

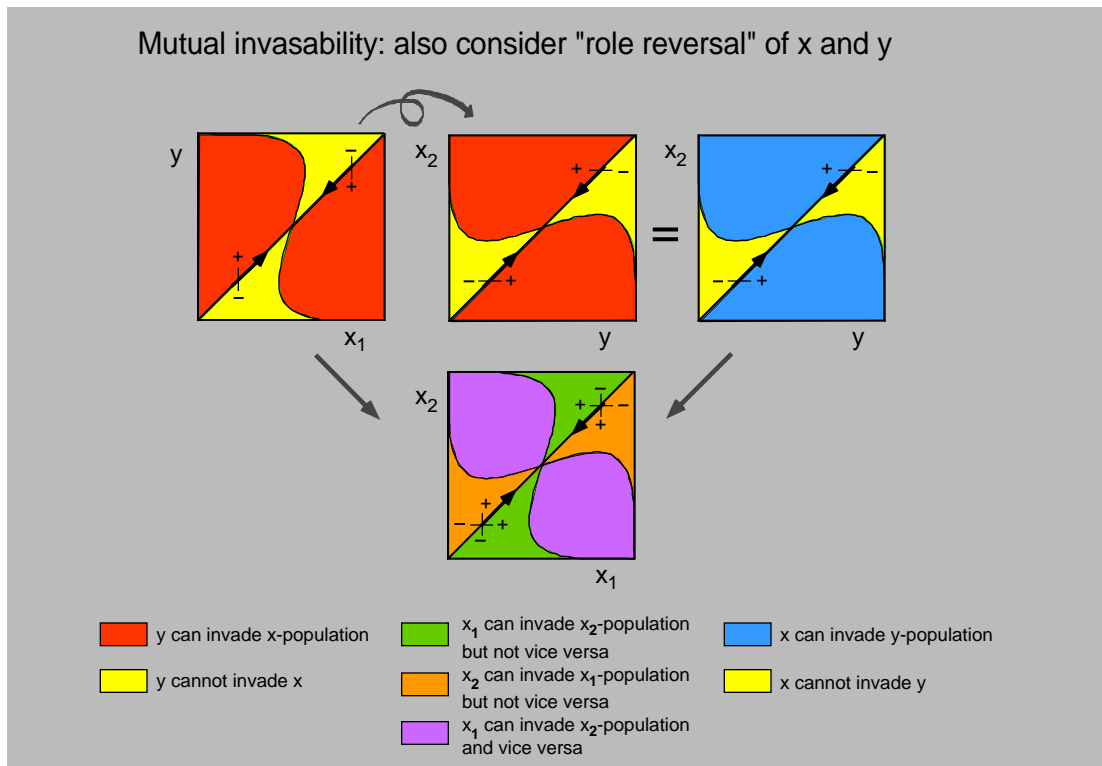
Bifurcations of
Evolutionarily Singular
& multivariate
adaptive dynamics

Hans Metz

ADN
IIASA

IEES
Leiden University

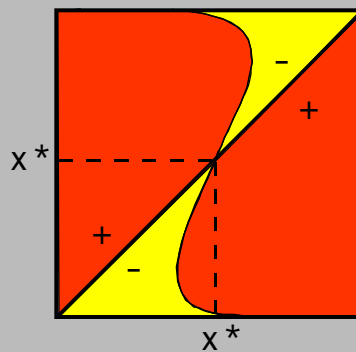
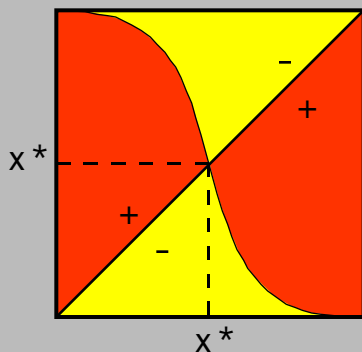
First a note about the colour coding:



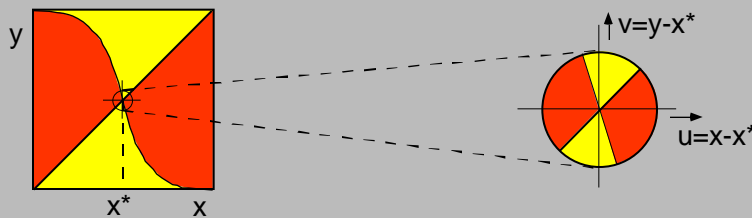
The classification of evolutionarily singular points,
an algebraic approach

x^* is a **singular point** iff

$$\left. \frac{ds_x(y)}{dy} \right|_{y=x=x^*} = 0 \quad (x^* \text{ is an extremum in the } y\text{-direction})$$



Linearization around $x = y = x^*$



$$s_u(v) = a + b_1u + b_0v + c_{11}u^2 + 2c_{10}uv + c_{00}v^2 + \text{h.o.t.}$$

neutrality of resident

$$s_u(u) = 0 \rightarrow$$

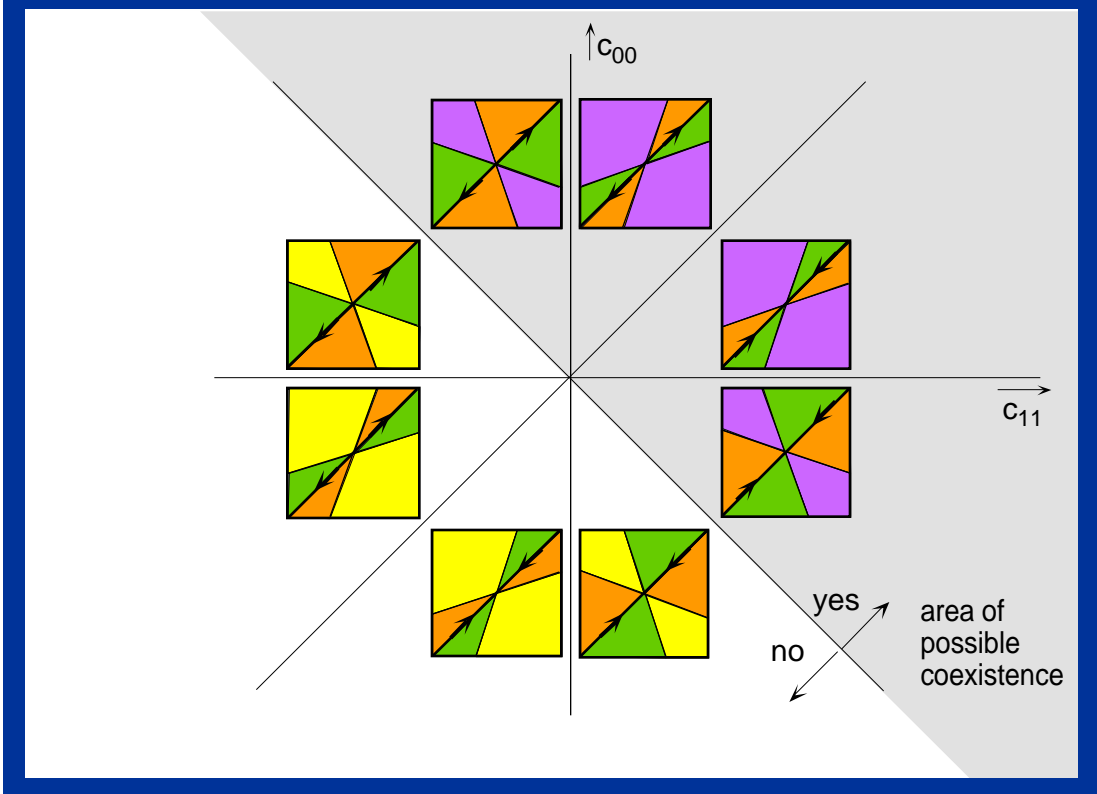
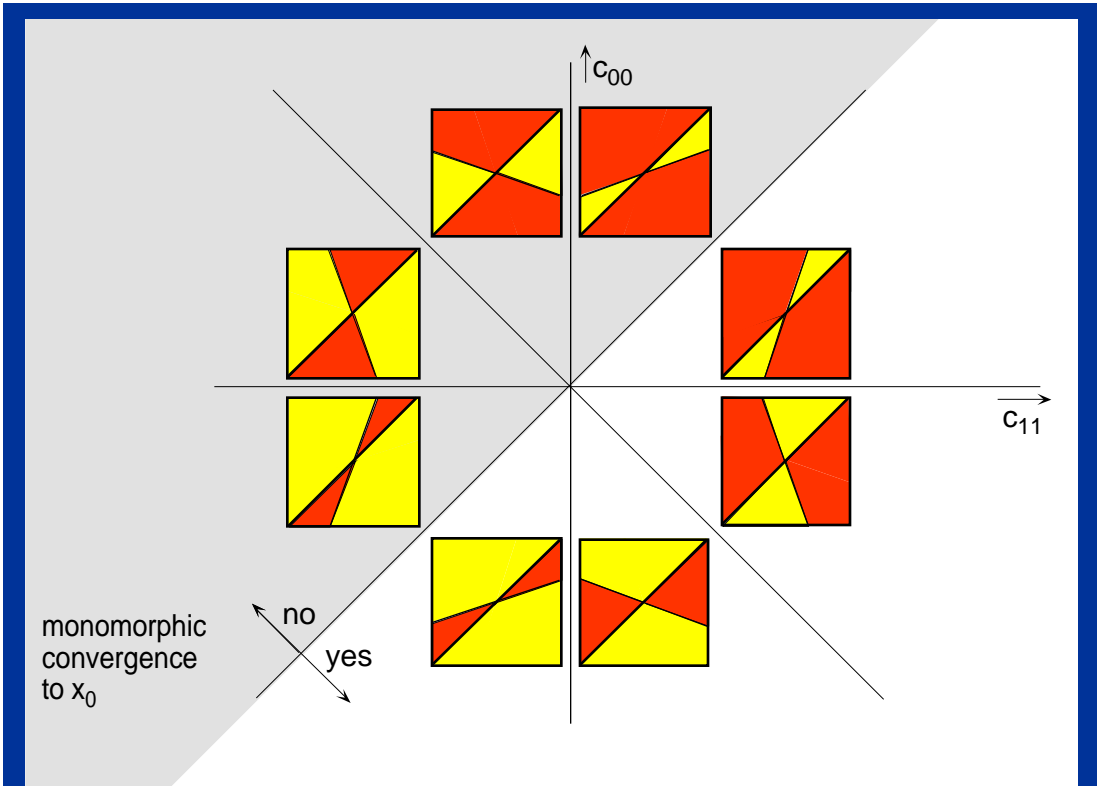
$$\begin{cases} a=0 \\ b_1+b_0=0 \\ c_{11}+2c_{10}+c_{00}=0 \end{cases}$$

x^* is an extremum in y

$$s_0(0) = 0 \rightarrow$$

$$b_1 = b_0 = 0$$

$$s_u(v) = c_{11}u^2 - (c_{11}+c_{00})uv + c_{00}v^2 + \text{h.o.t.}$$



Dimorphic linearisation around $x_1=x_2=y=x^*$, I:

Linearization: $v = y - x^*$ mutant
 $u_1 = x_1 - x^*$, $u_2 = x_2 - x^*$ residents

Only directional derivatives (!):

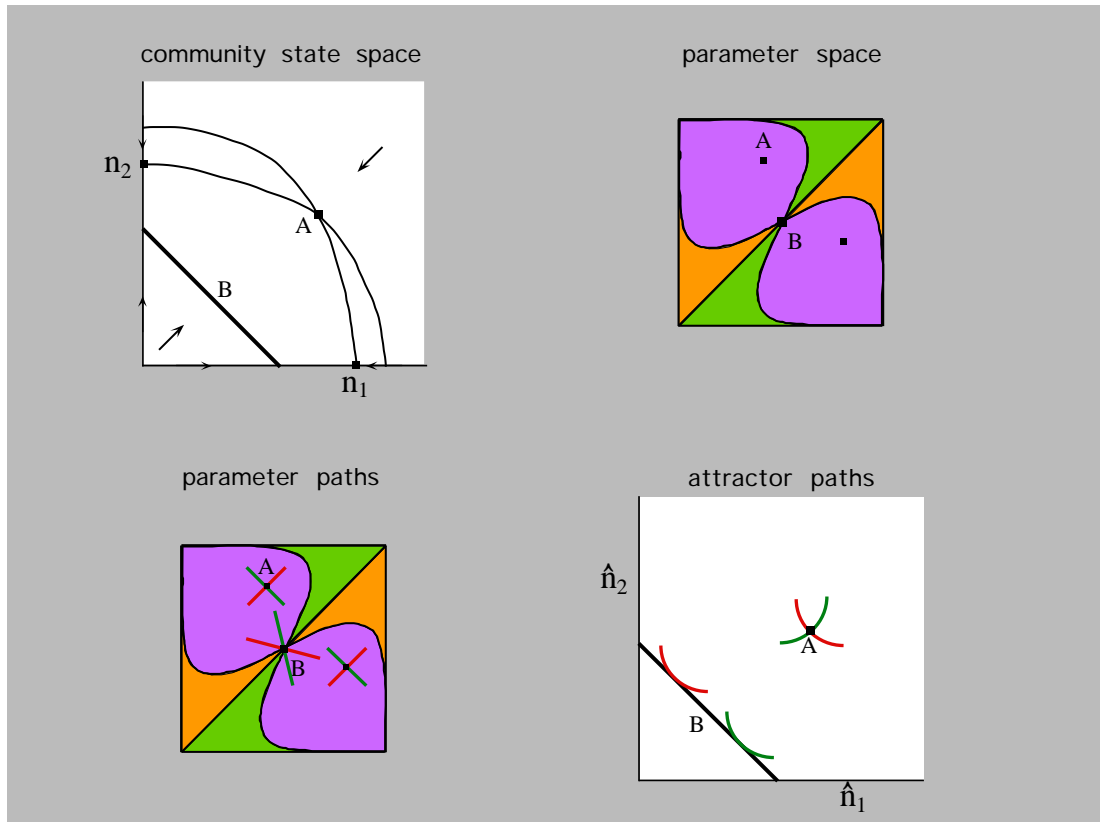
$$u_1 = u w_1, \quad u_2 = u w_2$$

$$s_{u_1, u_2}(v) = + \quad (*)$$

$$s_{11}(w_1, w_2) u^2 + s_{10}(w_1, w_2) u v + s_{00}(w_1, w_2) v^2 + \dots$$

h.o.t.

Why we may only use directional derivatives:



Dimorphic linearisation around $x_1 = x_2 = y = x^*$, II:

expansion formula (*)

symmetry

$$s_{u_1, u_2}(v) = s_{u_2, u_1}(v)$$

neutrality of residents

$$s_{u_1, u_2}(u_1) = 0 = s_{u_1, u_2}(u_2)$$

if $u_1 = u_2 = 0$ we are back in the monomorphic resident case

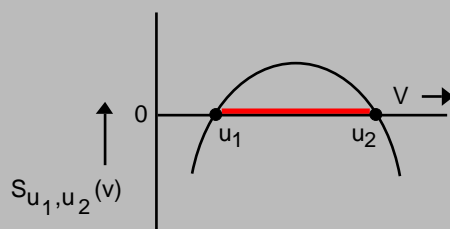
$$s_{00}(v) = s_0(v)$$

$$s_{u_1, u_2}(v) = (v - u_1)(v - u_2) [c_{00} + \text{h.o.t.}]$$

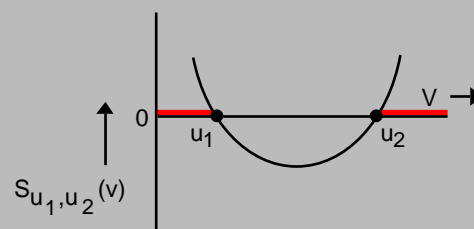
Dimorphic linearisation around $x_1 = x_2 = y = x^*$, III:

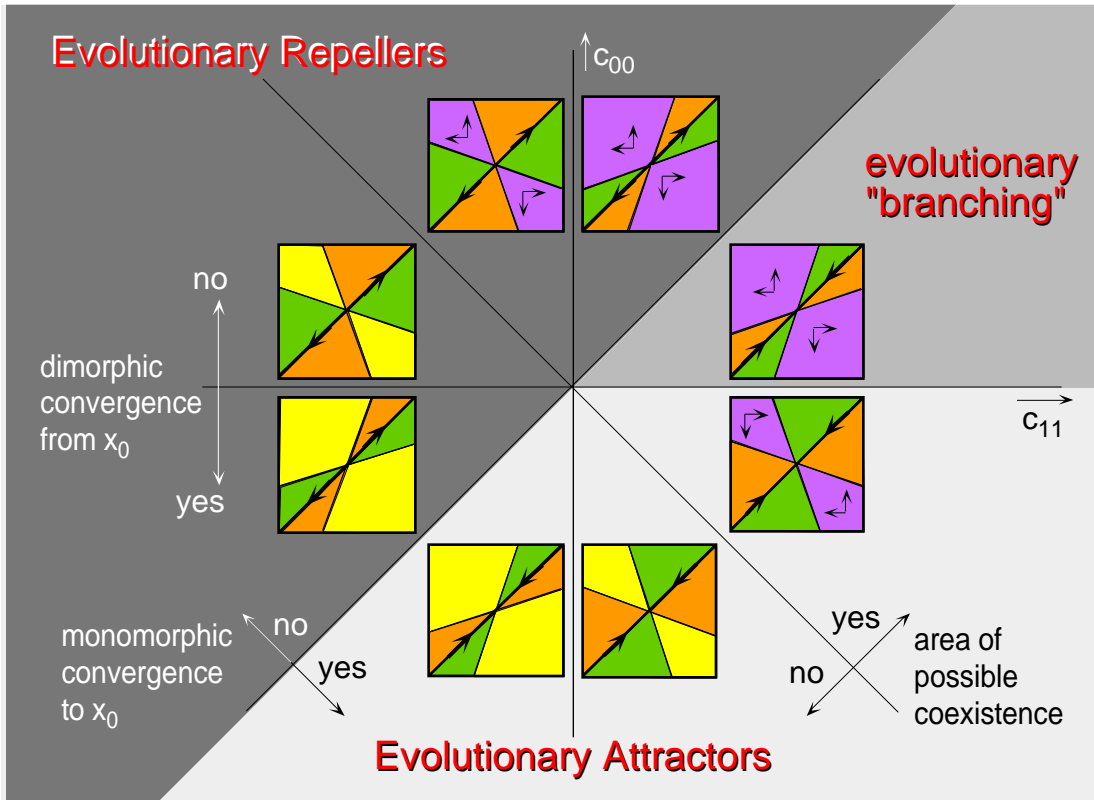
$$s_{u_1, u_2}(v) = (v - u_1)(v - u_2) [c_{00} + \text{h.o.t.}]$$

$c_{00} < 0$

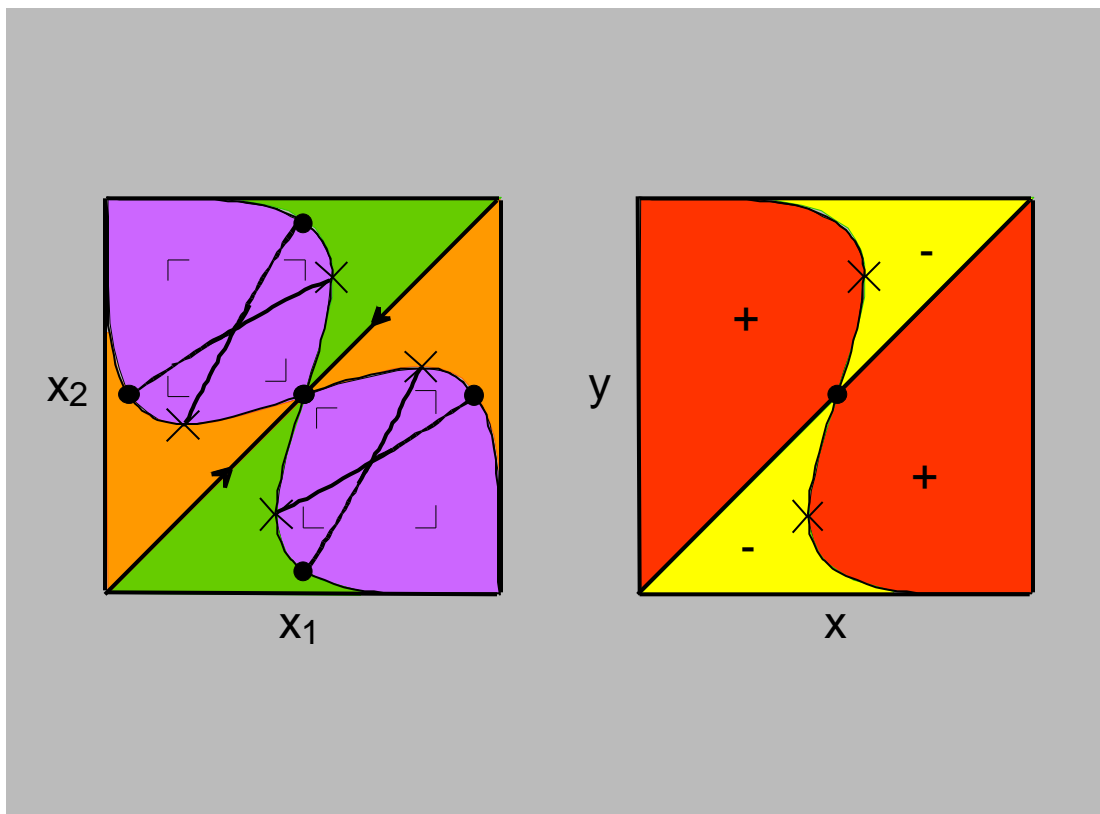


$c_{00} > 0$

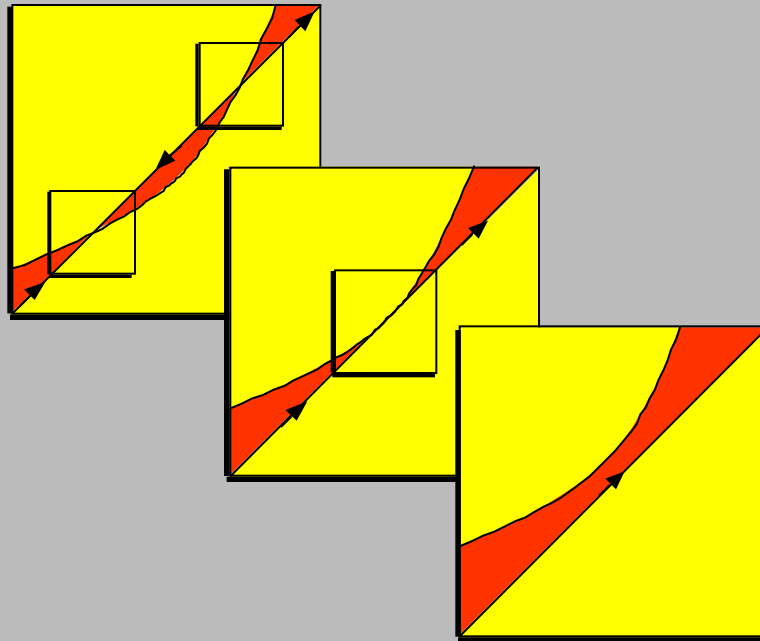
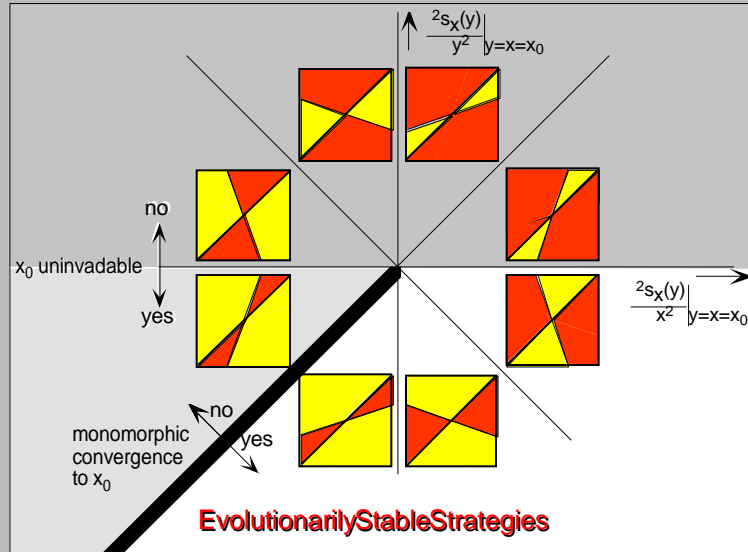


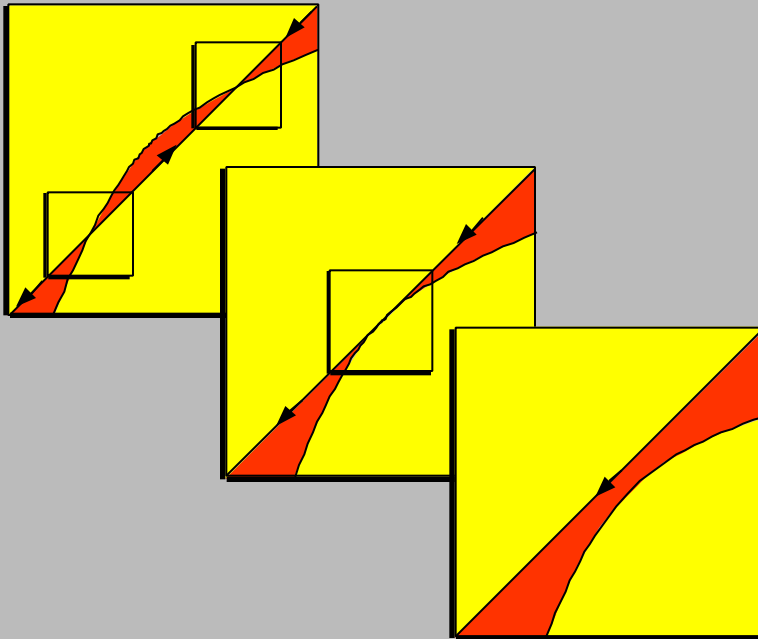
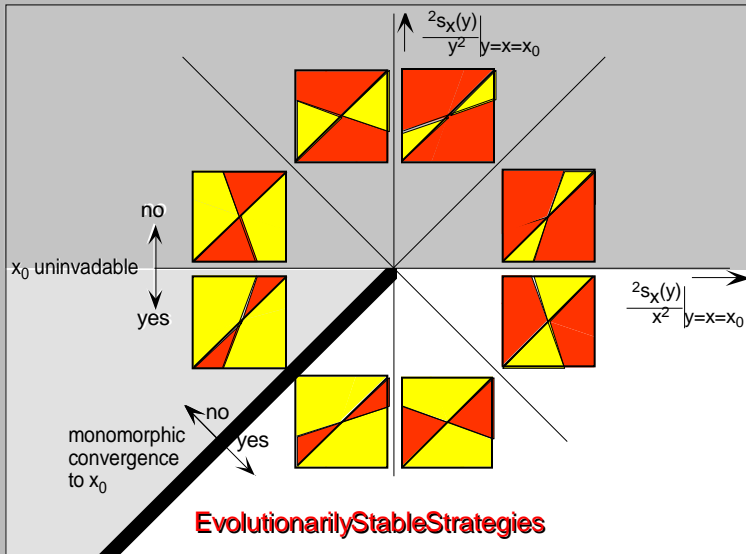


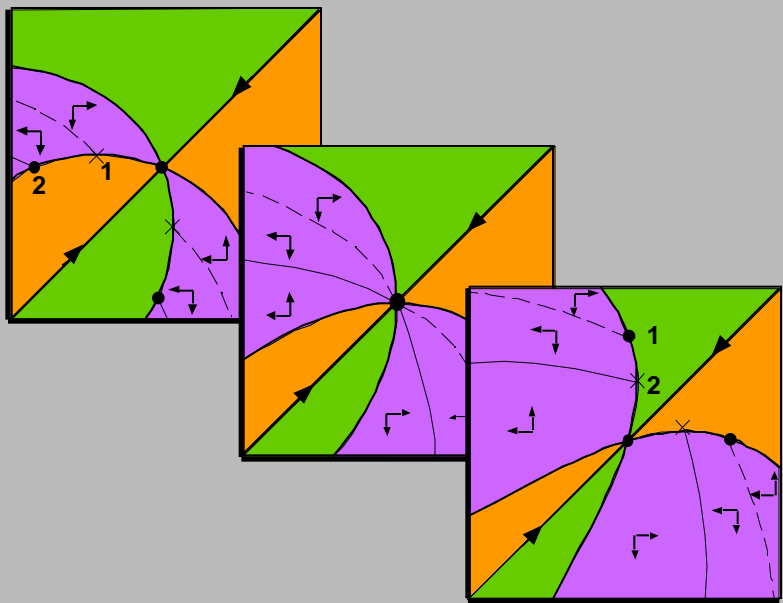
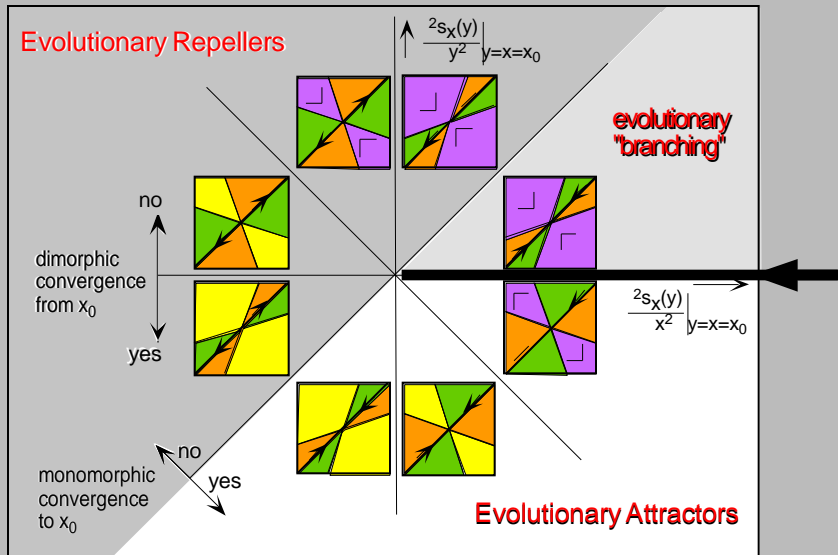
Some further useful consistency conditions:

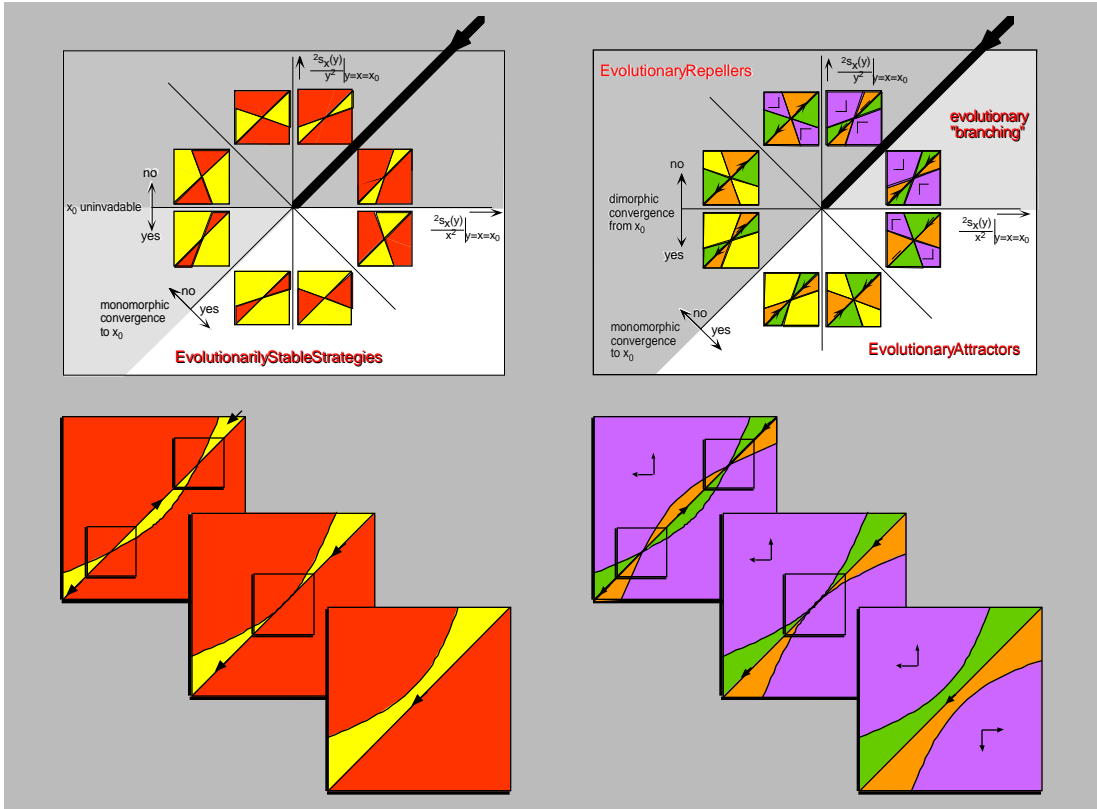


Bifurcations of evolutionarily singular points

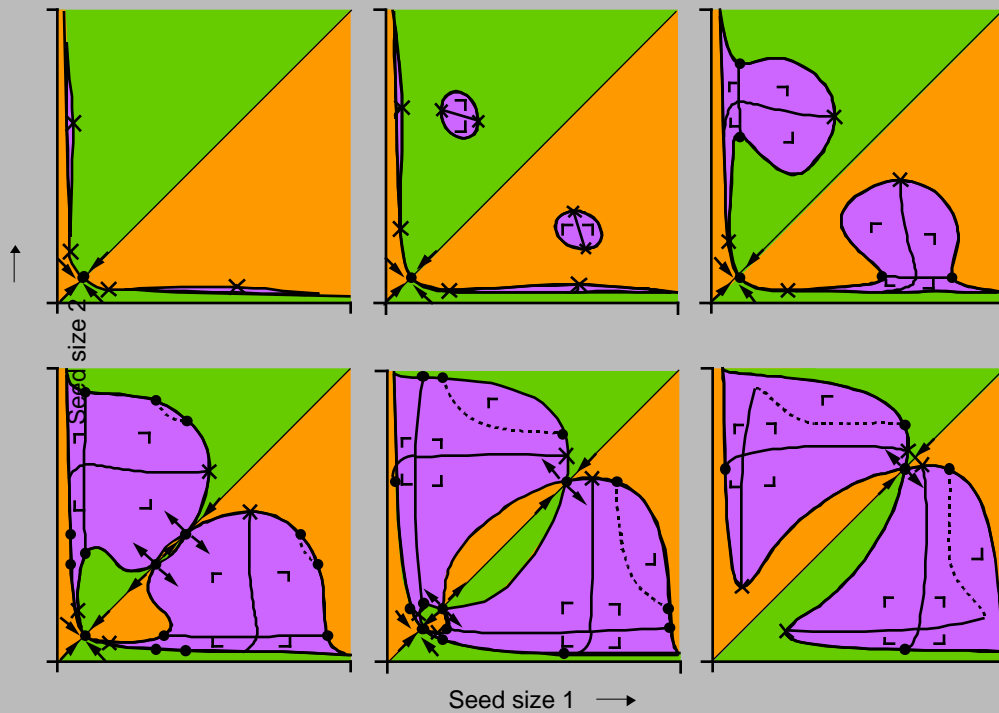








seed size evolution: Trait Evolution Plots



The Hawk-Dove game

Pay-off table:

	H	D
H	$\frac{1}{2}(V-C)$	V
D	0	$\frac{1}{2}V$

Population dynamics:

First round: Let \mathbf{P} be the probability to encounter a, temporary, Hawk. An individual with inborn probability p of playing Hawk accrues a contribution $p\mathbf{P}\frac{1}{2}(V-C) + p(1-\mathbf{P})V + 0 + (1-p)(1-\mathbf{P})\frac{1}{2}V$ to its effective fertility. To this is added a basic fertility $\frac{1}{2}B$ giving it an overall effective fertility $\frac{1}{2}[B + V(1-\mathbf{P}) + (V-C\mathbf{P})p]$.

Second round: Density dependence allows only a fraction $1/[\frac{1}{2}f(p_1, \dots; N_1, \dots; V, C; \dots)]$ to survive to the next generation.

$$n'_i = \frac{B + V(1-\mathbf{P}) + (V-C\mathbf{P})p_i}{f(p_1, \dots; N_1, \dots; V, C; \dots)} n_i \quad \text{with} \quad \mathbf{P} := \frac{p_i n_i}{n_i}$$

Fitness:

$$s_p(q) = \left\langle \ln \left[\frac{B + V(1-p) + (V-Cp)q}{f(p; N(t); V, C; \dots)} \right] \right\rangle_t =$$

$$\ln[B + V(1-p) + (V-Cp)q] - \left\langle \ln[f(p; N(t); V, C; \dots)] \right\rangle_t$$

$$s_p(p) = \ln[B + V(1-p) + (V-Cp)p] - \left\langle \ln[f(p; N(t); V, C; \dots)] \right\rangle_t =$$

$$\ln[B + V - Cp^2] - \left\langle \ln[f(p; N(t); V, C; \dots)] \right\rangle_t = 0.$$

$$s_p(q) = \ln \frac{B + V(1-p) + (V-Cp)q}{B + V - Cp^2}$$

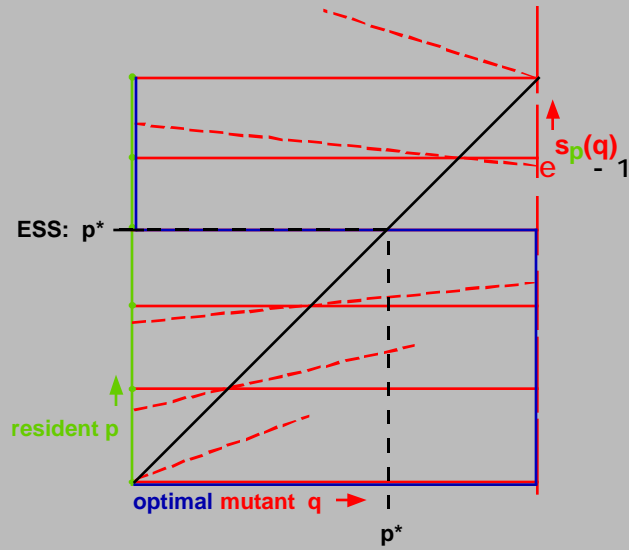
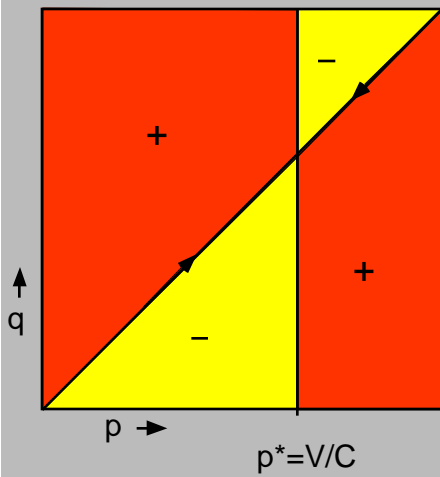
Special case: Evolutionary Game Theory:

Example: Hawk - Dove

	H	D
H	$\frac{1}{2}(V-C)$	V
D	0	$\frac{1}{2}V$

$$n_i = \frac{B + V(1-P) + (V-Cp) p_i}{f(p_1, \dots; N_1, \dots; V, C; \dots)} n_i \quad \text{with} \quad P := p_i n_i / n_i$$

$$s_p(q) = \ln \frac{B + V(1-p) + (V-Cp) q}{B + V - Cp^2}$$



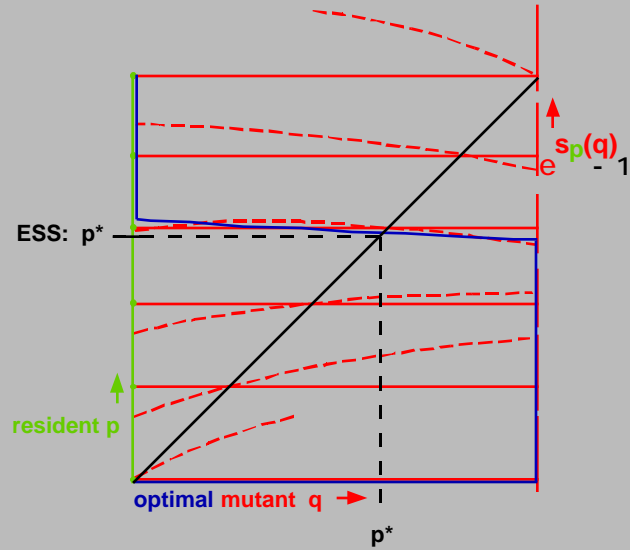
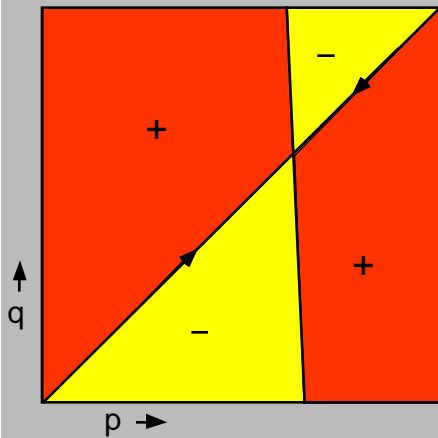
"Generic" Evolutionary Game Theory:

Hawk - Dove with between generation fluctuations in the pay-off

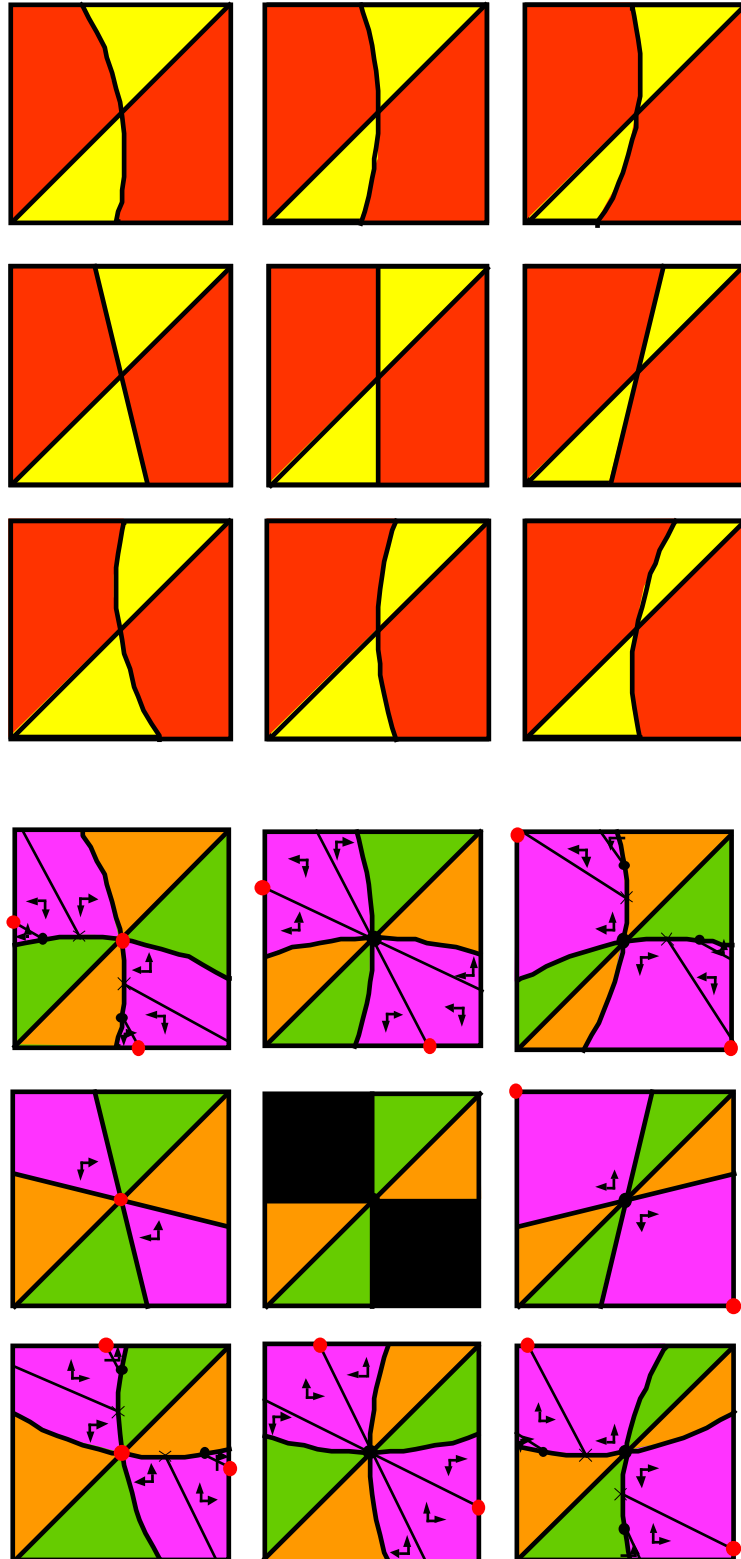
	H	D
H	$\frac{1}{2}(\underline{V}-C)$	\underline{V}
D	0	$\frac{1}{2}\underline{V}$

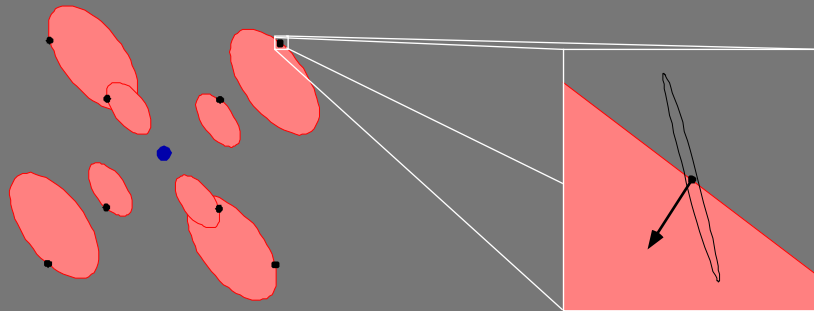
$$\underline{n}_i' = \frac{B + \underline{V}(1-\underline{P}) + (\underline{V}-C\underline{P}) p_i \underline{n}_i}{f(p_1, \dots; \underline{n}_1, \dots; \underline{V}, C, \dots)} \quad \text{with } \underline{P} := p_i \underline{n}_i / \underline{n}_i$$

$$s_p(q) = \mathbb{E} \ln \frac{B + \underline{V}(1-p) + (\underline{V}-Cp)q}{B + \underline{V} - Cp^2}$$



Unfolding the Degeneracy of Evolutionary Game Theory





To first order of approximation for small mutational steps:

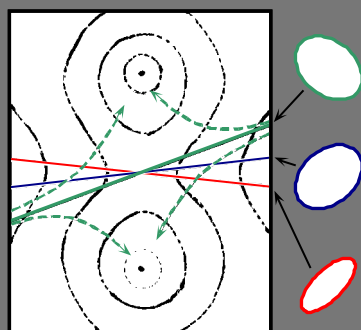
$$\frac{d\mathbf{X}}{dt} = \frac{1}{2} \bar{N}(\mathbf{X}) \mathbf{C} \left(\frac{s_{\mathbf{X}}(\mathbf{Y})}{\mathbf{Y}} \Big|_{\mathbf{Y}=\mathbf{X}} \right)^T$$

where $\frac{1}{2}$ is the probability of a mutation per birth event,
 \mathbf{C} is the mutational covariance matrix,
and $\bar{N}(\mathbf{X})$ depends on the relative reproductive variability.

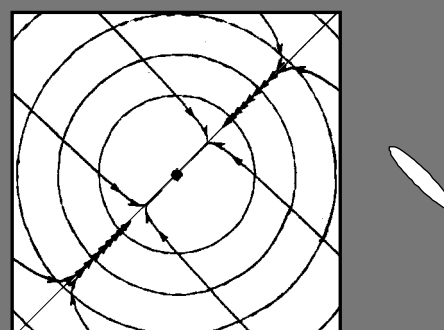
[When everybody is born equal & the community attractor is just a point:
 $\bar{N}(\mathbf{X}) = 2 / \text{Var}[\text{lifetime offspring number}]$.]

Two examples (from quantitative genetics, with a fixed shape of the fitness landscape) showing

that the domain of attraction of an adaptive peak will depend on the covariance matrix:



differences in evolutionary time scales due to an almost degenerate covariance matrix:



When the shape of the fitness landscape depends on the resident trait values, even the attractivity of a singular point may depend on the mutational/genetic covariance matrix.

Some matrix facts

A matrix is called symmetric if $A^T=A$,
where $A^T=(a_{ij})^T=(a_{ji})$ [the "transpose" of A].

Every square matrix can be decomposed into

$$\begin{array}{ll} \frac{1}{2}(A+A^T) & \text{the symmetric part} \\ \frac{1}{2}(A-A^T) & \text{the antisymmetric part} \end{array}$$

A symmetric matrix A is called positive [nonnegative] definite, written as $A>0$ [$A \geq 0$], if for all $X \neq 0$

$$X^T A X > 0 \quad [X^T A X \geq 0]$$

Covariance matrices are symmetric, as are (nonmixed) second derivatives of functions from vectors to scalars. Covariance matrices are moreover nonnegative definite.

For general matrices A one can only conclude from

$$X^T A X = 0 \quad \text{for all } X$$

that the symmetric part of A equals 0.

Some matrix facts II

For any quadratic form

$$(X-X_0)^T A (X-X_0) \quad (1)$$

with $\dim X = n$ there exists a linear transformation of coordinates such that this form can be written as

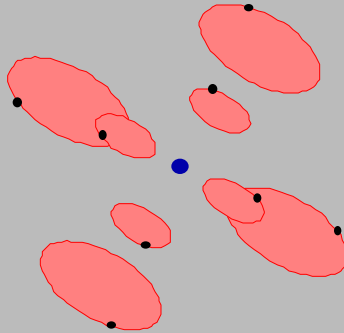
$$(X-X_1)^T \begin{bmatrix} I_h & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -I_k \end{bmatrix} (X-X_1) \quad (2)$$

$h+k = n$, with I_m the $m \times m$ identity matrix.

When $h=n$ or $k=0$ (A positive resp. negative definite), the level surfaces of (1) are ellipsoids, and those of (2) are spheres.

Some results for higher dimensional trait spaces 2:

- Near a singular point X^* :
 - The set of potential invaders into a given resident X is bounded by a quadratic surface, [in \mathbb{R}^2 an ellipse or a pair of hyperbolas].
 - The family of those sets, when X varies over a neighbourhood of X^* , is selfsimilar under uniform expansion:



- X^* is a local ESS (i.e., cannot be invaded by any nearby strategy Y) iff

$$C := \frac{2s_X(Y)}{Y^2} \Big|_{Y=X=X^*} \text{ is negative definite.}$$

- Convergence to an ESS is assured, whatever the mutational covariance matrix, iff

$$A := \frac{2s_X(Y)}{X^2} \Big|_{Y=X=X^*} - \frac{2s_X(Y)}{Y^2} \Big|_{Y=X=X^*} \text{ is positive definite.}$$

(Olof Leimar, in press)

- No mutual invasibility iff

$$B := \frac{2s_X(Y)}{X^2} \Big|_{Y=X=X^*} + \frac{2s_X(Y)}{Y^2} \Big|_{Y=X=X^*} \text{ is negative definite.}$$

- $A > 0 \ \& \ B > 0 \Rightarrow C < 0$

as in the one-dimensional case.

Normal form of the dimorphic s-function at a monomorphic singular point for vector traits

Let X^* be a singular point and let

$$X_1 = X^* + U_1, \quad X_2 = X^* + U_2, \quad Y = X^* + V,$$

and let

$$\bar{U} = \frac{1}{2}(U_1 + U_2), \quad \bar{V} = \frac{1}{2}(U_1 - U_2),$$

then

$$S_{X_1 X_2}(Y) = 2 \left\{ \bar{U}^T C_{11} \bar{U} - \bar{U}^T C_{00} + \right. \\ \left. 2 \left[\bar{U}^T C_{10} V + \frac{\bar{U}^T (C_{00} - C_{11} + C_{10} - C_{01})}{\bar{U}^T (C_{00} + C_{11})} \bar{U}^T C_{10} (V - \bar{U}) \right] + \right. \\ \left. V^T C_{00} V \right\} + \text{h.o.t}$$

with

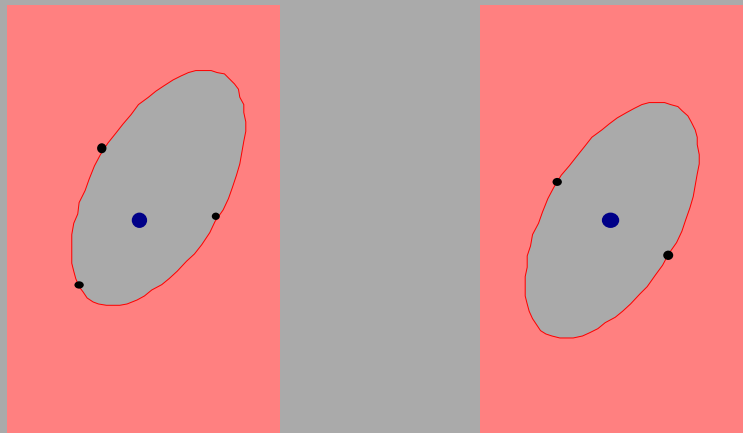
$$C_{01} = C_{10}^T \quad \text{and} \quad C_{11} \text{ and } C_{00} \text{ symmetric}$$

and

$$C_{11} + C_{01} + C_{10} + C_{00} = 0.$$

Some results for higher dimensional trait spaces 3:

- The number of types that can coexist around a monomorphic singular point is bounded from above by $\dim[X]+1$. (Freddy Bugge Christiansen & Volker Loeschcke, 1987)
- Near a singular point the sets of potential invaders into k-tuples (X_1, \dots, X_k) , $1 < k \leq \dim[X]+1$, are of the same form, bounded by the same quadratic surfaces (up to a scaling factor), independent of k or the choice of the X_1, \dots, X_k :



- The number of branches that can coexist and diverge is in principle equal to the number of positive eigenvalues of

$$C := \frac{2s_X(Y)}{Y^2} \Big|_{Y=X=X^*}$$

However in practice usually only 2 branches get started,

and there are indications that if more get started, usually only 2 remain.

Splitting in three has only been observed in the rotationally symmetric case (where the symmetry holds in the coordinate system where the covariance matrix becomes the identity matrix)

2D resource competition model
(Andras Vukics, Janos Asboth & Geza Meszena)

