

Microfoundations of Population Dynamics

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Synopsis: Population growth functions are fundamental tools in the study of animal and plant populations; however, they typically are chosen for mathematical convenience as opposed to being derived from individual behavior. An alternative is to start with the individuals and show how their behavior yields a population growth function. This approach is presented using a plant community wherein individuals behave as if they are maximizing the difference between energy inflow from their exposure to light and outflow from their respiration activities. Their behavior leads to resource competition, because each plant is vying for access to light, and as plants increase their biomass or as populations increase, the competition intensifies as light exposure declines, and this impinges upon further growth. Whether the net energy obtained by the representative individual in a population is positive or negative determines whether the population as a whole increases or decreases. Conditions for a short-run equilibrium show that plant biomass is positively related to the available space and shade tolerance and negatively related to variable respiration, while carrying capacity is positively related with the available space, and negatively related to the space taken by other populations and to fixed respiration and shade tolerance.

Keywords: optimizing behavior; exploitative competition; population ecology

1. Introduction

Population growth functions are fundamental tools in the study of animal and plant populations, and in bioeconomics they have allowed partial integration of ecology and economics to improve policymaking. For example, following the work of Gordon (1954), economists have made liberal use of the biology inherent in the familiar logistic growth function to describe optimal harvesting of fish and other species under a variety of economic conditions including alternative market structures and property right assignments.¹ However, these growth functions “are often ‘descriptive’ in the sense that they are not derived but are chosen as the mathematically most convenient expression that might in a very qualitative sense embody the appropriate ecological effect” (Schoener, 1986). They contain too little information about how competing individuals and populations of individuals compete for resources to be considered explanations of individual behavior.

Population growth functions are derived in a macro framework in the sense that the growth of the individual, i.e. the per capita growth, is based on entire populations occupying the individual’s community; how the interaction of the individual with the populations yields the resulting growth is left an open question.² An alternative to the macro approach is to start with the individuals and show how their behavior leads to the growth of the populations. This micro approach is developed here by assuming that individual plants behave as if they are maximizing the difference between energy inflow from photosynthesis and outflow to respiration. Whether the net energy obtained at the individual level is positive or negative then determines whether the population as a whole will increase or decrease.

The paper proceeds as follows. In the next section more background is given about how the micro approach differs from traditional approaches. Section 3 describes the optimizing behavior of individual plants in a short-run equilibrium, section 4 discusses using the optimization approach in ecology, and section 6 shows how optimizing behavior leads to population changes.

A long-run equilibrium is briefly covered in section 7 and section 8 is a final word about advantages and limitations of the micro approach. An appendix contains several mathematical derivations.

2. Background

Population growth sometimes follows a sigmoid curve, and Verhulst (1838) was first to propose a logistic equation to describe this growth. However, his work did not draw much attention until Pearl and Reed (1920) rediscovered the logistic equation. (See Kingsland (1982) for historical background.) The equation maintains that the growth rate of a population is a function of the population stock, and there is a carrying capacity that the population approaches but typically does not exceed. Depending on further assumptions, growth equations may take the form of the classic Verhulst-Pearl logistic equation (Royama, 1992) or its variants, and they may contain stochastic parameters to account for the uncertainties of recruitment and errors in estimating populations.³ In the Verhulst-Pearl equation:

$$\frac{dN}{dt} = rN(1 - N/K)$$

N is population, r an intrinsic growth rate and K the carrying capacity. The function has been derived from various mathematical constructs such as Lotka's Taylor series approximation (Lotka, 1925), and in some cases authors have interpreted the parameters to represent growth based on available space (Winsor, 1934) or on environmental resistance (Gause, 1934). In the equation, "any role of resources is subsumed in the idealized parameters r and K " (Grover, 1997). The same critique applies to Lotka-Volterra equations describing two species:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1} \right) \quad \text{and} \quad \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - \frac{\alpha_{21} N_1}{K_2} \right)$$

the role of resources and competition is hidden in the parameters.

Continuing in the Verhulst-Pearl and Lotka-Volterra tradition, more recent multi-species, dynamic population models begin with difference or differential growth equations, with one equation for each species in the model. Each equation contains as variables the population stocks of the other species in the model that are expected to impact, positively or negatively, the species represented by the equation. Because the population of a species is a function of the population of other species, these analyses mask individual behavior. To claim otherwise is to suggest that the individual, in order to make choices about its biomass growth and resource acquisition, takes an inventory of the surrounding populations. This is clearly unrealistic, and it explains why “the various parameters of the model can rarely be specified a priori” (Peters, 1991): there are no testable hypotheses that emerge from individual behavior that can be used to derive or place bounds on parameters in a growth equation.⁴

In recent years there has been a move away from aggregating individuals into a single state variable and toward individual-based models. These latter models may account for age and size structure or they may track large numbers of individuals with computer simulations. (See DeAngelis and Gross (1992) for a collection of papers on individual-based modeling.) While this literature adds much detail and richness to ecosystem processes, it does not include an underlying behavior or motivation on the part of the individual to explain its actions. For example, when Pacala and Silander (1990) regress the number of neighbors a plant has on the plant’s biomass in a hyperbolic function, we learn how the number of neighbors impact the individual’s biomass. However, what is missing is an underlying theory to explain why biomass is important to the plant. What is the plant’s motivation for accumulating biomass?⁵

In this paper we start with a behavioral theory that provides the motivation for why the plant accumulates biomass, and we show how this behavior yields functions of the type Pacala and Silander estimate. By starting at the behavioral level, refutable hypotheses in the form of restrictions on these functions are obtained. If the hypotheses are rejected, then the behavioral motivation assumed is called into question; if the hypotheses are accepted, then we have support

for why the individual behaves as it does. In developing the theory, we assume all individuals in a species are identical; therefore, we omit many details that might be included in individual-based models. How important is this omission will vary across species and communities, and will depend on the purpose of the model. We believe some of the richness ultimately can be included, but our main purpose here is to introduce a new methodology that accounts for underlying behaviors.

If individual behavior is to play a more prominent role in models of population growth and community structure, then we need to focus on what behavior is important and what it is that the individual is responding to if it is not entire populations. Schoener (1973) suggests intraspecific competition for resources as a useful mechanism to focus on, and we follow this suggestion below by assuming that individuals behave as if they are maximizing their net energy intake in a competitive environment. In his critique of lumped parameter models, Grover (1997) points out that the equations

“make no reference to any entities other than the densities of the two competing populations, and ...the parameters...cannot be estimated prospectively. ..What is needed are auxiliary hypotheses, postulating relations between the competition coefficients and some entities beyond the competitors’ population densities. An expanded theory, consisting of the (above) equation system plus rules for determining the competition coefficients independently, could then predict population trends under competition...(p. 13).

The optimization approach developed here is an auxiliary hypothesis that determines what are effectively competition coefficients in the population growth equations. The coefficients summarize the results of interactions between all members of all populations competing for the same resource, but they are derived from the individuals’ maximization problems that do not contain populations as parameters. Instead, the individuals are responding to energy availability that is

determined by the intensity of competition. The availability is beyond the control of individuals, yet its value is determined by the simultaneous interaction of all individuals.

3. Individual Behavior

The behavior of the individual will be developed in the context of plants, although with suitable modification, animal populations could also be used.⁶ Both biomass and population density are included in the model. Consider $m \geq 1$ plant species occupying a community of fixed size (space); thus, there is a limit on the amount of biomass that the space can contain. Population i consists of n_i identical individual plants, $i = 1, \dots, m$. The populations, n_i , are assumed to be constant in this section, and we use the term short run to describe the time over which populations do not vary.

The representative plant of species i is characterized by its *net energy function* R^i , where

$$r_i = R^i(e_i, x_i) \quad (1)$$

is the net energy (measured in energy time⁻¹ units, e.g., W) the plant obtains in the current period, where the index of its exposure to light energy (light exposure, for short) takes the value e_i (W gm⁻¹) and where x_i (gm) is the plant's biomass. The individual plant does not influence the light exposure as will become clear, but the plant does choose x_i . No distinction is made between above and below ground biomass, although this would make an interesting extension; and all plants are assumed to be mature so there is no age structure in the model, but this too would make an interesting extension. We concentrate on light, or access to light, as the resource being competed for because Huston and Smith (1987, p. 174) state that: "...light competition provides the clearest and most important example of the complexity of competitive ability for a single resource." And Grover (1997, p. 207) refers to light energy as "...a somewhat special resource" relative to nutrients and water in that it does not follow mass balance constraints, and it is an essential resource to almost all primary producers.

The net energy function R^i is assumed to have the following properties:

$$\text{R1: } R^i(0, x_i) < 0 \quad \text{for all } x_i \geq 0,$$

$$\text{R2: } R_{e_i}^i > 0, R_{x_i e_i}^i > 0,$$

$$\text{R3: } R_{x_i}^i|_{x_i=0} > 0, R_{x_i x_i}^i < 0 \quad \text{and} \quad \lim_{x_i \rightarrow \infty} R_{x_i x_i}^i < 0.$$

where subscripts denote partial derivatives. Assumption R1 says that net energy cannot be stored if the plant has no access to light ($e_i = 0$). According to R2 the plant's net energy rises with increasing light exposure when the plant's biomass is constant or increased at the margin. According to R3 when the plant's biomass increases its net energy may increase (for small x_i and sufficiently large e_i , at least), but will eventually shrink due to the plant's respiration that depends on its size.

The central 'behavioral' hypothesis is that the individual plants behave as if they maximize their net energy flow.⁷ In terms of the formal model, an individual of species i chooses the biomass

$$x_i = X^i(e_i) \equiv \arg \max_{x_i} R^i(e_i, x_i) \quad (2)$$

for every $e_i \geq 0$. Clearly, $X^i(e_i)$ exists and is unique by R3. From R2 we also know that $\partial X^i / \partial e_i > 0$; that is, the plants 'demand' for biomass, or its 'optimal' size, $X^i(e_i)$, is greater, the greater is its light exposure.

Light exposure and biomass can be related to models that examine shading in general. For example, Raulier and Ung (1997) develop a procedure to estimate total leaf area and apply it to sugar maples (*Acer saccharum* Marsh). When these authors estimate total leaf area (their equation (8)), essentially they are estimating the plant's demand function for biomass given by (2). The two major terms in their equation are: "the potential leaf area, i.e. the leaf area of a

crown entirely irradiated by an irradiance equal to that of the top cover” and “the reduction of potential leaf area caused by shading.” The first term contains the potential irradiance and the second the reduction in the potential due to transmittance, and these two measures of light are analogous to e_i that appears in the demand function, (2).

A major difference between the model presented here versus Raulier and Ung, or the Pacala and Silander paper alluded to in section 2 (although they stress number of neighbors and not shading directly), and many other papers that examine light and shading is the origin of the biomass demand function. We know that light is essential for most plants, and most models begin by constructing a biomass demand function that relates biomass with light variables and parameters. The model herein begins at a more underlying level by postulating that plants behave as if they maximize their net energy intake, and given their exposure to light they produce the amount of biomass that accomplishes the task. This postulate justifies formulating an objective function for the plant, and maximization procedures yield the plant’s biomass demand function.

Although the individual plant takes as given its light exposure, e_i , from the viewpoint of the plant community all plants’ exposures are endogenous. They depend on the populations’ capacities to make use of light energy, and also on the intensity of competition for access to light among all individual plants within their own population and across populations. An *exposure function*, E^i , for each population i formalizes these relations. Let

$$e_i = E^i(x, n) \quad i = 1, \dots, m \quad (3)$$

denote the energy exposure of each plant of population i where $x \equiv (x_1, \dots, x_i, \dots, x_m)$ is the vector of the representative plants’ biomasses and $n \equiv (n_1, \dots, n_i, \dots, n_m)$ is the vector of populations.

The basic idea of the exposure function is that increases in the size of representative individuals (x) and in the species populations (n) tend to generate congestion in the plant com-

munity after some threshold value of total population and/or total biomass across all species is passed. Prior to reaching the threshold, growth is density independent. Increasing competition for space results in a reduction of all species' access to light as represented by the exposure indexes, e_i . If biomass, x_i , is leaf area and/or plant height, for example, then the exposure function is similar to the Lambert-Beer law (Perry, Sellers and Blanchard, 1969) that determines the light available to an individual based on leaf area and the height of neighboring plants.

To capture this congestion feature we introduce the following properties for the function E^i :

E1: $E_b^i \leq 0$ and $E_{bb}^i \leq 0$ for $b = x, n$

E2: There is $D^i \equiv \{(x, n) \mid E^i(x, n) \geq 0\}$; D^i is compact, convex and contains the element $(x, n) = (0, 0)$.

E3: There is a proper subset D_o^i of D^i , such that $E^i(x, n) \begin{cases} = \bar{e}_i > 0, \text{ if } (x, n) \in D_o^i \\ < \bar{e}_i \text{ otherwise} \end{cases}$;

D_o^i is compact, convex and contains $(x, n) = (0, 0)$.

E1 implies that congestion diminishes the plant's access or exposure to light. E2 and E3 jointly specify that there are 'small' vectors (x, n) causing no congestion or so little that plants have at least some exposure to light; their access to solar energy may be impaired, but it is not entirely denied as long as $E^i(x, n)$ is positive. E3 secures a non-empty domain with maximum light exposure or, equivalently, without congestion. If (x, n) is not in D^i , crowding is so severe that plants have no access to light at all. Due to R2 they cannot survive in such an environment and it suffices, therefore, to focus on the domain D^i .

A particularly simple but not implausible class of exposure functions satisfying E1 - E3 is given by the set of all functions \tilde{E}^i for which e_i depends on (x, n) only through the total sum

of biomass across all species: $e_i = \tilde{E}^i \left(\sum_j x_j n_j \right)$. Figure 1 illustrates this type of exposure function. The segment OA in figure 1 corresponds to the set D_o^i and the segment OB to the set D^i . Clearly, this exposure function ignores the importance of height variations, and it omits the importance of the spatial distribution of plants by downplaying the role of near versus distant neighbors. (Although for some species, “knowledge of spatial distributions or the factors that determine them brings relatively little to an understanding of the processes that govern a ... community.” (Pacala and Silender, 1990)) Nevertheless, assuming that a plant’s light exposure is inversely related to the size and number of all neighbors in our simple model seems a reasonable description of the physical dimensions of the problem.

4. On Optimization

Optimization is not widely used in ecological modeling; therefore, the optimization framework adopted here as the organizing theme, and embodied in the assumption that plants behave as if they are maximizing net energy flow, deserves elaboration. In economics, formal mathematical models have been widely used for the better part of a century, and many of them have been useful as measured by their predictive ability. The central component in almost all of these models is consistent behavior. Given two situations where the consumer must choose among alternatives, the consumer will make the same choice if the circumstances defining the situations are identical with respect to all important parameters that might affect the consumer’s choice, such as income, prices, location, weather, etc. If the consumer were to make different choices consistently when faced with the same circumstances, then modeling the consumer’s behavior would be futile. The most common way to mathematically model consistent behavior is to use optimization techniques. Economic agents might maximize utility, maximize profit, minimize expenditures, and so on. An optimization framework captures the idea of consistent behavior succinctly. Thus, by assuming that a consumer is a utility maximizer, we are saying that the consumer behaves consistently.

Clearly, consumers do not always behave consistently, and the usefulness of the optimization approach depends on whether enough consumers behave consistently enough of the time. Moreover, we should not confuse inconsistent behavior with changing preferences over a lifetime, or with incomplete information. For example, consumers will make different choices at different stages of their lives, but within each stage of life may be acting consistently. This observation does not negate the usefulness of assuming consistent behavior and adopting the optimization framework.

The pertinent question is: Can an optimization framework be usefully applied to plants and animals? Do plants and animals behave consistently? We believe the answer is yes. In fact, we believe that consistent behavior is more applicable to plants and animals than it is to humans.⁸ Humans exhibit changing preferences for many reasons. A utility-maximizing consumer who wakes one morning with the thought that her diet needs changing from one full of fatty foods to one full of fruits and vegetables has altered her strategies to achieve maximum utility, and we can observe this preference reversal through her purchases. A model of this consumer's behavior is unlikely to predict this diet change. We believe that plants and animals are less likely to exhibit such unpredictable behavior. They do not have a wealth of strategies to choose from because they are limited by their habitat and the physiological and morphologic parameters that define them, and they are less likely in the first place to adopt a strategy that is inconsistent with their well being. As with the humans, plants and animal strategies certainly change over the stages of their lives, but this does not rule out consistent behavior within each stage.

In adopting the optimization framework, we must be careful in distinguishing between strategies and objectives. If a plant's objective is to maximize net energy, then its strategies will involve methods for exposing itself to light. In the real world of plants, some plants may be gleaners (shade tolerant species) and others may be opportunists (species with rapid juvenile growth in full light) and they may coexist (Grover, 1997). Some plants may allocate more biomass to roots versus shoots depending on environmental conditions, or they may adopt special

leaf characteristics defined by leaf area, thickness, hairiness, waxiness or angle to the sun. The point is that different plants adopting different strategies does not rule out that they may all have the same objective. The myriad ways they achieve their objective comprises the details that may or may not be important to include in a model depending principally on the magnitude and complexity of the community being studied and the purpose of the model. For example, in integrating plant communities with an economic system to determine how economic activity impacts the diversity or survivability of the community, the inclusion of very detailed descriptions of all strategies may not be necessary or even desirable to obtain a broad picture of how the community is prospering.

The model developed in this paper is very simple in that the plants have but one life stage, thus a rich set of strategies that plants may choose from at different life stages is omitted. Nevertheless, the optimization framework delivers numerous testable hypotheses even in this simple case, and it can be extended to include different strategies as well as plant age distributions.

The model also focuses on one resource, light, but this too could be extended to include additional resources. For instance, plants allocate energy to roots and shoots in differing proportions depending on environmental conditions. Clearly the model developed here is inadequate to capture this behavior, because it does not include a 'payoff' for the plant from manufacturing roots. There are at least two ways the model can be extended to capture the roots/shoots tradeoff. First, because most plants cannot have shoots without roots, a functional relationship could be imposed that requires a minimal root/shoot ratio to support the shoots. Second, and more useful perhaps, another resource could be appended. Suppose water is added and is indispensable for the plant's survival. Then the plant has two choice variables: above ground biomass and below ground biomass - both of which are lumped into one biomass in this paper. The plant's objective to maximize net energy still works, but now that energy must be allocated in two directions instead of one. (Tschirhart, 2001)

5. Short-run ecosystem equilibrium

The short-run ecosystem model is now completely described so that we turn to the issue of community equilibrium. For any given vector of populations, n , and exposures, $e = (e_1, \dots, e_i, \dots, e_m)$, a *short-run plant community equilibrium* is a pair of vectors (x, e) satisfying (2) und (3). Expressions (2) and (3) consist of $2m$ equations to solve for the $2m$ variables (x, e) . Under standard assumptions about the smoothness of the functions involved and about the compactness and convexity of these functions' relevant domains and ranges the existence of a solution can be secured using a suitable fixed-point argument. (Proof of existence is available from the authors.) Here, attention is restricted to the set of models for which unique solutions exist. With this qualification, we conclude that for every vector of populations, n , there exists a vector of light exposures,

$$e = \widehat{E}(n) = [\widehat{E}^1(n), \dots, \widehat{E}^m(n)] \quad (4)$$

such that the vectors $e = \widehat{E}(n)$ and $x = X[\widehat{E}(n)] \equiv [X^1[\widehat{E}^1(n)], \dots, X^m[\widehat{E}^m(n)]]$ constitute a short-run ecosystem equilibrium.

To offer more precise results, the function R^i from (1) and E^i from (3) are specified by

$$R^i(e_i, x_i) = e_i x_i - \frac{x_i^2}{2c_i} - \beta_i \quad i = 1, \dots, m \quad (5)$$

$$E^i(x, n) = \min \left[\bar{e}_i, h_i \left(\bar{a} - \sum_j x_j n_j \right) \right] \quad i = 1, \dots, m. \quad (6)$$

In (5) and (6), \bar{a} , β_i , c_i , \bar{e}_i , h_i are positive parameters satisfying $h_i \bar{a} > \bar{e}_i$. β_i is in energy time⁻¹ units (e.g., W), x is in biomass units (e.g., gm), and the e terms are energy per biomass units (e.g., W gm⁻¹). The energy required for the plant's respiration which includes growth, maintenance and reproduction, is divided into two parts: a variable portion that depends on the plant's biomass, $\frac{x_i^2}{2c_i}$, and a fixed portion, β_i , that represents energy lost to the atmosphere independent

of the biomass. (The constant c_i is in $\text{gm}^2 \text{W}^{-1}$.) The product $e_i x_i$ can be thought of as primary production in which case by (1) the primary production is allocated to energy lost in “preying” on light, fixed and variable respiration, and stored energy that is the maximand. Equation (6) implies that the light exposure for plant i in a congestion-free space is \bar{e}_i , but when the area of the total biomass of all plants, $\sum_j x_j n_j$, approaches the available area, \bar{a} , the light exposure begins to decline. The h_i (measured in $\text{W gm}^{-1} \text{m}^{-2}$) is a measure of the rate of decline and varies across species depending on their shade tolerance: a higher h_i implies greater shade tolerance.

Given (5) and (6), equation (2) is turned into:

$$X^i(e_i) = c_i e_i \quad (7)$$

Initially, suppose the light exposures in (4) yield a short-run equilibrium of the parametric model (5) – (7) (yet to be calculated) that exhibits⁹

$$\min [\bar{e}_i, h_i (\bar{a} - \sum_j x_j n_j)] = h_i (\bar{a} - \sum_j x_j n_j).$$

Then (6) and (7) yield

$$x_i = c_i e_i = \bar{a} c_i h_i - c_i h_i \sum_j x_j n_j \quad i = 1, \dots, m$$

and

$$\sum_j x_j n_j = \bar{a} - \frac{x_i}{c_i h_i} \quad i = 1, \dots, m. \quad (8)$$

Since the left side of (8) is the same for all i , the equations $\frac{x_i}{c_i h_i} = \frac{x_j}{c_j h_j}$ follow for $i, j = 1, \dots, m$.

Substitute $x_j = \frac{c_j h_j}{c_i h_i} x_i$ in (8) to obtain $\sum_j \frac{c_j h_j n_j}{c_i h_i} x_i = \bar{a} - \frac{x_i}{c_i h_i}$ and

$$x_i = X^i[\hat{E}(n)] = \frac{\bar{a} c_i h_i}{1 + \sum_j c_j h_j n_j} \quad i = 1, \dots, m. \quad (9)$$

In view of (7) and (9), \widehat{E}^i from (4) is specified as

$$e_i = \widehat{E}^i(n) = \frac{\bar{a}h_i}{1 + \sum_j c_j h_j n_j} \quad i = 1, \dots, m. \quad (10)$$

To sum up, (9) and (10) constitute the short-run ecosystem equilibrium, if for all i

$$\bar{e}_i \left(1 + \sum_j c_j h_j n_j \right) \geq \bar{a}h_i. \quad (11)$$

If the reverse inequality holds for all i , the equilibrium is given by¹⁰

$$e_i = \bar{e}_i \quad \text{and} \quad x_i = c_i \bar{e}_i, \quad i = 1, \dots, m. \quad (12)$$

Obviously, (12) characterizes a congestion-free short-run equilibrium in which the representative plant's energy exposure and optimal biomass (or size) is independent of the size and the populations of all species. Alternatively, in a congested short-run equilibrium (9) indicates that a plant's biomass increases with the available space, with its shade tolerance, and with decreases in its variable respiration, while the plant's biomass decreases with increases in the space taken up by other plants. The plant's biomass is independent of its fixed respiration in the short run, but as shown below this is not true in a long-run equilibrium.

6. Community dynamics

In short-run equilibrium the representative individual of population i develops the net energy $R^i \{ \widehat{E}^i(n), X^i [\widehat{E}^i(n)] \}$ that may be positive, zero or negative. We now show how the sign of net energy translates into the sign of population growth by deriving the population update equation:

$$\dot{n}_i = n_i \cdot \frac{\gamma_i R^i \{ \widehat{E}^i(n), X^i [\widehat{E}^i(n)] \}}{X^i [\widehat{E}^i(n)]} \quad i = 1, \dots, m, \quad (13)$$

where $\dot{n}_i \equiv dn_i/dt$ and where γ_i is a positive constant (gm cal⁻¹). The competition coefficient in the population growth equations referred to in Section 2 is $R^i(\cdot)/X^i(\cdot)$ in (13). As claimed in Section 2, the coefficient summarizes the results of interactions between all members of all

populations competing for light access, but it is derived from the individual's maximization problem. The term $\gamma_i R^i(\cdot)/X^i(\cdot)$ is the per capita growth rate. The idea is that because the optimum net energy in the numerator is energy available for reproduction above replacement levels (and it may be negative or zero), and because the size of the plant in the denominator, after being converted to a measure of energy using γ_i , is the energy spent to create new individuals, then the total number of new individuals from the representative plant is $\gamma_i R^i(\cdot)/X^i(\cdot)$. Including γ_i allows for interspecies differences in converting net energy to offspring. In other words, a population increase depends on individuals' abilities to convert energy into offspring (Schoener, 1986).

Growth equation (13) represents a system of m non-linear differential equations that determine the structure of the community over time. No attempt is made to characterize the general dynamics in the present paper. These can be computed, if at all, in numerical analysis with suitable computer algorithms. Here we proceed by asking the more modest but interesting question:

How does species i 's population increment over time, \dot{n}_i , depend on the size of species j , n_j , (with $j = i$ or $j \neq i$) provided that the populations of all other species k , $k \neq i, j$, remain constant?

To answer this question, differentiate (13) with respect to n_j and obtain, as shown in the appendix,

$$\frac{d\dot{n}_i}{dn_j} = \hat{n}_i \left[\frac{dn_i}{dn_j} + \frac{n_i}{n_j} \cdot \varepsilon(\dot{n}_i, e_i) \cdot \varepsilon(e_i, n_j) \right], \quad (14)$$

where $\varepsilon(\dot{n}_i, e_i) \equiv \frac{d\dot{n}_i}{de_i} \cdot \frac{e_i}{\dot{n}_i} = \varepsilon(r_i, e_i) - \varepsilon(x_i, e_i)$, $\varepsilon(r_i, e_i) \equiv \frac{e_i R_{e_i}^i}{R^i}$, $\varepsilon(x_i, e_i) \equiv \frac{e_i X_{e_i}^i}{x_i}$, $\varepsilon(e_i, n_j) \equiv \frac{n_j \hat{E}_{n_j}^i}{e_i}$,

$\hat{n}_i = \frac{\dot{n}_i}{n_i} = \frac{\gamma r_i}{x_i}$ (from (13)) and where $\frac{dn_i}{dn_j} = \begin{cases} 1, & \text{if } i = j \\ 0 & \text{otherwise} \end{cases}$.

To interpret (14) we distinguish uncongested and congested ecosystems. Suppose, first, the ecosystem is uncongested, i.e. the initial vector of populations is such that $n \in N_o^i \equiv \left\{ n \mid (X[\widehat{E}(n)], n) \in D_o^i \right\}$ (with $X[\widehat{E}(n)]$ as defined in (4)). Then $\varepsilon(e_i, n_j) = 0$ due to E3.

Hence, (14) yields

$$\frac{d\dot{n}_i}{dn_j} = \begin{cases} \hat{n}_i, & \text{if } i = j \\ 0 & \text{otherwise} \end{cases} \text{ for all } n \in N_o^i \quad (15)$$

For the relevant case $\dot{n}_i > 0$ it follows from (15) that in an uncongested ecosystem the development of species i is not disturbed by any other species. But the increment in species i 's population, \dot{n}_i , increases with its own population at the rate of population growth, \hat{n}_i . More specifically, since $e_i = \bar{e}_i$ for $n \in N_o^i$ (see E3) we infer from (13) and (15) that

$$\frac{d\dot{n}_i}{dn_i} = \hat{n}_o^i \equiv \frac{\gamma R^i[\bar{e}_i, X^i(\bar{e}_i)]}{X^i(\bar{e}_i)} = \text{constant for all } n \in N_o^i.$$

Summary 1: In an uncongested ecosystem each species grows at a constant species-specific rate, and this linear growth is unaffected by the growth of other species.

Suppose now the ecosystem is congested, i.e. $n \notin N_o^i$. In this case the sign and size of the elasticities $\varepsilon(\dot{n}_i, e_i)$ and $\varepsilon(e_i, n_j)$ from (14) turn out to be decisive for the sign and size of $d\dot{n}_i/dn_j$. As our detailed discussion of these elasticities in the appendix shows it is reasonable to assume $\varepsilon(\dot{n}_i, e_i) > 0$ and $\varepsilon(e_i, n_j) < 0$. With this qualification (14) yields

$$\frac{d\dot{n}_i}{dn_j} \begin{cases} < \\ > \end{cases} 0 \text{ if } R^i(\cdot) \begin{cases} > \\ < \end{cases} 0 \text{ and } i \neq j \text{ and } n \notin N_o^i, \quad (16)$$

$$\frac{d\dot{n}_i}{dn_j} \begin{cases} < \\ > \end{cases} \hat{n}_i \text{ if } R^i(\cdot) \begin{cases} > \\ < \end{cases} 0 \text{ and } i = j \text{ and } n \notin N_o^i. \quad (17)$$

(16) states that if species i is increasing $[R^i(\cdot) > 0]$ its population increase, ceteris paribus, is smaller the greater is the population of some species $j \neq i$. This reflects the competition for space among species that was absent under the conditions of (15). Comparing (15) for $i = j$ with (17) reveals that if species i increases $(R^i(\cdot) > 0)$ and aggravates congestion by increasing its own population $(dn_i > 0)$, its population increase slows down. More specifically, (17) implies for $i = j$ that

$$\frac{d\hat{n}_i}{dn_i} = \frac{1}{n_i} \left(\frac{d\dot{n}_i}{dn_i} - \hat{n}_i \right) < 0.$$

Hence, congestion causes the rate of population growth to slow down until \hat{n}_i will eventually become zero.

Summary 2: In a congested ecosystem species compete for space, and their growth is reduced, ceteris paribus, if the population of other species increases. When the populations of all other species are kept constant, the species under consideration grows at a positive rate when congestion sets in but its population growth then slows down and will eventually become zero.

These results exemplify plastic growth responses, and they are consistent with Clark (1990) who finds that more crowded stands of plants grow more slowly.

More specific results on how a species' growth is affected by its own (growing) population in a congested ecosystem can be obtained by resorting to the parametric model (5) – (7). It is shown in the appendix that under the condition that the populations of all other species remain unchanged the population growth curve for species i is characterized by

$$\frac{d\dot{n}_i}{dn_i} < 0 \text{ for all } n \notin N_o^i, \text{ for all } \dot{n}_i > 0 \quad \text{and} \quad \frac{d^2\dot{n}_i}{dn_i^2} < 0. \quad (18)$$

According to (18) the population increase of species i declines as soon as the community becomes congested. This decline is the more pronounced the greater is n_i . Consequently, there is some $\bar{n}_i > 0$ satisfying $\dot{n}_i = 0$. \bar{n}_i represents the *carrying capacity* which is calculated as

$$\bar{n}_i = \sqrt{\frac{\bar{a}^2}{2\beta_i c_i}} - \left(1 + \sum_{j \neq i} c_j h_j n_j\right) \frac{1}{c_i h_i}. \quad (19)$$

Thus, a population's carrying capacity is positively related with the available space, and negatively related to the space taken by other populations. Additionally, the carrying capacity is negatively related to a representative plant's fixed respiration and shade tolerance: the former because each plant must be larger to capture more energy to cover the greater fixed respiration, and the latter because greater shade tolerance means the plants can be more congested in equilibrium.

The population growth curve of plant species i is illustrated in figure 2. When the population n_i is small the ecosystem is uncongested and species i grows at the rate $\hat{n}_i^o \equiv \gamma R \left[\bar{e}_i, X^i(\bar{e}_i) \right] / X^i(\bar{e}_i)$, as demonstrated above, and in the figure $\tan \alpha = \hat{n}_i^o$. Congestion occurs when some threshold population, \tilde{n}_i in the figure, is exceeded. Starting at the point in time when \tilde{n}_i is reached, species i continues to grow, but at a declining rate. This is so, because for $n_i > \tilde{n}_i$

$$\frac{d\hat{n}_i}{dn_i} = \hat{n}_i \varepsilon(\hat{n}_i, e_i) \varepsilon(e_i, n_i) < 0.$$

Population growth continues but at ever declining rates, until eventually a steady state is reached at the maximum population \bar{n}_i as specified in (19).

7. Long-run Community Equilibrium

As mentioned above, the full-scale dynamic interactions of all species as described by (13) are too complex for non-numerical analysis. Under certain conditions (which we do not investigate here) the ecosystem reaches a long-run equilibrium defined by

$$\dot{n}_i = 0 \text{ for all } i. \quad (20)$$

To be more specific, suppose there are m species in a given uncongested ecosystem. Denote the set of these species by M . A long-run ecosystem equilibrium is defined by a vector of populations n^* and a set of species $N^* \subset M$ such that

- (i) $R^i \left\{ \widehat{E}^i(n^*), X^i \left[\widehat{E}^i(n^*) \right] \right\} = 0$ for all $i \in N^*$
- (ii) $n_i^* = x_i^* = 0$ for all $i \in M, i \notin N^*$.

In case of the parametric model, equilibrium condition (i) reads

$$\widehat{E}^i(n^*) = \sqrt{\frac{2\beta_i}{c_i}} \quad \text{for all } i \in N^*. \quad (21)$$

When combined with (10), (21) implies

$$1 + \sum_j c_j h_j n_j^* = \sqrt{\frac{\bar{a}^2 c_i h_i^2}{2\beta_i}} \quad i \in N^*. \quad (22)$$

With this information, a long-run equilibrium is characterized in the parametric model by $n^* \in \mathfrak{R}_+^m$ and $N^* \subset M$ such that

- (i) $\frac{c_i h_i^2}{\beta_i} = \frac{c_j h_j^2}{\beta_j}$ for all $i, j \in N^*$,
- (ii) $1 + \sum_j c_j h_j n_j^* > \sqrt{\frac{\bar{a}^2 c_i h_i^2}{2\beta_i}}$ for all $i, j \in M, i \notin N^*$.

Basically, the above conditions along with (10) and (21) state that if in a long-run equilibrium where plants other than plant i are earning zero net energy, and plant i 's energy exposure

is less than what it would require to earn zero net energy, then plant i cannot exist in the equilibrium. The conditions, therefore, shed light on what plants can coexist, and if the physiological parameters of the plants can be estimated, then predictions about coexistence would follow. Note that although there is only one resource being shared in this simple model, there is no limit on the number of coexisting species. This contrasts to the *competitive exclusion* principle that states “competition between consumers whose population growth rate is controlled only by resource availability invariably results in the extinction of all but one competitor.” (Gurney and Nisbet, 1998, p. 166) In approaches that begin with one differential equation for each species, and with only one resource, only one (non identical) species can have the lowest resource requirement.¹¹ Alternatively, here steady state occurs when the output of the maximization problem yields $R^i(\cdot) = 0$. But R_i depends on the behavioral parameters c_i , h_i and β_i , and there are infinite combinations of these three parameters yielding $R_i(\cdot) = 0$. This suggests that plants adapt to find a combination of these parameters that permit their success in the competitive environment. If experimental evidence supported the theory presented here with respect to coexistence of more species than resources, then the results may help explain what Hutchinson (1959) labeled the paradox of diversity with respect to animals, but which applies to plants as well. (Barbour et al., 1999).

A simulation was performed for a single species and the results for population, biomass and exposure over forty periods are shown in Figure 3. Panel a has the population starting below the steady state and Panel b has the population starting above the steady state value of 1740. When the population in Panel a starts at 5, there is no congestion and the population grows rapidly, but when congestion sets in around period 15 the growth slows down. This is in accordance with Summaries 1 and 2 above. In Panel b self thinning occurs as density decreases while simultaneously the survivors have greater biomass (See Clark, J.S., 1990). The reader can verify that the steady state values for population, exposure and biomass satisfy (19), (21) and $x = c E$.

8. Final Word

The success of a micro approach in deriving population growth curves is limited by the availability of key parameters. Bounds on parameter values for the exposure index and respiration functions can be found: 1) from observations about the relationships between population densities and light access; 2) based on necessary and sufficient conditions for a maximum to the net energy problem; and 3) using estimates of ecological efficiencies, if herbivores and predators are introduced. Laboratory and field experiments will be necessary to obtain parameter estimates within the theoretical bounds. (Finnoff and Tschirhart (2001) obtain parameter estimates from diverse ecological studies to describe an eight species Alaskan marine ecosystem.)

We believe that obtaining estimates is worthwhile, because the micro approach has several advantages over the traditional macro approach. First, it is behaviorally more basic in that it provides a picture of how a population changes by linking the changes with the individual's responses it receives about scarce resources. For example, carrying capacity for a single species is shown to depend on individual behavior determined by physiological parameters. In practice, if these parameters can be estimated, then improved predictions of population changes may follow. Second, the modeling framework allows any number of species to be easily linked (Tschirhart, 2000). Third, the micro approach is useful for identifying variables that may be important in the competition for resources. Fourth, relating to parameter estimation, the first- and second-order conditions from the maximization problems provide both guidance on the form of the functions describing resource use, and bounds on the functions' parameters; plus, there is a voluminous literature on optimization techniques from which to draw further insights about population growth. Fifth, by starting with a behavioral postulate, in this case net energy maximization, there is the opportunity to reject the postulate. Thus, if repeated attempts at estimating alternative functional forms yield poor predictions, then the behavioral postulate is called into question and an alternative postulate should be examined (Southwood, 1980). And sixth, the modeling framework is similar to the framework of microeconomic models, and this permits easier integration of the ecosystem and economic models (Finnoff and Tschirhart, 2001).

Appendix

Derivation of equation (14): We differentiate $\dot{n}_i = n_i \frac{\gamma R^i \{ \widehat{E}^i(n), X^i [\widehat{E}^i(n)] \}}{X^i [\widehat{E}^i(n)]}$ from (13)

with respect to n_j for any $j = 1, \dots, m$:

$$\frac{d\dot{n}_i}{dn_j} = \frac{dn_i}{dn_j} \frac{\gamma r_i}{x_i} + \frac{n_i \gamma}{x_i^2} [x_i (R_{e_i}^i \widehat{E}_{n_j}^i + R_{x_i}^i X_{e_i}^i \widehat{E}_{n_j}^i) - r_i X_{e_i}^i \widehat{E}_{n_j}^i]$$

Since $R_{x_i}^i = 0$ (net energy maximization), we obtain

$$\frac{d\dot{n}_i}{dn_j} = \frac{\gamma r_i}{x_i} \left[\frac{dn_i}{dn_j} + \frac{n_i}{n_j} \frac{n_j \widehat{E}_{n_j}^i}{e_i} \left(\frac{e_i R_{e_i}^i}{r_i} - \frac{e_i X_{e_i}^i}{x_i} \right) \right] \quad (\text{A.1})$$

Define $\varepsilon(e_i, n_j) := \frac{n_j \widehat{E}_{n_j}^i}{e_i}$, $\varepsilon(r_i, e_i) := \frac{e_i R_{e_i}^i}{r_i}$, $\varepsilon(x_i, e_i) := \frac{e_i X_{e_i}^i}{x_i}$ and $\hat{n}_i = \frac{\dot{n}_i}{n_i} = \frac{\gamma r_i}{x_i}$ (from (13)) to

rewrite (A.1):

$$\frac{d\dot{n}_i}{dn_j} = \hat{n}_i \left\{ \frac{dn_i}{dn_j} + \frac{n_i \varepsilon(e_i, n_j)}{n_j} [\varepsilon(r_i, e_i) - \varepsilon(x_i, e_i)] \right\}$$

Define $\varepsilon(\dot{n}_i, e_i) := \frac{d\dot{n}_i}{de_i} \frac{e_i}{\dot{n}_i}$. To demonstrate that $\varepsilon(\dot{n}_i, e_i) = \varepsilon(r_i, e_i) - \varepsilon(x_i, e_i)$ we calculate

$$\frac{d\dot{n}_i}{de_i} = \frac{\gamma n_i}{x_i^2} [x_i (R_{e_i}^i + R_{x_i}^i X_{e_i}^i) - r_i X_{e_i}^i] = \frac{\gamma n_i r_i}{x_i} \left(\frac{R_{e_i}^i}{r_i} - \frac{X_{e_i}^i}{x_i} \right) = \frac{\dot{n}_i}{e_i} [\varepsilon(r_i, e_i) - \varepsilon(x_i, e_i)].$$

The elasticities $\varepsilon(e_i, n_j)$ and $\varepsilon(\dot{n}_i, e_i)$: To specify $\varepsilon(e_i, n_j)$ we need to determine $\widehat{E}_{n_j}^i$. For that purpose one would differentiate $E^i \{ X [\widehat{E}(n)] n \}$, $i = 1, \dots, m$, with respect to n , and this amounts to a system of m equations. Therefore, the sign of $\widehat{E}_{n_j}^i$ will be indeterminate, if a large class of functions, E^i , is considered that have the properties E1 - E3. To obtain specific results, therefore, we focus on less general exposure functions. For the parametric model (5) - (7) $\widehat{E}^i(n)$ was

given by (10) implying unambiguously $\widehat{E}_{n_j}^i < 0$ for all j . In what follows, we show that this result extends to non-parametric models if the exposure functions take the form $e_i = \widetilde{E}^i(a)$ with $a \equiv \sum_j x_j n_j$ (see figure 1). Define $\widehat{E}^i(n) \equiv \widetilde{E}^i \left\{ \sum_j X^j \left[\widehat{E}^j(n) \right] n \right\}$ and differentiate with respect to n_k :

$$\widehat{E}_{n_k}^i = \widetilde{E}_a^i \sum_j \left(X_{e_j}^j \widehat{E}_{n_k}^j n_j + x_j \frac{dn_j}{dn_k} \right)$$

Since $\frac{dn_j}{dn_k} = 0$ for $j \neq k$ and $\frac{dn_j}{dn_k} = 1$ for $j = k$, the above equation can be turned into

$$\frac{\widehat{E}_{n_k}^i}{\widetilde{E}_a^i} = \sum_j X_{e_j}^j \widehat{E}_{n_k}^j n_j + x_k \quad \text{for } i = 1, \dots, m \quad (\text{A.2})$$

in case of congestion ($\widetilde{E}_a^i < 0$). Observe that the right side of (A.2) is the same for all i . Therefore, it follows that

$$\frac{\widehat{E}_{n_k}^i}{\widetilde{E}_a^i} = \frac{\widehat{E}_{n_k}^h}{\widetilde{E}_a^h} \text{ and } \text{sign } \widehat{E}_{n_k}^i = \text{sign } \widehat{E}_{n_k}^h \text{ for all } i, h = 1, \dots, m.$$

To demonstrate that $\widehat{E}_{n_k}^i < 0$ for all $j = 1, \dots, m$, suppose the contrary. Then the right side of (A.2) is positive and so is $\widehat{E}_{n_k}^i / \widetilde{E}_a^i$. But $\widetilde{E}_a^i < 0$ by assumption. Hence $\widehat{E}_{n_k}^i < 0$ for all $j = 1, \dots, m$. Quite obviously, $E^i(x, n)$ from (6) is a special case of \widehat{E}^i , and it is not surprising, therefore, that combined with (7) the implied function $\widehat{E}^i(n)$ from (10) exhibits $\widehat{E}_{n_k}^i < 0$ for all k .

Consider now the elasticity $\varepsilon(\dot{n}_i, e_i)$ in (14). It is plausible to assume that if species i 's access to light improves, then its population grows faster, i.e., $\varepsilon(\dot{n}_i, e_i) > 0$. In fact, this hypothesis is implicit in the parametric model (5) - (7), because in this case $\varepsilon(r_i, e_i) = \gamma_i / \hat{n}_i$ and

$$\varepsilon(x_i, e_i) = 1 \text{ imply } \varepsilon(\dot{n}_i, e_i) = \left(\frac{\gamma_i}{\hat{n}_i} - 1 \right). \text{ This term is positive because } \hat{n}_i = \frac{\gamma_i}{2} - \frac{\gamma \beta_i}{x_i} < \gamma_i.$$

Population growth with congestion in the parametric model: For $i=j$, equation (14) reads $\frac{d\hat{n}_i}{dn_i} = \hat{n}_i \{1 + [\varepsilon(r_i, e_i) - \varepsilon(x_i, e_i)]\varepsilon(e_i, n_i)\}$. In view of (5) - (7) we calculate $\varepsilon(r_i, e_i) = \frac{e_i x_i}{r_i} = \frac{\gamma e_i}{\hat{n}_i}$,

$\varepsilon(e_i, n_i) = -\frac{c_i e_i n_i}{\bar{a}}$ and $\varepsilon(x_i, e_i) = 1$. Hence

$$\frac{d\hat{n}_i}{dn_i} = \hat{n}_i \left[1 - \left(\frac{\gamma e_i}{\hat{n}_i} - 1 \right) \frac{c_i e_i n_i}{\bar{a}} \right] \quad \text{or} \quad \frac{d\hat{n}_i}{dn_i} = \hat{n}_i \left(1 + \frac{x_i n_i}{\bar{a}} \right) - \frac{\gamma e_i x_i n_i}{\bar{a}}.$$

We now consider $\hat{n}_i = \frac{\gamma e_i}{2} - \frac{\gamma \beta_i}{x_i}$ from (7) and (13) and write

$$\begin{aligned} \frac{d\hat{n}_i}{dn_i} &= \gamma \left[\left(\frac{e_i}{2} - \frac{\beta_i}{x_i} \right) \left(1 + \frac{x_i n_i}{\bar{a}} \right) - \frac{e_i x_i n_i}{\bar{a}} \right] = \gamma \left[\frac{e_i}{2} + \frac{e_i x_i n_i}{2\bar{a}} - \frac{e_i x_i n_i}{\bar{a}} - \frac{\beta_i}{x_i} \left(1 + \frac{x_i n_i}{\bar{a}} \right) \right] \\ &= \gamma \left[\frac{e_i}{2} \left(1 - \frac{x_i n_i}{\bar{a}} \right) - \frac{\beta_i}{x_i} \left(1 + \frac{x_i n_i}{\bar{a}} \right) \right] \end{aligned} \quad (\text{A.3})$$

Observe that $e_i > 0$ presupposes $\bar{a} > x_i n_i$ (from (6)). Therefore, $1 > x_i n_i / \bar{a}$, and the inequality

$$\gamma \left(\frac{e_i}{2} - \frac{\beta_i}{x_i} \right) \left(1 - \frac{x_i n_i}{\bar{a}} \right) > \frac{d\hat{n}_i}{dn_i}$$

holds. The left side of this inequality is non-positive, if and only if $e_i^2 \geq \frac{2\beta_i}{c_i}$ which is equivalent to $R^i[e_i, X^i(e_i)] \geq 0$ or $\dot{n}_i \geq 0$. Hence we established that for the parametric model (5) - (7) it is true that

$$\frac{d\hat{n}_i}{dn_i} < 0 \quad \text{for all } n \notin N_o^i \quad \text{and for all } \dot{n}_i > 0 \quad (\text{A.4})$$

To determine the sign of the second derivative of \hat{n}_i with respect to n_i we rearrange (A.3),

$$\frac{d\hat{n}_i}{dn_i} = \gamma \left[\frac{e_i}{2} - \frac{\beta_i}{c_i e_i} - \frac{\beta_i n_i}{\bar{a}} - \frac{c_i e_i^2 n_i}{2\bar{a}} \right], \quad \text{and differentiate:}$$

$$\frac{d^2 \hat{n}_i}{dn_i^2} = \gamma \left[\frac{1}{2} \hat{E}_{n_i}^i + \frac{\beta_i}{c_i e_i^2} \hat{E}_{n_i}^i - \frac{\beta_i}{\bar{a}} - \frac{c_i}{2\bar{a}} (2e_i n_i \hat{E}_{n_i}^i + e_i^2) \right] = \gamma \left[\left(\frac{1}{2} + \frac{\beta_i}{x_i e_i} - \frac{x_i n_i}{\bar{a}} \right) \hat{E}_{n_i}^i - \frac{\beta_i}{\bar{a}} - \frac{x_i e_i}{2\bar{a}} \right].$$

Since $\hat{E}_{n_i}^i = -\frac{x_i e_i}{\bar{a}}$, the last equation is equivalent to

$$\frac{d^2 \hat{n}_i}{dn_i^2} = -\gamma \left[\left(\frac{1}{2} + \frac{\beta_i}{x_i e_i} - \frac{x_i n_i}{\bar{a}} \right) \frac{x_i e_i}{\bar{a}} + \frac{\beta_i}{\bar{a}} + \frac{x_i e_i}{2\bar{a}} \right] = -\gamma \left[\left(1 - \frac{x_i n_i}{\bar{a}} \right) + \frac{2\beta_i}{\bar{a}} \right] < 0.$$

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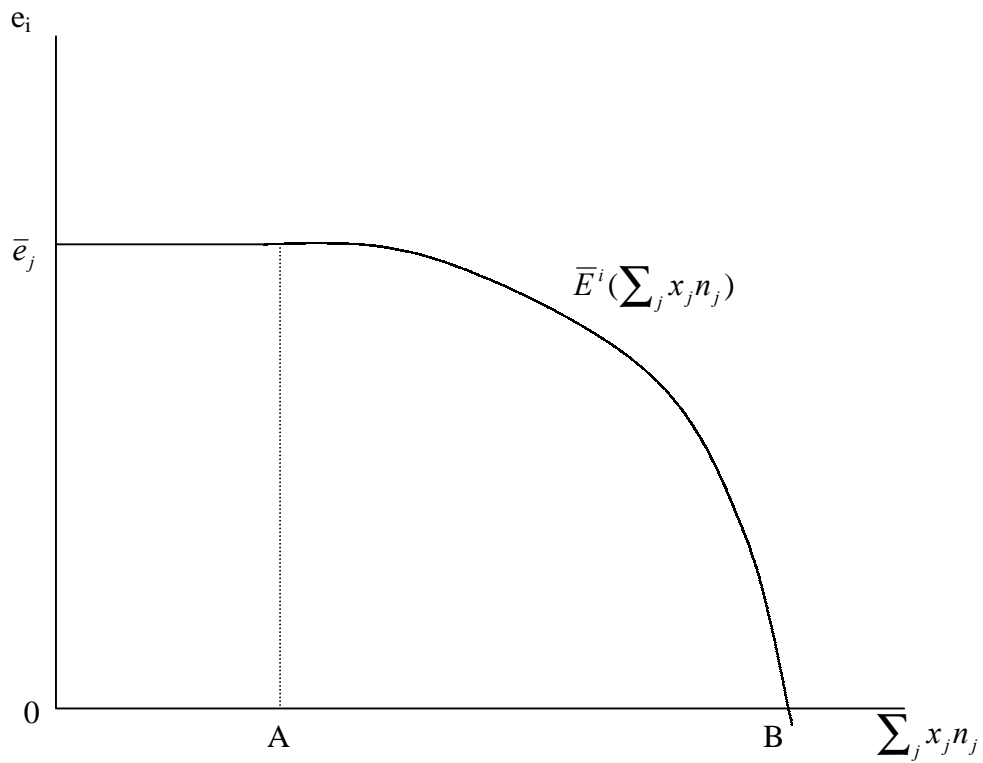


Figure 1.

Light exposure depending on the biomass of all plants in the community. From the origin to point A the community is uncongested and plant i absorbs light energy \bar{e}_j . As the total biomass increases along the horizontal axis, the community space fills, competition for light intensifies, and the absorbed light begins to fall and eventually reaches zero at point B.

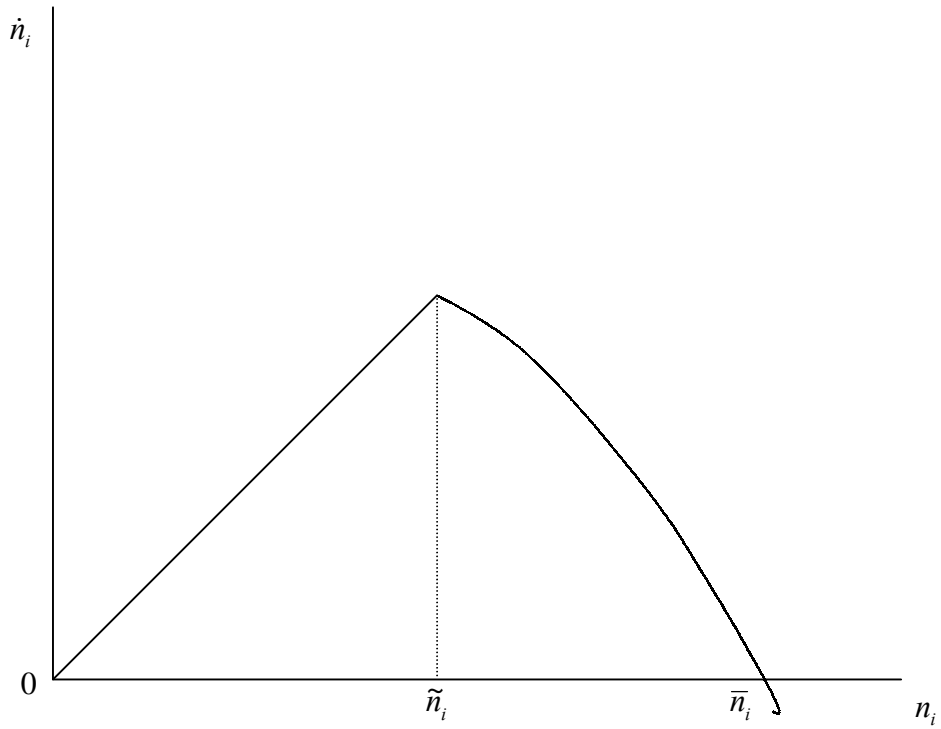


Figure 2.

The population growth curve for population i based on optimizing plants competing for access to light. From the origin to the peak the community is uncongested and the population exhibits exponential growth. After the peak, congestion sets in and competition intensifies so that the rate of growth slows until a carrying capacity is reached.

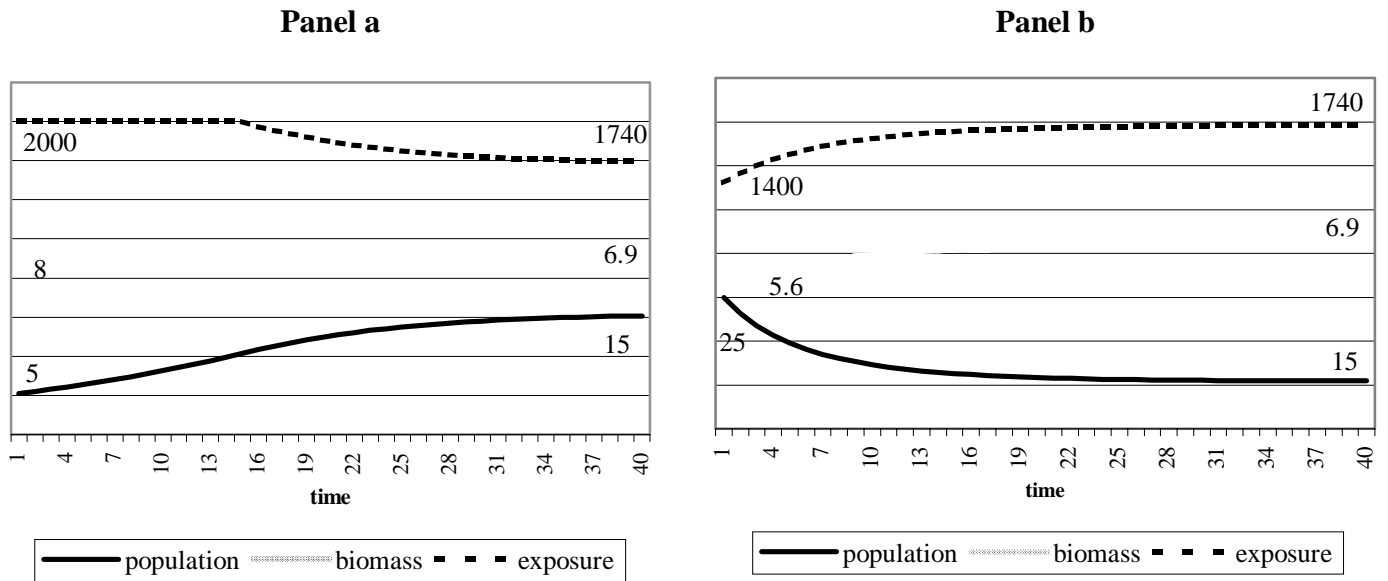


Figure 3

The graphs display populations (n), plant biomass (x) and the light exposure (e) over time for two cases that differ by the initial populations. All other parameters are held constant at values: $h = 10$, $a = 280$, $c = 0.004$, $\beta = 6000$ and $\gamma = 0.0002$. Values on the vertical axes are rescaled so only trends are significant. The steady-state population is approximately 15 which is the carrying capacity. More intense competition (lower e) results in smaller plants. In panel a the plant population starts below steady state and then increases rapidly; in panel b the plant population starts above steady state and self thinning occurs.

¹ See Munro and Scott (1985) or Brown (2000) for synopses.

² One could liken this to macroeconomic models wherein unemployment, consumption and other aggregate concepts are not derived from the behavior of individual actors in the economy.

³ See Pielou (1977), Clark, C. (1990) or Conrad (1999a) for the development and use of growth functions, and Conrad (1999b) or Costello, Polasky and Solow (2000) for recent studies using a stochastic growth function.

⁴ Schoener (1972) derives the logistic growth equation in a mechanistic way, one that employs individual ecological concepts. Nevertheless, his starting point is also a differential equation describing growth that contains entire populations.

⁵ The analogy in consumer theory, for example, would be to start with consumer demand functions and omit how consumer preferences yield those demand functions.

⁶ Caughley and Lawton (1976) indicate the same concepts inherent in Lotka-Volterra models apply to plants as well as animals.

⁷ Energy is singled out as a resource for several reasons. As long ago as Cowles (1899), light has been referred to as one of the main limiting resources in succession (along with nitrogen), and the importance of energy efficiency has its roots in the pioneering work of Lotka (1922). According to Herendeen (1991) energy has been the most frequently chosen maximand in ecological optimization models, and the individual-based, energy-maximizing hypothesis adopted below is closely aligned with Hannon (1973, 1976) and expanded to multiple species in Tschirhart and Crocker (1987), Crocker and Tschirhart (1992) and Tschirhart (2000).

⁸ Economists make simplifying assumptions about human behavior to develop mathematically tractable models. These simplifying assumptions “may be more reasonable for plant systems than for human systems.” (Bloom et al., 1985)

⁹ The conditions under which this presupposition turns out to be correct will be spelled out after the calculations.

¹⁰ Intermediate cases where only some but not all species suffer under congestion may occur but will not be considered here.

¹¹ Gurney and Nisbet point to experiments by Goulden et al. (1982) in which species of zooplankton (*Daphnia galeata mendotae* and *Bosmina longirostris*) competed for one algal food source. The experiment did not run long enough to yield unambiguous results, but *Daphnia* began to numerically dominate suggesting that competitive exclusion may have been operating.