

## Lecture 15 – Network modules (3-spp.)

### Today:

- Competition for explicit resources
- Trophic chain
- Intraguild predation

### Concepts:

- Competitive exclusion principle
- Bottom-up and top-down effects
- Temporal niche partitioning (Armstrong-McGehee effects)

### Method:

- Graphical analysis
  - Invasibility analysis
- 

### Recall:

2-spp. LV competition with implicit resource

⇒ Intra > Inter-specific competition for coexistence

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

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

⇒ More zero off-diagonals (lower connectance), the more likely  $\text{Det}(A) > 0 \Rightarrow$  more stable.

### Exploitative Competition for Explicit Resource

Start with 2 consumer 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? (⇒ What are they symbolically?)
2. When can each species invade? (⇒ When are equilibria stable?)

In other words: **How can two consumers coexist 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 20-30 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:  $\frac{1}{N} \frac{dN}{dt} > 0$

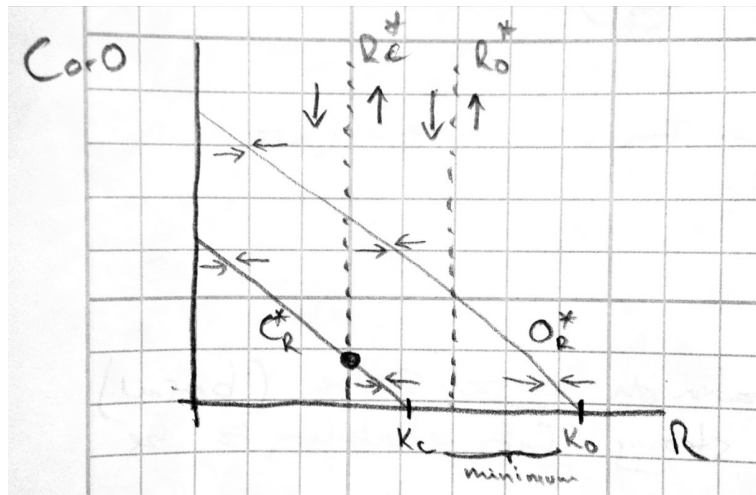
Predator isoclines: (Not really *isoclines*, but rather *isoplanes*.)

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

Prey isocline(s):

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

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* (i.e. one or the other) 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

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

Intuition from previous (exploitative competition) model:

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

Empirically, ~90% of energy is lost at each trophic transfer.

### Questions:

1. How many equilibria and what are they (*qualitatively*)?
2. What level of productivity ( $K$ ) is needed for each consumer to invade (*symbolically*)?

.....  
① Trivial equilibrium  $\Rightarrow R_{eq}^* = C_{eq}^* = O_{eq}^* = 0$

② Resource-only  $\Rightarrow R_{eq}^* = K$

③ When can  $C$  invade  $R$ -only system?

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

Consumer isocline:

$$\frac{1}{C} \frac{dC}{dt} = e_{RC}a_{RC}R - \cancel{a_{CO}CO}^0 - m_C = 0 \quad \Rightarrow \quad R_C^* = \frac{m_C}{e_{RC}a_{RC}}$$

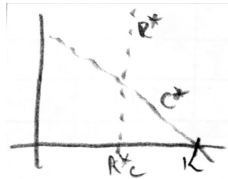
Resource isocline:

$$\frac{1}{R} \frac{dR}{dt} = r - \frac{rR}{K} - a_{RC}C = 0 \quad \Rightarrow \quad C_R^* = \frac{r - \frac{r}{K}R}{a_{RC}} = \frac{r}{a_{RC}} - \frac{r}{Ka_{RC}}R$$

Conclusion:

$C$  can invade when  $K > R_C^*$ .

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:

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

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

Invasion threshold  $C_O^*$ :

$$\frac{1}{O} \frac{dO}{dt} = 0 \quad \Rightarrow \quad C_O^* = \frac{m_O}{e_{CO}a_{CO}}$$

When does invasion threshold equal equilibrium (ie.  $C_O^* = C_{eq}^*$ )?

$$C^* = \frac{m_O}{e_{CO}a_{CO}} = \frac{r(a_{RC}e_{RC}K - m_C)}{a_{RC}^2e_{RC}K}$$

$$m_Oa_{RC}^2e_{RC}K = e_{CO}a_{CO}ra_{RC}e_{RC}K - e_{CO}a_{CO}rm_C$$

$$m_Oa_{RC} = e_{CO}a_{CO}r - \frac{e_{CO}a_{CO}rm_C}{a_{RC}e_{RC}K}$$

$$\frac{m_Oa_{RC}}{e_{RO}a_{RO}} = r - \frac{rm_C}{a_{RC}e_{RC}K}$$

$$\Rightarrow r - \frac{rm_C}{a_{RC}e_{RC}K} - \frac{m_Oa_{RC}}{e_{RO}a_{RO}} \geq 0$$

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  $K$

$$m_Oa_{RC}^2e_{RC}K = e_{CO}a_{CO}ra_{RC}e_{RC}K - rm_Ce_{CO}a_{CO}$$

$$K(m_Oa_{RC}^2e_{RC} - e_{CO}a_{CO}ra_{RC}e_{RC}) = -rm_Ce_{CO}a_{CO}$$

$$K \geq \frac{-rm_Ce_{CO}a_{CO}}{(m_Oa_{RC}^2e_{RC} - e_{CO}a_{CO}ra_{RC}e_{RC})} = \frac{rm_Ce_{CO}a_{CO}}{(e_{CO}a_{CO}ra_{RC}e_{RC} - m_Oa_{RC}^2e_{RC})}$$

Repeat with Mathematica

### Intraguild predation

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

$$\frac{dO}{dt} = e_{RO}a_{RO}RO + e_{CO}a_{CO}CO - m_OO$$

$$\frac{dC}{dt} = e_{RC}a_{RC}RC - a_{CO}CO - m_CC$$

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

Questions:

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

①②

Intuition from exploitative competition model:

Invasion thresholds in absence of other consumer:

$$\frac{1}{O} \frac{dO}{dt} = 0 \quad \Rightarrow \quad R_O^* = \frac{m_O}{e_{RO}a_{RO}}$$

$$\frac{1}{C} \frac{dC}{dt} = 0 \quad \Rightarrow \quad R_C^* = \frac{m_C}{e_{RC}a_{RC}}$$

If  $K$  is low enough,  $R$ -only is stable. (i.e. if  $K < \min(R_i^*)$ )

Consumer with lower  $R^*$  invades first. ③④

If both consumers are present:

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

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):

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

Invasion threshold

$$\frac{1}{O} \frac{dO}{dt} = 0 \Rightarrow C_O^* = \dots \text{Mathematica}$$

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  $K$ :

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

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.

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

$\Rightarrow$  Mathematica Handling time induces positive density-dependence in prey, 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.