Discrete Population Models

- Cooperation
- Competition
- Population Genetics

Let x and y denote the sizes for two populations which reproduce at discrete time intervals. A system of nonlinear difference equations describes the rule by which these populations change from one generation to the next. The population sizes evolve in time according to the iterates of the nonlinear map on the right side of the system of difference equations. A familiar 1-dimensional model is logistic population growth, i.e.,

$$x_{n+1} = \lambda\, x_n\, (1 - x_n)\,.$$

For simplicity, let "$'$" indicate the population size in the next generation.

Cooperation

$$x' = \frac{y}{a+y}\,x\,, \qquad y' = \frac{x}{b+x}\,y\,. \qquad \text{(Coop)}$$

Notice that each per capita transition function is increasing in the other population. If $f(x,y)$ represents the transition map in (Coop) then the derivative matrix of f is positive for all $x, y > 0$, i.e.,

$$Df(x,y) = \begin{bmatrix} \frac{y}{(a+y)} & \frac{ax}{(a+y)^2} \\ \frac{by}{(b+x)^2} & \frac{x}{(b+x)} \end{bmatrix} = \begin{bmatrix} + & + \\ + & + \end{bmatrix}.$$

This property holds for any 2-dimensional cooperative system without self-repression.

Competition

$$x' = \frac{1}{a+y}\,x\,, \qquad y' = \frac{1}{b+x}\,y\,. \qquad \text{(Com)}$$

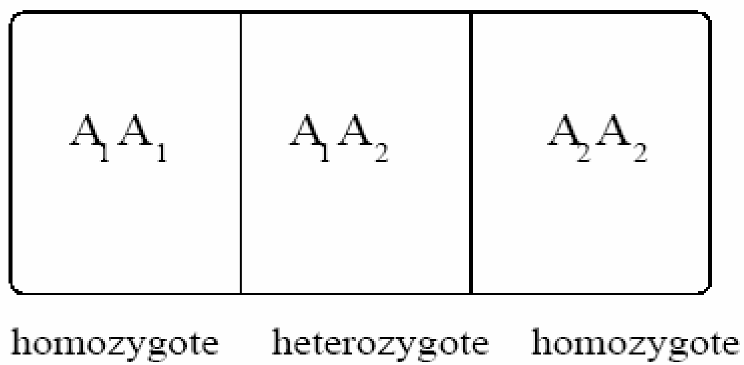
Here each per capita transition function is decreasing in the other population and the derivative matrix of f has the form

$$Df(x,y) = \begin{bmatrix} \frac{1}{(a+y)} & \frac{-x}{(a+y)^2} \\ \frac{-y}{(b+x)^2} & \frac{1}{(b+x)} \end{bmatrix} = \begin{bmatrix} + & - \\ - & + \end{bmatrix}.$$

Because of these sign symmetries in the derivative matrices, solution orbits of (Coop) and (Com) preserve appropriate partial orders on the positive quadrant.

Population Genetics

Consider a single locus, two-allele selection model with female and male viability differences. A population of size x is divided into three subpopulations based on allele pairing.



$P_{ij} =$ frequency of A_iA_j genotype at birth (independent of sex)

$v_{ij} =$ probability that A_iA_j genotype reaches reproductive age (called viability and depends on sex)

$p_i =$ frequency of A_i allele among adults

$$= \frac{\#\ A_i \text{ alleles}}{\text{total } \#\text{ alleles}} = \frac{2v_{ii}P_{ii}x + v_{12}P_{12}x}{2v_{11}P_{11}x + 2v_{12}P_{12}x + 2v_{22}P_{22}x}$$

$$= \frac{v_{ii}P_{ii} + 0.5v_{12}P_{12}}{v_{11}P_{11} + v_{12}P_{12} + v_{22}P_{22}}$$

$\overline{v} =$ mean viability or fitness $= v_{11}P_{11} + v_{12}P_{12} + v_{22}P_{22}$

Viability Differences

Genotype	A_1A_1	A_1A_2	A_2A_2
Female viability	$v_{11}^{♀}$	$v_{12}^{♀}$	$v_{22}^{♀}$
Male viability	$v_{11}^{♂}$	$v_{12}^{♂}$	$v_{22}^{♂}$
Normalized parameters			
Female viability	$a/2$	1	$b/2$
Male viability	$c/2$	1	$d/2$

$p_i =$ frequency of A_i allele among adults

$$= \frac{\#\ A_i \text{ alleles}}{\text{total } \# \text{ alleles}} = \frac{2v_{ii}P_{ii}x + v_{12}P_{12}x}{2v_{11}P_{11}x + 2v_{12}P_{12}x + 2v_{22}P_{22}x}$$

$$= \frac{v_{ii}P_{ii} + 0.5v_{12}P_{12}}{v_{11}P_{11} + v_{12}P_{12} + v_{22}P_{22}}$$

$\overline{v} =$ mean viability or fitness $= v_{11}P_{11} + v_{12}P_{12} + v_{22}P_{22}$

$p_i^{♀} =$ frequency of A_i allele among adult females

$= (v_{ii}^{♀}P_{ii} + 0.5v_{12}^{♀}P_{12})/\overline{v}^{♀}$

$p_i^{♂} = (v_{ii}^{♂}P_{ii} + 0.5v_{12}^{♂}P_{12})/\overline{v}^{♂}$

Assume random mating to determine the next generation, i.e., a genotype in the next generation is formed by the random union of adult alleles in the present generation. So

$$P'_{ii} = p_i^{\female} p_i^{\male} \qquad \text{and} \qquad P'_{12} = p_1^{\female} p_2^{\male} + p_2^{\female} p_1^{\male}\,.$$

The transition equations for $p_i^{\female\,\prime}$ and $p_i^{\male\,\prime}$ in terms of $p_i^{\female}$ and $p_i^{\male}$ of the previous generation are complicated and have no exploitable mathematical structure. Owen (*Heredity*, 1953) suggested using state variables

$$x = \frac{p_1^{\female}}{p_2^{\female}} = \frac{p_1^{\female}}{1 - p_1^{\female}} \qquad \text{and} \qquad y = \frac{p_1^{\male}}{p_2^{\male}} = \frac{p_1^{\male}}{1 - p_1^{\male}}\,.$$

So x increases (decreases) if and only if $p_1^{\female}$ increases (decreases).

$$x' = \frac{p_1^{\female\,\prime}}{p_2^{\female\,\prime}} = \frac{0.5\,a\,p_1^{\female}p_1^{\male} + 0.5\left(p_1^{\female}p_2^{\male} + p_1^{\male}\,p_2^{\female}\right)}{0.5\,b\,p_2^{\female}p_2^{\male} + 0.5\left(p_1^{\female}p_2^{\male} + p_1^{\male}\,p_2^{\female}\right)} \cdot \frac{\frac{1}{p_2^{\female}p_2^{\male}}}{\frac{1}{p_2^{\female}p_2^{\male}}}$$

and the transition equation in the variables x, y is

$$\begin{aligned} x' &= \frac{axy + x + y}{b + x + y} \\ y' &= \frac{cxy + x + y}{d + x + y}\,. \end{aligned} \qquad \text{(Gen)}$$

If $g(x, y)$ denotes the transition map in (Gen) then the derivative matrix of g is positive for all $x, y > 0$, i.e.,

$$Dg(x,y) = \begin{bmatrix} \frac{aby+ay^2+b}{(b+x+y)^2} & \frac{abx+ax^2+b}{(b+x+y)^2} \\ \\ \frac{cdy+cy^2+d}{(d+x+y)^2} & \frac{cdx+x^2+d}{(d+x+y)^2} \end{bmatrix} = \begin{bmatrix} + & + \\ + & + \end{bmatrix}.$$

Define two partial orders on $\mathbf{R}^2_+$. For g which represents the genetics and the cooperative systems define

$$(x_1, y_1) \leq_g (x_2, y_2) \quad \text{if} \quad x_1 \leq x_2 \text{ and } y_1 \leq y_2 .$$

Also define $<_g$ and $<<_g$ in the natural way.

For f which represents the competitive system, define

$$(x_1, y_1) \leq_f (x_2, y_2) \quad \text{if} \quad x_1 \leq x_2 \text{ and } y_2 \leq y_1 .$$

Also define $<_f$ and $<<_f$.

A map T is strongly monotone if $(x_1, y_1) < (x_2, y_2)$ implies $T(x_1, y_1) << T(x_2, y_2)$. If T is strongly monotone and if $(x_0, y_0) < T(x_0, y_0)$ then the orbit $T^n(x_0, y_0)$ is increasing and converges to a fixed point if bounded.

Result: The maps g and f are strongly monotone for the appropriate orders on the interior of $\mathbf{R}^2_+$.

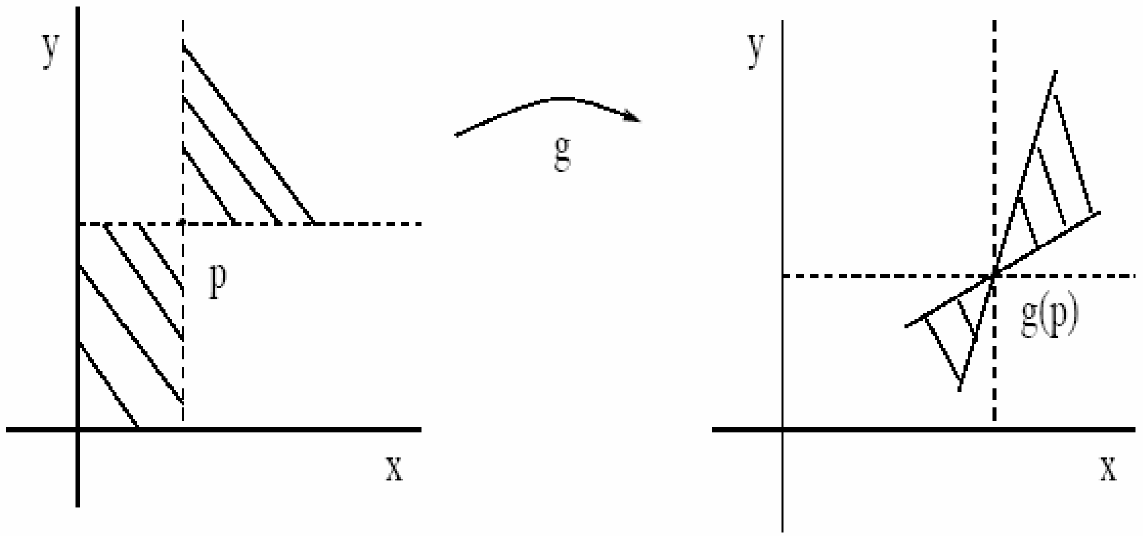
Verification

Suppose $(x_1, y_1) <_g (x_2, y_2)$. Then by the mean value theorem on $\mathbf{R}^2_+$.

$$g_i(x_2, y_2) - g_i(x_1, y_1) = \frac{\partial g_i}{\partial x}(x_2 - x_1) + \frac{\partial g_i}{\partial y}(y_2 - y_1).$$

$$+ \qquad + \qquad + \qquad + \qquad > 0$$

Hence $g_i(x_1, y_1) < g_i(x_2, y_2)$ so $g(x_1, y_1) <<_g g(x_2, y_2)$.

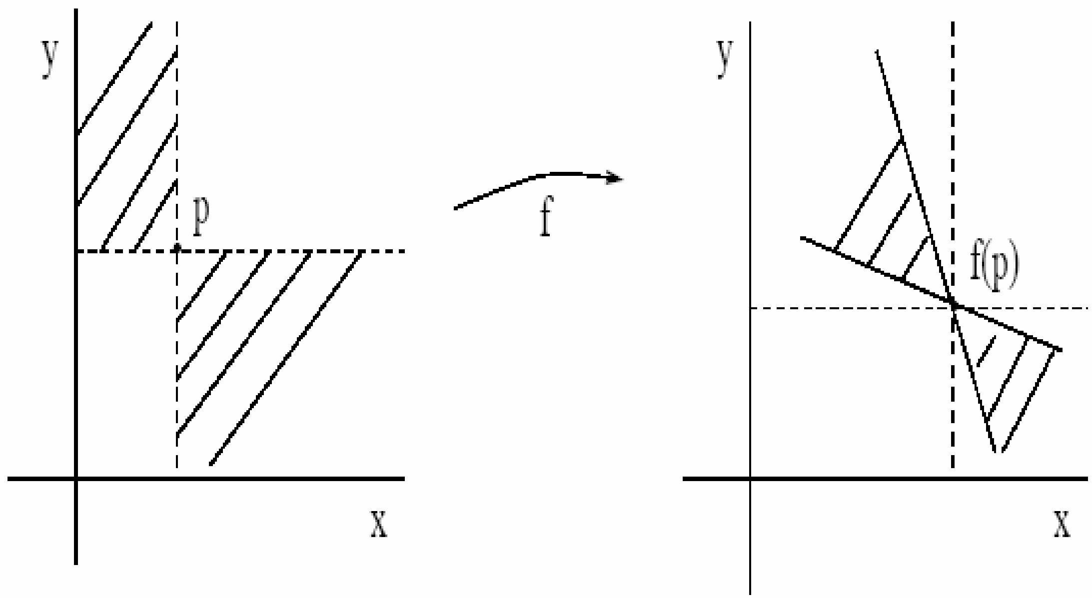


And for f, if $(x_1, y_1) <_f (x_2, y_2)$ then

$$f_i(x_2, y_2) - f_i(x_1, y_1) = \frac{\partial f_i}{\partial x}(x_2 - x_1) + \frac{\partial f_i}{\partial y}(y_2 - y_1).$$

$$\begin{array}{llllll}
\text{for } i = 1 & + & + & - & - & > 0 \\
\text{for } i = 2 & - & + & + & - & < 0
\end{array}$$

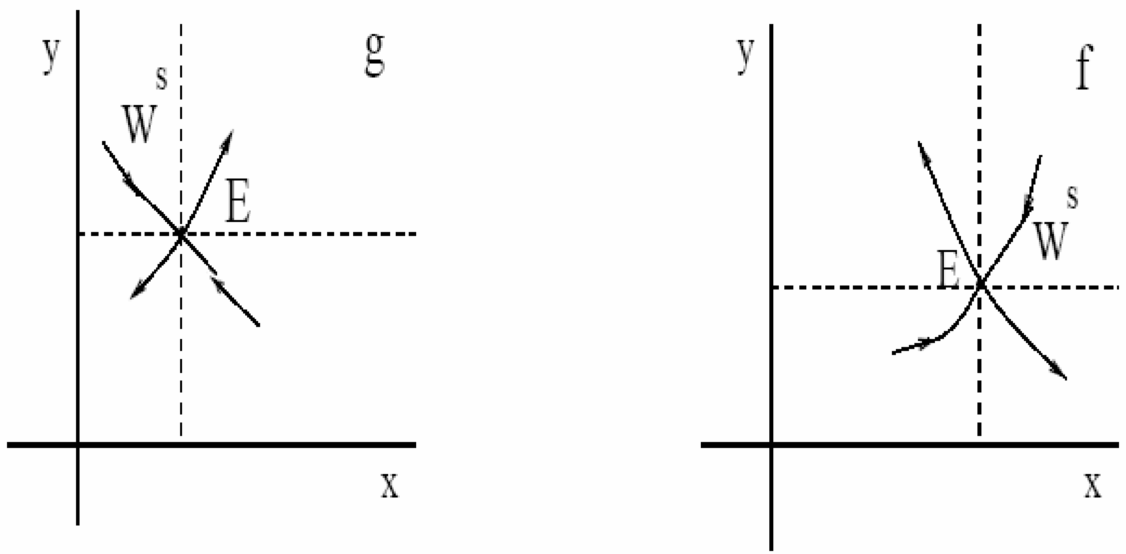
Hence $f(x_1, y_1) <<_f f(x_2, y_2)$.



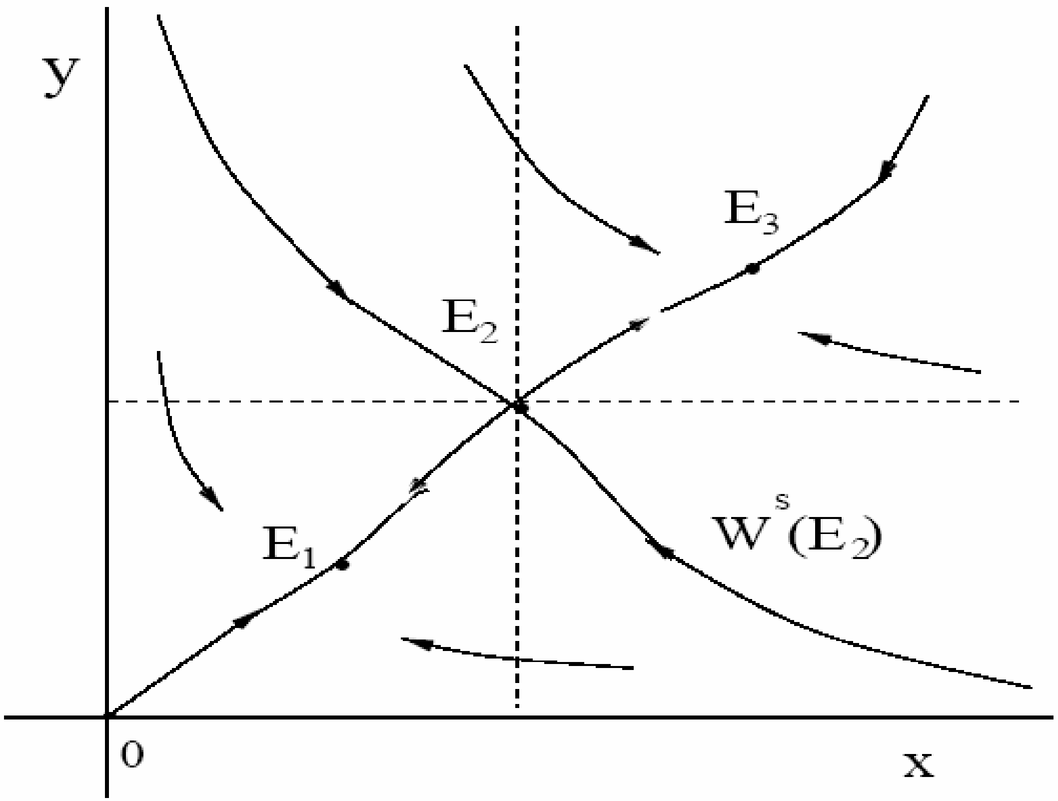
$p, q \in \mathbf{R}^2_+$ are related if $p < q$ or $q < p$. Being related is preserved by a monotone map.

Let E be a saddle point for g or f and let $W^s(E)$ and $W^u(E)$ denote its stable and unstable manifolds, respectively.

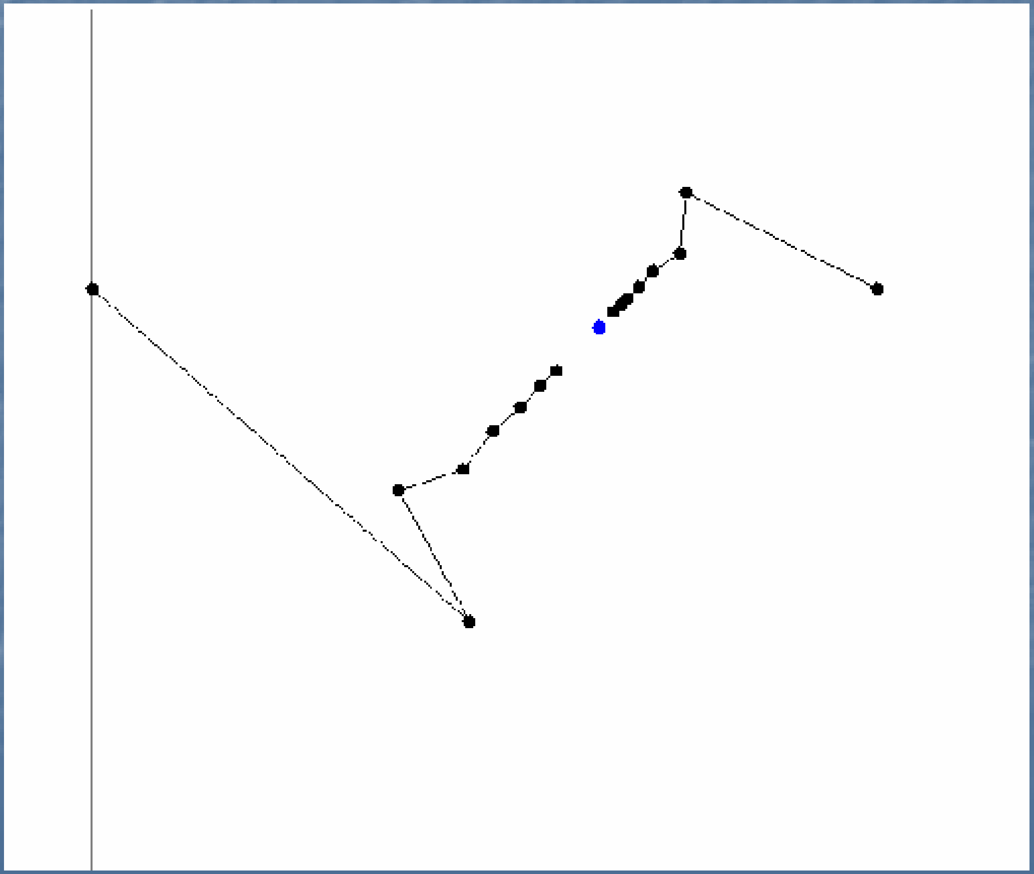
Result: $W^s(E)$ contains no related points. $W^u(E) \setminus E$ consists of orbits which are monotonically increasing or decreasing.



For the genetics system (Gen), there are at most 3 equilibria in the interior of R^2_+ and they are ordered. Each orbit converges to an equilibrium and the stable manifolds of saddles separate the domains of attraction of sinks.



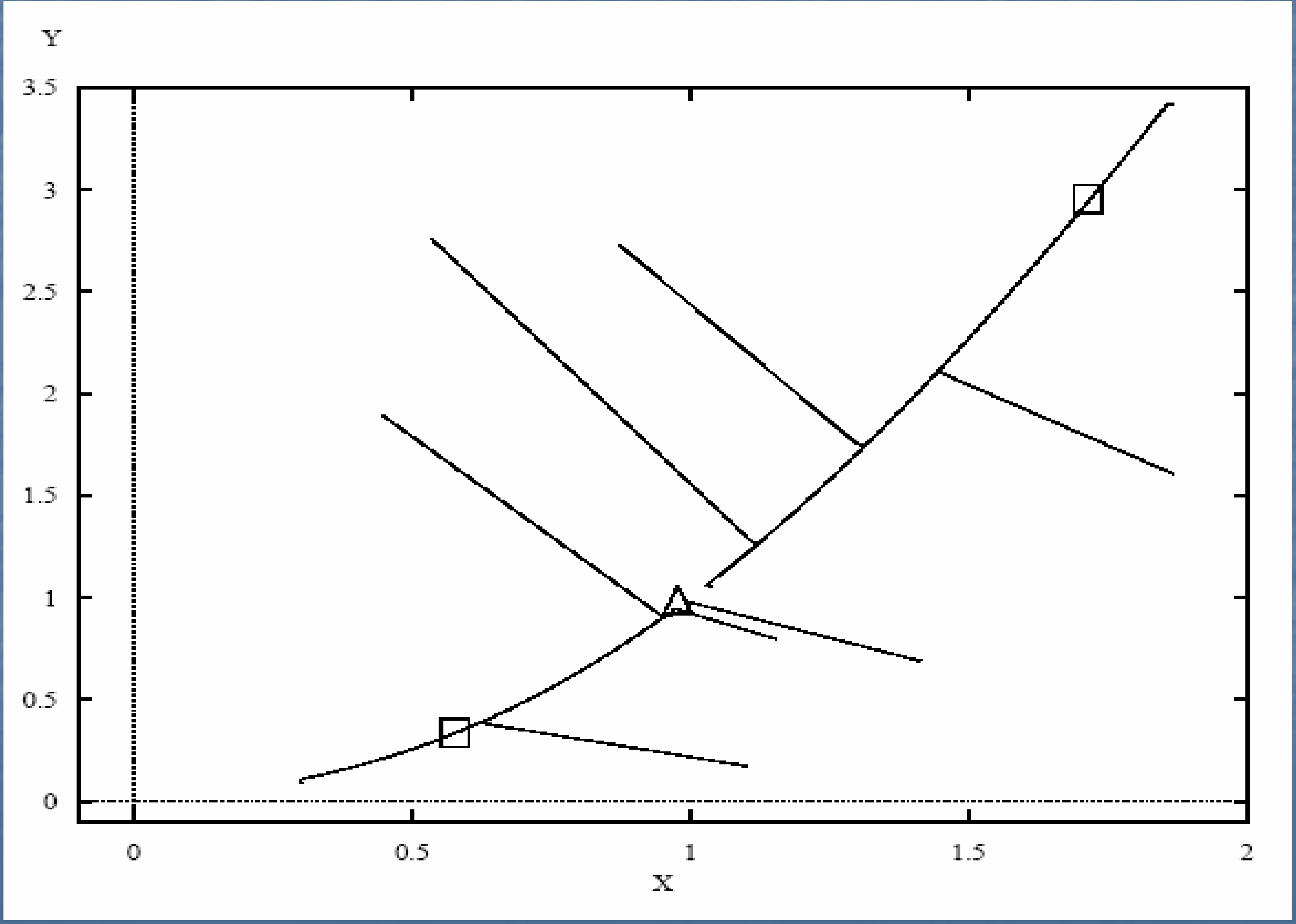
Damped oscillations may occur transverse to the positive direction. This corresponds to oscillations of the heterozygote frequencies. For example, if x decreases and y increases then $p_1^{\female}$ decreases and $p_1^{\male}$ increases. Hence, the frequency of new born $A_1^{\female}A_2^{\male}$ decreases and the frequency of $A_1^{\male}A_2^{\female}$ increases.



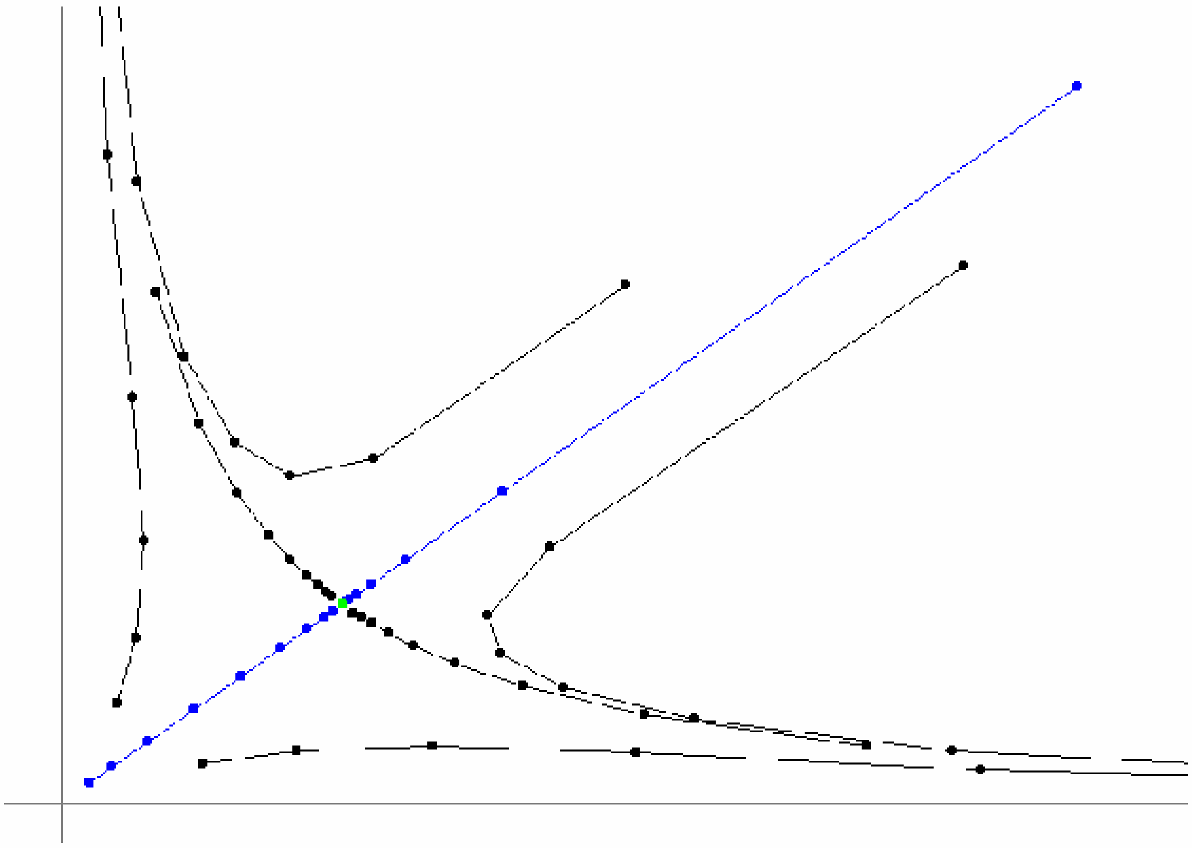
a=b=0.5

c=d=3

If $a = b = 1$ and $c = d = 4.3$, two stable equilibria ($\square$) exist with domains of attraction separated by the stable manifold of a saddle ($\triangle$).



For (Com), if $a, b < 1$ then $E = (1-b, 1-a)$ is a saddle with stable manifold in the first and third quadrants based at E, which separates the domains of attraction of $(x, y) = (0, \infty)$ and of $(x, y) = (\infty, 0)$. Let $a = b = 0.5$.



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