Origins and dynamics of new Self-Incompatibility alleles in plants

An example of diversification with coevolution

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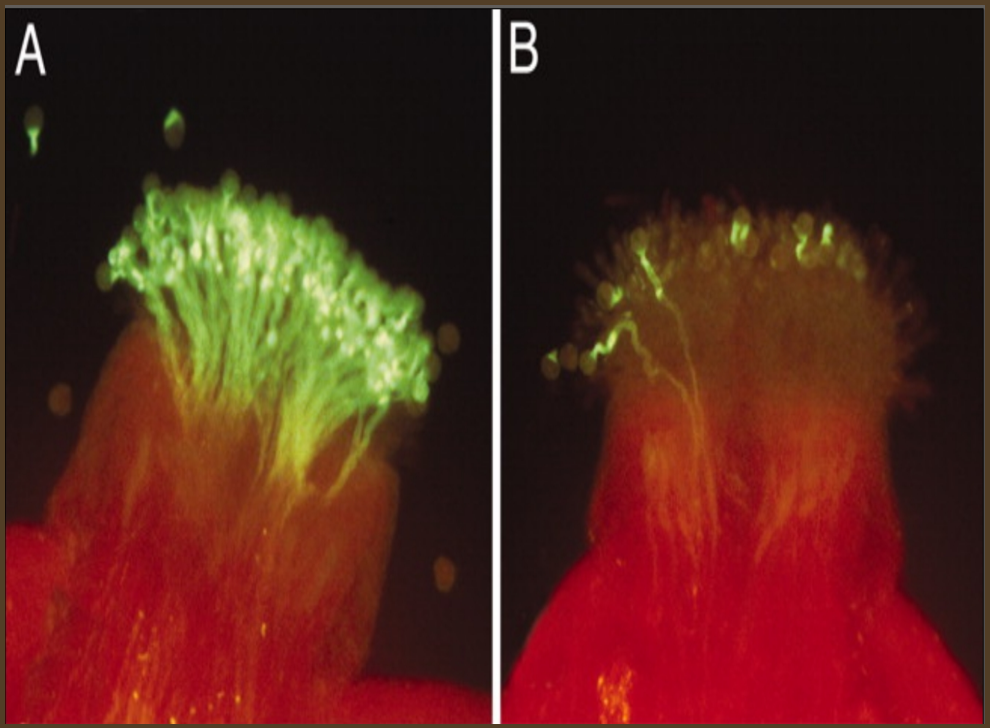
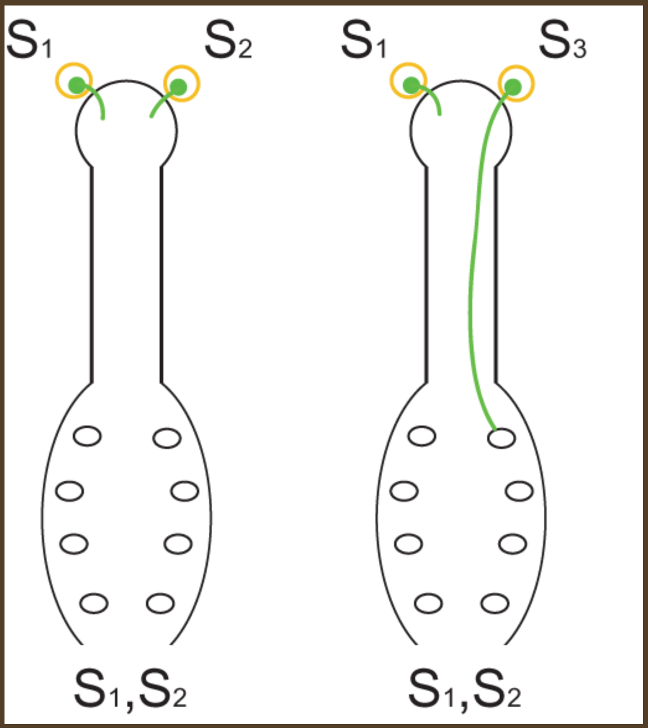
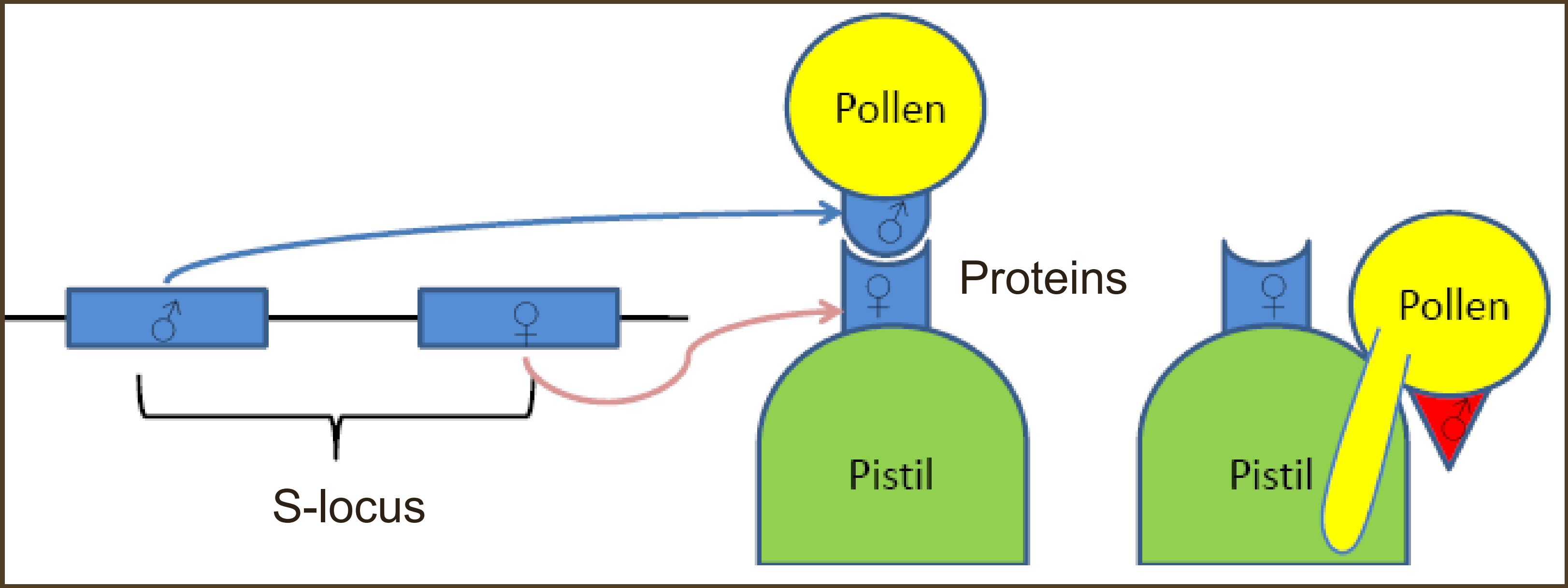




- Present in dozens Angiosperms families

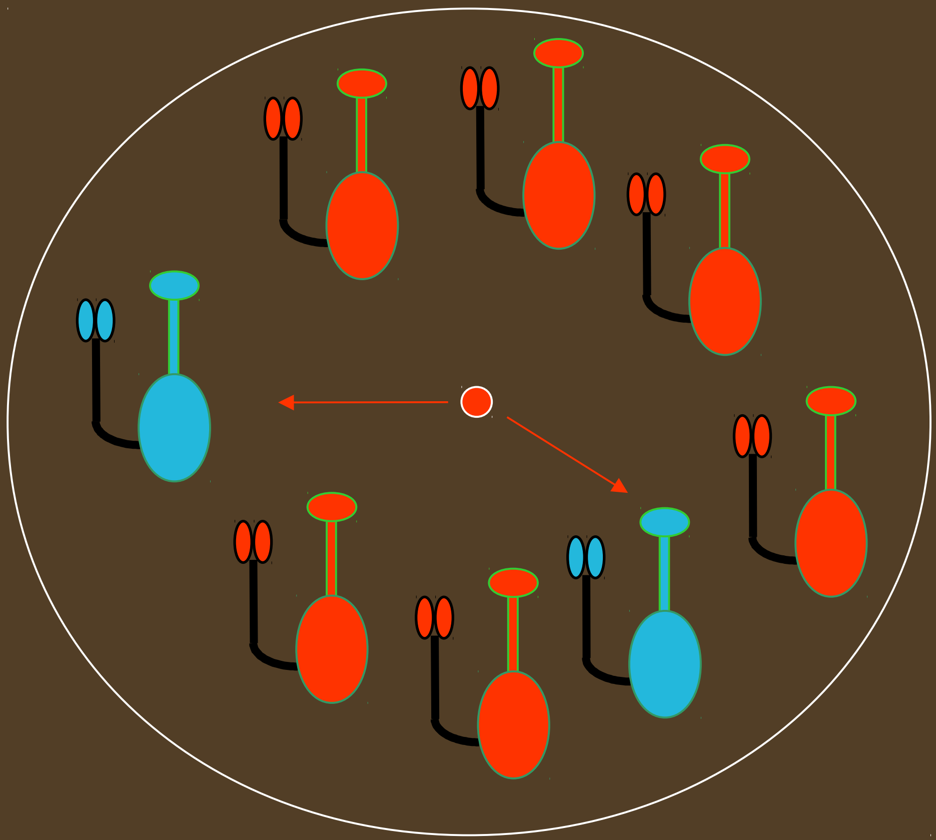
  (e.g. Solanaceae, Brassicaceae, ...)

Self-Incompatibility in plants



- Molecular recognition that prevents selfing and some cross-fertilization
- Up to 200 SI haplotypes thanks to the advantage of the rare (Wright 1939)

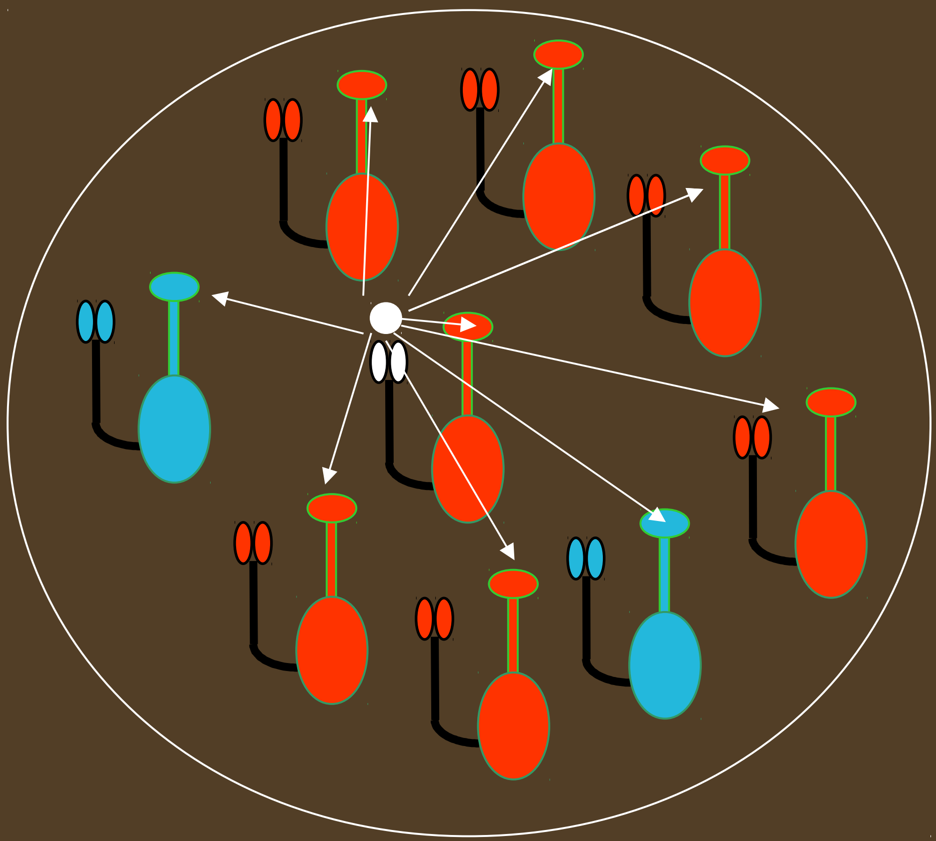
(or negative frequency dependent-selection)



Red phenotype is common

→ - potential mates

→ unfavored



White is self-compatible and compatible with anyone

The problem of S diversification

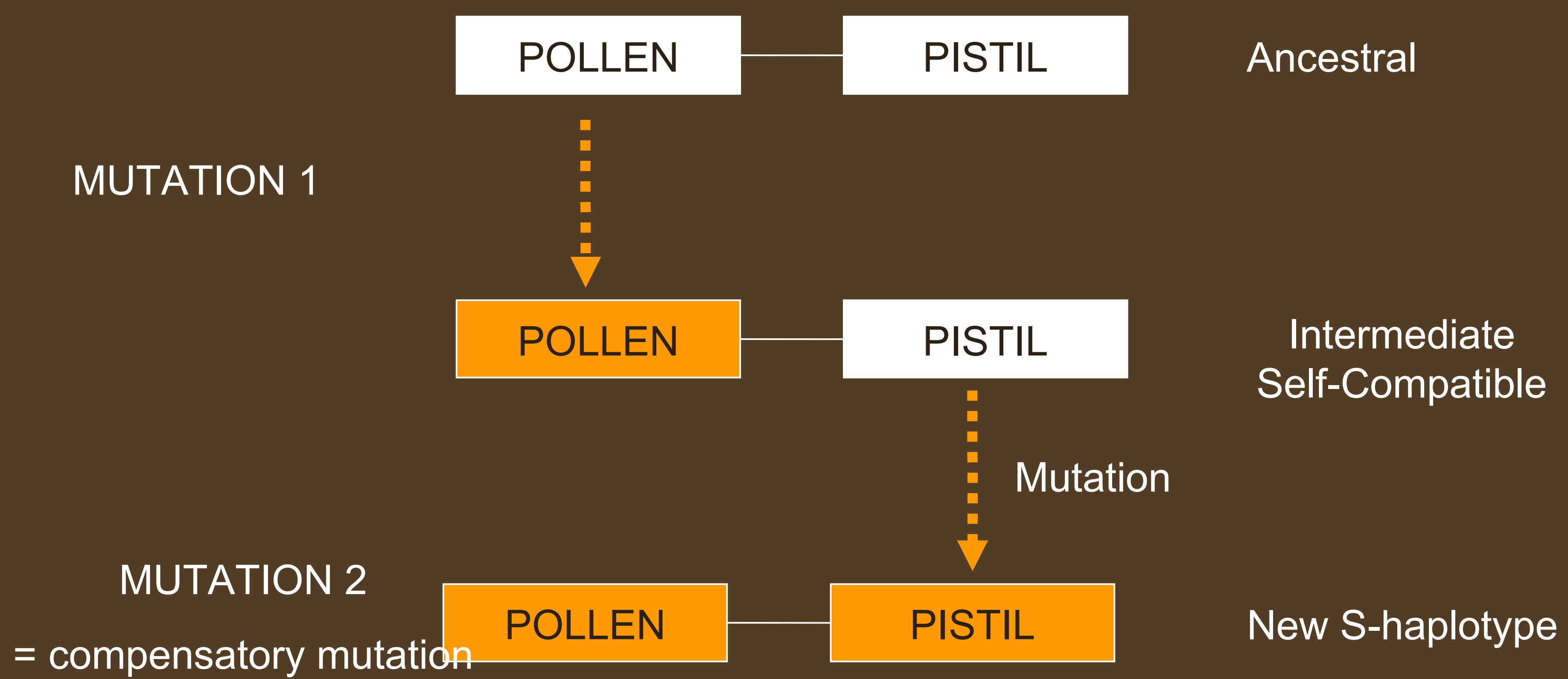
- Easy to understand how such a large diversity is maintained (Wright 1939)
- Hard to understand how it can be generated (sir R.A. Fisher 1961)

Mutation

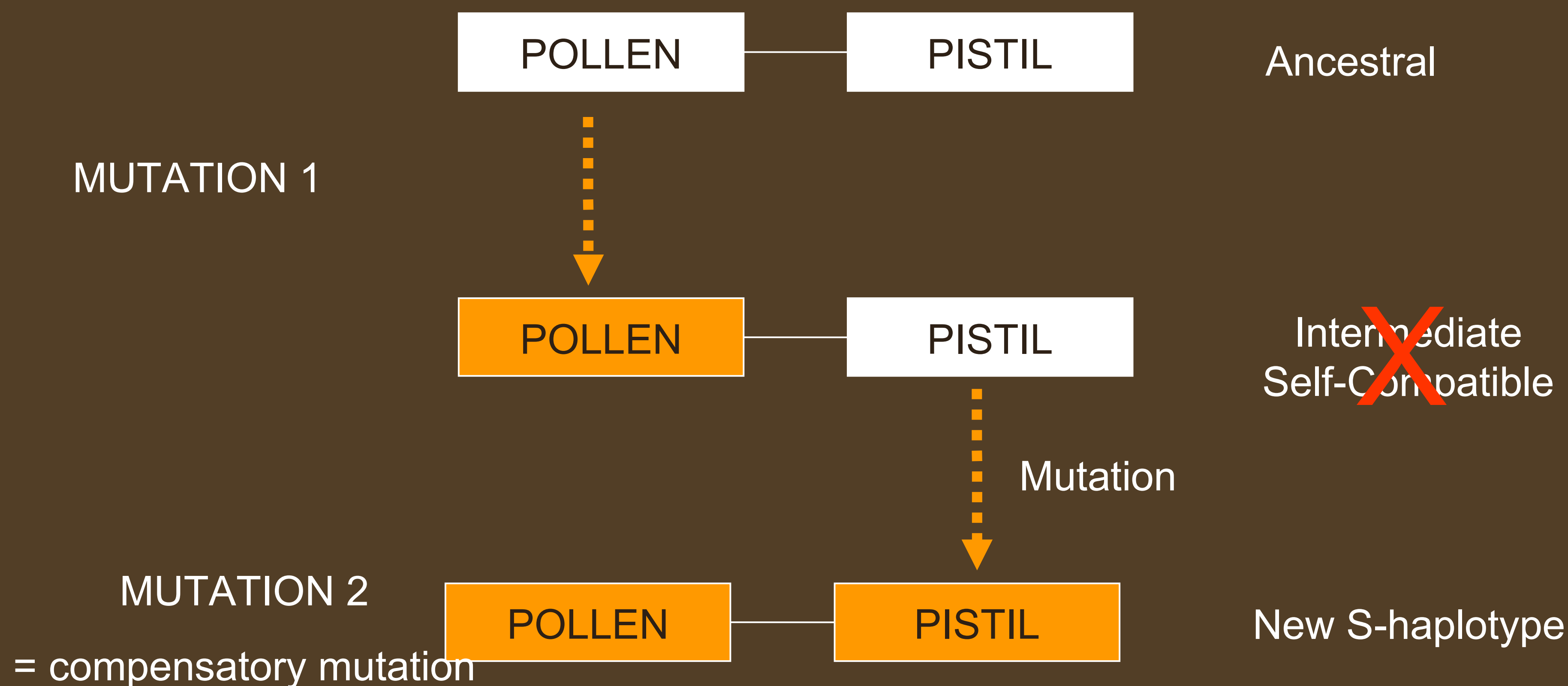
POLLEN	—	PISTIL	Recognition: Self-Incompatible
POLLEN	—	PISTIL	Non- Recognition: Self-Compatible

Self-Compatible haplotype can invade ⟶ SI Loss ⟶ Coevolution is necessary

Uyenoyama et al. (2001)'s model

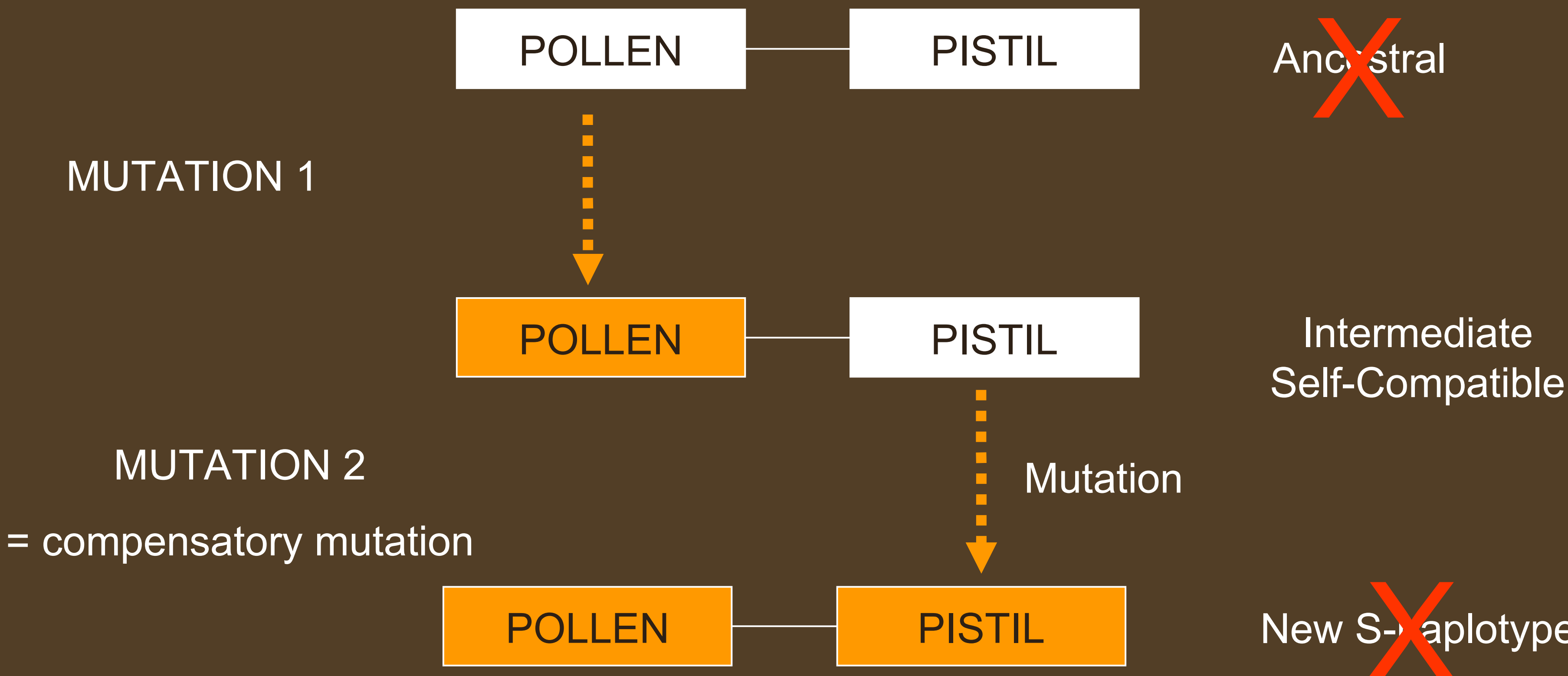


Uyenoyama et al. (2001)'s model



→ SI system remains unchanged

Uyenoyama et al. (2001)'s model



→ SI system is lost

The model (*based on Uyenoyama et al.2001)*

<u>ASSUMPTIONS</u>

-Unstructured population with *S* diploid individuals

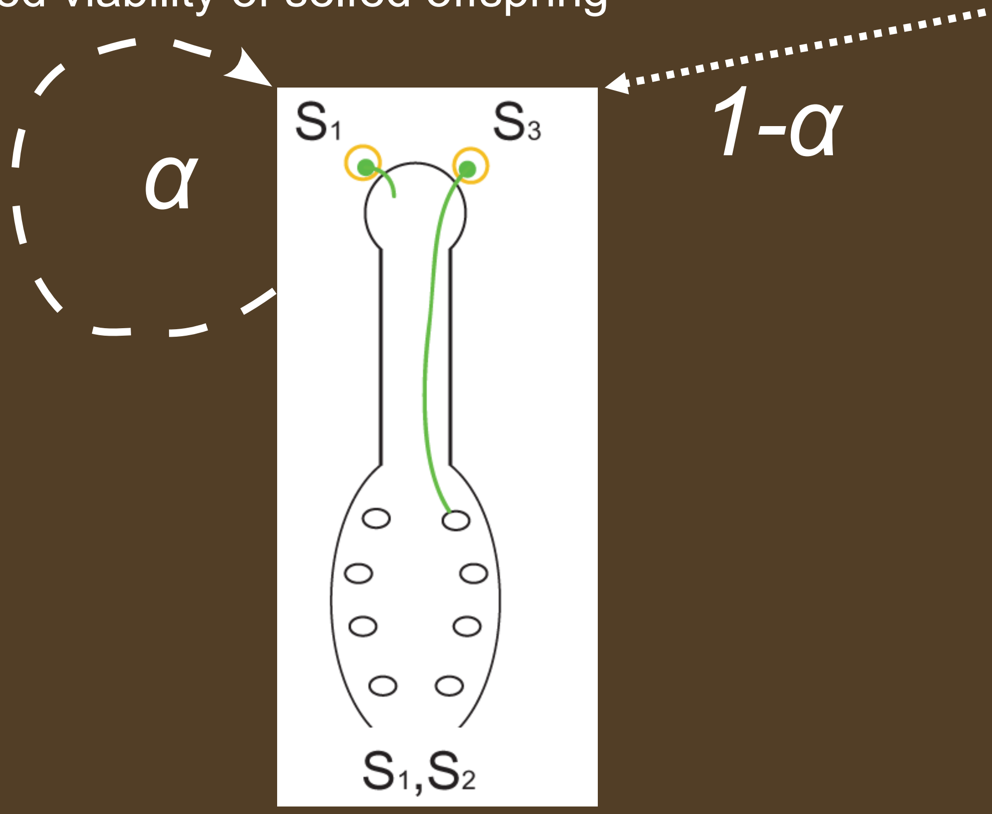
- Bipartite S-locus POLLEN — PISTIL

- Inbreeding depression *δ* = decreased viability of selfed offspring

- Self-pollination rate *α*

-Initial number of S-haplotypes *n*

-Max number of different alleles *K*



Description

$$X^t = \begin{pmatrix} x_{ij}^t \\ x_{bb}^t \\ x_{bi}^t \\ x_{ni}^t \\ x_{bn+1}^t \\ x_{nn+1}^t \\ x_{in+1}^t \\ \ldots \end{pmatrix}$$

i	POLLEN *i*	PISTIL *i*
j	POLLEN *j*	PISTIL *j*
n (ancestral)	POLLEN *n*	PISTIL *n*
b	POLLEN *n+1*	PISTIL *n*
n+1 (new)	POLLEN *n+1*	PISTIL *n+1*

What may happen...

$$X^t = \begin{pmatrix} x^t_{ij} \\ x^t_{bb} \\ x^t_{bi} \\ x^t_{ni} \\ x^t_{bn+1} \\ x^t_{nn+1} \\ x^t_{in+1} \\ \dots \end{pmatrix}$$

i	POLLEN *i*	PISTIL *i*
j	POLLEN *j*	PISTIL *j*
n (ancestral)	POLLEN *n*	PISTIL *n*
b	POLLEN *n+1*	PISTIL *n*
n+1 (new)	POLLEN *n+1*	PISTIL *n+1*

$$X^{t+1} \sim \frac{1}{S} M\left(X^{t} + \underbrace{R(X^{t}, \delta, \alpha)}_{\substack{\text{Reproduction} \\ \text{+ Viability selection}}} + \underbrace{U(X^{t}, u)}_{\substack{\text{Recurrent} \\ \text{Mutation}}}, S\right)$$

$$X^{t+1} \sim \frac{1}{S} M\left(X^t + R(X^t, \delta, \alpha) + U(X^t, u), S\right)$$

$$u = 0$$

$$S \to \infty$$

$$X^t = \begin{pmatrix} x^t_{ij} \\ x^t_{bb} \\ x^t_{bi} \\ x^t_{ni} \\ x^t_{bn+1} \\ x^t_{nn+1} \\ x^t_{in+1} \end{pmatrix}$$

$$R(X^t,\delta,\alpha) = \left(\begin{array}{l}
\frac{1}{\bar{W}}\left(x_{ij}\frac{(n-3)p}{N_{ij}} + x_{bi}(1-s_{bi})\,\frac{(n-2)p}{2N_{bi}} + x_{ni}\frac{(n-2)p}{2N_{ni}} + x_{in+1}\frac{(n-2)p}{2N_{in+1}}\right) \\
\frac{1}{\bar{W}}\left(x_{bb}\left(s_{bb}(1-\delta) + (1-s_{bb})\,\frac{p_b}{N_{bb}}\right) + \frac{x_{bn}}{2}\left(s_{bn}(1-\delta) + (1-s_{bn})\,\frac{p_b}{N_{bn}}\right) + \right. \\
\left.\frac{x_{bi}}{2}\left(s_{bi}(1-\delta) + (1-s_{bi})\,\frac{p_b}{N_{bi}}\right)\right) x'_{bn} = \frac{1}{\bar{W}}\left(\frac{x_{bn}}{2}\left(s_{bn}(1-\delta) + (1-s_{bn})\,\frac{p_b}{N_{bn}}\right) + x_{ni}\frac{p_b}{2N_{ni}}\right) \\
\frac{1}{\bar{W}}\left(x_{ij}\frac{p_b}{N_{ij}} + x_{bb}(1-s_{bb})\,\frac{(n-1)p}{N_{bb}} + x_{bn}(1-s_{bn})\,\frac{(n-1)p}{2N_{bn}}\right. \\
\qquad \left. + \frac{x_{bi}}{2}\left(s_{bi}(1-\delta) + (1-s_{bi})\,\frac{(p_b + (n-2)p)}{N_{bi}}\right) + x_{ni}\frac{p_b}{2N_{ni}} + x_{bn+1}\frac{(n-1)p}{2N_{bn+1}}\right) \\
\frac{1}{\bar{W}}\left(x_{ij}\frac{p_n}{N_{ij}} + x_{bn}(1-s_{bn})\,\frac{(n-1)p}{2N_{bn}} + x_{ni}\frac{(n-2)p}{2N_{ni}} + x_{nn+1}\frac{(n-1)p}{2N_{nn+1}} + x_{in+1}\frac{p_n}{2N_{in+1}}\right) \\
\frac{1}{\bar{W}}\left(x_{bb}(1-s_{bb})\,\frac{p_{n+1}}{N_{bb}} + x_{bn}(1-s_{bn})\,\frac{p_{n+1}}{2N_{bn}} + x_{bi}(1-s_{bi})\,\frac{p_{n+1}}{2N_{bi}}\right) \\
\frac{1}{\bar{W}}\left(x_{bn}(1-s_{bn})\,\frac{p_{n+1}}{2N_{bn}} + x_{ni}\frac{p_{n+1}}{2N_{ni}} + x_{in+1}\frac{p_n}{2N_{in+1}}\right) \\
\frac{1}{\bar{W}}\left(x_{ij}\frac{p_{n+1}}{N_{ij}} + x_{bi}(1-s_{bi})\,\frac{p_{n+1}}{2N_{bi}} + x_{ni}\frac{p_{n+1}}{2N_{ni}} + x_{bn+1}\frac{(n-1)p}{2N_{bn+1}} + x_{nn\,+\,1}\frac{(n-1)p}{2N_{nn+1}}\right. \\
\qquad \left. + x_{in+1}\frac{(n-2)p}{2N_{in+1}}\right),
\end{array} \right)$$

$$x'_{bi} = \frac{1}{\bar{W}}\left(x_{ij}\frac{p_b}{N_{ij}} + x_{bb}(1 - s_{bb})\,\frac{(n-1)p}{N_{bb}} + x_{bn}(1 - s_{bn})\,\frac{(n-1)p}{2N_{bn}}\right.$$
$$\left. + \frac{x_{bi}}{2}\left(s_{bi}(1-\delta) + (1 - s_{bi})\,\frac{(p_b + (n-2)p)}{N_{bi}}\right) + x_{ni}\frac{p_b}{2N_{ni}} + x_{bn+1}\frac{(n-1)p}{2N_{bn+1}}\right)$$

x_{uv} *frequency of genotype uv*

S_{uv} selfing rate of genotype *uv*

N_{uv} *proportion of compatible pollen received by genotype uv*

p_b frequency of allele *b*

p frequency of allele i

W mean fitness (normalization term because of selection)

4 interesting equilibria

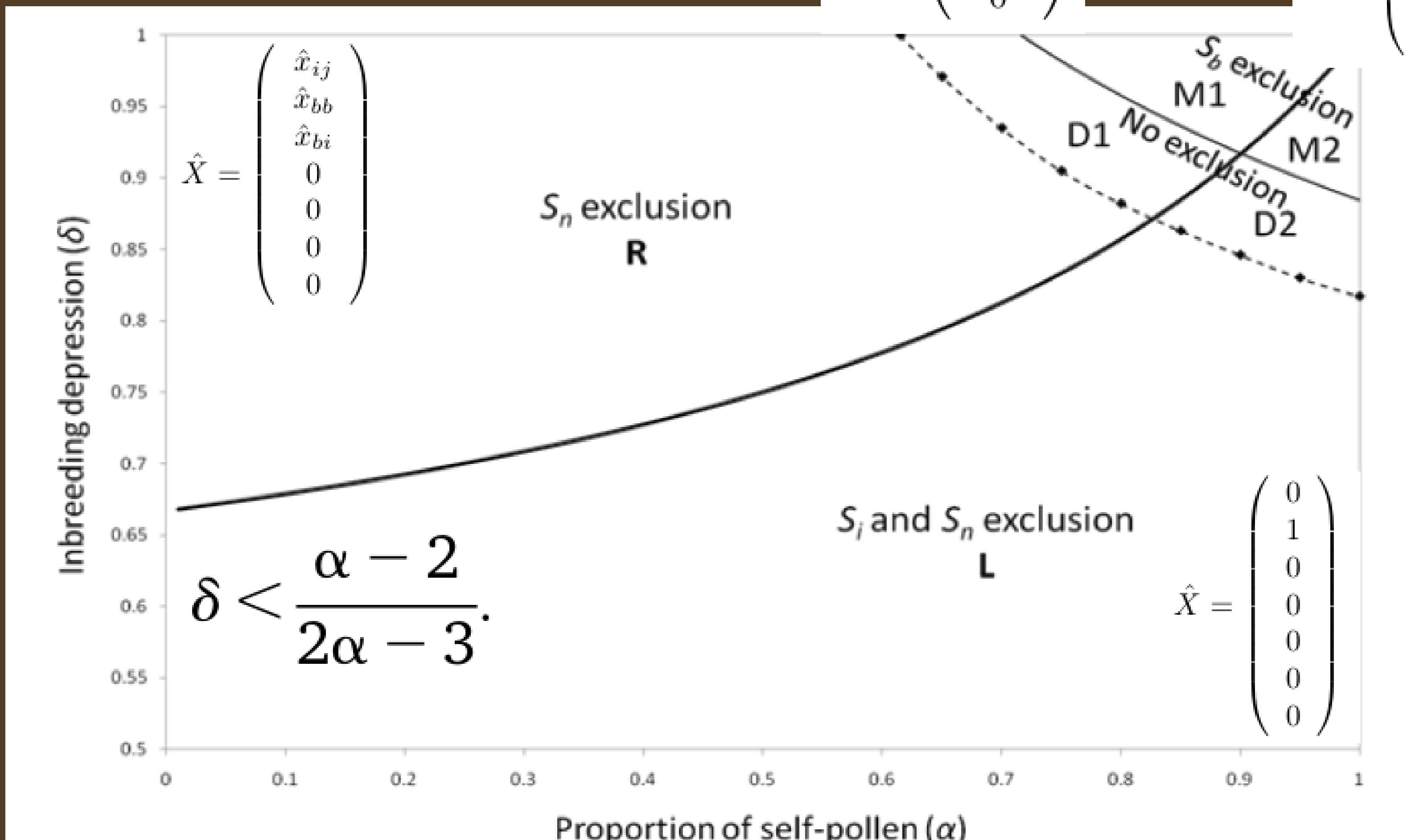
$$X^t = \begin{pmatrix} x_{ij}^t \\ x_{bb}^t \\ x_{bi}^t \\ x_{ni}^t \\ x_{bn+1}^t \\ x_{nn+1}^t \\ x_{in+1}^t \end{pmatrix}$$

$$\hat{X} = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} \qquad \hat{X} = \begin{pmatrix} 0 \\ 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} \qquad \hat{X} = \begin{pmatrix} \hat{x}_{ij} \\ \hat{x}_{bb} \\ \hat{x}_{bi} \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} \qquad \hat{X} = \begin{pmatrix} \hat{x}_{ij} \\ \hat{x}_{bb} \\ \hat{x}_{bi} \\ \hat{x}_{ni} \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

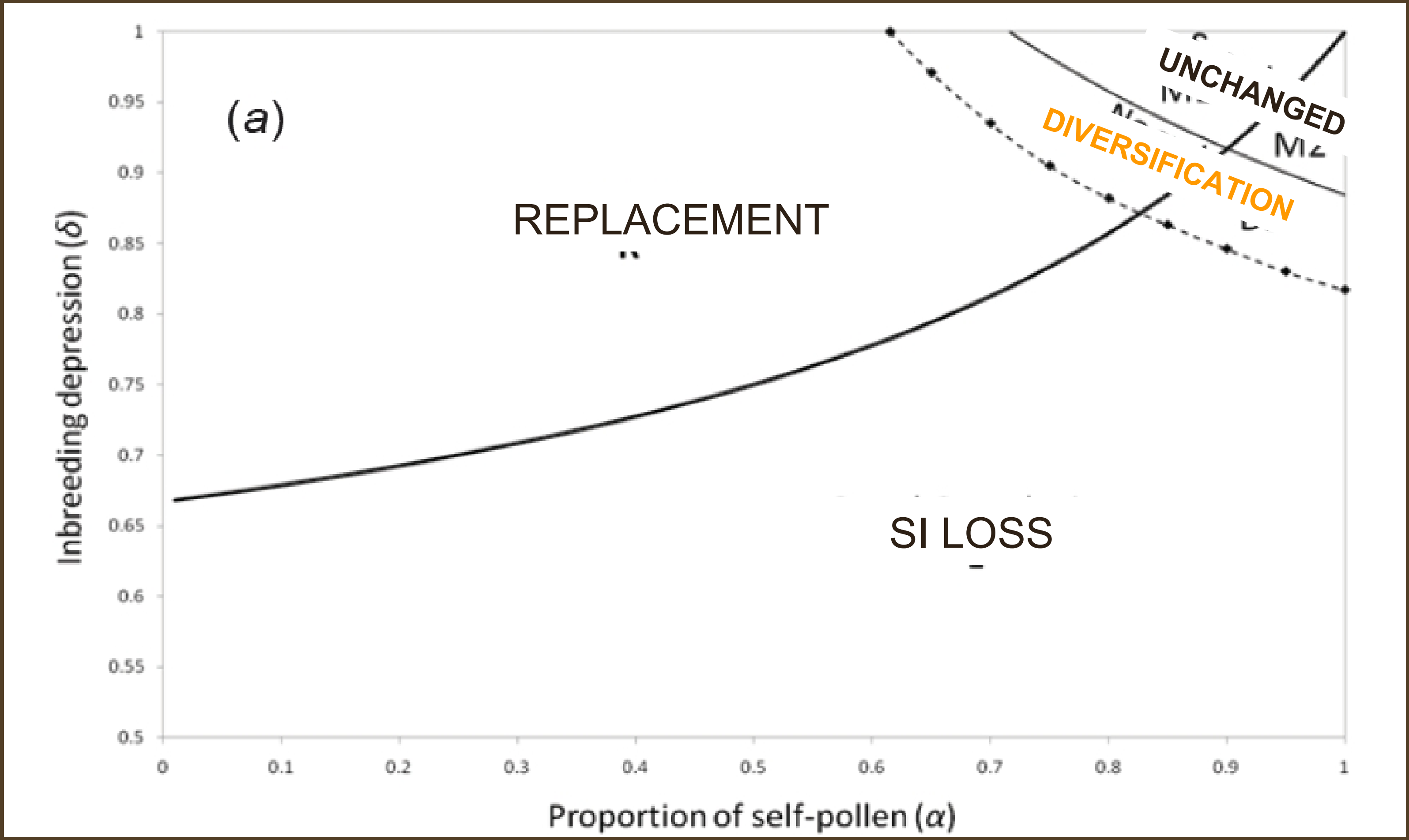
deterministic outcomes

$n = 5$

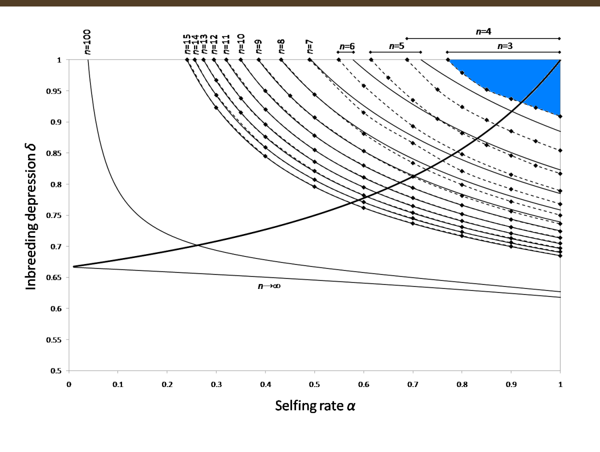
$$\hat{X} = \begin{pmatrix} \hat{x}_{ij} \\ \hat{x}_{bb} \\ \hat{x}_{bi} \\ \hat{x}_{ni} \\ 0 \\ 0 \\ 0 \end{pmatrix} \qquad \hat{X} = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$



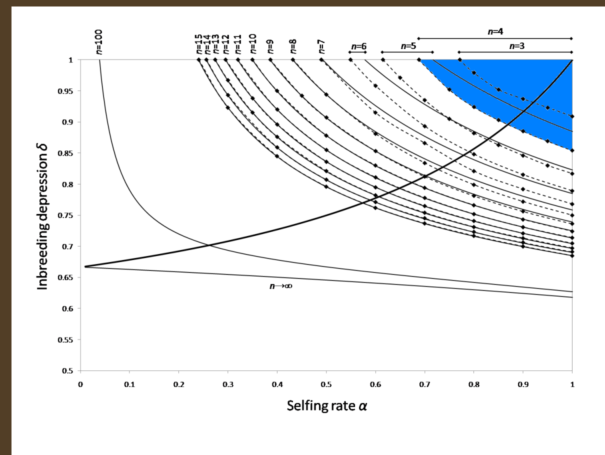
$n = 5$


(a)
REPLACEMENT
SI LOSS
UNCHANGED
DIVERSIFICATION
Inbreeding depression (δ)
Proportion of self-pollen (α)
1
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0.6
0.55
0.5
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

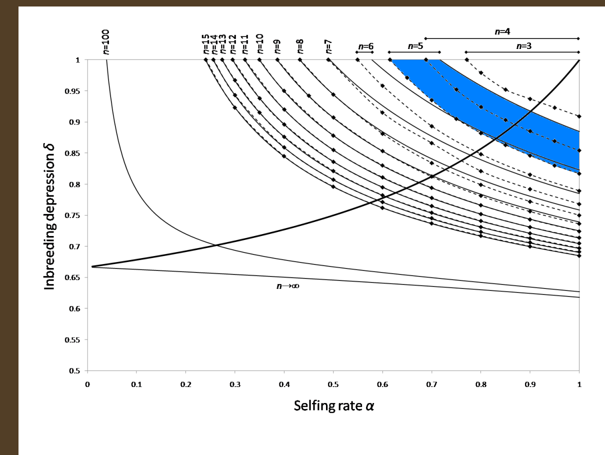
n = 3



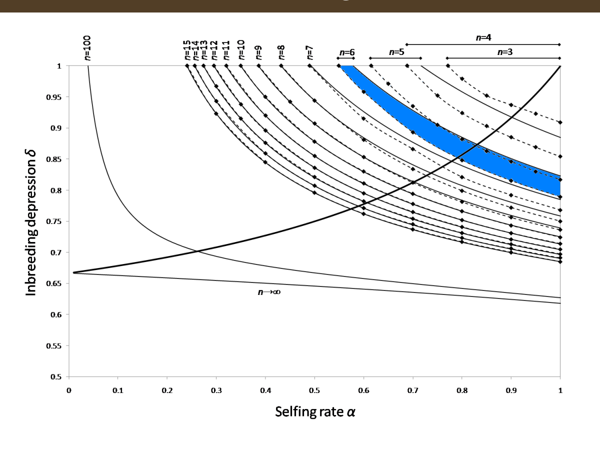
n = 4



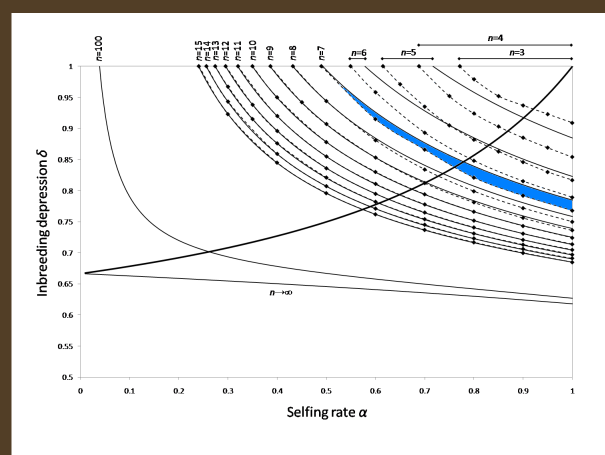
n = 5



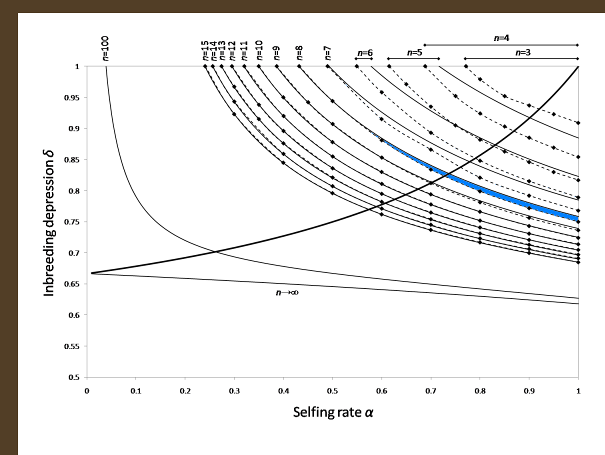
n = 6



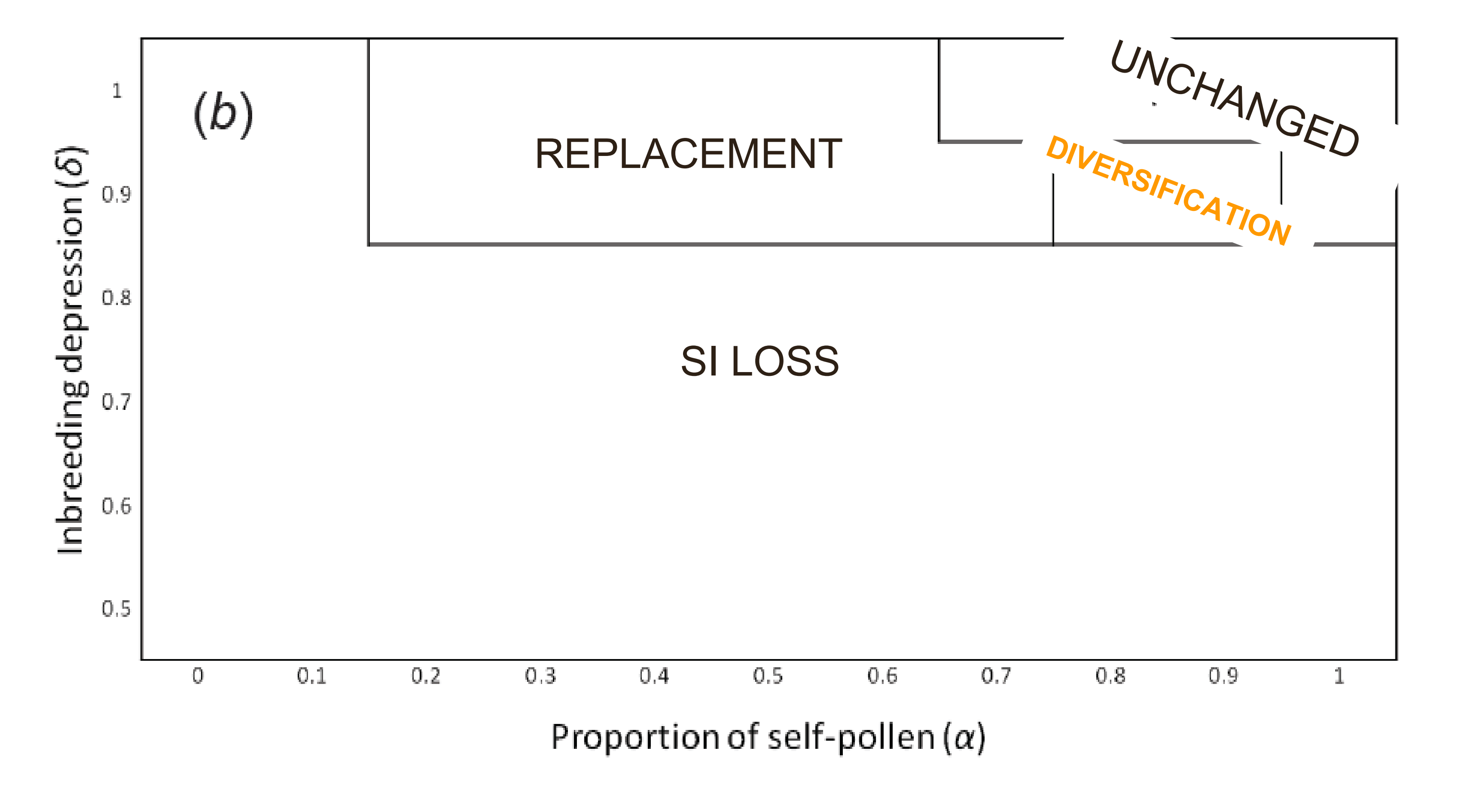
n = 7



n = 8



$N = 5, K=20, u=5.10^{-7}, S=5000$



Diversification probability in finite populations

100 replicates

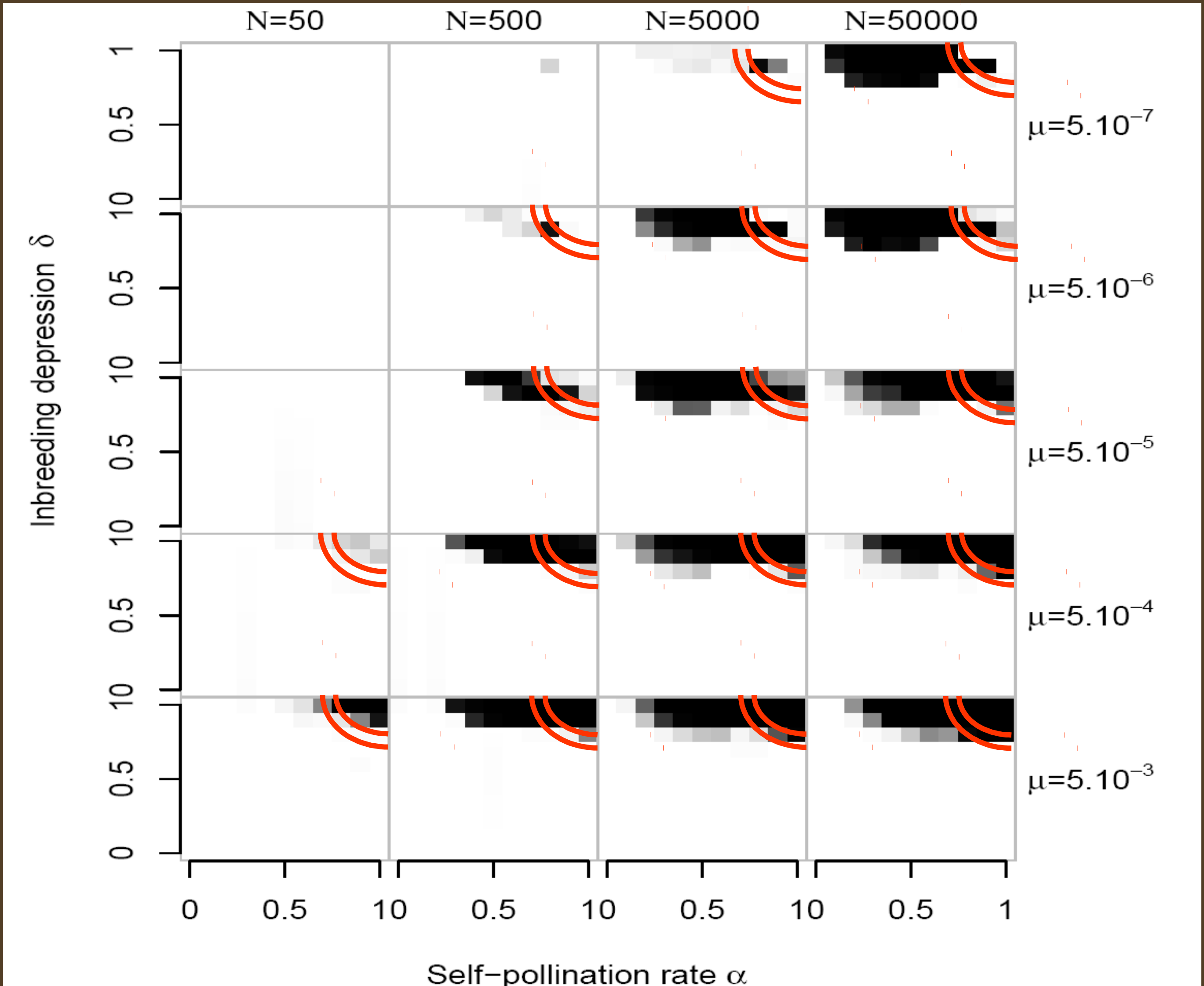
n = 5

100% diversification

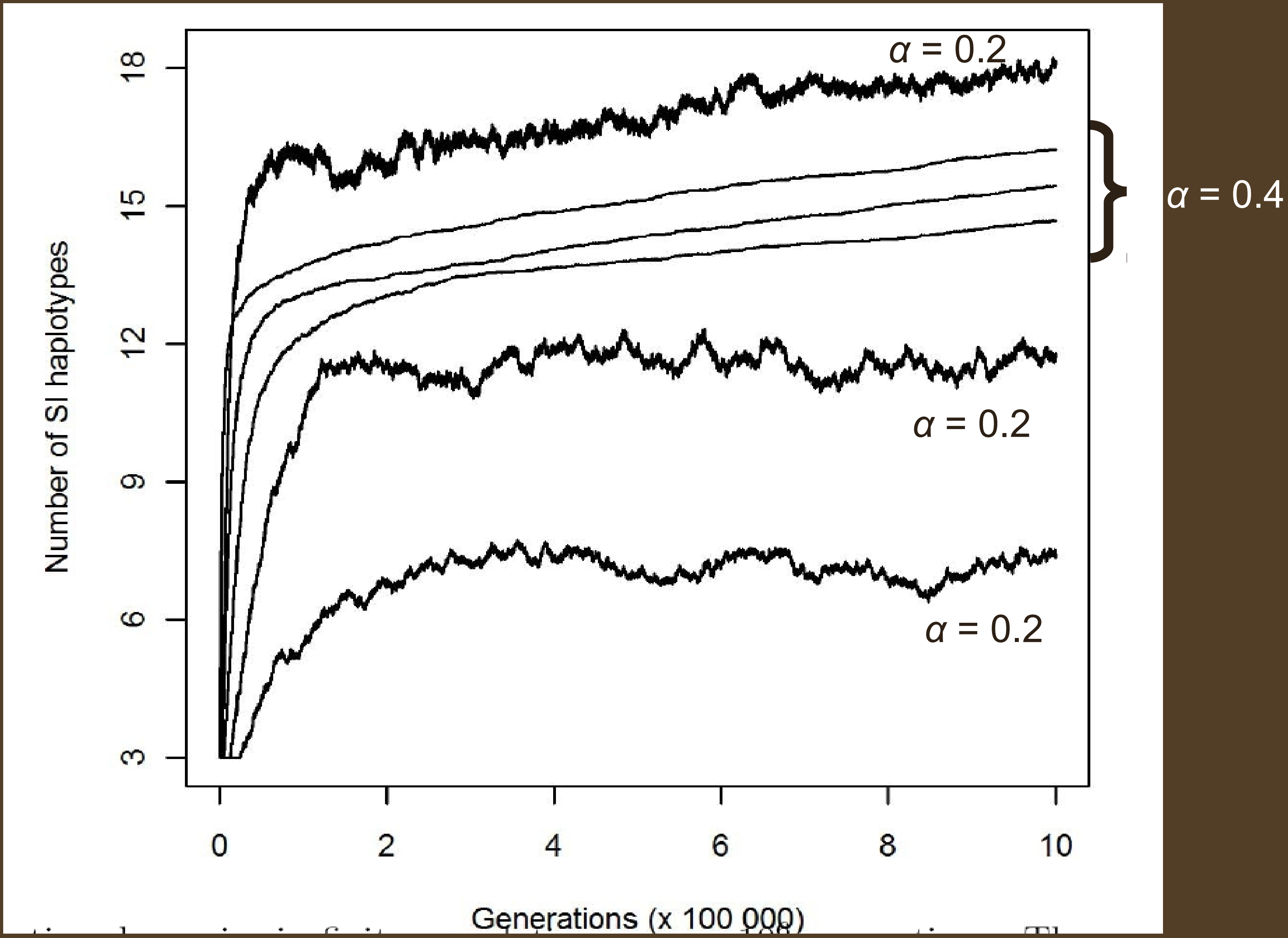
(n > 5)

0% diversification

(0 < n < 5)

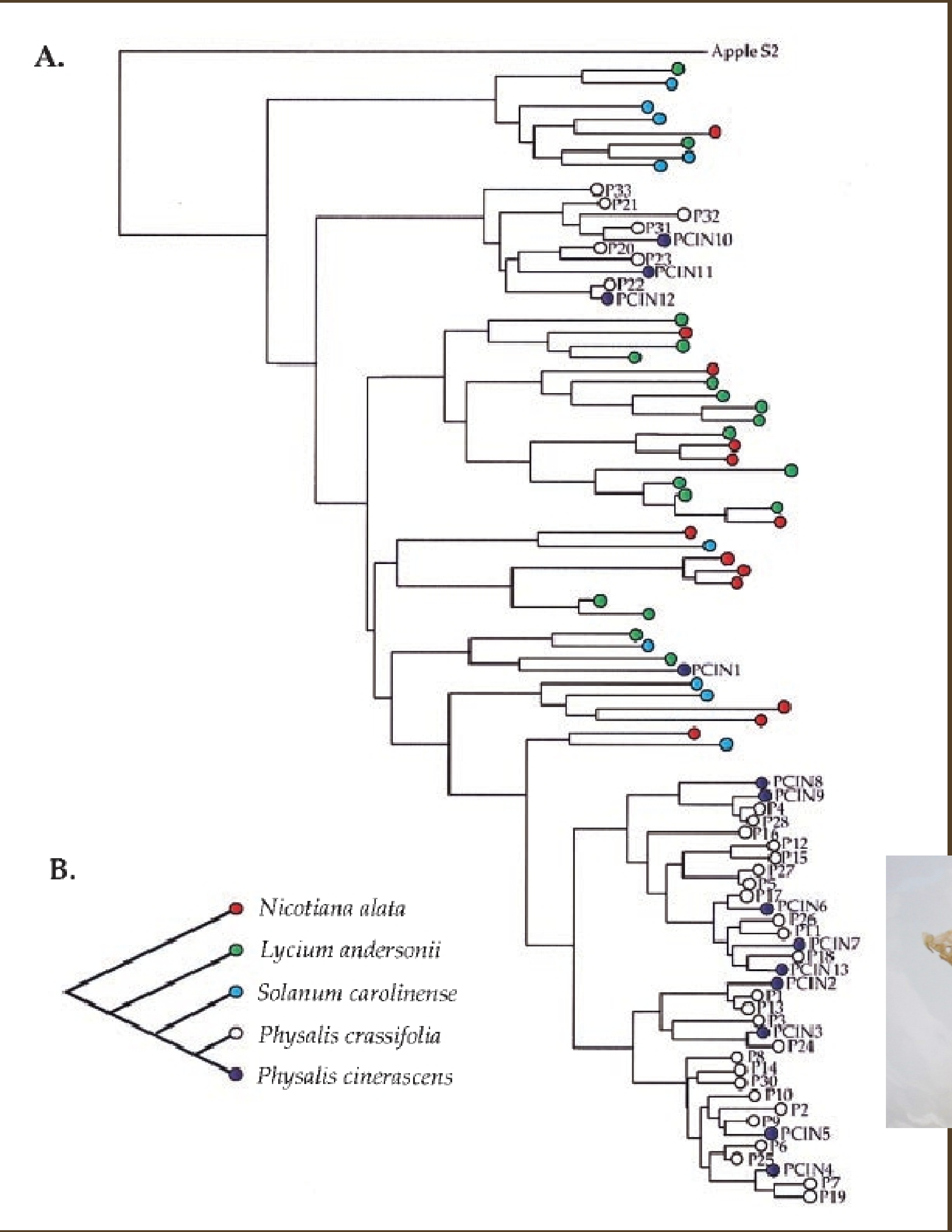


n with time


α = 0.2
α = 0.4
α = 0.2
α = 0.2
Number of SI haplotypes
18
15
12
9
6
3
0
2
4
6
8
10
Generations (x 100 000)

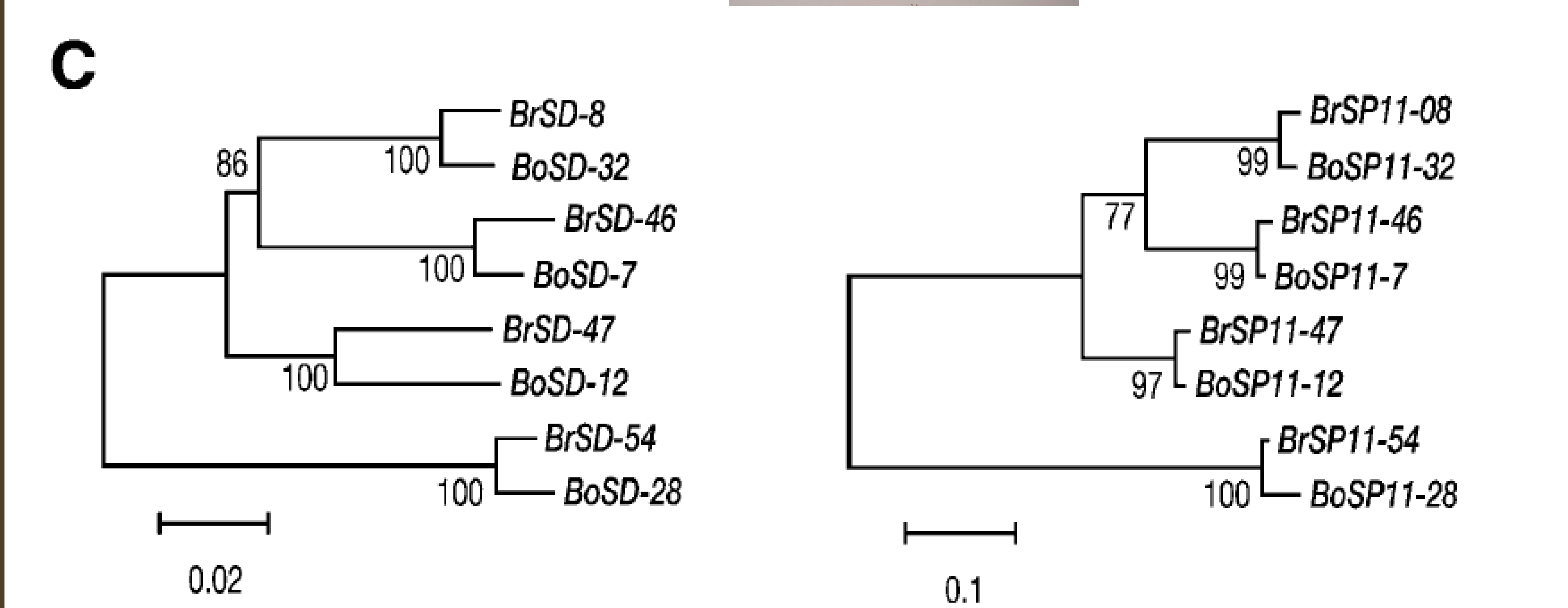
back to data

e.g. In Solanaceae
(Richman & Kohn 1999)



back to data

e.g. In Brassicaceae (*B. rapa*)
(Takuno et al. 2007)



PISTIL

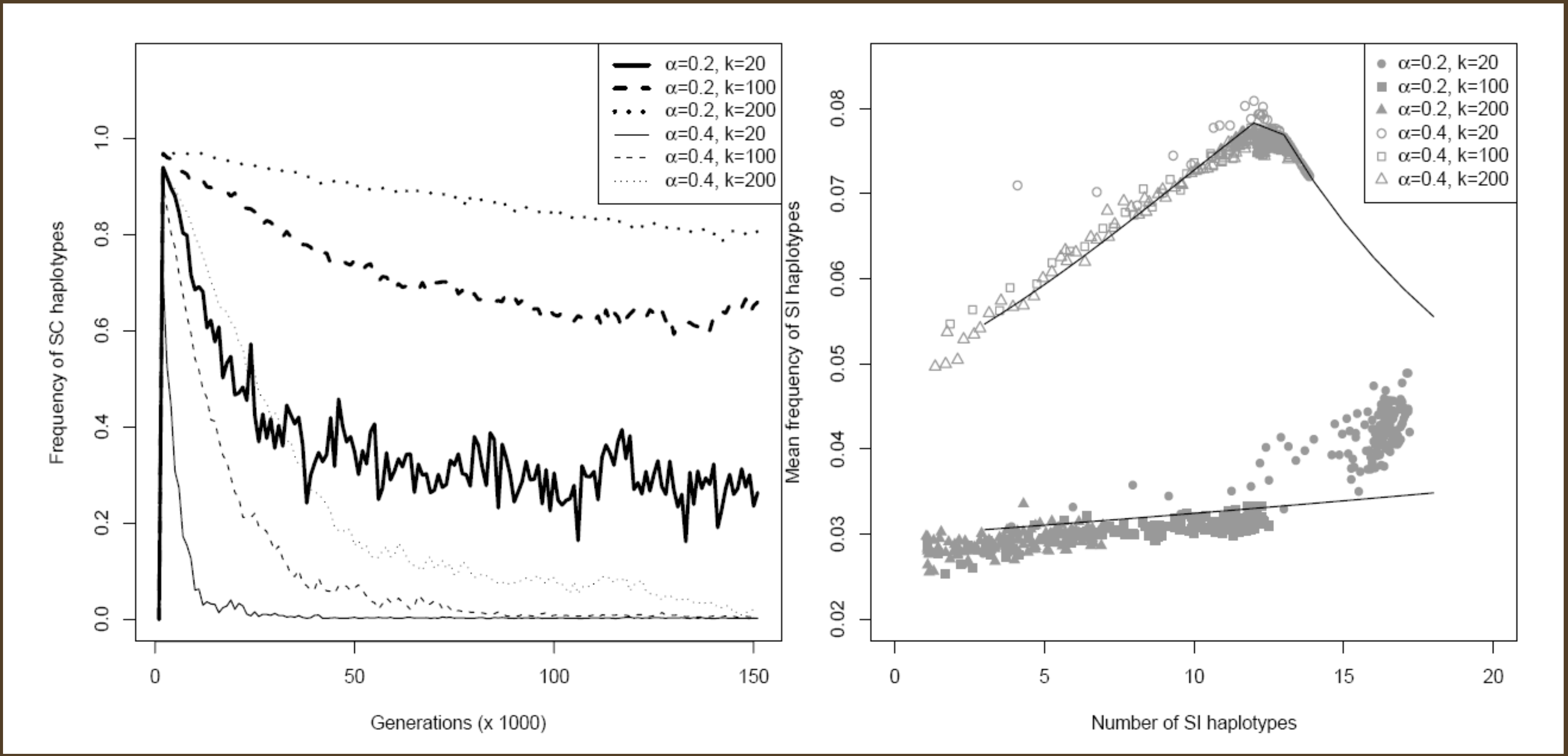
POLLEN

back to data

Allele number

(Castric & Vekemans 2004)

Species	N_{ind}	$n_{alleles}$
Gametophytic SI system		
Crataegus monogyna	13	17
Lycium andersonii	16	22
Oenothera organensis	67	34
Papaver rhoeas	51	31
Phlox drummondii	24	30
Physalis cinerascens	14	13
Physalis crassifolia	22	28
Prunus lannesiana	67	21
Solanum carolinense	24	12
Sorbus aucuparia	20	20
Trifolium repens	25	36
Witheringia maculata	12	10

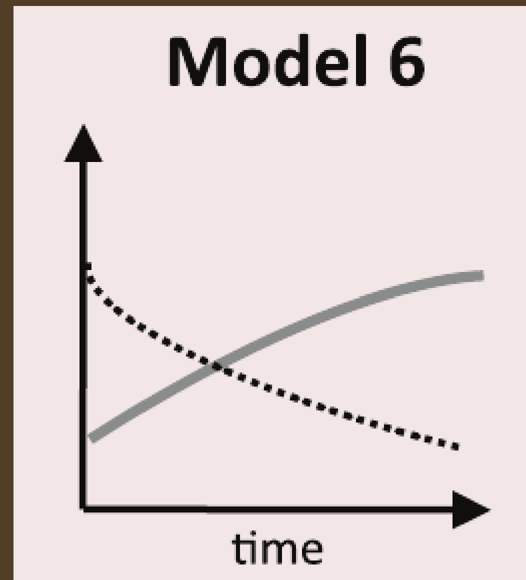


Frequency of SC haplotypes
Generations (x 1000)
α=0.2, k=20
α=0.2, k=100
α=0.2, k=200
α=0.4, k=20
α=0.4, k=100
α=0.4, k=200
Mean frequency of SI haplotypes
Number of SI haplotypes

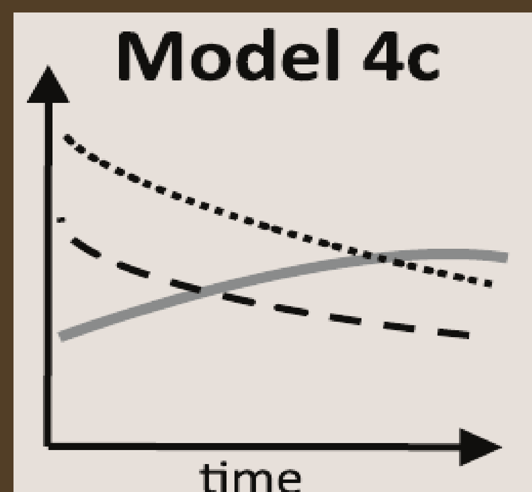
going further

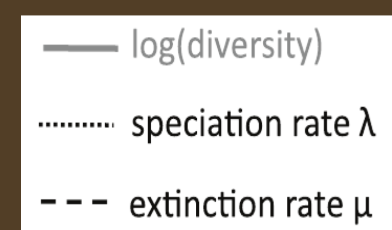
Decaying diversification rate with increasing diversity: a general property?

Best model of speciation
(Morlon et al. 2010)



Best model of diversification
at the S-locus?





Decaying diversification rate with increasing diversity: a general property?

Looking for analogs: speciation with coevolution?