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Identifying, preventing and controlling invasive plant species using their physiological traits

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Abstract

A model of a plant community that is biologically reasonable and easily adaptable to economic models is presented. The model includes optimization, competition, stochastic limiting resources, and identification of redundant and invasive species. Species exhibit a rich array of traits that make them suited for some set of environmental factors and not for other sets. And because environmental factors are constantly changing, species that are very successful under one set of factors become redundant under another set, implying that an ecosystem needs redundant species as insurance. Invasive species are the flip side of redundant species as they are successful, at least under some environmental conditions. Identification depends on four physiological parameters defining each plant: two respiration parameters, a parameter that gives the plant's ideal level of the stochastic limiting resource, and the specific leaf area. The parameters are terms in an expression that gives the net energy intake of an individual plant, and the plant behaves as if it optimizes this by choosing its individual biomass. Success of species is judged based on the biomass of the species in steady state. An application extends the range management literature by incorporating the model into a rangeland manager's decision problem extends the range management literature. The model allows for multiple plant species, addresses the influence of limiting resources (other than density dependence), and tracks the response of the entire system to human and natural system perturbations. The methods allow simple predictions of community composition in the face of jointly determined economic/ecological behavior. The power of the method is demonstrated through stylized examples of alternative invasion control techniques.

Keywords: Plant competition; Redundancy; Invasive species; Individual optimization

1. Introduction

Invasive species—harmful species introduced from elsewhere—are increasing worldwide, contributing to biodiversity loss and environmental change. Resource managers are being challenged to answer key policy questions of how to allocate society's resources to combat invasive species, and how best to mix ex ante and ex post strategies. To do a reasonable job, managers require knowledge of both economic and ecological systems. Human activities invariably impact ecosystems. The ecosys-

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tems respond to the impacts, in turn causing new human activity, and the process repeats. Capturing this linked economic system–ecosystem interaction requires one to account for adaptation and feedbacks within and between the systems. The issues are substantially complicated for the case of invasive species, where accurate predictions of biological system response to invasion are critical to efficient management. The ecosystem consequences of invasion can be better understood by recognizing that species exhibit a rich array of traits that make each of them ideally suited for some set of environmental factors and species composition and not for other sets and compositions (an early example is Gutierrez and Yaninek, 1983). Because environmental factors and species composition change over time, successful and unsuccessful species, including invaders, may trade places. Less successful species can be viewed as providing biodiversity insurance for the day when environmental factors or species composition change and the less successful replace the previously successful. We refer to these backup species as redundant. At any point in time, if a species is redundant in the community, it cannot be a successful invader, whereas a species that is a successful invader cannot be redundant.

In this paper a theory is developed and applied in a range management setting that can be used for identifying redundant and successful invasive plant species. Identification depends on four physiological parameters defining each plant: two respiration parameters, a parameter describing the plant's solar energy intake, and a parameter that gives the plant's ideal level of an environmental factor. The parameters are terms in an expression that gives the net energy intake of an individual plant, and the plant behaves as if it is maximizing this net energy by choosing their individual biomass.[1] The major difference between the theory presented here and most other theories of plant population dynamics is what underpins the population update equations. Most other theories take the update equations as their starting point. The equations include state variables for species populations, and they are formed by assuming that the changes in a population depend on the populations of other species in the community and on resource availability.

In the plant community model herein, the theory starts prior to population updates by first assuming the individual plant behaves as if it is choosing its optimum biomass. Optimization is done given the plant's parameters and the presence of other competing plants in its own and other species. The optimum amount of biomass is found to be where the marginal energy gain from growing another unit of biomass equals the marginal energy loss to respiration from that unit. The success of the individual in processing energy efficiently determines the species growth rate in the update equation.

The plant community occupies a fixed space, and as plants grow more biomass and/or become more numerous, the space fills up. As the space fills, each new unit of biomass grown becomes less effective in absorbing energy owing to shading from other plants. The loss in effectiveness is labeled the shading energy loss (SEL), and it represents the "price" the plant must pay to obtain energy. No single plant has any control over the SEL because it is only one of many plants in its vicinity and the value of the SEL depends on the aggregate action of all plants. Specifically, SEL is determined by equating the sum of all plants' optimum biomasses, or their "demands" for biomass, to the supply of space. When there are few plants in the space, SEL is zero and there is no competition. As plant biomasses and populations increase, however, SEL turns positive, and the greater the aggregate biomass demands, the greater is SEL and the more intense is the competition.

Populations change according to the success of the plants in storing net energy, and their optimum net energy is inversely related to SEL. Thus, when there is no competition and SEL is zero, net energies are positive and the populations grow. When there is competition, SEL turns positive and net energies fall. If they fall below zero, populations shrink. The interaction between the plants' demands and the supply of space tend to move net energies to zero and to a steady state.

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[1] Gutierrez and Baumgärtner (1984), Gutierrez (1992), and Gutierrez et al. (1994) present a similar method, where genetically determined maximum demands are constrained by current ecosystem conditions. Realized demands (realized functional responses) in the short-run depend on a parameter describing the accessibility of prey to the predator, and the ratio of the prey mass to the predator mass. For given maximum demands and levels of accessibility, the functional response is determined solely by the mass ratio in the absence of any optimization.

If one species' plants have positive net energies while another species' plants have negative net energies, the former species will eventually drive out the latter species. Which species dominate and which species are redundant or invaders can be predicted based on the parameters in their net energy function. Basically, species that respire relatively little per unit of their biomass, or species that absorb more energy per unit of their biomass, will be nonredundant or successful invaders.

2. One plant species

In an application, the range management literature is extended by incorporating the model into a rangeland manager's decision problem. The model allows for multiple plant species, addresses the influence of limiting resources (other than density dependence), and tracks the response of the entire system to human and natural system perturbations. The methods allow simple predictions of community composition in the face of jointly determined economic/ecological behavior. The power of the method is demonstrated through a stylized example of alternative invasion control strategies.

2.1. The individual plant

All else equal, plants that use energy more efficiently are more successful. Efficient use of energy is modeled by assuming that each plant behaves as if it is maximizing net energy intake per unit time. Energy per time is a power unit, although in keeping with the literature, we will simply refer to the plants as maximizing energy. There is a long history of energy as a maximand (see e.g., Hannon, 1973, 1976; Herendeen, 1991), but there are genetic limits (Gutierrez, 1992). The advantages of an optimization approach are discussed in Tschirhart (2000, 2002). Maximizing net energy does not preclude that other resources are vital. In fact, any number of resources (water, nitrogen, etc.) can be added to each plant's optimization problem. Rather, energy is a currency much like money is a currency in economic systems. An economic firm is assumed to maximize monetary profit, not because money is intrinsically desirable, but because money can be exchanged for productive inputs (land, labor, capital) that are needed to produce marketable outputs (food, shelter, and clothing). If profit is positive, meaning that market revenue from selling outputs exceeds the monetary costs of inputs, the excess can be used to grow the firm and "give birth" to new firms. Similarly, for a plant, energy is needed to acquire other resources, and any "excess" energy can be used for growth and reproduction. The resource that is being competed over in the formulation herein is access to light energy.

All plants in a species are assumed to be identical, so the analysis is carried out for the representative plant. In addition, only the mature plant is modeled, no earlier stages of growth are considered. A plant belonging to species i maximizes net energy flow (e.g., Watts W) and is linear in photosynthesis and in the conversion constant,

$$R_i = (ea_i - e_0)x_i - f_i(x_i) - \beta_i. \tag{1}$$

In Eq. (1), x_i is the plant's biomass (in gm units), and it is the choice variable: other things equal, the greater the biomass, the greater the exposure to light energy. The e is the flow of both direct and indirect solar radiation arriving at the surface of the plant for each unit of area (W cm^{-2} or kcal time^{-1} cm^{-2}). Because light availability is random, the model could be extended to make e a stochastic variable.

The a_i (m^2 gm^{-1}) is the plant's specific leaf area (SLA). SLA can vary by an order of magnitude across species based on leaf cell structures (Asner and Wessman, 1997). Here, the a_i is species-specific and assumed constant. Not examined here is the tradeoff between SLA and leaf longevity that has been studied as another choice strategy in plant behavior (Westoby et al., 2000).

The e_0 (W g^{-1}) is the SEL. Because of mutual shading among plants, they potentially incur this loss in competing for access to light. Each plant takes e_0 as a parameter in its optimization problem; but e_0 varies across periods and, as described below, may be zero or positive depending on the intensity of competition that is determined by the simultaneous behavior of all plants. Thus, $(ea_i - e_0)$ is an example of what Bendoricchio and Jorgensen (1997) indicate is needed in modeling ecosystems—a parameter that addresses how ecosystems change their properties to meet changing environmental conditions.

Conceptually, the value of SEL is measured as follows. Suppose a plant expends energy [accounted for in $f_i(x_i)$] to produce a leaf of one biomass unit. Suppose further that 1 W g^{-1} of radiant energy strikes the leaf of which 0.8 are absorbed to fix CO_2. If the same plant produces the same unit leaf area under more competitive conditions (e_0 is larger and there is more shading) and only absorbs 0.4 W g^{-1} from the potential 1 W g^{-1} arriving at the leaf surface, then the SEL incurred is 0.8−0.4=0.4 W g^{-1}.

The energy required for the plant's respiration, which includes growth, maintenance, and replacement reproduction, is divided into two parts, both measured in Watts: a variable portion, $f_i(x_i)$, that depends on the plant's biomass and a fixed portion, β_i, that represents energy lost to the atmosphere independent of the biomass. The function $f_i(x_i)$ is assumed to be increasing and continuously twice-differentiable. The product $(ea_i-e_0)x_i$ in Eq. (1) can be thought of as an individual plant's primary production. By Eq. (1), primary production is allocated to energy lost in "preying" on the sun, fixed and variable respiration, and net energy which is the maximand.

The necessary first-order derivative condition for a maximum of Eq. (1) is,

$$(ea_i - e_0) - \frac{\mathrm{d}f_i(x)}{\mathrm{d}x_i} = 0, \tag{2}$$

implying that biomass is increased to the point where the net marginal energy fixed from the last unit of biomass equals the marginal respiration loss from that unit. The net marginal energy is the difference between the gross energy from fixing the last unit of energy minus the loss the plant incurs to fix energy. All maximizing plants in all time periods follow this balance of marginal benefit and marginal cost in their behavior.

To be more specific and for analytical tractability let,

$$f_i(x_i) = \alpha_i x_i^2, \tag{3}$$

for $\alpha_i>0$. The parameter α_i (W gm^{-2}) converts the plant's biomass to respiration and is species-specific. Other things equal, a plant with a lower α_i respires less for each unit of biomass it accumulates. The functional form of Eq. (3) satisfies sufficient second-order conditions for a maximum, and using Eq. (3) in Eq. (2) gives the plant's demand for biomass,

$$\hat{x}_i(e,e_0,\alpha_i,a_i) = \frac{ea_i - e_0}{2\alpha_i}. \tag{4}$$

Substituting this demand into the objective function yields the optimum net energy,

$$\hat{\mathrm{R}}_i = (ea_i - e_0)\hat{x}_i(\cdot) - \alpha_i\hat{x}_i^2(\cdot) - \beta_i. \tag{5}$$

2.2. One plant species and population updates

The plant is part of a population that occupies a community of fixed physical size, thus there is a limit on the amount of biomass that the community's area can contain. If N_i is the ith species population, then this limit is expressed as,

$$N_i a_i x_i \le A. \tag{6}$$

where A (m^2) is the maximum physical area available to the community. If the model was extended to account for the vertical nature of light, then volume would be the constraining measure. The plants are competing for light by building biomass, although it is space that is in limited supply, and A can be thought of as the resource plants compete over. Thus, although light may not follow a mass-balance constraint (Grover, 1997), the space needed to access light does follow a mass-balance constraint given by Eq. (6) (Beer's Law).

The success of the representative plant as measured by its optimum net energy in Eq. (5) determines whether the plant's species reproduces more than replacement levels to increase its population. In other words, a population increase depends on individuals' abilities to convert energy into offspring (Schoener, 1986). If the optimum net energy, $\hat{\mathrm{R}}_i$, is positive, the representative individual channels the surplus energy to reproduction above replacement levels, and the population increases. Alternatively, if the optimum net energy is negative, this subtracts from the energy needed for replacement, and the population decreases. It follows that zero optimum net energy implies no change in the population. Thus, the success associated with accumulating energy is made operational here by linking net energy to population changes.

The dynamic growth process proceeds by using discrete population update equations that follow from the individuals' objective functions. In steady state, it must be the case that births equal deaths in each time period, and if s_i is the lifespan of the representative individual, then the total number of births and deaths must be N_i/s_i. Dividing the totals by N_i yields the per capita steady state birth and death rates,

$$1/s_i. \tag{7}$$

The plant's maximized net energy is given by $\hat{R}_i$ from Eq. (5). In the steady state, $\hat{R}_i=0$ and all energy for reproduction comes out of variable respiration, consistent with the definitions of the terms in Eq. (5). For $\hat{R}_i>0$ ($\hat{R}_i<0$) there is additional (less) energy available for reproduction (Tschirhart, 2002). Let r_i^{ss} be the steady state variable respiration, and let ρr_i^{ss} be the proportion of this variable respiration devoted to reproduction. Thus, in steady state, the energy given by ρr_i^{ss} yields a per capita birth rate of $1/s_i$. Next, suppose the plant is not in steady state and that $\hat{R}_i\neq 0$ and variable respiration is r_i. Assuming that the proportion of $\hat{R}_i$ that is available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy now available for reproduction is $\rho[\hat{R}_i+r_i]$. Finally, assuming that reproduction is linear in available energy, then it follows that if ρr_i^{ss} yields a per capita birth rate $1/s_i$, then $\rho[\hat{R}_i+r_i]$ yields a per capita birth rate of,

$$\left(\frac{1}{s_i}\right)\frac{[\hat{R}_i+r_i]}{r_i^{ss}}. \tag{8}$$

The change in population is obtained by multiplying the population by the difference between the birth and death rates, where the latter rate is assumed to be independent of energy available for reproduction. Therefore, using Eq. (8), the population adjustment equation is,

$$\begin{aligned} N_i^{t+1} &= N_i^t + N_i^t\left[\frac{1}{s_i}\frac{\hat{R}_i+r_i}{r_i^{ss}} - \frac{1}{s_i}\right] \\ &= N_i^t + N_i^t\frac{1}{s_i}\left[\frac{\hat{R}_i+r_i}{r_i^{ss}} - 1\right]. \end{aligned} \tag{9}$$

Expression (9) reduces to the steady state if $\hat{R}_i=0$ (in which case $r_i=r_i^{ss}$) because the bracketed term is zero. Alternatively, $\hat{R}_i>(<)0$ implies that $r_i>(<)r_i^{ss}$, in which case, population increases (decreases).

Like other ecological models, the populations are updated at the beginning of every period; however, unlike other ecological models, within each period, an equilibrium is calculated wherein each individual maximizes its net energy and the space constraint is satisfied. The results of the equilibrium calculation yield the optimum net energies for each individual from Eq. (5), and these net energies are used in Eq. (9) to update the populations. Thus, in the update equations there are no fixed parameters apart from lifespan and steady state variable respiration; instead, the terms change period-to-period depending on environmental conditions and competition. Note that the within-period equilibriums do not imply steady state; the steady state is attained when the period-to-period populations are unchanging, or the optimum net energies in the within- period equilibrium calculations are all zero.

3. Steady state and coexistence

A steady state is characterized by three conditions: the available space is filled, each plant is maximizing its net energy, and net energies are zero. To solve for the steady state for one species, set Eq. (1) to zero, and use Eqs. (2) and (6) as equalities to obtain biomass, SEL and population,

$$\hat{x}_i^s = \left(\frac{\beta_i}{\alpha_i}\right)^{0.5} \qquad \hat{e}_0^s = ea_i - 2\left(\alpha_i\beta_i\right)^{0.5}$$
$$N_i^s = \left(\frac{\alpha_i}{\beta_i}\right)^{0.5}\frac{A}{a_i}. \tag{10}$$

The results in Eq. (10) illustrate that the steady state optimum plant biomass (which can only be attained in the competitive state because there is exponential growth in the noncompetitive state) depends on the respiration attributes of the individual plant, and it is independent of the SEL, the SLA, and the physical space. The steady-state SEL in the middle equation in Eq. (10) is also independent of the physical space, but does depend on all three individual plant parameters. The steady-state population does depend on ecosystem size A as well as the respiration attributes of individual plants and the SLA. In the absence of any other species, the steady state population can be thought of as the carrying capacity.

Simulations illustrating population changes for a single species in both the competitive and noncompetitive states can be found in Tschirhart (2002).

To introduce multiple species, each representative plant in each species has an objective function of the type shown in Eq. (1), and the space constraint becomes,

$$\sum_{i=1}^{m} N_i a_i x_i \leq A. \tag{11}$$

where m is the number of species and subscripts refer to the ith species. Each species has an update difference equation given in Eq. (9). A pertinent question is what parameter values for the species allow for species coexistence in a steady state? Generally, coexistence of species in a steady state community requires that each plant in each species is maximizing its net energy and the net energies are equal to zero. When this occurs, the populations are unchanging and a multispecies steady state is attained. From Eq. (10), in a steady state, each plant is maximizing net energy, and net energy is zero when $\hat{e}_0^s = ea_i - 2(\alpha_i\beta_i)^{0.5}$. If the community determined SEL $\hat{e}_0^s > ea_i - 2(\alpha_i\beta_i)^{0.5}$, then the plant is earning negative net energy and its species' population is decreasing. Therefore, as competition intensifies with the growth of species populations and $\hat{e}_0$ increases toward $\hat{e}_0^s$, any species for which the term $ea_i - 2(\alpha_i\beta_i)^{0.5}$ is below $\hat{e}_0^s$ dies off given persistent negative net energies. In the steady state, only the species with the highest $ea_i - 2(\alpha_i\beta_i)^{0.5}$ remain. The value of $ea_i - 2(\alpha_i\beta_i)^{0.5}$ leads to a definition of efficiency. More efficient plants have greater $ea_i - 2(\alpha_i\beta_i)^{0.5}$, implying that more efficient plants exhibit a combination of larger SLAs, or for a given amount of energy fixed have relatively low variable respiration (α_i) or have relatively low fixed respiration (β_i). These results are summarized in the following principles (Tschirhart, 2002):

Principle 1. If at the outset of the noncompetitive state there are m species present, then species i, $i \in \{1,\ldots,m\}$ will still be present in the steady state community if,

$$\frac{ea_i - 2(a_i\beta_i)^{0.5}}{a_i}, \tag{12}$$

is a maximum over all m species; that is, i is the species that earns zero net energy at the highest SEL generated by the demands and supplies in the competition for space. All other potential species earn negative net energy at this SEL and are driven to extinction before steady state.

Principle 2. More than one species will be present in the steady state community if the maximum of Eq. (12) over all m species is not unique.

Principle 3. In a multispecies steady state in a community with limited space, the mix of species present depends on the attributes of the individual plants, including the plants' respiration parameters and SLA. The mix of species present depends neither on plant growth rates nor the original species present in the noncompetitive state and their populations. The final populations of the steady state species, however, do depend on the original species present and their populations and growth rates.

Using the above results, an introduced jth species will be a successful invader if,

$$ea_j - 2\left(\alpha_j\beta_j\right)^{0.5} > ea_i - 2(\alpha_i\beta_i)^{0.5}, \tag{13}$$

for all i=1, ...,m, $i \neq j$. However, success for an invader is likely to depend on other attributes of the plant beyond the three parameters shown. Environmental factors and parameters that define its ability to process nutrients will also be important. In the next section, temperature as an environmental factor is introduced, and this will lead to a rich set of possible outcomes for plant coexistence and redundancy.

4. Temperature

Tilman (1980, 1985, 1988) developed the resource-ratio hypothesis that underscores the importance of limiting resources for explaining community structure. The plant maximization problem is flexible in that additional resources can be introduced into a variety of ways, although here, it is assumed that when a plant is stressed by a shortage of nutrients or by temperature variations, the plant will require additional energy for any biomass it produces. Here, we concentrate on temperature, which is not a resource but does affect respiration, growth, and photosynthesis separately from light availability, and it has been shown to be important in determining competitive success (see Chpt. 3 in Grover, 1997 for a summary). Because biological processes increase with rising temperatures above freezing, then flatten out before starting to decrease (Ellert and Bettany, 1992), we assume that there is an optimum temperature for each plant, and that movements away from the optimum increase energy losses via respiration. Temperature, therefore, enters the individual plant's maximization problem. This is opposed to introducing temperature into the more aggregated population adjustment equation, as in Pacala and Tilman (1994).

Let t be actual temperature and rewrite the respiration function from Eq. (3) as,

$$f_i(x_i,t) = \alpha x_i^2\left[\left(t-t_i\right)^2+1\right]. \qquad (3')$$

The t_i is plant i's ideal temperature, and when $t=t_i$, the plant's variable respiration is at a minimum with respect to temperature. When $t<t_i$, the temperature is below the ideal, and when $t>t_i$, the temperature is above the ideal; in either case, the squared term in parentheses implies that deviations from the ideal stress the plant and increase respiration.

Principles 1 and 2 that state the conditions for coexistence in a steady state can be extended to include temperature. Solving for steady state values as in Eq. (10) but now using Eq. (3') instead of Eq. (3) yields $\hat{e}_0^s = ea_i - 2(\alpha_i\beta_i)^{0.5}[(t-t_i)^2+1]^{0.5}$ for species i, and m species coexisting in a steady state community requires,

$$\begin{aligned} &ea_1 - 2(\alpha_1\beta_1)^{0.5}[(t-t_1)^2+1]^{0.5} \\ &\quad = ea_2 - 2(\alpha_2\beta_2)^{0.5}[(t-t_2)^2+1]^{0.5} = \cdots \\ &\quad = ea_m - 2(\alpha_m\beta_m)^{0.5}[(t-t_m)^2+1]^{0.5}. \qquad (14) \end{aligned}$$

Going through the same maximization problem as above but now using Eq. (3'), the plant's demand for biomass from Eq. (4) becomes,

$$\hat{x}(e,e_0,\alpha_i) = \frac{ea_i - e_0}{2\alpha_i[(t-t_i)^2+1]}. \qquad (15)$$

and the steady state plant size and SEL from Eq. (10) become,

$$\hat{x}_i^s = \left(\frac{\beta_i}{\alpha_i[(t-t_i)^2+1]}\right)^{0.5} \text{ and}$$
$$\hat{e}_0^s = ea_i - 2(\alpha_i\beta_i)^{0.5}[(t-t_i)^2+1]^{0.5}. \qquad (16)$$

Thus, growth rates, steady state plant size, and SEL are functions of a time-dependent environmental factor, as in Norberg et al. (2001).

The second expression in Eq. (16) exhibits a parabolic relationship between temperature and the steady state SEL as displayed in Fig. 1. In the top diagram, the parabola shows all the values of e_0 and t for which one representative plant earns zero net energy, and its species' population is therefore in steady state. The ideal temperature is t_1, and at this temperature, competition among individuals would drive the steady state SEL to e_{01}. Any deviation of temperature from t_1 increases the plant's respiration for a given plant size; therefore, to maintain zero net energy, SEL must be lower to offset the temperature stress. For example, if temperature drops to t' or rises to t'', then SEL must drop to e_0' for individuals

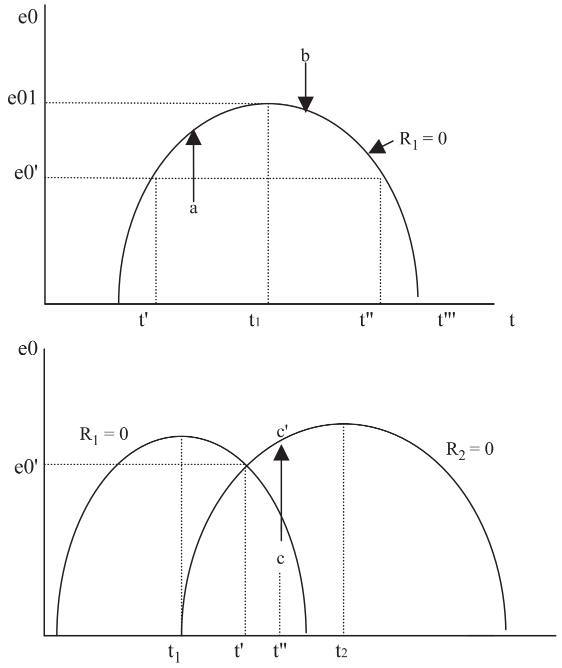

Fig. 1. Temperature and SEL.

to maintain zero net energy. At point a inside the parabola, the plant is enjoying positive net energy and population is increasing.[2] Assuming that the temperature does not change from what it is at point a, then the increased population will drive up SEL through demand and supply interactions until the point on the parabola directly above point a is reached and steady state obtains. At point b, the plant earns negative net energy, and again, if the temperature does not change, then population will decrease, SEL will fall, and e_0 will move to the parabola and the species to a steady state. If the temperature is t''', net energy is negative, and the plant population will decline to zero if the temperature does not drop.

The bottom diagram shows two competing species that have different ideal temperatures: species 1 (2) does better at lower (higher) temperatures. Both species must be earning zero net energy to coexist; hence, the only temperature that allows coexistence is t' where the two parabolas intersect. Notice that, at point c, where the temperature is t'', both plants are enjoying positive net energy and both populations are increasing; however, if the temperature remains at t'', the rising SEL owing to the increasing competition moves plant 1 above its zero net energy parabola so that its population decreases while plant 2 population continues to increase until point c′ is reached, in which case, plant 1 moves toward extinction and plant 2 is in steady state.

A long-standing ecological principle is that the maximum number of coexisting populations in steady state cannot exceed the number of resources (Levin, 1970; Armstrong and McGehee, 1980). Some authors have noted this result to be too restrictive (Tilman, 1982; Huston and DeAngelis, 1994). In the theory presented here, although there are but two "resources" (temperature and light), there is no limit on the number of species that can coexist because any number of parabolas can be drawn through the same point in the e_0-t plane. This follows because the shape and position of the parabolas are determined by the a_i, α_i, and β_i in the second term of Eq. (16), and there are infinite combinations of these parameters giving the same $\hat{e}_0^s$. The intersecting parabolas in Fig. 1 are convenient tools for exploring substitutes and compliments among species and for introducing successful invaders.

5. Dominant species

Fig. 2 shows the classic distribution of species abundance in a community wherein a few species make up the majority of the biomass. If biomass is used as an indicator of ecosystem function, then these few abundant species are functionally important. However, the minor species occupying the low end of the distribution are also important because under a different set of environmental conditions, the abundant and the tail end species may reverse their places; thus, the tail end species are providing insurance for continued ecosystem function (Main, 1982; Walker et al., 1999). Moreover, the small number of dominant species at any given time may have dissimilar attributes that determine their ecosystem function, but each dominant species has attributes similar to some of the species in the low end of the tail. These low-end species are waiting for a change in environmental conditions to perform their role as substitutes, and therefore, they contribute to ecosystem resilience (Walker et al., 1999).

The net energy optimization model can be used to analytically describe those species in a community that are ecological equivalents and dominate the biomass, those species that are redundant (as defined herein) and waiting to substitute for the dominant species, and those species that can successfully invade the community, possibly by driving out existing species. In addition, whether a species is in the

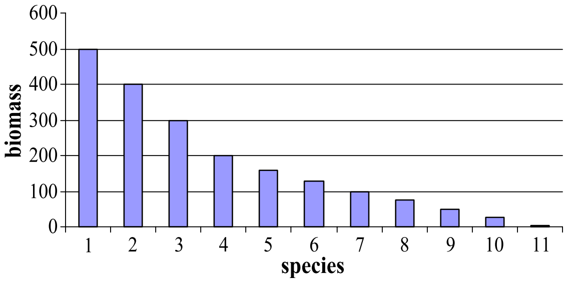

Fig. 2. Classic species distribution.

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[2] An anonymous referee pointed out the similarities with this concept and the growth indices developed in Fitzpatrick and Nix (1970), Gutierrez et al. (1974), Gutierrez and Yaninek (1983), and Gutierrez (1992).

dominant or redundant category, or in the invader category, will depend on time-dependent environmental factors. Continuing to use temperature to represent environmental factors, species that are ecological equivalents under one temperature may have a dominant/redundant relationship under another temperature. The physiological traits in Eqs. (1) and (3′) govern what category a species falls into; therefore, knowing these traits for each species and the temperature, or temperature distribution, completely determines community structure. The traits include a_i the SLA, α_i and β_i, the respiration parameters, and t_i, the plant's ideal temperature.

The key to categorizing the species can be understood by again referring to Fig. 1. From Eq. (16), the parabola for a representative plant in any species is given by,

$$p_i(a_i, \alpha_i, \beta_i, t_i) = ea_i - 2(\alpha_i\beta_i)^{0.5}[(t - t_i)^2 + 1]^{0.5}. \tag{17}$$

which is interpreted as the maximum SEL for the representative plant in species i at which the species population does not decrease. And from the previous section, if $p_i(a_i,\alpha_i,\beta_i,t_i)>(=,<)\hat{e}_0^s$, the population increases (remains constant, decreases). Also from the previous section, for a constant temperature those species with the greatest values of $p_i(a_i,\alpha_i,\beta_i,t_i)$ will dominate, and eventually drive out all other species. If the greatest value of $p_i(a_i,\alpha_i,\beta_i,t_i)$ is unique, then only one species will dominate and exist in steady state. Of course, a one-species community is unrealistic but so is holding temperature constant. A more likely scenario is that temperature changes according to some distribution, in which case a steady state involving but one species is less likely. With a changing temperature, the dominant, redundant, and invading species can still be ascertained probabilistically by calculating an expected value $p_i(a_i,\alpha_i,\beta_i,t_i)$, using the temperature probability density function. In other words, the term that determines the plant categories is the expected value of the maximum SEL at which the species population does not decrease. For example, if temperature exhibits a uniform distribution, then the plant with the largest area under its parabola between the highest and lowest possible temperatures (including the horizontal axis) will eventually dominate.

6. Simulations

6.1. Six diverse species

The above principles can be illustrated by simulating competing species. Table 1 contains parameters for six diverse species defined by the SLAs, respiration parameters α_i and β_i, and ideal temperature t_i. Fig. 3a shows the $p_i(\cdot)$ functions for i=i,. . ., 6.

Gitay et al. (1996) raise several questions about what evidence should be used in attempting to identify what species are redundant. One approach is to remove a plant species from a community, either on an experimental plot or in a simulated community, and observe what remains of the community post removal. In carrying out this approach, the authors point out that removing a species under only one set of conditions is not sufficient. Species perform differently under different conditions, and in real communities, environmental conditions are constantly changing. Therefore, in the simulations, we allow for changing environmental conditions by randomly drawing in each period a value for temperature.

Three simulations are shown in the bottom of Fig. 3a, with temperature drawn from a uniform distribution with support on [0, 6]. Thus, at the beginning of each time period a new temperature is randomly chosen implying that relative to the previous period, plants may move away from or closer to their ideal temperature. Each of the three simulations was run for 10 periods, and all populations were initialized at 50 for each run. Populations and biomasses for each species in the terminal period were recorded and plotted in the lower graphs (biomass is the product of population and biomass, or N_i x_i, i= 1,. . ., 6). Biomass and populations differ because individual plants choose different optimum biomasses or x_i.

Table 1
Parameters for six diverse species and e=2000

Plant	a_i (SLA)	α_i	β_i	t_i	s_i
1	1.0	125	6000	1.0	4
2	1.0	5500	120	3.0	4
3	0.15	8	300	3.0	4
4	0.18	14	500	3.6	4
5	0.18	14	500	2.4	4
6	1.0	125	6800	5.0	4

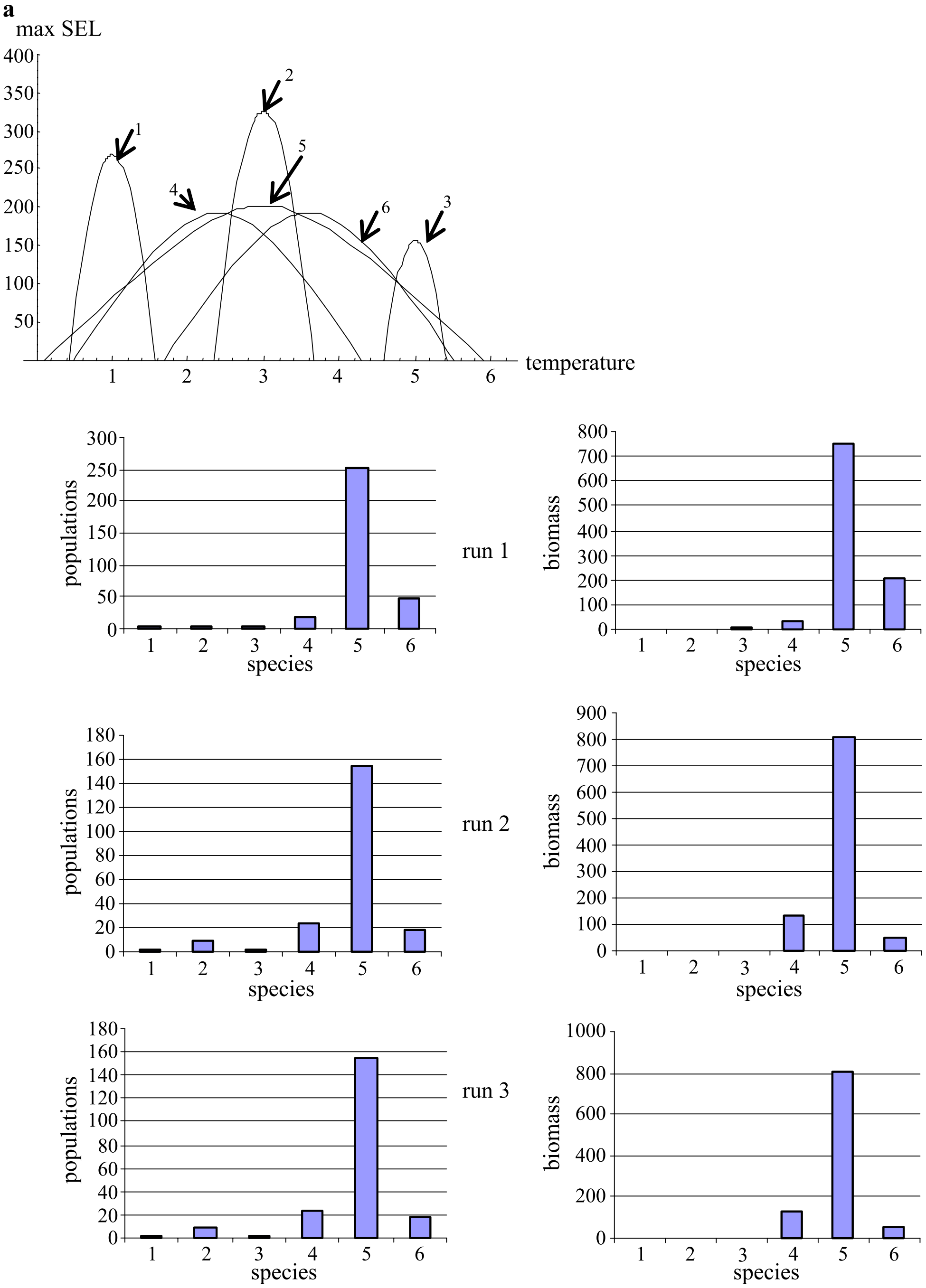

Fig. 3. (a) Six diverse species and redundancy. Temperature is uniformly distributed on (0, 6) and each run consists of 10 periods. Initial populations are each 50. (b) Six diverse species and redundancy. Temperature is normally distributed with parameters (3, 0.75) and each run consists of 10 periods. Initial populations are each 50.

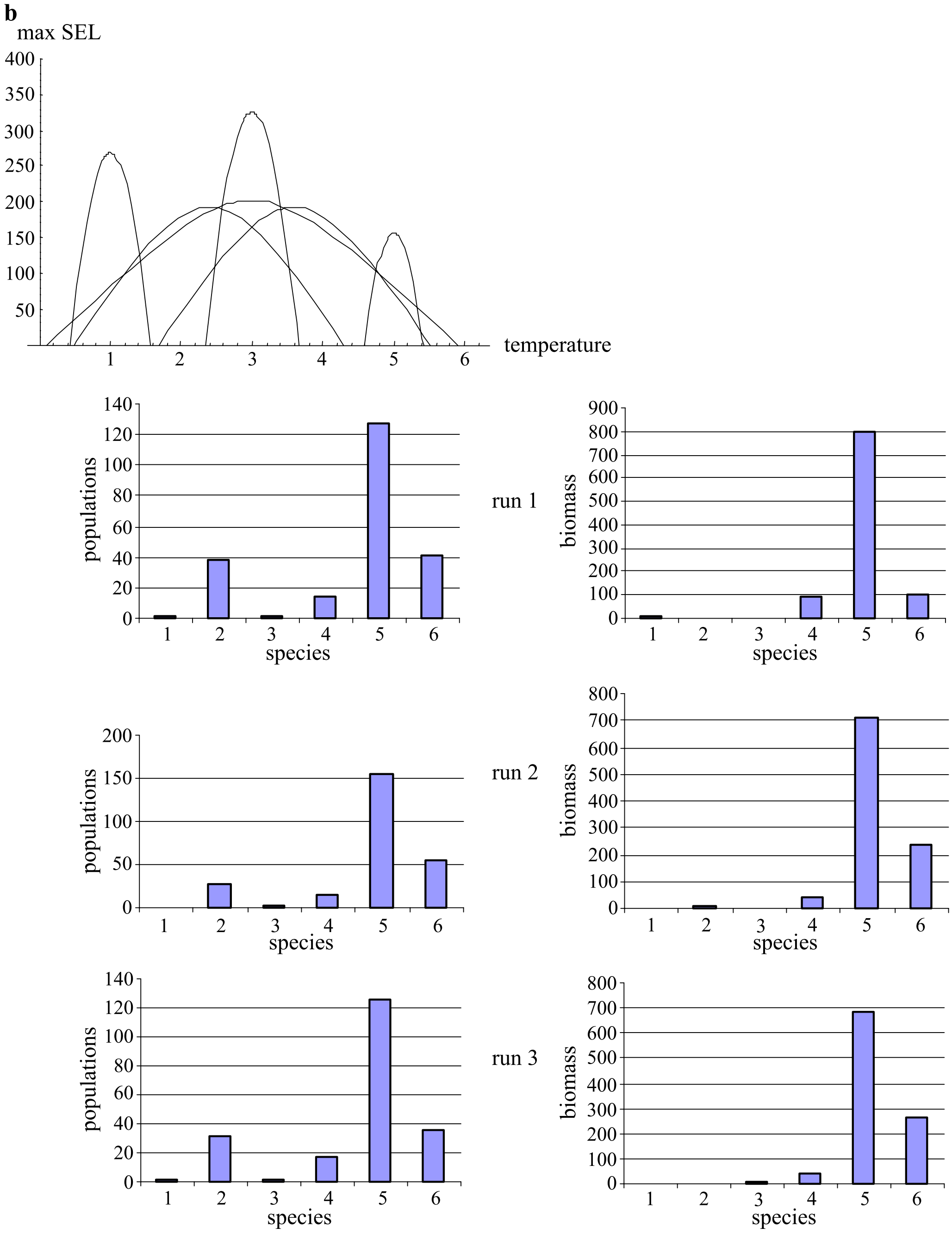

Fig. 3 (*continued*).

In all runs, plant 5 dominates its competitors. Interestingly, plant 5's parabola lies below the parabolas of one or more plants over all but the most extreme high and low temperatures. Thus, if temperature were held at t=2, plant 4 would dominate, if temperature were held at t=3, plant 2 would dominate, if temperature were held at t=5, plant 3 would dominate, and so on. But when temperature is random, the more realistic case, all these other plants are dominated by plant 5. This observation underscores the importance of allowing environmental factors to change, as pointed out by Gitnay et al. That plant 5 dominates follows from calculating the expected values for the $p_i(\cdot)$. Using the density function from the uniform distribution on [0, 6], the expected values are calculated as,

$$E[p_i(\cdot)] = \int_0^6 \left\{ ea_i - 2(\alpha_i\beta_i)^{0.5}[(t-t_i)^2+1]^{0.5} \right\} \frac{1}{6}\mathrm{d}t. \tag{18}$$

for i=1,..., 6. Substituting in parameter values from Table 1 yields the expected values shown in Table 2.

As reflected in Fig. 3a, plants 1, 2, and 3 are driven out relatively quickly by the other three plants that have much higher expected values, but of these other three, plant 5 has the highest expected value and dominates. In multiple simulations with 35 or more runs, the populations asymptotically converge to steady states wherein plant 5 is the only one left standing.

Another set of simulations was run using the same six diverse species; however, temperature was normally distributed with mean and standard deviation [3, 0.75]. The normal distribution allowed for temperatures that were more favorable for plant 2 whose $p_i(\cdot)$ value has a tall peak at t=3. In the population and biomass charts in Fig. 3b, plant 2 does better than when the temperature was uniformly distributed, although its population still moves close to zero in only 10 periods. The biomass of plant 2 remains low since it is a small plant relative to the others.

Fig. 4 shows a set of simulations in which dominant species 5 was removed. Temperature was again uniformly distributed with each simulation run going 10 periods and populations initialized at 50, similar to Fig. 3a. With plant 5 removed, plants 4 and 6 now become dominant. Moreover, in repeated simulations over many periods (not shown), plants 4 and 6 both survive as is expected. As Table 2 indicates, those plants have positive expected values, which now are also the maximum over the five species presented. They were not able to survive in the presence of plant 5 because they were inferior competitors. Competition drives up the SEL, and plant 5 can tolerate a higher SEL than plants 4 and 6.

The total biomasses over all plants in Fig. 4, measured by the sum of the bar heights, varies from a low of about 400 in run 1 to a high of 1000 in run 2 (the maximum possible total biomass is A=1000). In repeated runs over many periods, the total biomasses continually fluctuate from about 250–1000 with the changing temperatures. The fluctuations were less in the presence of species 5, and as Fig. 3a shows, the total biomasses tended to stay at or near 1000.

Gitnay et al. offer four criteria for defining whether a species is redundant. These include: (1) removal of the species has no effect on the abundance of remaining species; (2) remaining species are still present with no new species added; (3) some measure of ecosystem function should remain constant; and (4) some species should remain. The criteria go from the most to the least stringent requirements. These criteria do not provide clear guidelines, and each has pros and cons. If we adopt the second criteria and if we start from arbitrary population levels and move to steady states with temperature uniformly distributed, then of the six species in the simulations, all but species 5 are redundant. Alternatively, in the absence of species 5, species 1, 2, and 3 are redundant while species 4 and 6 are not. Redundancy will depend on the starting point and the initial species and also on the way that the environmental factor varies over time. At this point, we conjecture the species with the maximum $E[p_i(\cdot)]$ as the only nonredundant species, although if $E[p_i(\cdot)]$ is not unique, then there can be multiple nonredundant species.

Table 2
Expected values

Plant	1	2	3	4	5	6
$E[p_i(\cdot)]$	−14,070	−6668	−15,754	211	692	211

6.2. Invasives

Invasions are the flip side of redundancy. To paraphrase the above criteria, the success of an invader

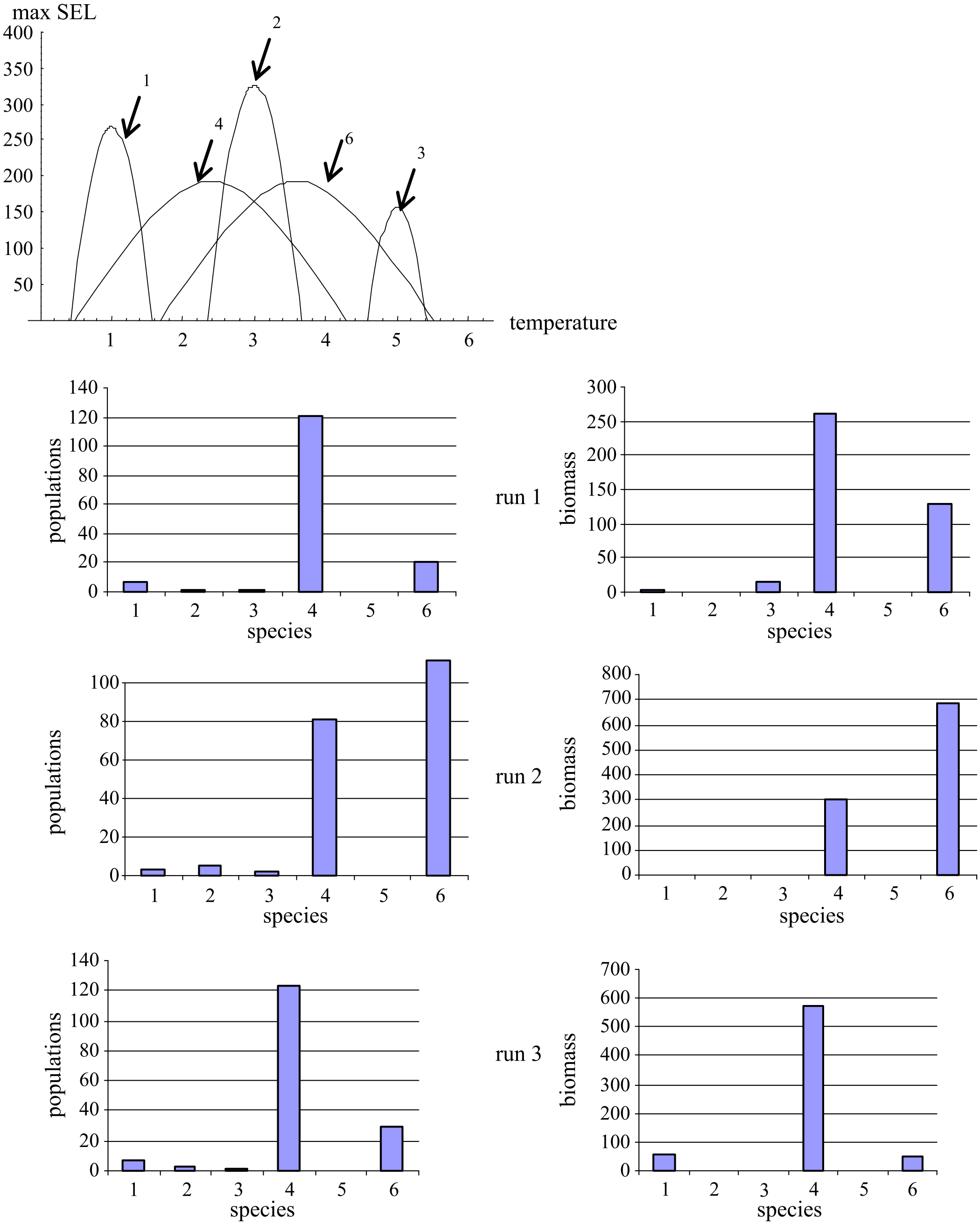

Fig. 4. Dominant species 5 removed. Temperature is uniformly distributed on (0, 6) and each run consists of 10 periods. Initial populations are each 50.

is determined by: (1) addition of the species has no effect on the abundance of initial species; (2) initial species are still present although affected; (3) some measures of ecosystem function is changed; and (4) no initial species remain. In the above simulations, if the initial species are all but five and then 5 is added, none of the initial species will remain, so 5 is completely successful by criterion (4). If the initial species include

1, 2, 3, and 4 and 6 is added, species 4 and 6 will remain; however, the biomass of species 4 will decrease. Species 6 in this case is a successful invader, although not to the degree of species 5 in the first case.

We illustrate the invasion process by letting species 5 be an invader and the remaining species comprise a native community. Simulations of the native community, under temperature drawn from the uniform and normal distributions, are run for 25 periods (from initial populations of 50) after which the invader is introduced and a further 25-periods run. Fig. 5 shows the biomass of each species over the entire 50 periods.

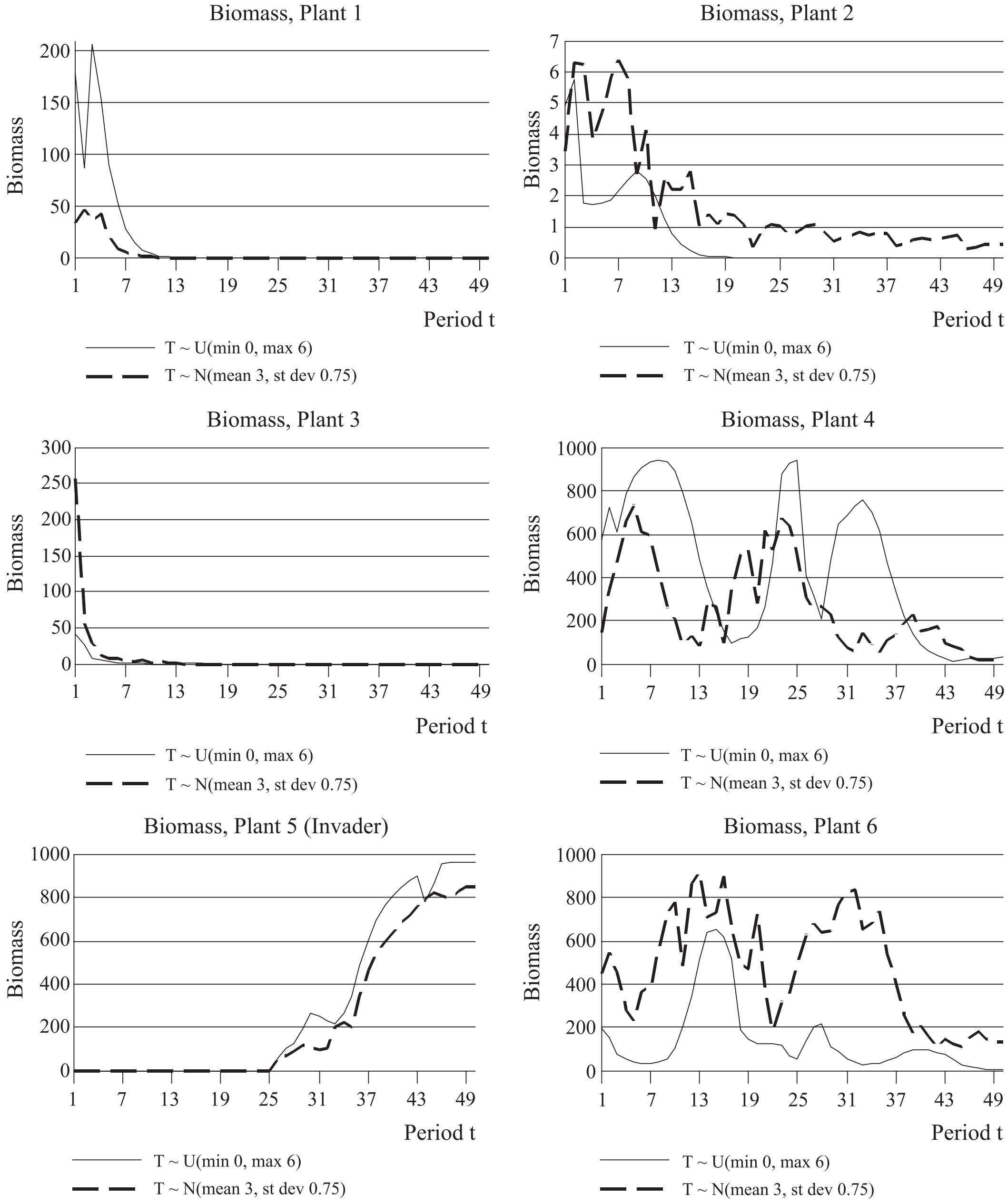

Fig. 5. Hypothetical invasion.

As the theory above predicts, prior to an invasion, under both temperature distributions, species 4 and 6 jointly dominate, the others forced into redundancy. Interestingly, when species 4 does well (large biomass), species 6 does not do so well and vice versa. Following the introduction of species 5, it rapidly gains biomass as the community SEL is pushed above the max for species 4 and 6, eventually leading to 5 solely dominating under both temperature scenarios.

7. Humans

The foremost applications of plant succession in economic methods concern agricultural questions of integrated pest management (IPM) and range management (RM). The IPM literature has centered on the damage function approach, where the damages pests cause are proportional to the pest stock, realized through production losses. Managers abate damages through pesticide or herbicide applications, generally modeled through reductions in pest populations. Applied both statically and dynamically, the static approaches have used theories of economic thresholds to determine the minimum pest density at which the marginal value of avoided damages equals the marginal costs of treatment (reviewed in Carlson et al., 1993). The dynamic approaches have relied primarily on deterministic and stochastic dynamic programming to determine optimal (or near optimal) management responses to pest infestations. These approaches have demonstrated the importance of an intertemporal perspective and timing in pest control when the pest populations are dynamically dependent (Fisher and Lee, 1981; Taylor and Burt, 1984; Pandey and Medd, 1991). Wu (2001) brings together static and dynamic IPM methods in a deterministic framework. Analytical results demonstrate that managers' optimal weed control measures will be more stringent if weed dynamics are included in the analysis, in comparison to a static decision rule.

Perhaps the closest examples of IPM to the methods herein is the work of Regev et al. (for examples concerning pest management see Regev et al., 1976, 1983). A general formulation of the ecological and economic behavior of the model is found in Regev et al. (1998), and for a general treatment of biological control of invasions, see Schreiber and Gutierrez (1998). These models are cast in an optimal control format and solved analytically. They are based on the ecological models originally outlined by Gutierrez and Baumgärtner (1984) and Gutierrez (1992). In this literature, the authors use intricately specified equations of motion for the age-structured pests and plants, where pesticide application reduces the number of adult pests. The methods also account for pesticide resistance on the part of the pest. In principle, the model is based on behavior at the level of the individual and has been extended to multiple plants and species (Gutierrez et al., 1999). Species behavior is guided by constrained individual maximum per capita demands for limiting resources or biomass. Maximal rates are constrained by factors influencing resource acquisition on the part of the individual, including "..the effects of random search, variable resource availability and demand for the resource, as well as intratrophic level competition for resource acquisition. . ." (Regev et al., 1998, p. 230).

The effects of temperature light and other resources have been outlined in Gutierrez et al. (1994) and Gutierrez (1996). The main difference between the Regev et al. work and that presented here is that in the former, there is no explicit representation of a choice process. The mechanics of resource competition are probabilistic as resource acquisition is determined by a random search model with the time varying ratio of catchable prey biomass to the maximum demand determining the proportion of the maximum genetic demand at time *t* obtained.

Interconnections between rangeland productivity, rangeland quality, stocking rates, and successful invasion of plant annuals dominates the relevant range management literature. Early examples (Karp and Pope III, 1984; Torell et al., 1991) focused on stocking rates and general rangeland improvement/treatment options available to managers in stochastic (Karp and Pope) and deterministic (Torell, Lyon, and Godfrey) settings. While capturing the interdependent evolutionary processes of managers' decision variables and rangeland, Huffacker and Cooper (1995) significantly extend the methods by incorporating an explicit model of plant succession (Boyd, 1991). Using optimal control with multiple interdependent differential equations, the impacts of grazing decisions on short-term productivity of perennials and annuals are shown to impact the long-term competitive success of plants.

Herein, the existing literature is extended by incorporating the model of plant competition as developed above into the rangeland manager's decision problem. The model allows an explicit representation of the rangeland plant community (including more than two plant species), the influence of limiting resources (other than density dependence), and the response of the entire system to human and natural system perturbations. The methods allow simple predictions of community composition in the face of jointly determined economic/ecological behavior. The power of the method is demonstrated through a stylized example.

Consider a benevolent policy maker (resource manager) who allocates scarce resources to maximize expected social welfare EW from an area of rangeland subject to the risk of invasion. Social welfare is a function of stochastic rangeland conditions, as captured by a hypothetical plant community consisting of five native species, whose annual populations are denoted N_1^t, N_2^t, N_3^t, N_4^t, and N_5^t. The presence and magnitude of the invader N_6^t serve to lower social benefits of the rangeland (the species notion is deliberately differentiated in this section from those in proceeding sections; note that species 6 is now the invader).

The manager can reduce the risks of invasion through costly application of prevention effort, control effort, or some combination of the two. Prevention effort X^t refers to a vector of strategies available to the manager that reduce the probability of invasion $P^I(X^t)$.[3] In a similar fashion, the manager can employ a vector of control strategies H^t to reduce the realized severity of invasion (for example herbicide applications).[4]

To simplify the problem, consider only two states: noninvaded and invaded. Assuming separable social benefits and costs, let benefits in the noninvaded state be given by $B(N_1^t,N_2^t,N_3^t,N_4^t,N_5^t)$ and in the invaded state given by $B(N_1^t,N_2^t,N_3^t,N_4^t,N_5^t,N_6^t)$, where both functions are concave in their arguments and benefits in the noninvaded state are greater than those in the invaded state due to the impacts of the invader. As there is no need for control in the noninvaded state, costs are solely a function of prevention or $C(X^t)$. In the invaded state, the manager can employ control strategies H^t to adapt to the invasion. Assume H^t only serves to negatively affect success of the invader, and adds to costs in the invaded state $C(X^t,H^t,N_6^t)$, assumed to be convex in its arguments.

Given initial community populations, the manager's problem is to choose vectors of prevention and control treatments to maximize expected social welfare as given by,

$$\begin{aligned}\max_{X^tH^t} EW = \sum_{t=0}^{\infty} \rho^t \Big[& (1 - P^I(X^t))(B(N_1^t, N_2^t, N_3^t, N_4^t, N_5^t) \\ & - C(X^t)) + P^I(X^t)(B(N_1^t, N_2^t, N_3^t, N_4^t, N_5^t, N_6^t) \\ & - C(X^t, H^t, N_6^t)) \Big]\end{aligned}$$

$s.t$

$$N_i^t = \left\{ \begin{array}{r} \text{No Invasion} \rightarrow N_i^{t+1} - G^i(N_1^t,\ldots,N_5^t) \\ \text{Invasion} \rightarrow N_i^{t+1} - G^i(N_1^t,\ldots,N_6^t) \end{array} \right. \quad i \neq 6$$

$$N_6^t = N_6^{t+1} - G^6(N_1^t,\ldots,N_6^t;H^t)$$

$$G^i(.) = N_i^t \frac{1}{s_i}\left[\frac{\hat{R}_i + r_i(.)}{r_i^{ss}} - 1\right]. \qquad (19)$$

where ρ^t is the discount factor, $G^i(.)$ are species-specific growth functions given in Eq. (9), and the stock dynamics have been rearranged for expositional purposes. Compounding the uncertainty of invasion, species growth functions depend on all species $G^i(N_1,.., N_6)$ and in the invaded state indirectly on the control choices of the manager. The problem can be simplified by substituting the constraints into the objective function,

$$\begin{aligned}\max_{X^tH^t} EW = \sum_{t=0}^{\infty} \rho^t \Big[& (1 - P^I(X^t))[B(N_1^{t+1} - G^1 \\ & \times (N_1^t,\ldots,N_5^t),\ldots,N_5^{t+1} - G^5(N_1^t,\ldots,N_5^t)) \\ & - C(X^t)] + P^I(X^t)[B(N_1^{t+1} \\ & - G^1(N_1^t,\ldots,N_6^{t+1} - G^6(N_1^t,\ldots,N_6^t;H^t)),\ldots, \\ & N_6^{t+1} - G^6(N_1^t,\ldots,N_6^t;H^t))) \\ & - C(X^t,H^t,N_6^{t+1} - G^6(N_1^t,\ldots,N_6^t;H^t))] \Big]. \end{aligned} \qquad (20)$$

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[3] Where reducing stocking rates are an example, and $\partial P^I(\mathbf{X}^t)/\partial \mathbf{X}^t < 0$.

[4] While there may be examples of actions that influence both the probability and outcomes of invasions, for a tractable model, we assume these sets are independent.

The following conventions are employed to describe benefits and costs in each state,

$$B^0 = B(N_1^{t+1} - G^1(N_1^t,\ldots,N_5^t),\ldots,N_5^{t+1} - G^5(N_1^t,\ldots,N_5^t))$$

$$\begin{aligned} B^1 = B(&N_1^{t+1} - G^1(N_1^t,\ldots,N_6^{t+1} \\ &- G^6(N_1^t,\ldots,N_6^t;H^t)),\ldots,N_6^{t+1} \\ &- G^6(N_1^t,\ldots,N_6^t;H^t))) \end{aligned}$$

$$C^0 = C(X^t)$$

$$C^1 = C\big(X^t, H^t, N_6^{t+1} - G^6\big(N_1^t,\ldots,N_6^t;H^t\big)\big).$$

For any period t, using the Kuhn–Tucker conditions with respect to X^t and H^t, and assuming X^t, $H^t>0$ at the optimum, yields the conditions:

$$P^I_{X^t}((B^1 - C^1) - (B^0 - C^0)) = C^0_{X^t} + P^I(C^1_{X^t} - C^0_{X^t}), \tag{21}$$

$$\begin{aligned} [&B^1_{N_1^t} N^t_{1_{G^1}} G^1_{G^6} G^6_{H^t} + B^1_{N_2^t} N^t_{2_{G^2}} G^2_{G^6} G^6_{H^t} + B^1_{N_3^t} N^t_{3_{G^3}} G^3_{G^6} G^6_{H^t} \\ &+ B^1_{N_4^t} N^t_{4_{G^4}} G^4_{G^6} G^6_{H^t} + B^1_{N_5^t} N^t_{5_{G^5}} G^5_{G^6} G^6_{H^t} \\ &- B^1_{N_6^t} N^t_{6_{G^6}} G^6_{H^t}] = C^1_{H^t} - C^1_{G^6} G^6_{H^t}, \end{aligned} \tag{22}$$

where all subscript variables indicate partial derivatives. Eq. (21) requires the manager to apply mitigation/preventative efforts up to the level that balances the expected net marginal benefits of its employment (left hand side, arising from the increased chance of attaining the noninvaded state, remembering that ${P^I}_X{}^t<0$) against its expected marginal costs. Eq. (22) requires control effort to be applied until the marginal benefits from its application (left hand side) are exactly offset by its marginal costs. Marginal benefits arise from how changes in control directly impact the growth of the invader and indirectly impact the growth of all species in the community.

A major difficulty with implementing this stylized analysis is the difficulty in constructing appropriate functional forms for the growth functions. The model developed above provides the appropriate functions. Further, the steady state conditions and propositions can be extended to understand steady state control rates. Herein, control is limited to consider only direct harvesting and herbicide applications. Harvesting/killing the invader can be modeled as human appropriation of individual plant biomass in the plants objective function,

$$R_6 = (ea_6 - e_0)x_6 - \alpha_6 x_6^2[(t - t_6)^2 + 1] - \beta_6 - e_6 h^t. \tag{23}$$

Harvests on an individual basis h^t (in biomass units, g) are converted to watts by e_6, the energy embodied in a unit of biomass. In this formulation, the harvests are taken as exogenous by the individual plant, and the steady state conditions become:

$$\hat{x}_6^s = \left(\frac{\beta_6 + e_6 h^t}{\alpha_6[(t - t_6)^2 + 1]}\right)^{0.5} \text{ and}$$

$$e_0^s = ea_6 - 2(\beta_6 + e_6 h^t)^{0.5} \alpha_6^{0.5}[(t - t_6)^2 + 1]^{0.5}. \tag{24}$$

The consequences of harvests are twofold. First, if the plant exists in the steady state (determined by the relationship between its max SEL and the community determined SEL), its steady state size/biomass is increased by the additional term in the numerator of $\hat{x}_6^s$. The increase in steady state size is necessary to compensate for the loss of biomass to humans. Second, harvests serve to lower the plant's maximum steady state SEL. For example, let the native community consist of the five native species coexisting, and the steady state SEL parabolas for representative plants in each species are given by p_i. As defined above, the expected values of each parabola between the minimum and maximum temperatures are equal across community species, or $\int_{t_{\min}}^{t_{\max}} p_1 \mathrm{d}T = \int_{t_{\min}}^{t_{\max}} p_2 \mathrm{d}T = \int_{t_{\min}}^{t_{\max}} p_3 \mathrm{d}T = \int_{t_{\min}}^{t_{\max}} p_4 \mathrm{d}T = \int_{t_{\min}}^{t_{\max}} p_5 \mathrm{d}T$. A sketch of the parabolas for the community's five species and the invader is given in Fig. 6. Direct biomass harvests serve to shift p_6 downwards, moving species 6 from a successful invader to a redundant species.

Harvests can also be represented through a more traditional format where harvests serve to reduce plant population growth,

$$N_6^{t+1} - N_6^t = N_6^t \frac{1}{s_i}\left[\frac{\hat{R}_6(.) + r_6(.)}{r_6^{ss}} - 1\right] - H^t. \tag{23b}$$

In this formulation, while the steady state conditions would not be altered directly, the realized SEL will be impacted due to the lowered invader populations, delaying the invaders rise to dominance.

In the alternate case of herbicide use, while there are a multitude of direct impacts of herbicide

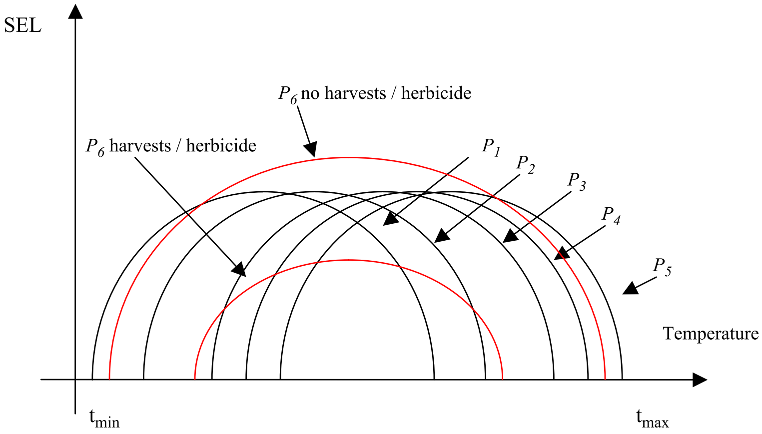

Fig. 6. Suppressing an invader in a rangeland community.

applications on the invader, specific physiological impacts depend on the herbicide. A basic formulation is one that depicts herbicide h_b as acting to increase the invader's energy losses to respiration,

$$R_6 = (ea_6 - e_0)x_6 - \alpha_6 x_6^2[(t-t_6)^2+1]\exp^{ch_b^t} - \beta_6, \tag{23c}$$

where exp is the exponential function, and c an effectiveness constant. In this setting, the steady state conditions become:

$$\hat{x}_6^s = \left(\frac{\beta_6}{\alpha_6[(t-t_6)^2+1]\exp^{ch_b^t}}\right)^{0.5} \text{ and}$$

$$\hat{e}_0^s = ea_6 - 2(\alpha_6\beta_6)^{0.5}[(t-t_6)^2+1]^{0.5}\exp^{0.5(ch_b^t)}. \tag{24}$$

Increasing the application of herbicide will both reduce the steady state size of the invader and lower its maximum steady state SEL. In a similar manner as for the above example concerning biomass harvests, herbicide serves to shift p_6 downwards, moving species 6 from a successful invader to a redundant species.

8. Conclusions

The theory developed in this paper describes a model of plant resource competition and how energy capture and allocation efficiency can determine the outcome of this competition. The method allows an analyst to identify species that are likely to be successful invaders based on their individual physiological parameters. In many instances, the parameters can be found in the existing botany literature or determined through experimentation. After identifying successful invaders, the most effective means of preventing their spread or controlling them once they are established can be related to how the means impact the physiological parameters.

There are shortcomings to the theory as it stands, including that there are no age structured populations, that essential nutrients such as nitrogen or phosphorus are omitted, that biomass is uniform as opposed to dividing it into above- and belowground portions, and herbivores are absent. These shortcomings and others ought to be the target of future research. In spite of the shortcomings, the model has the advantage of using concepts and techniques drawn from both ecology and economics. Additionally, its structure allows for a straightforward integration with agricultural or natural resource economic models.

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