Lecture 15 – Graphical Analysis of Network modules (3-spp.)

Today:

Paper discussion, then...

- Competition for explicit resources
- Trophic chain
- Intraguild predation

Concepts:

- Competitive exclusion principle (niche partitioning)
- Determining invasibility and coexistence criteria
- Temporal niche partitioning (Armstrong-McGehee effects)

Exploitative Competition for Explicit Resource

Recall:

2-spp. LV competition with implicit resource

$\Rightarrow$ Intra > Inter-specific competition for coexistence

Same general insight from n-spp. community matrix analysis.

$$\lambda^2 - \underbrace{(A_{11} + A_{22})}_{\text{Trace}}\lambda + \underbrace{A_{11}A_{22} - A_{12}A_{21}}_{\text{Determinant}}$$

$\Longrightarrow$ More zero off-diagonals (lower connectance), the more likely $Det(A) > 0 \implies$ more stable.

Today:

Start with 2 species competing for explicit resource.

Include self-limitation in resource

(Know that strong self-limitation on some species is needed for stable coexistence to be possible).

$$\begin{aligned}
\frac{dO}{dt} &= \overbrace{e_{RO}a_{RO}RO}^{\text{linear intxn}} - \overbrace{m_oO}^{\text{exponential}}\\
\frac{dC}{dt} &= e_{RC}a_{RC}RC - m_cC\\
\frac{dR}{dt} &= rR\left(1 - \frac{R}{K}\right) - a_{RC}RC - a_{RO}RO
\end{aligned}$$

Today's class is going to be *'Active learning'* style

Groups of 4-5 people. (1 whiteboard per group.)

Use the methods we've learned in class to answer (referring to notes is okay)...

Questions for each module:

1. How many equilibria exist? ($\Longrightarrow$ What are they symbolically?)
2. When can each species invade? ($\Longrightarrow$ When are equilibria stable?)

In other words: **How can both species coexists on a single resource?**

Method: Graphical analysis of isoclines

Hint: Best to start analyzing $\frac{dO}{dt}$ and $\frac{dC}{dt}$ rather than $\frac{dR}{dt}$

. . . .

Let groups work for 20 min.(?) before volunteer group explains to rest, or work through it together.

. . . .

Answer:
In order for a species to invade, its per capita growth rate must be positive: $\frac{1}{N}\frac{dN}{dt} > 0$

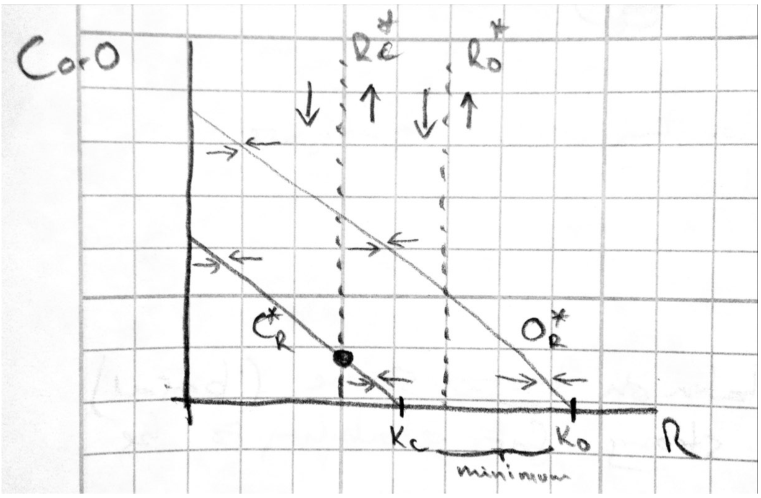
Predator isoclines: (Not really *isoclines*, but rather *isoplanes*.)

$$
\begin{aligned}
\frac{1}{O}\frac{dO}{dt} &= e_{RO}a_{RO} - m_0 = 0 \qquad &\Rightarrow \qquad R_O^* &= \frac{m_O}{e_{RO}a_{RO}} \\
\frac{1}{C}\frac{dC}{dt} &= e_{RC}a_{RC} - m_C = 0 \qquad &\Rightarrow \qquad R_C^* &= \frac{m_C}{e_{RC}a_{RC}}
\end{aligned}
$$

Prey isocline(s):

$$
\begin{aligned}
\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) = a_{RC}RC + a_{RO}RO = 0 \qquad &= \qquad r - \frac{rR}{K} - a_{RC}C - a_{RO}O \\
&\Rightarrow \qquad O_R^* = \frac{r - \frac{rR}{K} - a_{RC}C}{a_{RO}} \\
&\Rightarrow \qquad C_R^* = \frac{r - \frac{rR}{K} - a_{RO}O}{a_{RC}}
\end{aligned}
$$

Note that O_R^* and C_R^* are linearly declining functions of both R and C or O.
Look at marginal view of phase portrait (i.e. 3D in 2D):



Conclusions:

1. K_C and K_O are minimum carrying capacities needed for coexistence of either consumer with R.
2. Whichever species has the lower R^* out-competes the other!
3. R^* is a metric for competitive superiority.
   C out-competes O if $R_C^* < R_O^*$ ...which means that $m_C < m_O$ and/or $e_{RC}a_{RC} > e_{RO}a_{RO}$.
4. Competitive exclusion occurs regardless of carrying capacity (K doesn't show up in either R_i^*).
   As long as $K > \min R_i^*$, there will be only 1 consumer species.

But note assumption of linear species intxns. (Will get back to this.)

Trophic Chain

$$\begin{aligned}
\frac{dO}{dt} &= e_{CO}a_{CO}CO - m_o O \\
\frac{dC}{dt} &= e_{RC}a_{RC}RC - a_{CO}CO - m_c C \\
\frac{dR}{dt} &= rR\left(1 - \frac{R}{K}\right) - a_{RC}RC
\end{aligned}$$

Intuition from previous (exploitative competition) model:

Need some minimum amount of energy/productivity to support higher trophic levels.

Since middle-school probably know that ∼90% of energy is lost at each trophic transfer.

Questions:

1. How many equilibria and what are they (*qualitatively*)?
2. What level of productivity (K_i) allows each consumer to invade (*symbolically*)?

....

1 Trivial equilibrium ⇒ $R^*_{eq} = C^*_{eq} = O^*_{eq} = 0$

2 Resource-only ⇒ $R^*_{eq} = K$

3 When can C invade R-only system?

In order to invade $\frac{1}{C}\frac{dC}{dt} > 0$.

Consumer isocline:

$$\frac{1}{C}\frac{dC}{dt} = e_{RC}a_{RC}R - \cancelto{0}{a_{CO}CO} - m_C = 0 \qquad \Rightarrow \qquad R^*_C = \frac{m_C}{e_{RC}a_{RC}}$$

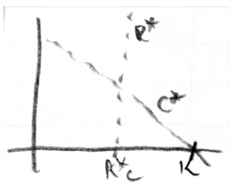
Resource isocline:

$$\frac{dR}{dt} = rR - \frac{rR^2}{K} - a_{RC}RC = 0 \qquad \Rightarrow \qquad C^*_R = \frac{r - \frac{rR}{K}}{a_{RC}} = \frac{r}{a_{RC}} - \frac{r}{K}R$$

Conclusion:

C can invade when $K \geq R^*_C$.

The R-only system becomes *unstable* when $K \geq R^*_C$.



4 O can't invade R-only system. When can O invade an RC-system at equilibrium?

RC equilibria:

$$R^*_{eq} = \frac{m_C}{a_{RC}e_{RC}}$$

$$C^*_{eq} = \frac{r - \frac{rR^*}{K}}{a_{RC}} = \frac{r - \frac{r\frac{m_C}{a_{RC}e_{RC}}}{K}}{a_{RC}} = \frac{r}{a_{RC}} - \frac{rm_C}{a^2_{RC}e_{RC}K} = \frac{r(a_{RC}e_{RC}K - m_C)}{a^2_{RC}e_{RC}K}$$

Invasion threshold C^*_O:

$$\frac{1}{O}\frac{dO}{dt} = 0 \qquad \Rightarrow \qquad C^*_O = \frac{m_O}{e_{CO}a_{CO}}$$

When does invasion threshold equal equilibrium (ie. $C^*_O = C^*_{eq}$)?

$$
\begin{aligned}
C^* = \frac{m_O}{e_{CO}a_{CO}} &= \frac{r(a_{RC}e_{RC}K - m_C)}{a_{RC}^2 e_{RC}K} \\
m_O a_{RC}^2 e_{RC} K &= e_{CO}a_{CO}r a_{RC}e_{RC}K - e_{CO}a_{CO}r m_C \\
m_O a_{RC} &= e_{CO}a_{CO}r - \frac{e_{CO}a_{CO}r m_C}{a_{RC}e_{RC}K} \\
\frac{m_O a_{RC}}{e_{RO}a_{RO}} &= r - \frac{r m_C}{a_{RC}e_{RC}K} \\
\Rightarrow \quad & r - \frac{r m_C}{a_{RC}e_{RC}K} - \frac{m_O a_{RC}}{e_{RO}a_{RO}} \geq 0
\end{aligned}
$$

$$
\text{Invasion promoted by } \begin{cases} \text{Higher productivity } (K) \\ \text{Higher conversion efficiencies } (e_{RC} \text{ and } e_{RO}) \\ \text{Lower mortality rates } (m_C \text{ and } m_O) \end{cases}
$$

Note that conversion efficiencies and mortality rates contribute to *'ecosystem efficiency'*
Effects of r and a_{RC} depend on mortality rates.

4b At what K can O invade?
Solve $C^*_O - C^*_{eq} = 0$ for K

$$
\begin{aligned}
m_O a_{RC}^2 e_{RC} K &= e_{CO}a_{CO}r a_{RC}e_{RC}K - r m_C e_{CO}a_{CO} \\
K(m_O a_{RC}^2 e_{RC} - e_{CO}a_{CO}r a_{RC}e_{RC}) &= -r m_C e_{CO}a_{CO} \\
K \geq \frac{-r m_C e_{CO}a_{CO}}{(m_O a_{RC}^2 e_{RC} - e_{CO}a_{CO}r a_{RC}e_{RC})} &= \frac{r m_C e_{CO}a_{CO}}{(e_{CO}a_{CO}r a_{RC}e_{RC} - m_O a_{RC}^2 e_{RC})}
\end{aligned}
$$

Repeat with Mathematica

Intraguild predation

Contains exploitative competition, trophic chain *and* apparent competition module!

$$
\begin{aligned}
\frac{dO}{dt} &= e_{RO}a_{RO}RO + e_{CO}a_{CO}CO - m_o O \\
\frac{dC}{dt} &= e_{RC}a_{RC}RC - a_{CO}CO - m_c C \\
\frac{dR}{dt} &= rR\left(1 - \frac{R}{K}\right) - a_{RC}RC - a_{RO}RO
\end{aligned}
$$

Questions:

1. How many equilibria and what are they (*qualitatively*)?
2. What level of productivity (K_i) allows each consumer to invade (*symbolically*)?

....

1 2
Intuition from exploitative competition model:
Invasion thresholds in absence of other consumer:

$$
\begin{aligned}
\frac{1}{O}\frac{dO}{dt} = 0 \quad &\Rightarrow \quad R^*_O = \frac{m_O}{e_{RO}a_{RO}} \\
\frac{1}{C}\frac{dC}{dt} = 0 \quad &\Rightarrow \quad R^*_C = \frac{m_C}{e_{RC}a_{RC}}
\end{aligned}
$$

If K is low enough, R-only is stable. (i.e. if $K < \min(R^*_i)$)
Consumer with lower R^* invades first. 3 4

If both consumers are present:

$$\frac{1}{O}\frac{dO}{dt} = 0 \qquad \Rightarrow \qquad R_O^* = \frac{m_O \boxed{-a_{CO}e_{CO}C}}{e_{RO}a_{RO}}$$

$$\frac{1}{C}\frac{dC}{dt} = 0 \qquad \Rightarrow \qquad R_C^* = \frac{m_C \boxed{+a_{CO}O}}{e_{RC}a_{RC}}$$

Therefore, C can never invade RO-equilibrium *unless...*

$$\frac{m_C}{e_{RC}a_{RC}} << \frac{m_O}{e_{RO}a_{RO}}$$

...which means that either $m_C << m_O$ and/or $e_{RC}a_{RC} >> e_{RO}a_{RO}$.

Conclusion: Coexistence requires that IGprey is be superior competitor for shared resource.
Otherwise RO-system occurs.

5
When can O invade stable RC-system?
RC-system at equilibrium (exactly as for trophic chain):

$$R_{eq}^* = \frac{m_C}{a_{RC}e_{RC}} \qquad\qquad C_{eq}^* = \frac{r(a_{RC}e_{RC}K - m_C)}{a_{RC}^2 e_{RC}K}$$

Invasion threshold

$$\frac{1}{O}\frac{dO}{dt} = 0 \qquad \Rightarrow \qquad C_O^* = ... \textbf{\textit{Mathematica}}$$

Solve $C_O^* - C_{eq}^* = 0$ for K...

$$K \geq \frac{a_{CO}e_{CO}m_C r}{a_{RC}(a_{RO}e_{RO}m_C - a_{RC}e_{RC}m_O + a_{CO}e_{CO}e_{RC}r)}$$

Show in Mathematica

6
When does C go extinct at high K?
Solve $C_{eq}^* = 0$ from RCO-equilibrium for K:

$$K \geq \frac{a_{CO}\overbrace{\quad\quad\;\;\,}m_O r}{\underbrace{a_{RO}}(a_{RO}e_{RO}m_C - a_{RC}e_{RC}m_O + a_{CO}e_{CO}\underbrace{\quad\quad\;\;}r)}$$

compare to solution in 5

Temporal niche partitioning

Conclusion from exploitative competition model: $n \geq 2$ consumers cannot coexist on 1 resource.
But, among assumptions of this model was that interactions were linear.

Add Type II functional response to one of the two consumers.

$$\frac{dO}{dt} = e_{RO}\frac{a_{RO}RO}{1 + a_{RO}h_{RO}R} - m_o O$$

$$\frac{dC}{dt} = e_{RC}a_{RC}RC - m_c C$$

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - a_{RC}RC - \frac{a_{RO}RO}{1 + a_{RO}h_{RO}R}RO$$

$\Rightarrow$ Mathematica Handling time induces a lag, which induces cycles.
Cycles of RO system induces cycles in C
C utilize resource when O is at low abundance and R is high.
Armstrong & McGehee 1980 also showed that $n \geq 4$ consumers can coexist on 4 resources.
