Chapter 9: Competition

From: Gause 1934
Competitive exclusion and co-existence

Asterionella formosa

Synedra ulna

Together
Competitive exclusion: several consumers using 1 resource

Closed system with fixed amount of resource $K$:

$$F = K - \sum_{i}^{n} e_{i}N_{i}, \quad \frac{dN_{i}}{dt} = N_{i}(b_{i}F - d_{i}), \quad \text{for } i = 1, 2, \ldots, n, \quad R_{0i} = \frac{b_{i}K}{d_{i}}$$

Since for each species $\bar{F} = d_{i}/b_{i} = K/R_{0i}$ they have to exclude each other

$$b_{i}\bar{F} - d_{i} > 0 \quad \text{or} \quad b_{i}\frac{d_{1}}{b_{1}} - d_{i} > 0 \quad \text{or} \quad b_{i}\frac{d_{1}}{d_{i}} > 1 \quad \text{or} \quad \frac{b_{i}}{d_{i}} > \frac{b_{1}}{d_{1}}.$$
Closed system with fixed amount of resource $K$:

\[
F = K - \sum_{i}^{n} e_i N_i , \quad \frac{dN_i}{dt} = N_i(b_i F - d_i) , \quad \text{for } i = 1, 2, \ldots, n ,
\]

Carrying capacity of one species:

\[
K_i = \bar{N}_i = \frac{K - d_i/b_i}{e_i} = \frac{K(1 - 1/R_{0i})}{e_i}
\]
Nullclines for 2-D closed system

\[ F = K - \sum_{i}^{n} e_i N_i , \quad \frac{dN_i}{dt} = N_i(b_i F - d_i) , \quad \text{for } i = 1, 2, \ldots, n , \quad (9.1) \]

\[ F = K - e_1 N_1 - e_2 N_2 \]

\[ N_2 = \frac{K - d_1/b_1}{e_2} - \frac{e_1}{e_2} N_1 = \frac{K(1 - 1/R_{01})}{e_2} - \frac{e_1}{e_2} N_1 \quad \text{and} \quad N_2 = \frac{K(1 - 1/R_{02})}{e_2} - \frac{e_1}{e_2} N_1 , \quad (9.4) \]
Nullclines for 2-D closed system

\[
F = K - \sum_i^n e_i N_i, \quad \frac{dN_i}{dt} = N_i(b_i F - d_i), \quad \text{for } i = 1, 2, \ldots, n, \quad (9.1)
\]

\[
F = K - e_1 N_1 - e_2 N_2
\]

\[
N_2 = \frac{K - d_1/b_1 - e_1}{e_2} N_1 = \frac{K(1 - 1/R_{01})}{e_2} - \frac{e_1}{e_2} N_1 \quad \text{and} \quad N_2 = \frac{K(1 - 1/R_{02})}{e_2} - \frac{e_1}{e_2} N_1, \quad (9.4)
\]
Competitive exclusion when birth rate is saturated (closed)

\[ F = K - \sum_{i}^{n} e_i N_i, \quad \frac{dN_i}{dt} = N_i \left( \frac{b_i F}{h_i + F} - d_i \right) \]

Carrying capacity of one species, and the corresponding steady state for \( F \):

\[ \bar{N}_i = \frac{K(R_{0i} - 1) - h_i}{e_i(R_{0i} - 1)} \]

\[ \bar{F} = \frac{h_i}{R_{0i} - 1} \]

Thus the consumer with the lowest \( h_i \) over \( R_0-1 \) ratio depletes the resource most.

At the lowest \( \bar{F} \) the other species cannot invade:

\[ \frac{b_j \bar{F}}{h_j + \bar{F}} > d_j \quad \text{or} \quad \bar{F} > \frac{h_j}{R_{0j} - 1} \]
Competition in open systems (one resource)

\[
\frac{dR}{dt} = s - dR - R \sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{dN_i}{dt} = N_i \left( \frac{b_i c_i R}{h_i + c_i R} - d_i \right) \quad \text{or}
\]

\[
\frac{dR}{dt} = s - dR - R \sum_{i=1}^{n} \frac{c_i N_i}{h_i + R} \quad \text{with} \quad \frac{dN_i}{dt} = N_i \left( \frac{b_i R}{h_i + R} - d_i \right) \quad \text{or}
\]

\[
\frac{dR}{dt} = rR(1 - R/K) - R \sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{dN_i}{dt} = N_i \left( \frac{b_i c_i R}{h_i + c_i R} - d_i \right) \quad \text{or}
\]

\[
\frac{dR}{dt} = rR(1 - R/K) - R \sum_{i=1}^{n} \frac{c_i N_i}{h_i + R} \quad \text{with} \quad \frac{dN_i}{dt} = N_i \left( \frac{b_i R}{h_i + R} - d_i \right),
\]

Exclusion because

\[
R_i^* = \frac{h_i/c_i}{R_{0_i} - 1} \quad \text{or} \quad R_i^* = \frac{h_i}{R_{0_i} - 1}, \quad \text{where} \quad R_{0_i} = \frac{b_i}{d_i},
\]
9.1 Competitive exclusion

To test the stability of the steady states of a 3-dimensional phase space one has to resort to an invasion criterion and apply that to each of the steady states (that are marked by circles or bullets):

1. In Fig. 9.1d the origin is unstable because $dR/dt > 0$ in its neighborhood (note that the origin is not a steady state in Fig. 9.1c).

2. The carrying capacity of the resource in Fig. 9.1c and d is unstable because it is located above the consumer planes, i.e., both $dN_1/dt > 0$ and $dN_2/dt > 0$ when $R = s/d$ or $R = K$.

3. The circled intersection point of the $N_2$ and the $R$-nullcline in the front plane is unstable because it is located on the right side of the $N_1$-nullcline, i.e., if $N_1$ were introduced in this state it would grow and invade.

4. The intersection point marked by a bullet in the $N_2 = 0$ plane at the bottom is stable because...
Quasi steady state to reveal interactions: resource with source

\[ \frac{dR}{dt} = s - dR - R \sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{dN_i}{dt} = N_i \left( \frac{b_i c_i R}{h_i + c_i R} - d_i \right) \]

\[ \hat{R} = \frac{s}{d + \sum c_i N_i} \]

\[ \frac{dN_i}{dt} = N_i \left( \frac{b_i s}{s + (h_i/c_i)(d + \sum c_j N_j)} - d_i \right) = N_i \left( \frac{\beta_i}{1 + \sum N_j/k_j} - d_i \right) \]

\[ K_i = \frac{s}{h_i} \left( R_{0i} - 1 \right) - \frac{d}{c_i} = \frac{s}{c_i R_i^*} - \frac{d}{c_i} \]
Quasi steady state to reveal interactions: logistic resource

\[ \frac{dR}{dt} = rR(1 - R/K) - R \sum_{i=1}^{n} c_i N_i \quad \text{with} \quad \frac{dN_i}{dt} = N_i \left( \frac{b_i c_i R}{h_i + c_i R} - d_i \right) \]

\[ \hat{R} = K \left( 1 - \frac{1}{r} \sum c_i N_i \right) \]

\[ \frac{dN_i}{dt} = N_i \left( \frac{b_i (r - \sum c_i N_i)}{(h_i/c_i)(r/K) + r - \sum c_j N_j} - d_i \right) \]

\[ \bar{N}_i = \frac{r}{c_i} \left( 1 - \frac{R_i^*}{K} \right) \]
Lotka-Volterra competition model

\[ \frac{dN_i}{dt} = r_i N_i \left( 1 - \sum_{j=1}^{n} A_{ij} N_j \right) \]

\[ N_2 = \frac{1}{A_{12}} - \frac{A_{11}}{A_{12}} N_1 = \frac{1}{A_{12}} (1 - N_1) \]

\[ N_2 = \frac{1}{A_{22}} - \frac{A_{21}}{A_{22}} N_1 = (1 - A_{21} N_1) \]
Several consumers on two substitutable resources

\[
\frac{dN_i}{dt} = \left( \beta_i \frac{\sum_j c_{ij} R_j}{h_i + \sum_j c_{ij} R_j} - \delta_i \right) N_i, \quad \frac{dR_j}{dt} = s_j - d_j R_j - \sum_i c_{ij} N_i R_j
\]

Consumer nullcline depends on resources only:

\[
R_2 = \frac{h_i}{c_{i2}(R_{0i} - 1)} - \frac{c_{i1}}{c_{i2}} R_1 \quad \text{Straight line with slope } -\frac{c_{i1}}{c_{i2}}
\]

where \( R_{0i} = \beta_i/\delta_i \)

Starting and ending at critical resource density:

\[
R_{ij}^* = \frac{h_i}{c_{ij}(R_{0i} - 1)}
\]

Simplified nullcline:

\[
R_2 = R_{i2}^* - \frac{c_{i1}}{c_{i2}} R_1
\]
Several consumers with same diet $c_{i1}$ and $c_{i2}$.

(a) Tilman diagram

(b) QSSA

$h_1 < h_2 < h_3$
Several consumers having different diets $c_{i1}$ and $c_{i2}$.

Generically only one intersection point between all nullclines:

maximally two co-existing species on two resources.

Lowest intersection not invadable by other consumers (but no guarantee that this is a steady state).
Essential resources

Several consumers:

\[ \frac{dN_i}{dt} = \left( \beta_i \prod_j \frac{c_{ij}R_j}{h_{ij} + c_{ij}R_j} - \delta_i \right) N_i , \quad \frac{dR_j}{dt} = s_j - d_j R_j - \sum_i c_{ij} N_i R_j \]

Two consumers using two resources:

\[ \begin{align*}
\frac{dN_1}{dt} &= \left( \beta_1 \frac{c_{11}R_1}{h_{11} + c_{11}R_1} - \frac{c_{12}R_2}{h_{12} + c_{12}R_2} - \delta_1 \right) N_1 \\
\frac{dN_2}{dt} &= \left( \beta_2 \frac{c_{21}R_1}{h_{21} + c_{21}R_1} - \frac{c_{22}R_2}{h_{22} + c_{22}R_2} - \delta_2 \right) N_2
\end{align*} \]
Essential resources

\[
\begin{align*}
\frac{dN_1}{dt} &= \left( \beta_1 \frac{c_{11} R_1}{h_{11} + c_{11} R_1} \frac{c_{12} R_2}{h_{12} + c_{12} R_2} - \delta_1 \right) N_1 \\
\frac{dN_2}{dt} &= \left( \beta_2 \frac{c_{21} R_1}{h_{21} + c_{21} R_1} \frac{c_{22} R_2}{h_{22} + c_{22} R_2} - \delta_2 \right) N_2
\end{align*}
\]

Asymptotes defined by letting
\[
R_1 \to \infty \text{ or } R_2 \to \infty
\]

\( c_{11} > c_{12}, \ c_{22} > c_{21} \) and \( c_{31} \approx c_{32} \),

Local steepness defines stability
4-dimensional Jacobian

\[
\begin{align*}
\frac{dR_1}{dt} &= s_1 - d_1 R_1 - c_{11} N_1 R_1 - c_{21} N_2 R_1, \\
\frac{dR_2}{dt} &= s_2 - d_2 R_2 - c_{12} N_1 R_2 - c_{22} N_2 R_2, \\
\frac{dN_1}{dt} &= (\beta_1 \frac{c_{11} R_1 + c_{12} R_2}{h_1 + c_{11} R_1 + c_{12} R_2} - \delta_1) N_1, \\
\frac{dN_2}{dt} &= (\beta_2 \frac{c_{21} R_1 + c_{22} R_2}{h_2 + c_{21} R_1 + c_{22} R_2} - \delta_2) N_2,
\end{align*}
\]

where

\[
J = \begin{pmatrix}
\partial_{R_1} R'_1 & \ldots & \partial_{N_2} R'_1 \\
\vdots & \ddots & \vdots \\
\partial_{R_1} N'_2 & \ldots & \partial_{N_2} N'_2
\end{pmatrix} = \begin{pmatrix}
-d_1 - c_{11} \bar{N}_1 - c_{21} \bar{N}_2 & 0 & -c_{11} \bar{R}_1 & -c_{21} \bar{R}_1 \\
0 & -d_2 - c_{12} \bar{N}_1 - c_{22} \bar{N}_2 & -c_{12} \bar{R}_2 & -c_{22} \bar{R}_2 \\
\Phi_1 c_{11} & \Phi_1 c_{12} & 0 & 0 \\
\Phi_2 c_{21} & \Phi_2 c_{22} & 0 & 0
\end{pmatrix}
\]

and

\[
\Phi_1 = \frac{\beta_1 h_1 \bar{N}_1}{(h_1 + c_{11} \bar{R}_1 + c_{12} \bar{R}_2)^2} \quad \text{and} \quad \Phi_2 = \frac{\beta_2 h_2 \bar{N}_2}{(h_2 + c_{21} \bar{R}_1 + c_{22} \bar{R}_2)^2}
\]

\[
J = \begin{pmatrix}
-\rho_1 & 0 & -\gamma_{11} & -\gamma_{21} \\
0 & -\rho_2 & -\gamma_{12} & -\gamma_{22} \\
\phi_{11} & \phi_{12} & 0 & 0 \\
\phi_{21} & \phi_{22} & 0 & 0
\end{pmatrix}
\]

\[
\lambda^4 + a_3 \lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0 = 0
\]

\[
a_0 = (\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21})(\phi_{11} \phi_{22} - \phi_{12} \phi_{21})
\]
where
\[ (\partial R_1 N_1' \quad \partial R_2 N_1' \quad \partial R_1 N_2' \quad \partial R_2 N_2') = \begin{pmatrix} \Phi_1 & \frac{R_2}{1+c_{11}R_1/h_{11}} & \Phi_1 & \frac{R_1}{1+c_{12}R_2/h_{12}} \\ \Phi_2 & \frac{R_2}{1+c_{21}R_1/h_{21}} & \Phi_2 & \frac{R_1}{1+c_{22}R_2/h_{22}} \end{pmatrix} = \begin{pmatrix} \phi_{11} & \phi_{12} \\ \phi_{21} & \phi_{22} \end{pmatrix} \]

where
\[ \Phi_1 = \frac{\beta_1 N_1 c_{11} c_{12}}{(h_{11} + c_{11} R_1)(h_{12} + c_{12} R_2)} \quad \text{and} \quad \Phi_2 = \frac{\beta_2 N_2 c_{21} c_{22}}{(h_{21} + c_{21} R_1)(h_{22} + c_{22} R_2)} \]

\[ c_{11} > c_{12} \text{ and } c_{22} > c_{21} \]

\[ J = \begin{pmatrix} -\rho_1 & 0 & -\gamma_{11} & -\gamma_{21} \\ 0 & -\rho_2 & -\gamma_{12} & -\gamma_{22} \\ \phi_{11} & \phi_{12} & 0 & 0 \\ \phi_{21} & \phi_{22} & 0 & 0 \end{pmatrix} \]

\[ \lambda^4 + a_3 \lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0 = 0 \]

\[ a_0 = (\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21})(\phi_{11}\phi_{22} - \phi_{12}\phi_{21}) \]

Unknown sign: \( \phi_{11}\phi_{22} - \phi_{12}\phi_{21} \)

If negative unstable steady state.