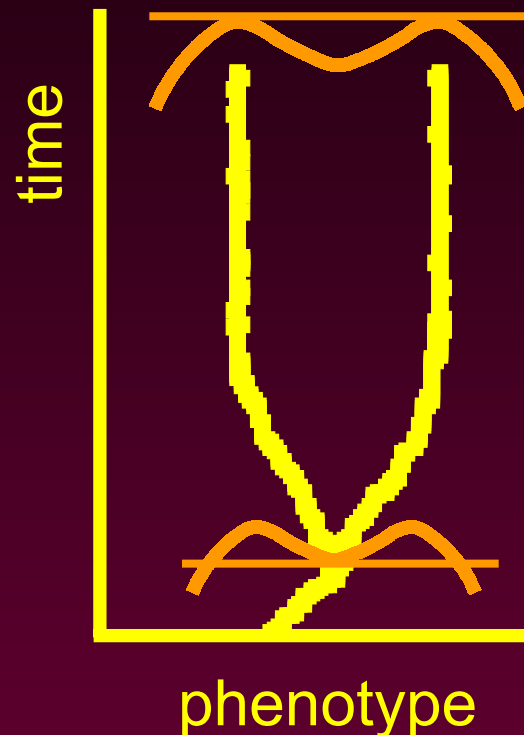


From disruptive selection to the origin of species



evolution to a fitness minimum:
disruptive selection

AD: evolutionary branching

(non-allopatric) speciation???



Evolutionary branching is common in clonal models

<i>Resource competition</i>	● Christiansen & Loeschcke 1980 ● Abrams et al. 1993 ● Metz et al. 1996 ● Meszéna & Metz 1996 ● Dieckmann & Doebeli 1999 ● Day 2000 ● Day 2001 ● Drossel & McKane 2000
<i>Asymmetric competition</i>	● Abrams et al. 1993 ● Geritz et al. 1999 ● Kisdi 1999 ● Jansen & Mulder 1999 ● Kisdi & Geritz 2001
<i>Predation</i>	● Abrams et al. 1993 ● Doebeli & Dieckmann 2000
<i>Host-parasite systems</i>	● Boots & Haraguci 1999
<i>Mutualism</i>	● Doebeli & Dieckmann 2000 ● Law et al. 2001
<i>Spatial heterogeneity</i>	● Brown & Pavlovic 1992 ● Meszéna et al. 1997 ● Geritz et al. 1998 ● Kisdi & Geritz 1999 ● Geritz & Kisdi 2000 ● Kisdi 2001 ● Mathias & Kisdi 2002
<i>Temporal fluctuations</i>	● Kisdi <i>in prep.</i>
<i>Metapopulations</i>	● Cohen & Levin 1991 ● Doebeli & Ruxton 1997 ● Parvinen 1999 ● Mathias et al. 2001 ● Kisdi 2002 ● Parvinen in press
<i>Mating systems</i>	● Hoekstra 1980 ● Metz et al. 1992 ● Cheptou & Mathias 2001 ● De Jong & Geritz 2001 ● Maire et al. 2001
<i>Sexual selection</i>	● Van Doorn & Weissing 2001
<i>Prebiotic replicators</i>	● Meszéna & Szathmáry 2001

One locus, many alleles: Genetic polymorphism



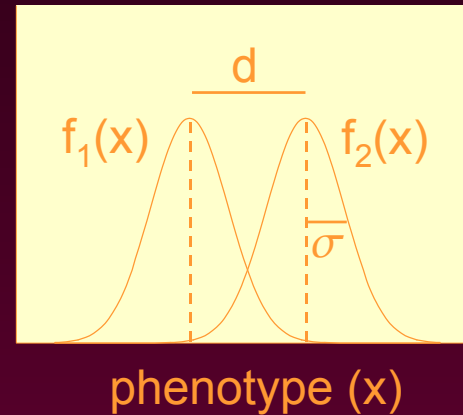
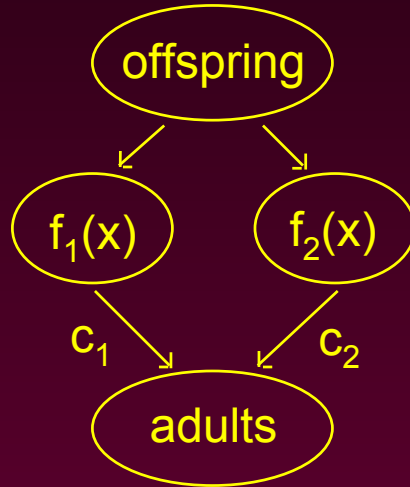
Invasion fitness of a rare mutant allele y
= invasion fitness of a rare phenotype $(x+y)/2$

Evolutionary branching with clonal inheritance
= evolutionary branching of alleles
= genetic polymorphism

Evolution in a polymorphic population:
clonal and diploid sexual cases are different

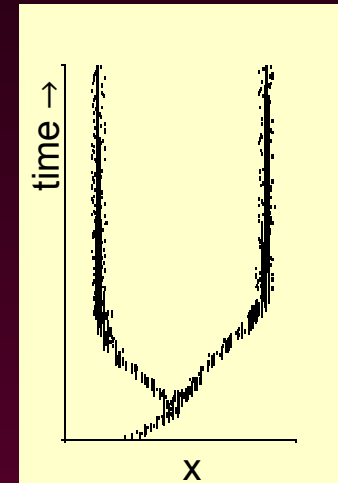
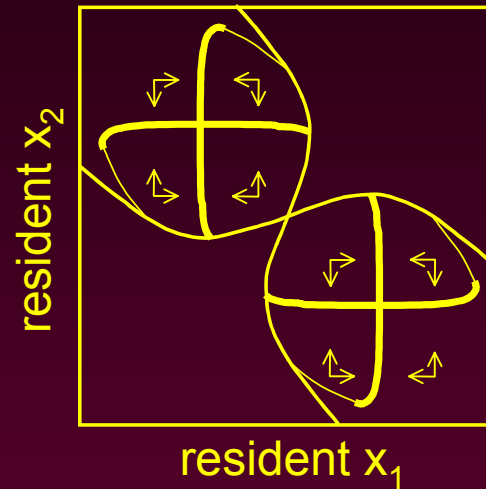
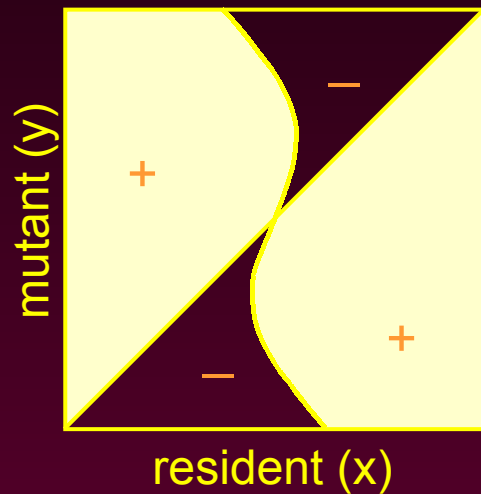
Two-patch soft selection model (Levene-model)

- random dispersal to two patches
- within-patch selection
- within-patch competition: fixed number of emerging adults



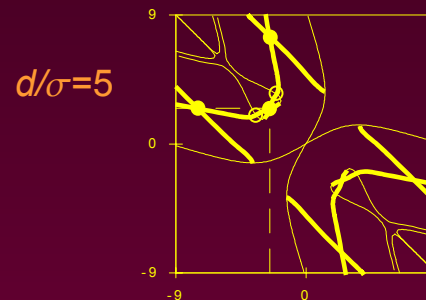
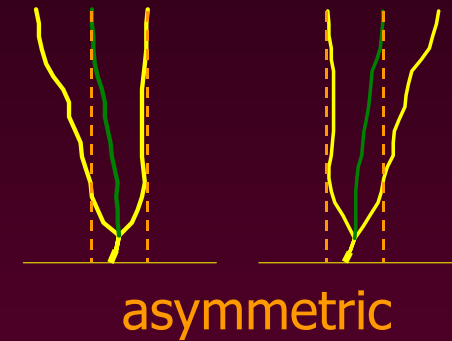
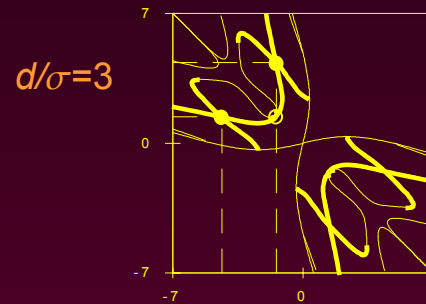
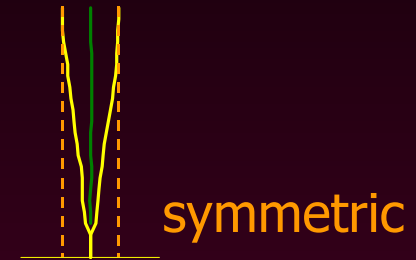
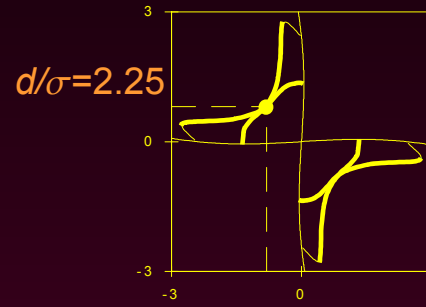
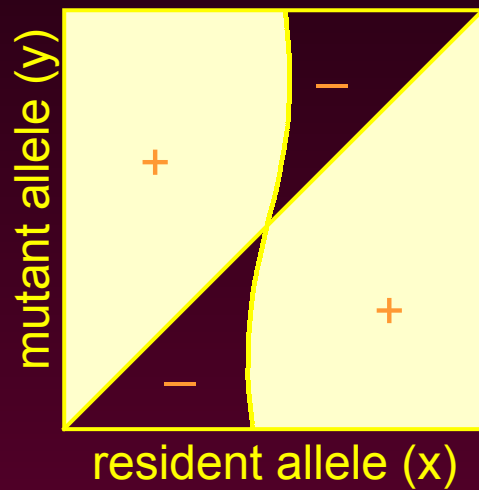
Two-patch soft selection model (Levene-model)

Clonal version



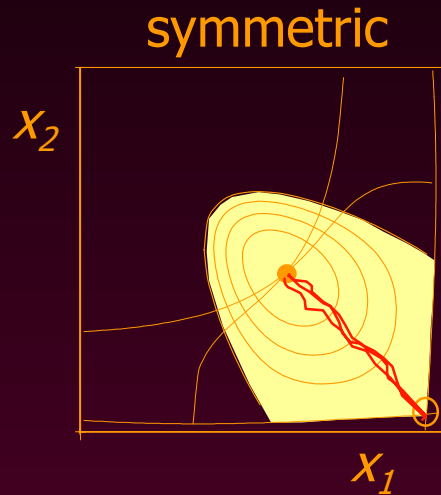
Two-patch soft selection model (Levene-model)

Diploid version



symmetric + asymmetric

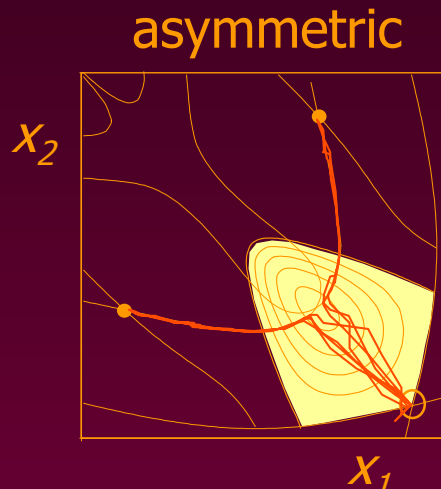
Selection against hybrids (Levene-model)



Selection against intermediate phenotypes
= selection against heterozygotes

→ Evolution of dominance
full dominance \equiv clonal dynamics

→ Evolution of assortative mating



- heterozygote disadvantage
- evolutionary trajectory
- branching point
- evolutionarily stable polymorphism

The evolution of assortative mating

- **Mate choice depends on the ecological trait**

Branching = speciation

e.g. body size (benthic-limnetic sticklebacks)

- **“One-allele” mechanisms**

Branching = speciation

e.g. less dispersal: local mating with similar individuals

- **“Two-allele” mechanisms**

mating is based on an independently segregating trait

e.g. flowering time in plants

??? may be under disruptive selection

(*Mimulus guttatus* metal-tolerant race)



**recombination between the ecological and the mating locus
-- strong selection / tight linkage needed**

Speciation

Biological species concept: Reproductive isolation

Ecological stability: Niche differentiation

Speciation by sexual selection yields ecologically identical sister species. If it happens at a branching point, subsequent divergence ensures differentiation

Multilocus genetics: Directional evolution

Quantitative Genetics (with separate species):

$$\Delta \bar{z}_i = V_{Ai} \left. \frac{\partial W(z; \bar{z}_1, \dots, \bar{z}_n)}{\partial z} \right|_{z=\bar{z}_i}$$

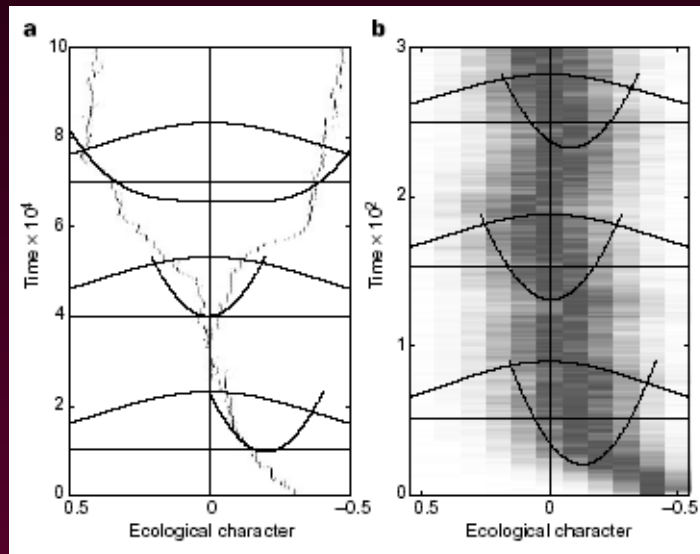
Canonical Equation of Mutation-Limited Evolution:

$$\frac{dx_i}{dt} = \frac{1}{2} \mu_i \sigma_i^2 \hat{N}_i(x_1, \dots, x_n) \left. \frac{\partial s_{x_1, \dots, x_n}(y)}{\partial y} \right|_{y=x_i}$$

Multilocus genetics: Branching?

clonal model

multilocus model



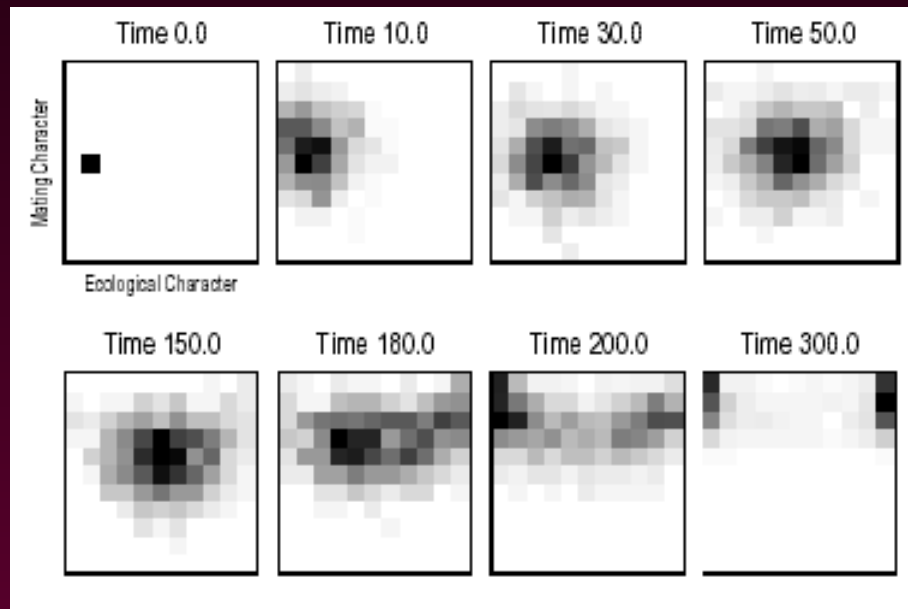
recombination between the ecological loci prevents branching

assortative mating needed for evolutionary branching itself (and then it is speciation)

Lotka-Volterra resource competition model

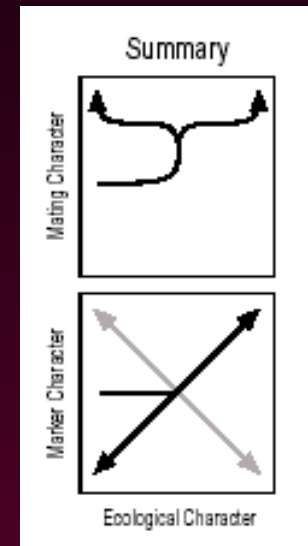
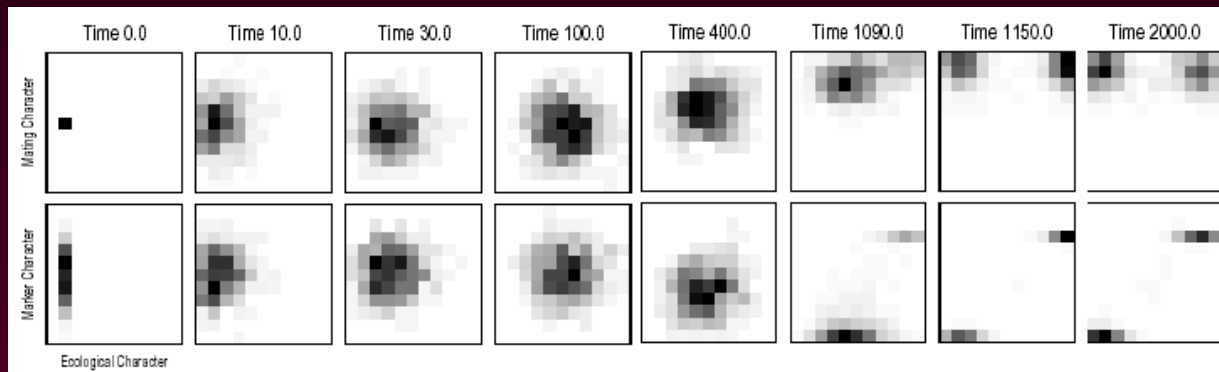
Multilocus genetics & assortative mating

I. Mate choice based on the ecological trait



Multilocus genetics & assortative mating

II. Mate choice based on a neutral marker character



Multilocus genetics & assortative mating

Mate choice based on a neutral marker character

- grim expectation from classic models:

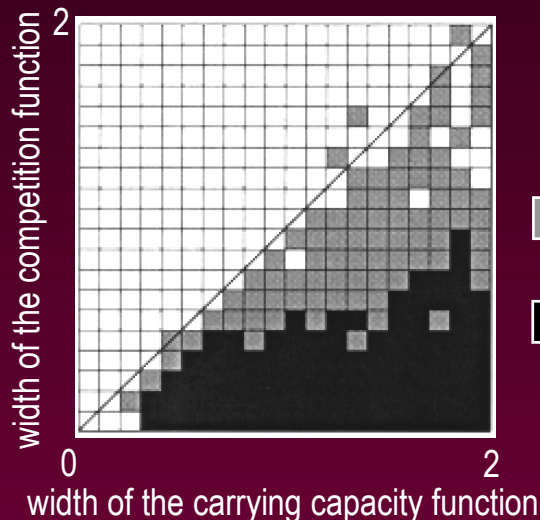


Weak selection at the branching point - no linkage

No linkage - mating is not assortative by the ecological trait

No assortative mating - no branching

Finite population size: initial linkage by genetic drift - it works



■ assortative mating based on the ecological trait

■ assortative mating based on a marker trait
(linkage disequilibrium necessary)

Take Home



Adaptive Dynamics



evolution to fitness minima is common

Evolution of diversity



within-species genetic polymorphism
speciation

References

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Kisdi E. & S. A. H. Geritz. 1999. Adaptive dynamics in allele space: Evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution* 53:993-1008.

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