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 $K$:

$$ F = K - \sum_{i}^{n} e_i N_i , \quad \frac{dN_i}{dt} = N_i (b_i F - d_i) , \quad \text{for} \quad i = 1, 2, \ldots, n , \quad R_{0_i} = \frac{b_i K}{d_i} $$

Since for each species $\bar{F} = d_i / b_i = K / R_{0_i}$ they have to exclude each other

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

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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

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

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

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

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

Exclusion because

\[ R_i^* = \frac{h_i/c_i}{R_0 - 1} \quad \text{or} \quad R_i^* = \frac{h_i}{R_0 - 1}, \quad \text{where} \quad R_0 = \frac{b_i}{d_i}, \]
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 \( \frac{dR}{dt} > 0 \) 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 \( \frac{dN_1}{dt} > 0 \) and \( \frac{dN_2}{dt} > 0 \) when \( R = \frac{s}{d} \) or \( R = \frac{K}{d} \).
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

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

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

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

\[ K_i = \frac{s}{h_i} \left( R_{0i} - 1 \right) - \frac{d}{c_i} = \frac{s}{c_i R_i^*} - \frac{d}{c_i} \]
9.1 Competitive exclusion

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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 $N_1 > N_2$.
Quasi steady state to reveal interactions: logistic resource

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

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

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

\[ \bar{N}_i = \frac{r}{c_i} \left( 1 - \frac{R_i^*}{K} \right) \]
9.1 Competitive exclusion

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4. The intersection point marked by a bullet in the $N_2 = 0$ plane at the bottom is stable because 

\[ N_1 \geq 0 \]
that the growth rates, because of their non-mass-action interaction terms (see also (O’Dwyer, 2018)). Finally, the fact Grind model with an arbitrary number of species, in the absence of interspecific competition Eq. (9.19) simplifies to logistic growth equations, where the interaction matrix, of Fig. 9.2, such a situation would correspond to perpendicular nullclines intersecting in stable of their unique resource, their consumption and that they do not compete and each approach a carrying capacity defined by the availability extreme example would be that they specialize on using just one of the two resources, implying because the species that initially has the highest abundance has the highest chance to exclude because the species that initially has the highest abundance has the highest chance to exclude (Tilman, 1980, 1982). First consider the red line and the blue lines depict the d

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

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

\[
N_2 = \frac{1}{A_{22}} - \frac{A_{21}}{A_{22}} N_1 = \left(1 - A_{21} N_1 \right)
\]
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).

\[
\begin{align*}
\frac{dN_i}{dt} &= \left( c_{ij} R_j - h_{ij} + c_{ij} N_i R_j \right), \\
\frac{dR_j}{dt} &= s_j R_j - c_{ij} N_i R_j.
\end{align*}
\] (9.24a,b)
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:

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

\[
\frac{dN_2}{dt} = \left( \beta_2 \frac{c_{21} R_1}{h_{21} + c_{21} R_1} \frac{c_{22} R_2}{h_{22} + c_{22} R_2} - \delta_2 \right) N_2
\]
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} \text{ and } c_{31} \approx c_{32},

Local steepness defines stability