

## Lecture 10 – Two-species competition

**Today:** Graphical analysis of two-species competition.

**Next:** 2-D stability analysis

**Concepts for the road ahead:**

Coexistence, Invasibility, Priority effects, Alternative Stable States

Phase diagrams & Zero Net Growth Isoclines (ZNGI's)

### Two-species competition

Motivate with Crombie (1946) flour beetle experiments. 2 slides.

Extend 1 sp. logistic to 2 spp.

$$\frac{dN_1}{dt} = r_1 N_1 \left( 1 - \frac{N_1}{K_1} - \alpha_{12} \frac{N_2}{K_1} \right) \quad \frac{dN_2}{dt} = r_2 N_2 \left( 1 - \frac{N_2}{K_2} - \alpha_{21} \frac{N_1}{K_2} \right)$$

Or in slightly different general form:

$$\frac{dN_i}{dt} = r_i N_i \left( 1 - \frac{N_i}{K_i} - \alpha_{ij} \frac{N_j}{K_i} \right) \quad \text{for } i \neq j.$$

Contrast *intra*-specific density-dependence (self-limitation) vs. *inter*-specific competition

$\alpha_{ij}$  - effect of 1 average  $j$  individual on 1 average  $i$  individual relative to effect that  $i$  has on self.

= per capita effect

'How much of  $K_i$  does each  $j$  individual use?'

e.g., if 10  $j$  individuals consume equivalent to 1  $i$  individual, then  $\alpha_{ij} = \frac{1}{10}$ .

This is a model of **exploitation** with *implicit* resources.

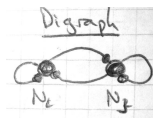
**Implicit** - Resource dynamics are *not* modeled

- Phenomenological model depiction of resources

- e.g.,  $K$  - 'carrying capacity'

That is:

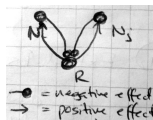
$$\frac{dN_i}{dt} = f_i(N_i, N_j)$$



**Explicit** - Resource dynamics *are* modeled

e.g. Consumer-resource models ( next class )

$$\frac{dN_i}{dt} = f_i(N_i, R) \quad \frac{dR}{dt} = f_R(N_i, N_j, R)$$



**Exploitation** - Indirect negative interaction through joint use of shared *limiting* resource(s).

**Interference** - Direct negative interaction preventing use of resource(s).

### Today's Q:

When can two species coexist on the same shared resource(s)?

When can Sp. 1 invade a community consisting of Sp. 2?

⇒ How many equilibria are there?

⇒ Are equilibria stable or unstable?

Hand out and work through quiz as group: (a)

$$\frac{dN_i}{dt} = r_i N_i \left( 1 - \frac{N_i}{K_i} - \alpha_{ij} \frac{N_j}{K_i} \right)$$

Qualitatively...

$$(N_i^*, N_j^*) = \begin{cases} 0, & 0 \\ N_i^* > 0, & 0 \\ 0, & N_j^* > 0 \\ N_i^* > 0, & N_j^* > 0 \end{cases}$$

(b)

When  $N_j = 0 \Rightarrow$  reduces to 1 sp. logistic:

$$\begin{aligned} \frac{dN_i}{dt} &= r_i N_i \left( 1 - \frac{N_i}{K_i} \right) \\ N_i^* &= K_i \end{aligned}$$

(c)

Replace  $i$  for  $j$ ,  $\Rightarrow N_j^* = K_j$  in absence of  $i$ .

(d)

Want  $N_i^* > 0$  &  $N_j^* > 0$

A: Solve for one as function of the other:

$$\begin{aligned} r_i N_i - \frac{r_i N_i N_i}{K_i} - \frac{r_i \alpha_{ij} N_i N_j}{K_i} &= 0 \\ r_i N_i K_i &= r_i N_i N_i + r_i \alpha_{ij} N_i N_j \quad (\text{move and multiply by } K_i) \\ K_i &= N_i + \alpha_{ij} N_j \quad (\text{divide by } r_i \text{ and } N_i) \\ N_i^* &= K_i - \alpha_{ij} N_j \quad \text{and similarly } N_j^* = K_j - \alpha_{ji} N_i \end{aligned}$$

or, rearranging differently

$$\begin{aligned} K_i - N_i^* &= \alpha_{ij} N_j \\ N_j &= \frac{K_i - N_i^*}{\alpha_{ij}} \quad \text{and } N_i = \frac{K_j - N_j^*}{\alpha_{ji}} \end{aligned}$$

Note intuitive meaning of  $\alpha_{ij}$ !

Note also that we can't solve for one species without knowing the other.

$\Rightarrow$  need to solve for  $N_i^*$  and  $N_j^*$  jointly.

Plug solution to  $N_j^*$  into solution for  $N_i^*$  and vice versa.

Solution:

$$N_i^* = \frac{K_j \alpha_{ij} - K_i}{\alpha_{ij} \alpha_{ji} - 1} = \frac{K_i - K_j \alpha_{ij}}{1 - \alpha_{ij} \alpha_{ji}}$$

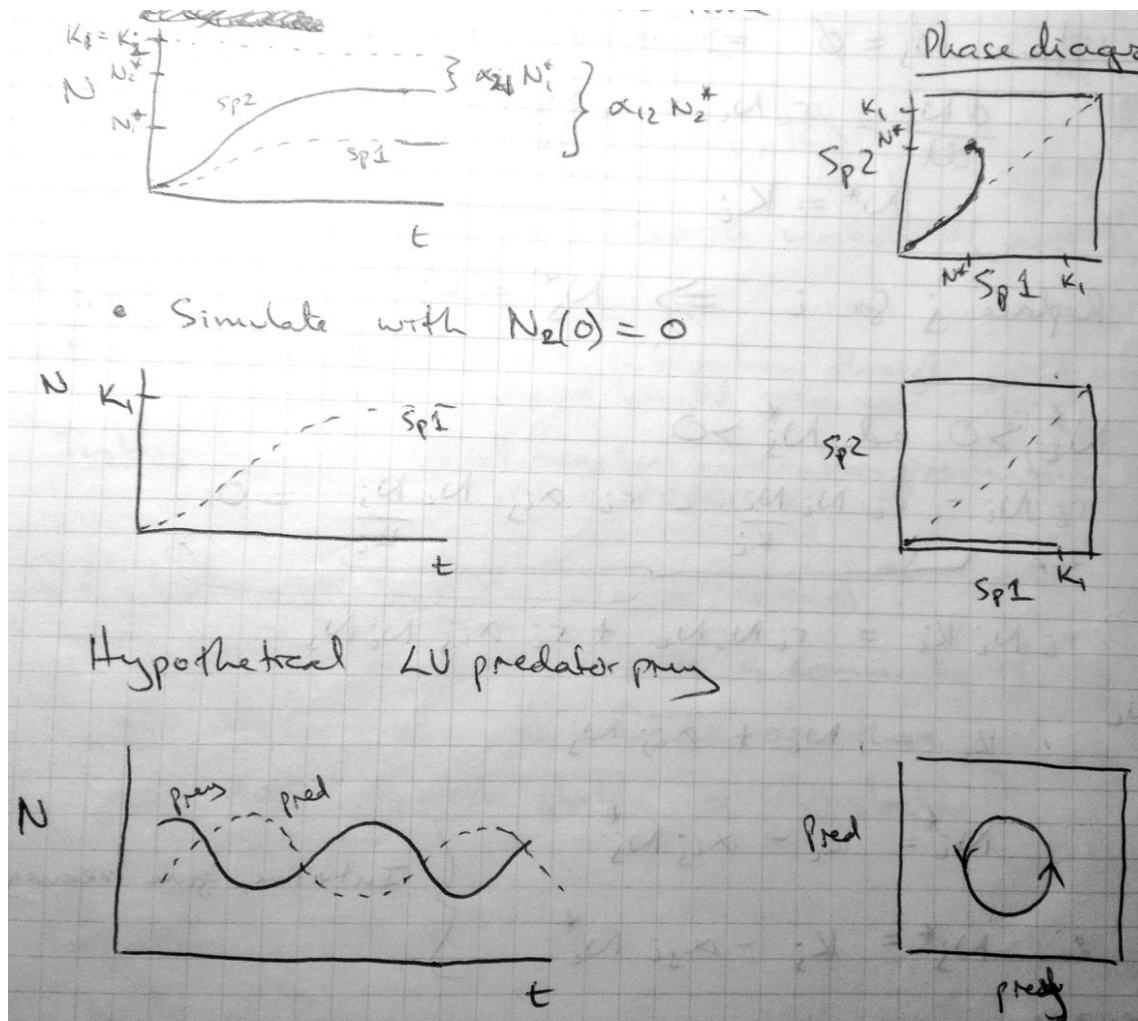
...where 2nd equation is as given in Case. Multiply top and bottom by  $-1$ .

## Phase portraits/diagrams

### R-code demonstration

Work through ode-solver code

Simulate coexistence over time



Return to main questions:

- When can both spp. coexist?
- When can sp 1 out-compete sp 2?
- When can sp 1 invade sp 2?

## Naive simulations

R-demonstration - Walk through first set of parameter values. "Naive simulations"

Then show full table before showing results with R code for other parameters.

With  $r_1 = r_2 = K_1 = K_2 = 1$  and  $N_1(0) = N_2(0) = 0.01$

$\alpha_{21}$	$\alpha_{12}$	Outcome	
0.5	0.7	coexist	
1.5	0.5	sp1	
0.5	1.5	sp2	$N_1(0) = N_2(0)$
1.5	1.7	sp2	
1.5	1.7	sp1	$N_1(0) > N_2(0)$

⇒ Priority effect

⇒ Alternative stable states

## Graphical Analysis

Earlier we showed that from  $\frac{dN_i}{dt} = 0$  that:

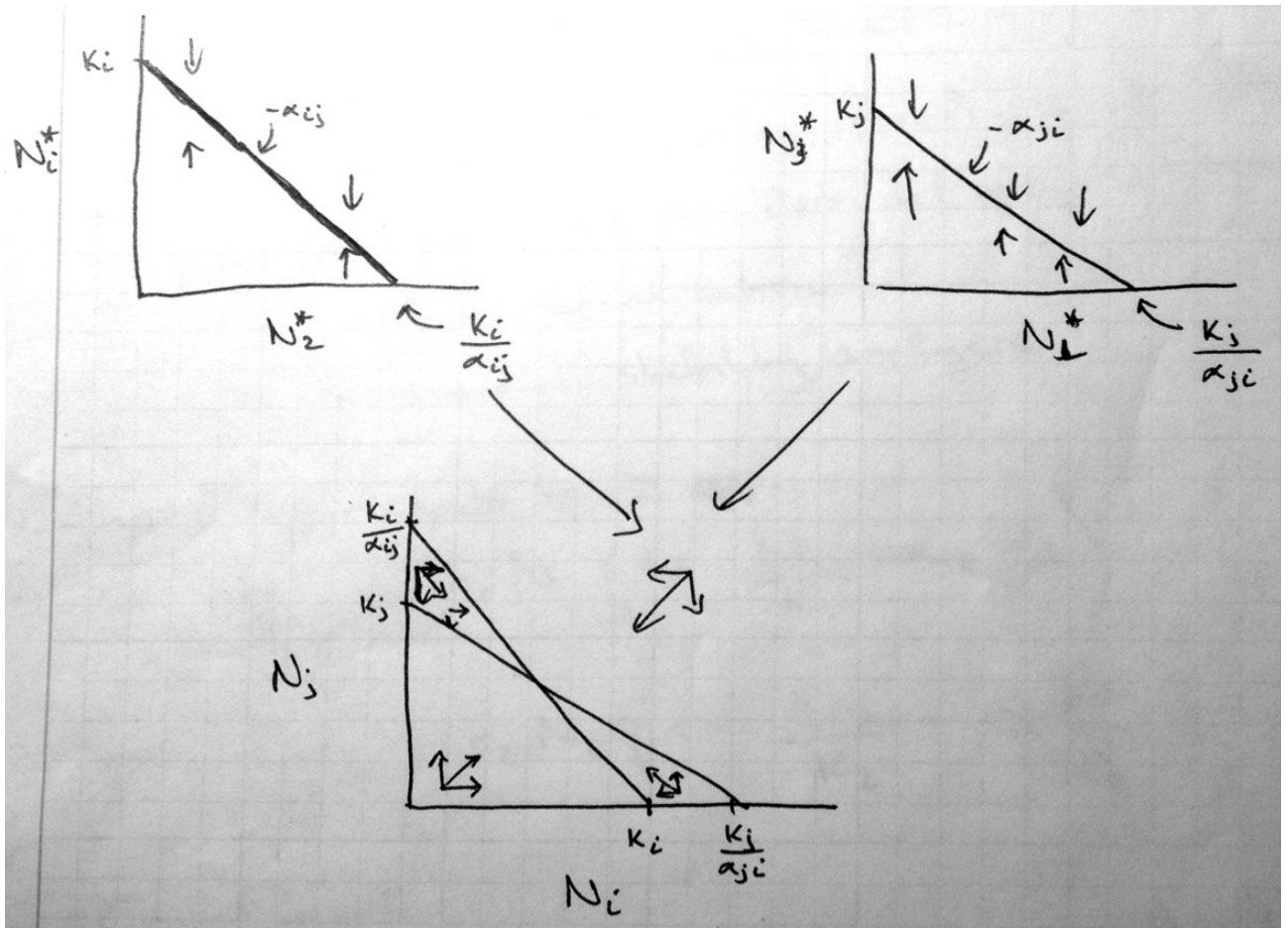
$$N_i^* = K_i - \alpha_{ij}N_j$$

$$\Rightarrow N_j = \frac{K_i - N_i^*}{\alpha_{ij}}$$

Thus isocline intersects x-axis at

$$N_j = \frac{K_i - 0}{\alpha_{ij}} = \frac{K_i}{\alpha_{ij}}$$

Same goes for 2nd species.



R-code: Work through other parameter values

## Inferences/Conclusions:

Coexistence:	intra > inter for both species (i.e. $\frac{K_i}{\alpha_{ii}} = \frac{K_i}{1} < \frac{K_j}{\alpha_{ji}} \Rightarrow \alpha_{ii} > \alpha_{ji}$ )
Sp <i>i</i> dominance:	intra > inter for <i>i</i> & intra < inter for <i>j</i>
Priority effect:	intra < inter for both (i.e. $\frac{K_i}{\alpha_{ii}} = \frac{K_i}{1} > \frac{K_j}{\alpha_{ji}} \Rightarrow \alpha_{ii} < \alpha_{ji}$ )