Mathematical and Statistical Modeling in Biology

Competitive Exclusion, Coexistence, Estimation, and Control

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Principle of Competitive Exclusion

- When two or more species compete for the same basic resources, the “strongest” survives; the weaker species is driven to extinction.

- Biologist G. F. Gause (1932, 1934) illustrates various competitive outcomes when the competing species are yeasts, e.g., *Saccharomyces cervisiae* and *Schizosaccharomyces kephir*.

Equilibrium Analysis

Recall for a differential equation of the form

$x' = f(x)$, solutions $\bar{x}$ that satisfy $f(\bar{x}) = 0$

are called equilibrium points or steady state solutions.

$f'(\bar{x}) < 0$ implies $\bar{x}$ is locally stable.

$f'(\bar{x}) > 0$ implies $\bar{x}$ is unstable.

Equilibrium Analysis of a System

Given a system $x' = f(x, y) \quad and \quad y' = g(x, y)$

and an equilibrium $(\bar{x}, \bar{y})$, the Jacobian

$$J(\bar{x}, \bar{y}) = \begin{bmatrix} f_x(\bar{x}, \bar{y}) & f_y(\bar{x}, \bar{y}) \\ g_x(\bar{x}, \bar{y}) & g_y(\bar{x}, \bar{y}) \end{bmatrix}$$

is used to determine stability.

If the eigenvalues satisfy $\operatorname{Re}\lambda_1, \operatorname{Re}\lambda_2 < 0$

Or alternatively, if Det(J) > 0 and Tr(J) < 0, then $(\bar{x}, \bar{y})$

Then the equilibrium point is locally stable.

Review

- Recall the classical logistic model,

$$x' = rx\left(1 - \frac{x}{K}\right)$$

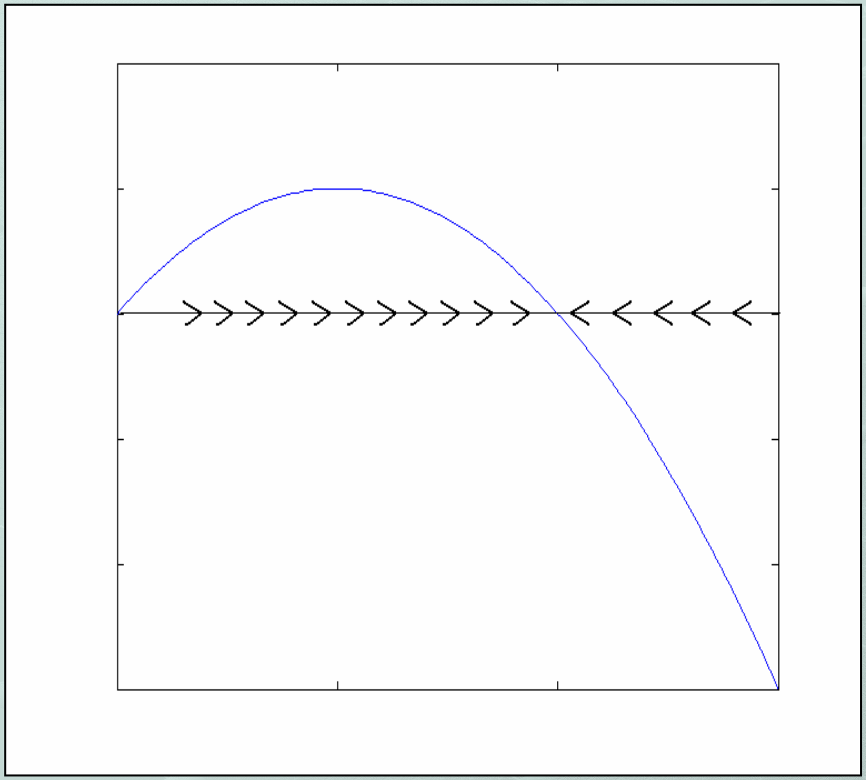
- Equilibria for this model are:

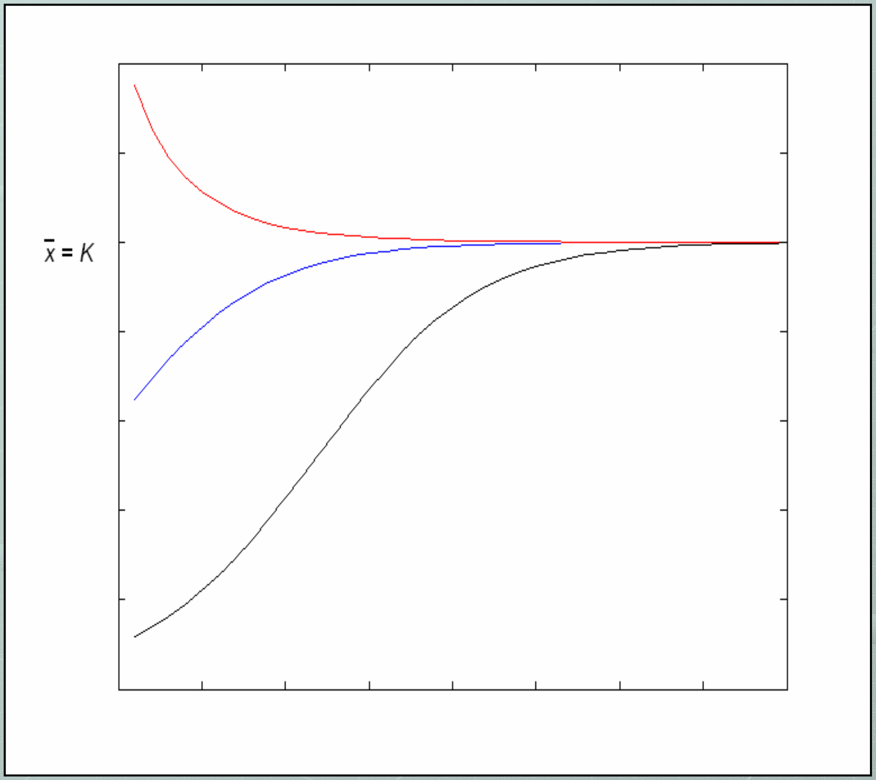
$$\bar{x} = 0 \quad and \quad \bar{x} = K$$

- Furthermore, stability analysis gives:

$$\bar{x} = 0 \quad unstable, \quad \bar{x} = K \quad globally\ stable$$

Logistic Continued





Lotka-Volterra Model for 2-Species: x_1 and x_2

$$\frac{dx_1}{dt} = r_1 x_1 \left(\frac{K_1 - x_1 - \beta_{12} x_2}{K_1} \right)$$

$$\frac{dx_2}{dt} = r_2 x_2 \left(\frac{K_2 - x_2 - \beta_{21} x_1}{K_2} \right)$$

where ….

Lotka-Volterra Model for 2-Species: x_1 and x_2

$$r_i, K_i, \beta_{ij} > 0$$

r_i is the intrinsic growth rate (births – deaths) of species *i*

K_i is the carrying capacity of species *i*

$\frac{\beta_{ij}}{K_i}$ is the competition coefficient of species *i*

Lotka-Volterra Model for 2-Species: x_1 and x_2

- The per capita growth rate

$$\frac{1}{x_i}\frac{dx_i}{dt} = f_i(x_1, x_2)$$ is linear.

- Also $\frac{\partial f_i}{\partial x_j} < 0 \; for \; i \neq j$ therefore this is a *competition* model.

- Equilibria are:

$$(0,0) \quad (K_1,0) \quad (0,K_2) \quad \left(\frac{K_1-\beta_{12}K_2}{1-\beta_{12}\beta_{21}}, \frac{K_2-\beta_{21}K_1}{1-\beta_{12}\beta_{21}}\right)$$

Lotka-Volterra Model for 2-Species: x_1 and x_2

For species x_1, isoclines are

$$x_1 = 0 \quad and \quad K_1 = x_1 + \beta_{12} x_2$$

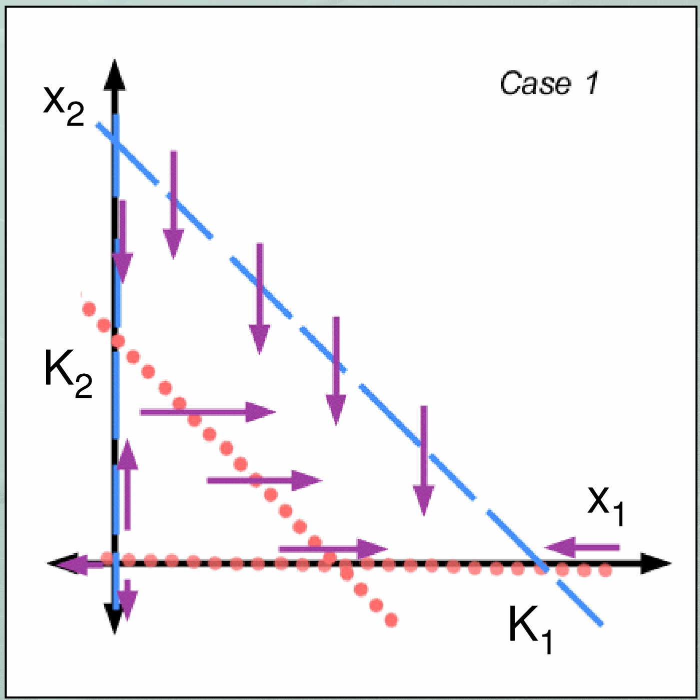
For species x_2, isoclines are

$$x_2 = 0 \quad and \quad K_2 = x_2 + \beta_{21} x_1$$

There are four cases to consider depending on how isoclines intersect in the 1^{st} quadrant …

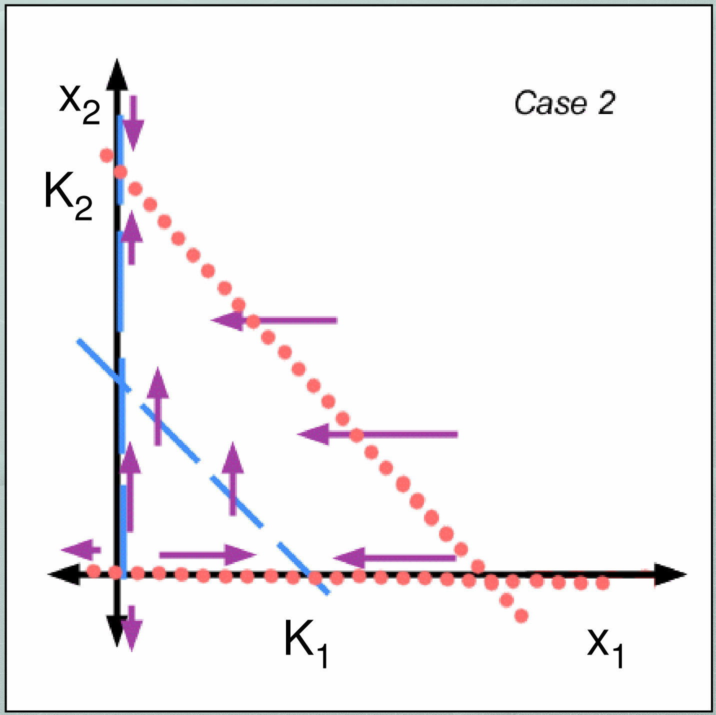
Lotka-Volterra Model for 2-Species: x_1 and x_2

Case 1 – Positive solutions approach equilibrium (K_1,0); species 1 always dominates (competitive exclusion).



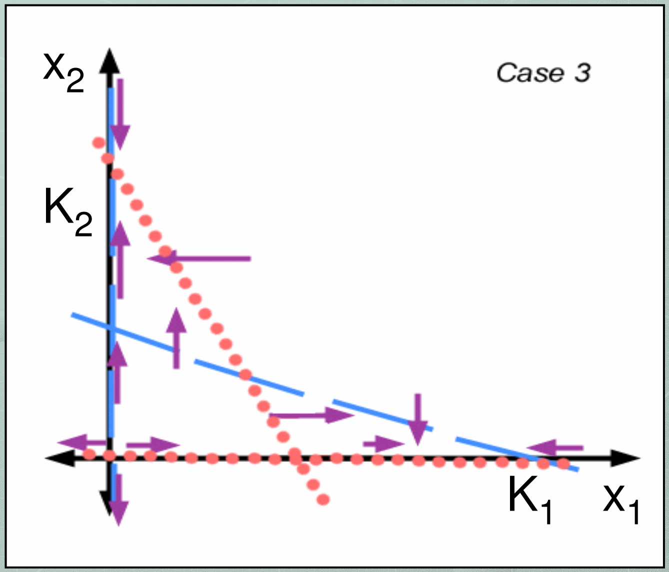
Lotka-Volterra Model for 2-Species: x_1 and x_2

Case 2 – Positive solutions approach equilibrium (0, K_2); species 2 always dominates (competitive exclusion).



Lotka-Volterra Model for 2-Species: x_1 and x_2

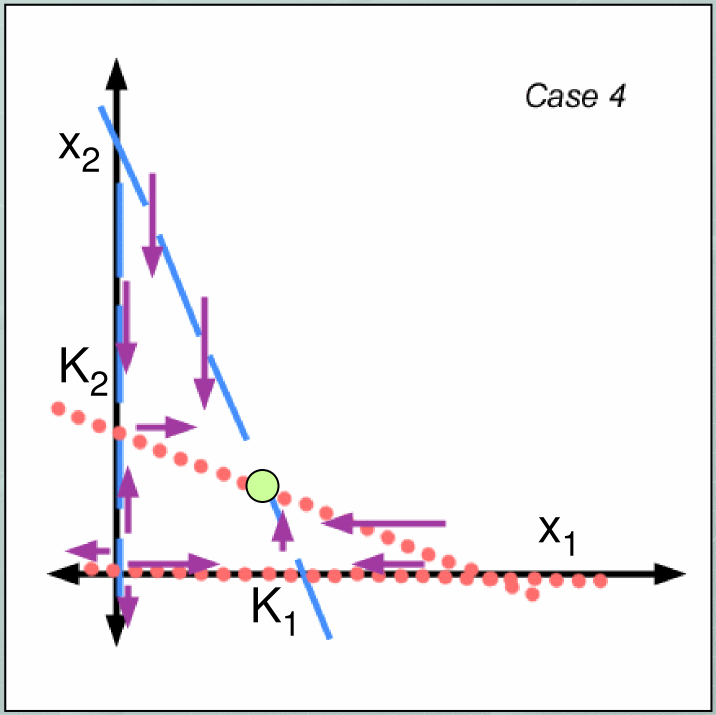
Case 3 – Positive solutions approach either equilibrium $(K_1,0)$ or $(0,K_2)$. The outcome depends on initial conditions, referred to as the *Founder Effect*. The species first to establish itself (the founder) has an advantage and will be the superior competitor.



Lotka-Volterra Model for 2-Species: x_1 and x_2

Case 4 – Positive solutions approach the equilibrium

$$\left(\frac{K_1 - \beta_{12} K_2}{1 - \beta_{12}\beta_{21}}, \frac{K_2 - \beta_{21} K_1}{1 - \beta_{12}\beta_{21}} \right)$$



Lotka-Volterra Predator-Prey Models

Review of Classical Lotka-Volterra Predator-Prey Model

$$\frac{dX(t)}{dt} = X(t)[a - bY(t)] \quad \frac{dY(t)}{dt} = Y(t)[-c + dX(t)]$$

$$X(0) = X^0, \quad Y(0) = Y^0$$

X(t) and ***Y(t)*** denote prey population size and predator population size, respectively at $t \geq 0$.

For **prey**: ***a*** and ***b*** are fixed growth and mortality rates, respectively.

For **predator**: ***d*** and ***c*** are fixed growth and mortality rates, respectively.

Review of Classical Lotka-Volterra Predator-Prey Model

Equilibria: $(0,0)$, $\left(\frac{c}{d},\frac{a}{b}\right)$

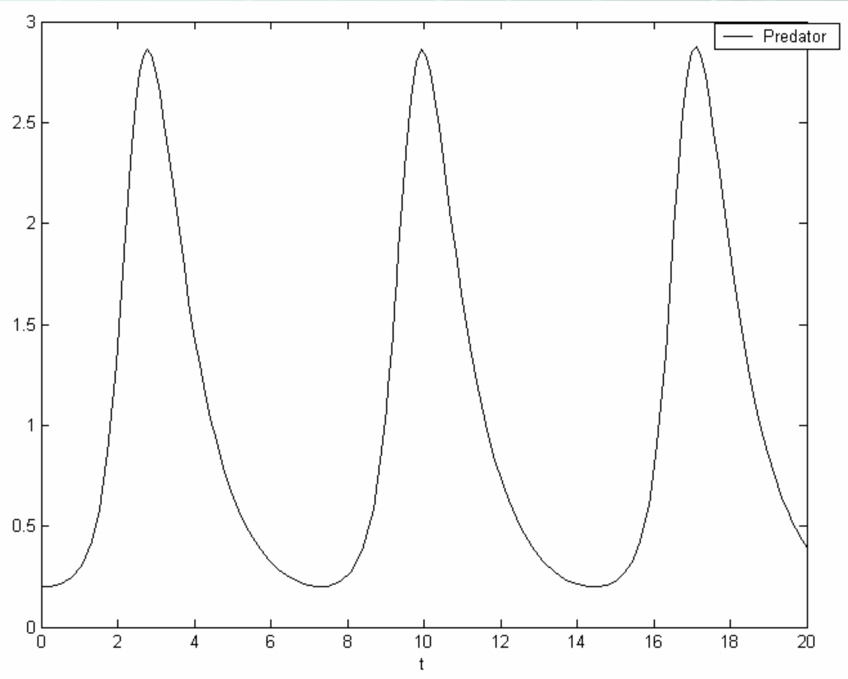
It is well known that the solution is a closed curve in satisfying $\mathrm{int}R^2{}_+$

$$dX + bY - c\ln X - a\ln Y = k,$$

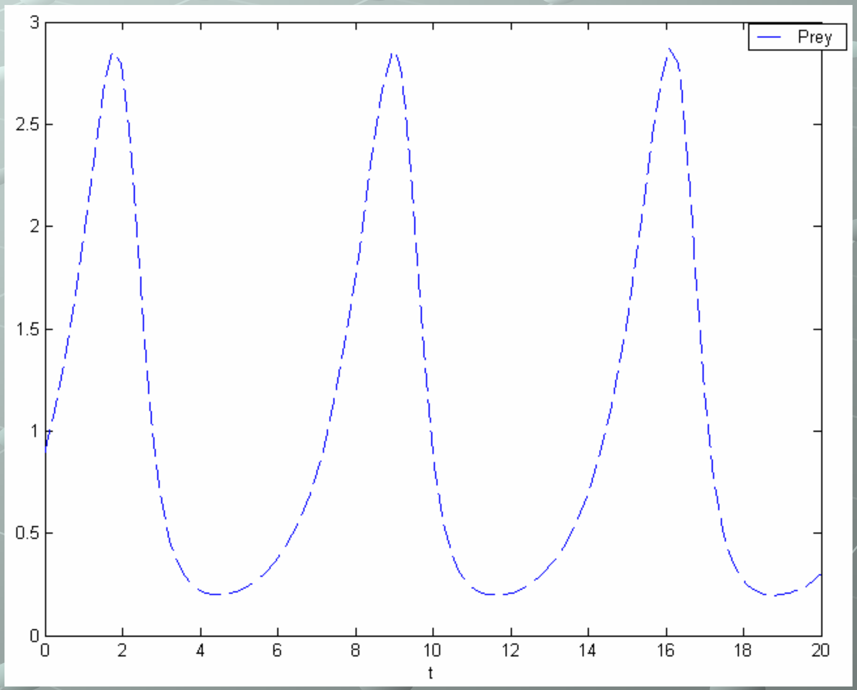
where k is a constant depending upon initial conditions and the point $\left(\frac{c}{d},\frac{a}{b}\right)$ is interior to the curve.

Hint: Solve $\frac{dX}{dY} = \frac{X(a-bY)}{Y(-c+dX)}$

Review of Classical Lotka-Volterra Predator-Prey Model

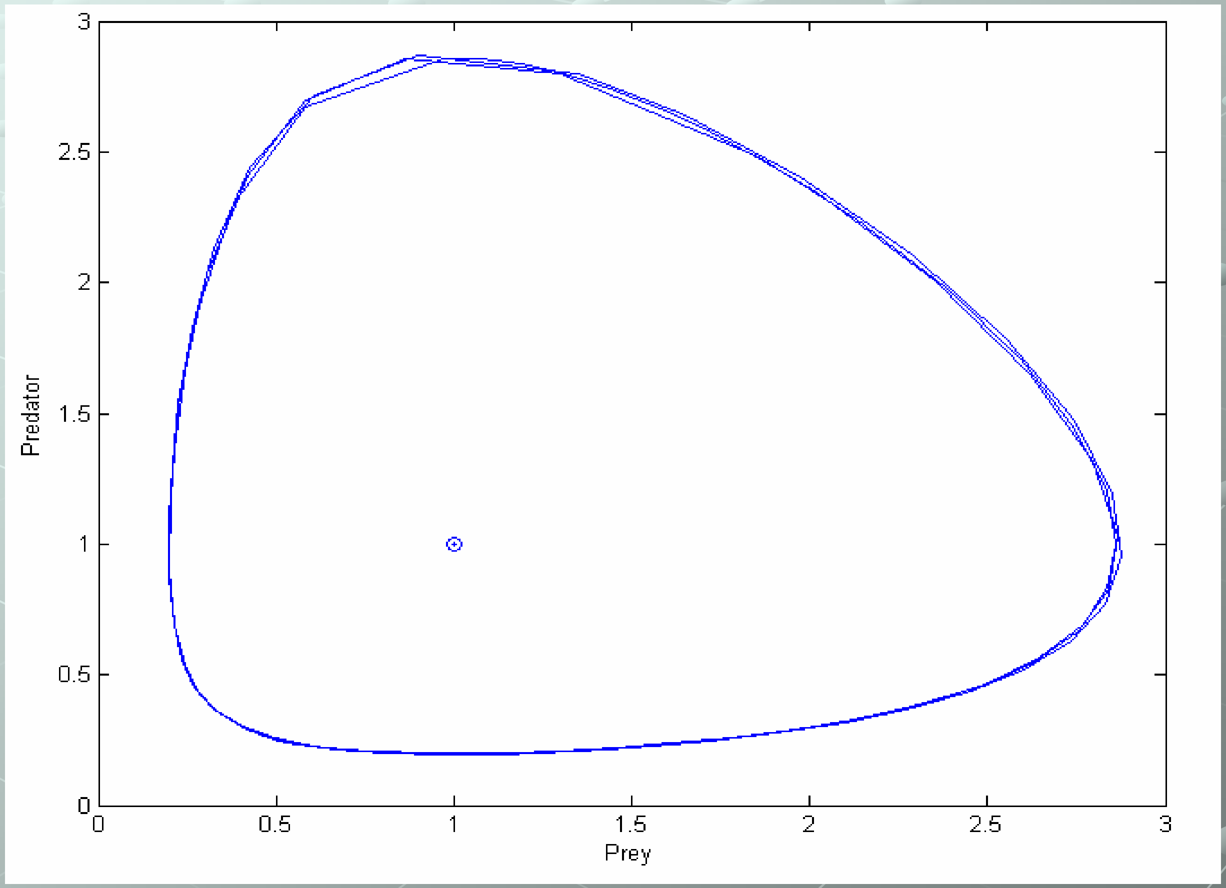


Predator Y(t) vs Time



Prey X(t) vs Time

Review of Classical Lotka-Volterra Predator-Prey Model



Predator Y(t) vs Prey X(t)

Generalized Lotka-Volterra Predator-Prey Model

Assume**:* Prey and predator populations are divided into ***M and ***N*** subpopulations respectively.

• ***Growth for prey*** is subpopulation specific, while ***mortality*** is driven by interaction with entire predator subpopulation.

• ***Growth for predator*** is driven by interaction with entire prey population; ***mortality*** is subpopulation specific.

Let $x_i(t)$ and $y_j(t)$ be the sizes of the i^{th} prey subpopulation and the j^{th} predator subpopulation at time $t \geq 0$, where $i = 1, \ldots, M$ and $j = 1, \ldots, N$.

Let $x(t) = (x_1(t), \ldots, x_M(t))$ and $y(t) = (y_1(t), \ldots, y_N(t))$.

Generalized Lotka-Volterra Predator-Prey Model

Let $X(t) = \sum_{i=1}^{M} x_i(t)$ be the total prey population size.

Let $Y(t) = \sum_{j=1}^{N} y_j(t)$ be the total predator population size.

$$\frac{dx_i(t)}{dt} = x_i(t)[a_i - b_i Y(t)], \qquad i = 1,\ldots, M; \quad x(0) = (x_1(0),\ldots, x_M(0))$$

$$\frac{dy_j(t)}{dt} = y_j(t)[-c_j + d_j X(t)], \quad j = 1,\ldots, N; \quad y(0) = (y_1(0),\ldots, y_N(0))$$

Dominance and Extinction of Non-dominant Subpopulation

Suppose subpopulations are ordered such that:

$$\frac{a_1}{b_1} > \frac{a_k}{b_k} \quad , k = 2, \ldots, M$$

$$\frac{d_1}{c_1} > \frac{d_k}{c_k} \quad , k = 2, \ldots, N$$

x_1 and y_1 are ***dominant*** in the sense that they have the highest *growth to mortality ratios* within the prey and predator classes, respectively.

Dominance and Extinction of Non-dominant Subpopulation

$x_k(t) \to 0 \quad as \quad t \to \infty \quad and \quad y_k(t) \to 0 \quad as \quad t \to \infty$

For $k \neq 1$

- x_1 and y_1 remain bounded and strictly positive.

This is why:

For any $t \geq 0$, define $H(t) = \Gamma(t) + \Lambda(t) + \Phi(t) + \Psi(t)$

where

$$\Gamma(t) = \frac{d_1}{b_1}\left(x_1(t) - \frac{c_1}{d_1} - \frac{c_1}{d_1}\ln\left(\frac{d_1 x_1(t)}{c_1}\right)\right)$$

$$\Lambda(t) = \frac{d_1}{b_1}\left(y_1(t) - \frac{a_1}{b_1} - \frac{a_1}{b_1}\ln\left(\frac{b_1 y_1(t)}{a_1}\right)\right)$$

$$\Phi(t) = \sum_{i=2}^{M} \frac{d_1}{b_i} x_i(t) \qquad \Psi(t) = \sum_{j=2}^{N} \frac{c_1}{c_j} x_j(t)$$

and observe that $H \in C^1([0,\infty); R_+)$.

Dominance and Extinction of Non-dominant Subpopulation

The total derivative of *H* along any solution of the system is negative. That is,

$$H'(t) = \frac{\partial H}{\partial x_1}\frac{dx_1}{dt} + \ldots + \frac{\partial H}{\partial x_M}\frac{dx_M}{dt} + \frac{\partial H}{\partial y_1}\frac{dy_1}{dt} + \ldots + \frac{\partial H}{\partial y_N}\frac{dy_N}{dt} < 0$$

for all $t \geq 0$. Hence, the auxiliary function *H* is bounded above on $[0, \infty)$.

Dominance and Extinction of Non-dominant Subpopulation

$$x_k(t) \to 0 \quad as \quad t \to \infty \quad and \quad y_k(t) \to 0 \quad as \quad t \to \infty$$

We begin by considering the prey case. Use the ratio

$$r(t) = \frac{x_k^{\frac{1}{b_k}}(t)}{x_1^{\frac{1}{b_1}}(t)}$$

to establish a comparison between $x_1(t)$ and $x_k(t)$ and the use the fact that $x_1(t)$ is bounded on [0, ∞), along with the comparison result, to conclude that $x_k(t) \to 0$ as $t \to \infty$. If k is in {2,…, M}, then …

Dominance and Extinction of Non-dominant Subpopulation

$$\frac{d}{dt}\left[\frac{x_k^{\frac{1}{b_k}}}{x_1^{\frac{1}{b_1}}}\right]=\left[\frac{1}{b_k}x_k^{\frac{1}{b_k}}(a_k-b_kY)-\frac{1}{b_1}x_k^{\frac{1}{b_k}}(a_1-b_1Y)\right]\left(\frac{1}{x_1^{\frac{1}{b_1}}}\right)$$

$$=\left[\frac{x_k^{\frac{1}{b_k}}}{x_1^{\frac{1}{b_1}}}\right]\left(\frac{a_k}{b_k}-\frac{a_1}{b_1}\right)$$

Dominance and Extinction of Non-dominant Subpopulation

By the dominance of x_1, we have $\frac{a_k}{b_k} - \frac{a_1}{b_1} = -\lambda_k$,
where λ_k is a positive constant.

So we have a first order differential equation of the form $r'(t) = -\lambda_k r(t)$, whose solution is $r(t) = r(0)e^{-\lambda_k t}$. In terms of x, we have

$$\frac{x_k^{\frac{1}{b_k}}(t)}{x_1^{\frac{1}{b_1}}(t)} = \left[\frac{x_k^{\frac{1}{b_k}}(0)}{x_1^{\frac{1}{b_1}}(0)}\right] e^{-\lambda_k t}.$$

Dominance and Extinction of Non-dominant Subpopulation

Solving for x_k , we obtain $x_k(t) = \left[\dfrac{x_k(0)}{x_1^{\frac{b_k}{b_1}}(0)}\right] e^{-\lambda_k b_k t} x_1^{\frac{b_k}{b_1}}(t).$

Since $x_1(t)$ is bounded on $[0, \infty)$, there exists a positive constant A such that $x_k(t) \le Ae^{-\lambda_k b_k t}$,

for $t \geq 0$. So $x_k(t) \to 0 \quad as \quad t \to \infty$, for $k \neq 1$.

An analogous argument for the predator case yields $y_k(t) \to 0 \quad as \quad t \to \infty$, for $k \neq 1$.

Dominance and Extinction of Non-dominant Subpopulation

NUMERICAL RESULTS

- Given ten predator and prey subpopulations:

For the **dominant** prey subpopulation,

$$a_1 = 1,\ b_1 = 0.8$$

For the **dominant** predator subpopulation,

$$c_1 = 0.6,\ d_1 = 1.2$$

- Each $x_i(0)$, $i = 1,\ldots,M$ and $y_j(0)$, $j = 1,\ldots,N$ is set equal to 0.18.

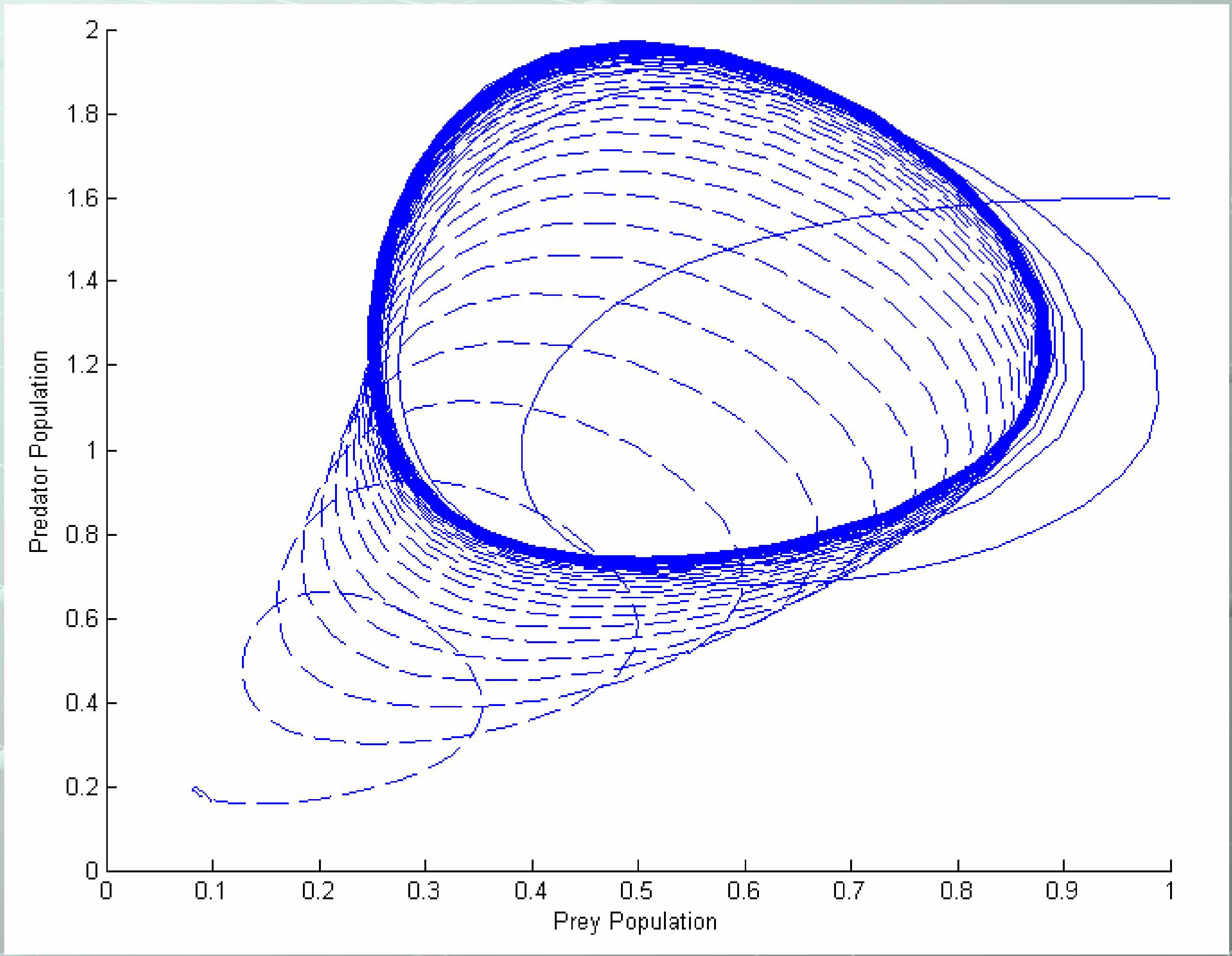
Dominance and Extinction of Non-dominant Subpopulation

- For **non-dominant** subpopulations …

$$a_n = a_{n-1} - 0.020(n-1)$$
$$b_n = b_{n-1} + 0.016(n-1)$$
$$c_n = c_{n-1} + 0.012(n-1)$$
$$d_n = d_{n-1} - 0.024(n-1)$$

$$n = 2,...,10$$

Dominance and Extinction of Non-dominant Subpopulation



- - - Dominant Subpopulations

----- Total Populations

<u>Figure 1</u>: Total and dominant population trajectories for t in [0,250]

Dominance and Extinction of Non-dominant Subpopulation

Figure 1 presents the ***predator population*** vs. ***prey population*** for t in [0,250].

• When $t = 0$, the total population trajectory starts at the point (X(0), Y(0)) = (1, 1.6) and moves in a counterclockwise fashion.

• When $t = 0$, the dominant subpopulations trajectory starts at $(x_1(0), y_1(0)) = (0.1, 0.1)$ and moves in a counterclockwise fashion as it approaches total population trajectory.

Dominance and Extinction of Non-dominant Subpopulation

- Since every prey subpopulation other than the dominant one approaches zero as $t \to \infty$ the dominant prey subpopulation must approach the total prey population as $t \to \infty$

- The predatory case is strictly analogous. So, the trajectories must approach one another.

Dominance and Extinction of Non-dominant Subpopulation

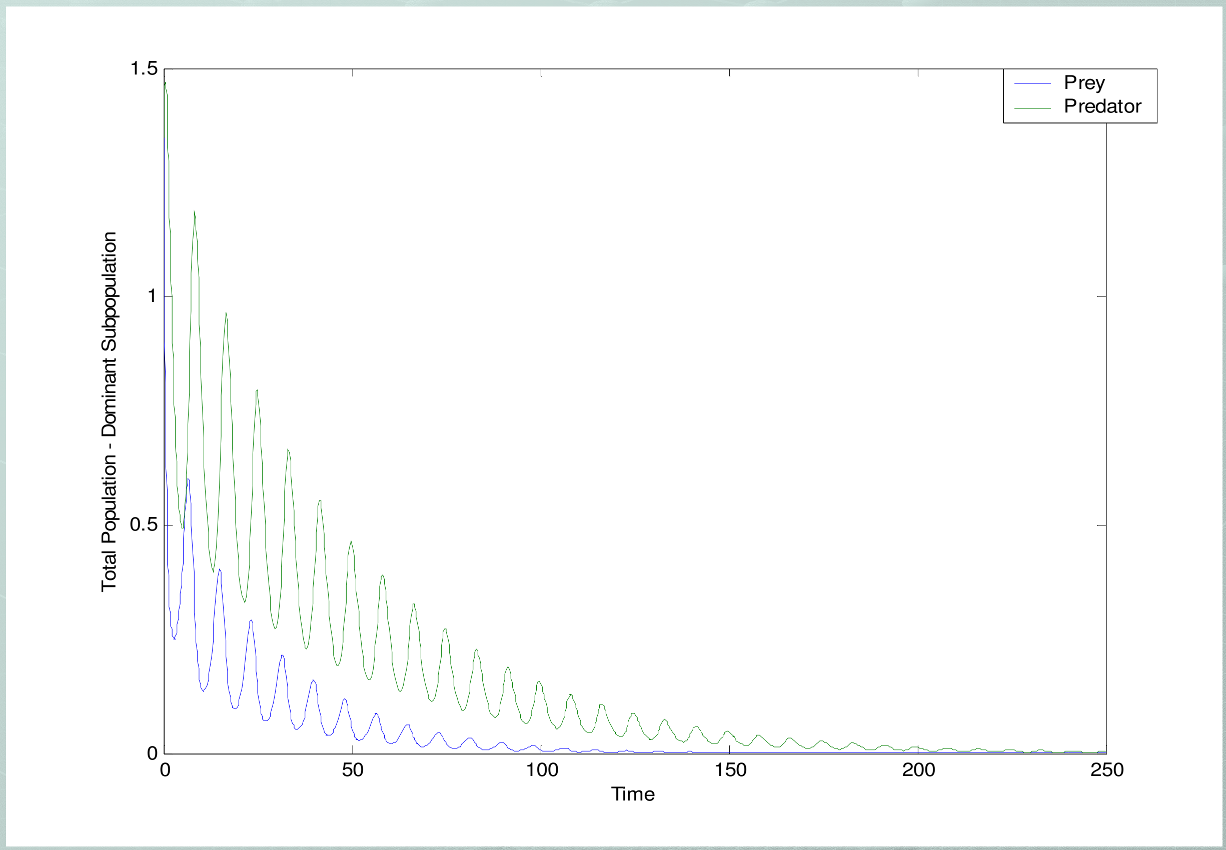


Figure 2: Population differences vs. time

Dominance and Extinction of Non-dominant Subpopulation

Let $a = a_1$, $b = b_1$, $c = c_1$, $d = d_1$ in the classical predator-prey system with initial conditions

$$(X(0), Y(0) = (x_1(250), y_1(250))$$

.

After enough time has passed, the trajectory for the dominant predator-prey pair from the generalized system closely approximates the solution curve of a classical predator-prey system with this initial condition.

Conclusion

- As seen from both theoretical and numerical results, all non-dominant subpopulations in the generalized predator-prey model are forced to extinction as $t \to \infty$ due to closed reproduction.

Closed reproduction/Selection - individuals with the highest growth to mortality ratio only produce more of themselves.

- This conclusion may change with an open reproduction.

Conclusion

• **Open reproduction/Mutation** - individuals in one subpopulation have a positive probability of producing individuals that belong to different subpopulations.

Hence, survival of the dominant species implies survival of some of the others. In this case, surviving subpopulations have an *oscillatory* behavior.

SELECTION MODELS

Selection Models

Consider a competition among ***N*** populations where the dynamics of each population is expressed in the following form:

$$x_i' = x_i(a_i - b_i X) \quad where \quad X = \sum_{i=1}^{N} x_i \qquad \frac{a_1}{b_1} > \frac{a_i}{b_i}$$

$$X = \sum x_i' = \sum x_i(a_i - b_i X)$$

$$\leq \sum x_i(\overline{a} - \underline{b} X)$$

$$= X(\overline{a} - \underline{b} X)$$

$$X \ is \ bounded.$$

Selection Models

As the asymptotic behavior shows, the population with the parameter (a_1, b_1) is the *fittest population*. That is, this is the only population that persists and the rest go to extinction.

Consider the ratio $\dfrac{x_i^{\xi}}{x_1^{\delta}}$. Thus $\dfrac{d}{dt}(x_i^{\xi} x_1^{-\delta}) = \xi\, x_i^{\xi-1} x_i{}' x_1^{-\delta} - \delta\, x_i^{\xi} x_1^{-\delta-1} x_1{}'$

If we let $x_i^{\xi} x_1^{-\delta} = \lambda$ then we arrive at

$$\frac{d}{dt}(\lambda) = \lambda\left(\xi a_i + \xi b_i X - \delta a_1 - \delta b_1 X\right)$$

Selection Models

Letting $\xi = \frac{1}{b_i}, \quad and \quad \delta = \frac{1}{b_1}$,

$$\frac{d\lambda}{dt} = \lambda\left(\frac{a_i}{b_i} + X - \frac{a_1}{b_1} - X\right)$$

$$= \lambda\left(\frac{a_i}{b_i} - \frac{a_1}{b_1}\right) = c\lambda$$

Since $\frac{a_1}{b_1} > \frac{a_i}{b_i}$, we have c < 0. Thus, $\frac{x_i^{\xi}}{x_1^{\delta}}$ approaches zero as

$t \longrightarrow \infty$. Because the denominator is bounded, the numerator must tend to zero at infinity. Thus, all non-dominant subpopulations die.

Selection Models

Now we show that the dominant subpopulation x_1 survives:

Recall $x_1' = x_1(a_1 - b_1 x_1 - b_1 \hat{X}) \quad \hat{X} = \sum_{j=2}^{n} x_j$

and consider $y' = y(a_1 - b_1 y)$

- Notice $x' \leq x_1(a_1 - b_1 x_1)$

$$Hence \;\; x(t) \leq y(t) \; by \; comparison.$$

Selection Models

Next, consider $$\frac{d}{dt}\ln\left(\frac{x_1}{y}\right)=\frac{x_1'}{x_1}-\frac{y_1'}{y}=(a_1-b_1x_1-b_1\hat{X})-(a_1-b_1y)$$

Making the substitution $\xi=\frac{1}{b_i},\quad and\quad \delta=\frac{1}{b_1}$ we arrive at

$$b_1(y-x_1)=b_1\hat{X}+\frac{d}{dt}\ln\left(\frac{x_1}{y}\right)$$

Selection Models

Integrating the equation from t_0 to t we arrive at:

$$\int_{t_0}^{t}\left(y(\tau)-x_1(\tau)\right)d\tau=\int_{t_0}^{t}\hat{X}(\tau)d\tau+\int_{t_0}^{t}\left(\frac{1}{b_1}\frac{d}{d\tau}\ln\left(\frac{x_1}{y}\right)\right)d\tau$$

$$=\frac{1}{b_1}\ln\left(\frac{x_1}{y}\right)\Bigg|_{t_0}^{t}+\int_{t_0}^{t}\hat{X}(\tau)d\tau$$

$$\leq\frac{1}{b_1}\ln\left(\frac{x_1}{y}\right)+\gamma\int_{t_0}^{t}\left(e^{-c\tau}d\tau\right)=\hat{M}$$

Since $0\leq\int_{t_0}^{\infty}(y-x_1)dt\leq\hat{M}$ and $(y'-x_1')$ are bounded,

we have $y-x_1\rightarrow 0 \quad as \quad t\rightarrow\infty$. Since y approaches a_1/b_1

in the long term, so too does x_1

EPIDEMIC MODELS

Competitive Exclusion for an Epidemic Model

Competitive Exclusion for an epidemic model

The model considered is of the **SIR** type, in that the host population consists of susceptible, **S**, individuals infected with strains 1 through n, $\mathbf{I_j}$, j=1,2. … , n and immune or removed individuals, **R**. In addition, it is assumed that there is mass action horizontal transmission:

$$\dot{S}(t) = S\left(f(N) - \sum_{j=1}^{n} \beta_j I_j \right) + \sum_{j=1}^{n} bI_j + bR$$

$$\dot{I}_j(t) = I_j\big(f(N) - b + \beta_j S_j - \gamma_j - \mu_j\big), \qquad j = 1, 2, \cdots, n.$$

$$\dot{R}(t) = R(f(N) - b) + \sum_{j=1}^{n} \gamma_j I_j$$

$$N = S + R + \sum_{j=1}^{n} I_j$$

$$\dot{N}(t) = Nf(N) - \sum_{j=1}^{n} \mu_j I_j$$

b is a birth rate, **f(N)** is the per capita growth rate, and **b-f(N)** is the natural death rate. β_j denotes the transmission rate for the i^{th} strain and γ_j is the recovery rate from infection with strain j. All parameters are positive.

Competitive Exclusion for an epidemic model

Competitive Exclusion

$$Let \quad c_j = b_j + \gamma_j + \mu_j > f(0)$$

Then the basic reproduction number for strain j is given by:

$$R_{0,j} = \frac{\beta_j}{c_j} K, \quad j = 1,2,...,n$$

We define

$$B_{0,j} = \frac{\beta_j K}{c_j - f(0)}, \quad j = 1,2,...,n$$

and assume for the rest of this section that for each j=2,…,n, one of the following conditions holds:

$$(3) \quad R_{0,1} > R_{0,j} \quad and \quad c_j > c_1$$

or

$$(4) \quad B_{0,1} > B_{0,j} \quad and \quad \beta_j > \beta_1$$

The following stronger conditions imply (3) or (4):

$$R_{0,1} > R_{0,j} \quad and \quad B_{0,1} > B_{0,j}$$

Competitive Exclusion for an epidemic model

$$S(t) \geq \underline{S} \;\; for \; t \in [0, \infty)$$

We show that all the strains, except possibly one, die out.

•*For j = 2, …, n;*

$$\lim_{t \to \infty} I_j(t) = 0.$$

•*First assume that the conditions in (3) hold for a fixed j and define* $\Gamma(t) = \dfrac{I_j^{\frac{1}{c_j}}}{I_1^{\frac{1}{c_1}}}$

$$\frac{d}{dt}\Gamma_1(t) = \frac{\frac{1}{c_j} I_j^{\frac{1}{c_j}}\left(f(N) + \beta_j S - c_j\right) I_1^{\frac{1}{c_1}} - \frac{1}{c_1} I_1^{\frac{1}{c_1}}\left(f(N) + \beta_1 S - c_1\right) I_j^{\frac{1}{c_j}}}{I_1^{\frac{2}{c_1}}}$$

$$= \frac{1}{c_j}\Gamma_1(t)\left(f(N) + \beta_j S - c_j\right) - \frac{1}{c_1}\Gamma_1(t)\left(f(N) + \beta_1 S - c_1\right)$$

Competitive Exclusion for an epidemic model

$$\frac{d}{dt}\Gamma_1(t) = \Gamma_1(t)\left(\frac{f(N)}{c_j} - \frac{f(N)}{c_1} + \left(\frac{\beta_j}{c_j} - \frac{\beta_1}{c_1}\right)S\right)$$

$$\leq \frac{1}{2}\Gamma_1(t)\left(\frac{\beta_j}{c_j} - \frac{\beta_1}{c_1}\right)\underline{S}$$

Expressed in terms of logarithms,

$$\frac{d\ln\Gamma_1(t)}{dt} \leq \frac{1}{2}\left(\frac{\beta_j}{c_j} - \frac{\beta_1}{c_1}\right)\underline{S}$$

Thus

$$\Gamma_1(t) \leq \Gamma_1(0)e^{\frac{1}{2}\left(\frac{\beta_j}{c_j} - \frac{\beta_1}{c_1}\right)\underline{S}\,t}; \qquad I_j^{\frac{1}{c_j}}(t) \leq I_1^{\frac{1}{c_1}}(t)\Gamma_1(0)e^{\frac{1}{2}\left(\frac{\beta_j}{c_j} - \frac{\beta_1}{c_1}\right)\underline{S}\,t}$$

Since I_1 is bounded, and $\left(\frac{\beta_j}{c_j} - \frac{\beta_1}{c_1}\right) < 0$ *we have* $\lim_{t\to\infty} I_j(t) = 0.$

Competitive Exclusion for an epidemic model

Now define $\Gamma(t) = \dfrac{I_j^{\frac{1}{\beta_j}}}{I_1^{\frac{1}{\beta_1}}}$

$$\frac{d}{dt}\Gamma_2(t) = \Gamma_2(t)\left(\frac{f(N)}{\beta_j} - \frac{f(N)}{\beta_1} + \left(\frac{c_1}{\beta_1} - \frac{c_j}{\beta_j}\right)S\right)$$

$$\leq \Gamma_2(t)\left(f(0)\left(\frac{1}{\beta_j} - \frac{1}{\beta_1}\right) + \left(\frac{c_1}{\beta_1} - \frac{c_j}{\beta_j}\right)\right)$$

$$= \Gamma_2(t)\left(\frac{c_1 - f(0)}{\beta_1} - \frac{c_j - f(0)}{\beta_j}\right)$$

Arguing as before we get $\lim_{t\to\infty} I_j(t) = 0.$

Competitive Exclusion for an Epidemic Model

Assume that

$$R_{0,1} > 1 \quad then \quad \liminf_{t\to\infty} I_1(t) > 0$$

Assume that $R_{0,1} < 1$

then

$$\lim_{t\to\infty}\left(S(t), \sum_{j=1}^{n} I_j(t), R(t) \right) = (K,0,0)$$

Competitive Exclusion for an Epidemic Model

Coexistence Case

Consider the following case with two strains (n=2). Let $f(N) = r\left(1 - \frac{N}{K}\right)$ where K = 100 and the intrinsic growth rate is r = 4.
Birth rate, b_j = 6 and the transmission rates and recovery rates for the two strains are:

$$\beta_1 = 2, \beta_2 = 1 \quad and \quad \gamma_1 = 1 = \gamma_2$$

Suppose strain 1 with the largest transmission rate also has the highest virulence, $\mu_1 = 10, \mu_2 = 3$. Clearly , in the case the reproduction number $R_{0,1}$ = 11.765 > 10 = $R_{0,2}$. But, C_1 = 17 > 10 = C_2. However, $B_{0,1}$ = 15.385 < 16.667 = $B_{0,2}$. But, $\beta_1 > \beta_2$ hence, neither condition (3) nor (4) are satisfied. Simple computations show that a positive steady state exists for this case and is given by

$$S = 7, I_1 = 4.929, I_2 = 8.571 \; and \; R = 4.5$$

Competitive Exclusion for an Epidemic Model

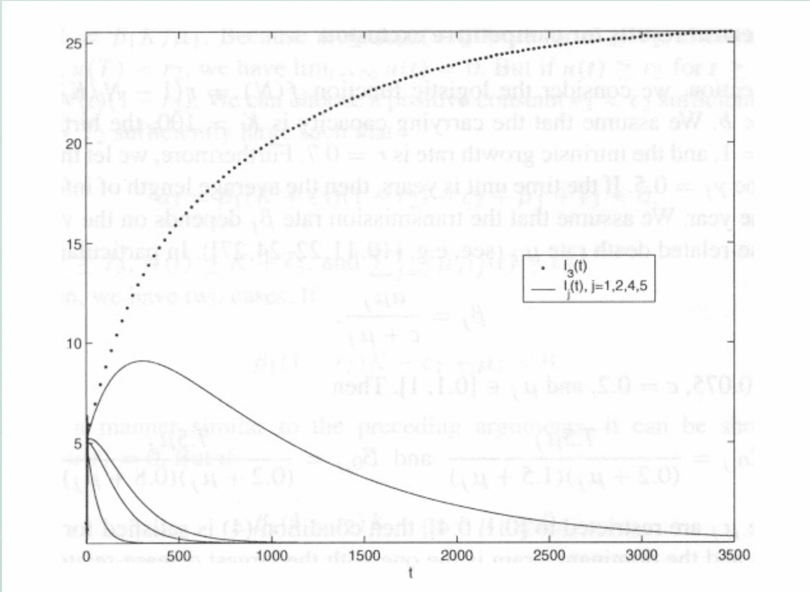


Fig. 1. Competitive exclusion when conditions (3) and (4) are not satisfied.

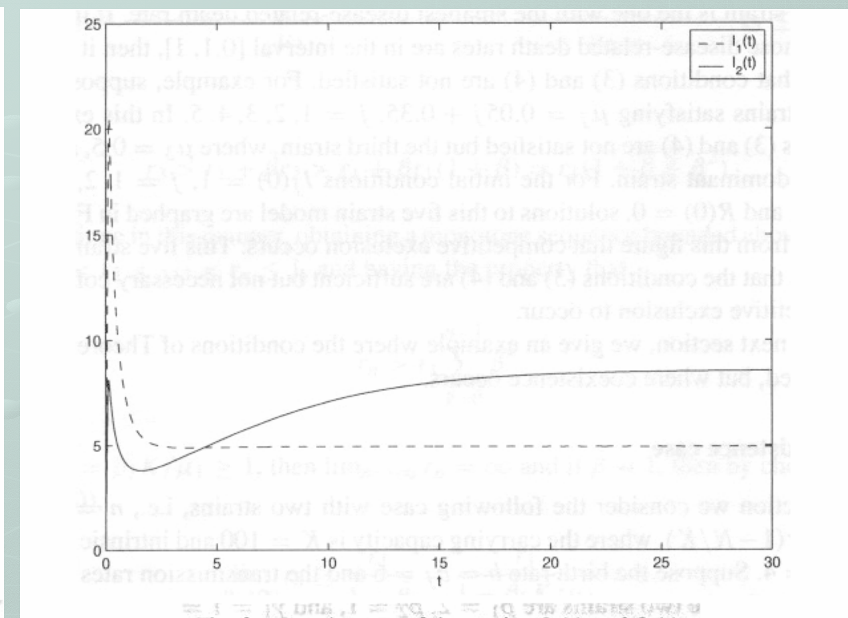


Fig. 2. Coexistence of the strains $I_1(t)$ and $I_2(t)$.

Local stability analysis proves that this positive steady state is locally asymptotically stable. In particular, the Jacobian matrix has eigen values given by

$$\lambda_1 = -8.657 + 6.833i,\ \lambda_2 = -8.657 - 6.833i,\ \lambda_3 = -1.899,\ \lambda_4 = -0.216$$

Our numerical results indicate that this equilibrium is indeed globally asymptotically stable.

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

Consider a species with ***n*** competing ecotypes.

For *i* = 1,2,…,*n*, we describe the dynamics of the subpopulation consisting of individuals of the i^{th} ecotype with the following individual size-structured model of the McKendrick-von Foerster type.

$$(u_i)_t + g_i(P(t))(u_i)_x + m_i(P(t))u_i = 0 \quad 0 < x < \infty, \quad t > 0$$

$$g_i(P(t))u_i(0,t) = \sum_{j=1}^{n} \int_0^{\infty} \gamma_{ij} \beta_j (P(t)) u_j(x,t)\,dx \quad t > 0$$

$$u_i(x,0) = u_{i0}(x) \quad 0 \le x < \infty$$

where $u_i(x,t)$ is the density of individuals of the i^{th} ecotype having size *x* at time *t*

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

$$P(t)=\sum_{i=1}^{n}\int_{0}^{\infty}u_i(x,t)dx$$ is the total number of individuals in the population at time *t.* For an individual in the *i*th subpopulation …

$g_i:$ is the *i*th growth rate

$m_i:$ is the *i*th mortality rate

$\beta_i:$ is the *i*th reproduction rate

$0\le\gamma_{i,j}\le 1:$ probability that an individual of the *j*th ecotype will reproduce an individual of the *i*th ecotype.

Clearly, $$\sum_{j=1}^{n}\gamma_{i,j}=\sum_{i=1}^{n}\gamma_{i,j}=1,\quad 1\le i,\quad j\le n$$

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

We focus on the asymptotic behavior of the population in two cases:

1. ***Closed reproduction***: offspring always belong to same ecotype as the parent.

$$\gamma_{i,i} \quad and \quad \gamma_{i,j} = 0 \quad for \quad i \neq j$$

2. ***Open reproduction***: individuals of ecotype *i* may reproduce individuals of ecotype *j.*

By integration of the PDE from 0 to infinity with respect to *t* and by making the following substitutions,

$$P(t) = \sum_{i=1}^{n} \int_{0}^{\infty} u_i(x,t)dx \quad and \quad P(t) = \int_{0}^{\infty} u_i(x,t)dx$$

we arrive at a system of *n* ODEs …

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

$$P_i'(t) = \sum_{j=1}^{n} (\gamma_{i,j} \beta_j(P) P_j) - m_i(P) P_i, \quad P_i(0) > 0, \quad i = 1,2,\ldots,n.$$

Asymptotic Behavior

In order to study the asymptotic behavior of the population, we consider the above system of coupled ordinary differential equations.

Assumptions for $0 \leq P < \infty$

$\beta_i(P)$ is non-increasing

$m_i(P)$ is increasing

There exists P_i^* such that $\beta_i(P_i^*) = m_i(P_i^*), \quad i = 1,2,\ldots,n.$

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

We first show that population ***P(t)*** is uniformly bounded.

Let $\overline{P} = \max_{1 \le i \le n} P_i^* \quad and \quad \underline{P} = \min_{1 \le i \le n} P_i^*.$

For any $0 < \varepsilon < 1$, define $I_\varepsilon = \left[\underline{P}(1-\varepsilon), \overline{P}(1+\varepsilon)\right]$.

Then there exists a finite time t_ε^* such that $P \in I_\varepsilon$ for $t \ge t_\varepsilon^*$.

Closed Reproduction Case

Recall that in the closed reproduction case,

$$\gamma_{i,i} \quad and \quad \gamma_{i,j} = 0 \quad for \quad i \ne j$$

Therefore the system of ODEs reduces to the following,

$$P_i' = \left(\beta_i(P) - m_i(P)\right)P_i \quad P_i(0) > 0, \quad i = 1,2,\ldots,n.$$

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

Under the assumption,

$$\frac{\beta_1(P)}{m_1(P)} > \frac{\beta_i(P)}{m_i(P)}, \quad i = 2,\dots,n\,;\ for\ any\ P \in I_0 = \left[\underline{P}, \overline{P}\right]$$

Then the solution of $P_i' = \left(\beta_i(P) - m_i(P)\right)P_i \quad P_i(0) > 0, \quad i = 1,2,\dots,n.$

satisfies that for each i = 2,…,n ; $P_i(t) \to 0$ as $t \to \infty$

To show this, it suffices to show that for i = 2,…,n ,

$\dfrac{P_i^{\sigma_i}}{P_1} \to 0$ as $t \to \infty$ for some positive constant σ_i

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

What's left is to show that $P_1(t) \to P_1^*$ as $t \to \infty$

This can be shown by considering the following initial value problem:

$$\begin{cases} y' = \left(\beta_1(y) - m_1(y)\right)y, \quad t_\varepsilon^* < t < \infty, \\ y(t_\varepsilon^*) = P_1(t_\varepsilon^*) \end{cases}$$

Clearly, $y(t) \to P_1^*$ as $t \longrightarrow \infty$. Furthermore, since

$P_1' \le \left(\beta_1(P_1) - m_1(P_1)\right)P_1$ by comparison $y(t) \ge P_1(t)$

for all $t \ge t_\varepsilon^*$. On the other hand we have:

$$\frac{d}{dt}\ln\left(\frac{P_1}{y}\right) = \frac{P_1'}{P_1} - \frac{y'}{y} = \left(\beta_1(P) - m_1(P)\right) - \left(\beta_1(y) - m_1(y)\right)$$

$$= \left(\beta_1(\hat{\xi}) - m_1'(\hat{\xi})\right)\left(P_1 - y\right) + \left(\beta_1'(\xi) - m_1'(\xi)\right)\sum_{j=2}^{n} P_j$$

Where ξ is between *P* and P_1 and $\hat{\xi}$ is between P_1 and *y*

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

Rearranging the terms, we arrive at

$$y - P_1 \le \frac{1}{c}\left(\frac{d}{dt}\ln(\frac{P_1}{y}) + (m_1'(\hat{\xi}) - \beta_1'(\hat{\xi}))\sum_{j=2}^{n} P_j \right)$$

Integrating from space to *t*, we get

$$\int_{t_\varepsilon^*}^{t} \big(y(\eta) - P_1(\eta)\big) d\eta \quad \le$$

$$\frac{1}{c}\left(\ln\left(\frac{P_1(t)}{y(t)}\right) + \sum_{j=2}^{n} \int_{t_\varepsilon^*}^{t} \big(\left[m_1'(\xi) - \beta_1'(\xi)\right] P_j(\eta)\big) d\eta \right) \le M < \infty$$

where *M* is independent of *t*.

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

Open Reproduction Case

In this case, we assume that reproduction is open under subpopulations, that is, individuals in the i^{th} subpopulation may also reproduce individuals in the j^{th} population. If the graph associated with the matrix $[\gamma_{i,j}]$ is strongly connected (the matrix is irreducible), then all ecotypes of the population coexist. For convenience, we assume the following:

Hypothesis 1:

$$\gamma_{1,2} > 0, \quad \gamma_{2,3} > 0, \ldots \quad \gamma_{n-1,n} > 0 \; and \; \gamma_{n,1} > 0. \quad otherwise$$
$$\gamma_{i,j} > 0, \quad 1 \le i, j \le n$$

If Hypothesis1 holds, then there exists a positive constant c such that

$$\lim \quad \inf_{t\to\infty} P_i(t) \ge c \quad for \quad i = 1,2,\ldots,n$$

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

NUMERICAL RESULTS

In the **closed reproduction** case, it is clear that subpopulations with smaller ratios $\frac{\beta_i(P)}{m_i(P)}$ will go to extinction.

This leads to the question:

What happens if two subpopulations have the same largest ratio?

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

We focus on the following subsystem consisting of two subpopulations with the largest ratio $\frac{\beta_1(P)}{m_1(P)} = \frac{\beta_2(P)}{m_2(P)}$

$$P_i' = (\beta_i(P) - m_i(P))P_i, \quad P_i(0) > 0, \quad i = 1,2.$$

In this case, both subpopulations should survive. However, the asymptotic behavior of this two-ecotype system depends on the initial conditions $P_i(0), \quad i = 1,2$.

Competitive Exclusion and Coexistence for a Quasilinear Size-Structured Population Model

In the **open reproduction** case, if the k^{th} $(1 \le k \le n)$ node in the graph associated with the matrix $[\gamma_{i,j}]$ is not connected to any other node, i.e.,

$$\gamma_{k,k} = 1 \; and \; \gamma_{k,j} = 1 \; for \; j = 1, \ldots, k-1, k+1, \ldots, n,$$

then the k^{th} subpopulation may become extinct.