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 $K$:

$$F = K - \sum_{i}^{n} e_i N_i , \quad \frac{dN_i}{dt} = N_i (b_i F - d_i) , \quad \text{for } i = 1, 2, \ldots, n , \quad R_0 = \frac{b_i K}{d_i}$$

Since for each species $\bar{F} = d_i / b_i = K / R_0$, they have to exclude each other

$$b_i \bar{F} - d_i > 0 \quad \text{or} \quad b_i \frac{d_1}{b_1} - d_i > 0 \quad \text{or} \quad b_i \frac{d_1}{d_i} \frac{b_1}{b_1} > 1 \quad \text{or} \quad \frac{b_i}{d_i} > \frac{b_1}{d_1} ,$$
Competitive exclusion: several consumers using 1 resource

Closed system with fixed amount of resource \( K \):

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

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

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

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

\[ N_2 = \frac{K - d_1/b_1}{e_2} - \frac{e_1}{e_2} N_1 = \frac{K(1 - 1/R_{01})}{e_2} - \frac{e_1}{e_2} N_1 \quad \text{and} \quad N_2 = \frac{K(1 - 1/R_{02})}{e_2} - \frac{e_1}{e_2} N_1, \quad (9.4) \]
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 \( F \):

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

Thus the consumer with the lowest \( h_i \) over \( R_{0_i} - 1 \) ratio depletes the resource most.

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

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

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

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

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

\[ R_i^* = \frac{h_i/c_i}{R_{0_i} - 1} \quad \text{or} \quad R_i^* = \frac{h_i}{R_{0_i} - 1}, \quad \text{where} \quad R_{0_i} = \frac{b_i}{d_i}, \]
Figure 9.1: Competitive exclusion in the simple model of Eq. (9.1) in Panels (a-b), and in 3-dimensional models of Eqs. (9.8) and (9.10) with a saturated functional response, for a non-replicating (c) and replicating (d) resource, respectively. This figure was made with the files comp.R and comp3d.R.

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

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

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

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

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

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

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

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

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

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

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

\[
N_2 = \frac{1}{A_{22}} - \frac{A_{21}}{A_{22}} \quad N_1 = (1 - A_{21} N_1)
\]
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: \( R_2 = R_{i2}^* - \frac{c_{i1}}{c_{i2}} R_1 \)
Because one cannot easily tell from a Tilman diagram whether or not an intersection point (Mylius & Diekmann, 1995), minimal density tend to win the competition, this has been coined as the pessimization principle.

Importantly, such a Tilman diagram can be made for any set of phase spaces (Fig. 9.4b–d). Importantly, such a Tilman diagram can be made for any set of consumers, and this analysis tells us (1) that the consumers depleting the resources the most are expected to be maintained by two resources. Because the consumer depleting resources to a steady state because it is located above the $d_i$ intersection point, this is not readily obvious from the Tilman diagram in Fig. 9.4a, the right-most intersection point, where $d_i = 0$, nullclines fail to intersect (see Panel (a)), and giving $N_i(0,0,0)$ an advantage over the other two consumers by setting $h_i = -c_{i1}/c_{i2}$. Thus, an intersection between two consumer nullclines need not be steady state of the full system, i.e., of Eq. (9.21) see the online tutorial). Using newton() again be confirmed by making a QSSA for the resources: and depicting all pairwise consumer nullclines, there is no steady state where several consumer co-exists, and that this is confirmed by making a QSSA for the resources and depicting the 3-dimensional consumer nullclines in (a), i.e., as a function of the resource densities they obey Eq. (9.22), and the nullcline of each consumer is defined by Eq. (9.21a). When depicted in a Tilman diagram in Panel (a), $N_i/R_i$ will decline at these resource densities. The left-most intersection point, where $d_i = 0$ nullcline, implying that $N_i = 0$, is not a steady state (see the online tutorial). These results can be again be confirmed by making a QSSA for the resources and depicting all pairwise consumer nullclines in (b). The three QSSA consumer nullcline planes fail to intersect, demonstrating that there is no combination of resource densities, where $d_i = 0$ nullcline, implying that $N_i = 0$, is an unstable steady state of Eq. (9.21) see the online tutorial). Using newton() again be confirmed by making a QSSA for the resources and depicting all pairwise consumer nullclines, there is no steady state where several consumer co-exists, and that

$-c_{i1}/c_{i2}$
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:

\[
\frac{dN_1}{dt} = \left( \beta_1 \frac{c_{11}R_1}{h_{11} + c_{11}R_1} \frac{c_{12}R_2}{h_{12} + c_{12}R_2} - \delta_1 \right) N_1
\]

\[
\frac{dN_2}{dt} = \left( \beta_2 \frac{c_{21}R_1}{h_{21} + c_{21}R_1} \frac{c_{22}R_2}{h_{22} + c_{22}R_2} - \delta_2 \right) N_2
\]
In all panels of Fig. 9.5 we have set $R_1, R_2$ respectively (see Fig. 9.5a and b). Whether or not the nullclines will intersect therefore depends on the minimal resource densities these consumers require. These asymptotes can be found by setting $d_R = 0$ nullcline more horizontal. The latter will create a situation where the nullclines intersect in the stable configuration of Fig. 9.3b. Note that setting the niche overlap to let each species eat most of the resource it requires most (which would be “optimal” in an evolutionary sense (see the chapter by Tilman in (McLean & May, 2007))). We have made the stable situation of Fig. 9.5a and c accordingly set $R_1, R_2$.

The other bullets and circles reflects a stability of steady state with consumers. The panels at upper corners depicts the (unstable) steady state of the resources in the absence of consumers. The panels at lower corners depicts the (stable) steady state of the resources in the presence of consumers. The panels at bottom provide the nullclines of Eqs. (9.24) and (9.25) after making a QSSA for the two species with the lowest requirements, $h_{11}, h_{22}, \ldots, n$. Decreasing the niche overlap further results in a situation where the nullclines fail to intersect.

Essential resources

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

Asymptotes defined by letting $R_1 \to \infty$ 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

\[ \frac{dR_1}{dt} = s_1 - d_1 R_1 - c_{11} N_1 R_1 - c_{21} N_2 R_1 , \]

\[ \frac{dR_2}{dt} = s_2 - d_2 R_2 - c_{12} N_1 R_2 - c_{22} N_2 R_2 , \]

\[ \frac{dN_1}{dt} = \left( \beta_1 \frac{c_{11} R_1 + c_{12} R_2}{h_1 + c_{11} R_1 + c_{12} R_2} - \delta_1 \right) N_1 , \]

\[ \frac{dN_2}{dt} = \left( \beta_2 \frac{c_{21} R_1 + c_{22} R_2}{h_2 + c_{21} R_1 + c_{22} R_2} - \delta_2 \right) N_2 , \]

where

\[ J = \begin{pmatrix} \partial R_1 R'_1 & \ldots & \partial N_2 R'_1 \\ \vdots & \ddots & \vdots \\ \partial R_1 N'_2 & \ldots & \partial N_2 N'_2 \end{pmatrix} \]

\[ = \begin{pmatrix} -d_1 - c_{11} \bar{N}_1 - c_{21} \bar{N}_2 & 0 & -c_{11} \bar{R}_1 & -c_{21} \bar{R}_1 \\ 0 & -d_2 - c_{12} \bar{N}_1 - c_{22} \bar{N}_2 & -c_{12} \bar{R}_2 & -c_{22} \bar{R}_2 \\ \Phi_1 c_{11} & \Phi_1 c_{12} & 0 & 0 \\ \Phi_2 c_{21} & \Phi_2 c_{22} & 0 & 0 \end{pmatrix} \]

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

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

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

\[ a_0 = (\gamma_{11} \gamma_{22} - \gamma_{12} \gamma_{21})(\phi_{11} \phi_{22} - \phi_{12} \phi_{21}) \]
4-dimensional Jacobian: essential resources

\[
\begin{pmatrix}
\frac{\partial R_1 N'_1}{\partial R_1} & \frac{\partial R_2 N'_1}{\partial R_1} \\
\frac{\partial R_1 N'_2}{\partial R_2} & \frac{\partial R_2 N'_2}{\partial R_2}
\end{pmatrix}
= \begin{pmatrix}
\Phi_1 \frac{\bar{R}_2}{1+R_1/H_{11}} & \Phi_1 \frac{\bar{R}_1}{1+R_1/H_{12}} \\
\Phi_2 \frac{\bar{R}_2}{1+R_1/H_{21}} & \Phi_2 \frac{\bar{R}_1}{1+R_2/H_{22}}
\end{pmatrix}
= \begin{pmatrix}
\phi_{11} & \phi_{12} \\
\phi_{21} & \phi_{22}
\end{pmatrix}
\]

\[
\frac{dN_1}{dt} = \left(\beta_1 \frac{c_{11} R_1}{h_{11} + c_{11} R_1} \frac{c_{12} R_2}{h_{12} + c_{12} R_2} - \delta_1\right) N_1
\]

\[
\frac{dN_2}{dt} = \left(\beta_2 \frac{c_{21} R_1}{h_{21} + c_{21} R_1} \frac{c_{22} R_2}{h_{22} + c_{22} R_2} - \delta_2\right) N_2
\]

\[H_{ij} = h_{ij}/c_{ij}\] and

\[\Phi_1 = \frac{\beta_1 \bar{N}_1}{(H_{11} + \bar{R}_1)(H_{12} + \bar{R}_2)} \quad \text{and} \quad \Phi_2 = \frac{\beta_2 \bar{N}_2}{(H_{21} + \bar{R}_1)(H_{22} + \bar{R}_2)}.
\]

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

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

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

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

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

If negative, steady state will be unstable.