

Three Compartment Models

Bio 534

Introduction

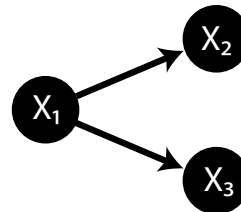
One and two entity models are useful for developing our understanding of the processes and their controls that affect entity growth and decay, but they rarely provide insight into the dynamics of complex ecosystems. Three entity models are the simplest models that meet this objective. There are four distinct configurations of such models that we need to consider, which are shown in Figure 1.

THREE COMPARTMENT MOTIFS

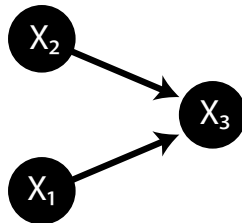
1. LINEAR CHAIN



2. RESOURCE COMPETITION



3. PREY CHOICE



4. CYCLE

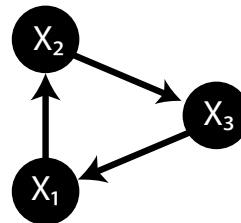


Figure 1: Four key configurations of three compartment models

1 The Chain

The chain is the simplest step from the two entity models we considered previously. This configuration might represent a system in which X_1 is a non-living resource or a primary producer, X_2 is a primary consumer, and X_3 is a secondary consumer as in classic trophic dynamics (Figure 2). In this case, there are no new processes to consider, but all the processes and controls we have previously considered can operate and combine to create interesting behaviors such as a trophic cascade. For a more concrete example, we can consider the Antarctic system in which Penguins (X_3) eat Krill (X_2), which in turn feeds on Diatoms (X_1).

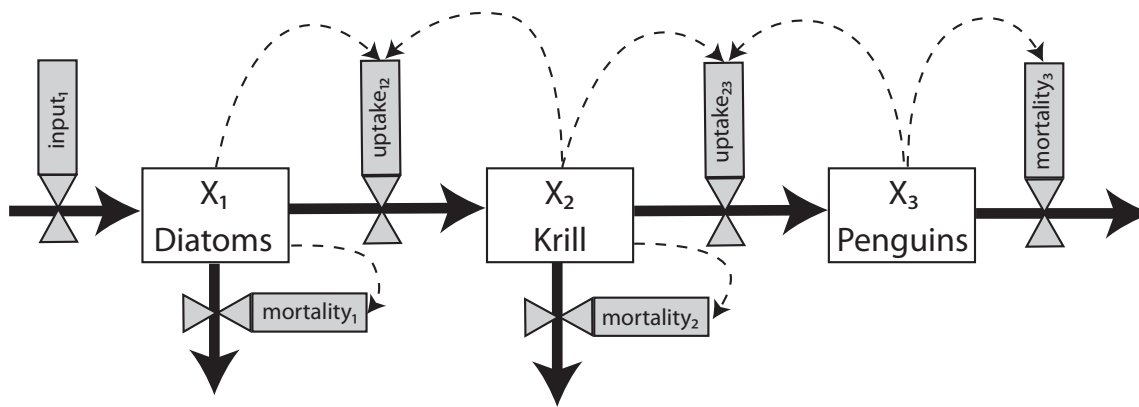


Figure 2: An example food chain isolated from the Antarctic ocean food web

In this case we can use the following equations written in terms of processes:

$$\dot{X}_1 = \text{growth}_1 - \text{uptake}_{12} \quad (1)$$

$$\dot{X}_2 = \text{conversion.efficiency}_{12} \cdot \text{uptake}_{12} - \text{uptake}_{23} - \text{mortality}_2 \quad (2)$$

$$\dot{X}_3 = \text{conversion.efficiency}_{23} \cdot \text{uptake}_{23} - \text{mortality}_3 \quad (3)$$

Here growth_1 is due to photosynthesis and uptake_{ij} represents consumption. Mortality $_i$ is both natural mortality and all other potential forms of loss.

We can rewrite these equations more specifically as:

$$\dot{X}_1 = (\mu_1 - \delta_1)X_1 - \Phi_1(X_1, X_2) \quad (4)$$

$$\dot{X}_2 = \gamma_2 \cdot \Phi_1(X_1, X_2) - \Phi_2(X_2, X_3) - \delta_2 X_2 \quad (5)$$

$$\dot{X}_3 = \gamma_3 \cdot \Phi_2(X_2, X_3) - \delta_3 X_3 \quad (6)$$

Where:

$\mu_1 = \mu_{max1} \cdot f(X_1)_a$ is the *specific growth rate* that is controlled by the **interference competition form of logistic equation**, $f(X_1)_a = \left(1 - w_1 \left(\frac{X_1}{K_1}\right)_+\right)_+$

in which w_1 is Wiegert's correction factor $\left(1 - \frac{\delta_1}{\mu}\right)$ and K_1 is the environmental carrying capacity. μ_{max_1} is the maximum growth rate assuming that all environmental conditions and resources are optimal.

$\Phi_1(X_1, X_2) = \tau_{12} \cdot f(X_{1b}) \cdot X_2$ is the effective predation or uptake rate modeled using the **exploitative form of the logistic equation** $f(X_{1b}) = \left(1 - \left(\frac{K_{12} - X_1}{K_{12} - \alpha_{12}}\right)_+\right)_+$ where K_{12} is the satiation level of X_2 on X_1 , and α_{12} is the prey refuge level.

γ_i is the ability of species i to convert the predated food into its own species or biomass.

$\Phi_2(X_2, X_3) = \tau_{23} \cdot f(X_2) \cdot f(X_3) \cdot X_3$ is the effective predation of X_2 by X_3 . Here, we will model the predation functional response $f(X_2)$ similarly to $f(X_{1b})$ such that $f(X_2) = \left(1 - \left(\frac{K_{23} - X_2}{K_{23} - \alpha_{23}}\right)_+\right)_+$ and further modify this predation rate by *interference competition* as $f(X_3) = \left(1 - w_3 \left(\frac{X_3 - \alpha_{33}}{K_3 - \alpha_{33}}\right)_+\right)_+$

Most of the individual functions used above have been described previously in class. Here, we are applying what we already have learned to a new situation. An important aspect of these equations is that we have begun to *combine* multiple control functions – multiple control factors can operate simultaneously in one process. Recall our conversation at the end of the *Control Functions* lecture regarding the ways to combine control functions and the dangers of using multiple multiplicative functions.

1.1 Two Forms of the Logistic

Notice that we are distinguishing between two forms of the logistic equation: **interference** and **exploitative**.

The exploitative form of the logistic models the feedback control of ingestion when the control is a function of the resource. Wiegert's correction term does not appear in the exploitative form. These controls can be summarized as follows

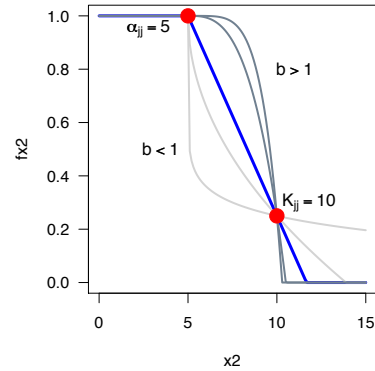
1.1.1 Interference Competition form of the Logistic

The logistic equation is most commonly used to represent feedback control on the ingestion, and thus growth, of a population as a consequence of increase in its size (represented as any manner — numbers, energy, carbon, etc.). The interference form uses Wiegert's modification to model the effects of interference competition on the gain term of the population growth rate (or here the photosynthetic rate).

In general terms where i is the resource and j is the consumer, we can write this control function as:

$$f(X_j) = \left[1 - \left(1 - \frac{\delta_j}{\tau_{ij}} \cdot (1 - \epsilon_{ij}) \right) \cdot \left(\frac{X_j - \alpha_{jj}}{K_{jj} - \alpha_{jj}} \right)_+^b \right]_+$$

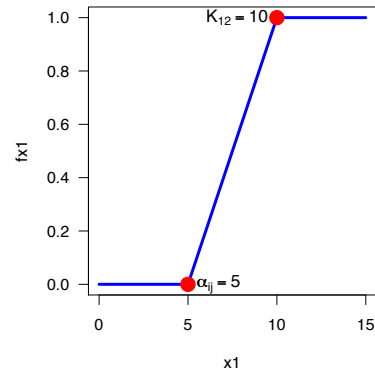
Notice that at the carrying capacity K_{jj} the $f(X_j) = 1 - w$ where $w = \left(1 - \frac{\delta_j}{\tau_{ij}} \cdot (1 - \epsilon_{ij}) \right)$ is Wiegert's correction factor.



1.1.2 Exploitative Competition form of the Logistic

The logistic can also be used as a feedback control of ingestion when control is a function of the availability of a material resource. As such, it represents a measure of the intraspecific exploitative control of ingestion. Since, in an exploitative situation, ingestion can indeed go to zero (resources at or below a refuge threshold), the exploitative form of the logistic control is somewhat simpler to write because no correction term is needed.

$$f(X_i) = \left[1 - \left(\frac{K_{ij} - X_i}{K_{ij} - \alpha_{ij}} \right)_+ \right]_+$$



2 Resource Competition

This configuration of three compartments (species or groups of species) represents two species competing for a common resource. Consider the system shown in Figure 3 in which turkey vultures (*Cathartes aura*; X_2) and common ravens (*Corvus corax*; X_3) both feed on carrion (X_1).

We can first write the equations describing this system by describing the processes involved:

$$\dot{X}_1 = \text{input}_1 - \text{loss}_1 - \text{uptake}_{12} - \text{uptake}_{13} \quad (7)$$

$$\dot{X}_2 = \text{conversion.efficiency}_{12} \cdot \text{uptake}_{12} - \text{mortality}_2 \quad (8)$$

$$\dot{X}_3 = \text{conversion.efficiency}_{13} \cdot \text{uptake}_{13} - \text{mortality}_3 \quad (9)$$

Now, we can quantify the processes involved using the mathematical functions we have previously discussed. For example, the input to the carrion compartment is not

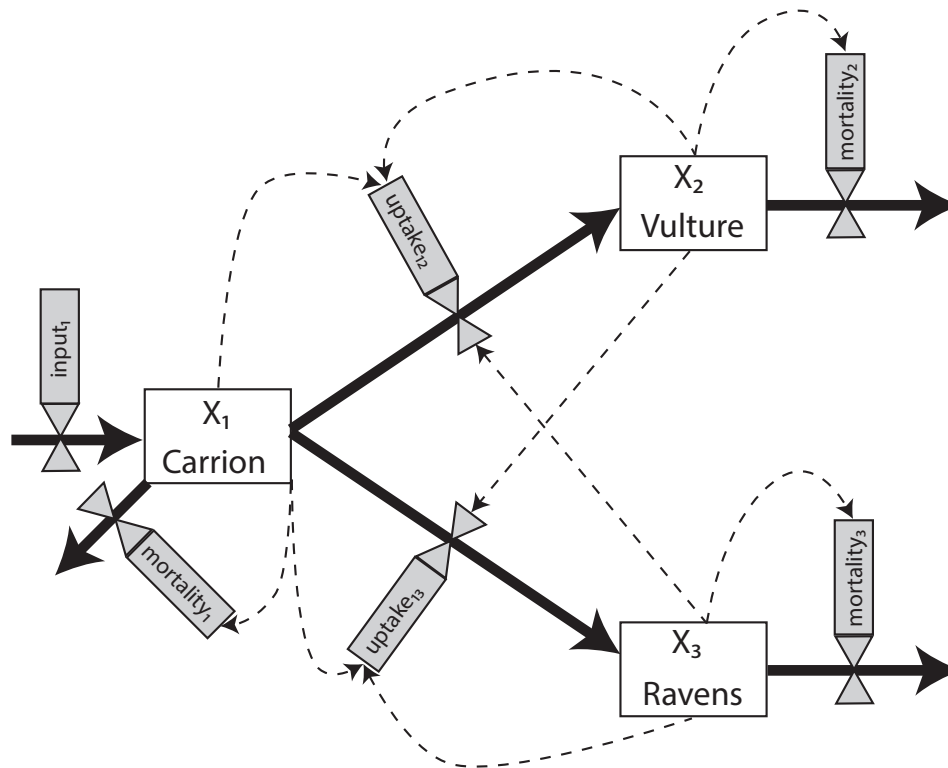


Figure 3: A model of two compartments competing for a common resource: resource–competitor model

influenced by the carrion density; instead we will consider it to be a constant input C_1 into the system. Carrion biomass is lost from the system in two ways: (1) the Vultures and Ravens both consume (*uptake*) the carrion and (2) there is an additional loss term from an unspecified process.

The Forrester type diagram in Figure 3 provides us with information about how the processes need to be formulated. For example, the input to carrion (X_1) is not controlled or regulated by the current carrion magnitude; In this model we will treat this as a constant input from a source outside the boundaries of our model. In contrast, the uptake fluxes are *recipient determined* and *donor–recipient controlled* — both the scarcity of resources and/or crowding by densities of X_2 and X_3 are possible controls of resource uptake. As both X_2 and X_3 are both using the same resource X_1 , we have *intraspecific competition* and *interspecific competition* for a limiting resource. In addition, the dotted lines from X_2 to uptake₁₃ and from X_3 to uptake₁₂ imply the possibility for *interspecific interference competition*.

2.1 Interspecific Interference Competition

Again, we have already considered how to model the interspecific interference competition that is shown in Figure 3. What is new here is incorporating it into a model with three state variables. Lets assume that the two interfering population are competing for the same unspecified resource such as **space**. Then we can modify the

logistic function as before to model intraspecific interference competition as

$$f(X_2, X_3) = \left[1 - w_2 \left(\frac{X_2 + \beta_3 X_3 - \alpha_{22}}{K_2 - \alpha_{22}} \right) \right]_{+} \quad (10)$$

$$f(X_3, X_2) = \left[1 - w_3 \left(\frac{X_3 + \beta_2 X_2 - \alpha_{33}}{K_3 - \alpha_{33}} \right) \right]_{+} \quad (11)$$

where β_i is the proportional effect of adding a unit of X_i on the growth of X_j and α_{ii} is a density threshold below which BOTH inter- and intraspecific competition do not occur. What is the ecological significance of $\beta_i < 1$? What if $\beta_i > 1$? With this formulation, how does our interpretation of K_i change? Again, equations (10) and (11) represent the *recipient* controls on the uptake process.

2.2 Resource Control of Uptake

We said earlier that uptake is donor–recipient controlled, so we must now consider how to model the donor control. In this case, we will use the *exploitative competition* form of the logistic as we are modeling resource competition control of uptake. Again, we can define our control functions as:

$$f(X_1)_a = \left[1 - \left(\frac{K_{12} - X_1}{K_{12} - \alpha_{12}} \right) \right]_{+} \quad (12)$$

$$f(X_1)_b = \left[1 - \left(\frac{K_{13} - X_1}{K_{13} - \alpha_{13}} \right) \right]_{+}. \quad (13)$$

What is the ecological interpretation of K_{12} and K_{13} ? What about α_{12} and α_{13} ? You could look back at your previous notes, but how could you use what you know to figure out the *roles* of these parameters in the equations?

2.3 Equations

Given this information, we can write the differential equations for the system as

$$\dot{X}_1 = C_1 - \delta_1 X_1 - \tau_{12} X_2 \cdot f(X_2, X_3) \cdot f(X_1)_a - \tau_{13} X_3 \cdot f(X_3, X_2) \cdot f(X_1)_b \quad (14)$$

$$\dot{X}_2 = \gamma_2 \tau_{12} X_2 \cdot f(X_2, X_3) \cdot f(X_1)_a - \delta_2 X_2 \quad (15)$$

$$\dot{X}_3 = \gamma_3 \tau_{13} X_3 \cdot f(X_3, X_2) \cdot f(X_1)_b - \delta_3 X_3 \quad (16)$$

Here,

C_1 is a constant input to X_1 , and

all other parameters are as previously discussed.

2.4 Model Analysis

Limitations We will consider three types of limitation in this system when all three state variables are at steady state $\dot{X}_i = 0$.

1. The resource entity X_1 is always greater than the largest of K_{12} and K_{13} – optimally enriched system.
2. The resource X_1 is the only limiting control; X_2 and X_3 never exceed α_{22} or α_{33} , respectively.
3. X_1 , X_2 , and X_3 are all at steady state at some value between the defining thresholds (scarcity of material resources and of space)

Graphical Analysis As we have already discovered, we can often learn quite a bit about the expected dynamics of a system of equations before we solve them numerically. Here, we again use the concept of *Zero Net Growth Isoclines* (ZNGI). This is sometimes referred to as *Null Cline Analysis* or graphical analysis. A zero growth isocline or null cline is a curve on a phase-plot that indicates when a variable remains unchanged from one time point to the next. Otto and Day (2007) state that “Along a null cline corresponding to the variable on the horizontal axis, the system can only move up or down, without any horizontal movement. Similarly, along the null cline corresponding to the variable on the vertical axis, the system can only move left or right, without any vertical movement” (p. 138).

In the first limitation type, $f(X_1)_a$ and $f(X_1)_b$ drop out of the equations because the system is optimally enriched, which leaves only intra- and interspecific competition. If we set equations (15) and (16) equal to zero and divide both sides by X_2 and X_3 , respectively, multiply through by respective τ values, rearranging and canceling terms we obtain:

$$\begin{aligned}\hat{X}_2 &= -\beta_3 X_3 + K_2 \\ \hat{X}_3 &= -\beta_2 X_2 + K_3\end{aligned}\tag{17}$$

These equations describe the line of zero growth for X_2 and X_3 for various combinations of the variables. Since both are straight lines, we can determine their intercepts on the X_2 and X_3 axes by setting one variable equal to zero. This generates four possible system configurations (Cases I-IV) shown below.

In three of four cases one species out-competes and excludes the other. According to Kot (2001), this is the basis for *Gause’s Principle* or the *Principle of Competitive Exclusion* (p. 203).

The same kind of analysis can be applied to with the second and third types of limitations we mentioned above, but the algebra is more complicated because resource competition must also be considered. What do you expect these to look like? Can you work them out?

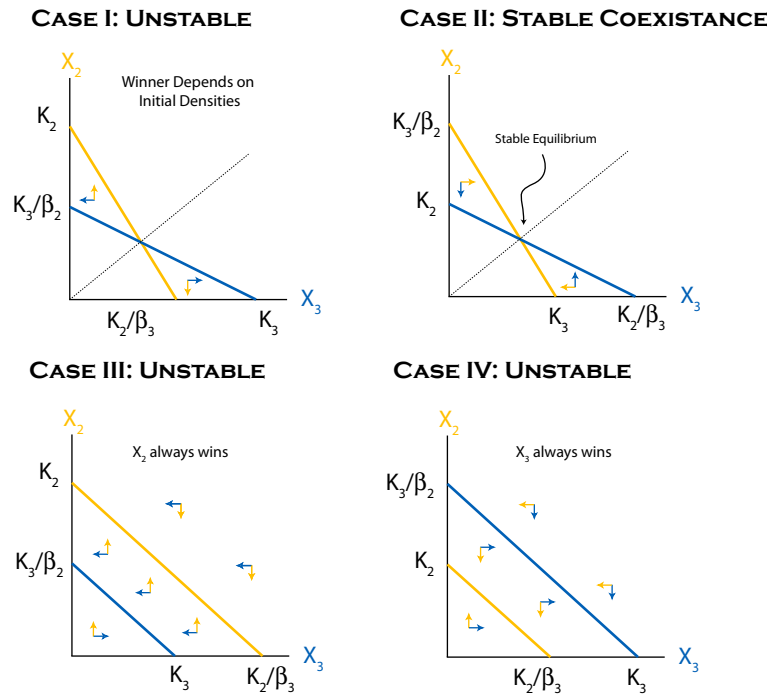


Figure 4: Four possible system configurations for interspecific competition

3 Prey Choice

When a consumer utilizes two resources as shown in the diagram at right, we must consider a new process that we will generically call *prey choice*. We touched upon this subject in when we discussed alternative forms of combining control functions, but here we will go one step further.

Recall the Michaelis–Menten predation functional response, which was

$$f(R) = \tau_{12} \left(\frac{R}{R + k_R} \right) \tag{18}$$

Where k_R is the 1/2 saturation constant and R is the resource concentration. To model the uptake of multiple resources that are *equally likely to be found*, we can weight their expected contribution to diet based on a factor w_{ij} , which represents the difference in consumption quantity based on nutritional differences (i.e. you have to eat more of less nutritious food). We represent this as

$$R = \sum_{i=1}^n w_{ij} R_i \tag{19}$$

When we substitute equation (19) into equation (18) we obtain

$$f(R) = \tau_{12} \left(\frac{\sum_{i=1}^n w_{ij} R_i}{\sum_{i=1}^n w_{ij} R_i + k_R} \right) \quad (20)$$

Notice that in this case, there is only one $1/2$ saturation constant for the set of resources. Also it is convenient to force $\sum_{i=1}^n w_{ij} = 1$.

When the resources are not all equally easy to find, we require more elaborate techniques. Unfortunately we do not have time to discuss these in class, but you can learn more about them in the following.

- O'Neill, R. V. 1969. Indirect estimation of energy fluxes in animal food webs. *Journal of Theoretical Biology* 22:284–290.
- Wiegert R.G. and Wetzel. 1979. *Marsh-Estuarine System Simulations*, UNC Press, p. 7-39.

4 Cycling

Cycle closure is the second major step in system formation. With this motif we do not necessarily have new processes to model, but we need to be cognizant of the impact cycle closure can have.

Energy-matter cycles create new pathways through which entities can affect each other indirectly, and an entity's actions can now indirectly feedback to affect its own behavior.

In the instance where the process connecting species is predation in which one species benefits and the other is harmed (+,−), it becomes an *autocatalytic cycle* or *hypercycle* (Figure 5). Collectively, the entities in the autocatalytic cycle become indirect mutualists because an increase in the abundance of one entity will lead to an abundance increase in all of the entities.

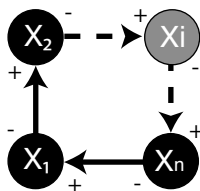


Figure 5: Hypercycle

This arrangement does seem to appear in natural systems. Borrett et al. (2007, *Journal of Theoretical Biology*) found cycles in 10 of 17 large empirical food webs drawn from the literature.