Lecture 10 – Two-species competition

Outline:

Do everything we did by hand last class in Mathematica.
The move on to Graphical analysis of two-species competition.

Concepts for the road ahead:

Coexistence, Invasibility, Priority effects, Alternative Stable States
Phase diagrams & Zero Net Growth Isoclines (ZNGI's)
2-D stability analysis

Intro to Mathematica - Local stability analysis of continuous logistic

Walk through Mathematica code: *'Class9-Stability-cLogistic.nb'*

Functions use square brackets [ ].
Important functions:

Solve[y=ax,x]
D[f(x),x]
Simplify
$func\ /.\ x \rightarrow y$
$var\ /.\ x$

Non-dimensionalization - 1 sp. logistic

The equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

] has 1 variable and 2 parameters (+1 that's implicit!).

$N : \#$ $\quad\quad r : \frac{\#}{\# time}$ $\quad\quad K : \#$

Define x to be the population size relative to the carrying capacity (i.e. fraction of the carrying capacity).:

$$x := \frac{N}{K}$$

x is dimensionless!

(Note: The symbol := means *define*. Sometimes the symbol $\equiv$ meaning *equivalent* is also used.)

Rearrange to $N = xK$ and substitute:

$$\frac{dxK}{dt} = rxK\left(1 - \frac{xK}{K}\right)$$
$$\frac{dx}{dt} = rx\,(1 - x)$$

Only 1 variable (x)and 1 parameter (r), same dynamical properties.
Can reduce further...

$$\tau := rt$$

(τ = 'tau') - dimensionless - the units of r are #'s per # per time ($= 1/t$).
That is,

$$\frac{d}{dt} = \frac{d}{d\tau} \cdot \frac{d\tau}{dt}$$

Rewriting $r = \tau/t = d\tau/dt$, this simplifies to

$$\frac{d}{dt} = \frac{d}{d\tau} r$$

Therefore

$$\frac{dx}{dt} = rx\,(1-x)$$
$$\frac{drx}{d\tau} = rx\,(1-x)$$
$$\frac{dx}{d\tau} = x\,(1-x)$$

Only 1 variable and 0 parameters!!!
Of course, 'time-scale' τ is tricky to conceptualize.
→ scaled realized rate of population dynamics (i.e. dN/dt or dx/dt)...
...relative to the maximum growth rate of the population (r).

Model is thus in terms of the realized growth relative to the maximum intrinsic growth.

Won't do all that much more non-dimensionalization (except in 2-spp. competition model, next), but can be extremely useful. (e.g., when absolute values of parameters are not known, but their relative values is (or can be approximated, or qualitatively known > 1 or < 1).)

Two-species competition Motivate with Crombie (1946) flour beetle experiments. 2 slides.
Extend 1 sp. logistic to 2 spp.

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

Or in slightly different general form:

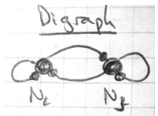
$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i} - \alpha_{ij}\frac{N_j}{K_i}\right) \qquad \text{for } i \neq j.$$

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

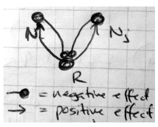
That is:

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



Explicit - Resource dynamics *are* modeled
e.g. Consumer-resource models (next class)

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



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:

$$\begin{aligned} r_i N_i - \frac{r_i N_i N_i}{K_i} - \frac{r_i \alpha_{ij} N_i N_j}{K_i} &= 0 \\ r_i N_i K_i &= r_i N_i N_i + r_i \alpha_{ij} N_i N_j \qquad \text{(move and multiply by } K_i\text{)} \\ K_i &= N_i + \alpha_{ij} N_j \qquad \text{(divide by } r_i \text{ and } N_i\text{)} \end{aligned}$$

$$N_i^* = K_i - \alpha_{ij} N_j \quad \text{ and similarly } N_j^* = K_j - \alpha_{ji} N_i$$

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 α_{ij}!

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

⇒ need to solve for N_i^* and N_j^* jointly.

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

Solution:

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

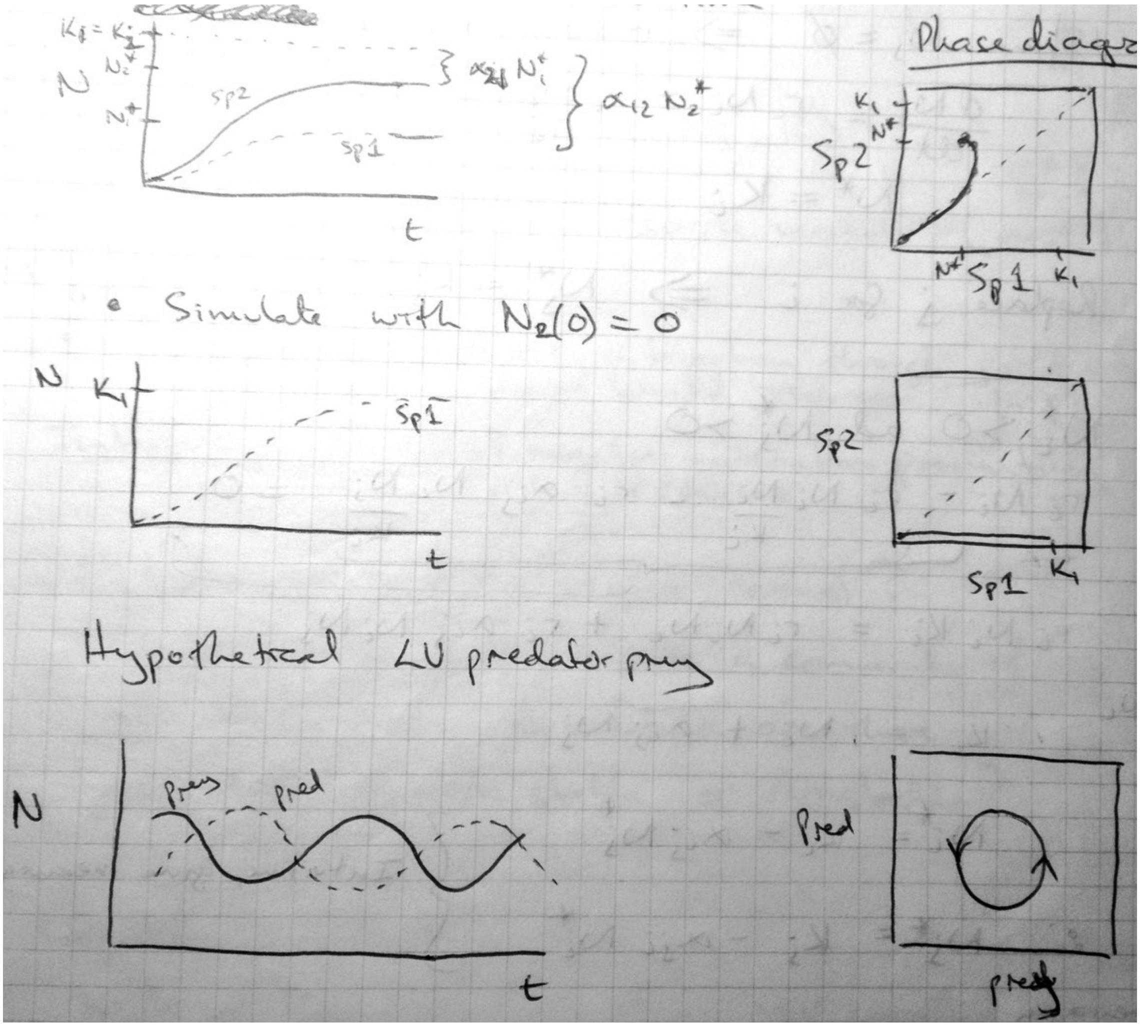
...where 2nd equation is as given in Case. Multiply top and bottom by -1.

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 $N_1(0) = N_2(0) = 0.01$

α_{21}	α_{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	$N_1(0) > N_2(0)$

$\Rightarrow$ Priority effect
$\Rightarrow$ Alternative stable states

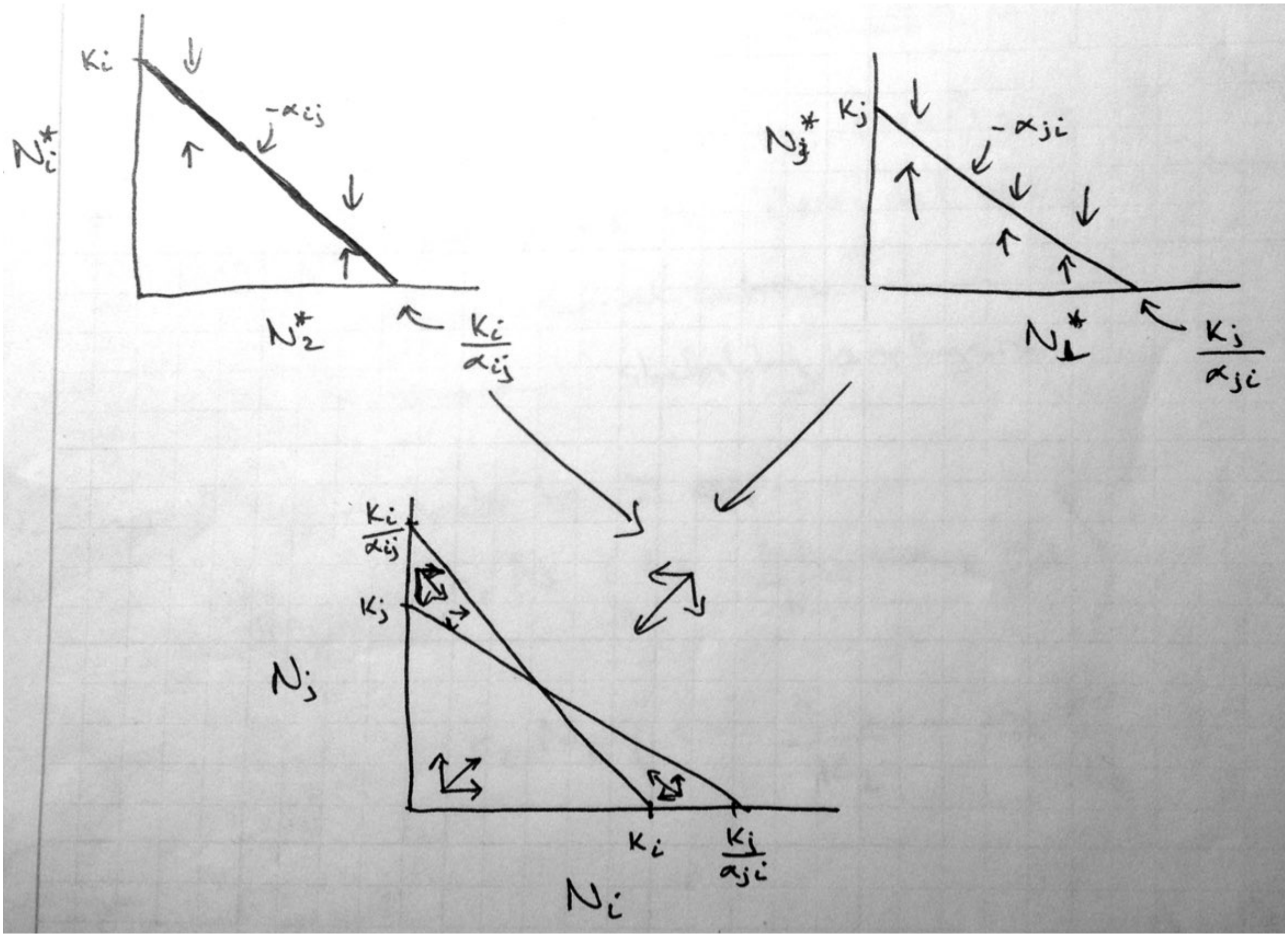
Graphical Analysis
Earlier we showed that from $\frac{dN_i}{dt} = 0$ that:

$$N_i^* = K_i - \alpha_{ij} N_j \quad \text{and} \quad N_j^* = K_j - \alpha_{ji} N_i$$
$$\Rightarrow N_j = \frac{K_j - N_i^*}{\alpha_{ij}}$$

Thus isocline interesects x-axis at

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

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