First a note about the colour coding:

**Mutual invasability:** also consider "role reversal" of x and y

- **y can invade x-population**
- **y cannot invade x**
- **x can invade y-population**
- **x cannot invade y**
- **x can invade x-population but not vice versa**
- **x can invade y-population but not vice versa**
- **x can invade x-population and vice versa**
The classification of evolutionarily singular points, an algebraic approach

\[ x^* \text{ is a singular point iff} \]

\[ \frac{ds_x(y)}{dy} \bigg|_{y=x=x^*} = 0 \quad (x^* \text{ is an extremum in the y-direction}) \]

Linearization around \( x = y = x^* \)

\[ s_u(v) = a + b_1 u + b_0 v + c_{11} u^2 + 2 c_{10} u v + c_{00} v^2 + \text{h.o.t} \]

neutrality of resident

\[ s_u(0) = 0 \quad a = 0 \quad b_1 + b_0 = 0 \quad c_{11} + c_{10} + c_{00} = 0 \]

\[ x^* \text{ is an extremum in y} \]

\[ s_0(0) = 0 \quad b_1 + b_0 = 0 \]
monomorphic convergence to $x_0$

area of possible coexistence

no  yes

no  yes
Dimorphic linearisation around $x_1 = x_2 = y = x^*$, I:

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

Only directional derivatives (!):
- $u_1 = u_1 w_1, \quad u_2 = u_2 w_2$

$s_{u_1, u_2}(v) = \alpha + \beta_1 (w_1, w_2) u + \beta_0 v + \gamma_{11} (w_1, w_2) u^2 + \gamma_{10} (w_1, w_2) u v + \gamma_{00} v^2 + \text{h.o.t.}$

---

**Community state space**

**Parameter space**

**Parameter paths**

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

Expansion formula ($\star$)

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

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

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:

- Evolutionary Attractors
- Evolutionary Repellers

- Monomorphic convergence to $x_0$:
  - No
  - Yes

- Dimorphic convergence from $x_0$:
  - No
  - Yes

- Evolutionary "branching":
  - Yes
  - No

- Area of possible coexistence:
  - Yes
  - No

- Evolutionary Attractors:

- Evolutionary Repellers:

---

$x_1$, $x_2$, $y$, $x$
Bifurcations of evolutionarily singular points

\[ \frac{\partial^2 s_x(y)}{\partial x^2} \bigg|_{y=x=x_0} \]

\[ \frac{\partial^2 s_x(y)}{\partial y^2} \bigg|_{y=x=x_0} \]

Evolutionarily Stable Strategies

\( x_0 \) uninvadable

\begin{align*}
\text{no} & \quad \text{yes} \\
\text{no} & \quad \text{yes}
\end{align*}

monomorphic convergence to \( x_0 \)
Evolutionarily Stable Strategies

$x_0$ invadable

monomorphic convergence to $x_0$

$\frac{\partial^2 s_x(y)}{\partial y^2} \bigg|_{x=x_0}$

$\frac{\partial^2 s_x(y)}{\partial x^2} \bigg|_{x=x_0}$

$\frac{\partial^2 s_x(y)}{\partial x \partial y} \bigg|_{x=x_0}$
Evolutionary Attractors

Evolutionary Repellers

Dimorphic convergence from $x_0$

Monomorphic convergence to $x_0$

Yes

No

Yes

No

$\frac{\partial^2 s(x(y))}{\partial x^2} |_{y=x=x_0}$

$\frac{\partial^2 s(x(y))}{\partial y^2} |_{y=x=x_0}$

Evolutionary "branching"
Evolutionarily Stable Strategies

Evolutionarily Repellers

Evolutionary Attractors

Seed size evolution: Trait Evolution Plots
The Hawk-Dove game

Pay-off table:

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>( \frac{1}{2} (V-C) )</td>
<td>V</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>( \frac{1}{2} V )</td>
</tr>
</tbody>
</table>

Population dynamics:

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

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

\[
n_i' = \frac{B + V(1-P) + (V-C)P_i}{f(p_1, \ldots; N_1, \ldots; V, C; \ldots)} n_i \quad \text{with} \quad P := \sum p_i n_i / \sum n_i.
\]

Fitness:

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

\[
s_p(p) = \ln[B + V(1-p) + (V-C)p] - \langle \ln[f(p;N(t);V,C;\ldots)] \rangle_t = \ln[B + V - C p^2] - \langle \ln[f(p;N(t);V,C;\ldots)] \rangle_t = 0.
\]
Special case: Evolutionary Game Theory:

Example: Hawk - Dove

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>(\frac{1}{2}(V-C))</td>
<td>V</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>(\frac{1}{2}V)</td>
</tr>
</tbody>
</table>

\[
n_i' = \frac{B + V(1-P) + (V-CP)p_i}{f(p_1,...;N_1,...;V,C;...)} n_i \quad \text{with} \quad P := \frac{\sum p_i n_i}{\sum n_i}.
\]

\[
s_p(q) = \ln \frac{B + V(1-p) + (V-Cp)q}{B + V - Cp^2}.
\]
"Generic" Evolutionary Game Theory:

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

<table>
<thead>
<tr>
<th></th>
<th>H</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>(\frac{1}{2}(V-C))</td>
<td>V</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>(\frac{1}{2}V)</td>
</tr>
</tbody>
</table>

\[ n_i' = B + V(1-P) + (V-CP)P_i \frac{n_i}{g(p_1,\ldots;n_1,\ldots;V,C;\ldots)} \]

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

ESS: \(p^*\)
Unfolding the Degeneracy of Evolutionary Game Theory
Higher Dimensional Trait Spaces

To first order of approximation for small mutational steps:

\[
\frac{dX}{dt} = \frac{1}{2} \alpha \varepsilon \bar{N}(X) C \left[ \frac{\partial s_X(Y)}{\partial Y} \bigg|_{Y=X} \right]^T
\]

where \( \varepsilon \) is the probability of a mutation per birth event, \( C \) is the mutational covariance matrix, and \( \alpha \) depends i.a. on the reproductive variability.

When everybody is born equal & the community attractor is just a point:

\[
\alpha = 2 \frac{T_f}{T_s \sigma^2}
\]

\( T_f \) = average age of giving birth, \( T_s \) = average lifetime
\( \sigma^2 = \text{Var}[\text{lifetime offspring number}] \).

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
\[
\frac{1}{2}(A+A^T) \quad \text{the symmetric part}
\]
\[
\frac{1}{2}(A-A^T) \quad \text{the antisymmetric part}
\]

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

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
\[
X^TAX = 0 \quad \text{for all } X
\]
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
\[
(X-X_1)^T \begin{bmatrix} I_h & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -I_k \end{bmatrix} (X-X_1) \quad (2)
\]

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

When $h=n$ or $k=n$ (A positive rep. negative definite), the level surfaces of (1) are elipsoids, 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, [$\text{in } \mathbb{R}^2$ 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
  $$C := \left. \frac{\partial^2 s_X(Y)}{\partial Y^2} \right|_{Y=X=X^*}$$
  is negative definite.

- Convergence to an ESS is assured, whatever the mutational covariance matrix, iff
  $$A := \left. \frac{\partial^2 s_X(Y)}{\partial X^2} \right|_{Y=X=X^*} - \left. \frac{\partial^2 s_X(Y)}{\partial Y^2} \right|_{Y=X=X^*}$$
  is positive definite.
  (Olof Leimar, in press)

- No mutual invasibility iff
  $$B := \left. \frac{\partial^2 s_X(Y)}{\partial X^2} \right|_{Y=X=X^*} + \left. \frac{\partial^2 s_X(Y)}{\partial Y^2} \right|_{Y=X=X^*}$$
  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
\[
X_1 = X^* + \varepsilon U_1, \quad X_2 = X^* + \varepsilon U_2, \quad Y = X^* + \varepsilon V,
\]
and let
\[
\bar{U} = \frac{1}{2}(U_1 + U_2), \quad \Delta = \frac{1}{2}(U_1 - U_2),
\]
then
\[
S_{X_1 X_2}(Y) = \varepsilon^2 \left\{ \bar{U}^T C_{11} \bar{U} - \Delta^T C_{00} \Delta + 2 \left[ \bar{U}^T C_{10} V + \frac{\bar{U}^T (C_{00} - C_{11} + C_{10} - C_{01}) \Delta}{\Delta^T (C_{00} + C_{11}) \Delta} \Delta^T C_{10} (V - U) \right] + V^T C_{00} V \right\} + \text{h.o.t}
\]
with \( C_{01} = C_{10}^T \) and \( C_{11} \) and \( C_{00} \) 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 \( \text{dim}[X]+1 \).
  (Freddy Bugge Christiansen & Volker Loeschcke, 1987)

- Near a singular point the sets of potential invaders into \( k \)-tuples \( (X_1, \ldots, X_k) \), \( 1 < k \leq \text{dim}[X]+1 \), are of the same form, bounded by the same quadratic surfaces (up to as scaling factor), independent of \( k \) or the choice of the \( X_1, \ldots, X_k \):

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

\[
C := \left. \frac{\partial^2 s_x(Y)}{\partial Y^2} \right|_{Y=X=X^*}
\]

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).