

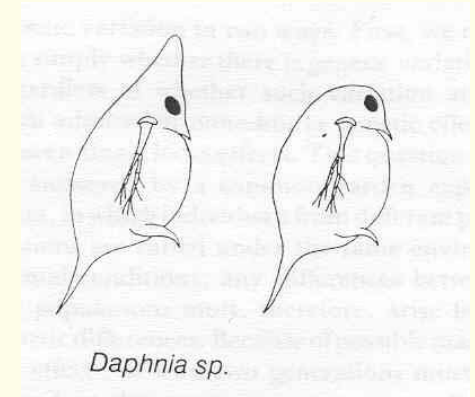
# Alternative phenotypes and the evolution of morph determination: an adaptive dynamics perspective

Olof Leimar

Department of Zoology, Stockholm University

**Alternative phenotypes**  
**Phenotypic polymorphism**  
**Heteromorphism**  
**Polyphenism**

**members of a population fall into two or more fairly distinct categories (morphs) with respect to some of their traits**



**Three systems**      **random, genetic, and environmental morph determination (combinations are possible)**

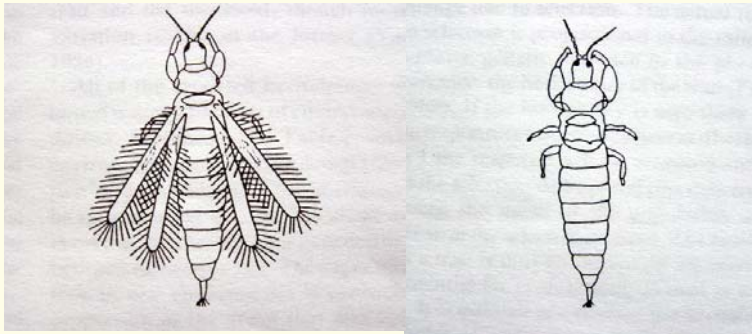
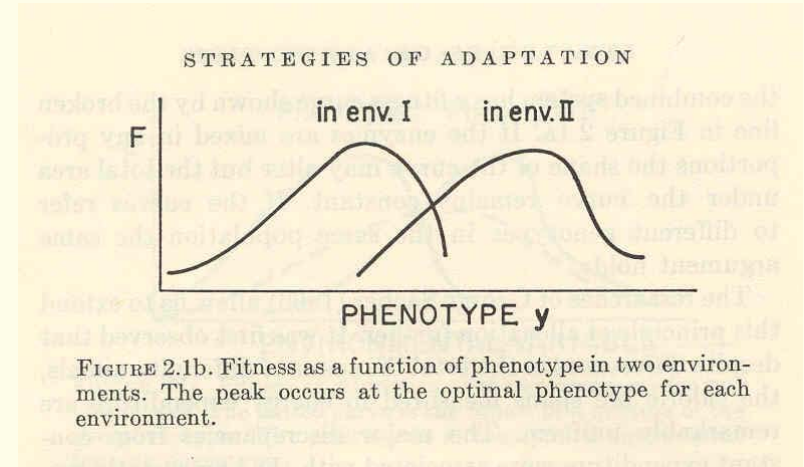
- **Summary and recapitulation of important ideas in the field**
- **Sketch unifying theory of the evolution of genetic vs. random morph determination**
  - based on evolutionary stability and evolutionary branching in different trait spaces
  - disruptive selection and related processes as unifying theme

# Phenotypic polymorphism

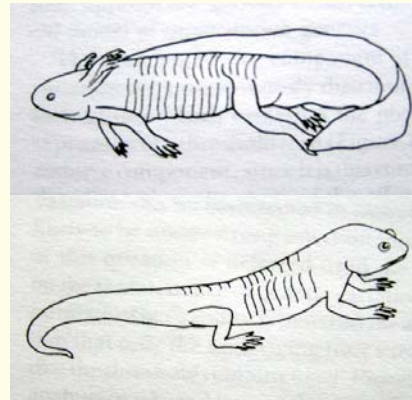
Basic idea: Some advantage from specialization

Levins, 1968, *Changing Environments*

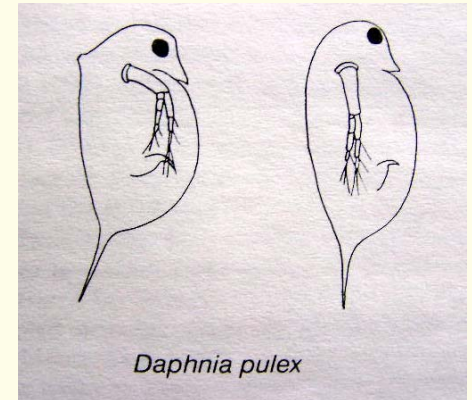
- **Levene (1953)**
  - multiple-niche polymorphism
- **Cohen (1966)**
  - bet-hedging in fluctuating environments
- **Fisher (1930), Shaw and Mohler (1953)**
  - frequency-dependent selection
- **West-Eberhard (1979)**
  - intraspecific character displacement



*Hoplothrips*



*Ambystoma*



*Daphnia pulex*

# Traditional views on morph determination

E. B. Ford, 1971, *Ecological Genetics*, 3rd ed.

## CHAPTER SIX

### The Theory of Genetic Polymorphism

The work on *Maniola jurtina* described in the last two chapters aimed at analysing the evolution of polygenic characters in wild populations. It is necessary also to consider how those controlled by major genes can be used for similar evolutionary studies. This can in fact be done in all instances of genetic polymorphism. A strict definition of that situation had proved a fundamental necessity. It was provided in the following terms: Genetic polymorphism is the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation (Ford, 1940a).

The implications of this definition must be assessed. Evidently it excludes geographical races, as well as continuous variation controlled by polygenes and falling within a curve of normal distribution, as with human height. It excludes also the segregation of rare recessives, or heterozygous conditions, eliminated by selection and maintained only by mutation-pressure. Thus the occurrence of Huntington's Chorea does not constitute a polymorphism in Man.

Discontinuous variation, which is nearly always genetic (Ford, 1965, pp. 11-12), must be maintained by some form of switch-mechanism, to which certain general conclusions are applicable whatever the nature of the controlling unit may be: whether a major gene, a super-gene or a chromosome reconstruction such as an inversion. Indeed the distinction between these is somewhat arbitrary and usually not ascertained.

E. B. Ford, 1965, *Genetic Polymorphism*

Discontinuous variation of this polymorphic kind, in which intermediates are nearly or completely absent, must be maintained by some type of switch-mechanism producing alternative forms. This, it might be thought, could be provided by environmental stimuli; yet it seems hardly ever to be so, doubtless owing to the difficulty of obtaining clear-cut and contrasted phases by such means. It is true that very distinct seasonal forms of butterflies are evoked by length of day ... However, in these circumstances, the whole of each generation is similar. **Far greater difficulties, requiring an extremely delicate adjustment to external conditions, would be encountered in producing in this way contrasted and discontinuous types within a single brood. Moreover, their proportions could not be accurately adjusted to meet changes in the ecological situation: a drawback fatal to the evolution of a polymorphism which, moreover, often arises automatically owing to the development of heterozygous advantage. On the contrary, therefore, the control of polymorphic phases is almost always genetic.**

# More recent views

## **West-Eberhard, 1989, Phenotypic plasticity and the origins of diversity**

The importance of facultative expression for the intraspecific evolution of divergent traits cannot be overemphasized. Condition sensitivity not only reduces negative selection by assuring that traits are expressed in appropriate conditions. It also contributes to divergence by increasing the consistency with which particular phenotypes are matched to the particular contrasting conditions which mold their divergent forms. For these reasons facultative expression should prove both more common and more often associated with complex alternatives than is allelic-switch control. Facultative expression is associated with “difficult to evolve” complex traits such as “altruism” (self-sacrificing beneficence) (225–227) and the ecological transitions often

## **West-Eberhard, 2003, Developmental Plasticity and Evolution**

**Alternative phenotypes epitomize the switch-controlled, environmentally sensitive, adaptive traits that characterize all of ontogeny ...**

**Several kinds of data are regularly mistaken for genotype-specific determination of alternatives and treated as if environmental influence is absent or negligible ...**

**Examples attributed to stochastic regulation often prove, upon further examination, to be conditional or genotype-specific alternatives.**

# Ideas about random morph determination

Walker, 1986, Stochastic polyphenism

Bet-hedging or "adaptive coin-flipping" can evolve as a result of temporally fluctuating environments (Cooper and Kaplan, 1982)

Spatial variation leads to genetic polymorphism but temporal variation can lead to random determination (Seger and Brockmann, 1987)

Sib competition may favor bet-hedging (Moran, 1992)

Mixed ESS and genetic polymorphism are alternative possibilities for the hawk-dove game (Maynard Smith, 1982)

Games between relatives sometimes have mixed ESS solutions only (Hines and Haigh, 1985)

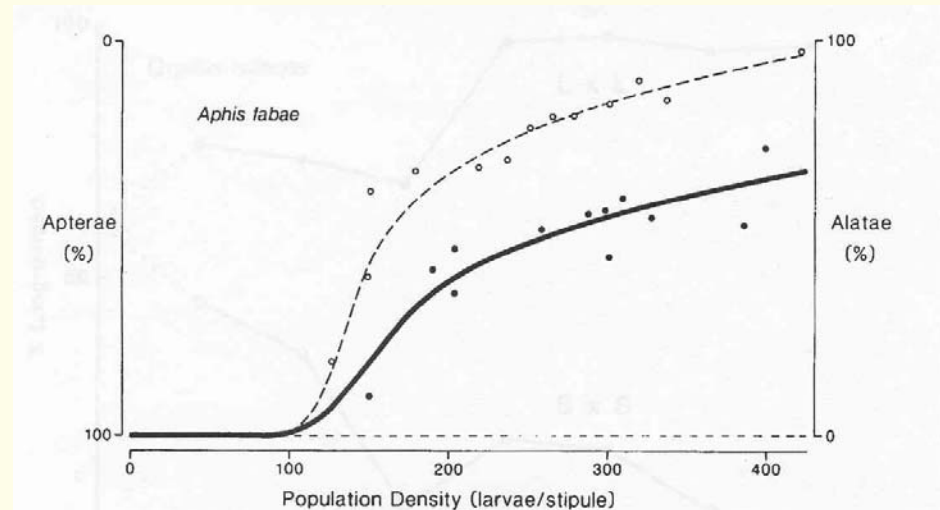
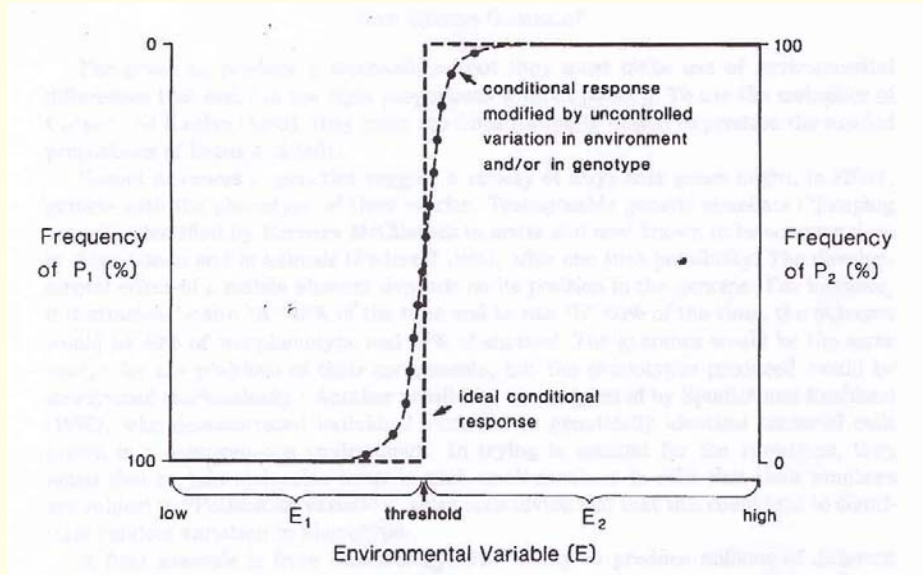


Fig. 3. Response of bean aphids to crowding (data from Shaw 1970a). Filled points and solid line are for the crowded progeny of uncrowded apterae. Open points and upper dashed line are for crowded progeny of apterae that were themselves crowded 100-400 per stipule. No alatae are produced at densities below 100 larvae/stipule. The difference between the two data sets shows that the environment of the mother influences the likelihood of her offspring being alatae. (The lower dashed line is for crowded offspring of alatae. Offspring of alatae are never alate, again demonstrating a maternal influence.) (Lines are eye-fitted.)

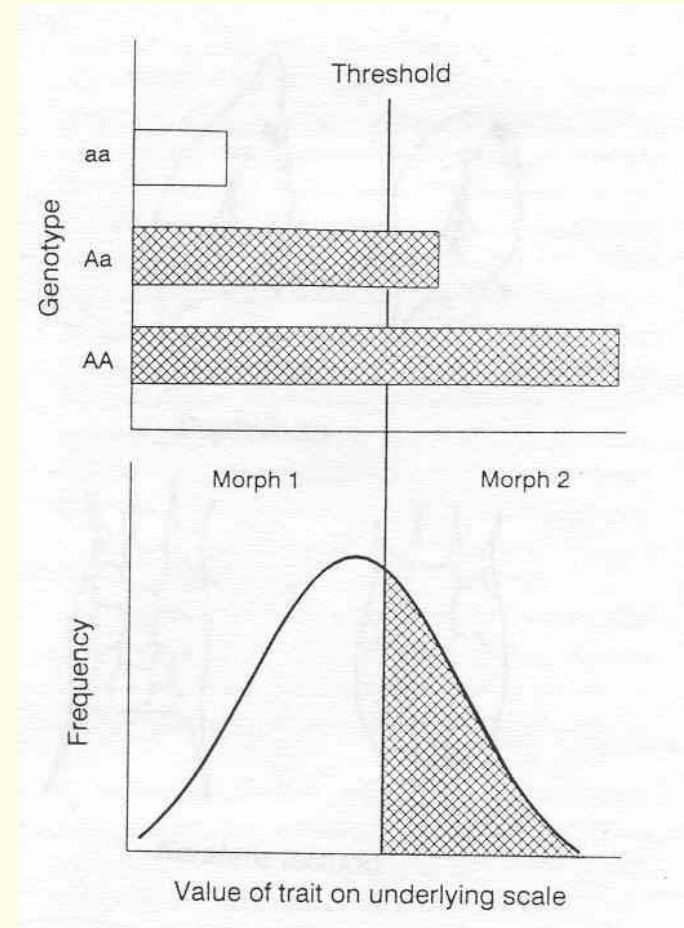


# Morphs as threshold traits

Walker, 1986



Roff, 1996



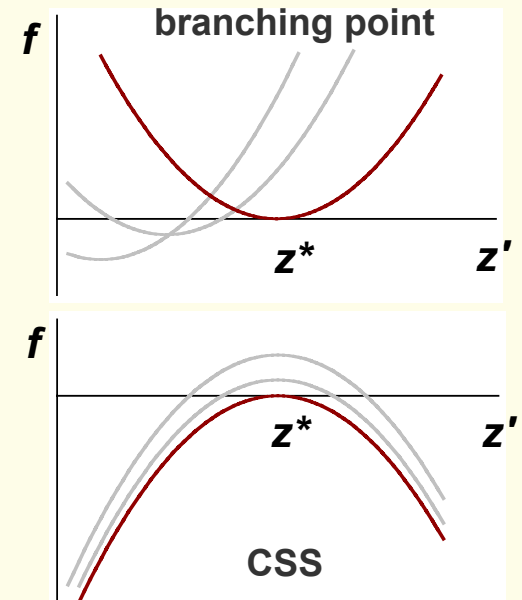
# Disruptive selection

The idea that disruptive selection and polymorphism are connected is not new

- **Mather (1955)**
  - Polymorphism as an outcome of disruptive selection
- **Maynard Smith (1962)**
  - Disruptive selection, polymorphism and sympatric speciation
- **Thoday (1972)**
  - Disruptive selection
- **Christiansen (1991)**
  - On conditions for evolutionary stability for a continuously varying character (combining concepts of convergence stability and polymorphism)
- **Abrams, Matsuda, and Harada (1993)**
  - Evolutionarily unstable fitness maxima and stable fitness minima

But the recent developments in adaptive dynamics have been crucial in moving disruptive selection to the forefront of evolutionary analysis

- **Metz, Geritz, Meszema, Jacobs, and Van Heerwaarden (1996)**
  - Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction
- **Geritz, Kisdi, Meszema, and Metz (1998)**
  - Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree



# Further development of adaptive dynamics: Classification of singular points in restricted and extended trait spaces

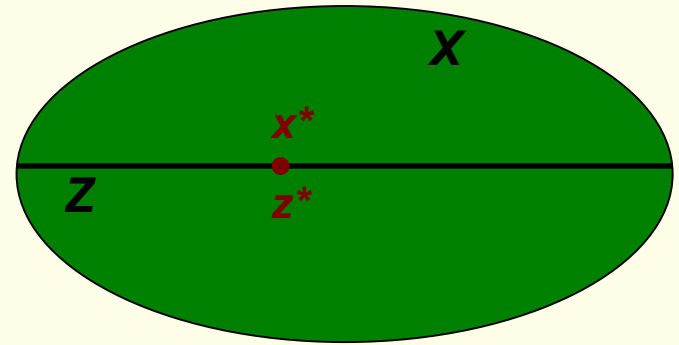
Restricted trait space  $Z$  embedded in  
extended trait space  $X$

Singular point  $z^*$  in  $Z$

Is the corresponding point  $x^*$  in  $X$  singular?

If  $z^*$  is a branching point, is  $x^*$  a branching point?

If  $z^*$  is a branching point, is  $x^*$  convergence stable?



$Z$  is a "primary" trait space (for ease of presentation,  $Z$  is one-dimensional)

$X$  is distributions on  $Z$

For simplicity, only "two-point" distributions will be considered

$x = (z_1, z_2; q_1, q_2)$ ,  $z_1$  with probability  $q_1$ ,  $z_2$  with probability  $q_2 = 1 - q_1$

$x = (z, z; q_1, q_2)$  corresponds to  $z$

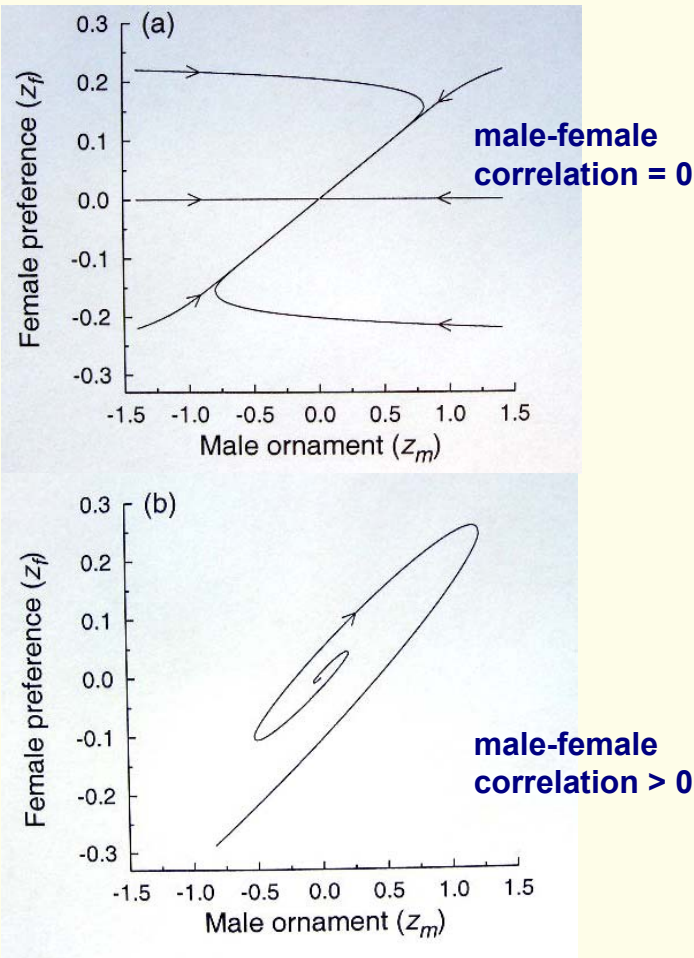
$f(z', z)$  invasion fitness in  $Z$

$F(x', x)$  invasion fitness in  $X$



# Multidimensional convergence stability

## Fisher's runaway process



After Pomiankowski, Iwasa, and Nee, 1991

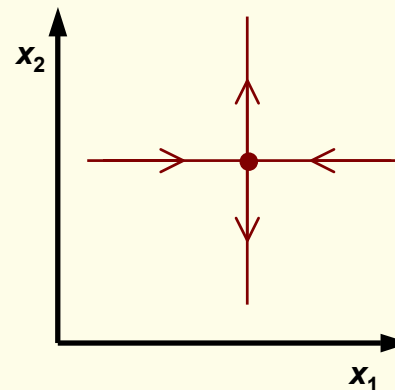
The distribution of mutational increments (pleiotropy, genetic correlations) can have a qualitative influence on multidimensional convergence stability

**A useful stability criterion is that there is convergence for evolutionary change constrained to any (one-dimensional) line through a point  $x^*$**

**Jacobian matrix of selection gradient negative definite**

This guarantees convergence for solutions to the canonical equation

**Convergence in some direction but divergence in other directions is a possibility**

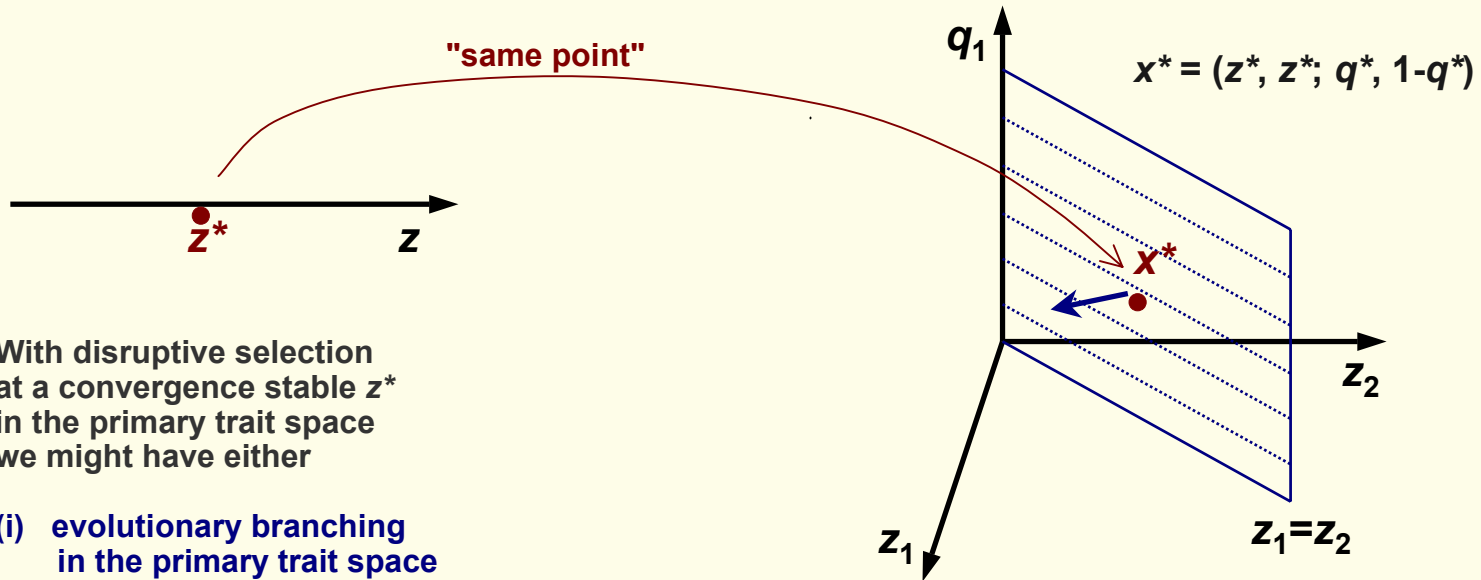


**If the trait space is restricted to this line, there would be convergence stability**

# Equilibria in primary and extended trait spaces

Primary trait:  $z$

Dimorphic randomization:  $z_1$  with probability  $q_1$   
 $z_2$  with probability  $q_2 = 1 - q_1$   
 $x = (z_1, z_2; q_1, q_2)$



With disruptive selection at a convergence stable  $z^*$  in the primary trait space we might have either

- (i) evolutionary branching in the primary trait space
- (ii) lack of convergence stability in the extended trait space
- (iii) branching along some other direction in the extended trait space

**Convenient coordinates**

mean primary trait	$\zeta = q_1 z_1 + q_2 z_2$
trait difference	$\eta = z_2 - z_1$
parameter for $q_1, q_2$	$\rho = 2q_2 - 1 = 1 - 2q_1$

# Invasion fitness in the extended trait space

An extended trait  $x$  is a probability distribution

Invasion fitness  $F(x', x)$  is a function of probability distributions

**What does a general (smooth) function of a probability distribution look like?**

Assume it looks like  $G(x) = \Gamma(H_1(x), \dots, H_K(x))$  where  $\Gamma(H_1, \dots, H_K)$

is a (smooth) function of several real variables, and the functions  $H_k(x)$

are some sort of averages of the following type: 
$$H(x) = \sum_{\{I_r\}} q_1 \cdots q_r h(z_{i_1}, \dots, z_{i_r})$$

$I_r = (i_1, \dots, i_r)$ , each  $i_m$  is 1 or 2

**Examples:**  $H(x) = q_1 h(z_1) + q_2 h(z_2)$

$H(x) = q_1 q_1 h(z_1, z_1) + q_1 q_2 h(z_1, z_2) + q_2 q_1 h(z_2, z_1) + q_2 q_2 h(z_2, z_2)$

(the second example is relevant for "kin grouping")

**Assume that  $F(x', x)$  depends on  $x'$  and  $x$  in a similar way as for  $G(x)$**

(this includes cases where a rare mutant interacts with itself)

# Derivatives of invasion fitness

## Primary trait space Z

$\left. \frac{\partial f(z', z)}{\partial z'} \right _{z'=z} = s(z)$	$\left. \frac{\partial^2 f(z', z)}{\partial z'^2} \right _{z'=z} = A(z)$	convergence stable	$A(\hat{z}) + D(\hat{z}) < 0$
Selection gradient		CSS	$A(\hat{z}) < 0$
equilibrium point: $s(\hat{z}) = 0$	$\left. \frac{\partial^2 f(z', z)}{\partial z' \partial z} \right _{z'=z} = D(z)$	branching	$A(\hat{z}) > 0$

## Extended trait space X

$$\zeta = q_1 z_1 + q_2 z_2, \quad \eta = z_2 - z_1, \quad \rho = 2q_2 - 1, \quad x = (\zeta, \eta, \rho)$$

Evaluate derivatives at "pure strategy"  $x = (z, 0, \rho)$

$\left. \frac{\partial F(x', x)}{\partial \zeta'} \right _{\eta'=\eta=0, \zeta'=\zeta=z} = S_\zeta(z) = s(z)$	$\left. \frac{\partial^2 F(x', x)}{\partial \zeta'^2} \right _{\eta'=\eta=0, \zeta'=\zeta=z} = A(z)$	"same as before"
$S_\eta = 0, \quad S_\rho = 0$	$\left. \frac{\partial^2 F(x', x)}{\partial \zeta' \partial \zeta} \right _{\eta'=\eta=0, \zeta'=\zeta=z} = D(z)$	
For an equilibrium in Z, the corresponding points in X are equilibria		
All other second derivatives needed for Hessian and Jacobian matrices are zero	$\left. \frac{\partial^2 F(x', x)}{\partial \eta'^2} \right _{\eta'=\eta=0, \zeta'=\zeta=z} = q'_1 q'_2 B(z)$	"new"

# Stability criteria at "pure-strategy" equilibrium

Look at a convergence stable equilibrium in primary trait space  $Z$

$$s(\hat{z}) = 0 \quad \Rightarrow$$

$$S_{\zeta}(\hat{z}) = 0, \quad S_{\eta}(\hat{z}) = 0, \quad S_{\rho}(\hat{z}) = 0$$

The corresponding points in the extended trait space  $X$  are equilibria

**Non-zero elements of Jacobian and Hessian matrices**

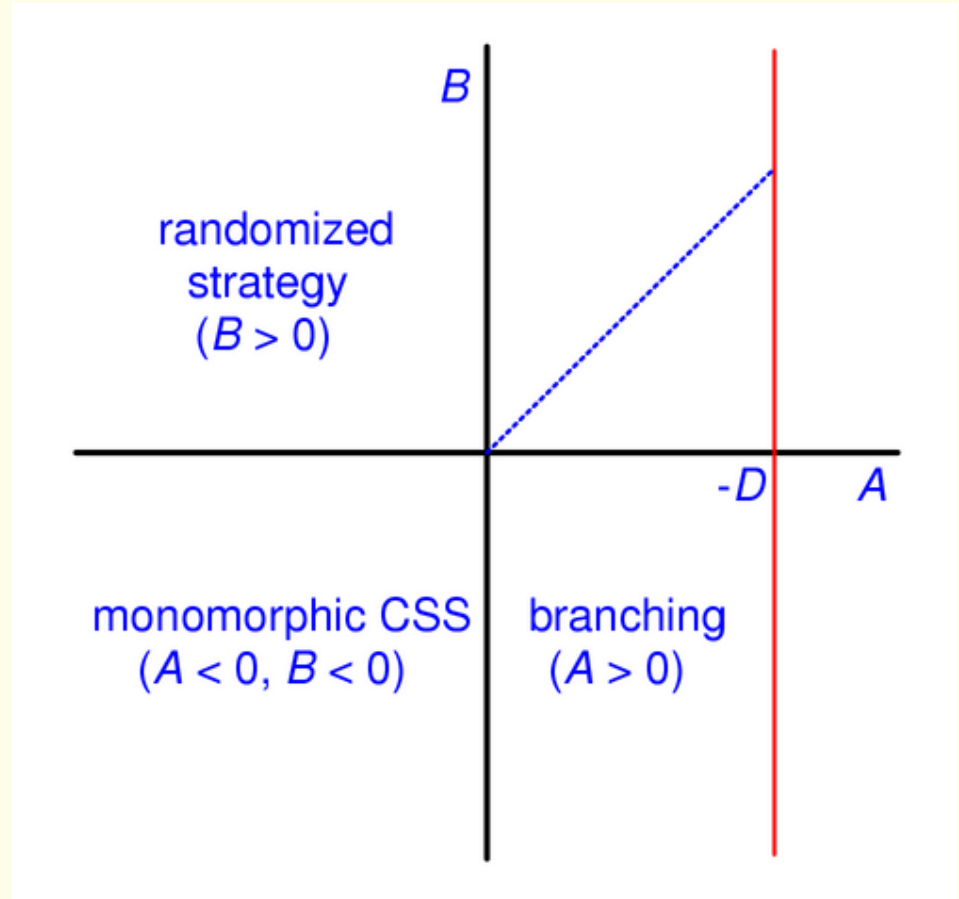
$$J_{\zeta\zeta} = A(\hat{z}) + D(\hat{z})$$

$$J_{\eta\eta} = q_1 q_2 B(\hat{z})$$

$$H_{\zeta\zeta} = A(\hat{z})$$

$$H_{\eta\eta} = q_1 q_2 B(\hat{z})$$

**Depending on the signs of  $A$  and  $B$ , we get different cases**



We might call  $A$  "branching disruptivity" and  $B$  "randomization disruptivity"

# Some comments on the fitness derivatives

In simple situations, we have  $A(\hat{z}) = B(\hat{z})$  (when the invasion fitness of a mutant trait is a function of the mutant's arithmetic average success in interactions with residents)

**Introduce**  $C(z) = A(z) - B(z)$  **so that**  $A(z) = B(z) + C(z)$

**We have the following second derivatives with respect to mutant traits**

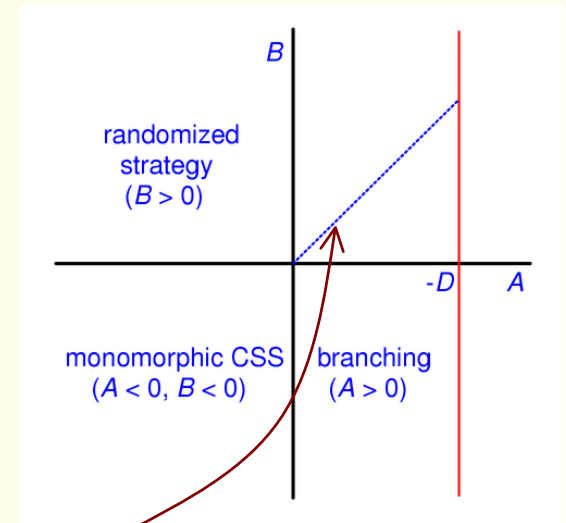
$$\left. \frac{\partial^2 F(x', x)}{\partial z_1'^2} \right|_{z_1' = z_2' = z_1 = z_2 = z} = q_1' B(z) + q_1'^2 C(z)$$

$$\left. \frac{\partial^2 F(x', x)}{\partial z_2'^2} \right|_{z_1' = z_2' = z_1 = z_2 = z} = q_2' B(z) + q_2'^2 C(z)$$

$$\left. \frac{\partial^2 F(x', x)}{\partial z_1' \partial z_2'} \right|_{z_1' = z_2' = z_1 = z_2 = z} = q_1' q_2' C(z)$$

Circumstances that give non-zero C at "pure strategy" equilibrium:

- kin-group structure
- "non-linearity" of fitness function (e.g. as a result of spatial or temporal fluctuations in conditions)

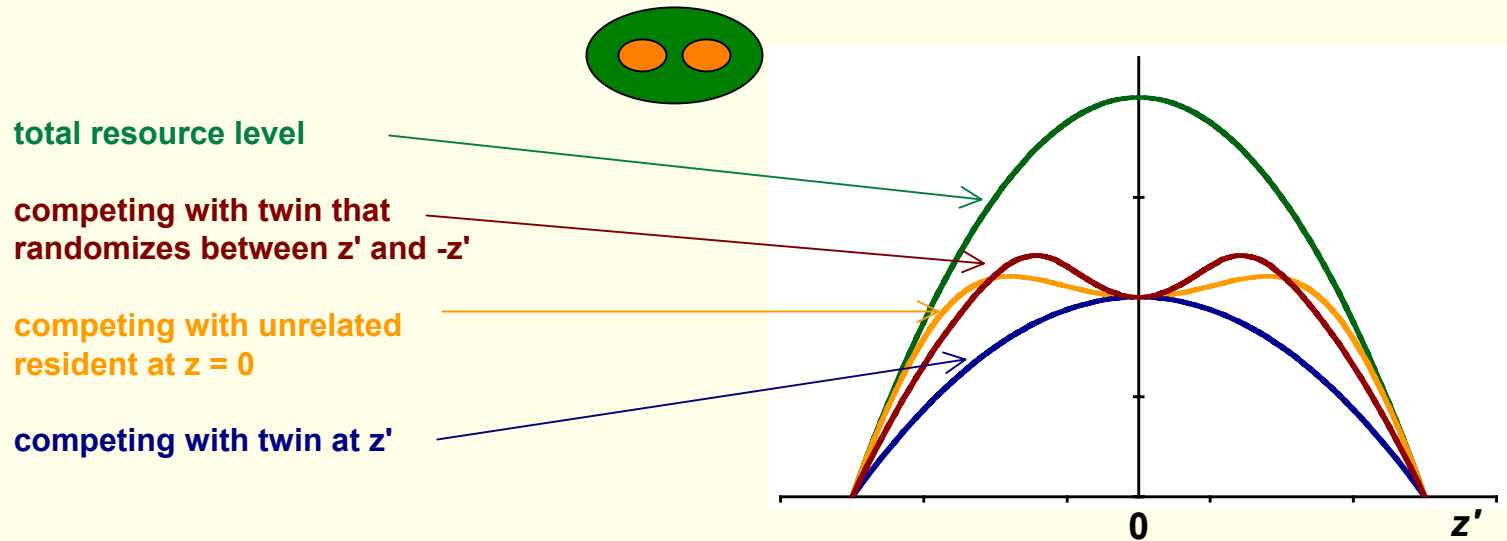


**For  $C = 0$ , there is either a CSS, or branching and the evolution of randomization are both possible**

**There is a relation between evolutionary branching in the primary trait space and a lack of convergence stability in the extended trait space**

# Different kinds of disruptivity

Example with trait-based competition between two possibly related individuals in a patch

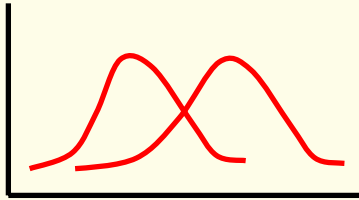


For unrelated individuals, there is disruptive selection at  $z^* = 0$

For twins, there is instead stabilizing selection in the primary trait space (blue curve) but disruptivity for a dimorphic randomization (red curve)

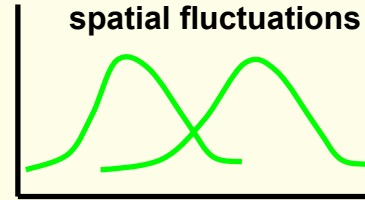
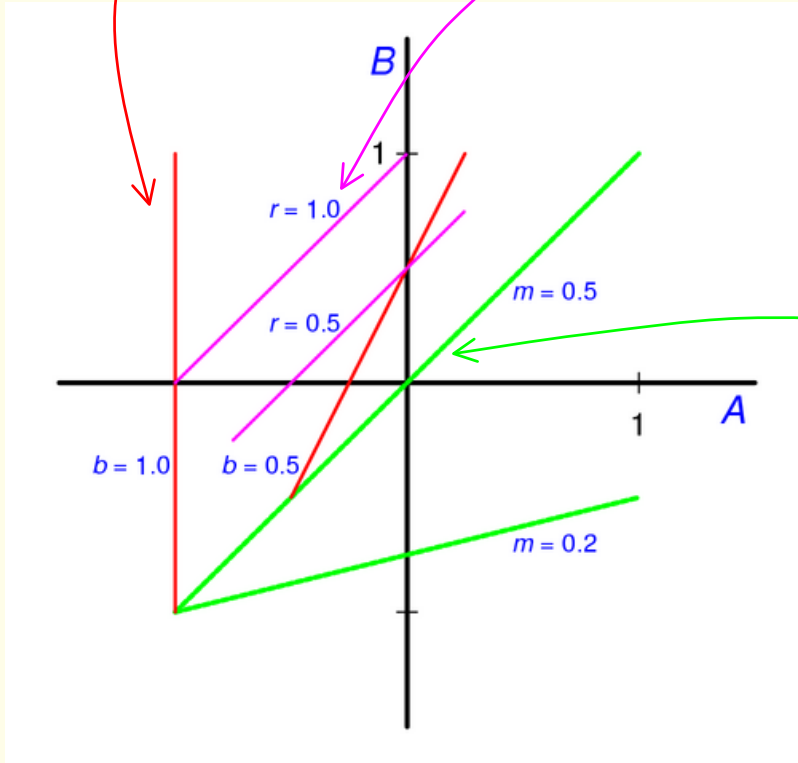
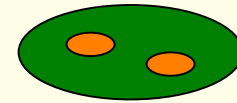
Temporal fluctuations or restricted gene flow between niches can have similar effects of differentiating between branching disruptivity and randomization disruptivity

# Examples

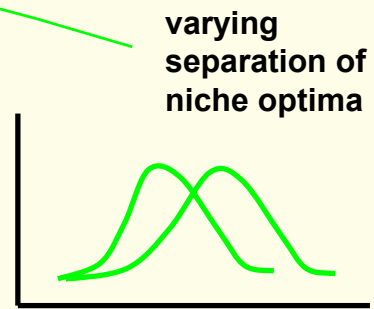


temporal fluctuations

Two individuals compete for resources in a patch



spatial fluctuations



varying separation of niche optima



# Two-patch model with soft selection

**Establishment  
survival in patch  $i$**

$$\alpha_i(z) = a \exp\left[-\frac{(z - \theta_i)^2}{2\sigma^2}\right], \quad \theta_1 = z_0 - \delta, \quad \theta_2 = z_0 + \delta$$
$$\beta_i(x) = q_1 \alpha_i(z_1) + q_2 \alpha_i(z_2)$$

**Invasion fitness**

$$\lambda(u_1, u_2) = (1 - m) \frac{u_1 + u_2}{2} + \sqrt{\frac{1}{4} (1 - m)^2 (u_1 - u_2)^2 + m^2 u_1 u_2}$$

$$F(x', x) = \log \lambda\left(\frac{\beta_1(x')}{\beta_1(x)}, \frac{\beta_2(x')}{\beta_2(x)}\right)$$

**Monomorphic  
equilibrium at  
 $x = (z_0, 0, 0)$**

**$C = 0$  for  $m = 0.5$**

$$B(z_0) = \frac{\delta^2}{\sigma^4} - \frac{1}{\sigma^2}$$

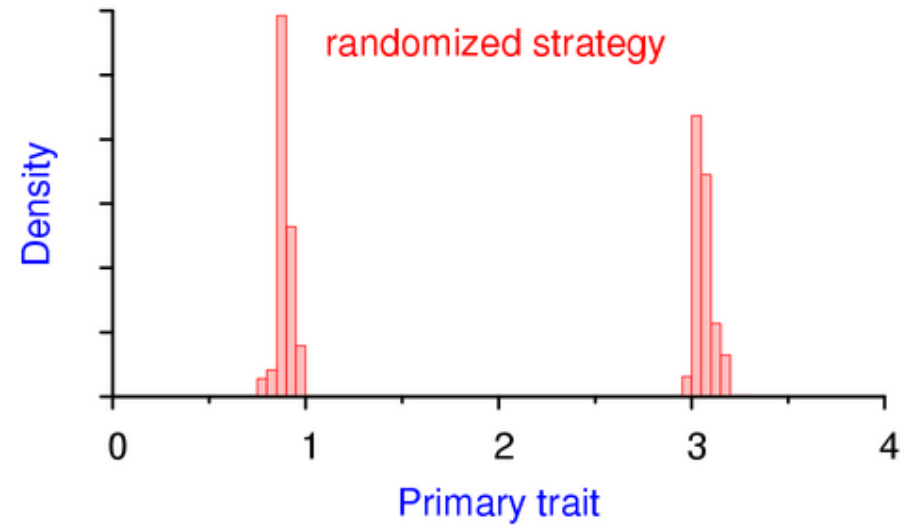
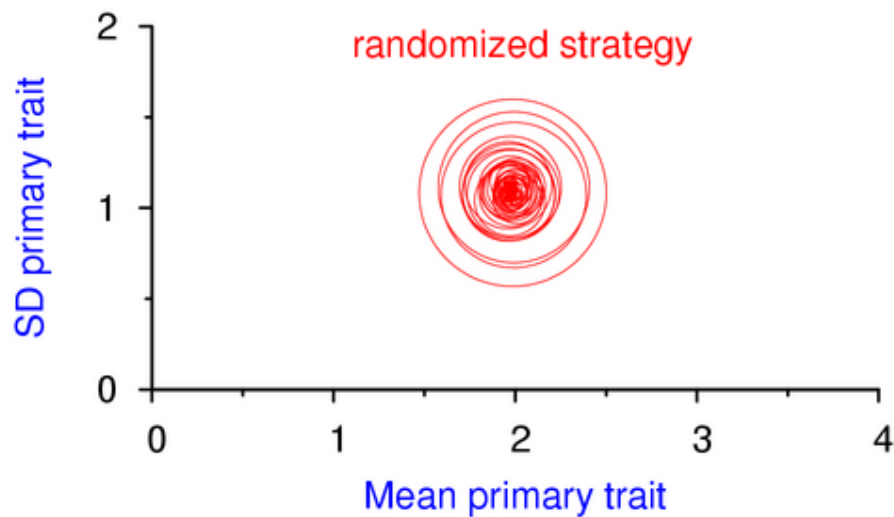
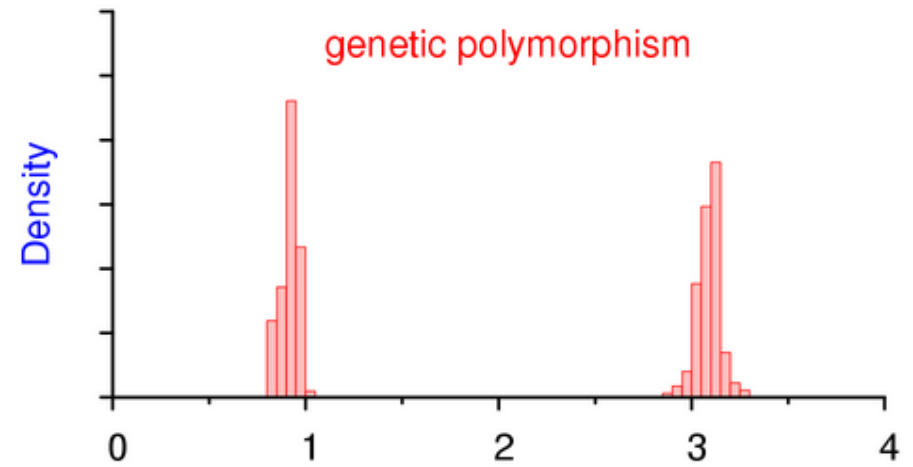
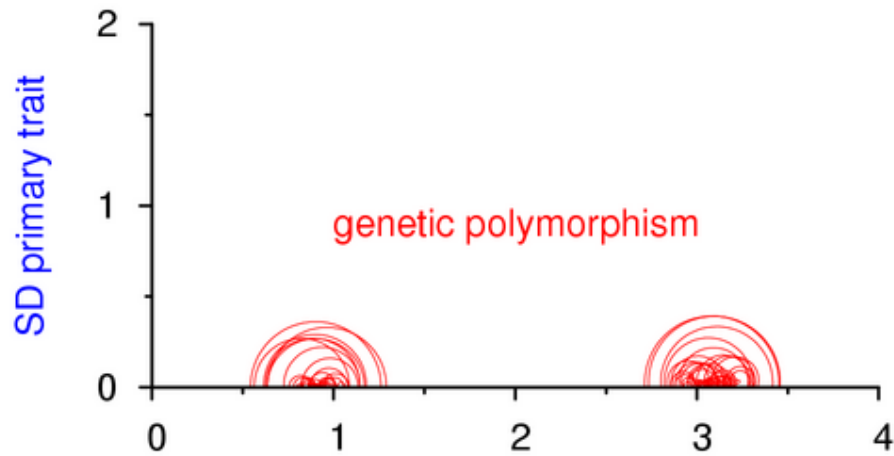
$$C(z_0) = \frac{1 - 2m}{m} \frac{\delta^2}{\sigma^4}$$

$$D(z_0) = \frac{m - 1}{m} \frac{\delta^2}{\sigma^4}$$

# Simulation: asexual individuals with random dispersal

Depending on the distribution of mutational increments, either genetic or stochastic dimorphism may evolve ( $A = B = 0.5625$ )

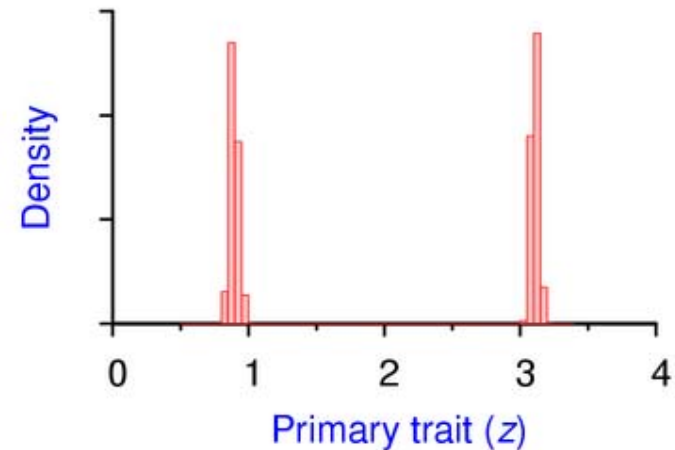
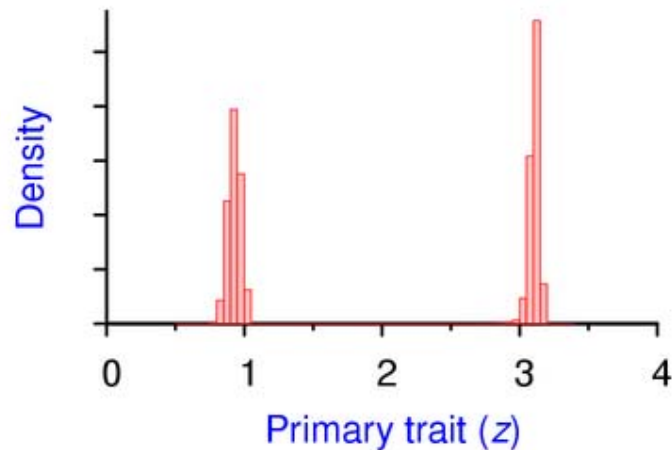
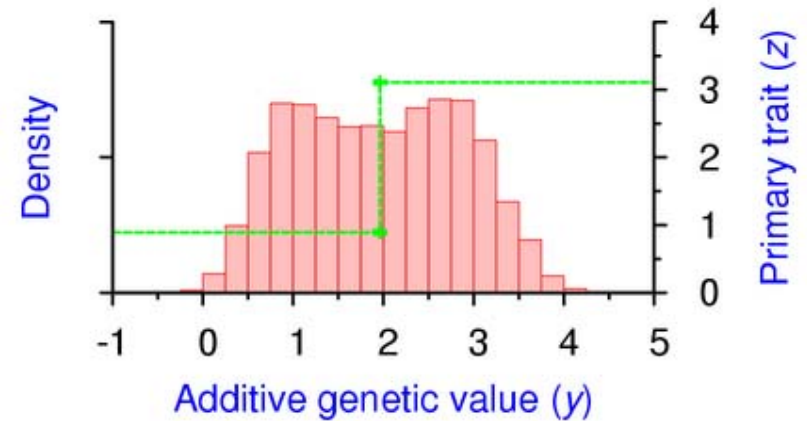
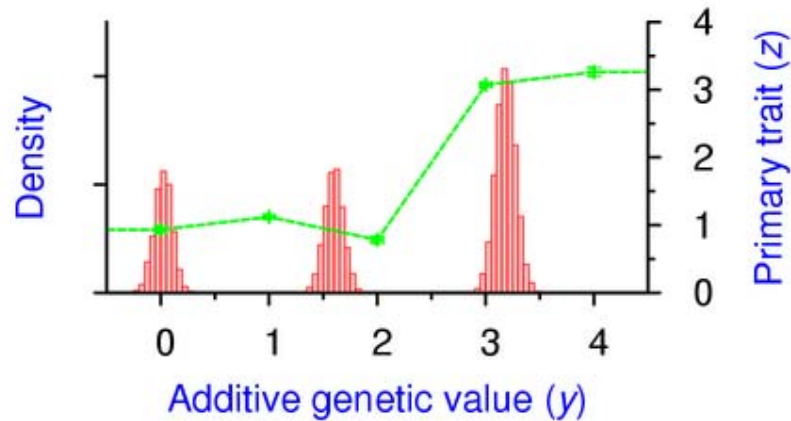
$$\sqrt{(1-\rho^2)\eta^2}/2$$



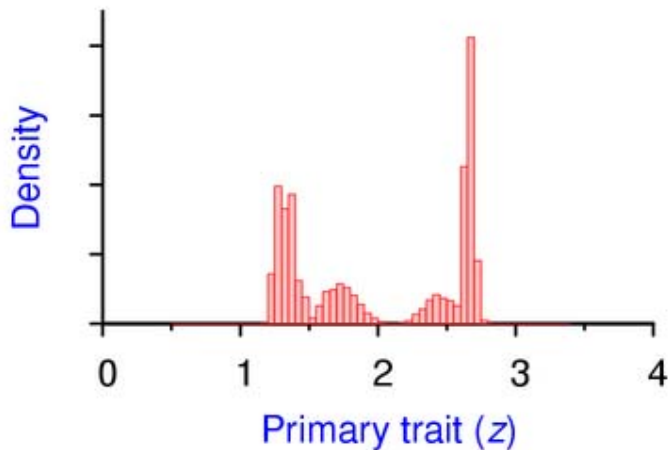
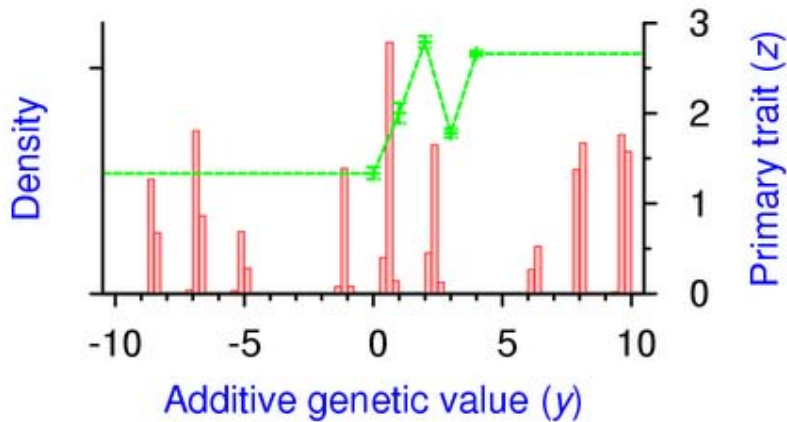
# Simulation: hermaphroditic individuals with random dispersal

There are five unlinked loci coding for the "additive effect"  $y$ , and an additional locus coding for a "genotype-phenotype" mapping

The result is a genetic polymorphism, either a "major-gene effect" or a "polygenic switch"



## Hermaphroditic individuals with restricted dispersal ( $m = 0.2$ )



A genetic polymorphism is possible ( $A = 1.54$ ) but there is no randomization disruptivity ( $B = -0.36$ )

For this simulation, a rather "sloppy" genetic polymorphism evolved (about  $5 \cdot 10^5$  generations)

An analysis of evolutionary stability and evolutionary change near to an equilibrium point in the trait space gives only some information about eventual evolutionary outcomes

This can be seen as an advantage of an analysis of polymorphism based on the situation near a monomorphic equilibrium: one gets a general theory by sacrificing many (possibly relevant) details

# "Lottery model"

The environment fluctuates randomly between two conditions (same as the patches in the previous model)

A proportion  $b$  of the population is recruited each season, whereas the remaining proportion  $1 - b$  survives

Selection operates on recruited juveniles

**Invasion fitness**

$$F(x', x) = \frac{1}{2} \log \left( 1 - b + b \frac{\beta_1(x')}{\beta_1(x)} \right) + \frac{1}{2} \log \left( 1 - b + b \frac{\beta_2(x')}{\beta_2(x)} \right)$$

**Monomorphic equilibrium at  $x = (z_0, 0, 0)$**

$$B(z_0) = b \left( \frac{\delta^2}{\sigma^4} - \frac{1}{\sigma^2} \right)$$

$$C(z_0) = -b^2 \frac{\delta^2}{\sigma^4}$$

**C approaches 0 when  $b$  approaches 0**

$$D(z_0) = -b(1 - b) \frac{\delta^2}{\sigma^4}$$

# Competition between relatives

**Fecundity**  $\alpha(z', z) = g(z') \frac{1}{1 + c(z', z)}$

**Competition coefficient**  $c(z', z) = \exp\left[-\frac{(z' - z)^2}{2\sigma^2}\right]$

**Resource density**  $g(z) = \begin{cases} 1 - \frac{1}{2}\gamma(z - z_0)^2 & \text{if } |z - z_0| < \sqrt{2/\gamma} \\ 0 & \text{otherwise} \end{cases}$

$$\beta(x', x) = q'_1 q_1 \alpha(z'_1, z_1) + q'_1 q_2 \alpha(z'_1, z_2) + q'_2 q_1 \alpha(z'_2, z_1) + q'_2 q_2 \alpha(z'_2, z_2)$$

**Invasion fitness**

$$w(x', x) = \frac{(1 - r)\beta(x', x) + r\beta(x', x')}{\beta(x, x)}$$

$$F(x', x) = \log w(x', x)$$

**Monomorphic equilibrium at  $\mathbf{x} = (z_0, 0, 0)$**

**C = 0 for  $r = 0$**

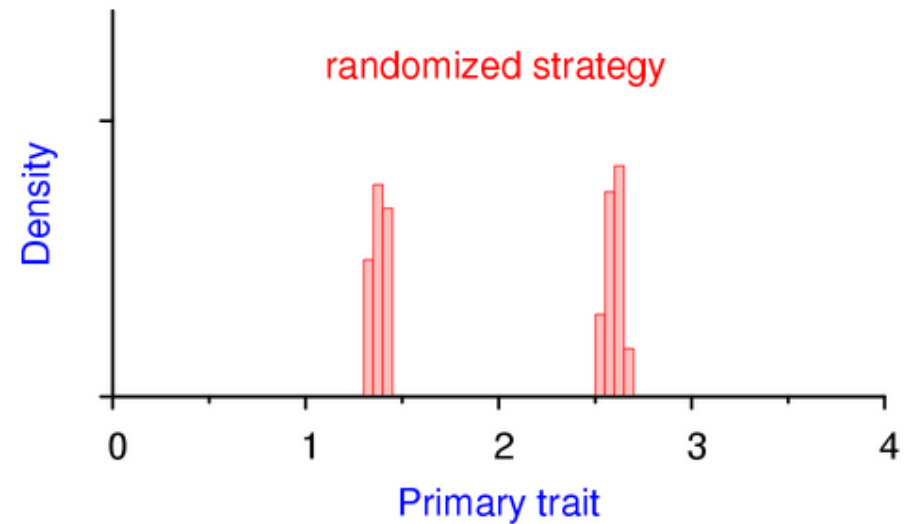
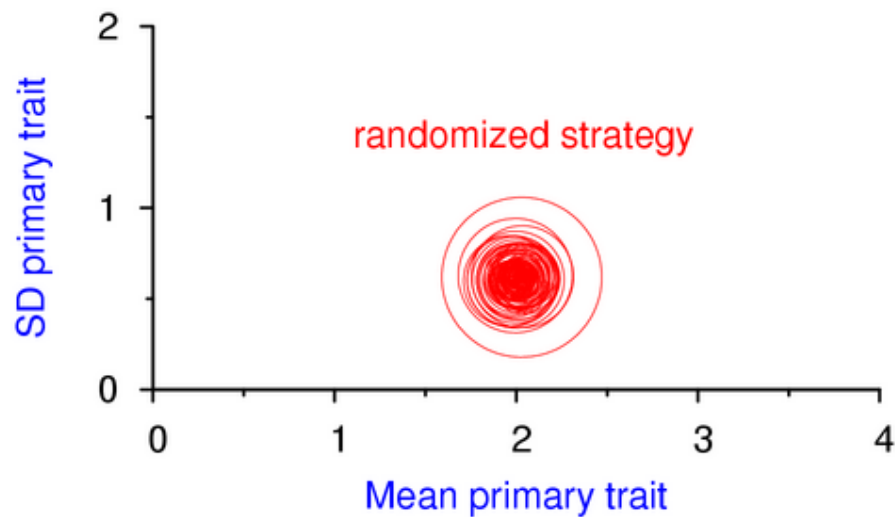
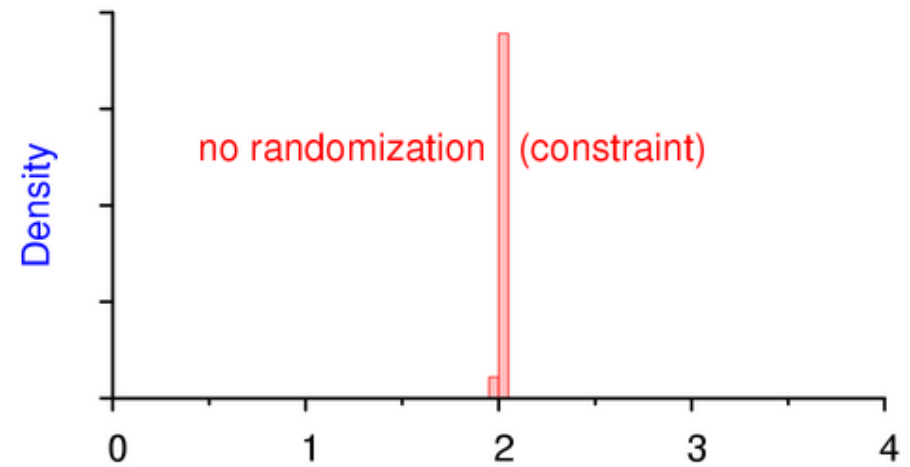
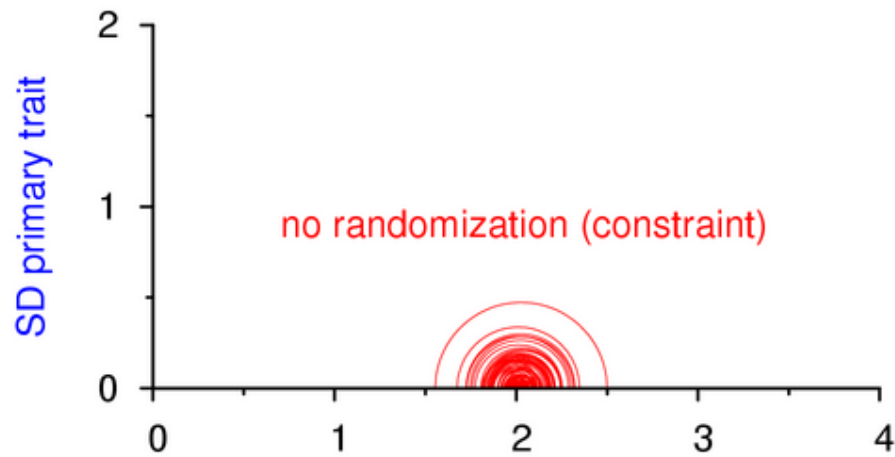
$$B(z_0) = -\gamma + (1 + r) \frac{1}{2\sigma^2}$$

$$C(z_0) = -r \frac{1}{\sigma^2}$$

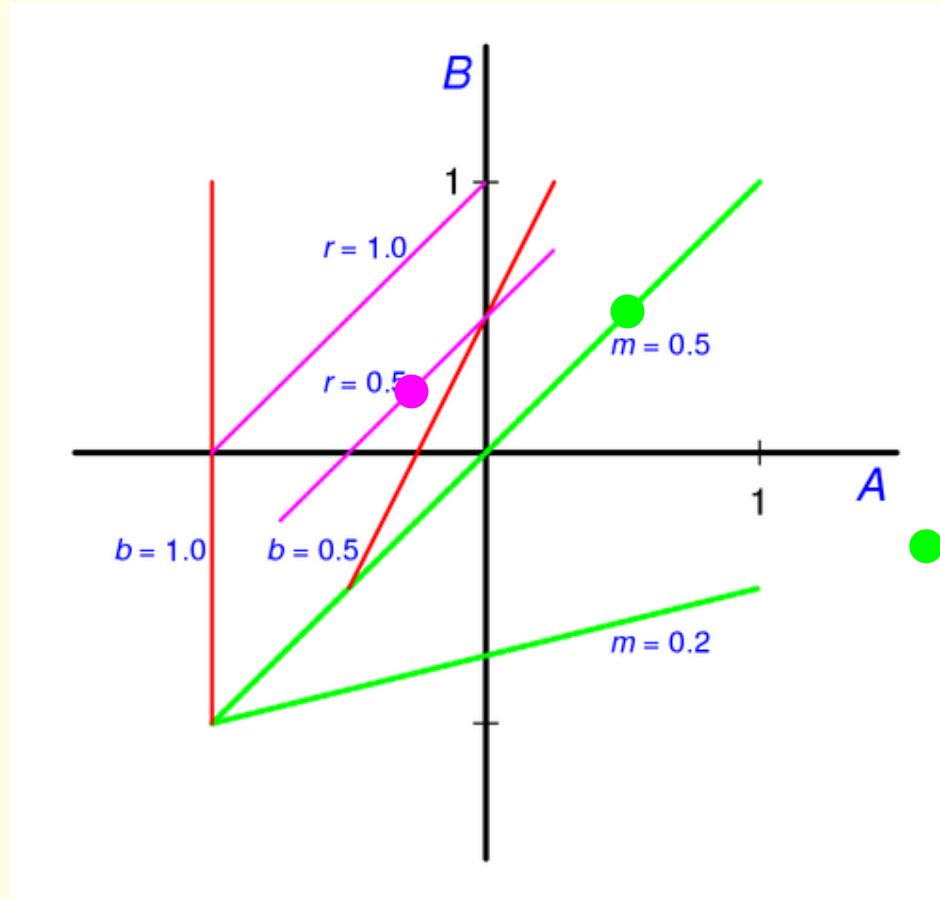
$$D(z_0) = -(1 - r) \frac{1}{2\sigma^2}$$

# Relatives ( $r=0.5$ ) competing for resources in a patch

There is randomization disruptivity ( $B = 0.25$ ) but no branching disruptivity ( $A = -0.25$ )



# Classification of the simulations



My impression is that the classification of the monomorphic equilibrium gives a good prediction of the evolutionary outcome in a simulation



# Sum up

- Local analysis: branching versus lack of convergence stability as a result of disruptivity
- "General" fitness function  $F(x',x)$  in extended trait space
- Branching ( $A$ ) and randomization ( $B$ ) disruptivities may differ for two qualitatively different types of reasons
  - Interactions between relatives, which tend to favor evolution of randomization over evolutionary branching
  - "Non-linear" dependence of invasion fitness  $F(x',x)$  on  $x'$ 
    - Spatial and temporal variation in conditions are typical examples and tend to favor, respectively, evolutionary branching and the evolution of randomization
- Unified perspective on previous analyses of random versus genetic morph determination
- Adaptive dynamics approximations provide quite useful idealizations
- Particularities of genetics may nevertheless play an important role