General competition

Key concepts

- Interspecific competition
- Relative strength of inter- vs. intraspecific competition
- Phase-plane analysis and zero net growth isoclines (ZNGIs)
- Stable and unstable co-existence equilibrium
- Alternative stable states

A recent invasion of shore crabs

The green crab (*Carcinus maenas*) arrived in the US from Europe around 1850 due to increasing shipping traffic, and spread rapidly along the east coast to become a dominant crab species, feeding on abundant mussel populations. In the late 1980s, the shore crab (*Hemigrapsus sanguineus*) also arrived on the east coast of the US for the first time, and is in direct competition with the green crab for mussels. The shore crab appears to be successfully invading in spite of the presence of an established competitor, often reaching very high population densities compared to the green crab. Ecological rules describing competition between two species can help us understand how this scenario emerges, and what the long-term fate of each population is likely to be.

Figure 1: Shore crab (*Hemigrapsus sanguineus*).

Figure 2: Green crab (*Carcinus maenas*).

Lotka-Volterra competition

In the chapter on density-dependent population growth, we have already been introduced to the idea that individuals can regulate the rate of growth and carrying capacity of the population by competing with other individuals for a shared resource. In particular, we represented this idea with the following differential equation:

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

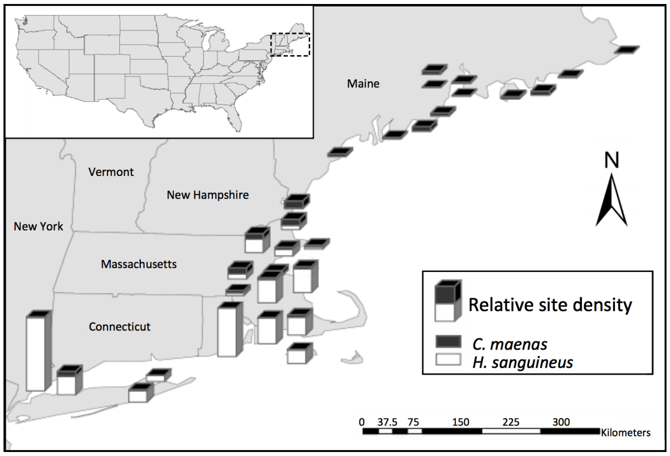

Figure 3: Density of *Carcinus maenas* and *Hemigrapsus sanguineus* at 30 sites throughout their invaded ranges. Heights of bars indicate relative mean values, n=16 values per site, Griffin and Delaney, 2007.

So, when N is far below the carrying capacity (K), then $K - N \approx K$ and the differential equation approximates exponential growth ($dN/dt \approx rN$). However, as N increases to a value close to K, then $K - N \approx 0$ and the differential equation approximates an equilibrium ($dN/dt \approx 0$) so the population stops growing.

We can extend this concept to competition between two species, N_1 and N_2, with a set of two, linked differential equations:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right) \tag{2}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \alpha_{21} N_1}{K_2} \right) \tag{3}$$

These equations describe generalized competition between two species, and are known as the Lotka-Volterra competition equations, named for the two mathematicians that developed the theory. In contrast to explicit resource competition (including R*-theory), the nature of the competition (resources or aggressive interactions) is implicit, because we only track population sizes of the two competitors and their effect on each other, and we don't define the biological details of the competition. In this way, it is a generalized form of competition. Note that each population has its own intrinsic growth rate (r_1, r_2) and carrying capacity (K_1, K_2).

Strength of competition

We see from equations 3 that population N_1 is negatively impacted by itself (intraspecific competition) and by population N_2 (interspecific competition), because in the parentheses the N_1 and N_2 terms are negative, meaning if either N_1 or N_2 becomes large, this acts to reduce the population growth rate of N_1 (the same principle applies to the second equation).

The reason we include the α parameters, is to provide some flexibility about how we describe interspecific competition relative to intraspecific competition. If the α parameters were absent, we would be stating that the addition of an N_1 **or** an N_2 individual to the community has the same effect on the population growth rate of the focal species, N_1, say. But this doesn't account for the fact that, on average, an individual of one species may be more aggressive or a more efficient predator.

The α parameters allow us to differentiate the competitive effects of each species on N_1 and N_2 and are known as relative-strength-of-competition parameters. The subscript indices of equations 3 are read backwards, so α_{12} is the relative effect of an individual of species 2 on species 1 (relative to the effect of an individual of species 1 on itself). For example, if it took the presence of 10 individuals of species 2 to reduce the population growth rate of species 1 by some factor, but it only took 1 individual of species 1 to achieve the same effect, then the relative-strength-of-competition parameter would be $\alpha_{12} = 1/10$. In such cases where $\alpha < 1$, we conclude that interspecific competition is weak relative to intraspecific competition. If the opposite situation were observed (10 conspecifics had the same competitive effect as 1 heterospecific individual) then we would use $\alpha_{12} = 10$, and conclude the interspecific competition is strong relative to intraspecific competition.

Phase-plane analysis

We can consider the two population equations dN_1/dt and dN_2/dt graphically to better understand how competition will play out. First, if we separately consider each population at equilibrium ($dN_1/dt = 0$ and $dN_2/dt = 0$) we note that rather than getting a single value (like $N = K$ in the case of logistic growth of a single population) we instead get a line (a relationship between N_1 and N_2). For example, when we separately assume N_1 is at equilibrium ($dN_1/dt = 0$) we have:

$$0 = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha_{12} N_2}{K_1} \right) \tag{4}$$

We're not particularly interested in the special case where the whole community is extinct (i.e., $N_1 = 0$, $N_2 = 0$ is an equilibrium, but not one in which we can learn much about competition). Instead, we'll focus on the parentheses equating to 0:

$$0 = \left(\frac{K_1 - N_1 - \alpha_{12}N_2}{K_1}\right) \tag{5}$$

$$0 = K_1 - N_1 - \alpha_{12}N_2 \tag{6}$$

This is the equation of a straight line. We can make this clearer, by preparing to plot N_1 on the x-axis and N_2 on the y-axis. Our generic straight line has the form $y = mx + b$, and here our y is going to be N_2, so we have to rearrange our equation accordingly:

$$N_2 = \frac{K_1 - N_1}{\alpha_{12}} \tag{7}$$

This line (called a zero net growth isocline - or ZNGI) intercepts the x-axis at $N_1 = K_1$ (i.e., x-axis intercept is found by setting $N_2 = 0$). Similarly, it intercepts the y-axis at K_1/α_{12} (i.e., the y-axis intercept is found by setting $N_1 = 0$). The line is illustrated in Fig. 4 (blue line). Remember, this ZNGI line is derived by setting $dN_1/dt = 0$ so it tells us that on this line, the N_1 population doesn't change (it doesn't tell us anything about the N_2 population). The line divides the $N_1 - N_2$ plane into two halves. As the N_1 population is measured on the x-axis, we can ask, what happens to N_1 when it is to the left of the ZNGI and what happens when it is to the right of the ZNGI? To answer this, we can look again at the N_1 equation of the original Lotka-Volterra equations (equations 3). The sign of this equation is determined by the parentheses; if K_1 dominates, it will be positive and if $-N_1 - \alpha_{12}N_2$ dominates, it will be negative. The ZNGI is the knife-edge, where the expression is exactly 0. If N_1 increases, then the balance will shift from =0 to <0 because N_1 appears as a negative term in the parentheses. This means the N_1 population will decrease, because dN_1/dt changes from =0 to <0. We can indicate this with arrows (Fig. 4, blue left-pointing arrows). Similarly, if N_1 decreases (i.e., is to the left of the ZNGI), then dN_1/dt changes from =0 to >0 and N_1 will increase in size. Again, we can indicate this with lines and arrows (Fig. 4, blue right-pointing arrows).

The same logic, from sketching the N_2 ZNGI line to evaluating what happens when N_2 is away from the line, can be applied to the N_2 equation. Because N_2 is plotted on the y-axis, we refer to change in the up-down direction. Its ZNGI is illustrated in Fig. 4 (red line) with associated arrows showing predicted changes to N_2, when away from the ZNGI.

Because the Lotka-Volterra competition equations (3) are coupled (N_2 appears in the dN_1/dt equation and vice versa), we need to put the N_1 and N_2 ZNGIs in one phase-plane to understand how the populations are predicted to interact, and establish the outcome of competition.

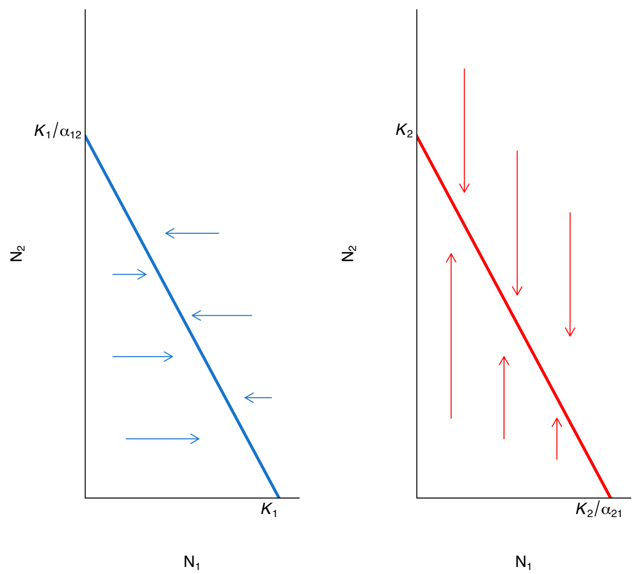

Figure 4: Phase-plane analysis for the Lotka-Volterra equations showing ZNGIs for N_1 (blue) and N_2 (red). The arrows illustrate how each population would move when away from the ZNGI.

Depending on the magnitude of K_1, K_2, α_{12}, and α_{21} there are four qualitatively different patterns to describe how the two populations will interact (Fig. 5, A-D).

We see in Fig. 5 panels A and B that the phase-plane is demarcated into 3 zones, and in panels C and D the phase-plane is demarcated into 4 zones. Any starting conditions (initial population sizes of N_1 and N_2) are defined by a point in the phase-plane. The black arrows are the resultant effects of combining the appropriate blue and red arrows in each zone, and describe how the populations N_1 and N_2 are predicted to change (move) in time.

A: N_1 excludes N_2

In Fig. 5, panel A, all starting conditions will eventually drift into the middle zone which points to bottom-right. The system of interacting N_1 and N_2 individuals will eventually reach a state where N_2 goes extinct and N_1 goes to its carrying capacity (K_1). The co-existence equilibrium is unstable.

B: N_2 excludes N_1

In Fig. 5, panel B, again all starting conditions will eventually drift into the middle zone which points to left. The system of interacting N_1 and N_2 individuals will eventually reach a state where N_1 goes extinct and N_2 goes to its carrying capacity (K_2). The co-existence

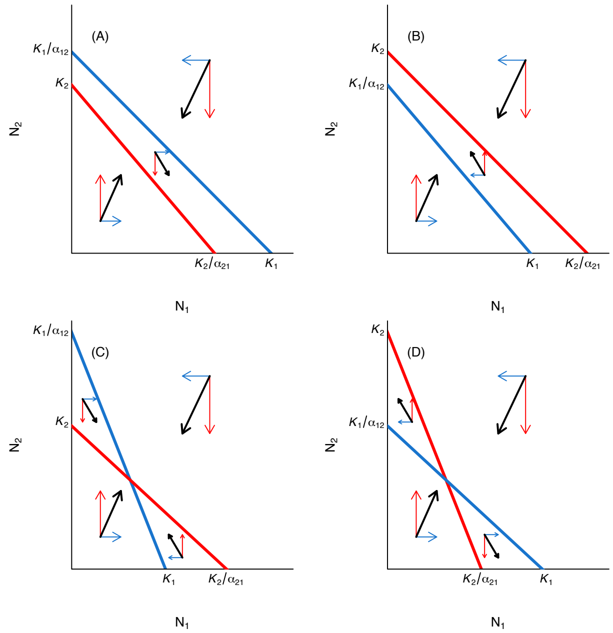

Figure 5: Four qualitatively different outcomes predicted by the Lotka-Volterra competition equations. In each panel, the blue line is the N_1 ZNGI and the red line is the N_2 ZNGI. The blue and red arrows indicate predicted population changes in the N_1 and N_2 directions, and the black arrows indicate the resultant change when the populations interact. A: N_1 excludes N_2 and grows to its carrying capacity, K_1; B: N_2 excludes N_1 and grows to its carrying capacity, K_2; C: Both species co-exist but at lower carrying capacities than they would attain by themselves; D: One population will go extinct and the other will go to its carrying capacity. The winner is determined by a combination of starting conditions and ZNGI orientations.

equilibrium is unstable.

C: Stable co-existence

In Fig. 5, panel C, the resultant black arrows all point towards the central area where the red and blue ZNGI lines cross. This crossing point is an equilibrium point since it satisfies the ZNGI conditions for both N_1 and N_2 (i.e., $dN_1/dt = 0$ and $dN_2/dt = 0$). In this case, the co-existence equilibrium is stable.

D: Alternative stable states

In Fig. 5, panel D, half of the resultant black arrows point towards the co-existence equilibrium and half point away. Depending on the starting conditions, the system will eventually move into one of the zones with arrows pointing away from the co-existence equilibrium. Depending on which of these two zones the system moves into, the system will resolve to one in which one species is extinct and the other is at its carrying capacity. However, the species that wins out is determined by the starting conditions, just as much as the rules that determine population changes. In this case, the co-existence equilibrium is unstable.

Interpretation of competition outcomes

Competitive exclusion

In outcomes A and B, one population goes extinct and the other grows to its carrying capacity. The winning species has the higher ZNGI, meaning that it has a larger value for both the x- and y-intercepts compared to the other ZNGI. Broadly, these conditions are likely to be met if the winning species has a relatively large carrying capacity, or the winning species has a strong competitive effect on the losing species (α value), or the losing species has a weak competitive effect on the winning species. Technically, for winner (W) and loser (L) we require: $K_W/\alpha_{WL} > K_L$ and $K_L/\alpha_{LW} > K_W$.

Constraint on stable coexistence

We note that in outcome C (stable co-existence), the ZNGIs cross each other and each population has the higher intercept value on its own axis. This means that the conditions:

$$K_1 < \frac{K_2}{\alpha_{21}} \tag{8}$$

$$K_2 < \frac{K_1}{\alpha_{12}} \tag{9}$$

must be met. We can perform a short analysis on these equations, assuming they are satisfied. If $K_2 < K_1/\alpha_{12}$, then we can substitute something larger on the right hand side, and still respect the inequality. We know that $K_2/\alpha_{21} > K_1$ so we can swap out the K_1 for K_2/α_{21} to get:

$$K_2 < \frac{K_2/\alpha_{21}}{\alpha_{12}} \tag{10}$$

which is algebraically equivalent to

$$K_2 < \frac{K_2}{\alpha_{12}\alpha_{21}} \tag{11}$$

and cancelling through by K_2 we arrive at:

$$1 < \frac{1}{\alpha_{12}\alpha_{21}} \tag{12}$$

Lastly, when we invert fractions in inequalities we need to reverse the inequality sign (e.g. $2/1 > 1$, but $1/2 < 1$), leading to:

$$1 > \alpha_{12}\alpha_{21} \tag{13}$$

This means that the overall effect of interspecific competition must be less than that of intraspecific competition for stable co-existence between the two populations. As often arises in population ecology, we see that intraspecific competition is a stabilizing force.

Alternative stable states

Of the 4 zones identified in outcome D, the top-left and bottom-right zones (Fig. 5 - panel D) will push the system to competitive exclusion (of N_1 and N_2, respectively). The key to understanding which outcome is more likely then, revolves around understanding which of those two zones the system will first encounter (assuming it starts in neither). Of those other 2 zones, in the top-right zone, the system moves towards the origin, and in the bottom-left zone it moves away from the origin. We see that for starting conditions where $N_2 > N_1$, there is a higher chance that N_2 wins (and vice versa for N_1). However, this is only a guideline. The exact positions of the ZNGIs (determined by K_1, K_2, α_{12}, and α_{21}) and the starting conditions together determine the final outcome.

Application of theory - competition between crab species

The shore crab invasion has been sufficiently well-studied that important components of the Lotka-Volterra model for green crab vs. shore crab competition may be qualitatively estimated (Fig. 3 and Fig. 6).

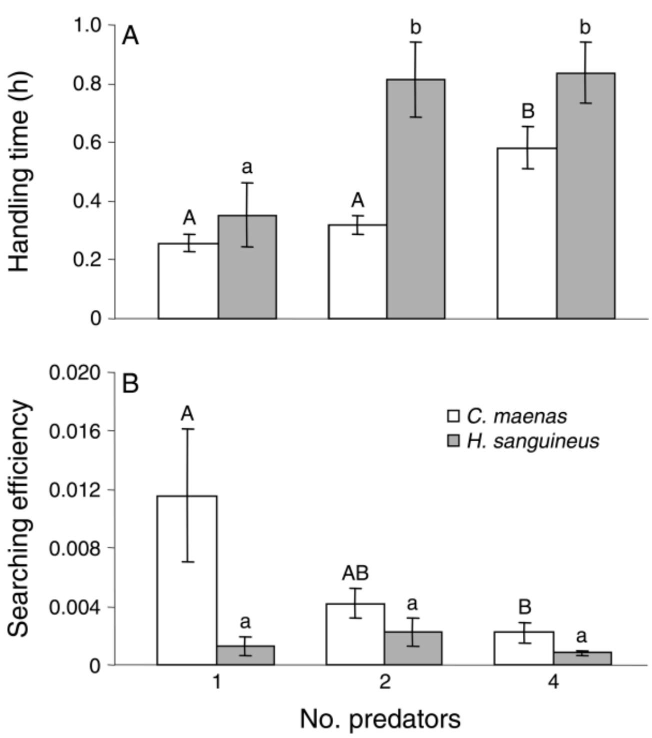

Figure 6: Estimates of handling time and searching efficiency for *Carcinus maenas* and *Hemigrapsus sanguineus* at different predator densities. Measurements were made in single-species experimental mesocosms (Griffin and Delaney 2007)

Fig. 3 tells us important information about the observed carrying capacities of each species, and Fig. 6 allows us to estimate the likely magnitudes of the α parameters. We leave it as an exercise for you (Homework question 1) to put these pieces of information together to evaluate the likely outcome of this competition as predicted by the Lotka-Volterra competition theory.

Homework

1. Articulate what you think the outcome of competition will be between green crabs and shore crabs on the east coast of the US. You should draw on evidence from Figs. 3 and 6 and make use of the phase plane analysis in this chapter to decide between outcomes A-D.

2. True or False: The Lotka-Volterra competition model predicts that coexistence between two competing species requires that overall, interspecific competition must be less than intraspecific competition.

3. Which of the following are potential outcomes of competition based on Lotka-Volterra theory? (circle ALL that apply)

(a) One species goes extinct, while the other goes to its carrying capacity

(b) Both species coexist at the same carrying capacities they would achieve in the absence of competition

(c) Outcomes may depend on initial population sizes

(d) Both species coexist at lower carrying capacities than they would achieve in the absence of competition

(e) Both species go extinct

4. In eastern Africa, lions and hyenas are in competition with one another. For the lion, $K_1 = 75$ and for the hyena, $K_2 = 300$. Competition parameters are $\alpha_{12} = 0.4$ and $\alpha_{21} = 0.8$ (where α_{12} represents the effect of species 2 on species 1). Suppose the initial population sizes at a site are 50 lions and 75 hyenas. Plotting lion abundance on the x-axis, and hyena abundance on the y-axis, plot the isoclines (ZNGIs) for each species, and plot these initial population sizes paying attention to details such as intercepts on the x and y-axis and accurate placement of initial conditions. Predict the short-term dynamics of each population and the final outcome of interspecific competition.

Glossary

- Conspecific - individual of the same species

- Explicit - implied though not plainly expressed
- Handling time - the amount of time it takes a predator to handle its prey, beginning from the time the predator finds the prey item to the time the prey item is eaten
- Heterospecific - individual of a different species
- Implicit - stated clearly and in detail, leaving no room for ambiguity
- Mescosm - an outdoor experimental system that examines the natural environment under controlled conditions
- Origin - reference point in a graph defined by $x = 0, y = 0$
- Phase-plane analysis - graphically determining the behavior of state variables (incl. population sizes) in the short- and long-term
- Searching efficiency - the rate at which the predator encounters prey items per unit of prey density
- Zero net growth isocline (ZNGI) - a line in a phase-plane where the associated state variable (e.g. population size) does not change

References

Griffen, B. D., and Delaney, D. G. 2007. Species Invasion Shifts the Importance of Predator Dependence. Ecology 88 (12): 3012-21