

7 Competition

(this chapter is still unfinished)

Species compete in many ways. Sometimes there are dramatic contests, such as when male bighorns compete for access to mates. That kind of competition, with direct encounters between individuals, is known as **interference competition**.

Other times the competition between species is more like a race to garner a particular resource, where the first one to take it acquires it. That mode of competition is generally known as **scramble competition**.

Very often, organisms are limited by their available food supply. As we saw in chapter 2, increasing population density decreases the resources available per individual, which in turn reduces their survival and/or reproduction. Eventually the population growth rate slows to zero and the population stabilizes at the carrying capacity of the environment.

But species are usually not alone. Consider the diverse herbivores that feed on prairie plants. Plants serve as food for a wide variety of herbivores, from large mammals to tiny insects, each of which reduces the available resources for all of the other species. When more than one species share the same resource, we must keep track of the density of all of the competitors in order to predict the population growth of a particular species.

Gary Belovsky, Jonathan Chase and Jennifer Slade studied grasshoppers on the short grass prairie of Montana. The prairie at the National Bison Range Wildlife Refuge contains several common species of grasses and broad leafed herbs (“forbs”). Those plants are utilized by mammalian herbivores as well as numerous insects. Belovsky and coworkers focused their attention on two species of grasshoppers: the migratory grasshopper (*Melanoplus sanguinipes*) and the white-whiskered grasshopper (*Ageneotettix deorum*). They are quite common. Those two species comprise about three-quarters of all of the grasshoppers in the area. On average you can find 5-10 of these grasshoppers in every square meter of prairie.

Figure 7.1



White Whiskered Grasshopper

National Bison Range

Migratory Grasshopper

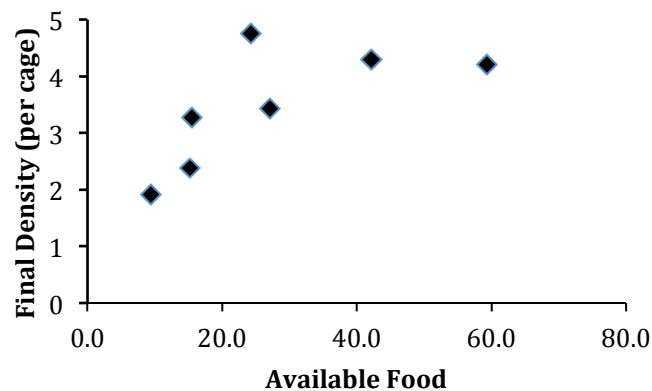
With such a density of grasshoppers, do they compete for food plants? It is not an obvious question. In a famous paper, Hairston, Smith and Slobodkin argued that herbivores are probably only rarely limited by food, because the world generally looks green. Because there appear to be lots of plants remaining as potential food for herbivores, they argued that herbivores must be limited by something else (perhaps predators, or density-independent

factors like weather). On the other hand, plants are often well-defended with toxins and other chemical deterrents. So not all of the plants may be effective food for all herbivores.

How could you test whether the grasshoppers on the Montana prairie were limited by food, and thus potential competitors for host plants?

The best evidence for food limitation in these grasshoppers comes from experiments where Belovsky and co-workers placed grasshoppers in small net cages on the prairie. They added excess nymphs at the beginning of the summer and monitored the density of grasshoppers as the summer progressed. Regardless of the starting density, the number of adult grasshoppers per cage would eventually stabilize at about 10 grasshoppers per m^2 . That is just about the natural density of grasshoppers at the site. Supplementing the available food in the cages (by watering some of the cages to increase the growth of the grasses) increased the survival and reproduction of the grasshoppers. So it appears that they are limited by their food supply, and that both species require approximately the same resources (Belovsky and Slade 1995).

*Fig 7.2 Density of *M. sanguinipes* depends on the available food. Cages with limited food support smaller populations of grasshoppers.*



7.1 Modeling Competition

Our approach to modeling competition will be similar to what we have seen in previous chapters. The main difference is that we will now need to keep track changes in population size of both of the species. We will use subscripts to identify species 1 and species 2, and each will now have its own population size, carrying capacity and intrinsic growth rate.

In chapter 2 we used the logistic equation for density dependent growth: $\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$

Now we will also have to include the density effects of the other species, The density-

regulated growth equation for species 1 becomes $\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{(\text{total density})}{K_1}\right)$ where the

total density is a weighted measure that takes into account the numbers of each species as well as their ability to use the shared resource.

Individuals of the different species may not use equal amounts of resources. Imagine ants competing with mice for seeds, or shrubs competing with trees for light. The addition of one extra tree may cause a greater reduction in growth rate than the addition of one extra shrub. Therefore we need a conversion factor, α , that translates the number of individuals of species 2 into “species 1 equivalents”. For example, each shrub may only have the effect of half a tree (or a tree may have the effect of 2 shrubs, etc). Therefore the available resources for the growth of species 1 will be reduced by the number of individuals of that species, as well as the weighted number of individuals of species 2:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{(N_1 + \alpha N_2)}{K_1} \right)$$

which can also be written as

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{(K_1 - N_1 - \alpha N_2)}{K_1} \right) \quad \text{eq 7.1}$$

If there are no individuals of species 2 present ($N_2=0$), how does eq. 7.1 compare to the regular equation for logistic growth from Chapter 2? _____

There is a corresponding equation for the growth rate of species 2:

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{(K_2 - N_2 - \beta N_1)}{K_2} \right) \quad \text{eq. 7.2}$$

Comparing equations 7.1 and 7.2, what is the meaning, in words, of the symbol β ? _____

Those equations can be used to describe the joint population growth of both species in mixture.

7.2 Phase planes and stability

By definition, species 1 will reach its equilibrium population size when $dN_1/dt=0$. Under what conditions will that be true? As we saw in chapter 2 that will be zero whenever $r_1=0$, $N_1=0$, or the quantity in parentheses $=0$. The interesting case is the non-zero equilibrium where $K_1 - N_1 - \alpha N_2 = 0$

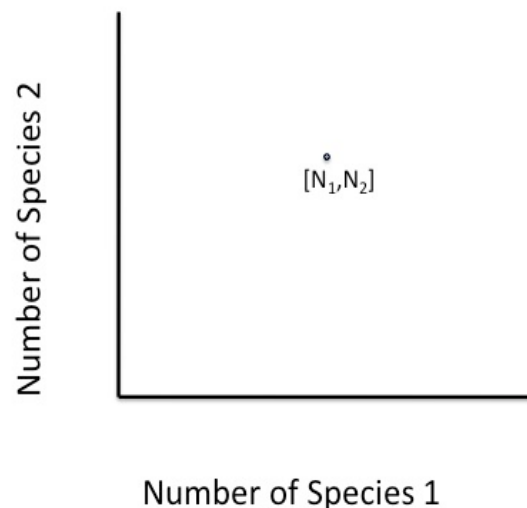
Solving for N_1 , we get

$$\hat{N}_1 = K_1 - \alpha N_2 \quad \text{eq. 7.3}$$

In our single species model we saw that the population growth was zero when $N_1=K_1$. Now, the effective carrying capacity for species 1 is reduced by the number of individuals of species 2. Moreover, the equilibrium number of species 1 is no longer a single number (K) but will change, depending on the number of species 2 that are also present.

To examine the joint effects of the two density of the two species, it is useful to make a graph with the number of species 1 along 1 axis and the number of individuals of species 2 on the other. The state of the joint system of two species can then be defined by a point in this “*phase plane*”. Any point in that space specifies a particular set of abundances of the two species $[N_1, N_2]$.

Figure 7.3 The two species “phase plane” graph. The current state of the system is indicated by a point in this space, showing the current population sizes of the two species.

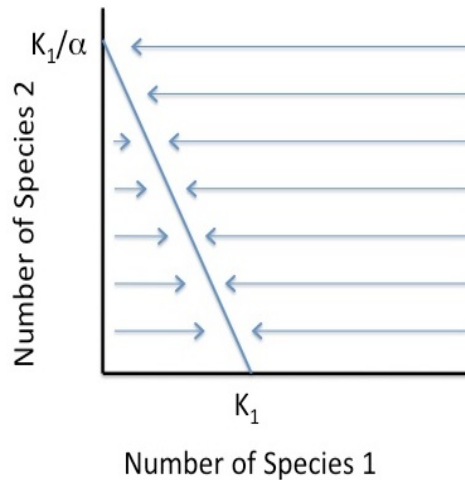


Equation 7.3 describes a straight line in this space which is known as a *zero growth isocline*. To draw that line on the phase plane, it is convenient to choose strategic points that minimize the arithmetic. One such point will be where it crosses the x-axis. At that point the number of

species 2 is 0. Let $N_2=0$ in eq 7.3. It then reduces to $N_1=K_1$. So we know it crosses the horizontal axis at K_1 . The line will cross the vertical axis when $N_1=0$. At that point $N_2=K_1/\alpha$.

The line connecting those two points (Fig. 7.4) describes the zero growth isocline for species 1. At any point along that line $\frac{dN_1}{dt}=0$ so species 1 will be at equilibrium. If the number of species 1 is below its isocline, then the population of species 1 will grow until it reaches the equilibrium. If the number of species 1 is above its zero growth isocline, N_1 will decrease back toward the equilibrium. Because we are looking only at changes in species 1, the state of the system will move either left or right in the phase plane graph.

Figure 7.4 Zero growth isocline for species 1. $dN_1/dt=0$ for any point along this isocline.

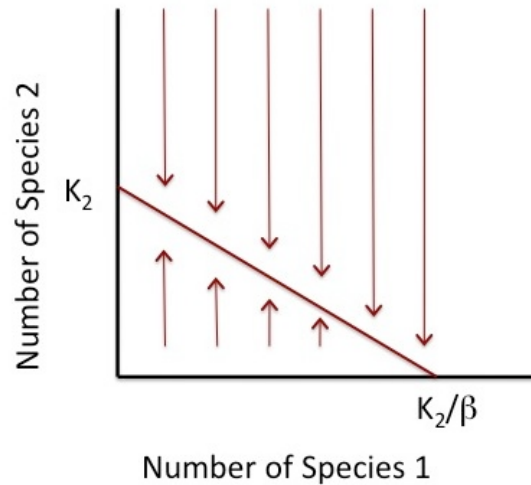


Now let's do the same thing for species 2. Starting with eq. 7.2 and using eq. 7.3 as a guide, write down the non-zero equilibrium for species 2. $\hat{N}_2 = \underline{\hspace{2cm}}$

The growth rate of species 2 will be zero when $N_2=K_2-\beta N_1$. We can draw that zero growth isocline for species 2 in the phase plane as we did for species 1. When $N_1=0$, the isocline is at $N_2=K_2$. When $N_2=0$ the isocline passes through $N_1=K_2/\beta$ (Fig. 7.5).

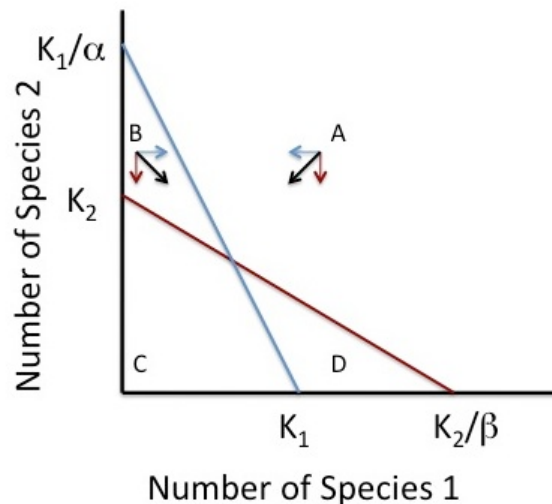
Again, if the number of species 2 is below its zero growth isocline, the growth rate will be positive and the population will increase towards the equilibrium. If the number of species 2 is above its zero growth isocline the growth rate will be negative and the population will decrease towards its isocline.

Figure 7.5 Zero growth isocline for species 2. $dN_2/dt=0$ for any point along this isocline.



How will the numbers of each species change when we consider both species simultaneously? The joint equilibrium for both species will occur where both $dN_1/dt=0$ and $dN_2/dt=0$. That point must fall on *both* of the zero growth isoclines, so it must be the intersection of the two lines.

Figure 7.6 Zero growth isoclines of the two species.



Starting at point A, N_1 is above its isocline, so the abundance of species 1 will decrease and the point representing the state of the system will move to the left. Similarly, N_2 is above its isocline so the abundance of species 2 will decrease and the point representing the state of the system will move down. The simultaneous change in both species will move the state of the system down and to the left, shown by the diagonal arrow from point A.

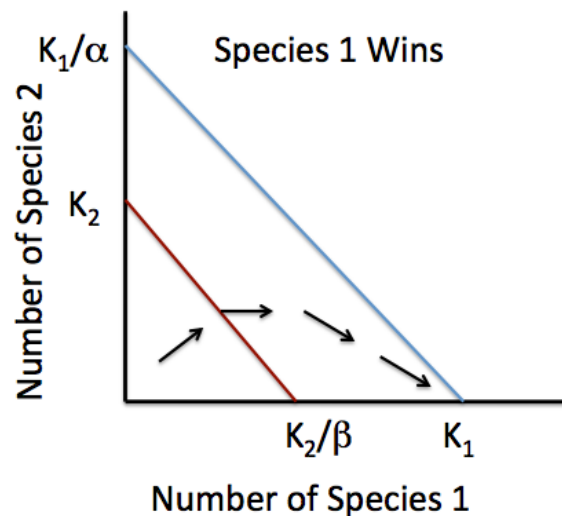
What will happen if the system starts at point B? Starting at B, species 1 is now below its isocline so the system will move to the right. Species 2 is above its isocline so it will decrease in abundance and the system will move down. The joint effect is to move the state of the system down and to the right.

Draw in the population change vectors for points C and D.

The set of isoclines in Figure 7.6 define a system where stable coexistence of the two competitors is possible. No matter where in the state space the system starts, the system will move toward the equilibrium. In other words, the joint equilibrium of the two species is globally stable.

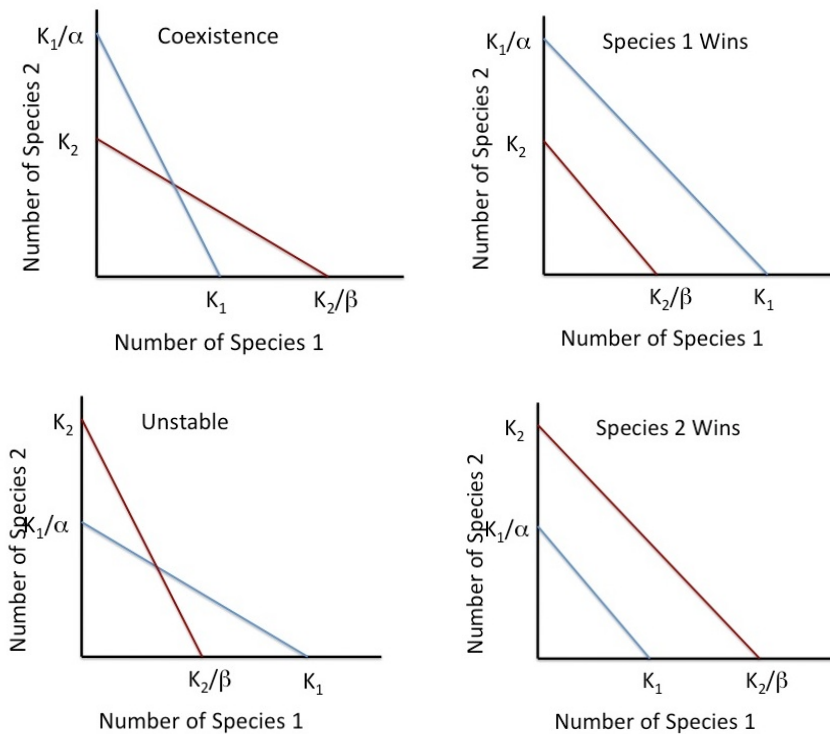
Let's look closely at a case where the isoclines do not intersect. In this situation the species with the higher zero growth isocline will eventually outcompete the other species. For example, in this scenario imagine we start the system with only a couple of individuals of each species. Initially, both species 1 and species 2 are below their isocline, so the abundance of both species will increase. Now consider a point when the joint abundances have changed and the system has reached the lower isocline. At this point species 1 can still increase but species 2 will stay constant. At the third position, species 2 is above its isocline so it will decrease in abundance while species 1 continues to increase. Eventually, species 2 will decline to extinction and species 1 will equilibrate at K_1 .

Figure 7.7



Depending on the values of K_1 , K_2 , α and β , there are four possible configuration of isoclines for two competitors (Figure 7.8).

Figure 7.8. Four possible arrangements of isoclines for two species in the phase plane.



Choose a starting point for each of those graphs and draw in the population trajectory.

7.3 An algebraic solution

We can also consider the stability of the joint equilibrium algebraically. At the joint equilibrium, both $dN_1/dt=0$ and $dN_2/dt=0$. Therefore both equations 7.3 and 7.4 must be satisfied. To find that joint equilibrium, substitute equation for N_1 (eq.7.3) into eq.7.4:

$$\begin{aligned}\hat{N}_2 &= K_2 - \beta(K_1 - \alpha N_2) \\ \hat{N}_2 &= K_2 - \beta K_1 + \alpha\beta N_2\end{aligned}$$

$$\hat{N}_2 = \frac{K_2 - \beta K_1}{1 - \alpha\beta} \quad \text{eq. 7.5}$$

By similar logic,

$$\hat{N}_1 = \frac{K_1 - \alpha K_2}{1 - \alpha\beta} \quad \text{eq. 7.6}$$

How can we make sense of those equations? First, notice that those criteria for coexistence don't depend on r . The growth rate of each population affects the rate of approach to the equilibrium, but r has no effect in determining which species is the better competitor or whether coexistence is possible.

Second, we can derive some general conditions for coexistence. Stable coexistence means that *both species should be able to increase when rare*. Imagine a case where species 1 is rare (so N_1 is approximately 0). Species 2 is common and without species 1 N_2 should equilibrate at approximately K_2 . Under those conditions, can an individual of species 1 invade?

Remember that the key part of eq. 7.1 in determining whether or not species 1 will increase was the part in parentheses. In particular, dN_1/dt will be positive when $(K_1 - N_1 - \alpha N_2)$ is positive. Now, can species 1 increase when rare (when $N_1 \approx 0$ and $N_2 \approx K_2$)? That will depend on the sign of $(K_1 - 0 - \alpha K_2)$. That expression will be positive when $K_1 > \alpha K_2$, or

$$K_1/K_2 > \alpha$$

You can also see this graphically. In order for species 1 to increase, its isocline must be above the current point. Examine Figure 7.8a and look along the vertical axis. If species 1 is rare the system will be at approximately $[0, K_2]$. Species 1 can increase only if its isocline is higher than that point: i.e. K_1/α must be greater than K_2 .

That can also be written

$$K_1/K_2 > \alpha$$

Similarly, if N_2 is close to zero, that means the system will be at approximately K_1 . In order for species 2 to increase when rare, its isocline must be higher than K_2 :

$$K_2/\beta > K_1.$$

or

$$1/\beta > K_1/K_2$$

With a little rearranging, those two expressions can be combined to yield the general criterion for coexistence of two competitors under the Lotka-Volterra competition model:

$$\alpha < \frac{K_1}{K_2} < \frac{1}{\beta} \quad \text{eq. 7.7}$$

7.4 Competitive exclusion

Equation 7.7 allows us to say a lot about the potential coexistence of two competitors. For example, imagine that the two species are identical in their use of resources. In that case, adding an extra individual of species 2 would have exactly the same effect on population growth as an addition individual of species 1: $\alpha=1.0$ and $\beta=1.0$.

Using equation 7.7, can those two species coexist when $\alpha=\beta=1.0$? _____

That result is sometimes known as the **competitive exclusion principle**: complete competitors cannot coexist.

Now imagine that the two species are quite similar, but not exactly identical. When two species are ecological similar and use approximately the same resources, α and β will be close

to 1.0. Let's imagine that $\alpha=\beta=0.9$. In that case coexistence is possible, but only if the carrying capacities are precisely matched. The ratio of carrying capacities must be between 0.9 and 1.11.

If two species are only weak competitors, alpha and beta will be much less than 1.0. In that case a much wider range of carrying capacities will still allow the species to coexist.

7.5 Back to grasshoppers

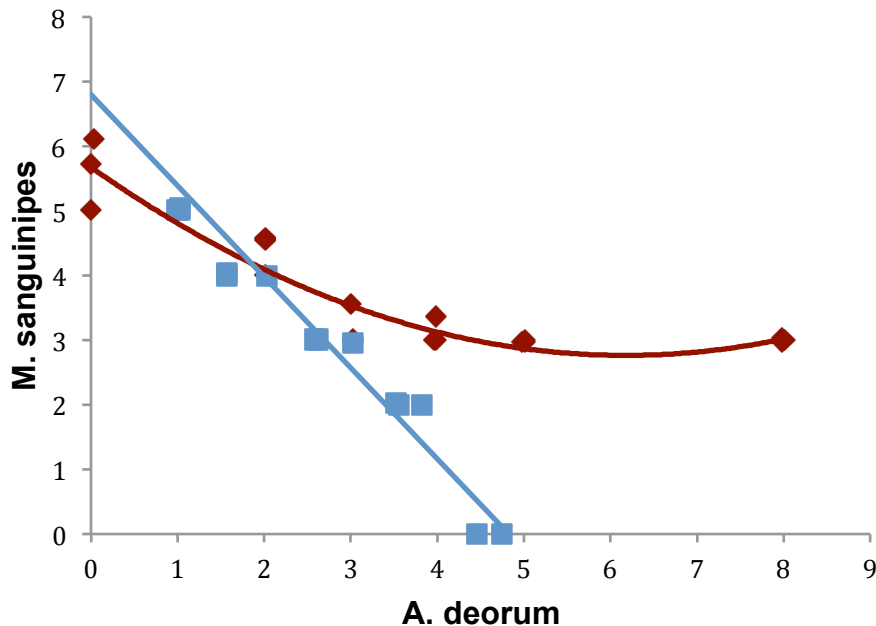


photo from G. Belovsky website

Belovsky and his students set up more grasshopper cages, this time starting with mixtures of the two species. They used many possible combinations of *Ageneotettix* and *Melanoplus* such that the total number of grasshoppers was about 10 per cage (10:0, 8:2, 5:5, etc). In some of the treatments *Ageneotettix* was kept at a constant density by replacing any grasshoppers that died or disappeared. In those cages the number of *Melanoplus* was allowed to decline to a constant density. (The idea was to mimic Figs 7.4 and 7.5.)

In other cages the number of *Melanoplus* was kept constant and *Ageneotettix* was allowed to decline toward its equilibrium density. They then allowed the density of grasshoppers to equilibrate and recorded the final number of each species. Their results are shown in Fig 7.9.

Figure 7.9. Competitive isoclines for two species of Montana grasshoppers. The isocline for *A. deorum* is shown with blue squares. The zero growth isocline for *M. sanguinipes* is shown by the red diamonds.



One important difference between this and figure 7.6 is that the changes in numbers of grasshoppers in the cages are entirely the result of mortality *within a generation*. But because mortality is an important component of population growth, the within generation changes in mortality should at least approximate the overall population growth.

The other obvious difference is that the observed isocline for *M. sanguinipes* is not straight.

Why are the isoclines for these grasshoppers curved? The logistic equation on which our competition model was based assumes linear density dependence. The grasshoppers show a non-linear response. One likely reason is because the two species feed on slightly different host plants. The Migratory grasshopper will eat almost all of the plants it encounters, both grasses and forbs. In contrast, the white-whiskered grasshopper prefers to eat grasses. In cages it will refuse to eat broad-leafed species even when it is running out of grass. In other words, *M. sanguinipes* has an unshared resource: forbs. That gives it a “reserve” so its numbers can’t be driven completely to zero by the addition of more *A. deorum*. It stabilizes at a minimum of about 3 per cage, regardless of the number of competitors.

(to be added eventually)

7.6 Extensions to the Lotka-Volterra competition model:

7.6.1 competition/colonization tradeoffs

7.6.2 temporal variation/storage effect

7.7 The niche.

7.8 Your turn

Further reading:

Belovsky, G. E. and J. B. Slade. 1995. Dynamics of two Montana grasshopper populations: relationships among weather, food abundance, and intraspecific competition. *Oecologia* 101: 383-396.

Chase, J. and G. E. Belovsky. 1994. Experimental evidence for the included niche. *Am. Nat.* 143:5143-527.

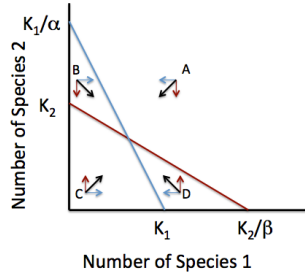
Hairston, N. G., Smith, F. E. and Slobodkin, L. B. 1960. Community structure, population control, and competition. *Am. Nat.* 94:421-425

Answers:

p 3. Eq. 7.1 reduces to the familiar logistic equation when $N_2=0$. $\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right)$

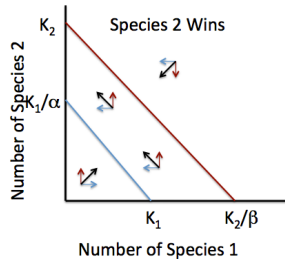
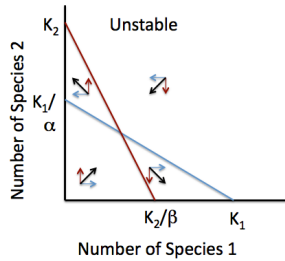
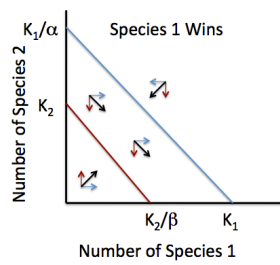
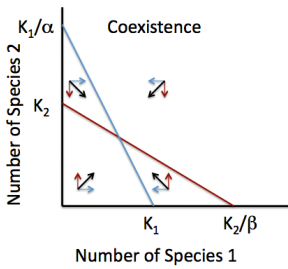
The coefficient β is a conversion factor that translates species 1 into “species 2 equivalents”

p 5. $dN_2/dt=0$ when $N_2 = K_2 - \beta N_1$



p 7

p 8 add four figs



p 9

No. They cannot coexist when there are complete competitors ($\alpha=\beta=1$).