

## CHAPTER 1

# Population and Ecosystem Approaches in Ecology

Building a theory that merges population, community, and ecosystem ecology requires at the very least that the fundamental descriptions of reality provided by the various subdisciplines be compatible with each other. But meeting this basic requirement is far from being a trivial issue given the widely different conceptual foundations and formalisms used by population and community ecology on the one hand and by ecosystem ecology on the other. In this introductory chapter, I first briefly revisit the foundations and formalisms of the population and ecosystem approaches in ecology. I then show how mass and energy budgets can bridge the gap between them. Last, I present a minimal ecosystem model to illustrate how an approach based on mass and energy budgets can be used to build simple models that combine the flexibility of demographic models and the physical realism of ecosystem models. The approach developed in this chapter will be the basis for most of the models presented in the rest of the book.

### THE FORMALISM OF POPULATION DYNAMICS: EXPONENTIAL AND DENSITY-DEPENDENT GROWTH

A population is a set of organisms from the same biological species in a given area. Since all individuals belonging to the same species are very similar to each other when considered over a whole life cycle, classical approaches to population ecology ignore variability among individuals and assume that these are identical. As a consequence, population dynamics focuses on changes in the number or density of individuals that make up the population. Thus, population ecology fundamentally has a demographic approach to reality, in which the basic unit of measurement is the individual.

Population dynamics is implicitly or explicitly based on the following balance equation, which tracks the fate of individuals from time  $t$  to time  $t + 1$ :

$$N_{t+1} = N_t + B + I - D - E. \quad (1.1)$$

In this equation,  $N_t$  is the number of individuals at time  $t$ , and  $B$ ,  $I$ ,  $D$ , and  $E$  are the numbers of births, immigrants, deaths, and emigrants, respectively, during the time interval from  $t$  to  $t + 1$ . The time unit is arbitrary; it may be a day, a year, or a generation, depending on the kind of organisms considered. This demographic balance equation simply states that the population at time  $t + 1$  is the population at time  $t$ , plus the individuals that have been added to the population by birth or immigration, minus the individuals that have been removed from the population by death or emigration.

In the simplest case, assume a closed population (no immigration or emigration), a constant environment, and density-independent growth; i.e., the per capita demographic parameters are independent of population density. In this case,  $I = E = 0$ ,  $B = bN_t$ , and  $D = dN_t$ , where  $b$  and  $d$  are constant per capita birth and death rates, respectively. Equation (1.1) then reduces to the familiar equation

$$N_{t+1} = N_t + bN_t - dN_t = \lambda N_t, \quad (1.2)$$

where  $\lambda = 1 + b - d$  is the finite rate of increase of the population.

This equation says that population size is multiplied by a factor  $\lambda$  during each time unit. Starting from  $t = 0$  and iterating the process over  $t$  time units yields

$$N_t = N_0 \lambda^t. \quad (1.3)$$

Thus, the population is predicted to grow geometrically at a rate  $\lambda$  per time unit.

An identical prediction is obtained assuming that demographic processes are continuous instead of discrete in time, which leads to the following differential equation:

$$\frac{dN}{dt} = \beta N - \delta N = rN, \quad (1.4)$$

where  $\beta$ ,  $\delta$ , and  $r$  are instantaneous per capita rates of birth, death, and population growth, respectively. This equation can be integrated to give

$$N(t) = N_0 e^{rt}, \quad (1.5)$$

which is identical to equation (1.3) with  $\lambda = e^r$ .

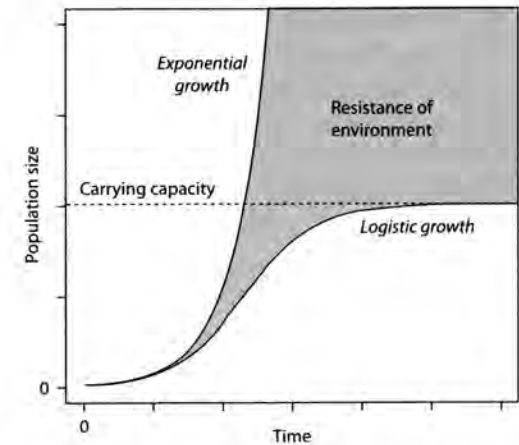


FIGURE 1.1. Exponential and logistic population growth. Populations tend to grow exponentially in the absence of environmental constraints, but logistically up to a carrying capacity when resources are finite. The difference between the two growth curves (gray area) can be interpreted as the resistance of the environment to unlimited growth. The carrying capacity, however, is a phenomenological abstraction that stands for a wealth of undefined ecological factors.

This fundamental equation of population dynamics, which is also known as Malthus's (1798) law, describes the inherent capacity of all organisms for exponential or geometric population growth (figure 1.1). *Exponential population growth* is a remarkably robust property as long as population processes are density-independent. It holds irrespective of spatial and temporal variations in demographic processes and population structure. If demographic processes vary in space or time, the finite and instantaneous population growth rates  $\lambda$  and  $r$  are simply replaced by appropriate spatial or temporal averages in equations (1.3) and (1.5). If age or stage structure is explicitly considered, the finite population growth rate  $\lambda$  is obtained from the projection matrix that describes transitions of individuals among age or stage classes (Caswell 1989). Exponential growth has been shown in numerous laboratory and natural populations under conditions of unlimited resource availability or low population density. The global human population itself is roughly experiencing exponential growth. More details on this topic can be found in theoretical ecology textbooks (e.g., Case 2000).

The propensity of populations to grow exponentially is an expression of the autocatalytic nature of biological systems and represents a fundamental

source of instability in ecological systems. Basically, all organisms multiply as much as they can—until something prevents them from continuing to do so. And that is where ecology comes into play. All organisms are embedded in a complex web of interactions with their environment, which includes other organisms as well as abiotic factors. As populations grow, they modify their own environment through these multiple interactions, which feeds back on their capacity to grow further.

Classical population ecology makes the simplest possible assumption regarding these environmental feedbacks: it assumes that they can be reduced to a dependence of demographic processes on the population's own density. As the population grows, it progressively exhausts resources such as space, food, and nutrients, and as a result it decreases its potential to grow further. This convenient assumption eliminates the need to consider the complex web of interactions that organisms maintain with their environment and focuses on their net effect on the population variable under consideration. *Density dependence* is formally defined as a dependence of the per capita population growth rate on population density. In the continuous formalism of equation (1.4), which is the formalism that I shall use in most of this book, density dependence is expressed as

$$\frac{dN}{Ndt} = f(N), \quad (1.6)$$

with  $f'(N) \leq 0$ ; i.e., the per capita growth rate monotonically decreases as population size increases.

The simplest form for the density-dependence function  $f(N)$  is a linear form, which yields the classical *logistic equation* proposed by Verhulst (1838):

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right). \quad (1.7)$$

In this equation,  $r$ , which is known as the intrinsic rate of natural increase, represents the maximum instantaneous population growth rate when population density is very low (close to zero), and  $K$  is known as the carrying capacity.

The logistic equation predicts a sigmoid growth pattern with a nearly exponential growth at low population size and a nearly exponential approach to a stable equilibrium population size equal to the carrying capacity (figure 1.1). This can be seen easily by noting that when population size is very small compared with the carrying capacity ( $N \ll K$ ), the term in parentheses in equation (1.7) vanishes, and equation (1.4) describing exponential growth is recovered. On the other hand, when  $N$  approaches  $K$ , a

first-order Taylor expansion of the right-hand side of equation (1.7) around  $K$  yields

$$\frac{dn}{dt} = -rn, \quad (1.8)$$

where  $n = N - K$  is a perturbation from the equilibrium value  $K$ . Thus, the logistic equation predicts an exponential decline of perturbations in the vicinity of the carrying capacity at the same rate as the exponential growth of population size at low density. In other words, density dependence stabilizes the population by counteracting its inherent tendency toward exponential growth and instability.

Logistic growth has been shown in numerous populations, especially in the laboratory under resource limitation. The reason why the logistic equation works so well under controlled laboratory conditions is simple: the linear density-dependence function in the logistic equation may be viewed as a first-order approximation to any form of density dependence. Logistic growth, however, is much less robust than density-independent exponential growth. Departures from the implicit assumptions of continuous demographic processes, constant environmental conditions, instantaneous operation of density dependence, and lack of population structure, can lead to periodic or chaotic population dynamics under logistic growth. These dynamical behaviors are qualitatively different from the stable equilibrium point predicted by the classical model. Again, more details on this topic can be found in theoretical ecology textbooks (e.g., Case 2000).

A more fundamental problem—from the perspective developed in this book—is that the density dependence included in the logistic equation in the form of the carrying capacity is a phenomenological abstraction. Parameter  $K$  is a condensed substitute for a wealth of factors and interactions that limit population growth, such as resources, competitors, mutualists, predators, parasites, and diseases. It is not even possible to disentangle the contributions of birth and death processes to density dependence in equation (1.7) since these are lumped into the parameters  $r$  and  $K$ .

Despite these limitations, the logistic equation has served as a basis for much of theoretical community ecology. The famous Lotka–Volterra models for interspecific competition or mutualism are direct extensions of the logistic equation in which the density-dependence function  $f(N)$  in equation (1.6) is simply expanded to become a linear function of the population sizes of other interacting species. The classical Lotka–Volterra model for predation does not include direct density dependence but is built on the same principle; i.e., per capita growth rates are linear functions of population sizes.



Although many refinements and developments have been added to the theoretical corpus of community ecology, community ecology is largely an outgrowth of population ecology in its conceptual and methodological foundations. Most dynamical models in community ecology are based on a demographic approach that implicitly takes into account demographic balance constraints of the kind encapsulated in equation (1.1), but they ignore explicit physical constraints such as mass and energy balance (although there are exceptions, of course). As a result, community ecology has a strong focus on the structure, dynamics, and complexity of ecological systems, but it generally does not consider their overall functioning.

#### THE FORMALISM OF ECOSYSTEM FUNCTIONING: MASS AND ENERGY FLOWS

Ecosystem ecology does not have a simple fundamental law equivalent to the Malthusian law of exponential growth in population dynamics. Consequently, the approaches developed to model ecosystems have been somewhat more variable than in population ecology. The simplest and most common approach, however, has been that of compartmental modeling, which was pioneered by Lotka (1925). Ecosystem ecology is mainly concerned with the stocks and fluxes of materials or energy through the system as a whole, and this is explicitly what compartmental models represent. A *compartmental model* describes a set of compartments, the size of which is measured by the stock of materials or energy they contain, which are connected by fluxes of materials or energy. *Mass or energy balance* is explicitly taken into account in the description of these fluxes.

The basic building block of these models is a single-compartment model open to material or energy exchanges with the outside world. As an example borrowed from DeAngelis (1992), take a water body with a constant volume  $V$  that contains a solute of concentration  $C$ , and through which water flows at a constant rate  $q'$  per unit time, and let  $C_I$  be the solute concentration in the inflowing water. The principle of conservation of mass states that the rate of change of the mass of solute in the compartment equals the rate at which mass enters that compartment minus the rate at which mass leaves that compartment. Since the mass of solute in the compartment is  $CV$ , this principle is expressed in the following dynamical equation:

$$\frac{d(CV)}{dt} = q'C_I - q'C. \quad (1.9)$$

Dividing both sides by the constant volume  $V$  and rescaling the water flow rate as  $q = q'/V$  yields

$$\frac{dC}{dt} = q(C_I - C), \quad (1.10)$$

which has the solution

$$C(t) = C_I + (C_0 - C_I)e^{-qt}. \quad (1.11)$$

This solution shows that the solute concentration in the water body tends asymptotically to the concentration in the inflowing water (the second term on the right-hand-side tends to zero as time goes to infinity, which leaves  $C = C_I$ ) and that the deviation between the initial ( $C_0$ ) and final ( $C_I$ ) concentrations declines exponentially with time at a rate  $q$ . Thus, this system smoothly approaches a stable equilibrium concentration set by the inflowing water, at a rate governed by water flow. The water flow rate  $q$  sets the characteristic time of the system. It measures the rate at which the system approaches its equilibrium, which is one common measure of resilience (DeAngelis 1992). It also determines the mean residence time of the solute in the compartment, also called the turnover time of the system, which is obtained as the ratio of the equilibrium mass of solute ( $C_I V$ ) over the equilibrium mass flow of solute ( $q' C_I = q C_I V$ ), i.e.,  $1/q$ .

This single-compartment model can easily be generalized to an arbitrary number of compartments coupled by material or energy flows. Take, for example, an ecosystem with two compartments 1 and 2, in which compartment 1 (say, plants) receives an input of a material such as carbon, part of the carbon contained in compartment 1 is transferred to compartment 2 (say, animal consumers) through some trophic interaction, and both compartments lose carbon to the external world through respiration or some other interaction (figure 1.2). Call  $X_i$  the carbon stock of compartment  $i$ ,  $f_{ij}$  the rate at which a unit of carbon is transferred from  $i$  to  $j$ , with 0 standing for the external world, and  $I_{01}$  the input of carbon to compartment 1 per unit time. The principle of conservation of mass then yields the following system of differential equations:

$$\begin{aligned} \frac{dX_1}{dt} &= I_{01} - f_{10}X_1 - f_{12}X_1, \\ \frac{dX_2}{dt} &= f_{12}X_1 - f_{20}X_2. \end{aligned} \quad (1.12)$$

This system can be rewritten in matrix form as

$$\frac{d\mathbf{X}}{dt} = \mathbf{F}\mathbf{X} + \mathbf{I}, \quad (1.13)$$

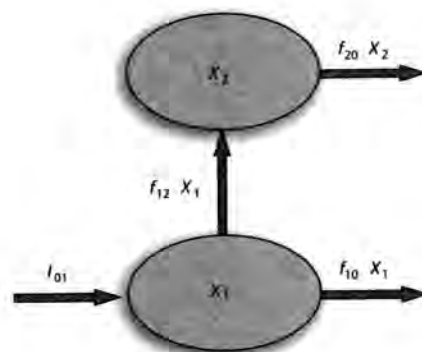


FIGURE 1.2. An abstract two-compartment ecosystem model. Circles represent energy or material stocks, while arrows represent energy or material flows.

where

$$\mathbf{X} = \begin{pmatrix} X_1 \\ X_2 \end{pmatrix}, \quad \mathbf{F} = \begin{pmatrix} -f_{10} & -f_{12} & 0 \\ f_{12} & & -f_{20} \end{pmatrix}, \quad \mathbf{I} = \begin{pmatrix} I_{01} \\ 0 \end{pmatrix}.$$

It is not difficult to show that this coupled system has similar properties as the previous single-compartment system. The equilibrium values (which will be denoted by an asterisk in this book following common usage) of the carbon stocks of the two compartments are easily obtained by setting the time derivatives equal to zero in equations (1.12) and solving for  $X_1^*$  and  $X_2^*$ :

$$\begin{aligned} X_1^* &= \frac{I_{01}}{f_{10} + f_{12}}, \\ X_2^* &= \frac{I_{01} f_{12}}{(f_{10} + f_{12}) f_{20}}. \end{aligned} \quad (1.14)$$

These equilibrium stocks are proportional to the carbon input into the system as before. The stability of the system is now governed by the eigenvalues of matrix  $\mathbf{F}$ , which contains the rate constants of carbon flows (except for the carbon input, which is independent of the system's dynamics). These eigenvalues can be shown to be both real and negative, thereby ensuring that the equilibrium is asymptotically stable (May 1973; Puccia and Levins 1985).

In contrast to population dynamical models, compartmental models used to describe mass and energy flows in ecosystems seem to be particularly stable and well behaved. This is, however, a consequence of the implicit or explicit assumptions about the physical constraints that govern these systems. For instance, the above single-compartment model is really a physical model based on the assumption that water flow drives the

dynamics of the solute. The two-compartment ecosystem model assumes that carbon flows are either constant (driven from outside) or linear functions of internal carbon stocks, which erases the complexity of biological interactions that might be involved in these transfers. Thus, the smooth behavior of ecosystem models is often a consequence of the perspective adopted by ecosystem modelers. Ecosystem ecology has traditionally been concerned with predictable whole-system functional processes, ignoring much of the diversity and dynamical complexity of the organisms that constitute them. Some have even argued that linearity is an intrinsic property of ecosystem processes (Patten 1975), but this is a viewpoint that cannot be taken at face value. We shall return to this issue of the stability and predictability of ecosystem processes with new insights derived from more rigorous theory in chapter 5.

#### MASS AND ENERGY BUDGETS AS A BASIS FOR UNIFYING POPULATION AND ECOSYSTEM APPROACHES

The demographic and functional perspectives offered by population and ecosystem ecology are rooted in different concepts and principles. But, clearly, population dynamics has to be compatible with the physical principles of conservation of mass and energy, just as ecosystem functioning has to be compatible with the demographic law of exponential growth. How, then, can we lay a bridge between these two approaches?

Ecosystem ecology is essentially a physiology of ecological systems. It analyzes the functioning of an ecosystem in ways similar to those of physiology for individual organisms. In particular, ecosystem ecology and ecophysiology share the concepts of mass and energy budgets as tools for understanding the acquisition, allocation, and disposal of materials and energy in the metabolism and life cycle of both organisms and ecosystems. On the other hand, growth and reproduction are the two processes at the individual level that are responsible for population growth, and these processes place high demands on energy and materials in the metabolism of individual organisms. Thus, the unification of population and ecosystem approaches should be rooted in the ecophysiology of organisms, in particular, in the constraints that govern the acquisition, allocation, and disposal of materials and energy.

The realization that generic physiological constraints should act across all levels of biological organization is the basis for the recent development of two successful areas of ecology, i.e., ecological stoichiometry and metabolic

theory. Ecological stoichiometry studies the balance among the chemical elements that make up living organisms (in particular, carbon, nitrogen, and phosphorus) and the constraints it generates for the functioning of biological systems, from cells to ecosystems (Sterner and Elser 2002). It is based on simple, fundamental physical and physiological laws, i.e., the conservation of mass and the homeostasis of living beings. The metabolic theory of ecology (Brown et al. 2004) is a quantitative theory that seeks to explain how metabolism varies with body size and temperature (essentially at macroecological scales) and constrains ecological processes at all levels of organization, from individuals to ecosystems. It is also based on simple constraints that govern the allocation of energy and materials in organisms.

The processing of energy and materials by individual organisms similarly constrains demographic processes at the population level. In principle, it should be possible to trace demography back to the *mass and energy budgets* of the individual organisms that make up the population. Energy budgets have been widely studied, especially in animals (Petrusewicz and Macfadyen 1970; Kooijman 2000). I am not so much interested here in the details of these budgets as in establishing simple approximate relationships between the parameters of classical population models and the components of these budgets. There have been several attempts to do so in the past (see Yodzis and Innes 1992 and references therein).

Here I start with a typical animal energy budget, which has the form (Petrusewicz and Macfadyen 1970)

$$C = A + Eg = P + R + Ex + Eg. \quad (1.15)$$

The amount of energy ingested by the organism (consumption,  $C$ ) during some time period can be divided into a part that is assimilated (assimilation,  $A$ ) and a part that is not. Nonassimilated energy is rejected without being digested (egestion,  $Eg$ ) and corresponds to feces in animals. Assimilated energy is used for production of new tissues (growth) and new individuals (reproduction) (combined in production,  $P$ ), respiration ( $R$ ), and excretion of urine or other metabolic products ( $Ex$ ). These elements of the energy budget are commonly used to define three measures of an organism's energetic efficiency: assimilation efficiency ( $A/C$ ), gross production efficiency ( $P/C$ ), and net production efficiency ( $P/A$ ).

All the elements of the energy budget do not respond in the same way to increased food consumption ( $C$ ). Part of the energy dissipated in respiration, and to a lesser extent in excretion and egestion, is used for basal metabolism, i.e., for the fixed energy costs of a living organism. Therefore, it is essentially constant. When food consumption is insufficient to match

basal metabolism, the organism loses weight and eventually dies. Its production is then negative. When food consumption is greater than basal metabolism, the excess energy is used in positive production and active metabolism. These then increase roughly in proportion to consumption above the threshold consumption necessary to compensate for basal metabolism (Warren 1971).

These empirical relationships can be expressed mathematically as follows. Call  $B$  biomass and  $\mu$  the mass-specific basal metabolic rate. Then if consumption is insufficient to match basal metabolism ( $C \leq \mu B$ ),  $R + Ex + Eg = \mu B$ , and by the conservation equation (1.15),

$$P = C - \mu B < 0. \quad (1.16)$$

On the other hand, if food consumption is greater than basal metabolism ( $C > \mu B$ ), the excess,  $C - \mu B$ , is used in active metabolism, a fraction of which is invested in production. Then

$$P = \varepsilon(C - \mu B) > 0, \quad (1.17)$$

where  $\varepsilon$  is the gross production efficiency for that part of consumption in excess of basal metabolism.

Since energy production is used for building new biomass, whether in the form of individual growth or reproduction, the contribution of the individual organism to the growth of biomass at the population level is  $P/\gamma$ , where  $\gamma$  is the energetic content of a unit biomass. Equation (1.17) can be scaled up to the population level if we make the simplifying assumption that all individuals are identical, as in classical population dynamical models. Subtracting losses due to mortality then yields

$$\frac{dB}{dt} = (\varepsilon/\gamma)C - (\varepsilon\mu/\gamma)B - \delta B, \quad (1.18)$$

where  $\delta$  is the mass-specific death rate. In this equation I assume that  $C > \mu B$ , and hence production is positive, which holds as long as the population is not abruptly declining from starvation.

Consumption itself is a dynamical function of resource availability, which is described traditionally by the consumer functional response (Holling 1959). Let the consumer functional response to variations in the biomass of their resources,  $R$ , be defined here in the form of a mass-specific function  $f(R)$ . Further assume for simplicity that resources have the same energetic content  $\gamma$  as consumers. Energy consumption by the consumer population is then  $\gamma f(R)B$ . Substituting this expression into equation (1.18) yields

$$\frac{dB}{dt} = \varepsilon f(R)B - mB, \quad (1.19)$$



where  $m = \epsilon\mu/\gamma + \delta$  is a mass-specific loss rate which measures the long-term maintenance cost of a unit biomass, including both basal metabolism and mortality. This equation has the same form as that used in classical population dynamics to describe the dynamics of a consumer population. Therefore, it provides an explicit link between the functional approach used in ecosystem ecology and the demographic approach used in population and community ecology.

This simple equation provides a number of valuable insights. In particular, note that it has a structure similar to that of equation (1.4). Thus, it predicts exponential growth of the consumer population as long as its resources are abundant and roughly constant. Population regulation, however, is included indirectly in this equation through the consumer functional response since resource biomass  $R$  is a variable that decreases as the consumer population increases. There is no need to add density dependence in the form of a carrying capacity: density dependence arises spontaneously through the dynamics of the resources.

Equation (1.19) also yields insights into the functional meaning of traditional demographic parameters. Of special interest is parameter  $m$ , the mass-specific loss rate, which is often interpreted as a mortality rate. This rate, however, includes both death due to starvation (failure to meet basal metabolism) and natural death from other causes. Population or community ecologists sometimes assume implicitly that the per capita death rate in their models represents natural death, but this rate may differ by several orders of magnitude from the rate at which individuals die once they are deprived of food. For instance, in humans, the life expectancy of well-fed individuals is about 70 years, but that of starved individuals is only a few weeks—a difference of more than three orders of magnitude! This shows that a functional perspective is important to avoid misinterpreting demographic parameters.

Note also, for terminological clarity, that the coefficient  $\epsilon$  in equation (1.19) has often been interpreted as the consumer's energy assimilation efficiency in the ecological literature (e.g., DeAngelis 1975; Yodzis and Innes 1992). The above derivation, however, shows that it actually represents its gross production efficiency for that part of consumption in excess of basal metabolism. I shall call it "production efficiency" in short in later chapters, although it does not correspond exactly to the definition of production efficiency in the energy budget literature.

As with any model, the great strength of a simple equation such as (1.19) is that it provides simple predictions and clear interpretations. Its corresponding weakness, of course, is that it does not provide a complete description of reality. Two important limitations need to be discussed here

because they can have significant consequences for the dynamics of the model populations, communities, and ecosystems built on this equation.

First, equation (1.19) is based on the simplifying assumption that functional and demographic processes in the consumer population, such as consumption and mortality, are proportional to consumer biomass. Some authors (e.g., Owen-Smith 2002) have argued that the rate of death due to starvation should be a nonlinear function of food consumption because mortality increases steeply as food consumption decreases. In fact, a comparison of equations (1.16) and (1.17) shows that both the growth and loss terms in equation (1.19) should increase by roughly a factor  $1/\epsilon$  when most of the population starves. Although the assumption of a constant mass-specific loss rate is obviously a simplification—as is any other feature of equation (1.19) or of any other model—it is nevertheless a reasonable one at the population level as long as starvation is not acute, because the dependence of net population growth on resource availability is already captured in the consumption term. When resource availability  $R$  is insufficient for consumption to compensate for maintenance costs [ $\epsilon f(R) < m$ ], the net population growth rate becomes negative, which amounts to an abrupt switching from growth to decline at the population level. A much stronger assumption is the lack of dependence of the mass-specific rates on population density or biomass in equation (1.19), which amounts to assuming that there is no interference among consumers, whether in the consumption or in the mortality process. There is no doubt that mutual interference does exist and can affect the dynamics of populations and communities qualitatively (DeAngelis et al. 1975; Arditi and Ginzburg 1989). Its prevalence and strength in nature, however, are controversial (Abrams and Ginzburg 2000), and its incorporation in population or ecosystem models complicates their analysis considerably. For the sake of simplicity, I shall accept in most of this book the traditional assumption that interference is negligible in trophic interactions.

Second, I have made explicit above another important assumption that is implicit in simple population dynamical models; i.e., all individuals are identical. This assumption is made for convenience because populations, or even whole functional groups (groups of species with similar functional roles in the ecosystem), will often be the basic unit in my representation of communities and ecosystems. This assumption is valid only to the extent that variation among individuals within a species or functional group is smaller than variation among species or functional groups. Alternative approaches when variation among individuals is significant include individual-based models (Huston et al. 1988; DeAngelis and Gross 1992) and physiologically

structured population models (Metz and Diekmann 1986; De Roos et al. 2003). These approaches have greater realism and flexibility, but they are also more complex and parameter-rich. Accordingly, they are generally applied to more specific situations in which detailed information on individual behavior and ontogeny is available and plays an important role in population dynamics. I shall ignore individual variability within populations in the rest of this book.

Last, I have provided a functional derivation and interpretation of the demographic equation (1.19) above based on animal energy budgets. Most of the models that I shall present in this book, however, will involve plants as the basal living compartment of ecosystems and will be based on mass budgets tracking the fate of limiting nutrients. It is straightforward to generalize the above approach to these situations. Plant energy budgets are traditionally defined differently than animal energy budgets, but they comprise essentially the same elements. Evapotranspiration is the part of the absorbed energy that is not assimilated by plants and thus is the functional equivalent of egestion in animals. Gross primary production and net primary production in plants correspond to assimilation and production, respectively, in animal energy budgets. Excretion is often ignored in plant energy budgets; it is implicitly regarded as a loss to net primary production.

Mass budgets have been less studied than energy budgets. For elements other than carbon, the main difference is that there is no equivalent for respiration. Otherwise, similar derivations of population-level dynamical equations are possible in principle for nutrients just as for energy. Primary production is thought to be limited by nitrogen or phosphorus in most ecosystems. Since nitrogen and phosphorus are not directly involved in the chemical reactions of photosynthesis and respiration, I shall assume in the rest of this book that the uptake of limiting nutrients by plants is proportional to net primary production, which is the equivalent of production (plus excretion) in animal energy budgets since these nutrients are used for growth and reproduction. Mass and energy transfers are simultaneous in animals since consumed food contains both energy and materials. Therefore, equations similar to equation (1.19) can be derived for the dynamics of nutrient stocks in animal populations.

#### A MINIMAL ECOSYSTEM MODEL

The above population dynamical model based on mass or energy budgets suggests a simple way to build ecosystem models that satisfy both the

physical laws of conservation of mass and energy and the demographic law of exponential growth at low population density or high resource availability: use the formalism of compartmental models but allow the dynamics of each compartment to be nonlinear functions of compartment sizes. All the complexity of biological interactions can be included in ecosystem models using this simple rule.

As the simplest possible application of this approach, consider a nutrient-limited ecosystem in which there is a single plant compartment with size  $P$  and an inorganic nutrient compartment with size  $N$  (H. T. Odum 1983). The size of each compartment is here measured by its nutrient stock. Assume that the ecosystem has a closed nutrient cycle (no input or output of nutrient) and that nutrient uptake by plants follows the law of mass action, i.e., is proportional to the product of  $P$  and  $N$ , as in standard Lotka-Volterra models (which corresponds to the linear part of a Holling type-I functional response). The dynamics of the system can be written as

$$\begin{aligned}\frac{dP}{dt} &= uNP - mP, \\ \frac{dN}{dt} &= mP - uNP,\end{aligned}\tag{1.20}$$

where  $u$  is the rate of nutrient uptake by plants per unit time per unit mass of nutrient, and  $m$  is the turnover rate of nutrient in plants due to basal metabolism and mortality.

Since the nutrient cycle is closed, any inflow to one compartment is an outflow from the other compartment, so that the equations for  $P$  and  $N$  are mirror images of each other. Summing the two equations, we see that the total quantity of nutrient in the system,  $P + N$ , is a constant, which I call  $Q$ :

$$\begin{aligned}\frac{d(P + N)}{dt} &= 0, \\ P + N &= Q.\end{aligned}\tag{1.21}$$

This conservation equation can now be used to substitute  $Q - P$  for  $N$  in the first of equations (1.20), yielding

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right),\tag{1.22}$$

where  $r = uK$ , and  $K = Q - m/u$ .

This is nothing else than the familiar logistic equation of population dynamics. Thus, we see that the logistic equation can be obtained as the result of explicit nutrient limitation in a closed ecosystem. On a more technical note, notice how the mass conservation constraint in a closed ecosystem



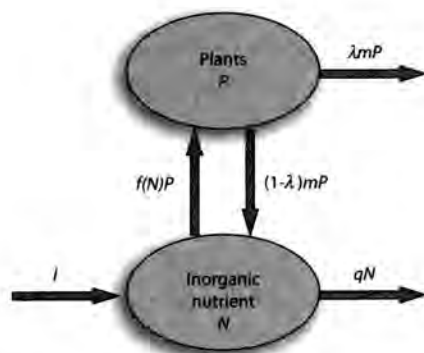


FIGURE 1.3. A minimal open, nutrient-limited ecosystem model. Circles represent nutrient stocks, while arrows represent nutrient flows.

reduces the effective dimensionality of the corresponding dynamical system (here, from two- to one-dimensional). Although incorporation of explicit ecosystem-level constraints may make population and community models look more complex at first sight, it may actually simplify their analysis under some conditions, just as incorporation of explicit resource dynamics may simplify the analysis of models of exploitation competition (Tilman 1982; Grover 1997). The reduction in dimensionality that results from incorporation of ecosystem-level mass-balance constraints is a trick that has been used in a number of theoretical studies in community and ecosystem ecology (e.g., Grover 1994; Holt et al. 1994; Loreau 1995).

The assumption of complete ecosystem closure to material exchanges with the outside world is of course unrealistic. A minimal ecosystem model that accounts for nutrient exchanges across ecosystem boundaries can be constructed as follows (figure 1.3). Assume that the inorganic nutrient pool is supplied with a constant input  $I$  of nutrient per unit time through processes such as water flow, dry deposition, and rock weathering and loses nutrient at a rate  $q$  per unit time through processes such as water flow, leaching, and volatilization. A fraction  $\lambda$  of nutrient is also lost from the ecosystem once released by plants, either before (e.g., through fire) or during (e.g., through leaching) the decomposition process. Let  $f(N)$  denote the functional response of plants to nutrient availability and let  $m$  denote the rate at which they release nutrient because of basal metabolism and mortality as before. The resulting ecosystem model is a nonlinear version of the abstract two-compartment model depicted in figure 1.2.

The diagram depicting these processes (figure 1.3) translates into mathematical equations by applying the principle of mass conservation and

setting the time derivative of compartment size equal to the sum of inflows minus the sum of outflows for each compartment. This provides the set of equations

$$\begin{aligned}\frac{dN}{dt} &= I - qN - f(N)P + (1 - \lambda)mP, \\ \frac{dP}{dt} &= f(N)P - mP.\end{aligned}\quad (1.23)$$

In the long run, this dynamical system reaches an equilibrium. This occurs when inflows balance outflows for each compartment, and hence the time derivatives in equations (1.23) vanish. Solving the resulting mass-balance equations provides the equilibrium nutrient stocks (denoted by an asterisk as before)

$$\begin{aligned}N^* &= f^{-1}(m), \\ P^* &= \frac{I - qN^*}{\lambda m},\end{aligned}\quad (1.24)$$

where  $f^{-1}$  denotes the inverse function of  $f$ , the plant functional response. It is easy to check, using standard graphical or mathematical analyses, that this equilibrium is always stable (May 1973; Puccia and Levins 1985).

Although the dynamics of this system can no longer be reduced to a simple logistic equation for plants as with model (1.20), indirect density dependence of plant growth also occurs through nutrient limitation in this case, leading to regulation of plant nutrient stock (and hence biomass) around an equilibrium value or "carrying capacity." This carrying capacity [equation (1.24)] is now determined by the parameters that govern the plant–nutrient interaction and by the parameters that govern nutrient exchanges across ecosystem boundaries.

Model (1.23) also allows analysis and prediction of primary production. Since net primary production generally increases in proportion to plant nutrient uptake, the nutrient flow corresponding to plant nutrient uptake,  $f(N)P$ , can be used to measure net primary production,  $\Phi_p$ . At equilibrium, the latter is simply

$$\Phi_p^* = mP^* = \frac{I - qN^*}{\lambda}. \quad (1.25)$$

This equation is easily interpreted. The numerator on the right-hand side of this equation is the excess of inflow of inorganic nutrient over its outflow at equilibrium; therefore it represents the net supply of nutrient in inorganic form available to plants at equilibrium. The denominator measures the fraction of nutrient lost from the plant compartment. Thus, equilibrium primary production is the product of two terms: (1) the net supply

of the limiting nutrient, and (2) the efficiency with which this limiting nutrient is conserved by plants within the ecosystem (as measured by the inverse of  $\lambda$ ). Equilibrium plant biomass [equation (1.24)] is then obtained simply by dividing primary production by the turnover rate of nutrient in plants. The implications of these equations will be further discussed in chapter 6.

### CONCLUSION

Although the conceptual and formal foundations of population dynamics and ecosystem functioning are very different, both are related, directly or indirectly, to the mass and energy budgets of individual organisms. The dynamics of a species' biomass is determined by the way individuals allocate the nutrients and energy they consume to various physiological and behavioral processes, which allows the demographic parameters of population dynamics to be given a functional interpretation in terms of mass and energy flows. In turn, the flows of mass and energy in an ecosystem are determined by the population dynamics and interactions of its component species, which makes it possible to incorporate the complexity of demographic processes in the functions that govern mass and energy flows. Consistent models that merge the community and ecosystem perspectives can then be obtained by coupling the formalism of compartmental models borrowed from ecosystem ecology and the versatility of nonlinear functions that determine mass and energy flows borrowed from population and community ecology.

Armed with these principles and methods, we may now examine more thoroughly the processes involved in the organization of ecosystems, and the causes and consequences of community-level processes such as biodiversity changes and species interactions within ecosystems.

### CHAPTER 2

## The Maintenance and Functional Consequences of Species Diversity

The core of community ecology is concerned with the question: why are there so many species on Earth? The tremendous diversity of life despite common constraints on the physiology and ecology of organisms is one of the hallmarks of living systems. Community ecology seeks to explain the maintenance of species diversity within ecological systems very much like population genetics seeks to explain the maintenance of genetic diversity within species. A large part of this diversity can be explained by geographical differences in environmental conditions across the globe and by historical circumstances. Many species and genetic variants, however, coexist in any given place and at any given time. Why do so many species and types coexist?

There are two main components to local species diversity, which I shall call vertical and horizontal, respectively. *Vertical diversity* is the diversity of functionally different types of organisms as defined by their trophic relationships or by other, nontrophic interactions (trophic levels, guilds, functional groups). The term "vertical" comes from the traditional representation of food chains in the form of vertical chains with plants at the bottom and carnivores at the top. By contrast, *horizontal diversity* is the diversity of species within trophic levels or functional groups. Vertical diversity concerns food webs and interaction networks and will be addressed in chapter 4. In this chapter I shall focus on the maintenance of horizontal diversity within ecological communities.

Explaining the coexistence of species with similar functional roles, or ecological niches, is the subject of *competition theory*. Competition theory is initially an extension of the theory of density dependence in population dynamics, in which intraspecific competitive interactions among individuals of a single species are extended to include interspecific competition among individuals of different species. This theory, however, has expanded

structured population models (Metz and Diekmann 1986; De Roos et al. 2003). These approaches have greater realism and flexibility, but they are also more complex and parameter-rich. Accordingly, they are generally applied to more specific situations in which detailed information on individual behavior and ontogeny is available and plays an important role in population dynamics. I shall ignore individual variability within populations in the rest of this book.

Last, I have provided a functional derivation and interpretation of the demographic equation (1.19) above based on animal energy budgets. Most of the models that I shall present in this book, however, will involve plants as the basal living compartment of ecosystems and will be based on mass budgets tracking the fate of limiting nutrients. It is straightforward to generalize the above approach to these situations. Plant energy budgets are traditionally defined differently than animal energy budgets, but they comprise essentially the same elements. Evapotranspiration is the part of the absorbed energy that is not assimilated by plants and thus is the functional equivalent of egestion in animals. Gross primary production and net primary production in plants correspond to assimilation and production, respectively, in animal energy budgets. Excretion is often ignored in plant energy budgets; it is implicitly regarded as a loss to net primary production.

Mass budgets have been less studied than energy budgets. For elements other than carbon, the main difference is that there is no equivalent for respiration. Otherwise, similar derivations of population-level dynamical equations are possible in principle for nutrients just as for energy. Primary production is thought to be limited by nitrogen or phosphorus in most ecosystems. Since nitrogen and phosphorus are not directly involved in the chemical reactions of photosynthesis and respiration, I shall assume in the rest of this book that the uptake of limiting nutrients by plants is proportional to net primary production, which is the equivalent of production (plus excretion) in animal energy budgets since these nutrients are used for growth and reproduction. Mass and energy transfers are simultaneous in animals since consumed food contains both energy and materials. Therefore, equations similar to equation (1.19) can be derived for the dynamics of nutrient stocks in animal populations.

### A MINIMAL ECOSYSTEM MODEL

The above population dynamical model based on mass or energy budgets suggests a simple way to build ecosystem models that satisfy both the

physical laws of conservation of mass and energy and the demographic law of exponential growth at low population density or high resource availability: use the formalism of compartmental models but allow the dynamics of each compartment to be nonlinear functions of compartment sizes. All the complexity of biological interactions can be included in ecosystem models using this simple rule.

As the simplest possible application of this approach, consider a nutrient-limited ecosystem in which there is a single plant compartment with size  $P$  and an inorganic nutrient compartment with size  $N$  (H. T. Odum 1983). The size of each compartment is here measured by its nutrient stock. Assume that the ecosystem has a closed nutrient cycle (no input or output of nutrient) and that nutrient uptake by plants follows the law of mass action, i.e., is proportional to the product of  $P$  and  $N$ , as in standard Lotka-Volterra models (which corresponds to the linear part of a Holling type-1 functional response). The dynamics of the system can be written as

$$\begin{aligned}\frac{dP}{dt} &= uNP - mP, \\ \frac{dN}{dt} &= mP - uNP,\end{aligned}\tag{1.20}$$

where  $u$  is the rate of nutrient uptake by plants per unit time per unit mass of nutrient, and  $m$  is the turnover rate of nutrient in plants due to basal metabolism and mortality.

Since the nutrient cycle is closed, any inflow to one compartment is an outflow from the other compartment, so that the equations for  $P$  and  $N$  are mirror images of each other. Summing the two equations, we see that the total quantity of nutrient in the system,  $P + N$ , is a constant, which I call  $Q$ :

$$\begin{aligned}\frac{d(P + N)}{dt} &= 0, \\ P + N &= Q.\end{aligned}\tag{1.21}$$

This conservation equation can now be used to substitute  $Q - P$  for  $N$  in the first of equations (1.20), yielding

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right),\tag{1.22}$$

where  $r = uK$ , and  $K = Q - m/u$ .

This is nothing else than the familiar logistic equation of population dynamics. Thus, we see that the logistic equation can be obtained as the result of explicit nutrient limitation in a closed ecosystem. On a more technical note, notice how the mass conservation constraint in a closed ecosystem