2

Models of simple and complex systems

2.1 Introduction

We have four objectives in this chapter. First, we present general approaches to developing the models that we will use throughout the book. The models will be deterministic models in nature, although they can be used and adapted to study the uncertainty of random fluctuations in the environment and in the parameters used to characterize the populations. Second, we discuss stability, the means that have been used to assess stability and other dynamic properties of the models, and special configurations of model systems that are inherently stable. Third, we will develop and assess the dynamics and stability of models that are based on primary producers and models that are based on detritus. Fourth, we will then compare the structure and dynamics of the two classes of models. We will revisit the approaches, concepts, and tools in the chapters that follow.

2.2 Model structure and assumptions

We describe two classes of models: one based on primary production and one based on detritus (Figure 2.1). Primary-producer-based models, as their name implies, start with populations of one or more primary producers that possess the ability to transform inorganic matter into an organic form. Detritus-based models start with one or more forms of nonliving organic matter (*aka* detritus) that originate from outside the system (an allochthonous source) and from within the system (an autochthonous source). The models will be based on variations of the familiar Lotka–Volterra form, by accommodating intraspecific competition and, in the case of nonliving materials, incorporating detritus. Furthermore, the models we will use possess a common currency of biomass (living or nonliving) bound by the conservation of matter and the first and second laws of thermodynamics. As such, whether viewed as open or closed to matter, a full accounting of inputs, outputs, and internal cycling of matter will be possible.

At this stage we will start with descriptions of the basal species and resources of the primary-producer-based and detritus-based models, and then follow with descriptions of the growth equations for the consumers of these resources. These descriptions will include a brief rationale for the structure and definitions of the parameters. The sections that follow provide a dimensional analysis of the growth

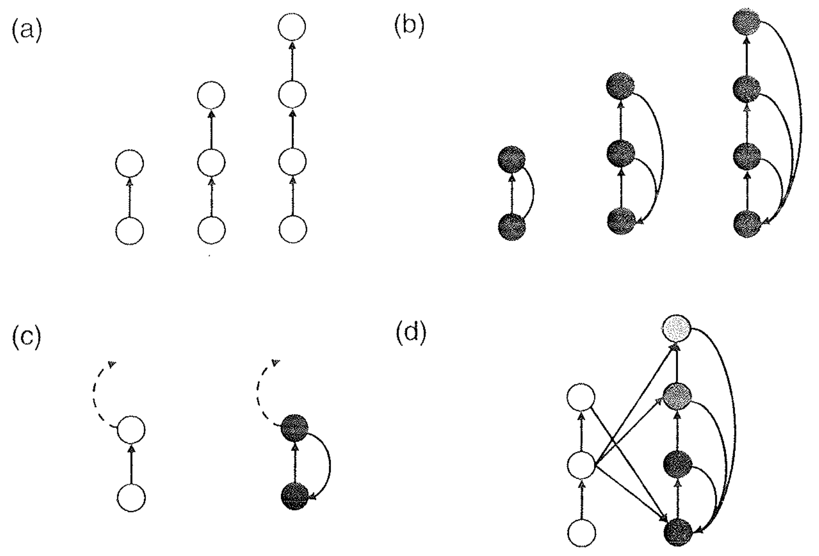


Figure 2.1 Simple food chains and food webs. Circles represent organisms or resources. Arrows represent flows of matter. Open circles are primary producers and their consumers. Black circles are detritus and their consumers. Shaded circles are consumers that consume or obtain energy from both types of food chains. (a) Primary-producer-based food chains of length 2, 3, and 4 include an autotroph at the base followed by consumers. (b) Detritus-based food chains of length 2, 3, and 4 include inputs of detritus from an outside (allochthonous) source, and cycled unassimilated organic matter and corpses from internal (autochthonous) sources. (c) Consumers in both types of food chains mineralize organic matter (dashed arrows, not depicted in the chains in a and b for clarity) and return unassimilated organic matter to the environment. For the detritus models, the unassimilated organic matter from consumption and the corpses of consumers is returned to the detritus pool as a basal resource. For the primary-producer-based models the unassimilated organic matter and corpses are accounted for but not included as an additional resource (i.e., they exit the system). (d) Models that link primary producers and detritus may cycle the unassimilated organic material and corpses through the detritus pool in an autochthonous manner or have a portion exit the system. The choices of the degrees to which organic material enters, cycles within, or leaves the system is entirely up to the modeler.

equations, and discussions on the functional responses, intraspecific competition coefficients, and the energetic efficiencies of fate of consumed matter.

The primary-producer-based models with n species will possess the following form:

$$\frac{dX_i}{dt} = r_i X_i - \sum_{i=1}^{n} f(X_i) X_j \tag{2.1}$$

where X_i and X_j represent the population densities of the primary producer and consumers, respectively, r_i is the specific growth rate of the primary producer, and $f(X_i)$

represents the functional response of the interaction between (species $i \neq j$) or within the populations (species $i = j$) (more of which we will discuss below).

The detritus-based models that include detritus and n species possess the following form presented by Moore et al. (1993):

$$\frac{dX_D}{dt} = R_D + \sum_{i=1}^{n}\sum_{j=1}^{n}(1 - a_j)f(X_i)X_j + \sum_{i=1}^{n} d_i X_i - \sum_{j=1}^{n} f(X_D)X_j \qquad (2.2)$$

Here we use the subscript D to simply highlight and keep track of where detritus arises in the equations. In subsequent chapters the subscript d may be replaced by the subscript 1. For the detritus based models, X_i and X_j represent the n living species and X_D is the nonliving detritus. Detritus enters the system from allochthonous and autochthonous sources. The allochthonous source, R_D, includes detritus that enters from outside the system. Examples might include kelp washing up onto a beach system, or leaves entering a stream. In this representation we include a single allochthonous source, but there is no reason that multiple sources could not be included. The model identifies two allochthonous sources, one from the unassimilated fractions of prey that are killed by consumers, $\sum_{i=1}^{n}\sum_{j=1}^{n}(1 - a_j)f(X_i)X_j$, which includes feces, orts, and leavings, and a second source from the corpses that die from causes other than predation, $\sum_{i=1}^{n} d_i X_i$. The functional response of the interactions between prey (living or nonliving) and consumers is presented by $f(X_i)$. Finally, the formulation for the direct consumption of detritus, $-\sum_{j=1}^{n} f(X_D)X_i$, resembles the consumption within the primary-producer-based equation (Equation 2.1).

We assume that detritus and living organisms within primary-producer-based systems and detritus-based systems are consumed in a density-dependent manner in the same way. For both classes of models the growth equations for consumers, X_i, can be described as follows:

$$\frac{dX_i}{dt} = -dX_i + \sum_{j=1}^{n} a_i p_i f(X_j)X_i - \sum_{j=1}^{n} f(X_j)X_i \qquad (2.3)$$

Consumer growth is offset by natural deaths represented by a specific death rate, d_i, and as a function of being consumed by other consumers, $-\sum_{j=1}^{n} f(X_j)X_i$, or is offset as a result of intraspecific competition (when $i = j$). In the case of intraspecific competition, the functional response, $f(X_i)$, is structured to model the impact of individuals of the same species (species i = species j) on their growth and dynamics, as above in Equation 2.1. The consumer populations grow in a density-dependent manner as a function of the living or nonliving prey that is consumed. This involves the summation of the consumption of individual prey types: $\sum_{j=1}^{n} a_i p_i f(X_j)X_i$. The consumption term incorporates the functional response, $f(X_i)$, found in Equations 2.1 and 2.2, but accounts for the assimilation efficiency, a_i, and consumption efficiency, p_i, of the consumer.

2.2.1 Dimensions of mass, area, and time

The dimensions of the models are expressed in units of biomass per area per time. The choice of units is arbitrary, but when scaled to the system under study they provide greater insight into the system. The population densities (X_i) and detritus densities (X_D) are expressed in terms of biomass per area. Biomass can be represented as the total live weight (e.g., g or kg), carbon (e.g., g C), nitrogen (e.g., g N), or another element, but on a dry weight basis. Area can be scaled to any set of units but generally is expressed in meters (m^2) or hectares (ha^2). Time is generally scaled to the birth and death rates of the primary producers at the base of the food web. For plant populations, we traditionally use an annual time step. Throughout the book the growth equations will be expressed as g C m^{-2} yr^{-1} or kg C ha^{-1} yr^{-1}.

The models possess two important rate-determining parameters: the specific birth (r_i) and specific death (d_i) rates. As explained below, these specific rates possess units of "per time." The specific birth rate (r_i), sometimes referred to as the intrinsic rate of increase, represents births minus deaths unrelated to consumption that is possible given the organism's life history and physiology within the chosen time step. The specific death rate (d_i) represents death not related to consumption. As a specific rate, it expresses the likelihood of the death of a unit of biomass per individual unit of biomass within the designated time step, having units of biomass per biomass per time, or simply per time. For the specific birth rate, we need to take into consideration the number (biomass) of progeny produced by an individual (biomass) within the time step. For the specific death rate, the inverse of the organism's life span is considered as a first approximation. We can also include deaths not related to consumption that are not explicitly included in the model (e.g., diseases, and deaths unaccounted for by predators).

2.2.2 Functional responses

The functional response, $f(X_i)$, characterizes how a predator adapts or adjusts its attack rate to changes in prey density. Many forms of functional responses have been proposed and their dynamic properties have been discussed at length elsewhere. Holling (1959) described three basic forms of functional responses, which he dubbed type I, type II, and type III (Figure 2.2). We will focus on these now, as each has important implications on how systems are structured and on their dynamic properties.

The type I, or linear functional, response is the simplest form of functional response, represented as follows:

$$f(X_i) = c_{ij}X_i \tag{2.4}$$

where c_{ij} represents the consumption coefficient with unit per biomass per time, and X_i represents the density in biomass of the prey species. The type I functional response depicts a relationship wherein the attack rate is constant, regardless of prey density. This approach has been criticized as being unrealistic, as consumers are likely to adapt their feeding rates with changes in prey density.

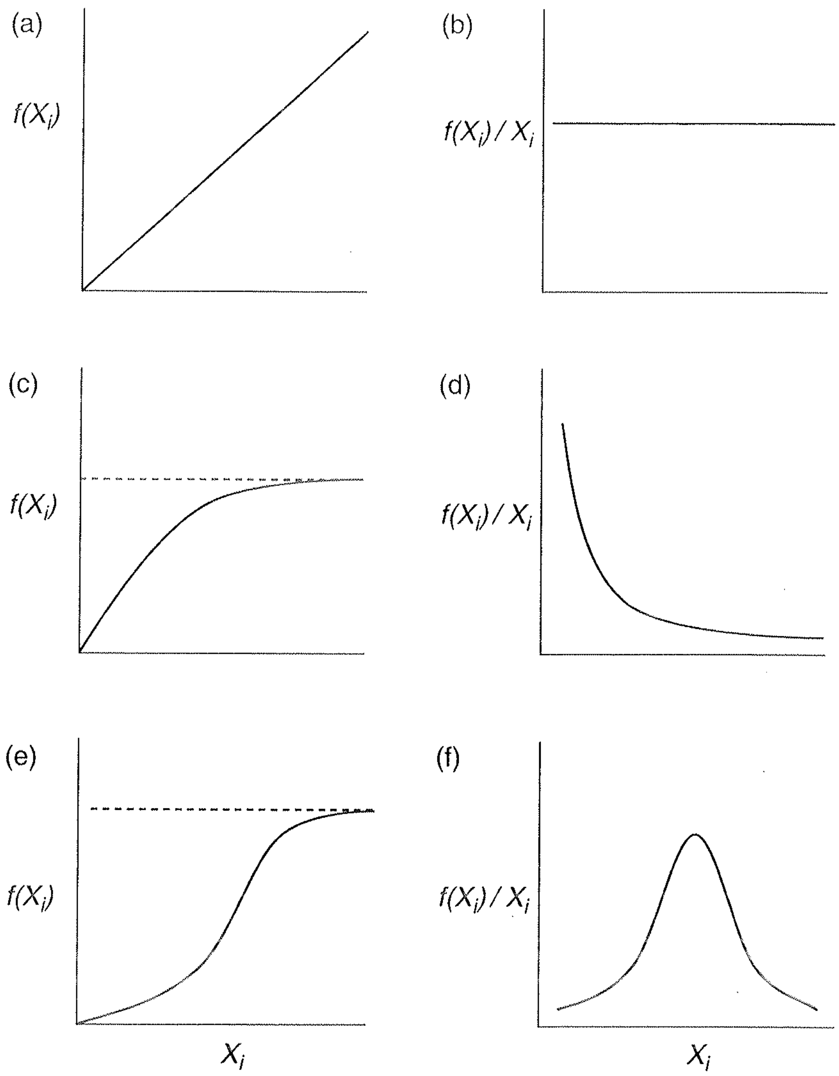


Figure 2.2 Functional response types described by Holling (1959). (a) Type 1 linear response: the feeding rate, $f(X_i)$, of the consumer increases linearly with prey density, X_i, and then becomes a constant value at the consumer's saturation point. (b) Relative mortality due to predation ($f(X_i)/X_i$) in the case of a type 1 linear response. (c) Hyperbolic type 2 functional response: the feeding rate increases with prey density but this increases continuously decreases until it becomes constant at saturation. (d) Relative mortality due to predation in the case of a type 2 hyperbolic response. (e) Sigmoid type 3 functional response: the feeding rate increases with prey density, first accelerating and then decelerating until the constant value is reached at the saturation level. (f) Relative mortality due to predation in the case of a type 3 sigmoid response.

The type II, or saturating functional, response is more realistic, and was originally represented by Holling (1959) as follows:

$$f(X_i) = \frac{cX_i}{1 + chX_i} \tag{2.5}$$

where c is the consumption or attack rate and h is the handling time. The type II functional response asserts that the attack rate increases with prey density to a point and then approaches a constant as the predator becomes satiated or is limited in its ability to process food. For this reason the form has all the properties of the Michaelis–Menton equations used to define enzyme kinetics. In fact with a little algebra, Equation 2.3 can be described by the Michaelis–Menton equation:

$$f(X_i) = \frac{\alpha X_i}{\beta + X_i} \tag{2.6}$$

where α is the maximum feeding rate when the consumer is satiated, and β is the prey density that generates half the maximum feeding rate, or the value of X where $\beta = \alpha/2$ defines the half-saturation point.

The type III, or switching functional, response can be derived directly from the generalized Michaelis–Menton equations as follows (Real, 1977):

$$f(X_i) = \frac{\alpha X_i^x}{\beta + X_i^x} \tag{2.7}$$

where x is the encounter rate where the predator is most efficient. When $x = 1$ the functional response is a Holling type II. When $x > 1$ the functional response is represented by a type III sigmoidal curve whose sill, like that of the type II functional response, is defined by handling time or satiation. The principal way it differs from the type II functional response is that its shape depicts an attack rate that is disproportionately low at low prey density, disproportionately high at high prey density, and constant when the predator is satiated. This type of response may represent a learning curve for consumers on prey types or switching behavior in cases where multiple prey are involved. The disproportionately low attack rate at low prey densities effectively serves as a refuge for the prey.

At first glance the graphical depictions of functional responses presented in Figure 2.2 might suggest that predators have a controlling effect on prey dynamics with increasing prey numbers, as the predation rate increases. From the standpoint of control or regulation, it is more important that we focus on how the *relative* mortality in the prey population, due to predation ($f(X_i)/X_i$), responds to changes in prey numbers (X_i). To illustrate this point, we have paired the traditional graphical representations of the different functional responses in Figure 2.2 with representations that show the relative contributions. For example, comparing the predation according to a type 1 linear response (Figure 2.2a) causes mortality that is neutral (Figure 2.2b), i.e., constant percentage-wise. The type 2 hyperbolic response (Figure 2.2c) means that mortality decreases with prey numbers, creating a destabilizing positive feedback (Figure 2.2d), i.e., the more prey the less mortality. The type 3 sigmoid response (Figure 2.2e), however, causes negative feedback at the relatively low prey numbers, i.e., the more prey (over that range) the higher the mortality (Figure 2.2f). This shows that a functional response has only a controlling effect on the prey numbers when the response has an accelerating shape and that an increase in prey numbers is followed by a disproportional increase in predation rate.

Functional responses have been established for many types of predator–prey systems and have been used to evaluate the consequences of the shape of the functional response for population dynamics and stability (e.g., Holling, 1965, Hassell, 1979). In most cases functional responses are established for single predator–prey interactions, but some include alternative prey from competitive predators (e.g., Hassell, 1979, Koen-Alonso, 2007). Measuring feeding rates through functional responses is a very laborious approach conducted under controlled field and laboratory conditions. Feeding rates have been based on direct observations of kills or consumption, and by indirect means including the number of corpses or amount of fecal deposition.

2.2.3 Energetic efficiency and conversion rates

The models take into consideration the energetic efficiencies of the trophic interactions. For our models we have defined the *energetic efficiency, e,* of a trophic interaction as the product of two components: the assimilation efficiency (a) and the production efficiency (p). Put another way, the energetic efficiency represents the ratio of immobilized matter or energy that forms new biomass in the form of individual growth or reproduction to the amount of matter or energy consumed, where

$$e = \frac{\text{Growth and Reproduction}}{\text{Consumed Biomass}} = ap \tag{2.8}$$

Equation 2.8 acknowledges that the energetic efficiencies of organisms are not perfect, yet must be greater than zero otherwise the organism dies, e.g., $0 < e < 1$. The fraction, $(1-e)$, represents the fraction of consumed prey or resource that remains in an organic form that is unassimilated (e.g., leavings and feces) by the consumer and the fraction that is assimilated by the consumer and mineralized to an inorganic form, i.e., the maintenance fraction.

$$(1-e) = \frac{\text{Unassimilated Consumption and Maintenance}}{\text{Consumed Biomass}} \tag{2.9}$$

Most models account for the energetic efficiencies of organisms. For our purposes, we need to refine the fractions further to account for fates of organic and inorganic matter. From Figure 2.3 we see that the matter that is consumed is separated into an assimilated fraction and an unassimilated fraction. *Consumption* of matter involves ingestion into a food vacuole or oral cavity, and then into a blind sac or gut. Not all the material that is consumed by an organism necessarily makes its way into the organism. For example, protozoa engulf materials into vacuoles or, in the case of amoebae, surround materials with pseudopodia. Once engulfed by the protozoan, materials are digested by enzymes secreted into the vacuole and move by diffusion

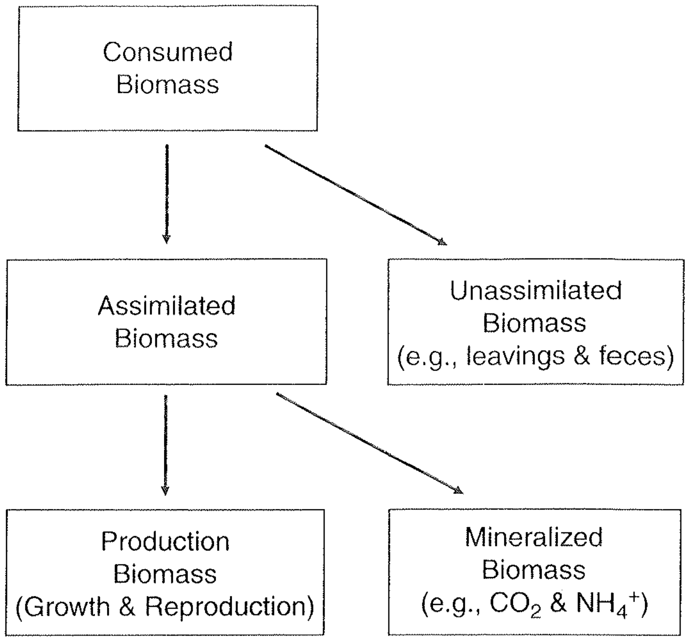


Figure 2.3 Scheme for the fate of consumed matter for given trophic interactions. The consumed biomass is divided into compartments determined by two energy conversion efficiencies. The assimilation efficiency defines the fraction of biomass of the prey or resource that is assimilated by the consumer. The unassimilated fraction is left behind, is egested, or passes through the consumer. The production efficiency is the fraction of assimilated that remains in the consumer and used for growth and reproduction. The remaining fraction is mineralized from organic to an inorganic form and returned to the environment. Estimates of these efficiencies for various taxa are readily available. If they are not available, they can be obtained through experimentation or approximated based on the body size, morphology, and physiology of the organisms.

across the cell membrane into the cytoplasm, with undigested materials remaining in the vacuole and then *egested*, or returned to the surroundings. Likewise, metazoans capture and kill prey, leaving unconsumed prey behind or returning the undigested prey to the environment as feces.

Of the material that has been *ingested*, a portion is used for growth, reproduction, and maintenance. *Assimilation* refers to the intake of molecules by an organism across cellular membranes so that they can then be used for these three processes. The *assimilation efficiency, a*, of an organism is the fraction of ingested or consumed matter that is assimilated.

$$a = \frac{\text{Assimilated Consumption}}{\text{Consumed Biomass}} \tag{2.10}$$

The unassimilated fraction, $(1 - a)$, represents the fraction that remains or is returned to the environment in either organic or inorganic form.

$$(1 - a) = \frac{\text{Egested Consumption}}{\text{Consumed Biomass}} \tag{2.11}$$

It is important to remember that the unassimilated material is organic material and is not lost to the environment, but rather serves as an energy source for other organisms. The unassimilated faction of consumed matter is left behind (leavings and orts), is evacuated from vacuoles (e.g., Protozoa) or gastric caecae (e.g., Cnidaria and Platyhelminthes), or is passed through the consumer as fecal material (e.g., protostomes and deuterostomes) and returned to the environment. These different forms of unassimilated organic compounds constitute either the autochthonous inputs of detritus that are returned to the labile or resistant detritus pool depending on their respective C:N ratios, or outputs (allochthonous inputs for another system) that leave the system. We have opted to assign a single value for the assimilation efficiency of a given taxon in our models. Clearly the assimilation efficiency will vary depending on the quality of the resource the taxon is consuming.

The second fate of consumed matter applies to the fraction that was assimilated. The assimilated fraction can be transformed into new biomass, i.e., *production*, as added biomass or reproduction, or can be used for maintenance. *Production* refers to the creation of new biomass as growth and reproduction from assimilated molecules. The *production efficiency, p,* of an organism is defined as the fraction of assimilated matter that is transformed into new biomass as growth and reproduction.

$$p = \frac{\text{Growth and Reproduction}}{\text{Assimilated Consumption}} \tag{2.12}$$

The maintenance fraction of the assimilated matter, $(1 - p)$, is the fraction that is returned to the environment in an inorganic form. For carbon, the maintenance fraction is the CO_2 respired; for nitrogen the fraction is nitrogenous waste (e.g., urea, ammonium).

$$(1 - p) = \frac{\text{Maintenance}}{\text{Assimilated Consumption}} \tag{2.13}$$

Coming full circle, we arrive at our definition for the *energetic efficiency, e,* of a trophic interaction presented in Equation 2.8 by taking into account both the assimilation efficiency, a, and the production efficiency, p.

The energy budget scheme presented above can be expanded on. We could define many more compartments than the four broad compartments used in this scheme. For example, we could further partition the unassimilated fractions into different forms, each serving as a separate basal resource. We could also expand the way in which the scheme is parameterized. Here we have opted to treat the assimilation and production efficiencies as constants. These were based on the physiology of the predator and the average quality of the prey. Prey types that are more recalcitrant than others might be assimilated differently and require greater metabolic energy for breakdown than more labile materials. The simplifications we used are arguably departures from reality, but for the purpose of the analyses, our assessment through sensitivity analyses leads us to believe that the impact of these simplifications on the outcome of the model is relatively small.

2.2.4 Intraspecific competition and self-limitation

Intraspecific competition, or self-limitation, represents the negative effects that individuals of a species within a population have on the growth of other individuals of the same species within the population. The process is modeled as being density dependent and tied to the acquisition or utilization for a resource including, but not limited to, a prey item, mates, space, essential nutrients, light, or water.

The original Lotka–Volterra models did not include intraspecific competition. Arguably, most, if not all, populations are subject to intraspecific competition and self-regulation to some degree. A simple representation starts with a model of a single species following Equation 2.1, with intraspecific competition modeled using a type I functional response (Equation 2.4):

$$\frac{dX_1}{dt} = r_1X_1 - c_{11}X_1X_1 \tag{2.14}$$

where c_{11} is the coefficient defining the degree of intraspecific competition. Equation 2.14 is a different representation of the equation of logistic population growth:

$$\frac{dX_1}{dt} = rX_1\left(1 - \frac{X_1}{K}\right) \tag{2.15}$$

where population equilibrium $X_1^* = r_1/c_{11}$, which is the carrying capacity K. What becomes clear from our discussion of stability, in the sections that follow, is that the functional response associated with intraspecific competition, $c_{11}X_1$, is central to the dynamics and stability of Equation 2.14. Below we will, in fact, demonstrate the importance of the functional responses for intraspecific competition, $c_{ii}X_i$, by extension of the systems of equations defining the interactions of multiple species.

2.3 Stability

Several definitions of stability have been developed and associated with ecological systems (McCann, 2000). Most meanings center on the ability of the system to maintain or return to a steady state in species composition, population size, and function in the face of perturbations. How we observe and study real ecosystems aligns well with our mathematical representations in models, but the fit is not perfect. Mathematical definitions of stability are less forgiving than those that we might base on observations given the assumptions on which they are based, and the contexts in which they are viewed. For example, many mathematical models of food webs often assume that the system operates at equilibrium or near equilibrium and are closed to immigration and emigration. In either case, if a species were to become locally extinct following a disturbance, the system would be deemed unstable in a mathematical sense. For real systems we might question the notion of a strict equilibrium and recognize that species often become locally extinct, only to return after some time. Other models do not take into consideration spatial variation or temporal variation in species composition, densities, or dynamics, but instead rely on spatial and temporal averaging. In these cases, local extinctions in space and time, and the ability of species to migrate from one locale to another may be important aspects of a systems dynamics and ability to persist, yet are missed when averages are employed.

Having said this, models require assumptions from which we can assess hypotheses and generate predictions. The challenge for us will be to select a framework or perspective to work with that captures enough biological realism and complexity and yet is tractable, both empirically and mathematically. As May (1973) pointed out, the factors that contribute to the stability at one level of resolution (locally) may not be the same as those that apply to the system as a whole (globally). That is, when a component of a system is viewed in isolation it may be stable, yet when coupled with others may not, and vice versa. We will review these notions of global and local stability, and properties of models that exhibit these types of dynamics.

2.3.1 Local stability

Local stability focuses on the dynamics of a system near equilibrium, regardless of the value of the equilibrium. For our purposes, we will focus on the subset of systems that have a feasible equilibrium, X_i^*, wherein all species have positive equilibrium densities ($X_i^* > 0$ for all i species). With local stability, if the system were disturbed causing any species to deviate, x_i, a small distance from its equilibrium ($x_i = X_i - X_i^*$) and in time the system returns to its original equilibrium, then the system is locally stable, and otherwise unstable. To model this we need to rewrite the system of equations using Taylor's expansion to represent the deviation (x_i) of a population (X_i) from its equilibrium (X_i^*), i.e., $x_i = X_i - X_i^*$. To understand the dynamics of the deviation it is useful to express these new equations in terms of their eigenvalues (λ_j) as follows:

$$\lambda x_i(t) = \sum_{j=1}^{m} \alpha_{ij} x_j(t). \qquad (2.16)$$

Equation 2.16 represents an nth order polynomial equation in λ of the Jacobian matrix A, whose elements are α_{ij}.

We can assess the local stability of a set of equations by analyzing the eigenvalues of the Jacobian matrix A as proposed by May (1972):

$$\frac{d\mathrm{x}}{dt} = A\mathrm{x} \qquad (2.17)$$

where x is the vector describing the state of the system in terms of the departures of the population sizes ($X_i - X_i^*$) from the equilibrium state (X_i^*), and A is the Jacobian matrix, in which the elements, α_{ij} describe the per capita effects of the populations upon one another under equilibrium conditions. The elements, α_{ij}, of A are defined as follows:

$$\alpha_{ij} = \left(\frac{\partial \frac{dX_i}{dt}}{\partial X_j} \right)^* \tag{2.18}$$

The stability of the system is governed by the eigenvalues (λ) of the matrix A. The eigenvalues are determined as follows:

$$\det|A - \lambda \mathrm{I}| = 0 \tag{2.19}$$

where I is the unit matrix with the same dimensions as A.

The eigenvalues may be complex numbers with real (ζ) and imaginary (ξ) parts, i.e., $\lambda = \zeta + i\xi$, each of which describes a component of the dynamics of the deviations x_i. The real part ζ influences the degree of exponential growth or decay in the deviation, while the imaginary part ξ introduces sinusoidal oscillations. If the real part ζ of all the eigenvalues is less than zero, the disturbance x_i decays and the system returns to its original equilibrium. The system is stable in the region of the equilibrium if the real parts of the eigenvalues, λ_i, of matrix A are negative. If one or more of the eigenvalues possess positive real parts, then the system is not stable, and if perturbed, will deviate from its original equilibrium. In this case we simply do not know what the configuration of the system will take over time, other than it will not return to its original state.

2.3.2 Qualitative stability

As expected, as the eigenvalues are defined in terms of the elements of A, there are conditions under which the patterns of the distribution and signs of the elements of A ensure stability. The Routh–Hurwitz criteria are based on one such patterning that can be used to gauge the stability of a system by knowing the signs of the interactions within the matrix A, without knowing the magnitudes of the elements of the matrix A. This can be useful as many of the published descriptions in the literature are connectedness descriptions devoid of any quantitative measures. For an $n \times n$ interaction matrix A with elements α_{ij} the conditions for local stability are as follows:

1. $\alpha_{ii} \leq 0$ for all species i.
2. $\alpha_{ii} \neq 0$ for at least one species
3. $\alpha_{ij}\alpha_{ji} \leq 0$ for all (i,j); $(i \neq j)$.
4. All sequences of three or more subscripts have cyclical products equal to zero, i.e., u, $v, w, \ldots, y, z$, such that $\alpha_{uv}\alpha_{vw} \ldots \alpha_{yz}\alpha_{zu} = 0$.
5. $\det A \neq 0$.

The biological meanings of the conditions are fairly straightforward. Condition 1 focuses on the diagonal elements of matrix A and requires that no species have a positive self-feedback term. If a positive feedback term were present, the deviation from equilibrium would simply grow in time. Condition 2 also focuses on the diagonal elements of matrix A, and further adds that at least one of the species is self-regulating, possessing a damping term. Without this condition the system could at best have positive terms, thereby violating Condition 1, or have all the terms equal to zero, leading to neutral stability wherein the population once disturbed cycles around the equilibrium, but never returns. Taken together Conditions 1 and 2 require that at least one of the species is constrained in some fashion by a limiting resource. Condition 3 requires that no two species that interact with one another have similar signs. This condition rules out direct inter-specific competition ($\alpha_{ij} < 0$ and $\alpha_{ji} < 0$) and mutualism ($\alpha_{ij} > 0$ and $\alpha_{ji} > 0$). Condition 4 eliminates the possibility of closed cycles of three or more species. This condition rules out most omnivorous interactions where a species preys on more than one species that occupy different trophic positions, and all such interactions within an isolated linear food chain or food chain embedded in a more complex web. Condition 5 insures that all species are either self-regulating and/or regulated by other species.

Qualitative stability is a useful tool for identifying stable configurations when the magnitudes of the elements of the community matrix are not known. However, we must remember that a system may be stable even though it is not considered to be qualitatively stable. In many cases, stability may depend on the magnitude of the elements and/or the patterning of elements of the community matrix.

2.3.3 Negative diagonal dominance and quasi-diagonal dominance

For descriptions that have estimates of the interactions' strengths the means to gauge stability are clear; evaluate the eigenvalues. There are cases where the configuration of the system ensures stability. For example, if the interaction matrix A possesses either a negative diagonal dominance configuration or a quasi-diagonal dominance configuration the equilibrium is stable. Both of these configurations involve assessing the relationships between the magnitudes of the diagonal elements to those of the off-diagonal elements of matrix A.

2.3.3.1 Diagonal dominance

A matrix A is diagonally dominant if the absolute value of each diagonal element is greater than the sum of the absolute values of the elements within its row:

$$|\alpha_{ii}| > \sum_{j \neq i} |\alpha_{ij}| \qquad (2.20)$$

McKenzie (1960) proposed the theorem that if a matrix A is dominant diagonally and the diagonal elements are all negative ($\alpha_{ii} < 0$ for all i), i.e., A is negative diagonally dominant, then the real parts of the eigenvalues of A are negative ($\lambda_i < 0$ for all i), hence A is stable.

This result has important implications when assessing the stability of ecological communities. At first glance the utility of McKenzie's theorem for ecological communities might appear tenuous, as the condition that all the diagonal elements are negative is rarely met. Traditional formulations of multispecies models include a negative self-limitation or intraspecific competition term along the diagonal for living basal species and consumption terms of detritivores on detritus that result in negative elements, $\alpha_{ii} < 0$, along the corresponding diagonal positions. The equations that describe the dynamics of the consumers in these descriptions often do not possess terms that lead to self-limitation or negative feedback along the diagonal, but typically result in $\alpha_{ii} = 0$.

The reason for the omissions appears grounded in part on a belief that not all species self-regulate at equilibrium and in part on a desire to simplify the equations. Regardless of the reason for the omissions, we argue that all living organisms exhibit some form of self-limitation due to crowding, the overexploitation of food resources or limiting nutrients, or a shortage of mates. If we add a density-dependent self-limitation term in the form of $-c_{ii}X_i^2$ to the equations for each living organism in the community, include feedback loops for their death, $-d_iX_i$, and unassimilated consumption to detritus, $(1-a_j)c_{ij}X_iX_j$, each of the diagonal elements of the Jacobian matrix A will be negative ($\alpha_{ii} < 0$ for all i). We will illustrate this point below for living species within the following three species omnivorous food chains:

$$\frac{dX_1}{dt} = r_1X_1 - c_{11}X_1^2 - c_{12}X_1X_2 - c_{13}X_1X_3 \tag{2.21a}$$

$$\frac{dX_2}{dt} = -d_2X_2 - c_{22}X_2^2 - c_{23}X_2X_3 + a_2p_2c_{12}X_1X_2 \tag{2.21b}$$

$$\frac{dX_3}{dt} = -d_3X_3 - c_{33}X_3^2 + a_3p_3c_{13}X_1X_3 + a_3p_3c_{23}X_2X_3 \tag{2.21c}$$

The Jacobian matrix A for this system of equations is:

$$A = \begin{bmatrix} -c_{11}X_1^* & -c_{12}X_1^* & -c_{13}X_1^* \\ a_2p_2c_{12}X_2^* & -c_{22}X_2^* & -c_{23}X_2^* \\ a_3p_3c_{13}X_3^* & a_3p_3c_{23}X_3^* & -c_{33}X_3^* \end{bmatrix} \tag{2.22}$$

The Jacobian matrix A presented in Equation 2.22 does not satisfy Condition 4 of the Routh–Hurwitz criteria for a qualitatively stable matrix and is, therefore, not qualitatively stable. Nonetheless the system may be stable depending on the magnitudes of the elements of matrix A, particularly since its diagonal elements are all negative. Matrix A would be negative diagonally dominant and therefore stable at equilibrium if, after some algebra, the following conditions were met:

$$\begin{aligned}
&1.\quad c_{11} > c_{12} + c_{13} \\
&2.\quad c_{22} > a_2 p_2 c_{12} + c_{23} \\
&3.\quad c_{33} > a_3 p_3 c_{13} + a_3 p_3 c_{23}
\end{aligned} \tag{2.23}$$

Most of the information required to evaluate the inequalities presented in Equation 2.23 can be readily obtained, as we will demonstrate in Chapter 4. The more difficult parameters to estimate are the coefficients for the self-limitation terms (c_{ii}). Knowing c_{ii} or having a convenient way to estimate it would simplify our analyses, but as we demonstrate below that all is not lost.

2.3.3.2 Quasi-diagonal dominance

An n x n matrix A representing community interactions with elements α_{ij} is quasi-diagonally dominant if there exists a set of n positive numbers $\pi_1, \pi_2, \ldots \pi_n$, such that the condition

$$\pi_i \alpha_{ii} + \sum_{j \neq i}^{n} \pi_j |\alpha_{ij}| < 0 \tag{2.24}$$

holds for every $i = 1,2,\ldots,n$. Moreover, if a matrix A is a negative diagonal matrix (i.e., all $\alpha_{ii} < 0$) and quasi-diagonally dominant, it is also stable (McKenzie, 1960).

DeAngelis (1975) conducted a series of analyses on models of simple food webs that provided plausible biological conditions (see inequalities presented in Equation 2.23) that would increase the likelihood of creating a system with a quasi-diagonal dominant matrix and meeting the conditions of Equation 2.24. These conditions included that: (1) consumers are inefficient either in terms of their energetic efficiencies or in terms of their capture rates, (2) consumers have high levels of self-limitations, and (3) the systems possessed donor-controlled dynamics. The first two conditions are apparent in the inequalities presented in Equation 2.23. The left-hand side of the inequalities contains the diagonal elements represented by the coefficients for self-limitation, c_{ii}. The right-hand side of the inequalities contains the off-diagonal elements composed of the consumption coefficients, c_{ij} and the predator energetic efficiencies, a_j and p_j. The first two conditions clearly tilt the system so that the diagonal elements of matrix A are large relative to the off-diagonal elements. The third condition deals with the impact of donor-controlled systems similar to those that involve detritus. We will discuss these types of systems in more detail below, but for now will leave the reader with the counterintuitive result that donor-controlled systems produce strong negative diagonal terms.

We will rely on the properties of negative diagonal dominance and quasi-diagonal dominance and employ variations of the procedures described above, offering a means for assessing and comparing the stability of complex multispecies models.

2.3.4 Quasi-diagonal dominance and loops

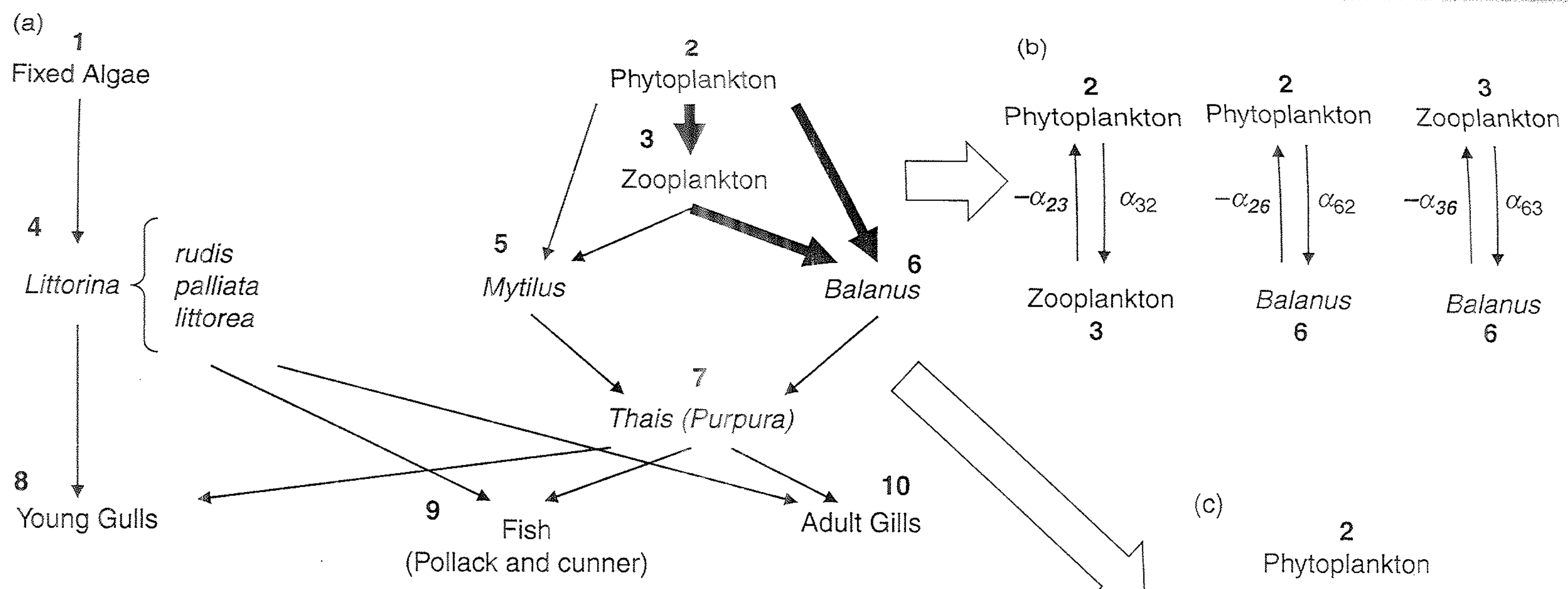
To understand the stability of complex communities, Neutel et al. (2002) studied food web structure in terms of trophic interaction loops. A trophic interaction loop is a closed chain of trophic links defined as a pathway of interactions that originate from a species through the web back to the same species without passing other species more than once (Figure 2.4). Being a pathway of interactions, an important distinction is that each step on the path going from one species to another refers to the interaction strength between the two species and not to the energy flux rate or to the feeding rate. For predator–prey interactions, the interaction loop includes the positive effects of prey on predators and the negative effects of predators on prey. Two important metrics of the trophic interaction loop are its length and weight. The length of a loop is the number of groups or species in the loop. Loop weight is a measure of the strengths of the interactions in the loop calculated as the geometric mean of the absolute values of the interaction strengths, (i.e., elements of matrix A) in the loop.

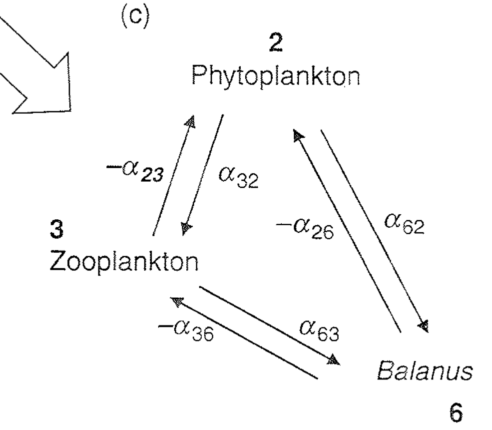
To illustrate these points, we turn to the example of a three-species omnivorous interaction within the food web by Colton (1916) that we presented in Chapter 1. The interactions among phytoplankton, zooplankton, and *Balanus* form two loops of length 3 (Figure 2.4). One of the loops consists of two top-down effects and one bottom-up effect; the other consists of two bottom-up effects and one top-down effect. The two loop weights for this omnivorous subsystem of length 3 can be calculated as:

$$W_1 = \sqrt[n]{(\alpha_{32}\alpha_{63}|\alpha_{26}|)} \tag{2.25}$$

$$W_2 = \sqrt[n]{(|\alpha_{23}||\alpha_{36}|\alpha_{62})} \tag{2.26}$$

The weights of the trophic interaction loops in food webs are an interesting property, as the maximum of all loop weights is an indicator for matrix stability (Neutel et al., 2002). By assuming $\alpha_{ii} = \alpha < 0$ for all i, and defining a positive matrix A with $\alpha_{ij} = |\alpha_{ij}|$ and $\alpha_{ii} = 0$, Neutel et al. (2002) argued that the dominant eigenvalue $\lambda_d(A)$ of A is the smallest value for intraspecific interaction necessary for A to be quasi-diagonally dominant and hence a sufficient condition for stability. In this way, the maximum loop weight provides an approximation of the level of intraspecific interaction, α_{ii}, sufficient for stability, and hence a means of estimating the α_{ii} elements of the A matrix at equilibrium. We will argue that the diagonal elements of the interaction matrices of our complex food webs can be expressed as $\alpha_{ii} = s_i d_i$, where d_i refers to all forms of nonpredatory death, both density-dependent and density-independent death, and s_i is the fraction that is density dependent. Hence for any food web with negative diagonal elements, we can adjust the value of s_i to find the critical values of s_i required for matrix stability.





$$A = \begin{bmatrix} -\alpha_{11} & 0 & 0 & -\alpha_{14} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -\alpha_{22} & -\alpha_{23} & 0 & -\alpha_{25} & -\alpha_{26} & 0 & 0 & 0 & 0 \\ 0 & \alpha_{32} & -\alpha_{33} & 0 & -\alpha_{35} & -\alpha_{36} & 0 & 0 & 0 & 0 \\ \alpha_{41} & 0 & 0 & -\alpha_{44} & 0 & 0 & 0 & -\alpha_{48} & -\alpha_{49} & -\alpha_{4,10} \\ 0 & \alpha_{52} & \alpha_{53} & 0 & -\alpha_{55} & 0 & -\alpha_{57} & 0 & 0 & 0 \\ 0 & \alpha_{62} & \alpha_{63} & 0 & 0 & -\alpha_{66} & -\alpha_{67} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \alpha_{75} & \alpha_{76} & -\alpha_{77} & -\alpha_{78} & -\alpha_{79} & -\alpha_{710} \\ 0 & 0 & 0 & \alpha_{84} & 0 & 0 & \alpha_{87} & -\alpha_{88} & 0 & 0 \\ 0 & 0 & 0 & \alpha_{94} & 0 & 0 & \alpha_{97} & 0 & -\alpha_{99} & 0 \\ 0 & 0 & 0 & \alpha_{104} & 0 & 0 & \alpha_{107} & 0 & 0 & -\alpha_{1010} \end{bmatrix}$$

Figure 2.4 Trophic loops in food webs based on feeding relationships. (a) The connectedness food web description of the Mount Desert Island, Maine, rocky intertidal (Colton, 1916) from Chapter 1 (upper panel) and the Jacobian matrix A derived from system of the differential equations that describe the trophic dynamics (lower panel). The black arrows isolate a three-species omnivorous trophic loop that includes phytoplankton, zooplankton, and *Balanus*. (b) Given that every two-species trophic interaction creates a simple trophic loop of length 2, the three-species omnivorous loop for three loops of length 2: $(\alpha_{3,2}, -\alpha_{2,3})$, $(\alpha_{3,2}, -\alpha_{2,3})$, and $(\alpha_{3,2}, -\alpha_{2,3})$. (c) The three-species omnivorous loop possess two loops of length 3: $(\alpha_{6,2}, -\alpha_{3,6}, -\alpha_{2,3})$ and $(-\alpha_{2,6}, \alpha_{6,3}, \alpha_{3,2})$.

2.3.4.1 Global stability

Global stability analyses study the system over a wider landscape, encompassing larger perturbations. A system that is globally stable will return to equilibrium from any initial condition, i.e., deviation from equilibrium, and not just those that are close to equilibrium. Complications arise in assessing global stability because the trajectory that the system takes following the disturbance may involve moving away from the equilibrium.

Physical analogies of landscapes are often invoked to convey the distinction between local and global stability (May, 1973, Pimm, 1982). Picture a hilly, sloping landscape pocked with craters. The analogy for a local stability analysis would be as follows. Assume our system were a round object nestled at the bottom of a crater (at equilibrium) that was pushed up the wall of the crater but not over its lip (a short distance from the equilibrium). If released, our system would return to its original position at the basin (locally stable). To be globally stable, the analysis would have to take into account what would happen to our system if it were pushed over the lip of the crater. In this case the trajectory is less clear, but if it were globally stable it would eventually return to the basin of the crater.

Global stability can be assessed by identifying a Lyapunov function, V, and determining whether the time derivative of V is less than or equal to zero, i.e, $dV/dt \leq 0$, provided that all the solutions are bounded for $t \geq 0$. We will demonstrate below that for simple food chains described as primary producer-based and detritus-based food chains Lyapunov functions have been identified that meet these conditions, indicating that both types of models are globally stable.

2.4 Simple food chains

Here we will explore the structural and dynamic properties of simple food chains based on primary producers and detritus (Figure 2.1). We will focus more attention on the discussion for the detritus-based models as the literature is replete with detailed descriptions and analyses of the primary producer-based models. More complex forms will be presented in Chapter 6.

The connectedness descriptions of the food chains are presented in Figure 2.1. The number of trophic levels refers to the number of energy states (sensu Odum, 1953) that the system possesses. Energy at the base of the system, whether from a primary producer or detritus, resides in the first trophic level. Energy from the first trophic level that is consumed and incorporated into the biomass of the consumer resides in the second trophic level. Energy from the second trophic level that is consumed and incorporated into the biomass of the consumer resides in the third trophic level, and so on. The trophic position of an organism is defined by the relative contribution of each trophic level plus 1 to its steady state biomass. For our simple linear food chain, the energy that resides in each trophic level corresponds to the organism's trophic position within the food chain. For systems that include omnivores (organisms that obtain energy from more than one trophic level) the concordance between trophic levels and the trophic positions of organisms abates.

Before delving much further into the discussion we first define the notion of feasibility as it is related to the densities of species at steady state (Roberts, 1974). A system is feasible if all the species possess positive densities at steady-state, i.e., $X_i^* > 0$ for all i species. This may seem like a trivial point, but it is important if we are to model systems that are biologically realistic. It does not make sense to model the dynamics of a system in which one or more of the populations possess negative densities, much less to try to define such circumstances biologically.

2.4.1 Primary-producer-based food chains

A simple two-species primary-producer-based food chain depicting a plant, X_1, (Equation 2.12a), and a herbivore, X_2, (Equation 2.12b) is given by:

$$\frac{dX_1}{dt} = r_1 X_1 - c_{11} X_1^2 - c_{12} X_1 X_2 \tag{2.27a}$$

$$\frac{dX_2}{dt} = -d_2 X_2 + a_2 p_2 c_{12} X_1 X_2 \tag{2.27b}$$

The equilibrium values are as follows:

$$X_1^* = \frac{d_2}{a_2 p_2 c_{12}} \tag{2.28a}$$

$$X_2^* = [(r_1 a_2 p_2 c_{12}) - (c_{11} d_2)]/(a_2 p_2 c_{12}^2) \tag{2.28b}$$

The Jacobian Matrix, A, is given by:

$$A = \begin{bmatrix} -c_{11} X_1^* & -c_{12} X_1^* \\ a_2 p_2 c_{12} X_2^* & 0 \end{bmatrix} \tag{2.29}$$

The critical eigenvalue, λ_{max}, that dominants the dynamics of this model is as follows:

$$\lambda_{max} = \frac{\alpha_{11} + \sqrt{\alpha_{11}{}^2 + 4\alpha_{12}\alpha_{21}}}{2} \tag{2.30}$$

The equilibrium of this two-species system is locally stable as both the eigenvalues are negative. Goh (1977) demonstrated that if food chains described using generalized Lotka–Volterra models of the form as those described above, are feasible (all $X_i^* > 0$), then the equilibrium is globally stable as well. If a Lotka–Volterra model for n interacting species has the following form:

$$\frac{dX_i}{dt} = r_i X_i + \sum_{i,j=2}^{k} c_{ij} X_i X_j \quad i = 1, ..., n \tag{2.31}$$

and has a nontrivial equilibrium (i.e., the system is feasible as all $X_i^* > 0$), then the Lyapunov function

$$V(X) = \sum_{i=1}^{n} l_i \left[X_i - X_i^* - X_i^* \ln \frac{X_i}{X_i^*} \right] \tag{2.32}$$

has the following time derivative expressed only in terms of the intraspecific parameters (Harrison 1979):

$$\frac{dV}{dt} = \sum_{i=1}^{n} l_i c_{ii} (X_i - X_i^*)^2 \tag{2.33}$$

As for the intraspecific competition coefficient, $c_{ii} \leq 0$, $dV/dt \leq 0$, the system is globally stable. Harrison (1979) went on to prove that simple food chains described in this manner with an intraspecific competition term at the first level assures global stability.

2.4.2 Detritus-based food chains, internal cycling, and donor control

Here we will discuss models that include detritus at the base, followed by detritivores and predators. While there are similarities in the ways in which detritus-based and primary-producer-based models behave, there are key differences that may have important implications.

We know that not all the energy that is captured by primary producers is consumed in the manner described above and not all the energy that sustains a food web arises directly from living primary producers within the ecosystem. Most primary production is not consumed while living, but rather is released into the environment as nonliving detritus to be consumed by a host of organisms. In many instances, detritus leaves the system from which it originated, only to enter another system. In fact, few ecosystems are based entirely on homegrown energy, but instead are a composite of internally (autochthonous) and externally (allochthonous) derived energy, a point we will discuss further below. Autochthonous inputs include feces, exuvia, fallen leaves, dead roots, orts, and corpses that remain in the system. Allochthonous inputs include the same materials imported from another system.

The balance between the levels of autochthonous and allochthonous inputs of energy into a food web creates an interesting array of dynamics. DeAngelis (1980) defined food chains and webs that are based on detritus inputs as donor-controlled systems. Under donor control, the population density and rate of input of the donor has an effect on the consumer population density and dynamics, whereas the population density and dynamics of the consumer has no direct effect on the dynamics of the donor population or resource. Odum (1969) noted that the balance of internal and external levels of detritus and nutrient inputs played a more important role in the maintenance—and, by implication, stability—of mature ecosystems. Although the empirical evidence supports the notion that the internal origins of detritus and nutrients become more prevalent in mature systems, the basis for the proposition that it is important to the stability and persistence of the system is not obvious from observation alone.

2.4.2.1 *Models of donor-control dynamics*

We will elaborate on the equations we introduced in Section 2.2 that included both allochthonous and autochthonous inputs, the conceptual model of which is presented in Figure 2.1. The equations for dynamics of the detritus pool and its consumers were defined as follows:

$$\frac{dX_1}{dt} = R_D - a_2 c_{12} X_1 X_2 + d_2 X_2 \tag{2.34a}$$

$$\frac{dX_2}{dt} = -d_2 X_2 + a_2 p_2 c_{12} X_1 X_2 \tag{2.34b}$$

where X_1 and X_2 are the densities of detritus and the consumer, respectively, R_D is the allochthonous input of detritus, d_2 is the specific death rate of the consumer, a_2 is the assimilation efficiency, p_2 is the production efficiency, and c_{12} is the consumption coefficient of the consumer on the detritus.

For a two-species linear detritus food chain based on Equations 2.34a and 2.34b, the equilibrium values for detritus (X_1) and the consumer (X_2) are as follows:

$$X_1^* = \frac{d_2}{a_2 p_2 c_{12}} \tag{2.35a}$$

$$X_2^* = \frac{R_D p_2}{d_2(1 - p_2)} \tag{2.35b}$$

The equilibrium for the detritus using this formulation is somewhat fixed, as it is solely dependent on the death rate, energetic efficiencies, and feeding behavior of the consumer. The equilibrium of the consumer is feasible for all R_D and d_2, as the production efficiency is defined as being $0 < p_2 < 1$, and increases as R_D increases.

The Jacobian matrix (A) for our two-species detritus-based system is as follows:

$$A = \begin{bmatrix} -a_2 c_{12} X_2^* & d_2 - a_2 c_{12} X_1^* \\ a_2 p_2 c_{12} X_2^* & 0 \end{bmatrix} \tag{2.36}$$

An interesting feature of the model is that the diagonal term of the interaction matrix corresponding to detritus (α_{11}) is negative even though the model does not possess a term for intraspecific competition (*aka* self-limitation). Instead, the negative diagonal term arises from the internal, or autochthonous, cycling of detritus.

Three important points that merit clarification and qualification emerge when discussing allochthonous inputs and donor-controlled systems. First, the definition of an allochthonous input is scale dependent and, more specifically, boundary dependent. The movement of resources across habitat boundaries is a common phenomenon. Leaf litter entering a soil system might be considered allochthonous if we consider the aboveground realm separate from the belowground realm. However, this is hardly the case, as consumption and utilization of leaf litter by detritivores and microorganisms provide crucial nutrients that impact plant growth and development (Coleman et al., 1983, Moore et al., 2003, Wardle et al., 2004). The corpses of microorganisms and invertebrates, and the unassimilated fraction of each trophic interaction, have the potential to feed back within the system, affecting plant growth.

Second, few ecosystems are devoid of allochthonous inputs and few are based entirely on them. Interestingly, the examples of systems that represent either end of the spectrum involve isolated aphotic systems such as deep-sea hydrothermal vents and caves. Those devoid of allochthonous inputs rely on chemolithotrophic microorganisms to obtain their energy from inorganic compounds. Sarbu et al. (1996) found that the Movile Cave ecosystem in Romania was based entirely on in situ chemoautotrophic energy sources with no allochthonous sources derived from photosynthetic or detritus sources. Sealed from the surface for over 5 million years, the chemoautotrophic bacteria use hydrogen sulfide as an energy source to fix inorganic carbon, resulting in thick mats of bacteria and fungi that float on the water surface. The mats support an assemblage of 48 species of invertebrates that include microbial grazers and predators. Cave ecosystems also provide examples of systems that rely entirely on allochthonous inputs from surface communities (Culver, 1982). Moore et al. (1996) found that the Wind Cave ecosystem in South Dakota was based largely on allochthonous energy sources in the form of windblown plant debris, hair, skin, and feces from rodents, and clothing fibers, hair, and skin from tourists. The allochthonous energy sources supported a diverse array of bacteria, fungi, and invertebrates (Jesser, 1998, Horton, 2005).

Finally, although not restricted to detritus, the majority of the cited examples of donor-controlled systems include detritus as the allochthonous energy source (Polis and Strong, 1996, Huxel and McCann, 1998, Moore et al., 2004). So it is not surprising that detritus-based systems are thought to be the quintessential model of donor-controlled systems. The original formulations of donor-controlled systems differed from our presentations in an important manner, as they often did not include the internal cycling of detritus. For this reason, we could argue that the detritus-based models presented here contain elements of a donor-controlled model, but are not strictly donor controlled.

2.4.2.2 The stability of donor control and detritus

The two-species system of detritus and decomposers described above in Equations 2.34a and 2.34b are not only locally stable, but globally stable as well (Neutel et al., 1994). A critical feature of the results hinged on the inclusion of the allochthonous input, R_D, and the internal cycling of materials due to natural death of the decomposers, d_2X_2. In their analysis, Neutel et al. (1994) noted that for the energy function V as defined by Goh (1977) to serve as a Lyapunov function, as in Equation 2.32, would require some substitutions, as the direct manner employed by Harrison (1979) for the Lotka–Volterra analogs could not be applied. Neutel et al. (1994) demonstrated that the two-species detritus-detritivore model is globally stable, as V is indeed a Lyapunov function applicable to this system with a time derivative as follows:

$$\frac{dV}{dt} = -l_1 \frac{(X_1 - X_1^*)^2}{X_1 X_1^*}(R_D + d_2 X_2) \leq 0. \tag{2.37}$$

Huxel and McCann (1998) add a different dimension to the influence of allochthonous resources, and detritus in particular, on the dynamics of a system. They studied simple tri-trophic models that coupled an allochthonous resource with an autochthonous resource through a common consumer, where each consumer–resource interaction used a type II functional response. The dynamics and stability of the system was governed by two factors: 1) the level of allochthonous input, and 2) the degree of the consumer's preference for the autochthonous source. If the flow of energy shifted too strongly from the autochthonous source towards the allochthonous source either through feeding preferences or increased rates of input of the allochthonous source, the food web was prone to collapse.

The rationale and discussion provided above gives us a place to start our assessment of Odum's proposition about the increasing importance of detritus and internal nutrient cycling to the maintenance and persistence of ecosystems during the early stages of development to their mature stage (Odum, 1969). Assume that a mature ecosystem is at a steady state in terms of primary production, the inputs that it receives from outside sources, and respiration. At a steady state the primary production of the system is in balance with respiration. If outside sources of detritus enter the system, and the system is at a steady state, then the composition of the decomposer community would adapt to compensate for the internally generated materials and the externally generated materials. In either case, net primary production equals respiration.

Recall that the stability of the system is governed by the eigenvalues (λ) of the matrix A. For our simple model of detritus and a detritivore (Equation 2.34) the eigenvalues are determined as follows:

$$\det|A - \lambda I| = 0 \tag{2.38}$$

where,

$$\lambda^2 + (a_2 c_{12} X_2^*)\lambda - (a_2 p_2 c_{12} X_2^*)(d_2 - a_2 c_{12} X_1^*) = 0 \tag{2.39}$$

The solution to the quadratic equation in λ, yields the following for the critical eigenvalue λ_{max}:

$$\lambda_{max} = \frac{-a_2c_{12}X_2^* + \sqrt{(-a_2c_{12}X_2^*)^2 + 4(a_2p_2c_{12}X_2^*)(d_j - a_2c_{12}X_1^*)}}{2} \tag{2.40}$$

As we discussed above, the equilibrium of the system is both locally stable and globally stable. The discriminant, μ, of Equation 2.40 is less than $-a_2c_{12}X_2^*$ as the constant of the quadratic is negative, and $X_2^* > 0$, hence λ_{max} is always negative. The rate that the deviation from steady state decays is governed by the linear coefficient $-a_2c_{12}X_2^*$, which at steady state (from Equation 2.35b) can be expressed as follows:

$$-c_{12}R_D\frac{e_2}{d_2\left(1-\frac{e_2}{a_2}\right)} \tag{2.41}$$

where $e_j = a_jp_j$ represents the energetic efficiency of the detritivore. Leading up to the steady state, the dynamics are dominated by the influence of the increased input of detritus, as seen for both the steady-state density of the detritivores and the linear coefficient of the solution to the quadratic for λ_{max}. If we were to view the system at a steady state with a fixed rate of consumption of detritus, $c_{12}R_1$, the dynamics are controlled internally by the ecological efficiency, e_2, and the specific death rate, d_2, of the detritivore, both of which reflects the rate of turnover of the of the detritivore and detritus. As $e_2 \rightarrow 1$ and $d_2 \rightarrow \infty$, the linear coefficient $\alpha_{11} \rightarrow 0$. Although our two-species detritus-based system is globally stable, as $\alpha_{11} \rightarrow 0$, the capacity of the system to stabilize more complex arrangements as proposed by Huxel and McCann (1998) at a given rate of input diminishes. This is a topic we will revisit.

2.5 The dynamics of primary-producer-based and detritus-based models

How different are the dynamics of primary-producer-based and detritus-based models? We will evaluate factors that affect the feasibility and resilience of our simple two-species, three-species, and four-species primary-producer-based and detritus-based food chains. We will follow a variation of the approach used by Pimm and Lawton (1977), wherein the feasibility and resilience of our simple two-species, three-species, and four-species primary-producer-based and detritus-based food chains were compared. For this exercise we constructed 10,000 food chains of each type using equations 2 and 3, where the consumer–resource interactions used type I functional responses. All parameters were sampled from a uniform distribution, I (0,1). We estimated resilience as the return time (RT) defined as RT = –1/real (λ_{max}), where real(λ_{max}) is the real part of the dominant (least negative) eigenvalue (Pimm and Lawton 1977). Under this definition, RT represents the time it takes the deviation x_i to decay to $1/e$ ($\approx$37%) of its original value.

At first glance the primary-producer-based and detritus-based food chains behaved similarly (Figure 2.5). In both cases, feasibility decreased and return times increased with increased food chain length. However, direct comparisons of the two types of food chains of the same length revealed that if a higher proportion of the detritus were feasible, the return times were shorter than for their primary-producer counterparts. The decline in feasibility for both types of food chains was precipitous, to the point that fewer than 5% of the detritus-based and 1% of the primary-producer-based food chains could persist under the parameter selection, and subsequent level of productivity, they represented. One surprising result is that all of the two-species detritus-based food chains were feasible over the range of productivity that we chose. As we will demonstrate in a subsequent analysis in Part II, this result recurs over a wide range of productivities and suggests that the lower limit of production (detritus input) needed to support a detritivore may indeed be a limit defined by minimum cell size and physiology.

We can draw three conclusions from this exercise. The first conclusion is that both the primary-producer-based and detritus-based food chains behave in a qualitatively similar manner for the measures that we employed. The second conclusion is that the decline in the proportion of feasible food chains with increased food chain length are consistent with the hypothesis that food chains are limited by the rate of production (Hutchinson, 1959). In this exercise the terms used to define the rate of production at the base of the food chain (r_i and R_D) were on average the same within each type of food chain, but the realized rates were higher on average for the detritus-based equations owing to the internal cycling of detritus and the way in which inputs were defined ($r_1X_1^*$ for the primary-producer-based food chains and R_D for the detritus-based food chains). Nonetheless, in both cases increasing the length of the food chains from two species to four species places a greater exploitative pressure on a fixed rate of production. The third conclusion is that the increase in the return times for both types of food chains with increased length suggests that dynamics cannot be ruled out as a limiting factor. To understand this we need to invoke the concepts of persistence and variability for the simple formulations that we used here. As Pimm (1982) pointed out, systems with long return times are neither more nor less vulnerable to disturbances than those with short return times, as both are stable. However, in a stochastic environment, systems with long return times are likely to experience the type of catastrophic perturbations that could occur in any system.

2.6 Summary and conclusions

We have developed primary-producer-based and detritus-based models that possess familiar forms in ways that meld the traditional approaches of theoreticians and empiricists in the fields of population, community, and ecosystem ecology. The models track the dynamics of living and nonliving biomass. Both classes of models are flexible in nature and could be adapted and scaled to a number of community and ecosystem types. In developing the equations and assessing their dynamics and

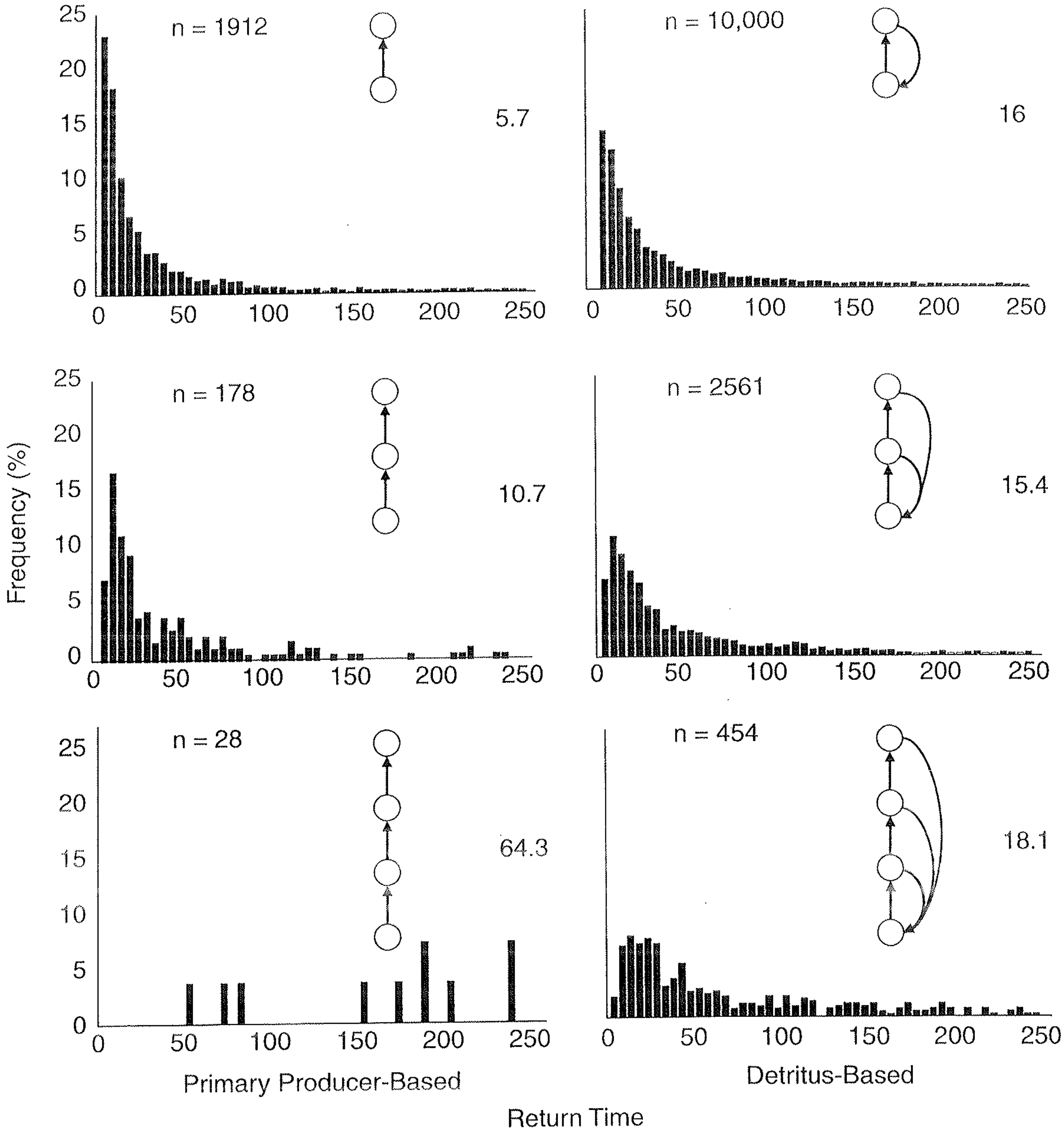


Figure 2.5 Frequency distributions of return times for the primary-producer-based and detritus-based food chains of length 2, 3, and 4 depicted in Figure 2.1 using Equations 2.1–2.3 with type I functional responses. All parameters in the models were assumed to possess a uniform distribution over the interval (0,1). The analysis included 10,000 trials for each food chain. The number of trails that produced feasible food chains (n) wherein each species possessed a positive equilibrium is presented in the upper left corner of each graph. The number to the right of the food chains represent the percentage of return times that exceeded 250 time units (the selection of 250 as a stopping point was arbitrary).

stability we are left with the unmistakable conclusion that trophic structure, dynamics, energy flow, and stability are interrelated.

We discussed the concept of stability, drawing on themes and approaches that have been treated at length elsewhere (May, 1973, Pimm, 1982, DeAngelis, 1992, Cushing et al., 2003). We assessed the stability of simple two-species primary-producer-based and an analogous simple two-species detritus-based model. The models were found to possess similar Jacobian matrices, and hence similar dynamic properties. The detritus-based models included elements that were donor controlled and elements that were density dependent. These attributes led to an interesting condition wherein the growth and dynamic of nonliving detritus is constrained in a self-limiting manner, much like living organisms.

At this stage we have treated primary producers and detritus separately, in part for pragmatic reasons to provide a historical perspective and a familiar basis for comparison. We will continue along these lines in later chapters, but will link the two in our discussions of complex multispecies food webs.