

## POPULUS Simulations of interspecific competition using the Lotka-Volterra model.

*Recall from Lecture:*

The logistic population growth equation is:

$$dN/dt = rN[(K-N)/K]$$

so that population growth slows as  $N \rightarrow K$  and *intraspecific* competition becomes more intense. Growth stops, due to intraspecific competition, when the population reaches carrying capacity.

(when  $N = K$ ,  $dN/dt = 0$ )

How do we modify the equation to take into account *interspecific* competition, as well as intraspecific competition? Suppose that we are dealing with an elk population, and that each elk competes with white-tailed deer for food, as well as competing with other elk. First, add a subscript 'e' to the variables that have to do with elk:

$$dN_e/dt = r_e N_e [(K_e - N_e)/K_e]$$

If an individual deer uses resources in exactly the same way as a elk, then the survival and reproduction of elk ( $dN_e/dt$ ) would be affected by deer numbers in the same way that it is affected by elk numbers. Can easily incorporate this simplified form of interspecific competition into the equation:

$$dN_e/dt = r_e N_e [(K_e - N_e - N_d)/K_e]$$

BUT, it's unlikely that a deer has exactly the same impact on resources as an elk does. Deer are much smaller, so they consume less food. Also, there is not complete overlap in the plant species they consume, so some of the resources used by deer have no impact on elk. When measuring the impact of interspecific competition on population growth, you must take into account differences between the competing species in:

1. **amount** of resources used by individuals of each species
2. **overlap** in the set of resources used by each species

To determine the effect of deer on elk, we basically need to convert deer numbers into 'elk equivalents'. We need to determine how many elk would have the same impact on resources (for other elk) that one deer has. In the equation, this is taken into account by multiplying the number of deer by a **competition coefficient**,  $\alpha_{ed}$ . The competition coefficient ranges from 0 to 1 (usually). If it's zero, then deer have no effect on elk at all. If it's 1, then each individual deer has exactly the same effect on elk as an individual elk would. Values greater than 0 but less than 1 indicate that each deer affects elk via

competition, but not as strongly as another elk would. Values greater than one are possible but not common -- what does a value  $> 1$  imply?

$$dN_e/dt = r_e N_e [(K_e - N_e - \alpha_{ed} N_d)/K_e]$$

Following the same logic used for elk, the equation for deer population growth is:

$$dN_d/dt = r_d N_d [(K_d - N_d - \alpha_{de} N_e)/K_d]$$

This pair of equations describe population growth for two species that are affected by both intraspecific and interspecific competition.

These are the *Lotka-Volterra equations*.

### ***POPULUS SIMULATIONS: EFFECTS OF INTERSPECIFIC COMPETITION ON POPULATION GROWTH.***

#### ***Getting Started:***

1. Use the instructions and links on the 'Populus software' link to download Populus onto your computer, if you have not already done so. Double click the Populus icon or shortcut to start the program.
2. Select "Multi-Species Interactions" from the Model tab on the menu.
3. Select "Lotka-Volterra Competition" from the pop-up menu.
4. Clicking the help icon (light bulb) will pop up a pdf file with a section on Lotka-Volterra competition.

### ***Variables you control:***

In the Lotka-Volterra competition equations, there are 4 variables controlling the population growth rate ( $dN/dt$ ):

1.  $N$  - the current size of the population. In *Populus*, this is labelled  $N_0$ , the population size at some arbitrary time zero.
2.  $r$  - the intrinsic rate of increase ( $r_{max}$  = per capita birth rate - per capita death rate under optimal conditions)
3.  $K$  - environmental carrying capacity (which reflects the strength of *intraspecific* competition)
4.  $\alpha$  and  $\beta$  – competition coefficients.  $\alpha$  is the effect on species 1 of species 2 ( $\alpha_{12}$ ).  $\beta$  = effect on species 2 of species 1 ( $\alpha_{21}$ ). These reflect the strength of *interspecific* competition.

The input panel allows you to change each of these variables, for each of the two competing species.

When you run the simulation "To steady state", it will run until population size is no longer changing for either species. Steady state means  $dN/dt = 0$  for both species. This can occur with competitive coexistence (both species persist), or competitive exclusion (one species is driven extinct). Where in the  $N_2$  vs  $N_1$  phase-plane plot are these outcomes located?

### **The goal of this exercise is to understand:**

- 1. How differences between the two species in each of these 4 variables affects the outcome of competition, and**
- 2. How the 4 variables affect the trajectory through which  $N_1$  and  $N_2$  change to reach that outcome.**

### ***Displays:***

For each run of the simulation, there are two output displays. Look at both displays for each simulation run, and **understand how they relate to each other.**

***From the input panel, run the simulation with the default settings and look at the displays as you read the following explanation.***

"N vs T" plots population size for each species against time.

" $N_2$  vs  $N_1$ " plots population size for species 2 against population size for species 1 (this is called a phase-plane). On the  $N_2$  vs  $N_1$ , there are three lines:

- a trajectory that shows how the numbers of the two species change through time (green),

- the zero-isocline for species 1 (red)
- the zero-isocline for species 2 (blue)

Remember that zero-isoclines show where population growth is zero. An isocline is a line that connects points with equal growth rates ( $dN/dt$ ): a zero-isocline connects points with  $dN/dt = 0$ . On one side of the isocline, the population grows; on the other side, it shrinks. With a plot of  $N_2$  vs  $N_1$ :

- For species 1, population growth is positive LEFT of the (red) isocline, and negative RIGHT the isocline. The red isocline refers to the X axis, and gives information about changes in  $N_1$ .
- For species 2, population growth is positive in areas BELOW the (blue) isocline, and negative in areas ABOVE the isocline. The blue isocline refers to the Y axis, and gives information about changes in  $N_2$ .
- For either species, the arrows are parallel to the axis that plots the numbers of that species.

### ***Stability Analysis:***

This is very useful for testing how well you understand the Lotka-Volterra competition model!

Select the  $N_2$  vs  $N_1$  “phase-plane” plot. Rather than running to steady state, run until time 1, then time 2, 3, etc, seeing if the trajectory follows the path you predicted ahead of time. Two valuable ways of going about this are:

- Leave everything else the same but change the initial population sizes. See if you can predict the trajectory correctly?
- Change one variable ( $r$ ,  $K$ ,  $\alpha$ ,  $\beta$ ) and see how the trajectory changes.

***SIMULATIONS:***

The default values for variables are:

|                 | Species 1 | Species 2 |
|-----------------|-----------|-----------|
| $N_0$           | 10        | 20        |
| $r$             | 0.9       | 0.5       |
| $K$             | 500       | 700       |
| $\alpha, \beta$ | 0.6       | 0.7       |

***Effect of initial population size (N1 and N2).***

1. Accept the default values for all variables (if you've changed values, the defaults are given above so you can reset them).
2. Run the simulation and examine both output displays. In the N2 vs N1 display, select different pairs of initial population sizes, and understand the trajectory of changes in population sizes through time from that starting point.

Use this approach to check outcomes from a wide range of initial population sizes.

3. Now set the input values to:

|                 | Species 1 | Species 2 |
|-----------------|-----------|-----------|
| $N_0$           | 10        | 10        |
| $r$             | 0.5       | 0.5       |
| $K$             | 700       | 700       |
| $\alpha, \beta$ | 0.7       | 0.7       |

4. Explore the effects of different initial population sizes for this set of conditions, using the same approach as before.
5. **How do the initial population sizes for species 1 and species 2 affect the outcome of competition?**

**B. Effect of intrinsic rate of increase ( $r$ ):**

1. Set the input values to:

|                 | Species 1 | Species 2 |
|-----------------|-----------|-----------|
| $N_0$           | 100       | 100       |
| $r$             | 0.5       | 0.5       |
| $K$             | 700       | 700       |
| $\alpha, \beta$ | 0.7       | 0.7       |

2. Run the simulation and examine the outcome. In particular, note the shape of the trajectory in the  $N_2$  vs  $N_1$  plot (equivalently, note the shapes of the two population growth curves vs time in the other plot... understand how the two plots relate).
3. Run the simulation several times, varying the intrinsic rate of increase ( $r$ ) for species 1 (be sure to include 0 and 1) and leaving everything else constant. Notice that the competition is symmetric, with only  $r$  differing between the species. The carrying capacities and competition coefficients are the same for each species...so competition itself is symmetrical in its effects on the two.
4. Restore the input values from step 1. Now re-run the simulation several times, varying the intrinsic rate of increase for species 2 (be sure to include 0 and 1)
5. **How does variation in the intrinsic rate of increase affect the outcome of competition? How does it affect the trajectory of population sizes?**

**C. Effects of competition coefficients ( $\alpha$  &  $\beta$ ) and carrying capacities ( $K$ ):**

1. Set the input values to:

|                 | Species 1 | Species 2 |
|-----------------|-----------|-----------|
| $N_0$           | 100       | 100       |
| $r$             | 0.5       | 0.7       |
| $K$             | 500       | 300       |
| $\alpha, \beta$ | 0.7       | 0.9       |

2. Run the simulation and inspect the outcome.
3. Rerun the simulation, decreasing the carrying capacity ( $K$ ) for species 1 by 100 each time (500, 400, 300, 200 & 100), and noting the outcome. Leave everything else constant.

**What effect does  $K$  have on the outcome of competition (all else equal)?**

4. Set the inputs to values in shown in below:

|                 | Species 1 | Species 2 |
|-----------------|-----------|-----------|
| $N_0$           | 100       | 100       |
| $r$             | 0.5       | 0.5       |
| $K$             | 500       | 500       |
| $\alpha, \beta$ | 0.5       | 0.5       |

5. Rerun the simulation, increasing the competition coefficient for the effect on species 2 of species 1 ( $\beta$ ) by 0.1 each time, and noting the changes. Run  $\beta$  values from 0.5 to 1.0. Leave everything else constant.
6. Now run  $\beta = 1.1$ . What does a competition coefficient greater than one mean?
8. Now set  $\beta = 1.0$ , and change the carrying capacity ( $K$ ) for species 1 to 600. How does this result compare with the previous one?

**What effect do  $\alpha$  and  $\beta$  have on the outcome of competition (all else equal)?  
How do competition coefficients interact with carrying capacities?**