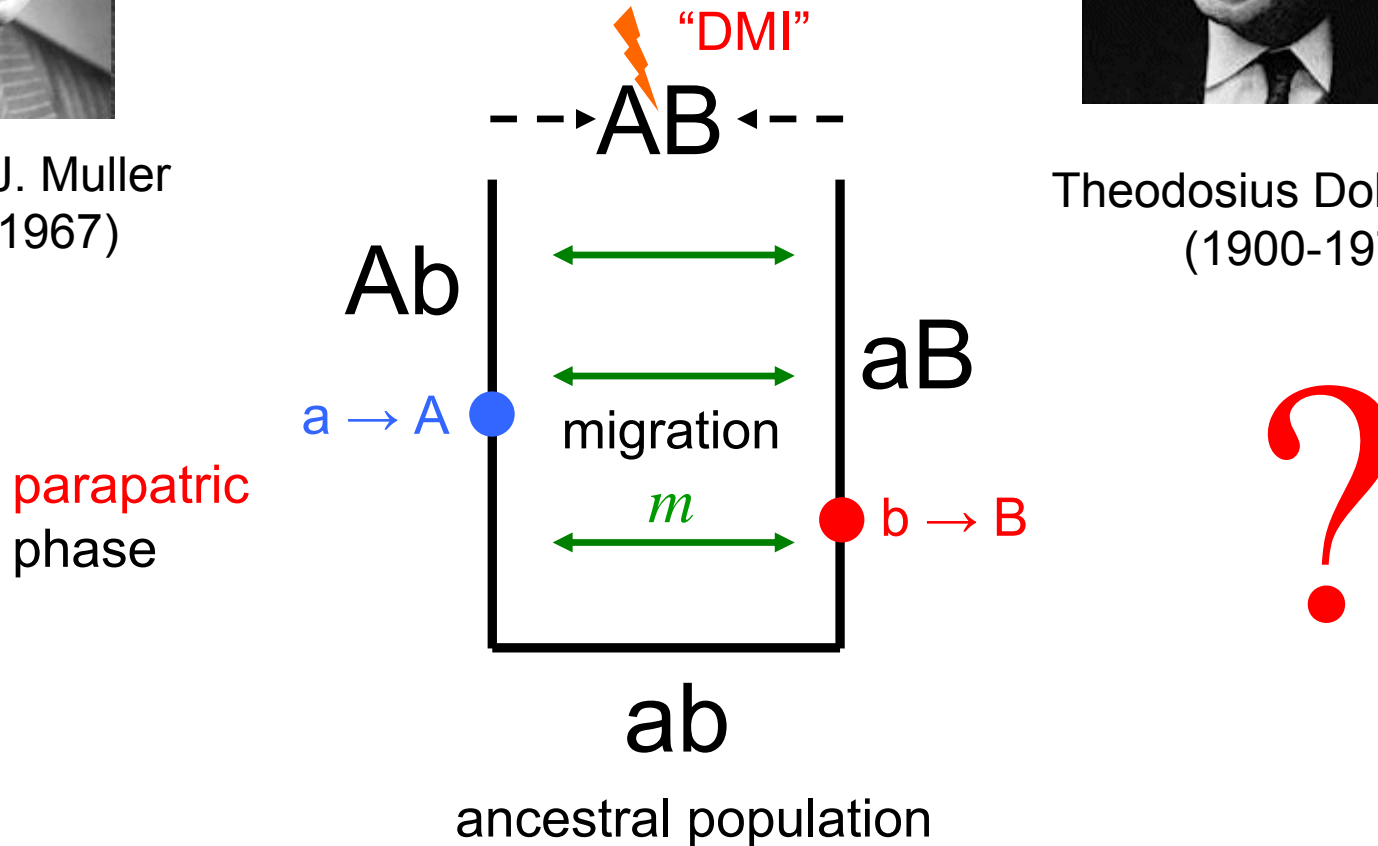


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Speciation due to genetic incompatibilities: **parapatry**

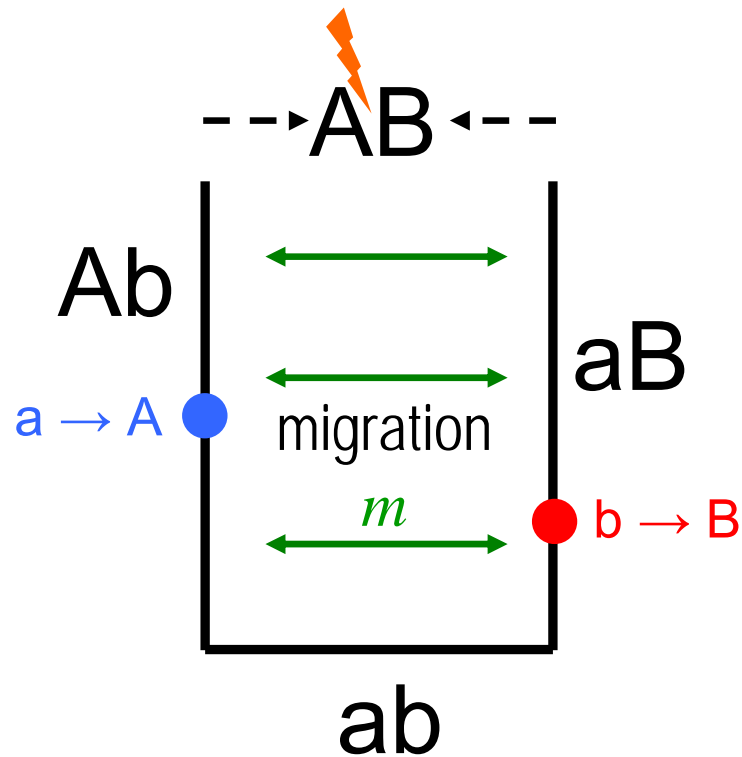


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Dobzhansky-Muller Incompatibilities in Parapatry

Origin and maintenance of DMI's in parapatry

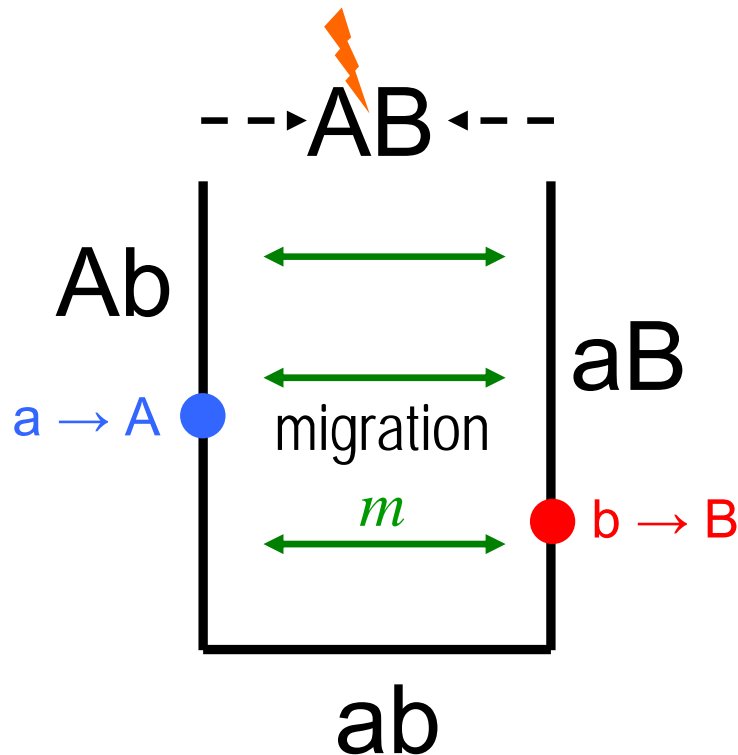


When does the mechanism work?

➤ Limiting rate of gene-flow m_{\max}

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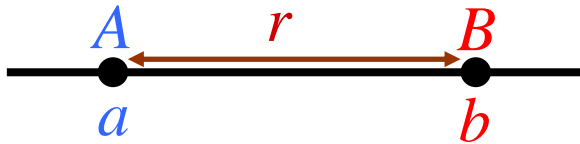
- influence of ecological factors
 - heterogeneous selection
- genetic factors
 - strength of incompatibility
 - recombination rate
- evolutionary history
 - order of substitution events



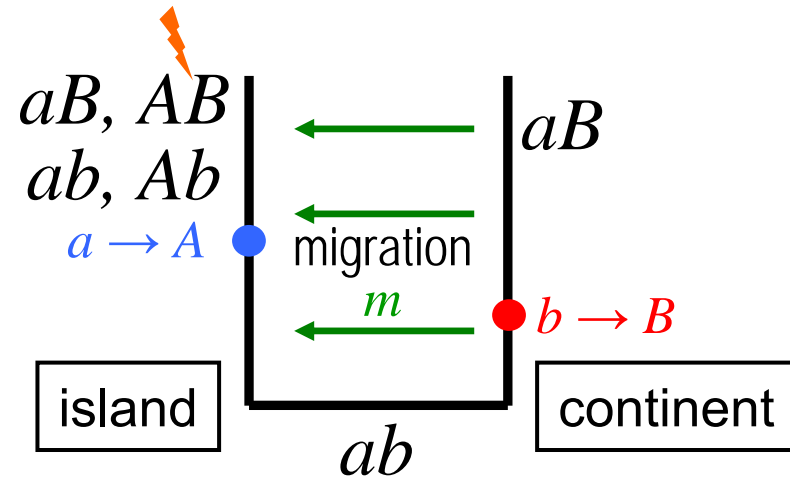
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Model: 1. Haploid Continent and Island

- 2 loci, 2 alleles, recomb. r



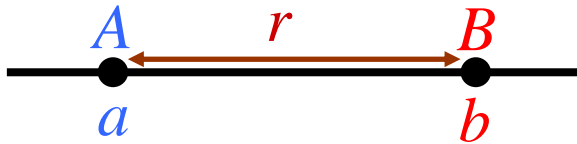
- unidirectional migration m



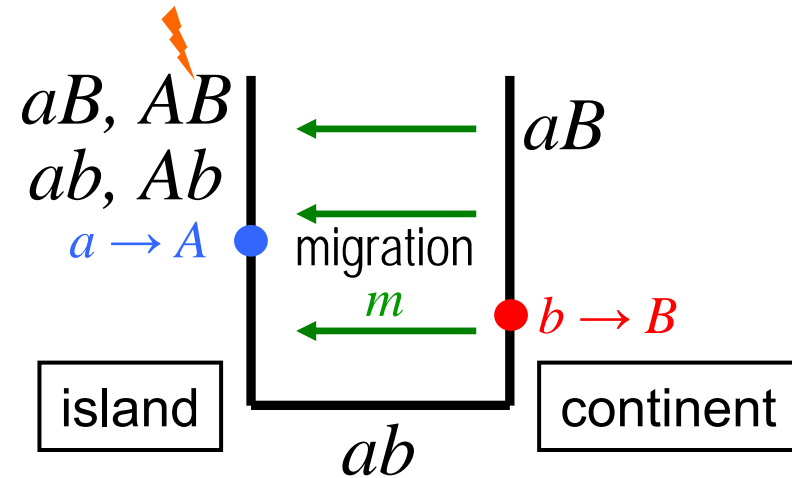
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Model: 1. Haploid Continent and Island

- 2 loci, 2 alleles, recomb. r



- **unidirectional** migration m
- fitness scheme on island:



haplotype	ab	aB	Ab	AB
	wildtype	continental	island	recombinant
fitness	$w_1 = 0$	$w_2 = \beta$	$w_3 = \alpha$	$w_4 = \alpha + \beta - \gamma$
frequency	x_1	x_2	x_3	x_4

β and α are circled in red.

ecological or extrinsic selection

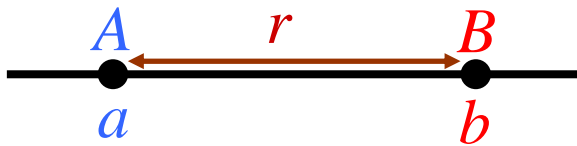
γ is circled in red.

incompatibility: intrinsic selection

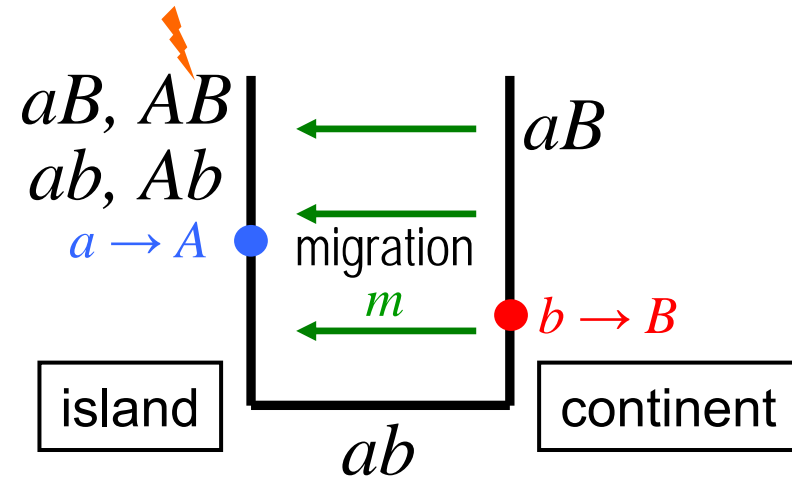
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Model: 2. Diploid Continent and Island

- 2 loci, 2 alleles, recomb. r



- **unidirectional** migration m
- fitness scheme on island:



	aa	aA	AA
bb	0	α	2α
bB	β	$\alpha + \beta - \gamma_1$	$2\alpha + \beta - \gamma_3$
BB	2β	$\alpha + 2\beta - \gamma_2$	$2\alpha + 2\beta - \gamma_4$

4 incompatibility parameters

γ_1 : double heterozygote $aAbB$

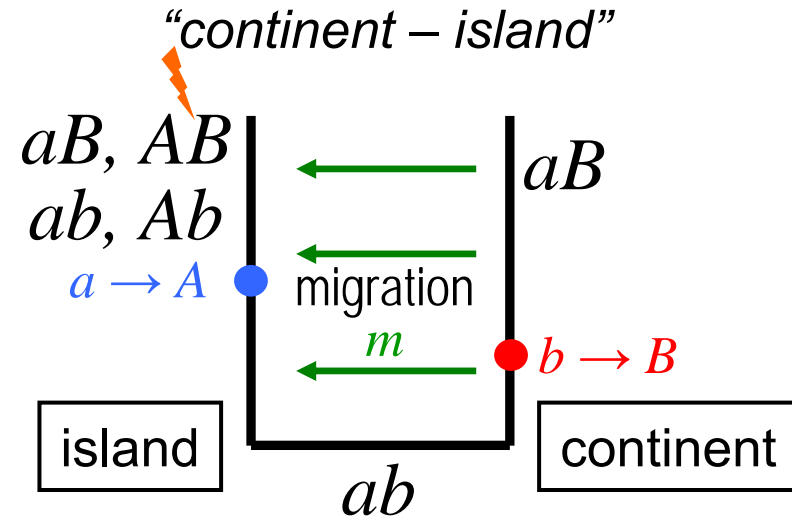
γ_2, γ_3 : hetero/ homo $AAbB, aABB$

γ_4 : double homozygote $AABB$

$$\gamma_1 < \gamma_2, \gamma_3 < \gamma_4$$

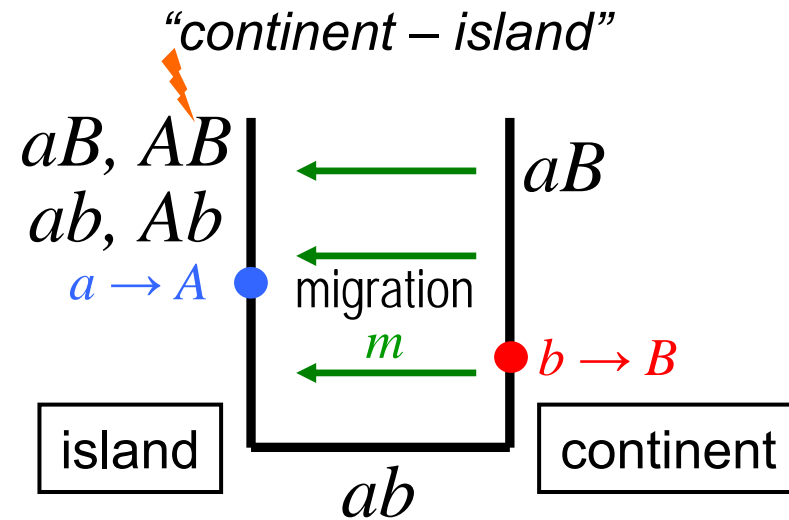
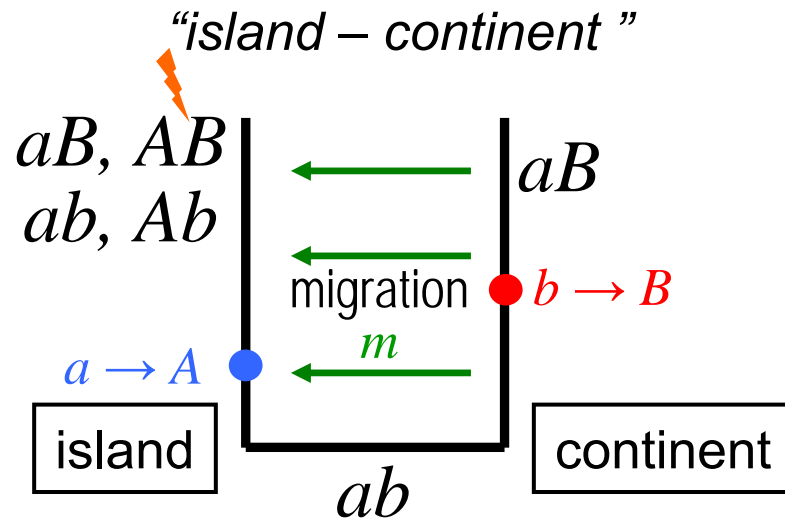
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Evolutionary Histories



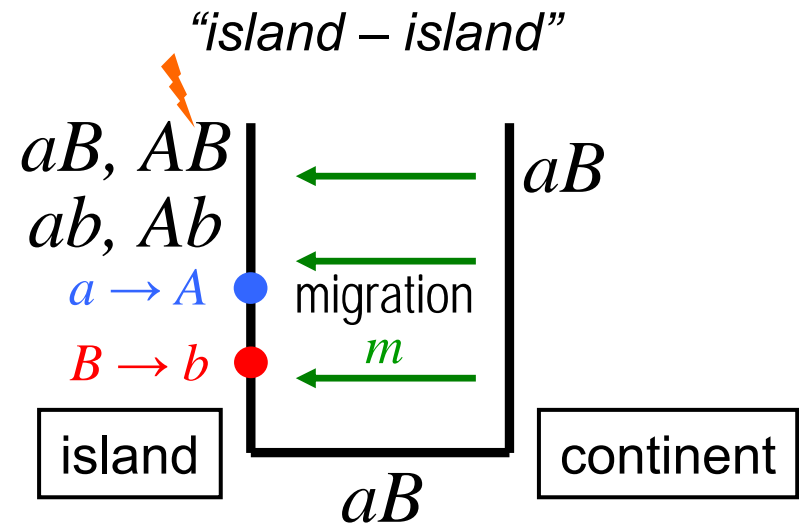
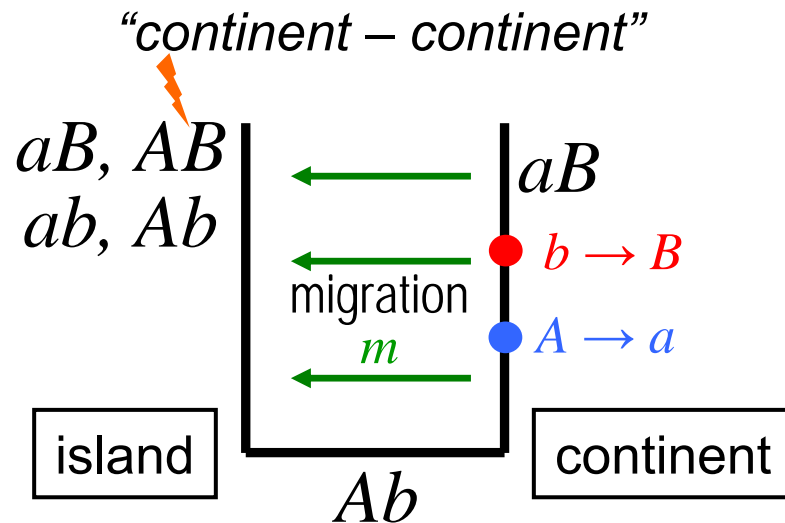
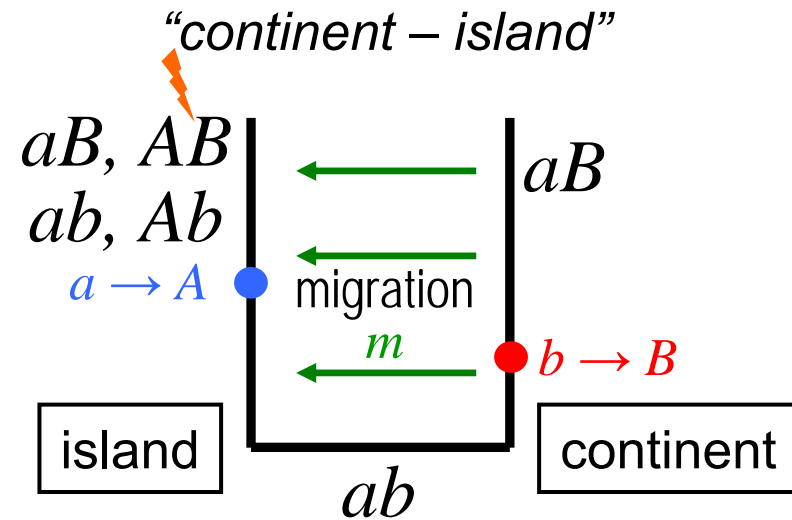
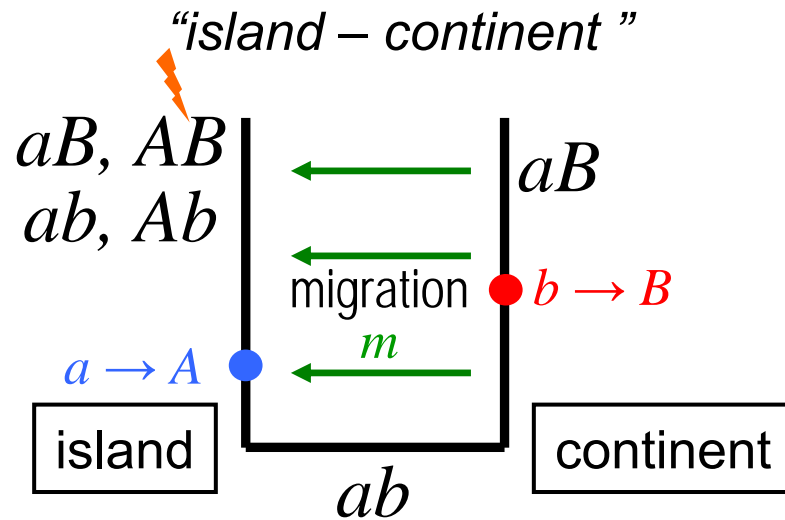
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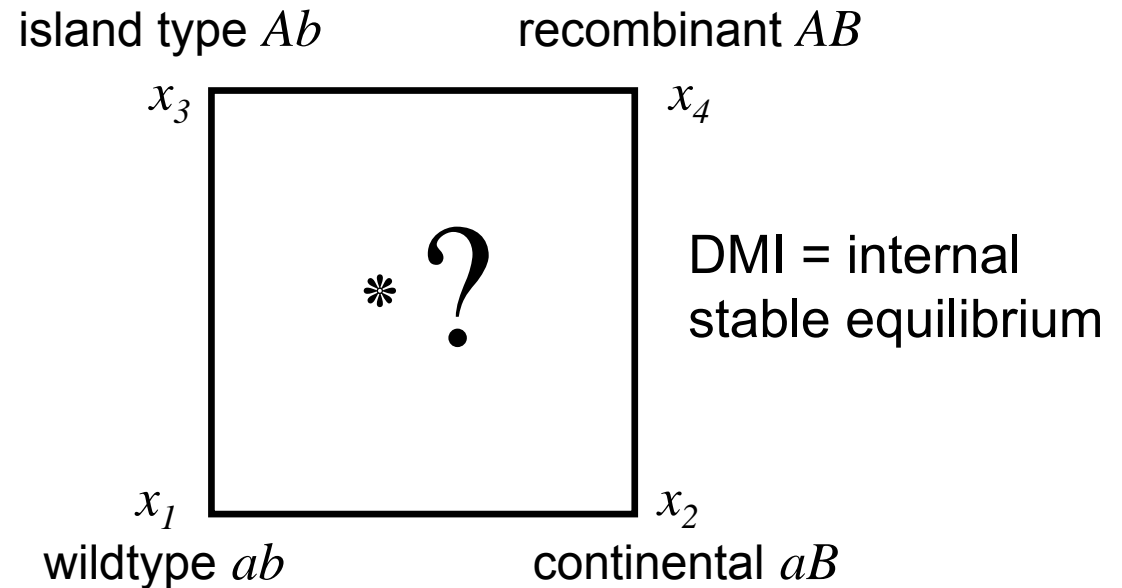
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Evolutionary Histories



Dobzhansky-Muller Incompatibilities in Parapatry

Evolutionary dynamics on the island

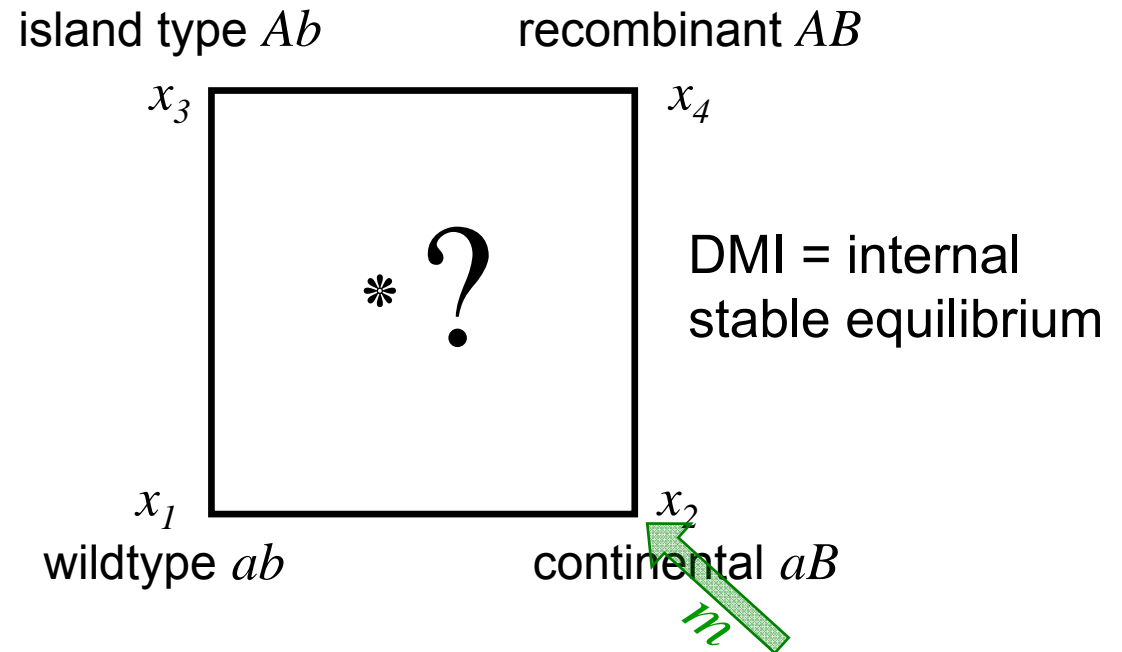


continuous time dynamics

$$\left\{ \begin{array}{l} \dot{x}_1 = x_1(w_1 - \bar{w} - m) - rD \quad ; \quad \dot{x}_2 = x_2(w_2 - \bar{w} - m) + rD + m \\ \dot{x}_3 = x_3(w_3 - \bar{w} - m) + rD \quad ; \quad \dot{x}_4 = x_4(w_4 - \bar{w} - m) - rD. \\ D = x_1x_4 - x_2x_3 \qquad \bar{w} = \beta x_2 + \alpha x_3 + (\alpha + \beta - \gamma)x_4 \end{array} \right.$$

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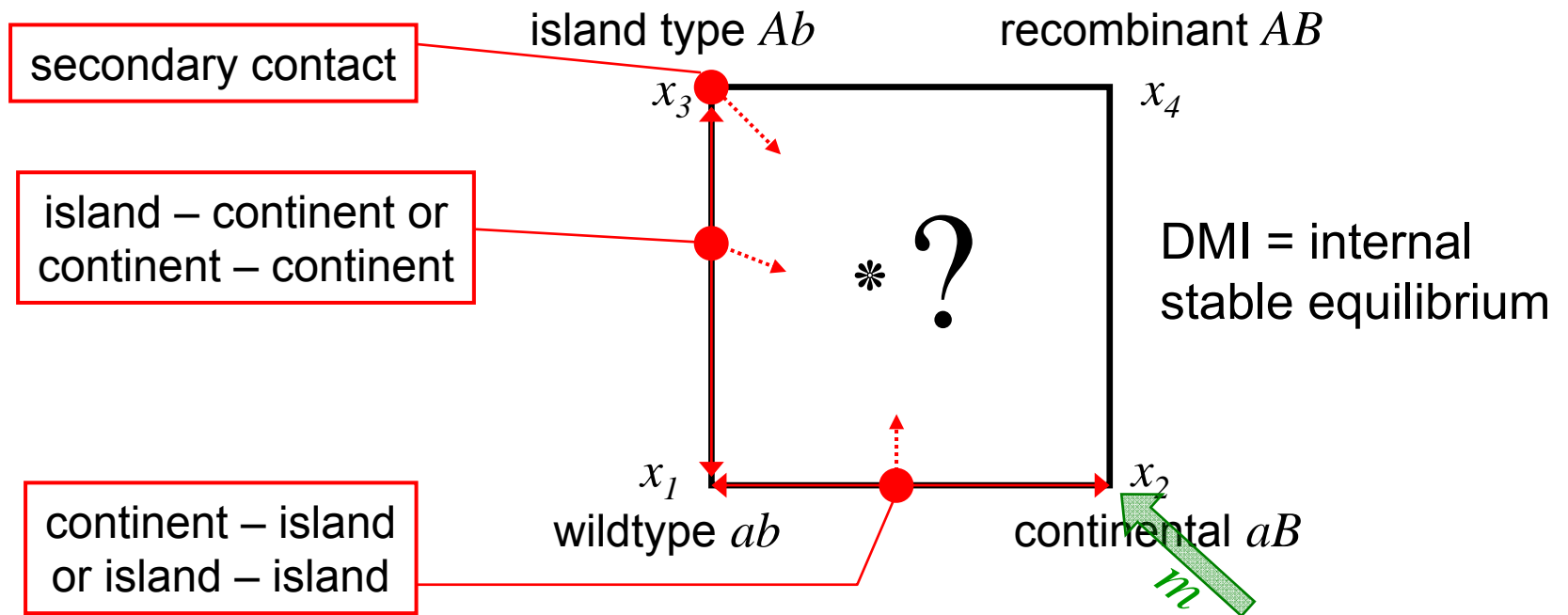


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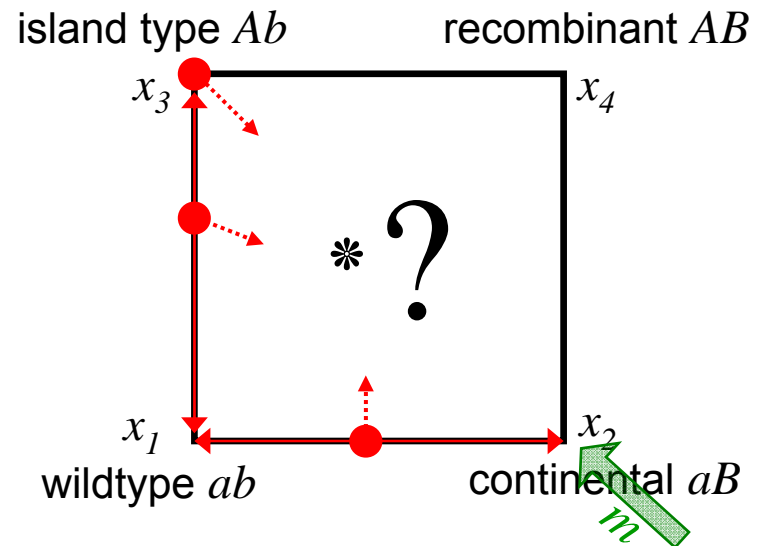
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Evolutionary dynamics on the island

Analytical results

- equilibria and stability analysis
- Lyapunov functions
- limiting cases: $m \rightarrow 0$, $r \rightarrow 0$, $D \rightarrow 0$
and perturbation theory

& numerical analysis



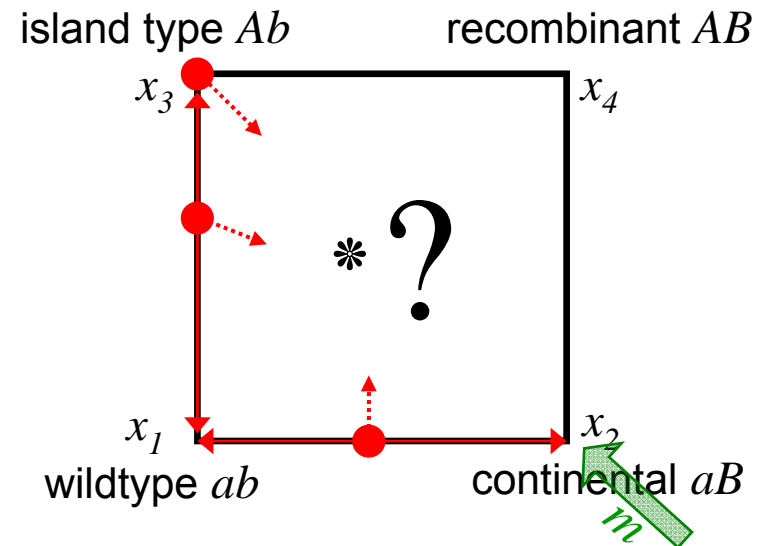
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Limiting migration rates m_{\max} for stable DMI:

- haploid: almost everything analytical
- diploid: only limiting cases analytical, full numerical overview

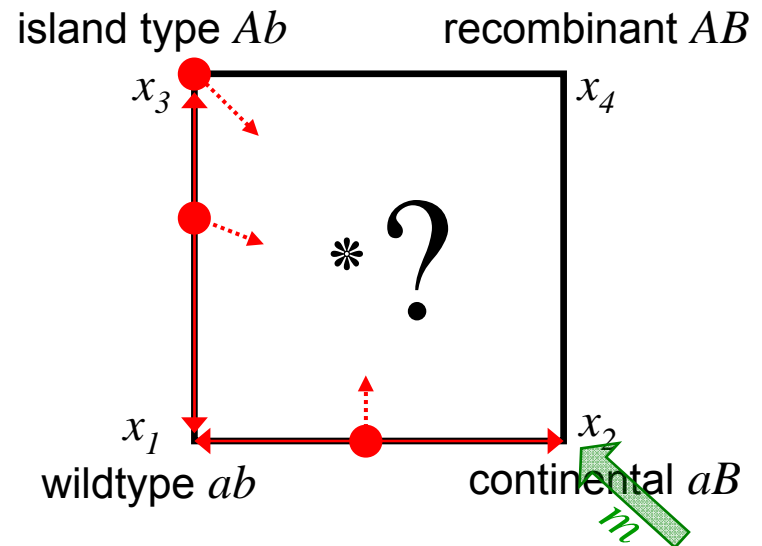
➤ at most a single stable DMI, which can be globally or locally stable

Dobzhansky-Muller Incompatibilities in Parapatry

Results: Types of parapatric speciation

1. Neutral DMI: $\alpha = \beta = 0$

- **never** for $m > 0$, unless $r = 0$
- flow: $Ab \rightarrow ab \rightarrow aB$
- general proof for diploid ?



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Results: Types of parapatric speciation

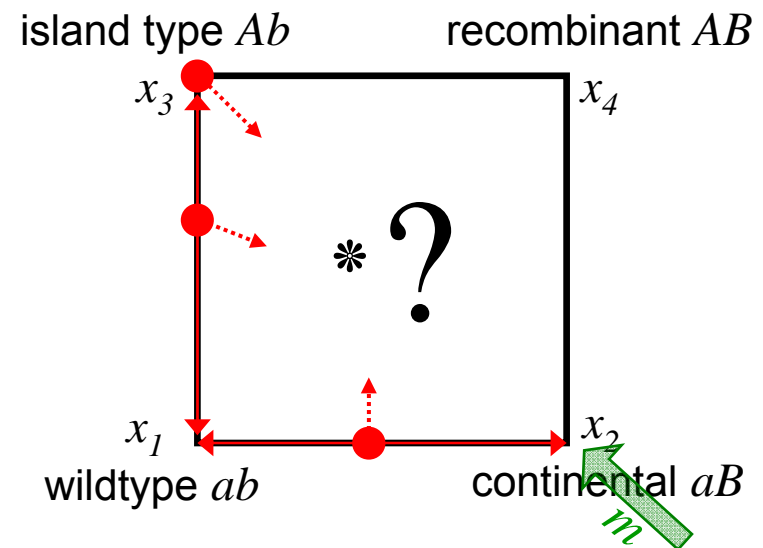
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2. Adaptive DMI [Schluter 2009]:

a) “Ecological speciation”

- globally stable DMI
- *Schluter*: for local adaptation ($\beta < 0 < \alpha$)



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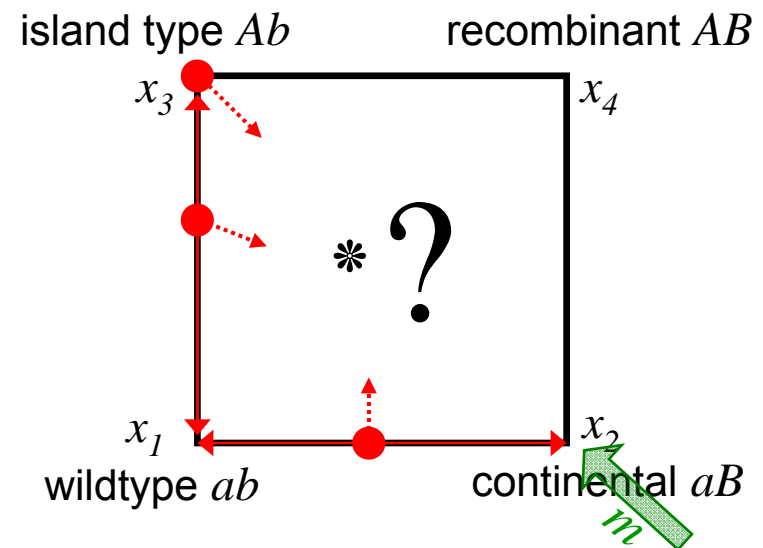
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- *Schluter*: for local adaptation ($\beta < 0 < \alpha$)

b) “Mutation order speciation”

- Origin of DMI depends on mutation order: **historical contingency**
- locally stable DMI: evolves only if second substitution on continent (island – continent, continent – continent, secondary contact)
- *Schluter*: for global adaptation ($0 < \alpha, \beta$)



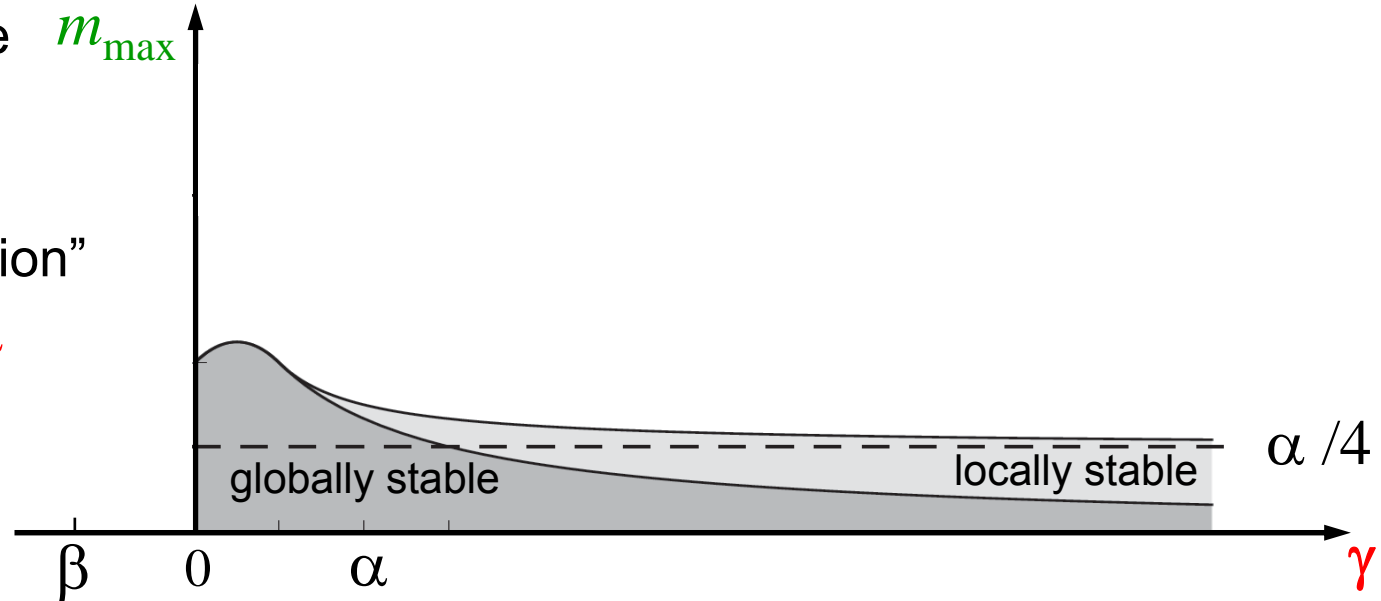
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Results: Fitness parameters (haploid)

$D = 0$ (linkage equilibrium) m_{\max}

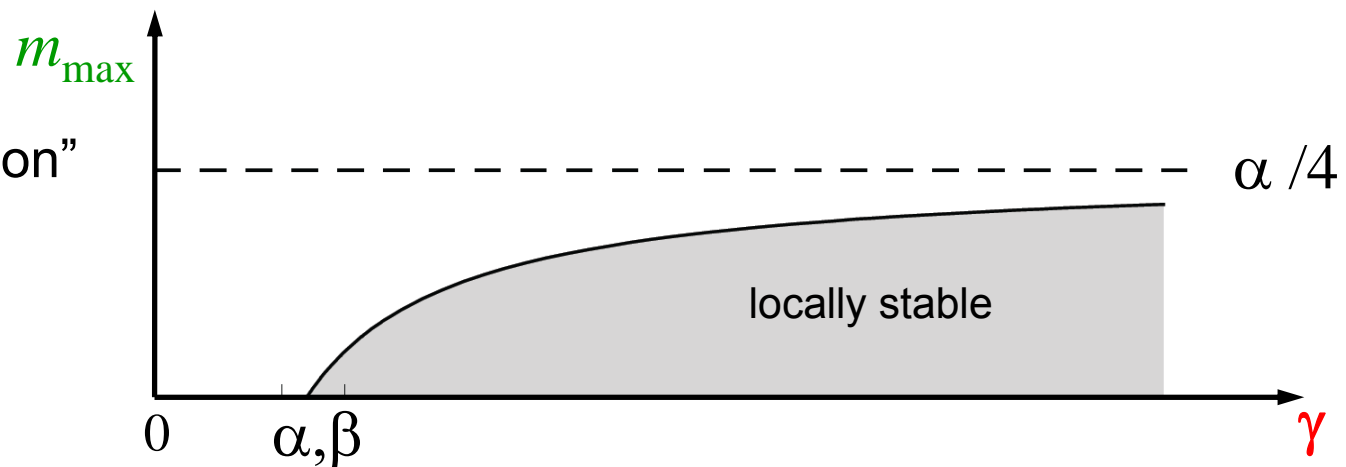
“local adaptation”

$$\beta < 0 < \alpha$$



“global adaptation”

$$0 < \alpha, \beta$$



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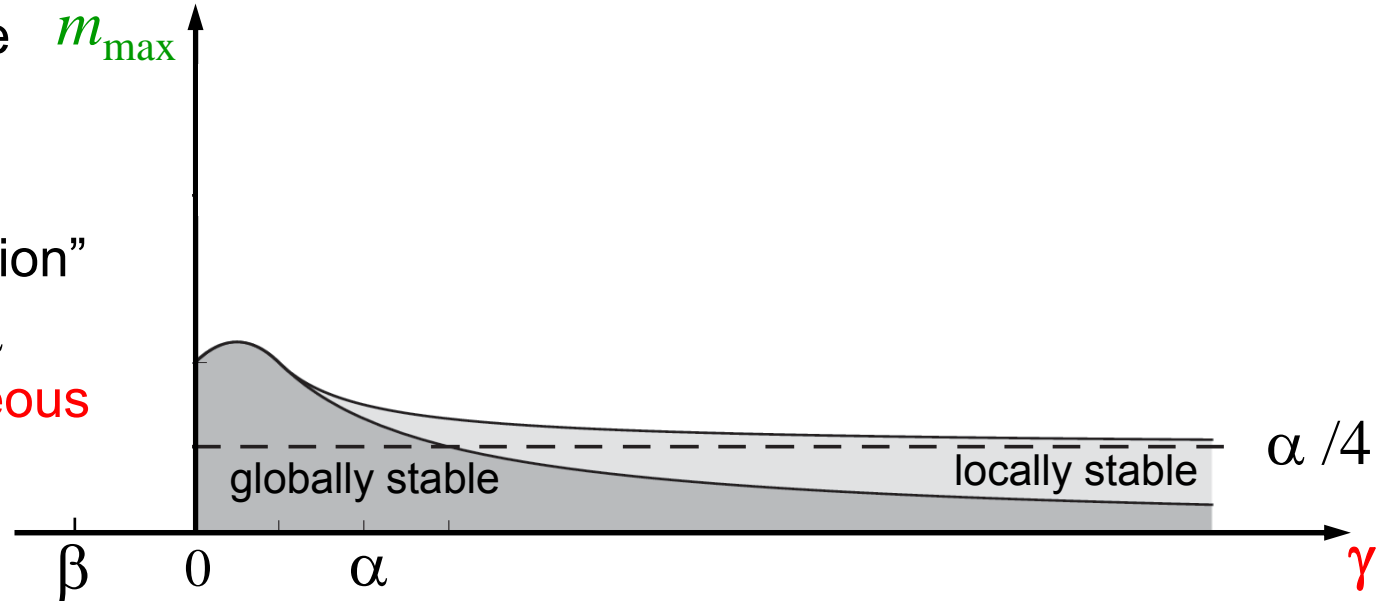
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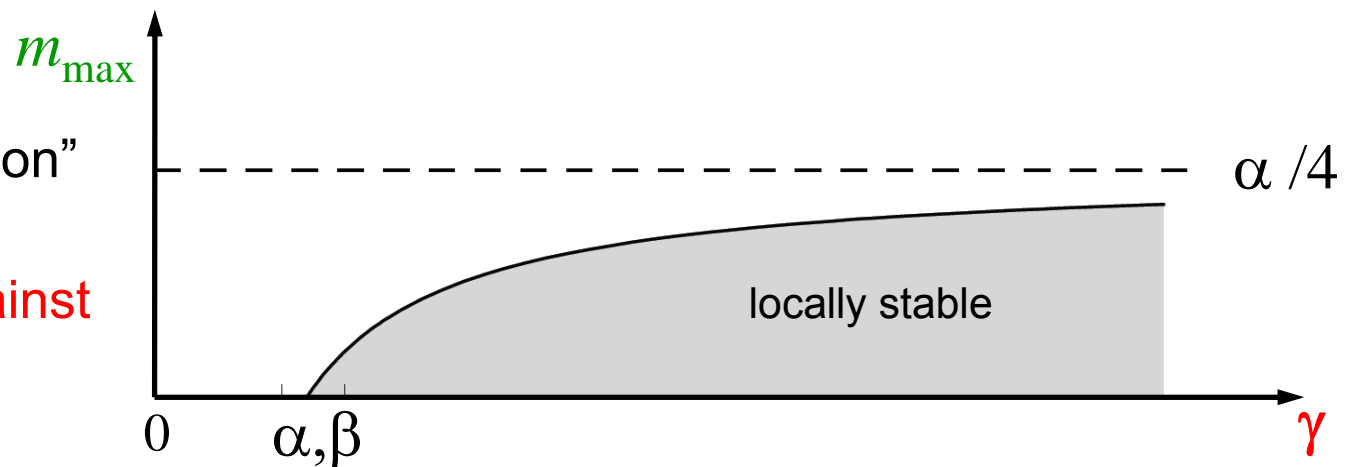
➤ heterogeneous selection



“global adaptation”

$$0 < \alpha, \beta$$

➤ selection against hybrids



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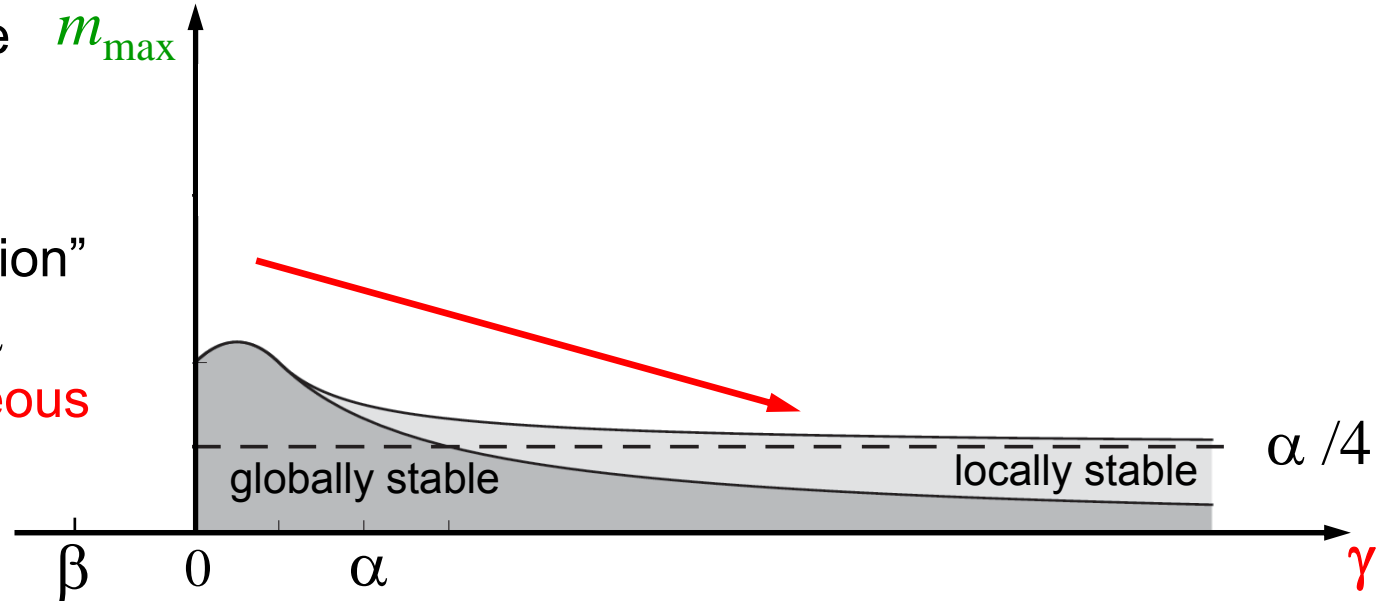
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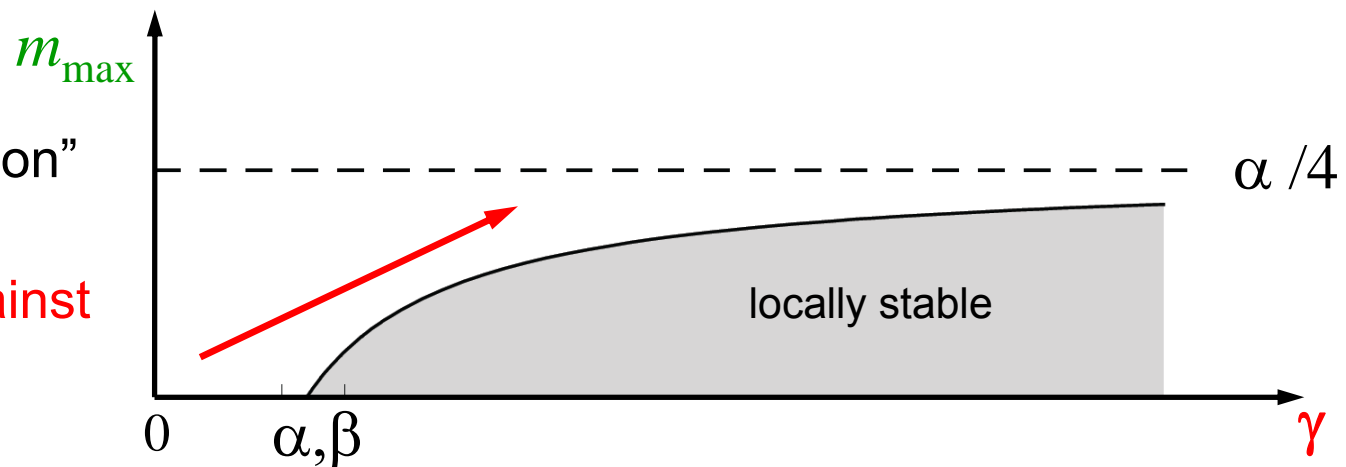
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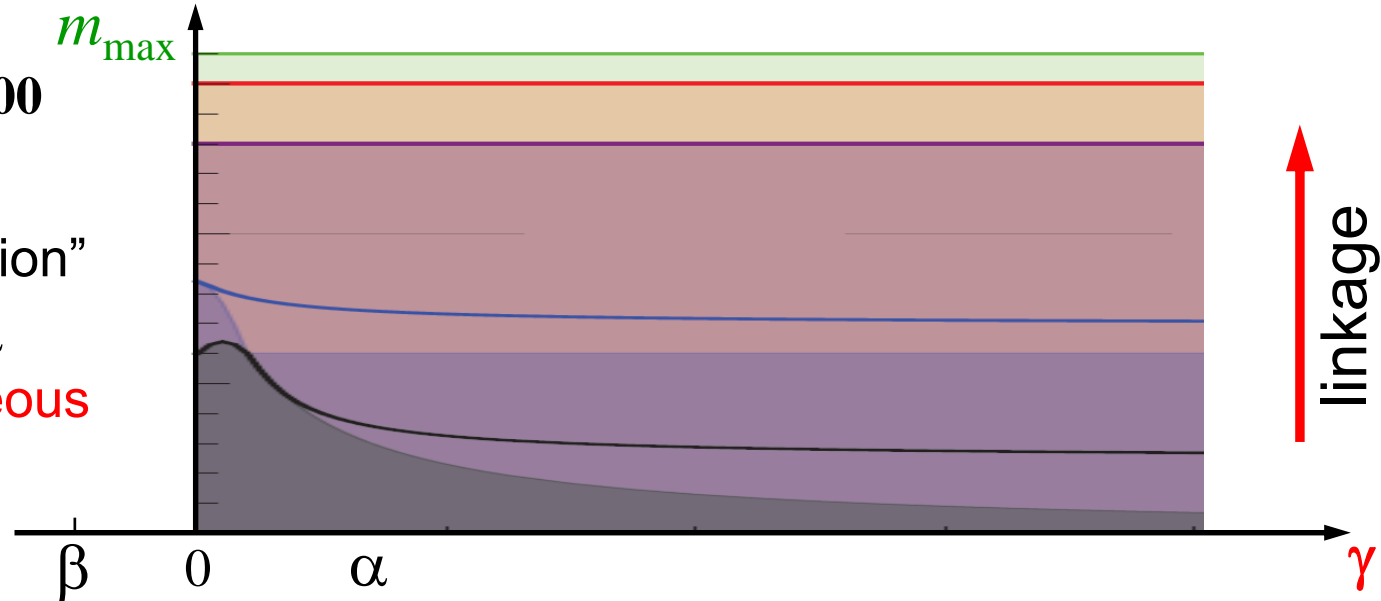
Results: Recombination & linkage (haploid)

$r = 0; 0.001; 0.003; 0.1; 100$; m_{\max}

“local adaptation”

$$\beta < 0 < \alpha$$

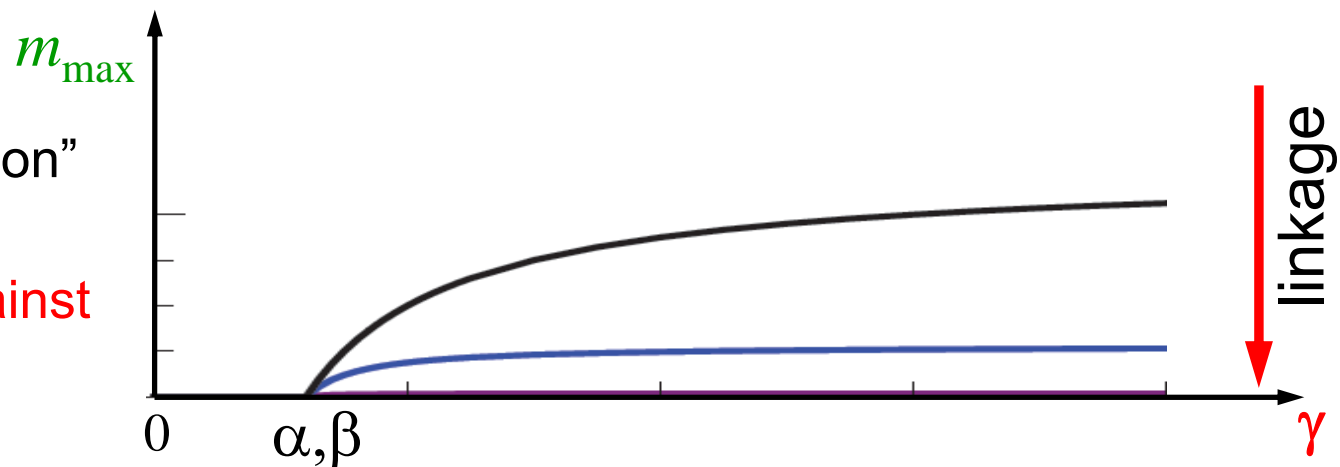
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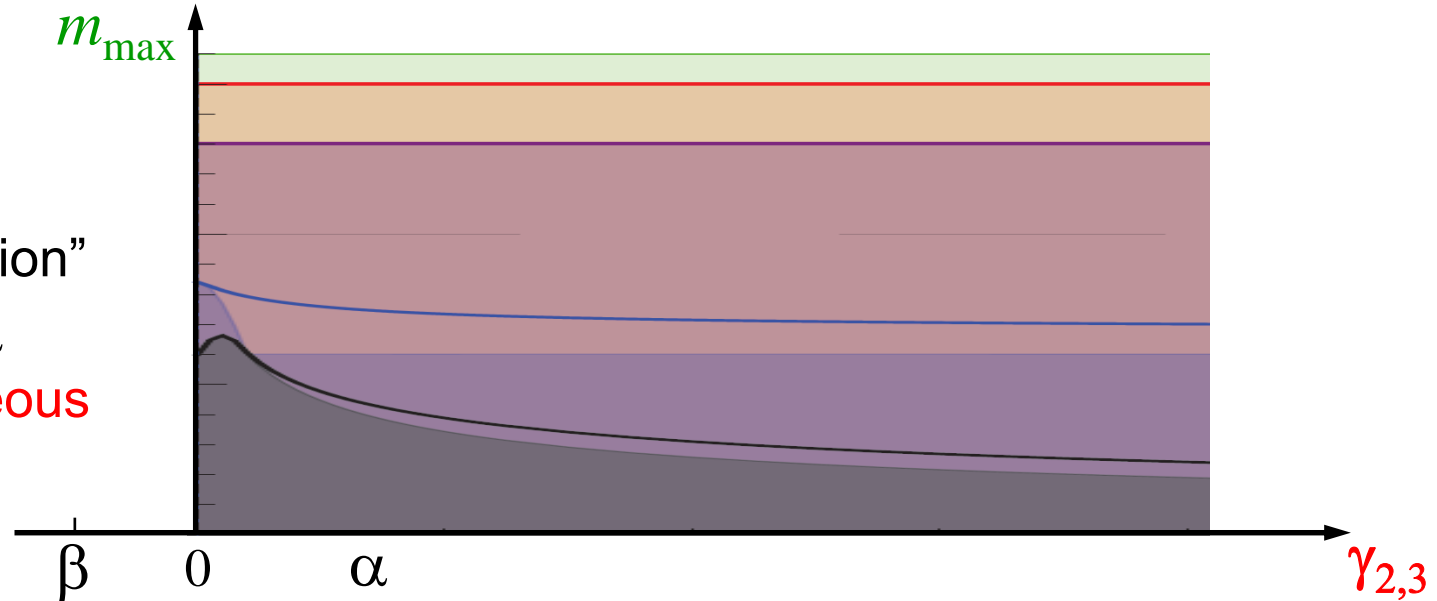
Results: Diploid, recessive DMI

$$\gamma_1 = 0;$$
$$\gamma_{2,3} = \gamma_4 / 2$$

“local adaptation”

$$\beta < 0 < \alpha$$

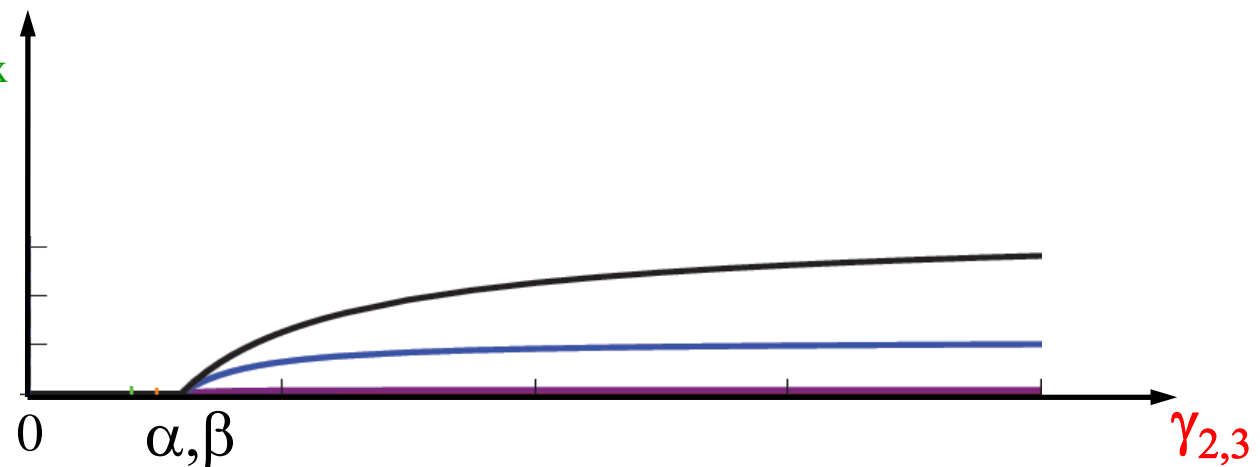
➤ heterogeneous selection



“global adaptation”

$$0 < \alpha, \beta$$

➤ selection against hybrids



Dobzhansky-Muller Incompatibilities in Parapatry

Results: Diploid, co-dominant DMI

$$\gamma_1 = \gamma_4 / 4; \quad m_{\max}$$

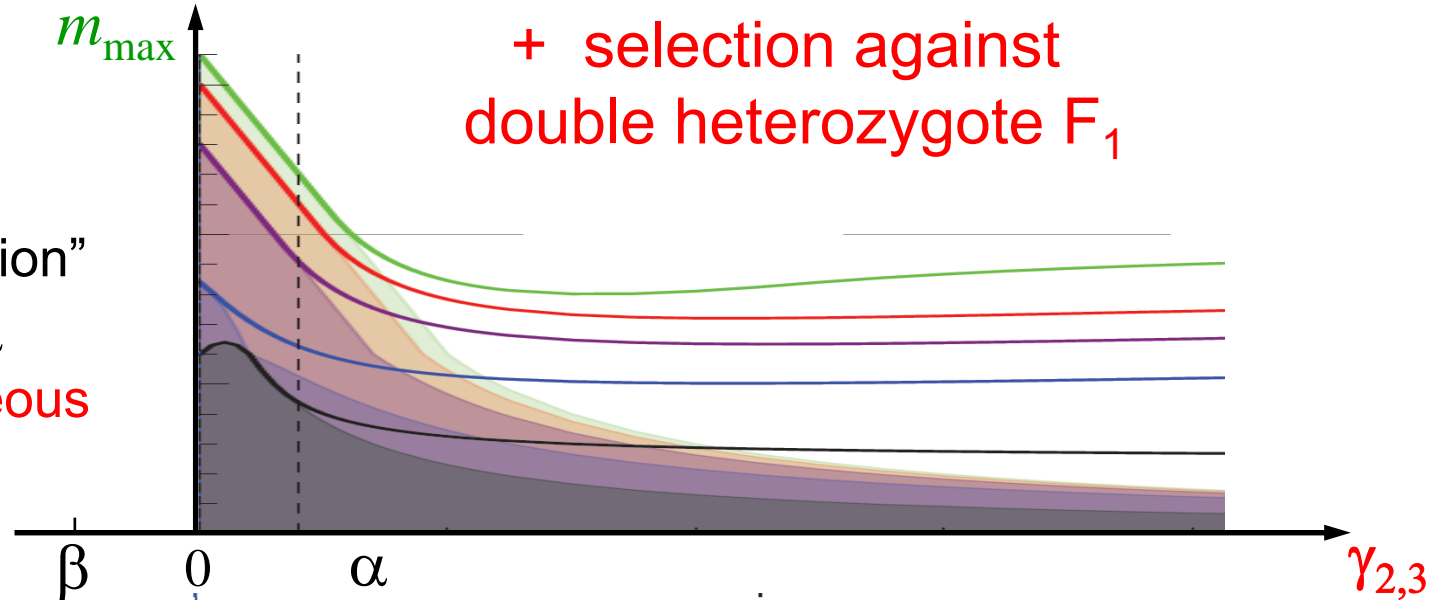
$$\gamma_{2,3} = \gamma_4 / 2$$

+ selection against double heterozygote F_1

“local adaptation”

$$\beta < 0 < \alpha$$

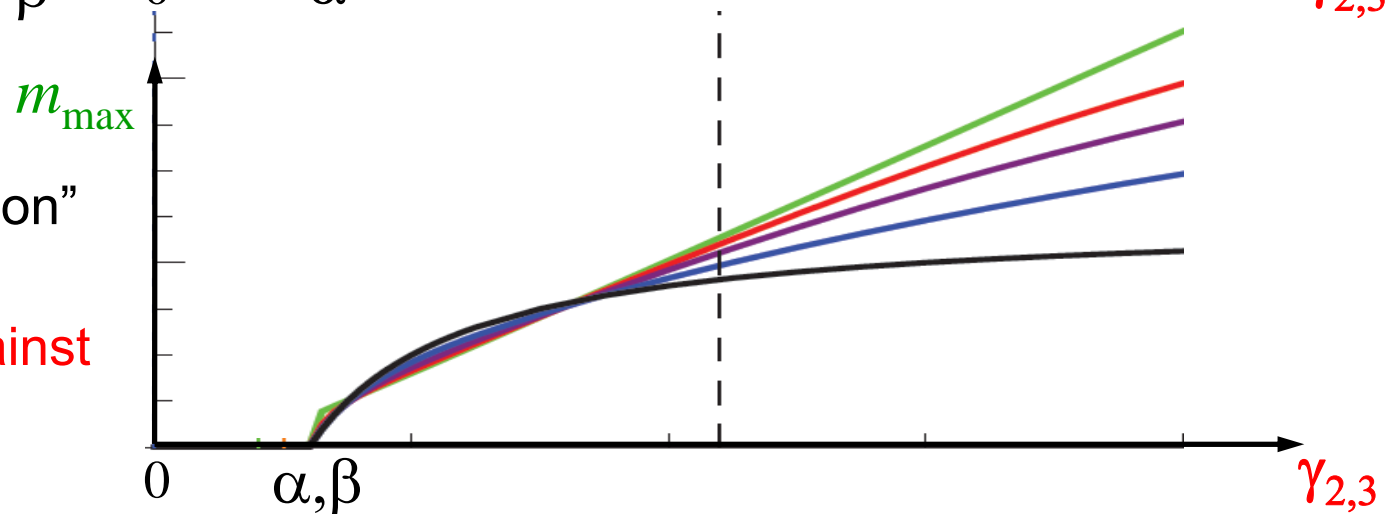
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Summary & Outlook

- No neutral DMI's with gene-flow

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- Two mechanisms for stable DMI's in parapatry:

Heterogeneous selection

- can be globally stable
- weak DMI favored
- tight linkage

Hybrid deficiency (intrinsic)

- mutation order important
- strong DMI favored
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 - costs for double heterozygotes $AaBb$ (γ_1) crucial
 - $\gamma_1 \gg 0$: DMIs due to deficient hybrids with **tight** linkage

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- Outlook:
 - two islands, X-linked DMI's, genetic drift, ...

Thanks !



Claudia Bank



Reinhard Bürger



Wiener Wissenschafts-, Forschungs- und Technologiefonds