Control Functions

Fundamentals of Ecological Modelling (BIO534)

Contents

1   Introduction

In this lesson, I explicitly introduce the notion of control functions and illustrate how they are used in ecological modeling. We will discuss a number of example control functions along with their applications and limitations. The assigned background reading for this lecture is Chapter 3 Bolker (2008).

At the end of this lesson, you should be able to:

1. Distinguish between process *determinants* and *controls*;

2. Identify the difference between *donor* and *recipient* determinants and controls;

3. Construct plots to evaluate how a control function operates;

4. Identify and characterize selected illustrative control functions;

5. Recognize the Monod Function (aka Michaelis-Mention) function, provide examples of its use in ecological modeling, and recall the advantages and disadvantages of this function.

6. Explain and use Wiegert's trick to make the logistic only operate on ingestion (births);

7. Utilize a consumer–resource ecological framework common in ecosystem ecology; and

8. Describe alternative ways of combining control functions and explain the rational for each.

In our previous discussions, we have approached the model construction using a **population ecology** framework in which the state variables were population abundances or densities (i.e., number of individuals per area). Today, we will use an **ecosystem perspective** in which the state variables represent the collective biomass of the group or compartment. To reinforce this distinction, we will represent the state variable as X in today's equations.

Conceptually, we could simply convert from one perspective to the other by multiplying the number of individuals N by the average biomass of an individual. However, we also start to consider different processes. Instead of the input process being *Births* and the loss process being *Deaths*, we substitute processes like *Ingestion* and *Natural Mortality*. Despite the differences in the notation and interpretation, there is a strong similarity in the underlying mathematics.

2   Determinants vs. Controls

The structure of a system interacts with the function to generate the **behavior** of the system. As previously discussed, any change in the state variable(s) X

(i.e., population size, concentration) such that $X_{t+1} \neq X_t$ can be considered a dynamic change of state or behavior.

Conceptually, the magnitude of change in a state variable is *determined* (determine = to set bounds or limits to; to limit in extent) by characteristics internal to the components of a model. In the case of biotic components, it is the genetic composition of the organism that sets these bounds. The maximum rate of growth under optimal conditions and resources (μ_{max}) is one such limit.

The changes produced by system and model behavior are kept within bounds by *controls*. These control functions take many forms, some are external (environmental limitations) and some are internal (i.e., intraspecific competition). We will examine such functional forms in detail.

One of the challenges of quantitative modeling is choosing the best functional forms to represent specific processes. Alternative functional forms make different assumptions about the ways the biological process works, and they each have strengths and weaknesses. In general, we use knowledge and data about the particular system to guide our selection of functions. Many modeling texts introduce a "Beastiary" of mathematical functions that might be useful for ecological modeling. For example, see Chapter 5 in Haefner (2005), Chapter 3 in Bolker (2008), and Chapter 3 in Jørgensen and Bendoricchio (2001).

2.1 Donor–Determined, Donor–Controlled

Some ecological processes can be modeled as both determined and controlled by the donor compartment including respiration, non-predatory mortality, excretion. When using this formulation, we are assuming that no other entity is involved in the process, such as the logistic model of population growth. Figure 1 shows a general example of this.
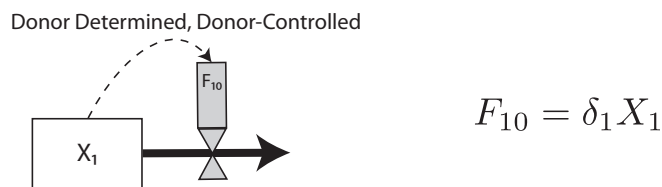

$$F_{10} = \delta_1 X_1$$

Figure 1: Examples of donor determined flows. In this figure, F_{10} is the flow or process, δ_1 is a specific process rate, and X_1 is the state variable.

2.2 Recipient–Determined

Processes such as ingestion or predation are often modeled as recipient determined because it is the recipient's basic biology determining what can occur.
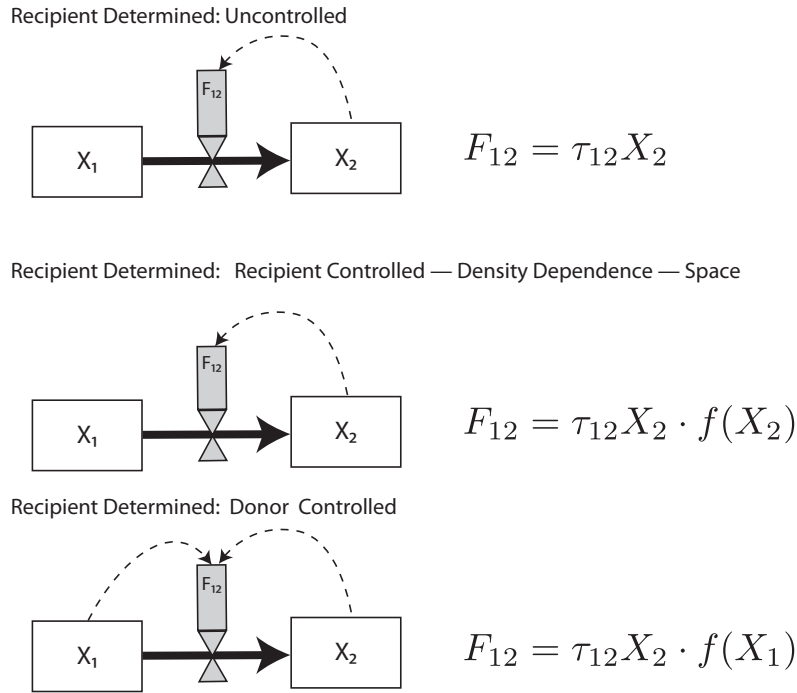
Recipient Determined: Uncontrolled

$$F_{12} = \tau_{12} X_2$$

Recipient Determined: Recipient Controlled — Density Dependence — Space

$$F_{12} = \tau_{12} X_2 \cdot f(X_2)$$

Recipient Determined: Donor Controlled

$$F_{12} = \tau_{12} X_2 \cdot f(X_1)$$

Figure 2: Examples of recipient determined flows. In this figure X_i $i = 1, 2$ are the state variables, F_{ij} is the process or flow, τ_{12} is a specific rate for the process, and $f(X_i)$ is a process control that is a function of X_i.

Figure 2 shows three examples of recipient determined flows with different types of controls.

3 Example Control Functions

In this section, I introduce a number of example formulations of process or flow controls. These controls will be added to the input or output process (flow) equations.

3.1 External Conditions or Resources

There are multiple functions for controlling a process by external conditions or resources such as temperature or light availability. We will discuss some of them in a different lecture. This simply serves as a place-holder for now. If you are curious, (Jørgensen and Bendoricchio, 2001) describes several functions for temperature and light in Chapter 3, and (Atanasova et al., 2006) presents a summary of useful functions.

3.2 Resource Controls

3.2.1 Michaelis-Menton or Monod

The Michaelis-Menton or Monod function is one of the more commonly used functions in ecological modeling. It was originally used by chemists to model reaction rate kinetics, but it is quite useful for many purposes. For this example, assume that there is some resources with concentration X_1, which could be a constant or a variable within our system, that might limit or control the growth of our system variable of interest.
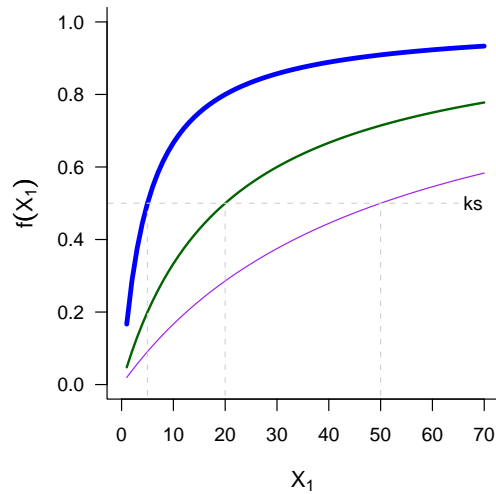
$$f(X_1) = k_{max}\frac{X_1}{(X_1 + ks)}$$

where ks is the 1/2 saturation constant. Notice that the curves are asymptotically growing to the $k_{max} = 1$ value.
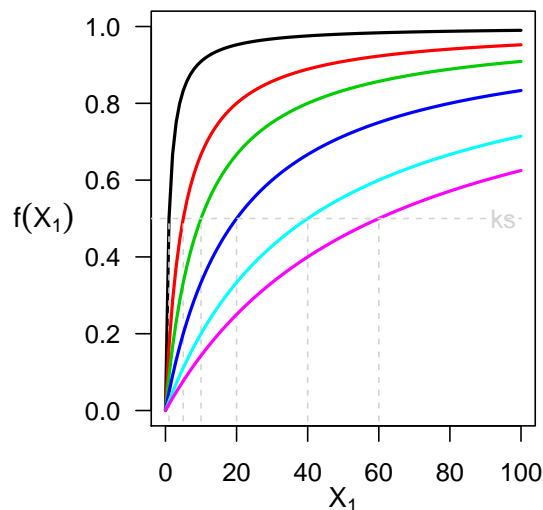
3.2.2 Hyperbolic form of the Michaelis–Menton Half Saturation

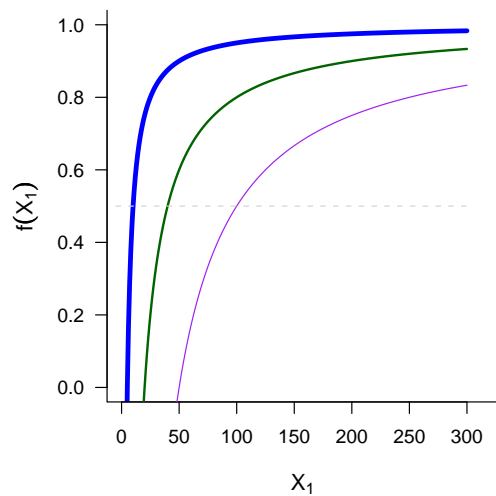$$f(X_1) = \left[1 - \frac{ks}{ks + X_1}\right]$$

Where ks is the $1/2$ saturation constant

3.2.3 Refuge form of the Hyperbolic Michaelis–Menton

$$f(X_1) = \left[1 - \frac{\alpha_{12}}{X_1}\right]$$

where α_{12} is a refuge concentration

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Assumptions

1. The maximum rate ($k_{max} = 1.0$) is not reached until resources are infinitely available. This is more problematic if we multiplicatively combine multiple control functions (see Section 5)

2. Limited to a convex upward hyperbolic curve, which may not match data.

3. If you use the refuge form, you cannot specify a half-saturation constant, but if you use the half-saturation form you cannot specify a refuge.

3.3   Logistic Function

Recall the original logistic equation that we discussed last meeting. This is an example of donor determined and donor controlled function. Gotelli (2008) presented the equation in standard form using population ecology notation as

$$\frac{dN}{dt} = rN * f(N) \tag{1}$$

$$f(N) = \left(1 - \frac{N}{K}\right) \tag{2}$$

where N is the population size, $r = b - d$ is the intrinsic growth rate, and K is the carrying capacity.

This equation makes most of the same assumptions as the exponential growth population equation as well as two others:

- constant carrying capacity, and

- linear density dependence.

For the ecosystem perspective, we can represent this equation as:

$$\dot{X}_2 = \frac{dX_2}{dt} = (\tau_{12} - \delta_2)X_2 * f(X_2) \tag{3}$$

$$f(X_2) = \left(1 - \frac{X_2}{K_2}\right). \tag{4}$$

In equation (4), X_2 is the state variable, τ_{12} is the ingestion or uptake rate, δ_2 is the specific loss rate, and K_2 is the carrying capacity. $\dot{X}_2$ is a convenient engineering notation that stands for $\frac{dX_2}{dt}$. I have also added subscripts to the parameters that refer to the variables to which they are related. For example, τ_{12} is the rate at which X_2 ingests material from a resource, which we indicate as subscript 1.

Notice that equations (2) and (4) are mathematically identical, we have just changed symbols and interpreted them slightly differently.

3.3.1 Wiegert's Problem and Trick for the Logistic Function

One of the assumptions of the logistic function is that the density dependent control operates simultaneously and equally on both births and deaths – or ingestion and loss rates in the ecosystem perspective. This may or may not be true for the specific system of interest. Further, there seems to be another more serious problem.

R.G. Wiegert, who was a pioneer of ecological modeling and a professor at the University of Georgia, suggested that there is a biological problem with the way that equation (4) is written. Given equation (4), it seems logical to write out the process rates as

$$\text{INGESTION} = \tau_{12}\left(1 - \frac{X_2}{K_2}\right), \text{ and} \tag{5}$$

$$\text{LOSS} = \delta_2\left(1 - \frac{X_2}{K_2}\right). \tag{6}$$

This satisfies the *mathematical* equation (4), but it violates the *biological* constraint that at equilibrium $\dot{X}_2/X_2 = 0$ both ingestion and the loss processes must be non-negative (≥ 0), even if the net growth rate is negative.

We can start to mathematically address this issue by rearranging the equations. First, we distribute and rearrange the terms on the RHS of equation (4) as:

$$\frac{\dot{X}_2}{X_2} = \underbrace{\left[\tau_{12}\left(1 - \frac{X_2}{K_2}\right)\right]}_{\text{Input}} - \underbrace{\left[\delta_2\left(1 - \frac{X_2}{K_2}\right)\right]}_{\text{Output}} \tag{7}$$

$$= \tau_{12} - \tau_{12}\frac{X_2}{K_2} + \delta_2\frac{X_2}{K_2} - \delta_2 \tag{8}$$

$$= \tau_{12} - (\tau_{12} - \delta_2)\frac{X_2}{K_2} - \delta_2 \tag{9}$$

$$= \tau_{12}\left(1 - \left(1 - \frac{\delta_2}{\tau_{12}}\right)\frac{X_2}{K_2}\right) - \delta_2 \tag{10}$$

Now, let $c = \left(1 - \frac{\delta_2}{\tau_{12}}\right)$ and we can rewrite equation (4) as

$$\frac{\dot{X}_2}{X_2} = \tau_{12}\left(1 - c\frac{X_2}{K_2}\right) - \delta_2 \tag{11}$$

and then the process rates are

$$\text{INGESTION} = \tau_{12}\left(1 - c\frac{X_2}{K_2}\right), \text{ and} \tag{12}$$

$$\text{LOSS} = \delta_2 \tag{13}$$

While this may seem like an overly complicated mathematical trick, we will discover that it can be quite useful. To make this idea more concrete, we will explore the details of Wiegert's trick in laboratory.

Egestion and Respiration   With our example above we are beginning to explicitly consider trophic processes. Our first process was ingestion, but as Odum's drawing in Figure 3 illustrates, not all ingested material is used by an organism to produce new organism biomass. Some energy–matter is egested or not used and another fraction of the input is lost through metabolic processes like respiration.

Unassimilated material is typically modeled as a fraction of ingested material that is loss from the donor but never enters the consumer. Thus, if τ_{12} is the maximum specific ingestion rate, then $\tau_{12}(1 - \epsilon_{12})$ is the effective assimilation rate where ϵ_{12} is the unassimilated fraction. What are the units of ϵ_{12}?

When we substitute this formulation of assimilation into equation (11) we generate

$$\frac{\dot{X}_2}{X_2} = \tau_{12}(1 - \epsilon_{12})\left(1 - c\frac{X_2}{K_2}\right) - \delta_2 \tag{14}$$

Respiration may be modeled as a separate loss processes, and is typically treated as an exponential function such that

$$\text{respiration} = \rho_2 * X_2. \tag{15}$$

However, it is probably more realistic to model respiration as a function of temperature. What mathematical formulation would you use? Why?

In equation (11) we are assuming that loss due to respiration is captured in our specific loss term δ_2.
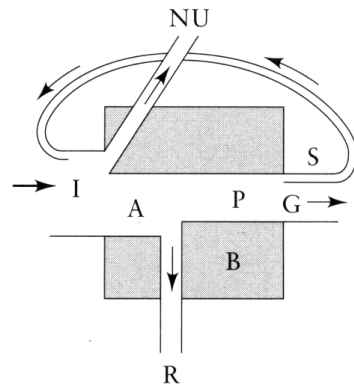
3.3.2   Generalized Logistic (non-linear relationships, refuges)

With these modifications to the logistic control of population growth, lets now add modifications including (1) adding a refuge α_{22}, (2) making the function capable of representing non-linear relationships, and (3) constraining the function to be positive using $+$.
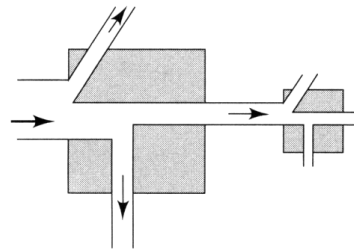
$$f(X_2) = \left[1 - c \cdot \left(\frac{X_2 - \alpha_{22}}{K_2 - \alpha_{22}}\right)^b_+\right]_+$$

$$c = \left[1 - \frac{\delta_2}{\tau_{12}(1 - \epsilon_{12})}\right]$$
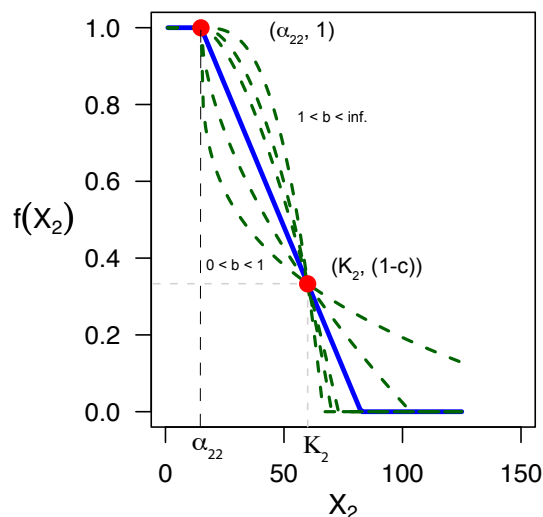
FIGURE 6.1 (a) E. P. Odum's "universal" model of ecological energy flow, which can be applied to any organism: I = ingestion; A = assimilation; P = production; NU = not used; R = respiration; G = growth; E = excreta; S = storage, as in the form of fat, for future use; and B = biomass.
(b) Representation of a food chain by Odum's energy flow models. The net production of one trophic level becomes the ingested energy of the next higher level. After E. P. Odum, *Am. Zool.* 8:11–18 (1968).

Figure 3: Odum's diagrammatic model of energy flowing through an organism.

In this formulation we have added (1) a refuge represented by α_{22}, (2) the exponent b, and (3) the $+$ notation. The refuge operates as a threshold below which density-dependent interference competition does not occur. b allows us to consider alternative shapes of the relationship between $f(X_2)$ and X_2. The $+$ notation indicates that we are keeping the function or part of the function positive. From a programming standpoint, we are using the maximum function as $\max(0, \left(\frac{X_2-\alpha_{22}}{K_2-\alpha_{22}}\right)^b)$. These modifications to the logistic address some of its short comings.

4 General Problems with "off the shelf" control functions

There are three main categories of problems[1]:

- The functions seldom incorporate thresholds, mainly because they were all developed and applied to ecological models of population growth and energy flow at a time when closed form solutions to sets of differential equations were the only practical means of manipulating such models.

- The functions usually commit the user to a single behavior of the control function, e.g. the logistic assumes a linear change with respect to change in density, the hyperbolic assumes a single convex upward asymptotic curve once either the half-saturation constant of refuge is chosen.

- Adequate consideration has seldom been given to the need for separate control functions to simulate the effects of resource limitation (exploitative competition) versus the effects of limits imposed by some form of scarcity of space (interference competition).

The control functions we have previously discussed in class try to address these three issues.

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[1]Wiegert 1999

5 Combining Control Functions

Once we have established how a particular factor effect the maximum process rate (μ_{max}), the next step is to consider how to combine multiple factors. Here we introduce three cases using the Michaelis–Menton 1/2 saturation function as an example. Figure 4 illustrates the mathematical consequences of the different combinations methods.

5.1 Essential

The first method of combining multiple resources is based on *Liebigs Law of the Minimum* which states "under conditions of equal temperature and light, the nutrient available in the smallest quantity relative to the requirement of the plant will limit productivity" (as quoted by H.R. Pulliam). This approach assumes that each resource is essential for growth. It is formulated as follows:

$$
\begin{aligned}
\mu(R_1, R_2) &= \mu_{max} \cdot \min[f(R_1), f(R_2)] & (16) \\
&= \mu_{max} \cdot \min\left[\frac{R_1}{R_1 + ks_1}, \frac{R_2}{R_2 + ks_2}\right] & (17)
\end{aligned}
$$

where R_1 and R_2 are two different factors (i.e., nutrient, temperature, etc.) and ks_1 and ks_2 are the respective 1/2 saturation constants.

Resources required in this fashion have been called *essential* or *complementary resources* in the literature.

5.2 Independent

Another possible way of combing limiting nutrients assumes that the effect of each resource is independent. Haefner (2005) refers to this case as multiplicative. In this case, both limitations operate simultaneously and are therefore multiplied together as shown in equation (18).

$$
\mu(R_1, R_2) = \mu_{max} \cdot \frac{R_1}{R_1 + ks_1} \cdot \frac{R_2}{R_2 + ks_2} \tag{18}
$$

The relative importance of the factors in determining the growth rate varies with the abundance of each. What do you think the disadvantage of this approach might be? Can you tell from Figure 4?

5.3 Substitutable

The final combination case we will discuss concerns completely substitutable resources: one resource will work just as well the other. Both resources are not required. H.R. Pulliam suggests that a good example of this is when a

predator can consume two types of prey that might differ in nutritional value. This combination is formulated as:

$$\mu(R_1, R_2) = \mu_{max} \cdot \frac{R_1 + (v_1/v_2)R_2}{R_1 + R_2 + ks} \tag{19}$$

Where v_1 and v_2 represent the size or nutritional contents of the prey types, and ks is a half-saturation constant. In the illustration below we assumed that $v_1 = v_2$. How would you expect the response surface to change when $v_1 \neq v_2$?
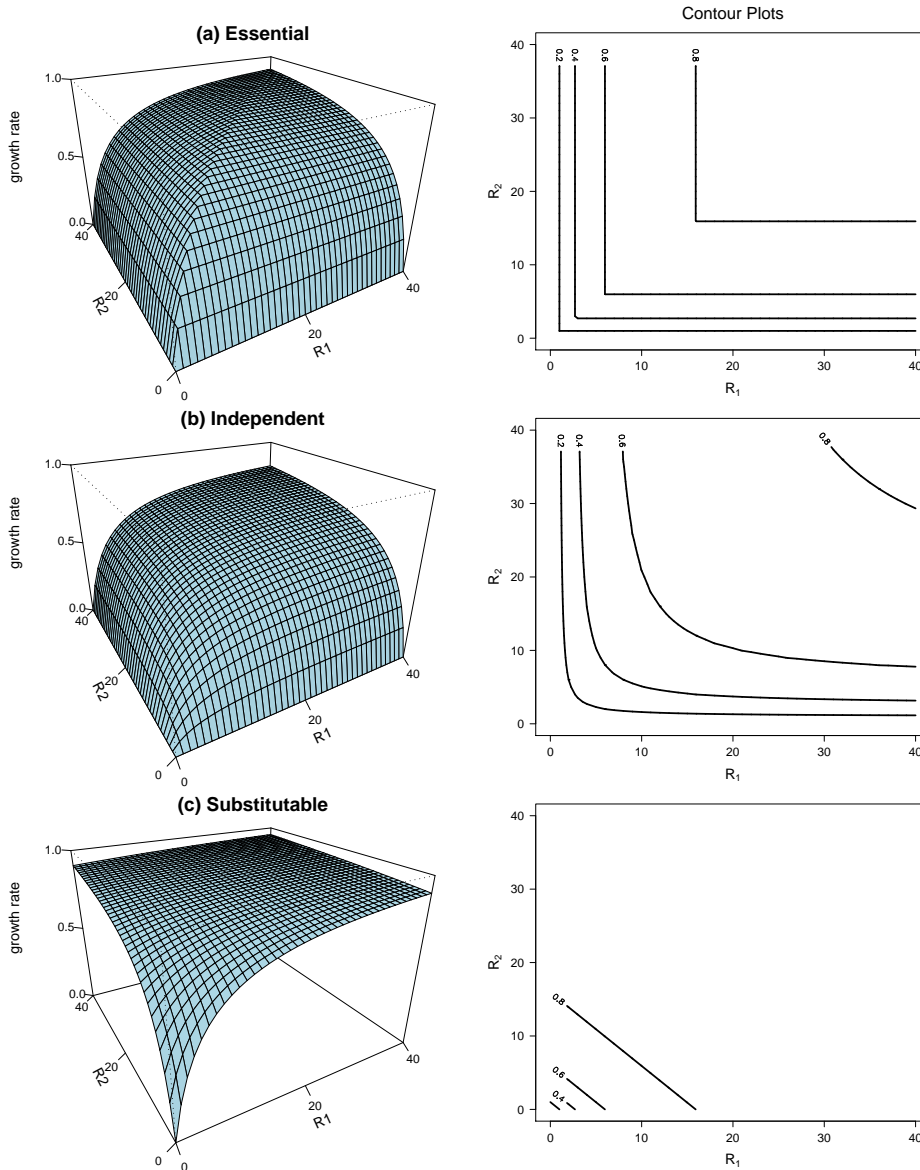

Figure 4: Result of combining two Michaelis–Menton functions assuming they are (a) essential, (b) independent, and (c) substitutable

References

Atanasova, N., Todorovski, L., Džeroski, S., Kompare, B., 2006. Constructing a library of domain knowledge for automated modelling of aquatic ecosystems. Ecol. Model. 194 (1), 14–36.

Bolker, B. M., 2008. Ecological models and data in R. Princeton University Press, Princeton.

Gotelli, N. J., 2008. A primer of ecology, 4th Edition. Sinauer Associates, Inc.

Haefner, J. W., 2005. Modeling Biological Systems: Principles and Applications, 2nd Edition. Springer, New York, NY.

Jørgensen, S., Bendoricchio, G., 2001. Fundamentals of ecological modelling. Vol. 21. Elsevier Science.

6   Appendix

6.1   Monod

```
# Monod Function Example
# Borrett | Sept. 23, 2014
# ---------------------
rm(list = ls())

X1 = 0:100    # select arbitrary values of the resource
ks = c(1, 5, 10, 20, 40, 60)  # selected 1/2 saturation values (same units as X1)
kmax = 1

fn <- "../figures/monod.pdf"         # file name
pdf(file=fn ,height=3.7, width=3.7)  # open PDF object
opar<-par(oma = c(0,0,0,0),
          mar = c(4,5,1,1),
          las = 1,
          cex.lab = 1.2)

for (i in 1:length(ks)){

  fx1 <- kmax * X1/(X1 + ks[i])

  if (i ==1) {
     plot(X1,fx1,
          type = "l", lwd = 2, col = i,
          xlab = "", ylab = "",
          ylim = c(0,kmax))
    mtext(bquote(f(X[1])), side = 2, line = 2.5, cex = 1.1)
    mtext(bquote(X[1]), side = 1, line = 2,cex = 1.1)
  } else {
     points(X1, fx1,
            type = "l", lwd = 2, col = i)
  }
  points(c(ks[i],ks[i]), c(-0.5, 0.5),
         type = "l", lty = 2, col = "lightgray")
}

  # -- Add Labels
points(c(-5, max(X1)), c(0.5, 0.5),
       type = "l", lty = 2, col = "lightgray")
text(95, 0.5,
     "ks", col = "lightgray")

dev.off()  # close PDF object

# open plot (on MAC)
```

```
cmd <- paste("open",fn)
system(cmd)

rm(opar)
```

6.2   Combining Control Functions

```
# Modeling Resource Control
# S.R. Borrett
# 10 October 2006
#
# This script shows growth rate surfaces in response to three ways of
# combining the effect of multiple resources. It is based on class
# notes from H.R. Pulliam.
###############################################################################
rm(list=ls())


R1 <- 0:40;  # resource
R2 <- 0:40;  # resource
k1 <- 4;       # 1/2 saturation constant
k2 <- k1
mu_max <- 1;   # maximum intrinsic growth rate of the species

# CASE 1: Liebig's Law of the Minimum
f1 <- function(R1,R2) {mu_max * pmin((R1/(R1+k1)), (R2/(R2+k2)))}
z1 <- outer(R1, R2, f1)
z1[is.na(z1)] <- 0


# CASE 2: Independent Resources
f2 <- function(R1,R2) {mu_max * (R1/(R1+k1)) * (R2/(R2+k2))}
z2 <- outer(R1, R2, f2)
z2[is.na(z2)] <- 0


# CASE 3: Substiutable Resources
v1 = 1;      # size or total nutritional content of R1
v2 = 1;   # size or total nutritional content of R2
f3 <- function(R1,R2) {mu_max * (R1+R2*(v1/v2))/(R1+R2+k1)}
z3 <- outer(R1, R2, f3)
z3[is.na(z3)] <- 0


##   PLOTS   ##
opar<-par(mfcol=c(3,2),las=1,
oma=c(1,2,3,1),mar=c(2,2,2,1),cex.main=2,
cex.axis=1.2,cex.lab=1.5)

persp(R1, R2, z1, theta = -30, phi = 25, expand = 0.7, col = "lightblue",
      ltheta = 120, lphi = 120, shade = 0.1, ticktype = "detailed",
      xlab = "R1", ylab = "R2", zlab = " ", main="(a) Essential",
      zlim=c(0,1),nticks=3)
mtext("growth rate",side=2,las=0,adj=0.75,line=1.5)

persp(R1, R2, z2, theta = -30, phi = 25, expand = 0.7, col = "lightblue",
      ltheta = 120, lphi = 120, shade = 0.1, ticktype = "detailed",
```

```
      xlab = "R1", ylab = "R2", zlab = "",main="(b) Independent",
      zlim=c(0,1),nticks=3)
mtext("growth rate",side=2,las=0,adj=0.75,line=1.5)


persp(R1, R2, z3, theta = -30, phi = 25, expand = 0.7, col = "lightblue",
      ltheta = 120, lphi = 120, shade = 0.1, ticktype = "detailed",
      xlab = "R1", ylab = "R2", zlab = "",main="(c) Substitutable",
      zlim=c(0,1),nticks=3)
mtext("growth rate",side=2,las=0,adj=0.75,line=1.5)


opar<-par(mar=c(5,5,1,1))
contour(R1,R2,z1,method="edge",
        levels=c(0.2,0.4,0.6,0.8,1),lwd=2,xlab=bquote(R[1]),
        ylab=bquote(R[2]),cex=1.2)
mtext("Contour Plots",line=1,side=3,cex=1.2)

contour(R1,R2,z2,method="edge",
        levels=c(0.2,0.4,0.6,0.8,1),lwd=2,xlab=bquote(R[1]),
        ylab=bquote(R[2]),cex=1.2)
contour(R1,R2,z3,method="edge",
        levels=c(0.2,0.4,0.6,0.8,1),lwd=2,xlab=bquote(R[1]),
        ylab=bquote(R[2]),cex=1.2)



##################

#opar<-par(mfrow=c(2,3),las=1,oma=c(1,1,1,1),mar=c(0,2,1,0),cex.axis=0.25)

#persp(R1,R2,Z1,theta = -20, phi = 10, expand = 0.7, col = "lightblue")
#opar<-par(oma=c(2,4,4,2))
#persp(R1, R2, z1, theta = -30, phi = 15, expand = 0.7, col = "lightblue" ,
#       ltheta = 120, lphi = 300, shade = 0.2, ticktype = "detailed",
#       xlab = "R1", ylab = "R2", zlab = "growth rate",main="Essential",
#       zlim=c(0,1),nticks=3) -> res
```