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Prey-Producing Predators: The Ecology of Human Intensification

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Abstract: *Economic growth theory and theoretical ecology represent independent traditions of modeling aggregate consumer-resource systems. Both focus on different but equally important forces underlying the dynamics of human societies. Though the two traditions have unknowingly converged in some ways, they each have curious conventions from the perspective of the other. These conventions are reviewed, and two separate modeling frameworks that integrate the two traditions in a simple and straightforward fashion are developed and analyzed. The resulting models represent a consumer species (e.g. humans) that both produces and consumes its resources and then reproduces biologically according to the consumption of its resources. Depending on the balance between production, consumption, and reproduction, the models can exhibit stagnant behavior, like some predator-prey models, or growth, like many mutualism and economic growth models. When growth occurs, in the long term it takes one of two forms. Either resources per capita grow and the human population size converges to a constant, which may be zero, or resources per capita converge to a constant and the human population grows. The difference depends on initial conditions and the particular mix of biological conditions and human technology.*

Key Words: economic growth, human population dynamics, human evolutionary ecology

INTRODUCTION

Various human societies in many different environments, under many different social institutions, and with many different productive technologies have expanded, stagnated, and collapsed (Barro & Sala-i-Martin, 2004; Diamond, 1997, 2005; Galor, 2005; Galor & Weil, 1999; Johnson & Earle, 2000; Turchin, 2003a). An elementary taxonomy of society dynamics might be based on two variables: the size of the human population and its resources per capita. Together these two variables give us some idea about how many people

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were present and how well they were doing. By extension these two variables give us basic information about the state of the society through time. When was it on the rise? When was it in decline? Is the claim, for example, that a society was in decline during a given period of time a statement about population dynamics, the dynamics of resources per capita, or both?

The objective of the present paper is to develop a theoretical framework for modeling society dynamics. In particular, the focus is on which types of dynamic are historically important and which arise readily from simple dynamical models derived from first principles. The modeling strategy is to develop two basic models that draw heavily from theoretical ecology and economic growth theory. Both theoretical ecology and economic growth theory represent mature theories of aggregate dynamics in consumer-resource systems. Unfortunately, little exchange exists between the two disciplines, and though they have converged in some ways each discipline makes curious assumptions from the perspective of the other. Ecology is extremely rich in theory that jointly considers resource dynamics, consumption, and reproduction as interrelated biological processes (Case, 2000; Kot, 2001; Thieme, 2003; Turchin, 2003b). Nonetheless it does not often work with consumer species that, in addition to consuming, also *produce* their biological resources. Economic growth theory, in contrast, has a rich theory of production (Barro & Sala-i-Martin, 2004; Jones, 1998), but it is chronically happy to ignore the biological realities of human behavior and human economic activities. This latter point, with the recent exception of fields like ecological and behavioral economics, is also true of economics more generally.

The paper is organized as follows. I first discuss consumer-resource modeling in economic growth theory and theoretical ecology and evaluate each tradition from the perspective of the other. I then develop two separate modeling frameworks that reconcile and generalize the two traditions. In both cases the idea is to focus on the dynamics of a species, like humans, that both produces and consumes some critical resource. The first modeling framework involves a neoclassical economic growth model modified in the simplest possible way to make it compatible with ecology. The second framework involves a predator-prey model modified in the simplest possible way to make it compatible with the human talent for economic productivity. The resulting pair of models produce a variety of dynamical regimes that always depend on the balance between production and consumption and in some cases also depend on initial conditions. I conclude by discussing model dynamics in relation to the broad qualitative features of human population dynamics and economic history.

THEORETICAL MISCELLANEA

Macroeconomies as Predator-Prey Systems as Macroeconomies

Consider a generic consumer-resource system with a resource stock, K, and a consumer stock, L, that change according to the model,

$$\begin{aligned} \dot{K} &= f(K,L) - c(K,L)L \\ \dot{L} &= g(K,L)c(K,L) - dL, \end{aligned} \qquad (1)$$

where $f(K,L)$ represents resources produced per unit of time, $c(K,L)$ summarizes resources consumed per consumer per unit of time, $g(K,L)$ specifies the consumers produced per unit of consumed resource, and d is an exogenous death rate for consumers. Importantly, the resource should be interpreted broadly and not necessarily conventionally as any stock that has either a direct or indirect positive influence on the population growth of a consumer species. We will focus on resources that have a positive effect on human population growth, but we will also have occasion to mention the resources of species that in turn serve as resources for humans. Cows, for example, are resources for humans, but so too is grass a resource for cows. This is a common idea in ecology. Any species of our choosing is both a resource and a consumer. What we choose to call it is a function of how we would like to think about it in a particular theoretical setting.

For convenience we will assume that the resource stock, K, is the same species that is produced at rate $f(K,L)$ and consumed at rate $c(K,L)L$. We will examine the idea of resources much more closely below, but for now note that they can be biological or abiological. In either case, the effect on human population dynamics will be positive, but how we model this positive effect will depend critically on whether or not we imagine the resource being modeled as a biological species.

As an interesting case of convergence in science, both economic growth theory and population biology have a tradition of using models with the generic structure of Eq. 1. In economic growth theory, one of the earliest and simplest models is the neoclassical model of Solow (1956) without technological progress. In this model, $f(K,L) = F(K,L) - \delta K$ where $F(K,L)$ is a production function homogeneous of degree 1 in K and L and δ is an exogenous rate of resource depreciation. In addition, Solow's model assumes a constant savings rate, S, which means $c(K,L)=(1-s)F(K,L)/L$. Lastly, the model assumes $g(K,L)c(K,L) - d = n$, where n is a constant exogenous rate of population growth. Using a conventional Cobb-Douglas production function, $F(K,L) = AK^{\alpha}L^{1-\alpha}$ where A is a technology parameter with units $[(\text{resources/consumer})]^{1-\alpha} \bullet [\text{time}]^{-1}$, the resulting model is

$$\begin{aligned} \dot{K} &= sAK^{a}L^{1-\alpha} - \delta K \\ \dot{L} &= nL. \end{aligned} \qquad (2)$$

Barro & Sala-i-Martin (2004) provide an extensive analysis of this model and its many derivatives.

From ecology, a general consumer-resource model with the structure of Eq. 1 is the model of DeAngelis, Goldstein, and O'Niell (1975). In this model,

$f(K,L) = rK(1\text{-}K/K_{\max})$, $c(K,L) = vaK/(1 + ahK + bwL)$ and $g(K,L) = q$, where r, $K_{\max}$, v, a, h, b, w, and q are parameters. The full model is

$$\dot{K} = rK\left(1 - \frac{K}{K_{\max}}\right) - \frac{vaKL}{1 + ahK + bwL}$$
$$\dot{L} = \frac{qvaKL}{1 + ahK + bwL} - dL. \tag{3}$$

In essence, conventional models of consumer-resource systems from both economics and ecology have the same generic structure. The details, however, differ tremendously. In particular, if we think of the systems as modeling human consumers and some resource critical for the relevant human society, each theoretical tradition makes curious assumptions from the perspective of the other.

Endless Cows, Endless Humans, Lazy Predators

From the perspective of theoretical ecology, the Solow (1956) model is strange in two ways. First, it assumes the per capita rate of increase among consumers is constant, $g(K,L)c(K,L) - d = n$. This assumption is widespread in economic growth theory even though growth economists recognize that the economy and human population dynamics are almost certainly not independent (Barro & Sala-i-Martin, 2004, Ch. 9). Additionally, much of theoretical ecology is devoted to an explication of why exogenous population growth is typically a bad assumption (Murdoch, Briggs, & Nisbet, 2003; Turchin, 2003b), a generalization that holds for humans as much as any other species. In essence, consumers need resources. Consumers do not appear spontaneously out of thin air. Thus a theoretical treatment of consumer population growth should generally reflect, either implicitly or explicitly, the fact that reproduction needs inputs just like any other type of production. Otherwise, if considering more than a few generations, we end up with exponential population growth in a purely hypothetical and unrealistic world of endless humans.

The fact that reproduction requires inputs lies behind my choice of denoting the resource as "K." Given that the resource should be broadly interpreted as any stock that, all else equal, has a positive effect on human population dynamics, we can think of K as a kind of input for a type of production typically referred to as biological reproduction. In this case we will be especially interested in the resource as some kind of input affecting human reproduction and by extension human population dynamics. How the input works, however, is a fundamental question to which we now turn.

The second way in which economic growth theory makes unusual assumptions from the perspective of ecology is that, as in Eq. 2, growth economists often assume the production function satisfies the Inada conditions (Inada, 1963). For present purposes, these conditions are important because they mean the following:

$$\forall K \in R_+ \quad \frac{\partial F}{\partial K} > 0, \quad \lim_{K \to 0^+} \frac{\partial F}{\partial K} = \infty, \quad \lim_{K \to \infty} \frac{\partial F}{\partial K} = 0. \tag{4}$$

If we think of the resource stock, *K,* as a biological resource like cattle, the problem becomes evident. With this example, the Inada conditions hold two implications. As the number of cows approaches 0, the rate at which the marginal cow produces new cows per unit of time approaches infinity. Essentially, in a world where cows are few and their resources (e.g. grass) are many, each cow reproduces at a nearly infinite rate. No intrinsic constraints such as gestation time limit reproduction. The Inada conditions are equally unsuitable when considering what happens as the number of cows approaches infinity. In this case, when the resource stock (cows in this example) gets very large, the rate at which new resources are produced per unit of existing resource per unit of time is very small *but still positive.* In a world where all ice-free terrestrial environments are covered with a seamless layer of cattle 10 kilometers thick, one more cow actually increases, by however small an amount, the rate at which cows produce new cows per unit of time. If we include the depreciation rate, $\lim_{K \to \infty} f(K, L) = -\delta$, where $\delta < 1$. A biological approach would posit, in stark contrast, that in a world with so many cows, cows would die at a staggering rate approaching negative infinity because they would be ridden with disease and have nothing to eat. In particular, the most important biologically minded assumptions would be $\exists \hat{K} > 0$ such that $\forall K > \hat{K}$, $\partial F / \partial K < 0$ and $\lim_{K \to \infty} \partial F / \partial K = -\infty$. These assumptions mean that the environment has a limited biological capacity, and the more this capacity is exceeded the greater the negative effects on the dynamics of the resource population. Environmental limitations are almost certainly variable and sensitive to human activities, but they are still limitations. They represent an ecological version of the economists' dictum, “There's no free lunch.”

Interestingly, however, the Inada conditions are completely at odds with the ecological version of the no-free-lunch premise and are thus not appropriate when modeling the production of a biological resource. Consequently, we must be clear about whether we think the capital stock (*K*) is something like machinery and infrastructure, in which case a neoclassical production function that satisfies the Inada conditions might be appropriate, or a biological stock, in which case such a function will typically not be suitable. Economists, of course, probably do not typically think of *K* as an input for a biological production process. For that reason a neoclassical production function might often approximate the process they have in mind sufficiently well. If the production process is biological, however, in the sense that the resource is a biological species, then a neoclassical function will not serve well. The Inada conditions are not simply useful approximations that are a little off in this case; they are wholly and utterly at odds with everything we know about biological production. Importantly, this does not mean we cannot use a neoclassical production function in our model. It simply means that, if we do, we cannot model human population dynamics by allowing humans to "eat" the resource as theoretical ecologists typically do in predator-prey models. This distinction represents the basic difference between the two modeling frameworks developed below. In the modified neoclassical model, the resource is abiological. It is still a resource because it affects human population growth positively, but this effect must be indirect precisely because the humans in the model do not and really cannot eat the resource. In the modified predator-prey model, however, humans do eat the resource. This is what makes it a predator-prey model, and it is also what requires us to abandon neoclassical production.

But what about ecology from the perspective of economic growth? Humans are, after all, a species with a talent for production. This fact surely plays a role in human population dynamics, the success of human societies, and the economist's widespread tendency to assume a constant rate of growth for the theoretical labor supply (i.e. L). This notion points toward what is strange about a predator-prey model like the DeAngelis et al. (1975) model from the perspective of economic growth theory. The model has no human-induced production. In short, $\delta f/\delta L = 0$. Many human societies, however, at least in the Holocene, share the fact that they put effort into producing the resources they consume. They have both a negative and positive effect on their resources, and in general $\partial f / \partial L \neq 0$.

The anomalies enumerated above are points of departure in the present study. In particular, I modify model Eq. 2 in a very simply way by adding implicit resource dependence for humans to make the model minimally compatible with theoretical ecology. I also modify Eq. 3 in a simple way by adding production to make it minimally compatible with economic growth theory. The result is two models that clarify the basic properties of a society composed of consumer-producers and their biological resources.

A MODIFIED NEOCLASSICAL GROWTH MODEL WITH IMPLICIT RESOURCE DEPENDENCE

If Eq. 2 unrealistically decouples consumer population dynamics and resource availability, we should link the two. Linking them as a predator-prey system, however, leaves us with the problem that resource production in the Solow model is not appropriate for a biological resource. Humans can eat cows, but they cannot each machines. To deal with this problem, assume that human population dynamics are implicitly resource dependent. Implicit resource dependence simply means that, all else equal, an increase in the consumer population reduces the per consumer rate of reproduction per unit of time because some unspecified resource is less available than it used to be. The generalized logistic equation (Gilpin & Ayala, 1973; Thieme, 2003) represents a venerable example of this approach, and I use it here to incorporate implicit resource dependence in humans. To capture an assumed positive effect of economic production on human population growth, let the carrying capacity for the human population be an increasing linear function of economic production, $C = C_0 + mAK^{\alpha}L^{1-\alpha}$. The parameter C_0 is a baseline carrying capacity in the absence of production, m is a technological parameter with units [humans]•[resources/time]$^{-1}$, and $AK^{\alpha}L^{1-\alpha}$ is a Cobb-Douglas production function with constant returns to scale, no technological progress (i.e. A is a parameter), and units [resources/time]. In short, the explicit resource, K, is not a consumable biological resource, but its production has a straightforward positive effect on the ability of the environment to sustain a human population. This might happen, for example, because production also improves conditions for some implicit biological resource (e.g. corn) that does have a direct positive effect on human population growth. The explicitly modeled resource, K, is in this case abiological because of how it is produced. It is still a resource, however, in the sense that it has a positive effect on human population dynamics. This effect is indirect because it is mediated by some implicit biological resource whose direct effects are summarized phenomenologically with the logistic equation.

Coupling these assumptions with the Solow model, the result is

$$\begin{aligned}\dot{K} &= sAK^{\alpha}L^{1-\alpha} - \delta K \\ \dot{L} &= nL\left(\frac{C_0 + mAK^{\alpha}L^{1-\alpha} - L}{C_0 + mAK^{\alpha}L^{1-\alpha}}\right).\end{aligned} \tag{5}$$

Our interest is in the dynamics of resources per capita, $k = K/L$, and the human population size, L. A dynamical system in these two variables is easily derived by noting that $d(K/L)/dt = \dot{K}/L - k(\dot{L}/L)$. To produce a non-dimensional equivalent of Eq. (5), define three non-dimensional parameter combinations. Namely, α is the same as before, $\lambda = n/\delta$, and

$$\beta = \left(\frac{\delta}{s}\right)^{\alpha/(1-\alpha)} \frac{1}{mA^{1/(1-\alpha)}}.$$

The resulting non-dimensional system (Efferson, 2007) in resources per capita and the human population size is

$$\begin{aligned}\dot{k} &= k^{\alpha} - (\lambda+1)k + \frac{\lambda\beta kL}{\beta + k^{\alpha}L} \\ \dot{L} &= \lambda L\left(1 - \frac{\beta L}{\beta + k^{\alpha}L}\right),\end{aligned} \tag{6}$$

where k and L are now dimensionless quantities. Because k is not defined when $L = 0$ we will limit our attention in (k,L) space to dynamics in $R_{+} \times R_{++}$.

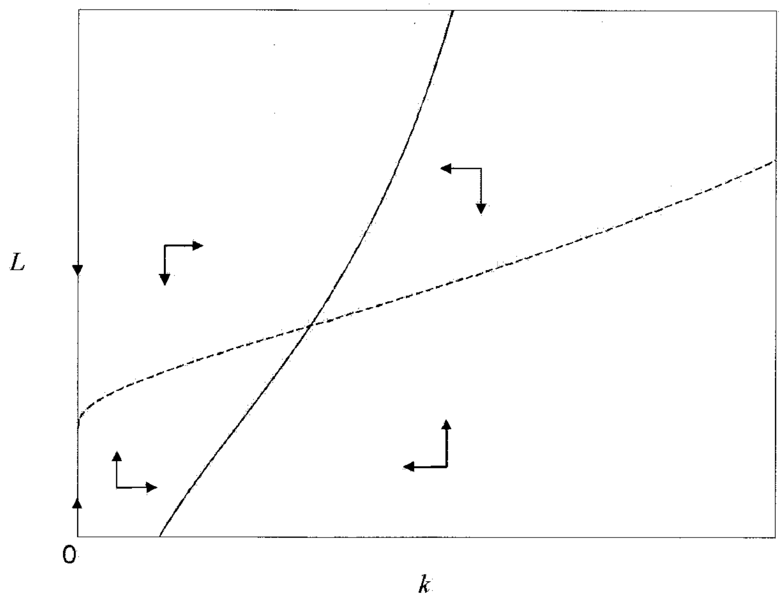

Fig. 1. The phase plane of the modified neoclassical growth model when β >1. The system has a unique and globally stable non-trivial steady state. The solid line is the $\dot{k}=0$ nullcline, while the dashed line is the $\dot{L}=0$ nullcline. The arrows show the direction of movement in each region of phase space.

The system defined by Eq. 6 has two dynamical regimes (Efferson, 2007). When β > 1, the system has a non-trivial stable node at $(\hat{k},\hat{L})$ = (1, β/(β-1)). This means both resources per capita, k, and the human population size, L, approach their steady-state values, and once they get there they stay there. Figure 1 shows the phase plane under these conditions.

The characteristics of such a society are exactly those characteristics that would lead β to be greater than 1. Namely, rapid resource depreciation (large δ), limited resource savings (small s), and poor technology (small m and A) could all contribute. The effects of α are more subtle. Specifically, one can easily verify that, if δ/s > A, then δβ/δα > 0. In contrast, if δ/s < A, then δβ/δα <0.

This dynamical regime with stable values of k and L is interesting because it characterizes most of human history. In particular, imagine a human society in this regime that enjoys a sudden improvement in its situation. So long as β remains greater than 1, the improvement is ultimately manifested exclusively as an increase in the steady-state human population size with no

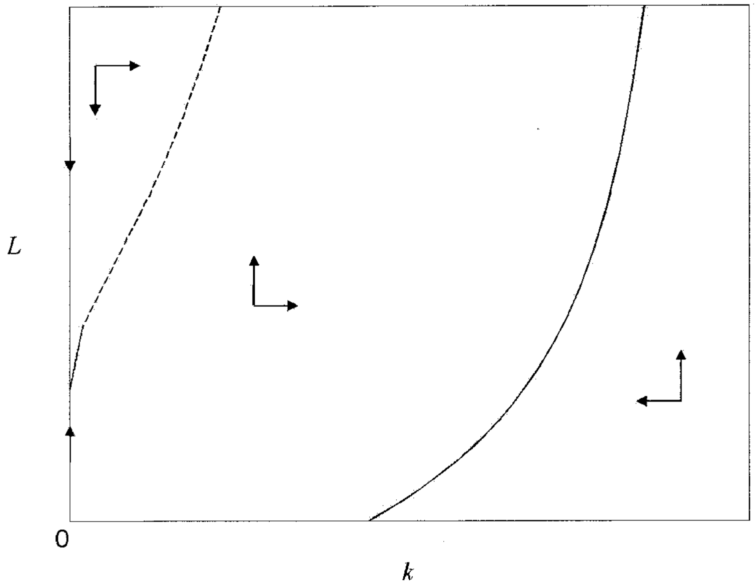

Fig. 2. The phase plane of the modified neoclassical growth model under the growth regime that holds when β <1. In this case the human population grows forever, and the resource per capita approach an asymptotic value as explained in the text. The solid line is the $\dot{k} = 0$ nullcline, while the dashed line is the $\dot{L} = 0$ nullcline.

long-term change in resources per capita. Say, for example, that some critical technology improves because of a recent innovation like a new weapon or a new hunting technique. This would be equivalent to an increase in m or A. This change in turn would decrease β. As $\beta \rightarrow 1^+$ the steady state level of the human population size (i.e. $\beta/(\beta - 1)$) increases, the steady state level of resources per capita (i.e. 1) remains exactly the same, and the system retains its stable steady state. The stable value of the human population changes, but the qualitative nature of the regime does not. This is one of the key features of what Galor & Weil (1999) call the ``Malthusian" regime. Any improvements in the economic, technological, or ecological circumstances of the society are translated into a larger, but stable consumer population with a level of resources per capita exactly the same as before the improvement. We might choose to describe such a society as expanding, but it is expanding in a very particular and limited sense.

Continued improvements, however, will eventually push the system across the critical threshold such that $\beta < 1$. Here the dynamics change dramatically. In this case we have a sustained growth regime. It is distinguished by the fact that the steady state no longer exists. Thus the system does not grow to a new steady state and stop growing. Rather, it grows and grows and grows. Asymptotically, however, all the growth takes the form of human population growth. Specifically, the population grows indefinitely, and resource per capita approach (Efferson, 2007) an endogenous asymptotic value, k_a, defined implicitly by

$$\lambda+1=\frac{1}{k_a^{1-\alpha}}+\frac{\lambda\beta}{k_a^{\alpha}}.$$

Because $\beta < 1$ in this dynamical regime, the inequalities $\beta < k_a^a$ and $k_a < 1$ must also hold for this equality to be true. Thus, under the sustained growth regime ($\beta < 1$), resources per capita endogenously approach an asymptotic value, k_a that is actually less than the steady state value, $k = 1$, under the steady-state regime ($\beta > 1$). The world has more and more people who lead lives that are, relatively speaking, asymptotically impoverished. Figure 2 shows the phase plane for this scenario.

A MODIFIED PREDATOR-PREY MODEL WITH PREY-PRODUCING PREDATORS

As mentioned above, much of consumer-resource theory in ecology does not concern itself with consumer species that both consume and produce their resource species (Murdoch et al., 2003; Turchin, 2003b). For this reason, conventional predator-prey models cannot be put forward as a theory of economic growth and society dynamics. Nonetheless, such models are typically derived by assuming that consumers divide their time among various activities associated with the consumption of prey. For example, a predator-prey modeler might assume that predators divide their total consumption time between time spent pursuing and capturing prey and time spent processing and eating prey (Case, 2000). This approach can be further generalized by assuming that consumers additionally divide their time between activities associated with consuming the resource and activities associated with producing the resource. Importantly, the resource in this case is biological. Humans can eat the resource, a critical feature of predator-prey models, and the resource thus has an explicit, direct, and positive effect on human population dynamics. For reasons enumerated earlier, this also means that production should not be neoclassical.

I have derived a model that allows consumers to divide their time between production and consumption (Efferson, 2007), and it turns out to be a generalization of the model specified in Eq. 3. It allows for predators (e.g. humans) who both consume and produce their resources, and in its complete dimensional form it looks like the following,

$$\begin{aligned}\dot{K} &= rK\left(\frac{K_{\max} - K + \phi mL}{K_{\max}}\right) - \frac{va(1-\phi)KL}{1+ahK+bwL} \\ \dot{L} &= \frac{qva(1-\phi)KL}{1+ahK+bwL} - dL.\end{aligned} \tag{7}$$

The quantity $\phi \in [0,1]$ summarizes how consumer-producers allocate their time. Focusing on time allocation under a time constraint is squarely in the tradition of theoretical ecology. In the present case, a proportion of time, ϕ, on average goes to producing the biological resource and the remaining proportion, $1 - \phi$, goes to consuming the resource. When $\phi = 0$, Eq. 7 reduces to Eq. 3. Several different treatments of ϕ are possible. One could make ϕ a choice variable under optimal control in the tradition of Ramsey (1928), Cass (1965), and Koopmans (1965). Alternatively, ϕ could be a population-level quantity evolving under the forces of cultural transmission and strategic decision making in the spirit of Boyd and Richerson (1985) and Bowles (2004). For the sake of starting at the beginning, let us assume ϕ is an exogenous constant. Additionally, *r, m, a, b*, and *q* are different kinds of technology parameters in the sense that they control how inputs of one sort or another yield outputs. The parameters *h* and *w* are additional quantities relevant to the question of time allocation.

I will work with a reduced form of the model that assumes *h, w,* = 0. Define the following non-dimensional parameter combinations: $\theta = r/d$, $\xi = va(1-\phi)K_{\max}/(dm\phi)$, and $\mu = qva(1-\phi)K_{\max}/d$. The resulting non-dimensional model in *k* and *L* is

$$\begin{aligned}\dot{k} &= \theta k(1-kL+L) + k - \xi kL - \mu k^2 L \\ \dot{L} &= \mu kL^2 - L,\end{aligned} \tag{8}$$

where *k* and *L* are now non-dimensional quantities. This model has four dynamical regimes (Efferson, 2007). The critical considerations determining which regime holds are whether ξ is less than or greater than θ and whether μ is less than or greater than 1.

The system has a non-trivial steady state at

$$(\hat{k},\hat{L}) = \left(\frac{\theta-\xi}{\theta(1-\mu)}, \frac{\theta(1-\mu)}{\mu(\theta-\xi)}\right). \tag{9}$$

This steady state is in the relevant region of phase space, namely $R_{+} \times R_{++}$, if and only if one of the following two conditions holds. Either (a) $\xi < \theta$ and $\mu < 1$, or (b) $\theta < \xi$ and $1 < \mu$. If neither of these conditions is true, the $\dot{k} = 0$ and $\dot{L} = 0$ nullclines do not intersect in $R_{+} \times R_{++}$.

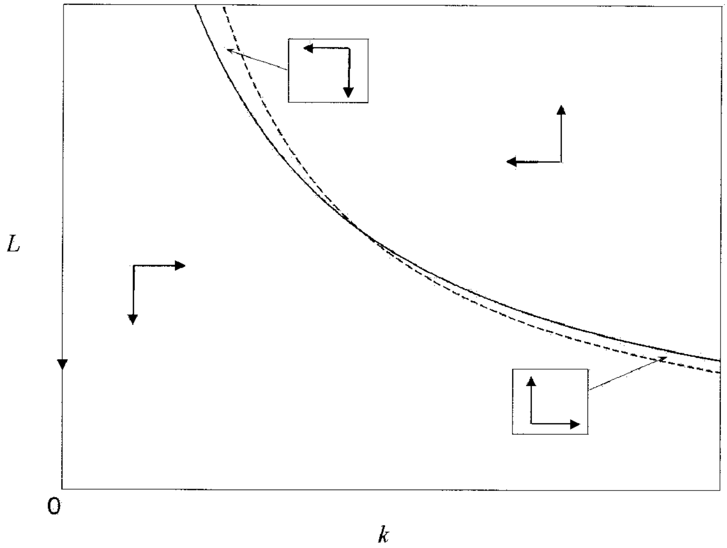

Fig. 3. The phase plane of the modified predator-prey model when $\theta < \xi$ and $1 < \mu$. The solid line is the $\dot{k} = 0$ nullcline and the dashed line the $\dot{L} = 0$ nullcline. The steady state is a focus and locally stable.

The first regime we consider occurs when $\theta < \xi \Rightarrow \phi < vaK_{\max}/(vaK_{\max} + rm)$ and $1 < \mu \Rightarrow \phi < (qvaK_{\max} - d)/(qvaK_{\max})$. In this case the steady state specified by Eq. 9 is in $R_{+} \times R_{++}$. Figure 3 shows the phase plane. A local stability analysis (Hoy et al., 2001) shows that the steady state is a stable focus (Efferson, 2007), and thus the system exhibits decaying oscillations toward the constant values of resources per capita and human population size specified by Eq. 9. In this regime, the balance between consumption and production favors consumption, and as a consequence the model behaves much like a conventional predator-prey model with a stable focus (Kot, 2001). Several factors can contribute to such a scenario. Namely, the time devoted to production is small (small ϕ), the environment has an high intrinsic capacity to support the resource species (large $K_{\max}$), the resource is easily attainable (large α), the resource species is high quality (large q), the resource species reproduces slowly (small r), the production technology is bad (small m), or the human death rate is low (small d).

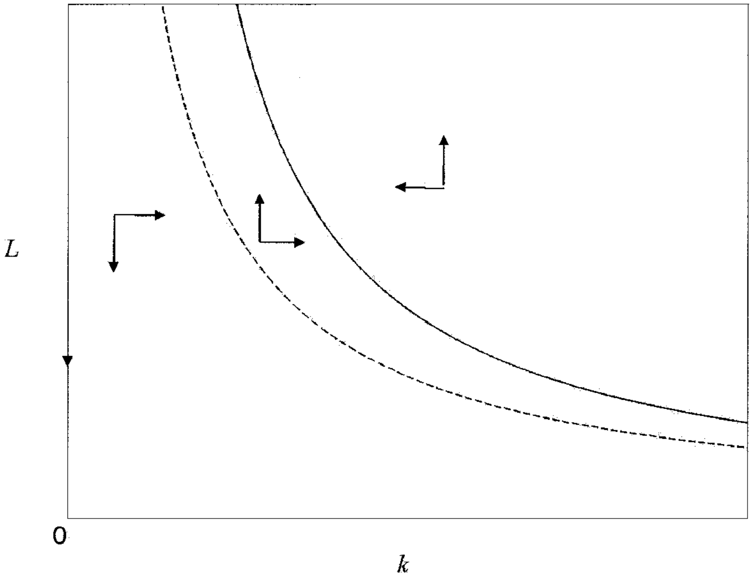

Fig. 4. The phase plane of the modified predator-prey model when $\xi < \theta$ and $1 < \mu$. The solid line is the $\dot{k} = 0$ nullcline and the dashed line the $\dot{L} = 0$ nullcline.

Second, when $\xi < \theta$ and $1 < \mu$, then $vaK_{\max}/(vaK_{\max} + rm) < \phi < (qvaK_{\max} - d)/qvaK_{\max})$. In this case the system has productive capacity beyond that of a conventional predator-prey system. This extra capacity sooner or later leads to an endlessly growing consumer population and an endogenous, asymptotic level of resources per capita defined by $k_a = (\theta - \xi)/(\theta + \mu)$. The phase plane for this scenario is shown in Fig. 4.

Notice that this scenario obtains when ϕ has an intermediate value between two non-dimensional parameter combinations. This will be feasible when $vaK_{\max}/(vaK_{\max} + rm)$ takes on a relatively small value and $(qvaK_{\max} - d)/(qvaK_{\max})$ takes on a relatively large value, which will be true under some combination of a good production technology (large m), a low death rate among humans (low d), and a rapidly reproducing, high-quality resource (large r and q).

Third, if $\theta < \xi$ and $\mu < 1$, then $(qvaK_{\max} - d)/(qvaK_{\max}) < \phi < vaK_{\max}/(vaK_{\max} + rm)$. Here the system once more involves a level of production beyond a regular predator-prey system. This time, however, as the phase plane in Fig. 5 shows, the extra capacity leads to a consumer population declining toward extinction as the resources per capita approach infinity. Again we have a situation in which ϕ takes an intermediate value between two non-dimensional parameter combinations, but the conditions are reversed. Now we need a relatively

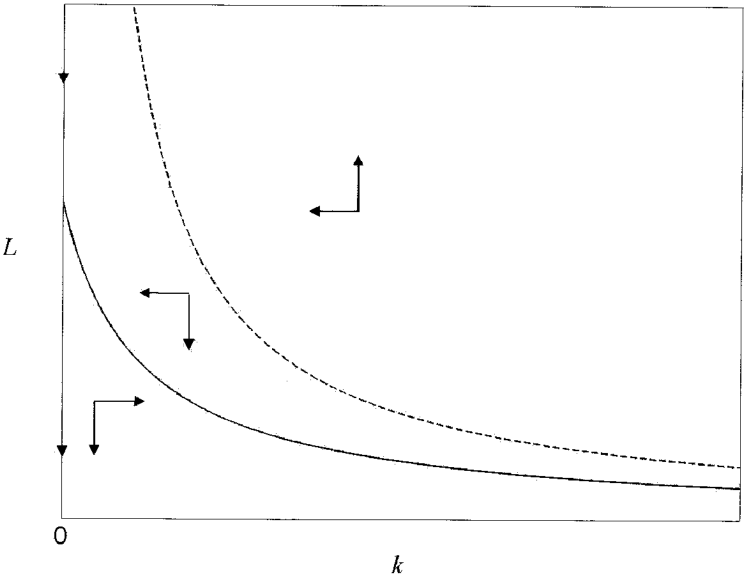

Fig. 5. The phase plane of the modified predator-prey model when $\theta < \xi$ and $\mu < 1$. The solid line is the $\dot{k} = 0$ nullcline and the dashed line the $\dot{L} = 0$ nullcline.

small value of $(qvaK_{\max} - d)/(qvaK_{\max})$ and a relatively large value of $vaK_{\max}/(vaK_{\max} + rm)$, which will hold under some combination of poor technology (small m), a high death rate among humans (large d), and a low-quality, slowly reproducing resource species (small q and r).

Fourth and finally, when $\xi < \theta \Rightarrow vaK_{\max}/(vaK_{\max} + rm) < \phi$ and $\mu < 1 \Rightarrow (qvaK_{\max} - d)/(qvaK_{\max}) < \phi$, the steady state specified by Eq. 9 is once again in $R_+ \times R_{++}$, but it is not locally stable. In this case, when consumer-predators are devoting a lot of time to production relative to the two non-dimensional parameter combinations, additional capacity can go toward either an endlessly growing consumer population and an asymptotic level of resources per capita or a consumer population declining toward extinction as resources per capita grow and grow. The difference depends only on initial conditions. Figure 6 shows the phase plane.

The dynamics of societies who meet the conditions of this final regime are predicted to depend strongly on historical contingencies. In particular, an initial bias toward per capita wealth and small population size can be reinforcing and lead to an even smaller, wealthier population. Analogously, an initial bias toward per capita poverty and large population size can also be reinforcing and lead to an even larger, poorer population. A particularly striking prediction is that two societies can be identical with respect to all parameters and evolve in completely different ways. Specifically, slight variations in initial conditions in the vicinity of the steady state can lead one society to specialize, so to speak, in population growth, while the other specializes in economic growth. This is characteristic of what Galor (2005) and others call the "Great Divergence" among the world's economies in the last two or three centuries. Some economies have excelled at population growth, while others have excelled in the growth of resources per capita. This has produced a dramatic rearrangement in the global distribution of resources and population, along with an associated divergence in terms of wealth and poverty.

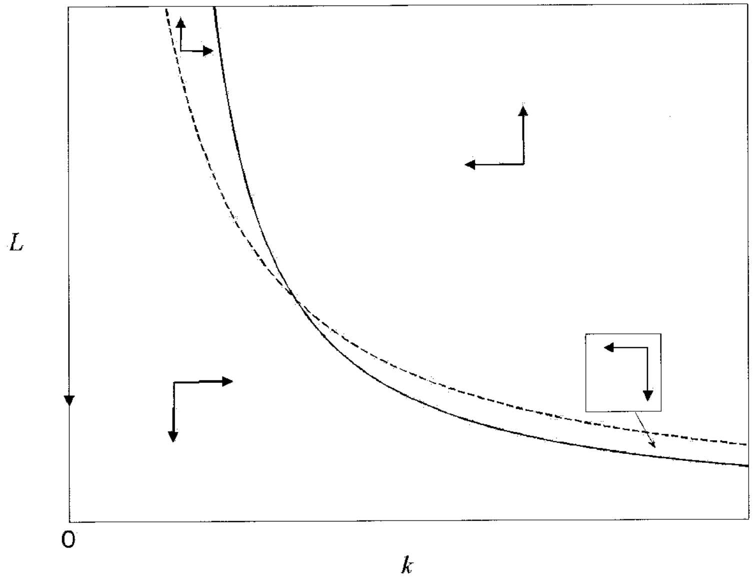

Fig. 6. The phase plane of the modified predator-prey model when $\xi < 0$ and $\mu < 1$. The solid line is the $\dot{k} = 0$ nullcline and the dashed line the $\dot{L} = 0$ nullcline.

DISCUSSION AND CONCLUSION

Societal dynamics have a pure ecological component related to the simple fact that humans consume and produce their resources and in turn require resources to reproduce. If consumption dominates production, the society can be interpreted as analogous to a kind of biologically limited, conventional predator-prey system. If the productive capacity is strong enough, however, the system takes on a mutualistic character, the consumer and resource populations are dominated by dual positive feedbacks, and the system can run away, at least for a while. The modified neoclassical growth model illustrates this result, and the parameter β is key. β summarizes the joint effects of several real-world forces: the depreciation of capital (δ), human consumption behavior (s), the returns to capital (α), the technology governing capital production (A), and the technology controlling how production translates into human carrying capacity (m). An improvement in any of these parameters yields growth of some sort. Initially, however, the effects do not change the qualitative behavior of the system. Instead, they simply change the steady state. The steady-state level of resources per capita remains constant ($k = 1$), and all improvements are funneled toward an increase in the steady state consumer population ($L = \beta/(\beta - 1)$), as shown in Fig. 1. This type of growth is one of the principal characteristics of Malthusian stagnation, one of the regimes identified by Galor and Weil (1999) and Galor (2005) as important for societies throughout much of human economic history. The Malthusian regime is "stagnant" in the sense that any productivity gains are quickly offset in terms of consumption per capita by a corresponding increase in the human population size.

Under continued productivity gains, $\beta \rightarrow 1^+$ and the steady state value of the consumer population gets increasingly large. If the threshold at $\beta = 1$ is crossed, the steady state vanishes, and the system enters a pure growth regime (Fig. 2). Importantly, the existence of this pure growth regime depends critically on the assumption that economic productivity expands the capacity of the environment to sustain a human population in a linear fashion. Over very long time periods, this must be wrong, and the carrying capacity effect should be diminishing (see Efferson, 2007). Nonetheless under a fortuitous confluence of technological progress and institutional improvements, the productivity effect could be approximately linear for notable periods of a society's history. A growth regime would be the outcome of this quasi-mutualistic exchange between humans and their resources, and the linear productivity effect might serve as a useful theoretical starting point.

Whatever the modified neoclassical economic growth model tells us about the transition from stagnation to growth, it has a restrictive set of dynamics. It cannot capture the fact that growth has taken the form of increases in resources per consumer in some cases, but increases in the consumer population in other cases. Galor (2005) has argued persuasively that these two different forms of growth represent an important means of distinguishing the nature of growth among different societies in the past few hundred years. The modified predator-prey model can produce this kind of divergence between different growth regimes. Again, when production is relatively limited (Fig. 3), a steady state exists. At intermediate and high productivity levels (Figs. 4 - 6), the system is in a pure growth regime. Growth, however, can take the form of an increase in resources per capita *or* an increase in the consumer population size, but not both. Which form growth takes depends on both the parameter values and initial conditions. When humans consume a lot per capita (large a) and invest heavily in each offspring (small q), for example, a situation plausibly represented by Figure 5, the consumer population shrinks even as it becomes increasingly rich in per capita terms. This is not the only way, however, to arrive at this scenario. The entire set of non-dimensional parameter combinations matters, as specified above in the model analysis. If the human death rate is high (large *d*) and the resource species has a low intrinsic rate of increase (small r), the human population once again shrinks even as it becomes increasingly wealthy in per capita terms. In contrast, imagine that humans invest little in each offspring (high *q*), the resource species is *r*-selected (high *r*), and human production of the resource is highly efficient (high *m*). Then, as shown in Fig. 4, the consumer population grows forever, and resources per capita approach a constant level asymptotically.

Whatever the parameter values controlling the ecological, technological, and consumption properties of the system, the consumer population can in principle always increase production (i.e., ϕ) to a sufficient degree that the scenario in Fig. 6 obtains. In this case, whether growth is growth in resources per capita or growth in the consumer population depends on initial conditions. A separatrix runs southwest to northeast in the phase plane in Fig. 6. Near the separatrix, even a slight bias toward a larger, less wealthy society can send the population off toward a big consumer population with no growth in resources per capita. A slight bias toward a smaller, more wealthy society can send the system in the opposite direction. Once again, long-term aggregate dynamics are highly sensitive to the interaction between the ecological, consumptive, and productive characteristics of the system. This interaction, in some cases coupled with differences in initial endowments, can mean the difference between population explosion and collapse, poverty and wealth.

In sum, the purely ecological interactions between humans and their resources can capture much about the biological forces controlling society dynamics. Importantly, I have left out a lot of what surely mattered in the economic history of humans for the last 100,000 years or so. I have parameterized technology and by extension ignored technological progress. I have parameterized consumption behavior, reproductive behavior, and production behavior. I have effectively reduced the intelligence of my agents to zero and consequently bypassed everything associated with contingent decision-making. I have ignored human capital, political institutions, and multi-sector production. I have removed history and disregarded culture. My intention is not to suggest that these forces were unimportant. They almost certainly were and are. Galor and Weil (2000) and Galor (2005) present some exciting recent work that incorporates many of these considerations in an economic setting. Turchin (2003a) has developed several interesting ecological models of agrarian empires that incorporate sociopolitical forces. My task, in contrast, has been to focus squarely on the ecological component of human success and growth. How far, in essence, can a purely ecological model of a consumer-resource-mutualist system take us?

Such systems, as I have formulated them, exhibit threshold effects. Low productivity systems, like the period of Malthusian stagnation, have steady states. Small improvements in, say, technology may change the steady state, but they do not initially change the dynamical regime. At some point, however, a critical threshold is crossed, and the mutualistic feedbacks between the consumer-producer and its resource species dominate the predatory interactions. This is a growth regime. The presence of a threshold between a steady-state regime and a growth regime seems to depend on production having a positive effect on the resource that is linear. Notice that in Eq. 5 production increases the carrying capacity of the consumer species in a linear fashion. Similarly, in Eq. 7 production alleviates density dependence in the resource species in a linear fashion. Over long time spans, some environmental constraint must eventually set in, even if it is only physical space itself. Thus the productivity effect should diminish at some point. In other words, it should be less than linear. I have experimented (Efferson, 2007) with such models as further variations on the models specified in Eqs. 5 and 7. They are sufficiently complex to be unilluminating analytically, but simulations suggest, with one important exception, that they exhibit many of the same qualitative features as Eqs. 5 and 7. The exception is the absence of dynamical regimes in which the consumer population grows indefinitely. Nonetheless the models do support enormous variation in the size of the consumer population, with growth toward a very large consumer population replacing the endless growth of the consumer population as the relevant concept. In this sense the models with linear productivity effects may be useful approximations for periods during which institutions, technology, and capital converged to improve a given society's circumstances dramatically. In the very long term, however, the approximation is too optimistic as a hypothesis about production as a means of relaxing ecological constraints.

Interestingly, neither of the models presented here can produce long-term growth in both resources per capita and the human population. Simulations, however, indicate that both models support such a situation as transitional dynamics. Both quantities can grow, but only for a while. Galor (2005) identifies regimes in which resources per capita and the consumer population grow as ``Post-Malthusian," and he argues that this state is one of the important periods in the economic histories of many modern societies. Nonetheless, human societies that grow in terms of both population size and per capita wealth typically undergo a demographic transition in which reproductive rates fall, often below replacement levels (Galor, 2005). Thus it is not at all clear that the "Post-Malthusian" regime is really a state that exists because of the fundamental properties of the system. It may simply be a transition. As Galor (2005) argues, the traditional focus among growth economists on increases in both the human population and per capita wealth stems from a narrow focus on the dynamics of human societies in the last two or three centuries. This represents a limited view of society dynamics. A richer view must in some sense recognize that a human society, as a dynamical economic system, is necessarily nested within a larger biological system with all the limitations and potential this fact implies.

REFERENCES

Barro, R. J., & Sala-i-Martin, X. (2004). *Economic growth (2^{nd} ed.)* Cambridge MA: MIT Press.

Bowles, S. (2004). *Microeconomics: Behavior, institutions, and evolution.* New York: Russell Sage.

Boyd, R. & Richerson, P. J. (1985). *Culture and the evolutionary process.* Chicago: University of Chicago Press.

Case, T. J. (2000). *An illustrated guide to theoretical ecology.* Oxford: Oxford University Press.

Cass, D. (1965). Optimum growth in an aggregative model of capital accumulation. *The Review of Economic Studies, 32,* 233-240.

DeAngelis, D. L., Goldstein, R. A., & O'Neill, R. V. (1975). A model for trophic interaction. *Ecology, 56,* 881-892.

Diamond, J. (1997). *Guns, germs, and steel: The fates of human societies.* New York: W. W. Norton.

Diamond, J. (2005). *Collapse: How societies choose to fail or suceed.* New York: Viking.

Efferson, C. (2007). *An analysis of two modeling frameworks combining economic growth theory and theoretical ecology.* Unpublished Manuscript. Santa Fe, NM: Santa Fe Institute. Retrieved 27 September 2007 from http://www.santafe.edu/~cmefferson/cmeSite/publications.html.

Galor, O. (2005). From stagnation to growth: unified growth theory. In P. Aghion & S. N. Durlauf (Eds.), *Handbook of economic growth* (pp.171-294). Amsterdam: Elsevier.

Galor, O., & Weil, D. N. (1999). From Malthusian stagnation to modern growth. *The American Economic Review, 89,* 150-154.

Galor, O., & Weil, D. N. (2000). Population, technology, and growth: from Malthusian stagnation to the demographic transition and beyond. *The American Economic Review, 90,* 806-828.

Gilpin, M. E., & Ayala, F. J. (1973). Global models of growth and competition. *Proceedings of the National Academy of Sciences, 71,* 3590-3593.

Hoy, M., Livernois, J., McKenna, C., Rees, R., & Stengos, T. (2001). *Mathematics for Economics (2^{nd} ed.).* Cambridge MA: MIT Press.

Inada, K.-I. (1963). On a two-sector model of economic growth: comments and a generalization. *The Review of Economic Studies,. 30,* 119-127.

Johnson, A. W., & Earle, T. (2000). *The evolution of human societies: From foraging group to agrarian state (4^{th} ed.).* Stanford: Stanford University Press.

Jones, C. I. (1998). *Introduction to economic growth.* New York: W. W. Norton.

Koopmans, T. C. (1965). On the concept of optimal economic growth. In *The econometric approach to development planning.* Amsterdam: North Holland.

Kot, M. (2001). *Elements of mathematical ecology.* Cambridge: Cambridge University Press.

Murdoch, W. W., Briggs, C. J., & Nisbet, R. M. (2003). *Consumer-resource dynamics.* Princeton: Princeton University Press.

Ramsey, F. P. (1928). A mathematical theory of saving. *The Economic Journal, 38,* 543-559.

Solow, R. M. (1956). A contribution to the theory of economic growth. *The Quarterly Journal of Economics, 70,* 65-94.

Thieme, H. R. (2003). *Mathematics in population biology.* Princeton: Princeton University Press.

Turchin, P. (2003a). *Complex population dynamics: A theoretical/empirical synthesis.* Princeton: Princeton University Press.

Turchin, P. (2003b). *Historical dynamics: Why states rise and fall.* Princeton: Princeton University Press.

An Analysis of Two Modeling Frameworks Combining Economic Growth Theory and Theoretical Ecology*

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1 Introduction

Economic growth theory and theoretical ecology represent independent traditions of modeling aggregate consumer-resource systems. Both focus on different but equally important forces underlying the dynamics of human societies. Though the two traditions have unknowingly converged in some ways, they each have curious conventions from the perspective of the other. Specifically, much of economic growth theory assumes exponential growth of the human population. Much of ecology is either directly or indirectly related to the study of why this assumption is usually bad for any species, including humans. Analogously, theoretical ecology often focuses on systems in which consumer species only consume but do not produce their resources, while economics has a rich and varied theory of production that is surely relevant to the study of human societies from at least the origin of agriculture until the present.

The present paper shows the derivation and analysis of two modeling frameworks I presented in another paper entitled, "Prey-Producing Predators: The Ecology of Human Intensification." First, I cover the technical material associated with a modified neoclassical growth model. This model is a simple Solow growth model (Solow, 1956) with resource-dependent population growth in the labor supply (i.e. humans). Second, I derive and analyze a modified predator-prey model. This model is a generalization of the predator-prey model by DeAngelis *et al.* (1975). The generalization consists of allowing the predators to both produce and consume their prey.

2 A modified neoclassical growth model with implicit resource dependence

In the following model, the presentation begins with a dimensional system. The state variables in this case are subscripted with "D" for "dimensional." In addition, with some conventional exceptions like the depreciation rate of capital (δ), dimensional parameters are Roman letters. Once an equivalent non-dimensional model is derived, the "D" is dropped from the state variables, and non-dimensional parameter combinations are Greek letters. This convention will also hold for the modified predator-prey model presented later.

2.1 Deriving the neoclassical model in k and L

Define $k_D = K_D/L_D$. Given the neoclassical growth model in K_D and L_D, the dynamics of k_D are $\dot{k}_D = \dot{K}_D/L_D - k_D(\dot{L}_D/L_D)$. Because k_D is not defined when $L_D = 0$, I will work with dynamics in (k, L) space and limit attention to $\mathbb{R}_+ \times \mathbb{R}_{++}$. Altogether the system in k_D and L_D is

$$\begin{aligned} \dot{k}_D &= sAk_D^\alpha - (n+\delta)k_D + \frac{nk_D L_D}{C_0 + mAk_D^\alpha L_D} \\ \dot{L}_D &= nL_D\left(1 - \frac{L_D}{C_0 + mAk_D^\alpha L_D}\right). \end{aligned} \tag{1}$$

To derive a non-dimensional equivalent, define the variables as $k_D = \bar{k}k,\ L_D = \bar{L}L$, and $t_D = \tau t$. The quantities $\bar{k},\ \bar{L}$, and τ are scaling constants with the same units as their associated variables, and $k,\ L$, and t are pure numbers without units. Basic algebra shows that model (1) is equivalent to the following non-dimensional system,

$$\begin{aligned}\dot{k} &= \tau \dot{k}_D/\bar{k} \\ \dot{L} &= \tau \dot{L}_D/\bar{L}.\end{aligned} \tag{2}$$

Further define the following set of scaling constants and dimensionless parameter combinations:

$$\bar{k} = (sA\tau)^{1/(1-\alpha)},\ \bar{L} = C_0,\ \tau = 1/\delta,\ \beta = 1/(mA\bar{k}^{\alpha}),\ \lambda = n\tau.$$

With these definitions in hand, system (2) is

$$\begin{aligned}\dot{k} &= k^{\alpha} - (\lambda+1)k + \frac{\lambda\beta k L}{\beta + k^{\alpha}L} \\ \dot{L} &= \lambda L\left(1 - \frac{\beta L}{\beta + k^{\alpha}L}\right).\end{aligned} \tag{3}$$

This is the model of primary interest in the main paper.

2.2 Nullclines

Setting $\dot{k} = 0$, the resulting nullclines are specified by $k = 0$ and

$$L = \frac{\beta - \beta(\lambda+1)k^{1-\alpha}}{(\lambda+1)k - k^{\alpha} - \lambda\beta k^{1-\alpha}}. \tag{4}$$

To get some analytical results for the second of these two nullclines, I consider the numerator, $N(k) = \beta - \beta(\lambda+1)k^{1-\alpha}$, and the denominator, $D(k) = (\lambda+1)k - k^{\alpha} - \lambda\beta k^{1-\alpha}$, separately. When $k = 0$, $N(0) = \beta$, and $\lim_{k\to\infty} N(k) = -\infty$. Moreover, $\forall k > 0,\ N'(k) = -(1-\alpha)\beta(\lambda+1)k^{-\alpha} < 0$ and $N''(k) = \alpha(1-\alpha)\beta(\lambda+1)k^{-\alpha-1} > 0$. These results indicate that the numerator is convex and monotonically decreasing, and $\forall\ k \in [0,\infty)$ it thus has a single root at

$$k_r = \left(\frac{1}{\lambda+1}\right)^{1/(1-\alpha)}.$$

For all $k \in (0, k_r),\ N(k) > 0$, and for $k > k_r,\ N(k) < 0$.

With respect to the denominator, $D(0) = 0$, and $\lim_{k\to\infty} D(k) = \infty$ so long as $\alpha \in (0,1)$, which is true by assumption. In addition, one can show that $\lim_{k\to 0^+} D'(k) = -\infty,\ \lim_{k\to\infty} D'(k) = \lambda + 1$, and that $\forall k > 0,\ D''(k) > 0$. These results tell us that, $\forall k > 0$, the denominator has a single root at k_a, which is defined implicitly by

$$\lambda + 1 = \frac{1}{k_a^{1-\alpha}} + \frac{\lambda\beta}{k_a^{\alpha}}. \tag{5}$$

For all $k \in (0, k_a),\ D(k) < 0$, and for $k > k_a,\ D(k) > 0$.

To characterize the $\dot{k} = 0$ nullcline further, we need to know the relation between k_r and k_a. In particular, is it possible for k_r to be greater than or equal to k_a? To examine this possibility, let us assume that it is and look for a contradiction. Specifically, let $k_a = \psi k_r$ for some $\psi \in (0, 1]$. Substituting into (5), the following must be true:

$$\begin{aligned}
\lambda + 1 &= \frac{1}{(\psi k_r)^{1-\alpha}} + \frac{\lambda\beta}{(\psi k_r)^{\alpha}} \\
&= \frac{\lambda+1}{\psi^{1-\alpha}} + \frac{\lambda\beta(\lambda+1)^{\alpha/(1-\alpha)}}{\psi^{\alpha}} \\
&= (\lambda+1)\left\{\frac{\psi^{\alpha} + \lambda\beta(\lambda+1)^{(2\alpha-1)/(1-\alpha)}\psi^{1-\alpha}}{\psi}\right\}
\end{aligned}$$

A few more manipulations, and the result is

$$\psi - \psi^{\alpha} = \lambda\beta\psi^{1-\alpha}(\lambda+1)^{(2\alpha-1)/(1-\alpha)},$$

which cannot be true because $\alpha \in (0,1)$ and $\psi \in (0,1]$ by assumption. This means the left-hand side of the equality must be non-positive, while the right-hand side must be positive because all parameters are positive. This is our contradiction, and it means that our initial assumption was wrong. Consequently, $0 < k_r < k_a$. To review, we know that $N(0) = \beta > 0$ and $D(0) = 0$. We know that $\forall k \in (0, k_r)$, $N(k) > 0$, $D(k) < 0$, and thus the nullcline is below the k-axis in (k, L) space. We also know that $N(k_r) = 0$ and $D(k_r) < 0$. In addition, $\forall k \in (k_r, k_a)$, $N(k) < 0$, $D(k) < 0$, and so the nullcline is *above* the k-axis. Lastly, when $k > k_a$, the numerator is negative and the denominator positive, and the nullcline is once again below the k-axis. In short, the non-trivial $\dot{k} = 0$ nullcline is only in $\mathbb{R}_+ \times \mathbb{R}_{++}$ when $k_r < k < k_a$.

The final question with respect to this nullcline is whether it is monotonic over the interval $k \in (k_r, k_a)$. By taking the derivative of (4) with respect to k, one can show that, as long as the derivative is defined (i.e. $k \neq k_a$), the derivative is positive when the following holds,

$$\frac{\alpha\beta\{(\lambda+1)k^{1-\alpha} - 1\}^2}{k^{1-\alpha}} + \frac{(1-\alpha)\lambda\beta^2}{k^\alpha} > 0. \tag{6}$$

Because all parameters are positive and $\alpha < 1$, this expression must be true, and so the nullcline specified by (4) is monotonically increasing over the relevant interval, $k \in (k_r, k_a)$.

Setting $\dot{L} = 0$, the relevant nullcline is defined by $L = \beta/(\beta - k^\alpha)$. This nullcline intersects the L-axis at $(0, 1)$, and $\forall k < \beta^{1/\alpha}$ it increases monotonically toward a vertical asymptote at $k = \beta^{1/\alpha} > 0$. For $k > \beta^{1/\alpha}$, the nullcline is not in $\mathbb{R}_+ \times \mathbb{R}_{++}$.

2.3 Steady states

Model (3) has two steady states in $\mathbb{R}_+ \times \mathbb{R}_{++}$. The first is $(\hat{k}, \hat{L}) = (0, 1)$. The phase plane from the main paper shows that this steady state is not stable. The other steady state of interest is $(\hat{k}, \hat{L}) = (1, \beta/(\beta - 1))$, which is only in the relevant part of phase space if $\beta > 1$. When this is true, the steady state is a stable node. Specifically, the trace of the Jacobian of (3) evaluated at the steady state is

$$\operatorname{tr}\left(J(1, \beta/(\beta-1))\right) = \frac{-\beta(1-\alpha) - \alpha\lambda - \lambda(\beta-1)}{\beta} < 0,$$

while the determinant is

$$\det\left(J(1, \beta(\beta-1))\right) = \frac{\lambda(\beta-1)(1-\alpha)}{\beta} > 0.$$

2.4 Effects of α on β

Taking the derivative of β with respect to α, we have

$$\frac{\partial\beta}{\partial\alpha} = \left(\frac{\delta}{s}\right)^{\alpha/(1-\alpha)} m^{-1} A^{-1/(1-\alpha)} (1-\alpha)^{-2} \left\{ \ln\left(\frac{\delta}{s}\right) - \ln A \right\}.$$

Because all parameters are positive and $\alpha < 1$ by assumption, this derivative is positive when $A < \delta/s$ and negative when $\delta/s < A$.

2.5 The carrying capacity as a concave function of economic production

Let the carrying capacity be $C_0 + bm(AK_D^\alpha L_D^{1-\alpha})^\eta$, where b has units $[\text{resources/time}]^{1-\eta}$ and $\eta \in (0,1)$. With this assumption the carrying capacity is a strictly concave function of $AK_D^\alpha L_D^{1-\alpha}$. With the additional non-dimensional parameter combination, $\gamma = \beta A^{1-\eta} \bar{k}^{\alpha(1-\eta)} \bar{L}^{1-\eta}/b$, the system is

$$\begin{aligned} \dot{k} &= k^\alpha - (\lambda+1)k + \frac{\lambda\gamma k L}{\gamma + k^{\alpha\eta} L^\eta} \qquad (7) \\ \dot{L} &= \lambda L \left(1 - \frac{\gamma L}{\gamma + k^{\alpha\eta} L^\eta}\right). \end{aligned}$$

Figures 1–S4 show simulations of this system for two values of η and four values of γ. Variation in neither η nor γ affects the final value of k. The transitional dynamics, however, vary dramatically, and as a consequence the final value of L is quite labile. Increasing η and decreasing γ (e.g. increasing b) both protract transitional dynamics by increasing the tendency for economic production to alleviate implicit resource dependence in the consumer population. The effect is striking because logistic growth behaves much like exponential growth at low population densities. Alleviating implicit resource dependence extends this quasi-exponential stage, and the explosiveness of exponential growth ensures the resulting variation is the final population size is substantial.

3 A modified predator-prey model with prey-producing predators

3.1 Deriving the model in k and L

Much of consumer-resource theory in ecology assumes that the direct effects of the predator on the prey are only negative. Because labor is a fundamental productive input in human economies, this assumption is not appropriate for our purposes. Consider an important biological resource in a given society like wheat in many agrarian societies or cows in many pastoralist societies. Humans have both a predatory and productive effect on the resource. People both eat and raise cows. To address this complication, I assume consumption and production are mutually exclusive activities with respect to time allocation. Although one could make alternative assumptions, this one will allow us to modify classic consumer-resource models from ecology in a straightforward and transparent fashion.

Posit a small interval of time per consumer, Δt_c, which a given consumer can allocate in only four mutually exclusive ways. A given consumer can spend time (1) acquiring the biological resource, t_a, (2) processing and handling the resource, t_h, (3) dealing with costly and potentially competitive social interactions involving conspecifics, t_s, or (4) contributing to the production of the resource, t_p. By definition, $\Delta t_c \equiv t_a + t_h + t_s + t_p$. Let $\Delta t_c = v\Delta t$, where v specifies the time available per consumer per unit time for these four activities.[1]

Assume the resources acquired per consumer during Δt_c satisfy $K_a = at_aK_D$, where a is the proportion of the resource stock acquired per unit of time spent acquiring resources.[2] Posit a constant expected handling time per resource, h, which thus yields an average handling time per consumer of $t_h = hK_a = aht_aK_D$.

Further assume the consumers encountered per consumer during Δt_c satisfy $L_e = bt_aL_D$, where b is the consumers encountered per consumer per unit of time spent acquiring resources. The fact that the consumers encountered varies positively with time spent acquiring resources reflects the idea that consumers compete for resources. The more time a consumer spends acquiring resources, the more time the consumer must spend with costly political interactions precipitated by resource competition with other consumers. Although other assumptions are certainly possible, this one should be relevant in many cases, and it has a long history in theoretical ecology. Under a constant expected interaction time, w, per consumer encountered, $t_s = wL_e = bwt_aL_D$. After substituting into $\Delta t_c = t_a + t_h + t_s + t_p$ and dividing both sides by Δt_c, time allocation per consumer satisfies the following:

$$\frac{\Delta t_c}{\Delta t_c} = \frac{t_a(1 + ahK_D + bwL_D)}{\Delta t_c} + \frac{t_p}{\Delta t_c}. \tag{8}$$

Define the fraction on the far right as $\phi = t_p/\Delta t_c \in [0, 1]$ and the remaining fraction as $1 - \phi$.

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[1] To my knowledge, v is always taken to be 1 in ecological models and indeed is generally not included as a separate quantity. Assuming $v = 1$ simply means time is not rival. Every minute you spend foraging, I can too. I include it explicitly here to be precise about units at all stages of model derivation.

[2] I ignore the negative effects of consumers acquiring resources on the resource stock. This approach means the discrete-time dynamics in model (9) are only approximate. The approximation, however, is increasingly accurate as Δt gets smaller, and as $\Delta t \to 0$ the approximation becomes exact.

To incorporate time allocation into a consumer-resource model, assume the dynamics are approximate as follows,

$$\begin{aligned}K_D(t+\Delta t) &\approx K_D(t) + \{B(K_D(t), L_D(t)) - D(K_D(t), L_D(t))\}K_D(t)\Delta t \\ &\quad - \ c(K_D(t), L_D(t))L_D(t)\Delta t \qquad (9) \\ L_D(t+\Delta t) &\approx L_D(t) + qc(K_D(t), L_D(t))L_D(t)\Delta t - dL_D(t)\Delta t.\end{aligned}$$

The functions $B(\cdot)$ and $D(\cdot)$ are respectively birth and death rates per unit of resource per unit of time, $c(\cdot)$ represents resources consumed per consumer per unit of time, q is a parameter that converts consumed resources in new consumers, and d is an exogenous death rate for consumers. Further assume the resource birth and death rates have a linear form,

$$\begin{aligned}B(K_D(t), L_D(t)) &= b_0 - b_1K_D(t) + b_2(\phi)L_D(t) \qquad (10) \\ D(K_D(t), L_D(t)) &= d_0 + d_1K_D(t) - d_2(\phi)L_D(t).\end{aligned}$$

In this formulation, $B(\cdot)$, $D(\cdot)$, b_0, and d_0 have units [resource]$\cdot$[resource]$^{-1}\cdot$[time]$^{-1}$. Correspondingly, b_1 and d_1 represent changes in $B(\cdot)$ and $D(\cdot)$ quantities per unit of resource, which mean the units are [resource]$^{-1}\cdot$[time]$^{-1}$. Analogously, $b_2(\phi)$ and $d_2(\phi)$ have units [consumer]$^{-1}\cdot$[time]$^{-1}$. All parameters are positive. If we remove predation by consumers from consideration for the moment, (10) means the net recruitment of the resource species satisfies

$$\begin{aligned}B(K_D(t), L_D(t)) - D(K_D(t), L_D(t)) &= b_0 - d_0 - (b_1 + d_1)K_D(t) \qquad (11) \\ &\quad + \ \{b_2(\phi) + d_2(\phi)\}L_D(t).\end{aligned}$$

Expressions (10) and (11) mean that, because of implicit resource competition for resources *among individuals of the resource species*, the prey birth rate decreases and the death rate increases linearly in K_D. Furthermore, because of productive activities on the part of the consumer species, the prey birth rate increases and the death rate decreases linearly in L_D. These latter rates of increase and decrease depend, in some currently unspecified way, on how consumer-producers proportion time between production and consumption as summarized by ϕ.

To complete model (9), define $r = b_0 - d_0$, $r/K_{\max} = b_1 + d_1$, and $rm\phi/K_{\max} = b_2(\phi) + d_2(\phi)$. The parameter m has units [resource/consumer]. In addition, $c(\cdot)$ is what ecologists call the "functional response." The functional response summarizes the prey consumed per predator per unit of time and thus by definition must satisfy

$$\begin{aligned} c(K_D(t), L_D(t)) \approx K_a/\Delta t = vat_aK_D(t)/\Delta t_c \\ = \frac{va(1-\phi)K_D(t)}{1 + ahK_D(t) + bwL_D(t)}, \end{aligned} \tag{12}$$

where these expressions follow from (8), the definition of ϕ, and the fact that $\Delta t_c = v\Delta t$. By rearranging (9), making the appropriate substitutions for (11) and $c(\cdot)$, and finally taking the limit as $\Delta t \to 0$, the exact dynamics of our predator-prey model with prey-producing predators result,

$$\begin{aligned} \dot{K}_D &= rK_D\left(\frac{K_{\max} - K_D + \phi mL_D}{K_{\max}}\right) - \frac{va(1-\phi)K_DL_D}{1 + ahK_D + bwL_D} \\ \dot{L}_D &= \frac{qva(1-\phi)K_DL_D}{1 + ahK_D + bwL_D} - dL_D. \end{aligned} \tag{13}$$

This model is an economic generalization of the DeAngelis *et al.* (1975) model discussed in the main paper. The only modification is that predators divide their time between predation and production as summarized by ϕ. At one extreme, if $\phi = 1$ the consumers have only a positive effect on their sole resource, but this abstemious behavior leads to the exponential decline of the consumer population. In contrast, if $\phi = 0$ the consumers are pure predators, and the model reduces to the classic predator-prey model of DeAngelis *et al.* (1975).[3]

To simplify matters, assume $h, w = 0$. In other words, people have to devote time to neither the act of consumption nor interactions with other people related to resource competition. Consequently, resources consumed per consumer per unit of time increase linearly with the resource stock, $c(K_D, L_D) = va(1-\phi)K_D$. This consumption function has a long history in theoretical ecology stretching all the way back to the early Lotka-Volterra models. Its primary shortcoming is that it implies an unlimited capacity to consume among predators, and the effects of this shortcoming are well understood (Kot, 2001; Roughgarden, 1979; Turchin, 2003). Essentially an unlimited capacity to consume dampens the oscillatory dynamics many real predator-prey systems exhibit. Insofar as humans are profligate consumers, the assumption may be correspondingly less serious. Alternatively, insofar as human economies past and present exhibit sustained oscillations, more complex functional responses could offer one theoretical approach to these oscillations.

As before we can convert our system (still assuming $h, w = 0$) into a system in k_D and L_D and then derive a non-dimensional equivalent. Define the following set of scaling constants and non-dimensional parameter combinations:

$$\bar{k} = K_{\max}/\bar{L}, \quad \bar{L} = K_{\max}/(m\phi), \quad \tau = 1/d$$

$$\theta = r\tau, \quad \xi = va\tau(1-\phi)\bar{L}, \quad \mu = qva\tau(1-\phi)K_{\max}.$$

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[3] If we assume $1 + ahK_D + bwL_D \approx ahK_D + bwL_D$, we can reformulate the functional response as $va(1-\phi)k_D/(bw + ahk_D)$, where only resources per consumer, k_D, matter. The empirical merits of this formulation remain a contested issue (Abrams and Ginzburg, 2000; Turchin, 2003).

The dimensionless model in k and L results,

$$\begin{aligned}\dot{k} &= \theta k(1 - kL + L) + k - \xi kL - \mu k^2 L \\ \dot{L} &= \mu k L^2 - L.\end{aligned} \tag{14}$$

3.2 Nullclines

Setting $\dot{k} = 0$, the corresponding nullclines satisfy $k = 0$ and

$$L = \frac{\theta + 1}{\xi - \theta + (\theta + \mu)k}.$$

In (k, L) space, this latter nullcline intercepts the L-axis at $(0, (\theta + 1)/(\xi - \theta))$. It has a vertical asymptote at $k_a = (\theta - \xi)/(\theta + \mu)$ and a horizontal asymptote at $L_a = 0$. If $\theta < \xi$, then $k_a < 0$, and $\forall\, k > k_a$ the nullcline is above the horizontal asymptote (i.e. the k-axis). Also, $\forall\, k < k_a$, it is below the horizontal asymptote. If $\theta > \xi$, then $k_a > 0$, and the nullcline is again $\forall\, k > k_a$ above the horizontal asymptote and $\forall\, k < k_a$ below.

Setting $\dot{L} = 0$, the relevant nullcline is $L = 1/(\mu k)$. This nullcline is a rectangular hyperbola.

3.3 Steady states

Model (14) has one non-trivial steady state. It is

$$(\hat{k}, \hat{L}) = \left(\frac{\theta - \xi}{\theta(1 - \mu)}, \frac{\theta(1 - \mu)}{\mu(\theta - \xi)} \right),$$

which is only defined and in $\mathbb{R}_+ \times \mathbb{R}_{++}$ if $\theta - \xi$ and $1 - \mu$ are either both positive or both negative. The trace of the Jacobian of (14) evaluated at this steady state is

$$\mathrm{tr}(J(\hat{k}, \hat{L})) = -\theta/\mu.$$

The determinant is

$$\det(J(\hat{k}, \hat{L})) = \theta(\mu - 1)/\mu.$$

Together these values indicate that the steady state is locally stable if $\mu > 1$.

3.4 Treating r a maximum rate of increase

In his discussion of mutualism models, Kot (2001) presents a formulation that prevents the rate of increase for a mutualistic species from exceeding the maximum rate of increase. Generalizing his approach for our modified predator-prey model, let

$$\begin{aligned} B(K_D(t), L_D(t)) &= b_0 - \frac{b_1 K_D(t)}{1 + f(\phi) L_D(t)} \qquad (15) \\ D(K_D(t), L_D(t)) &= d_0 + d_1 K_D(t). \end{aligned}$$

Under this formulation, b_1 has units [time]$^{-1}$ and $1 + f(\phi) L_D(t)$ has units [resource]. Again letting $f(\phi) = m\phi$ and $r = b_0 - d_0$, net recruitment into the resource population is

$$B(K_D(t), L_D(t)) - D(K_D(t), L_D(t)) = r - \frac{b_1 K_D(t)}{1 + m\phi L_D(t)} - d_1 K_D(t). \qquad (16)$$

By substituting into (9), letting h, $w = 0$ as before, and deriving a model in k and L, the result follows,

$$\dot{k} = \left(\theta - \frac{\pi k L}{1+L} - kL\right) k + k - \xi k L - \mu k^2 L \tag{17}$$

$$\dot{L} = \mu k L^2 - L,$$

where $\pi = b_1/d_1$, $\bar{k} = 1/(\tau d_1 \bar{L})$, and $\bar{L} = 1/(m\phi)$ (where the 1 has units [resource]). Other non-dimensional parameters are the same as those defined for the linear formulation.

The $\dot{k} = 0$ nullclines are $k = 0$ and

$$k(L) = \frac{(1+L)(\theta + 1 - \xi L)}{L\{\pi + (1+L)(1+\mu)\}}. \tag{18}$$

This function, $\forall\, L \geq 0$, is monotonically decreasing. It has a root at $L = (\theta+1)/\xi$, and $\lim_{L\to 0+} k(L) = \infty$. In (k, L) space, the nullcline intersects the vertical L-axis at $(0, (\theta+1)/\xi)$ and declines monotonically toward the k-axis as as k gets bigger. The relevant $\dot{L} = 0$ nullcline is defined by $k = 1/(\mu L)$.

The system has zero, one, or two steady states in $\mathbb{R}_+ \times \mathbb{R}_{++}$. If $(\mu(\theta+\xi)-1)^2 < 4\xi\mu\pi$, the system has no steady states in the relevant part of phase space, and the dynamics have the qualitative properties shown in Figure 5. If $4\xi\mu\pi < (\mu(\theta+\xi)-1)^2$, two additional steady states are

$$(\hat{k}, \hat{L}) = \left(\frac{1}{\mu\hat{L}}, \frac{\mu(\theta-\xi) - 1 \pm \{(\mu(\theta+\xi)-1)^2 - 4\xi\mu\pi\}^{1/2}}{2\xi\mu}\right). \tag{19}$$

When $\mu(\theta-\xi) < 1$ and $\mu\theta < \pi+1$, both of these steady states are in $\mathbb{R}^2_{--}$, and the dynamics in $\mathbb{R}_+ \times \mathbb{R}_{++}$ again have the qualitative properties shown in Figure 5. If $\pi + 1 < \mu\theta$, one non-trivial steady state is in $\mathbb{R}^2_{--}$ and the other in $\mathbb{R}^2_{++}$. In this case, dynamics exhibit the qualitative behavior shown in the phase plane of Figure 6.

Lastly, when $1 < \mu(\theta - \xi)$ and $\mu\theta < \pi + 1$, both steady states are in $\mathbb{R}^2_{++}$. In this case, the following steady state is unstable,

$$(\hat{k}, \hat{L}) = \left(\frac{1}{\mu \hat{L}}, \frac{\mu(\theta - \xi) - 1 - \{(\mu(\theta + \xi) - 1)^2 - 4\xi\mu\pi\}^{1/2}}{2\xi\mu} \right). \tag{20}$$

The remaining steady state,

$$(\hat{k}, \hat{L}) = \left(\frac{1}{\mu \hat{L}}, \frac{\mu(\theta - \xi) - 1 + \{(\mu(\theta + \xi) - 1)^2 - 4\xi\mu\pi\}^{1/2}}{2\xi\mu} \right), \tag{21}$$

is a focus. I have not derived local stability conditions for the focus, and I do not show a phase plane because in the specific numerical cases I have examined the nullclines are sufficiently close together to make the resulting figure unhelpful. Regardless, this brief analysis shows that, in contrast to model (14), model (17) cannot produce a human population that grows endogenously forever under any conditions. It does, however, seem to support variation in the long-term values of the state variables that is similar to the modified Solow model in which the carrying capacity is a concave function of income (7). Figures 7−S9 show three simulations involving either one steady state in $\mathbb{R}^2_{++}$ (i.e. Figure 7) or two steady states (Figures 8 and S9). Here we are not considering a case involving a human population declining to extinction, and the figures show limited variation in the long-term values of k but large variation in the long-term values of L.

References

Abrams, P. A. and Ginzburg, L. R. (2000). The Nature of Predation: Prey Dependent, Ratio Dependent or Neither? *Trends in Ecology and Evolution*, **15**(8), 337–341.

DeAngelis, D. L., Goldstein, R. A., and O'Neill, R. V. (1975). A Model for Trophic Interaction. *Ecology*, **56**(4), 881–892.

Kot, M. (2001). *Elements of Mathematical Ecology*. Cambridge: Cambridge University Press.

Roughgarden, J. (1979). *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Upper Saddle River, NJ: Prentice Hall.

Solow, R. M. (1956). A Contribution to the Theory of Economic Growth. *The Quarterly Journal of Economics*, **70**(1), 65–94.

Turchin, P. (2003). *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton: Princeton University Press.

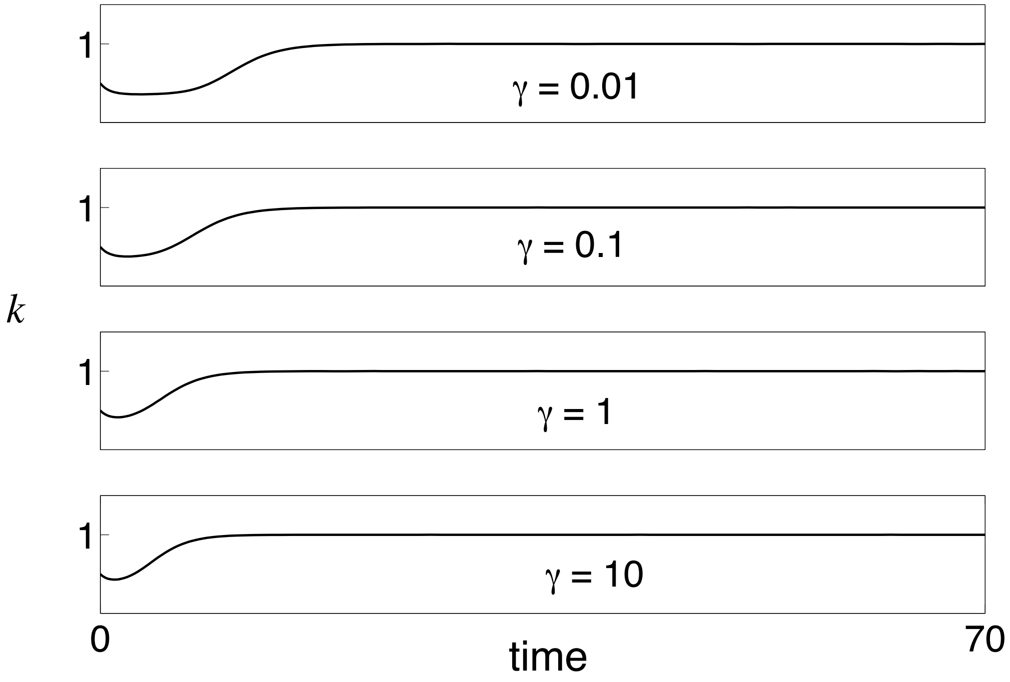

Figure 1: A simulation of model (7). Parameter values are $\alpha = 1/3$, $\lambda = 1$, and $\eta = 1/4$.

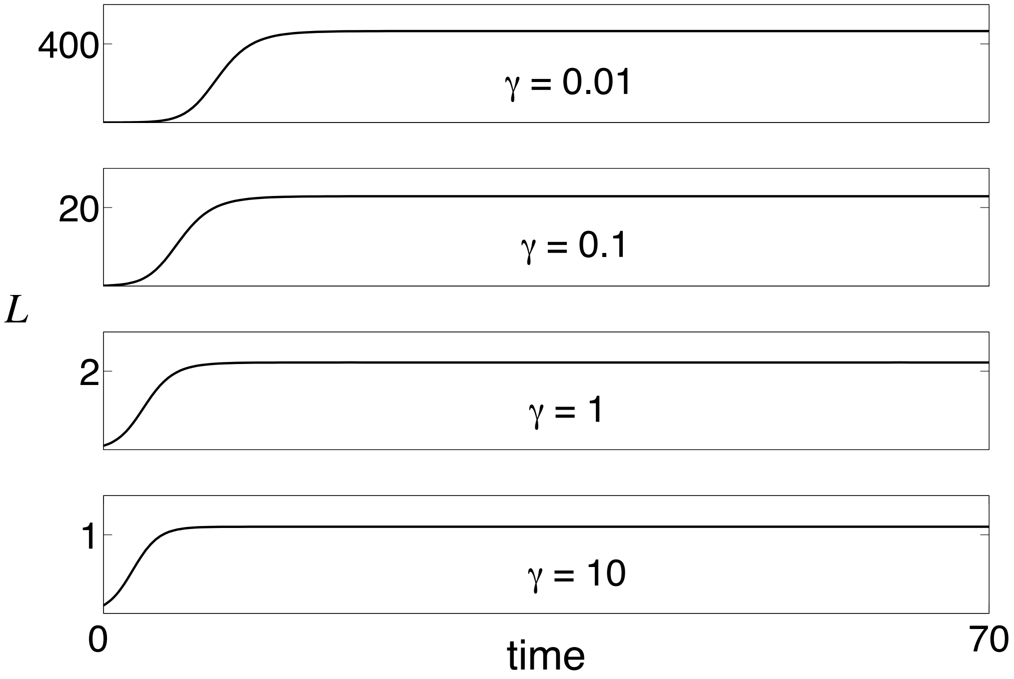

Figure 2: A simulation of model (7). Parameter values are $\alpha = 1/3$, $\lambda = 1$, and $\eta = 1/4$.

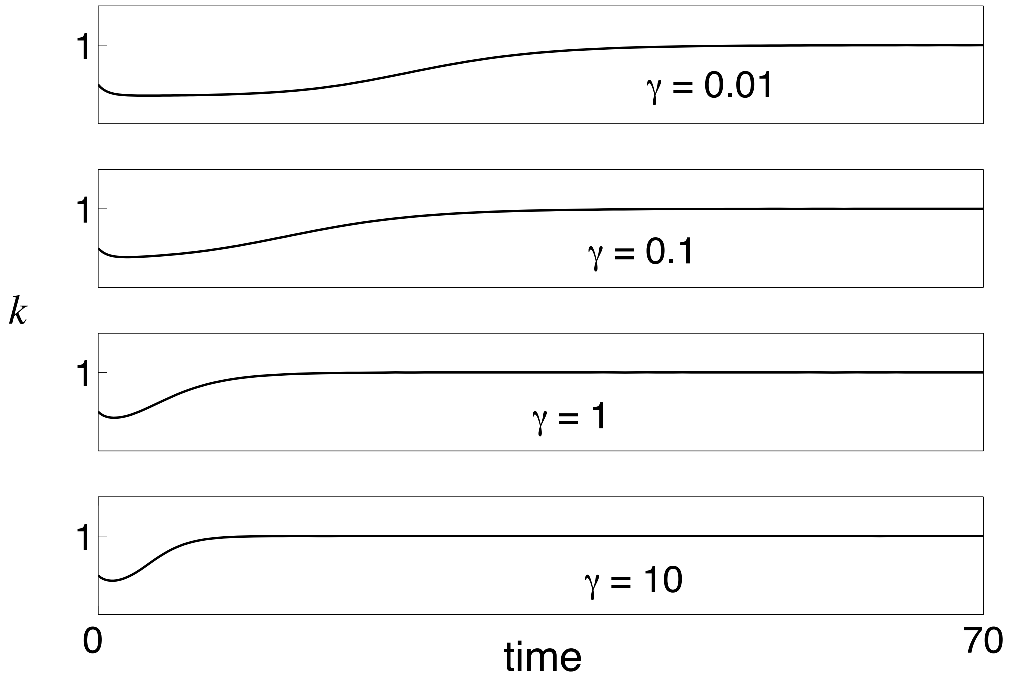

Figure 3: A simulation of model (7). Parameter values are $\alpha = 1/3$, $\lambda = 1$, and $\eta = 3/4$.

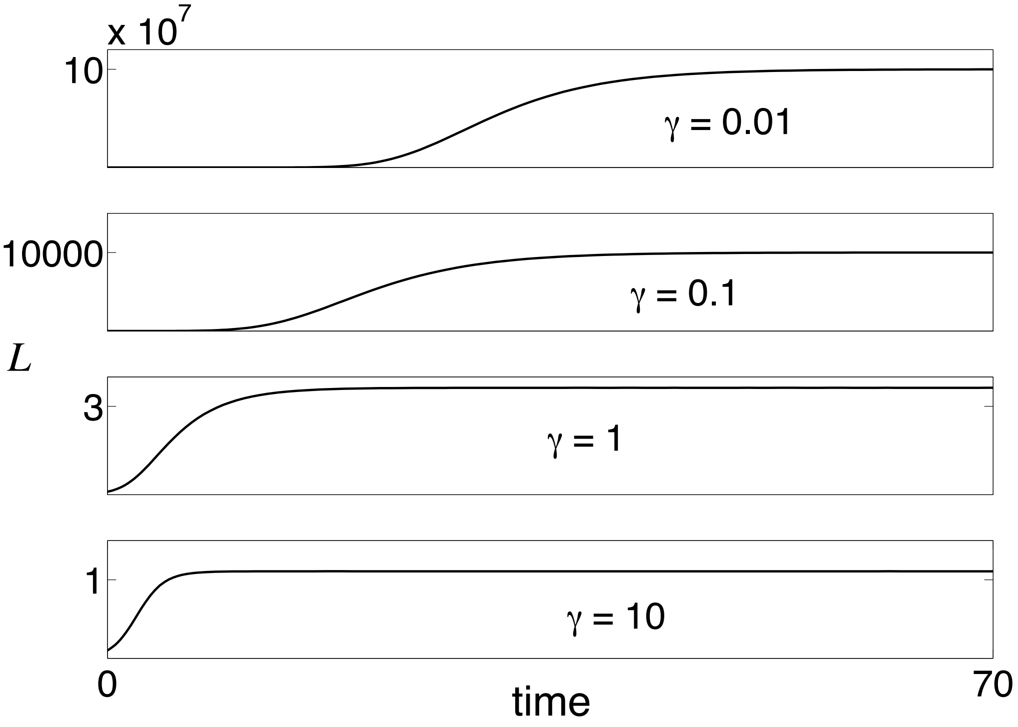

Figure 4: A simulation of model (7). Parameter values are $\alpha = 1/3$, $\lambda = 1$, and $\eta = 3/4$.

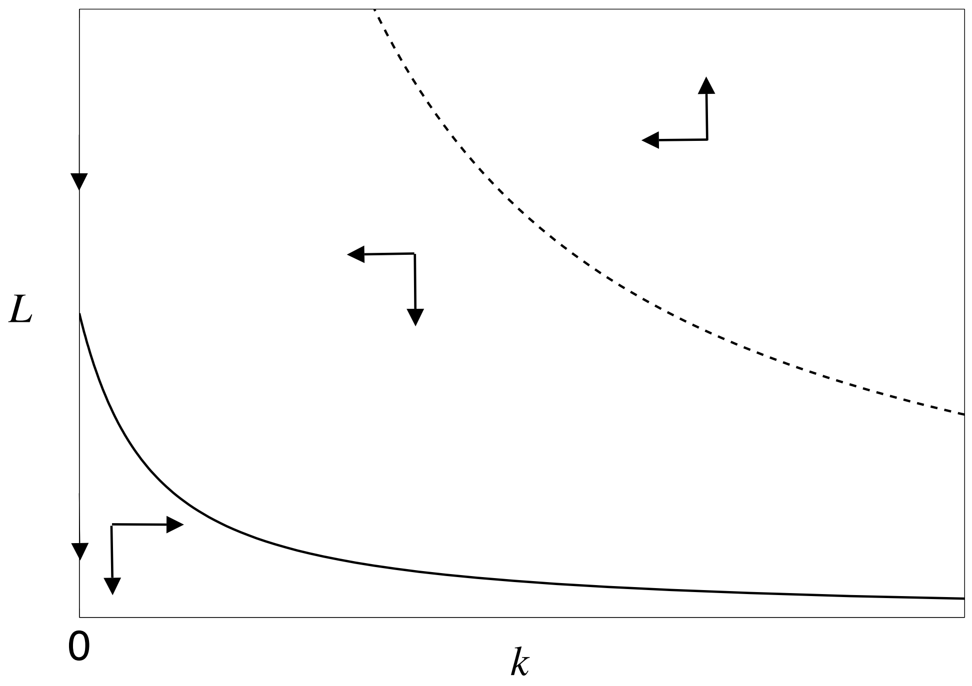

Figure 5: The phase plane for model (17) when it has no steady states in $\mathbb{R}_+ \times \mathbb{R}_{++}$.

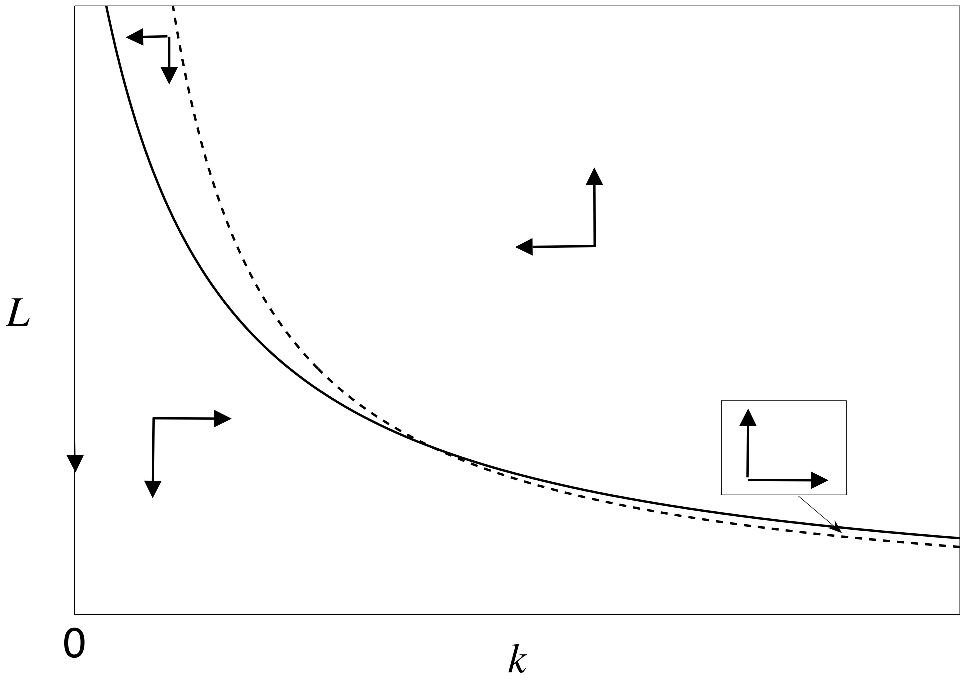

Figure 6: The phase plane for model (17) when it has one steady state in $\mathbb{R}_+ \times \mathbb{R}_{++}$.

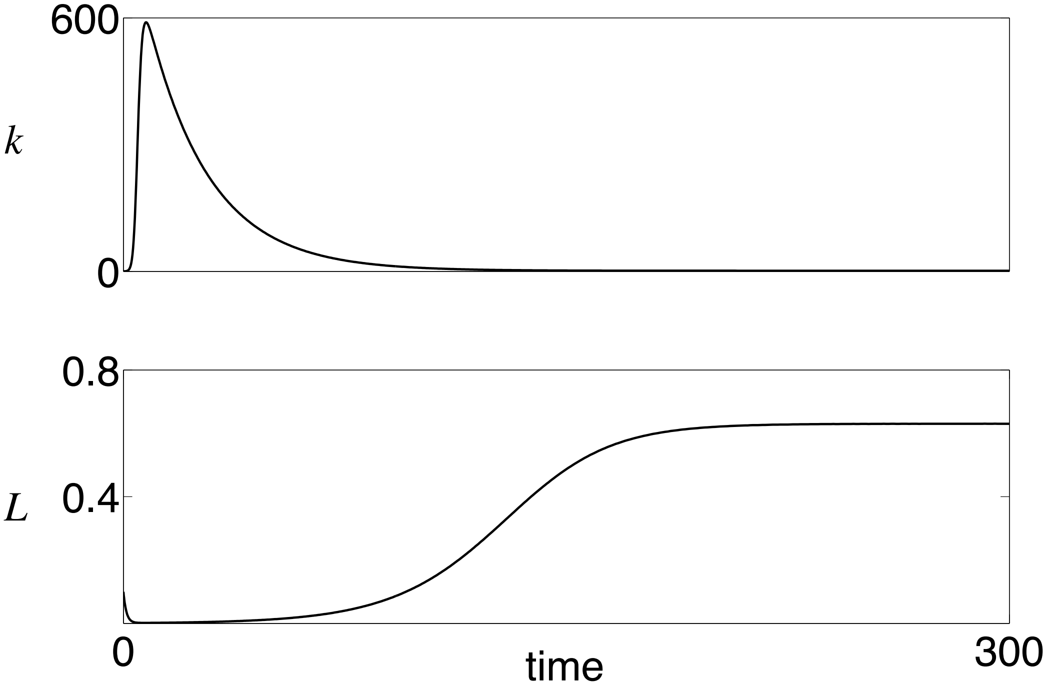

Figure 7: A simulation of model (17) when it has one steady state in $\mathbb{R}_+ \times \mathbb{R}_{++}$. Parameter values are $\theta = 1.1,\ \pi = 0.05,\ \xi = 0.11$, and $\mu = 1$.

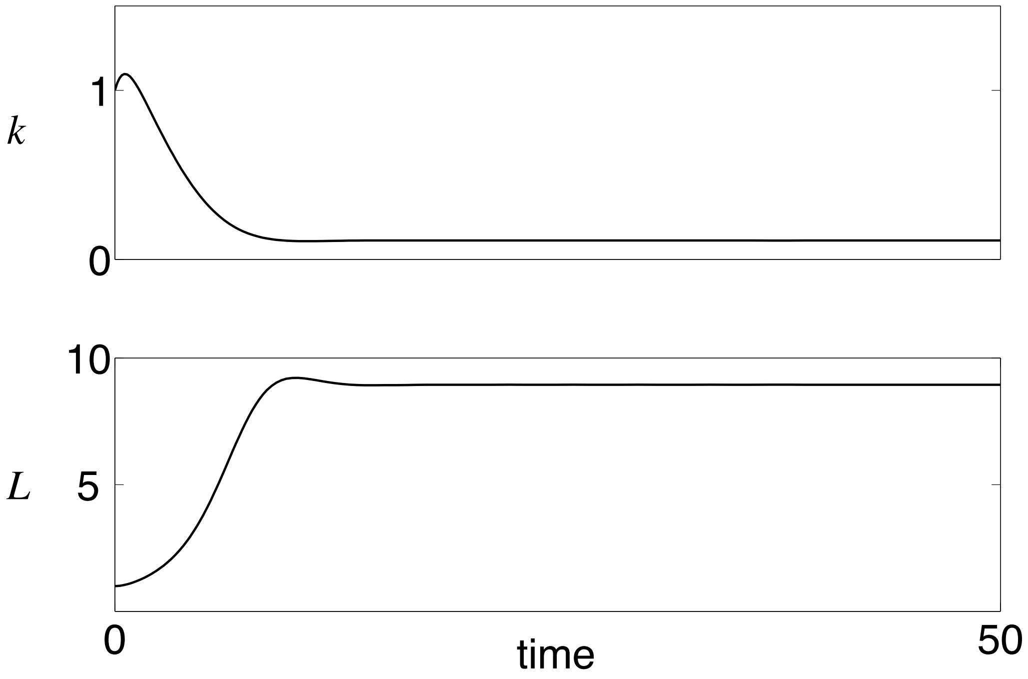

Figure 8: A simulation of model (17) when it has two steady states in $\mathbb{R}_+ \times \mathbb{R}_{++}$. Parameter values are $\theta = 2,\ \pi = 1.05,\ \xi = 0.01$, and $\mu = 1$.

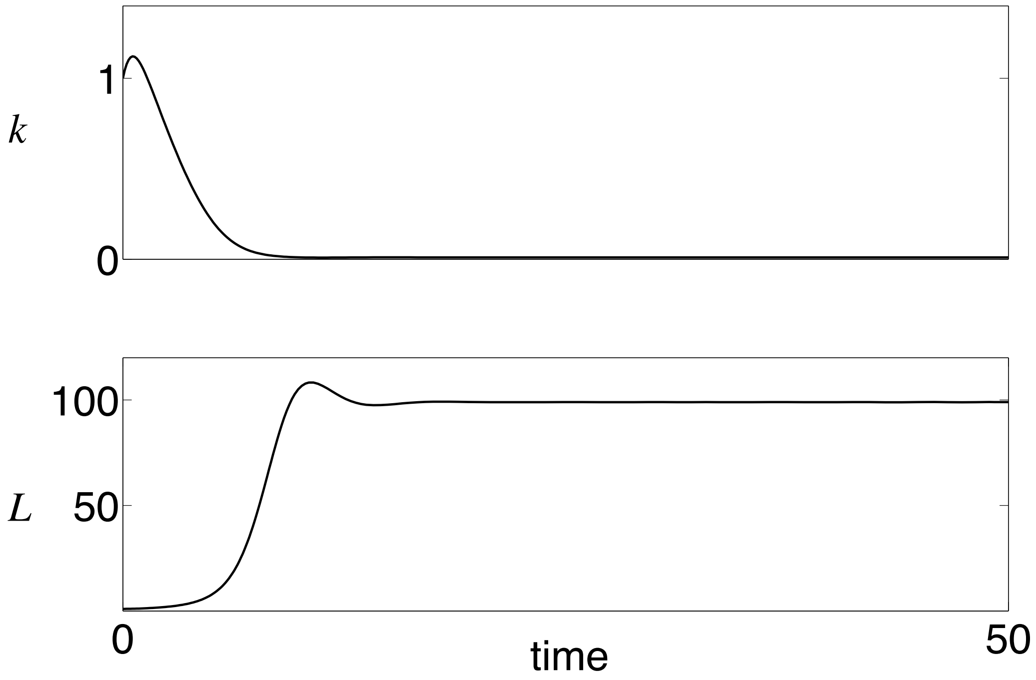

Figure 9: A simulation of model (17) when it has two steady states in $\mathbb{R}_+ \times \mathbb{R}_{++}$. Parameter values are $\theta = 2,\ \pi = 1.05,\ \xi = 0.1$, and $\mu = 1$.