

Problem Set #6: Continuous time population dynamics
 Biomathematics, Spring 2001

1. (a) At equilibrium the population size is constant, thus, $\frac{dN}{dt}(N^*) = 0$.

$$\frac{dN}{dt}(N^*) = rN^*[1 - (N^*/K)^\theta] = 0$$

$$rN^* - rN^* \left(\frac{N^*}{K}\right)^\theta = 0$$

$$\left(\frac{N^*}{K}\right)^\theta = 1$$

$$N^* = K$$

Another value for N that satisfies $\frac{dN}{dt}(N^*) = 0$, is $N^* = 0$.

To evaluate the equilibrium, let $\frac{dN}{dt} = rN[1 - (N/K)^\theta] = F(N)$, and

determine whether $\frac{dF}{dN}(N^*)$ is positive or negative. If $\frac{dF}{dN}(N^*)$

is positive this means that $\frac{dN}{dt}(N^*)$ is an increasing function

at N^* . Remembering that at N^* , $\frac{dN}{dt}(N^*) = 0$, if $\frac{dF}{dN}(N^*)$

is positive then any small perturbation to the left is associated with a negative $\frac{dN}{dt}$. Therefore any perturbation to the left of

N^* will move away from the equilibrium. A similar argument shows that if $\frac{dF}{dN}(N^*)$ is positive any perturbation to the right

of N^* will also move away from the equilibrium. If $\frac{dF}{dN}(N^*)$

is negative, the opposite dynamics will occur in that any small perturbation will return to the equilibrium, whether to the right or to the left.

Stability analysis of the equilibrium $N^* = K$:

$$\frac{dF}{dN}(N) = r - r \left(\frac{N}{K}\right)^\theta - r\theta \left(\frac{N}{K}\right)^{\theta-1}$$

$$\frac{dF}{dN}(N^*) = r - r - r\theta = -r\theta$$

Since both r and θ are positive $\frac{dF}{dN}(N^*)$ is negative, and since

$\frac{dF}{dN}(N^*)$ is negative the equilibrium, $N^* = K$, is stable.

Stability analysis of the equilibrium $N^* = 0$:

$$\frac{dF}{dN}(N^*) = r$$

Since r is positive, the equilibrium, $N^* = 0$, is unstable.

In figure 1, for $\theta = 1$ there is a linear decline in per capita growth rate with population size. For $\theta < 1$ the decline in growth rate is more rapid for small population size but becomes less as population size reaches the carrying capacity. For $\theta > 1$ the decline is less rapid for small population size but becomes greater as population size reaches the carrying capacity.

2. A plot of $\frac{dN}{dt}$ versus N is provided in figure 2.

(a) At equilibrium, $\frac{dN}{dt} = 0 = rN^*(N^* - a)(1 - N^*/K)$.

The equation is already factored for us leaving

$$rN^* = 0 \implies N^* = 0$$

$$N^* - a = 0 \implies N^* = a$$

$$(1 - N^*/K) = 0 \implies N^* = K$$

Thus we have three equilibrium at $N^* = \{0, a, K\}$.

(b) As with problem #1, we set $\frac{dN}{dt} = rN(N - a)(1 - N/K) = F(N)$, and take the derivative of $F(N)$ with respect to N . We then evaluate the derivative at the equilibrium points.

$$\frac{dF(N)}{dN} = r(N - a)(1 - N/K) + rN(1 - N/K) - \frac{rN(N - a)}{K}$$

The equilibrium $N^* = 0$:

$\frac{dF(0)}{dN} = r(-a)$. Thus $\frac{dF(0)}{dN}$ is always negative which means the equilibrium, $N^* = 0$, is stable.

The equilibrium $N^* = a$:

$$\frac{dF(a)}{dN} = r(a - a)(1 - a/K) + ra(1 - a/K) - \frac{rN(a - a)}{K}$$

$\frac{dF(a)}{dN} = ra(1 - a/K)$. In this case, $\frac{dF(a)}{dN}$ is always positive which means the equilibrium is unstable.

The equilibrium $N^* = K$:

$$\frac{dF(K)}{dN} = r(K - a)(1 - K/K) + rK(1 - K/K) - \frac{rK(K - a)}{K}$$

$= -r(K - a)$. Which is always negative for reasonable values of r , K , and a . Therefore this equilibrium is stable.

(c) In figure 3 we see that the per capita growth rate is negative for $N < a$ and $N > K$. In this figure $a = 20$ and $K = 100$.

(d) In the logistic model there were two equilibrium, whereas in the Allee model there are three. In the logistic model the per capita growth rate was positive until the population size grew larger than the carrying capacity, whereas in the Allee model the per capita growth rate is negative if $N < a$ or $N > K$.

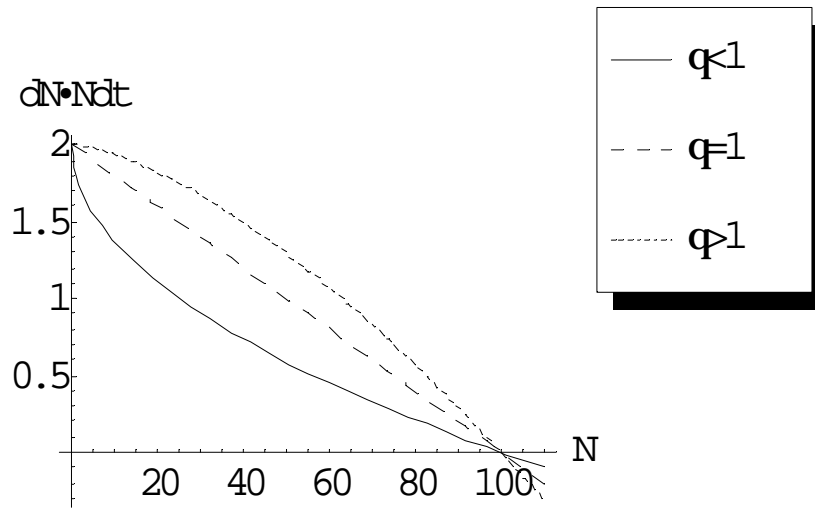


Figure 1:

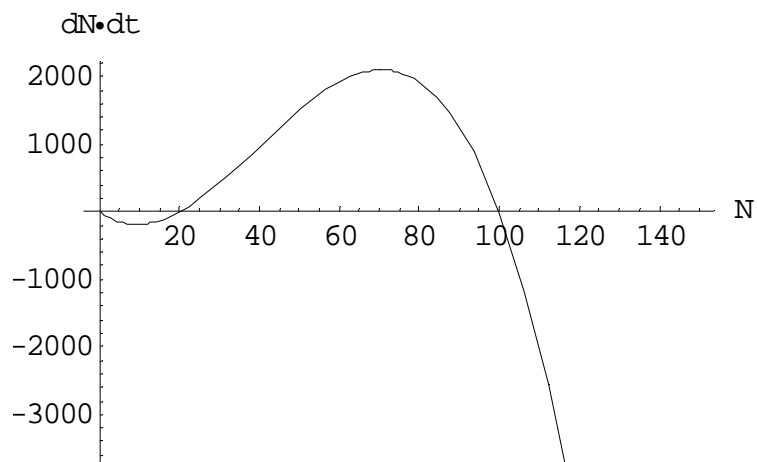


Figure 2:

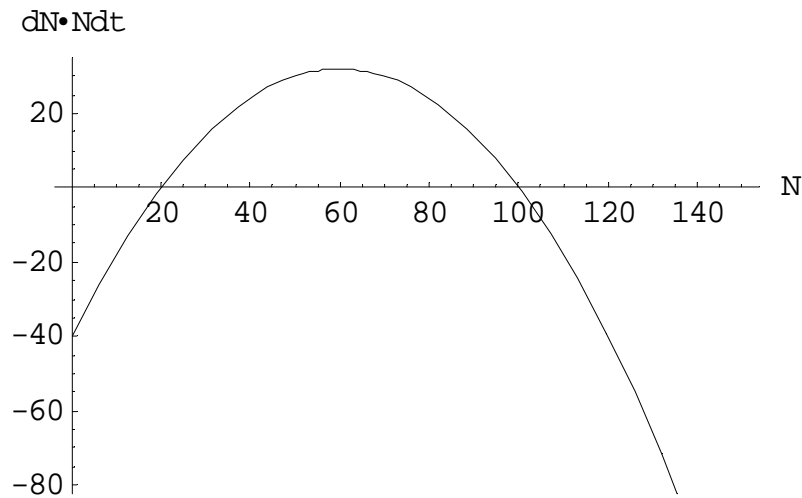


Figure 3:

3. -

(a) At equilibrium $\frac{dN}{dt} = 0 = rN^*(1 - N^*/K) - HN^*$

$$rN^*(1 - N^*/K) - HN^* = 0$$

$$rN^*(1 - N^*/K) = HN^*$$

$$r(1 - N^*/K) = H$$

$$\frac{N^*}{K} = 1 - \frac{H}{r}$$

$$N^* = K(1 - \frac{H}{r})$$

For this equilibrium to make sense, $0 < H < r$, otherwise $\frac{dN}{dt} < 0$ for all N , resulting in an equilibrium population size that is 0.

(b) If H is too large the harvested population will go extinct.

4. -

(a) At equilibrium, $\frac{dp}{dt} = 0 = mp^*(1 - p^*) - ep^*$.

$$-m(p^*)^2 + mp^* - ep^* = 0$$

$$p^*(-mp^* + m - e) = 0$$

$$p^* = 0$$

$$p^* = 1 - \frac{e}{m}$$

- (b) The parameter e must be less than the parameter m for p^* to take on a positive value. This makes sense because if the extinction rate (e) is greater than the migration rate (m) then there will be insufficient migration to balance extinction.

(c) Let $\frac{dp}{dt} = mp(1-p) - ep = F(p)$

$$\begin{aligned} \frac{dF}{dp}(p) &= m(1-p) - mp - e \\ &= m - e - 2mp \end{aligned}$$

Stability of the equilibrium $p^* = 0$:

$$\frac{dF}{dp}(0) = m - e. \text{ Which is positive (i.e., unstable) for } m > e \text{ and}$$

is negative (stable) for $m < e$. These dynamics make sense because if the migration rate is greater than the extinction rate then new subpopulations should be colonized at a greater rate than extinction, therefore the metapopulation will persist. Contrariwise, if the extinction rate is greater than the migration rate, the migration rate is insufficient to counteract extinction and the metapopulation will go extinct.

Stability for the equilibrium $p^* = 1 - \frac{e}{m}$:

$$\frac{dF}{dp}\left(1 - \frac{e}{m}\right) = m\left(1 - \left(1 - \frac{e}{m}\right)\right) - m\left(1 - \frac{e}{m}\right) - e$$

$= e - (m - e) - e = e - m$. In contrast with the equilibrium $p^* = 0$, the equilibrium at $1 - \frac{e}{m}$ is unstable if $m < e$ and is stable if $m > e$. This makes sense because for a nonzero equilibrium to persist the migration rate must be at least as great as the extinction rate.

- (d) In the logistic model there was a globally stable population size, namely K . Likewise in the metapopulation model, there is a globally stable metapopulation size, namely $1 - \frac{e}{m}$. The metapopulation model is related to the harvesting model in problem #3, in that the term ep acts similarly as the term HN .

5. The set of equations describing a 2-species model of competition for space is (see Hastings pgs. 147-148)

$$\begin{aligned} \frac{dp_1}{dt} &= m_1 p_1 (1 - p_1) - ep_1 \\ \frac{dp_2}{dt} &= m_2 p_2 (1 - p_1 - p_2) - m_1 p_1 p_2 - ep_2. \end{aligned}$$

- (a) The fraction of patches occupied by the dominant competitor is given by the variable p_1 . The differential equation describing the change in p_1 through time is given by $\frac{dp_1}{dt} = m_1 p_1 (1 - p_1) - ep_1$. The

equilibrium fraction of habitat occupied by the dominant competitor (p_1^*) occurs when $\frac{dp_1}{dt} = 0$.

$$p_1^*(m_1(1 - p_1^*) - e) = 0$$

$$p_1^* = 0$$

$$p_1^* = \frac{m_1 - e}{m_1}$$

The nonzero solution is $p_1^* = 1 - \frac{e}{m_1}$. As with problem #4, for the equilibrium value of p_1 to be positive then $m_1 > e$.

- (b) To determine the equilibrium fraction of habitat the subdominant competitor occupies when the dominant competitor is at its nonzero equilibrium proportion, substitute the equilibrium proportion for the dominant competitor in place of p_1 in the equation $\frac{dp_2}{dt} = m_2p_2(1 - p_1 - p_2) - m_1p_1p_2 - ep_2$ which describes the change in fraction of habitat occupied by the subdominant competitor and set $\frac{dp_2}{dt} = 0$.

$$\frac{dp_2}{dt} = m_2p_2^*\left(1 - \frac{m_1 - e}{m_1} - p_2^*\right) - m_1\frac{m_1 - e}{m_1}p_2^* - ep_2^* = 0$$

$$p_2^*(m_2\left(1 - \frac{m_1 - e}{m_1} - p_2^*\right) - m_1\frac{m_1 - e}{m_1} - e) = 0$$

$$p_2^* = 0$$

So one solution is $p_2^* = 0$, but this is rather uninteresting. Let's see if there is a nonzero equilibrium by finding the other root of the equation, $p_2^*(m_2\left(1 - \frac{m_1 - e}{m_1} - p_2^*\right) - m_1\frac{m_1 - e}{m_1} - e) = 0$:

$$m_2\left(1 - \frac{m_1 - e}{m_1} - p_2^*\right) - m_1 = 0$$

$$-m_2p_2^* = m_1 - m_2 + m_2\frac{m_1 - e}{m_1}$$

$$p_2^* = 1 - \frac{m_1}{m_2} - \frac{m_1 - e}{m_1}$$

$$p_2^* = \frac{e}{m_1} - \frac{m_1}{m_2}$$

Provided $\frac{e}{m_1} > \frac{m_1}{m_2}$, the other equilibrium, $p_2^* = \frac{e}{m_1} - \frac{m_1}{m_2}$ is a positive nonzero equilibrium for the subdominant competitor. Since e is less than m_1 for the superior competitor to have a nonzero equilibrium, this means that for the subdominant competitor to persist, $m_2 > m_1$, which makes sense because the subdominant competitor must make up for its competitive disadvantage by having a higher rate of migration.

- (c) There are several ways to analyze this question. One approach is to first numerically solve the set of differential equations and then observe the effect of changing e on the trajectory through time of

the proportion of subpopulations occupied by each species. This analysis shows that species 1 appears to decline to extinction as the extinction rate increased. Based on this observation, a more definite reason is sought by looking at the equilibrium equations for species 1 and 2. From these equations it is clear that given a starting point such that both species are coexisting, if you increase e species 1 will go extinct. The equilibrium proportion for species 1 is $1 - \frac{e}{m_1}$, whereas the equilibrium for species 2 is $\frac{e}{m_1} - \frac{m_1}{m_2}$, it is clear from these equations that given m_1 and m_2 are fixed as you increase e species 1 will decline to 0 and species 2 will increase.

- (d) The equilibrium of species 2 increases (see 5c). This makes sense because species 2 can only colonize uninhabited subpopulations, and for species 2 to coexist at all - its migration rate must be greater than that of species 1. Therefore, as the extinction rate of both species 1 and 2 increases, more habitat will be available for species 2 to colonize.

6. Let's add the terms $-mN_i$ to equations 7.5 and 7.6 because these are the ones we worked with in lecture.

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right) - m N_1 \quad (\text{eq. 6a})$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}\right) - m N_2 \quad (\text{ep. 6b})$$

For $m = 0$, equations 6a and 6b reduce to 7.5 and 7.6 in Hastings.

A graphical analysis of the dynamics of two species defined by differential equations 6a and 6b involves drawing isoclines. The simplest way to draw isoclines is to determine at what points on the N_1 and N_2 axes the lines cross. These points will also provide information regarding parameter values that allow coexistence. The point at which an isocline crosses the N_1 axes is when $N_2 = 0$; likewise, the point at which an isocline crosses the N_2 axes is when $N_1 = 0$.

A 0-isocline is a solution to the general differential equation $\frac{dN}{dt} = 0$.

For equation 6a, the 0-isocline is defined by the relation $r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}\right) - m N_1 = 0$. We seek the points where the line described by this relation crosses the N_1 and N_2 axes

To find the point at which it crosses the N_2 axis, set $N_1 = 0$ and solve for N_2 :

$$1 - \frac{\alpha_{12} N_2}{K_1} - \frac{m}{r_1} = 0 \text{ by dividing through by } r_1 N_1 \text{ and then substituting } N_1 = 0$$

$$N_2 = \frac{K_1(1 - \frac{m}{r_1})}{\alpha_{12}}$$

To determine at which point the relation $r_1 N_1(1 - \frac{N_1 + \alpha_{12} N_2}{K_1}) - m N_1 = 0$ crosses the N_1 axis, set $N_2 = 0$ and solve for N_1 :

$$1 - \frac{N_1}{K_1} - \frac{m}{r_1} = 0 \text{ by dividing through by } r_1 N_1 \text{ and then substituting } N_2 = 0$$

$$N_1 = K_1(1 - \frac{m}{r_1}).$$

For equation 6b, the points at which the 0-isocline crosses the N_1 and N_2 axes are found in a similar way as was done for equation 6a:

Solution for the point at which the relation $r_2 N_2(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}) - m N_2 = 0$ crosses the N_1 axis:

$$1 - \frac{\alpha_{21} N_1}{K_2} - \frac{m}{r_2} = 0 \text{ by dividing through by } r_2 N_2 \text{ and then substituting } N_2 = 0$$

$$N_1 = \frac{K_2(1 - \frac{m}{r_2})}{\alpha_{21}}$$

Solution for the point at which the relation $r_2 N_2(1 - \frac{N_2 + \alpha_{21} N_1}{K_2}) - m N_2 = 0$ crosses the N_2 axis:

$$1 - \frac{N_2}{K_2} - \frac{m}{r_2} = 0 \text{ by dividing through by } r_2 N_2 \text{ and then substituting } N_1 = 0$$

$$N_2 = K_2(1 - \frac{m}{r_2}).$$

Note that when we include rarefaction, K_1 is replaced by $K_1(1 - \frac{m}{r_1})$

and K_2 is replaced by $K_2(1 - \frac{m}{r_2})$ in comparison with the points at which the 0-isoclines cross the N_1 and N_2 axes in the standard Lotka-Volterra models. Provided m is small enough, a case where

coexistence is impossible is when $K_1(1 - \frac{m}{r_1}) > \frac{K_2(1 - \frac{m}{r_2})}{\alpha_{21}}$ and

$\frac{K_1(1 - \frac{m}{r_1})}{\alpha_{12}} > K_2(1 - \frac{m}{r_2})$. A schematic plot of the 0-isoclines looks

like figure 4 under these conditions. But as m is increased the points on the N_1 where the 0-isoclines cross switch arrangements resulting in an arrangement of 0-isoclines represented in figure 5. Under these conditions, a stable equilibrium is attained.

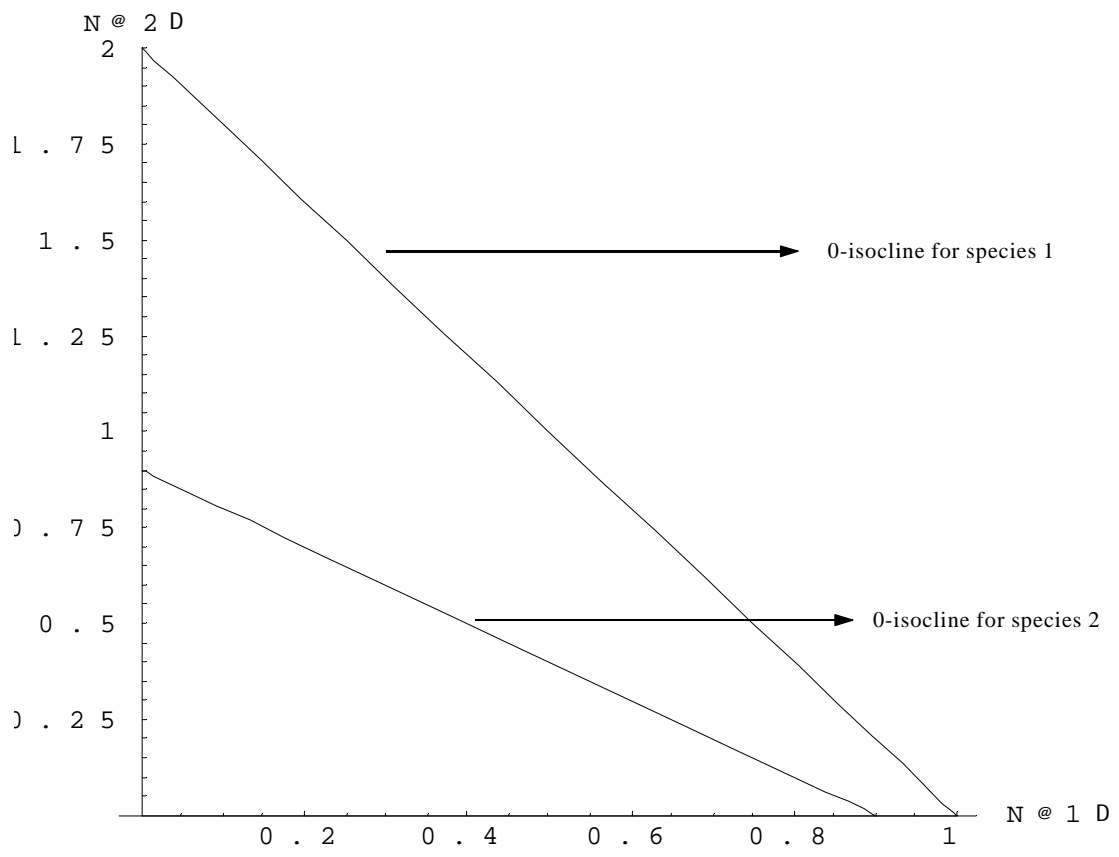


Figure 4:

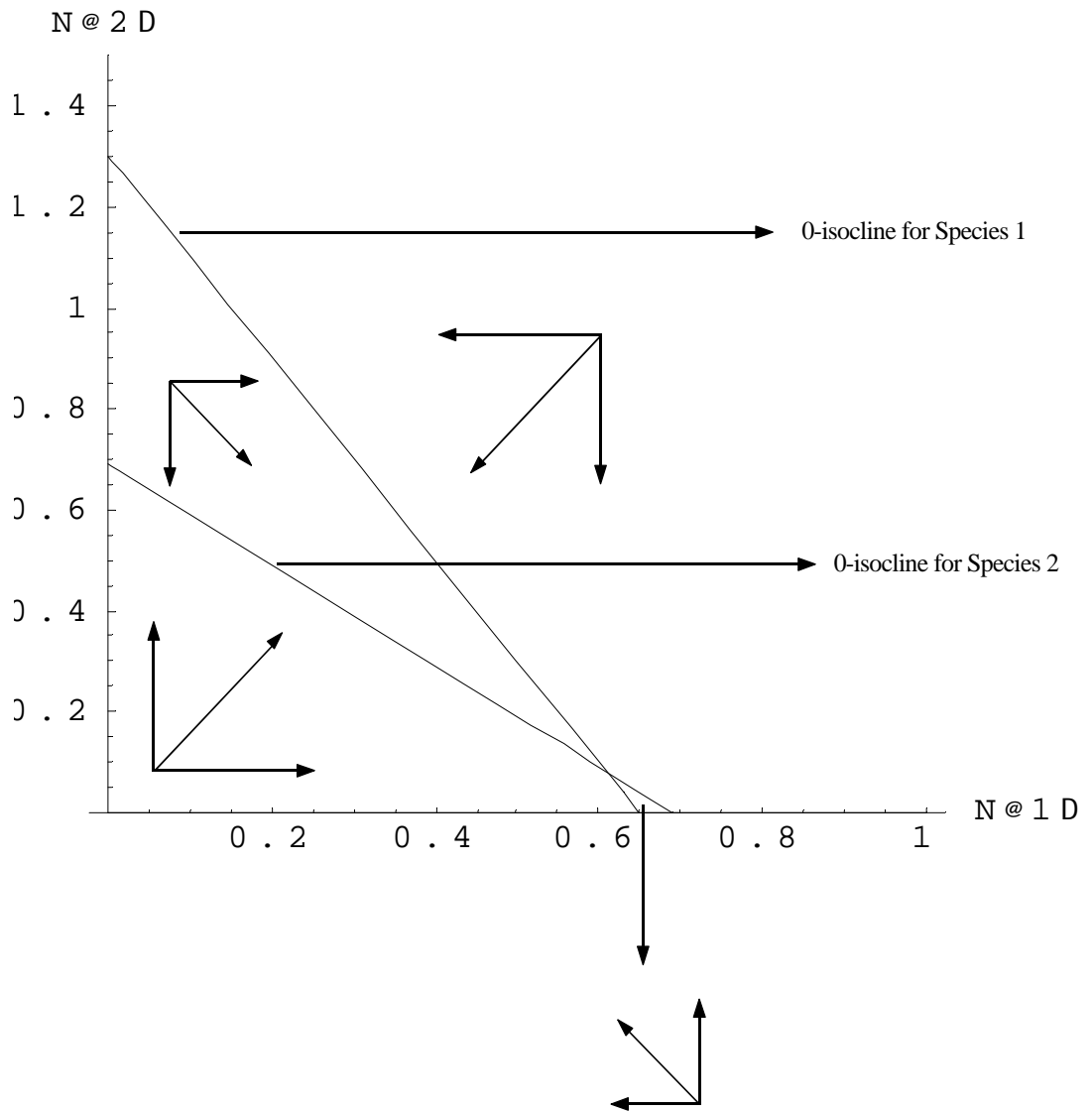


Figure 5: