# A MICROFOUNDATION OF PREDATOR-PREY DYNAMICS

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## Abstract

Predator-prey relationships account for an important part of all interactions between species. In this paper we provide a microfoundation for such predator-prey relations in a food chain. Basic entities of our analysis are representative organisms of species modelled similar to economic households. With prices as indicators of scarcity, organisms are assumed to behave as if they maximize their net biomass subject to constraints which express the organisms' risk of being preyed upon during predation. Like consumers, organisms face a 'budget constraint' requiring their expenditure on prey biomass not to exceed their revenue from supplying own biomass. Short-run ecosystem equilibria are defined and derived. The net biomass acquired by the representative organism in the short term determines the positive or negative population growth. Moving short-run equilibria constitute the dynamics of the predator-prey relations that are characterized in numerical analysis. The population dynamics derived here turn out to differ significantly from those assumed in the standard Lotka-Volterra model.

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# 1  Introduction

The dynamics of predator-prey interactions have a long tradition in the theoretical population biology and date back to the seminal works of Lotka (1925) and Volterra (1926). The original Lotka-Volterra model of natural predator-prey systems (May 1973, Clark 1976) turned out to be of limited value as a descriptive model and it therefore has been refined in several ways (May 1981, Kuang and Beretta 1998, Cantrell and Cosner 2001). The basic building blocks of these models of the Lotka-Volterra type are difference or differential equations. Each species is represented by a single equation containing as variables the own population and the population of its preys or predators. Hence these predator-prey models are macro-approaches in the sense that they take populations as basic units of analysis. Population growth is assumed rather than explained. Choosing populations as basic endogenous variables amounts to disregarding the transactions of individual organisms, fails to identify the types and scales of those transactions and does not answer the question as to how the interaction of individual organisms translates into population changes.

The present paper aims at providing a microfoundation of predator-prey dynamics in a unidirectional food chain by means of economic methodology. The starting point of our approach is the short-run ecosystem model in which populations are constant. The representative organisms are assumed to behave as if they maximize their net biomass as price takers subject to appropriate constraints.[2] Similar as in models of perfectly competitive economies a short-run ecosystem equilibrium is defined as a state where all organisms are maximizing their net biomass, and biomass demand of predators equals biomass supply of preys. Such equilibria are shown to exist. The equilibrium allocation of biomass transactions completely determines the net biomasses each species acquired during the short-run period. Net biomass represents (positive or negative) net offspring and hence population change. When the population change is linked to the populations that have prevailed and kept constant during the period under consideration, a sequence of short-run net biomasses constitutes the predator-prey dynamics.

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[2]The notion of organisms behaving as if they maximize some objective function has first been investigated in formal analysis by Hannon (1976), Crocker and Tschirhart (1992), Tschirhart (2000, 2002) and Pethig and Tschirhart (2001). These authors assume that organisms maximize net energy rather than net biomass. However, in our view net energy maximization can be considered equivalent to net biomass maximization. As-if maximization is also applied by Pethig (2003) and Eichner and Pethig (2003) but on the level of species rather than individual organisms. Their models deviate substantially from the present approach. A common feature of all these models are equilibrating ecosystem prices and price-taking behavior on the part of organisms or species. For an optimizing approach relying on Nash behavior without prices see Pethig (2003).

We take the view that there are remarkable similarities between a consumer's decision problem in the conventional economic household theory and an organism's decision problem. The problem faced by the consumer is to choose among all commodities that are available for purchase in the market. The consumer's purchase is financed by her capital income and/or labor income. Supplying labor is necessary for (most) consumers to earn their living and this is similar in case of organisms with their supply of own biomass. The link between demanding commodities and supplying labor is formally established in the budget constraint. In the ecosystem, an organism demands biomass of preys and supplies own biomass to predators. The ecological predation risk (Lima and Dik 1990) suggests that an organism's demand, capture and intake of prey biomass necessarily is correlated to its exposure to predators and hence necessarily entails the sacrifice of some own biomass. Introducing prices as scarcity indicators for each type of biomass the predation risk takes the form of a budget constraint requiring the expenditures for biomass of prey species not to exceed the income from supplying own biomass. The representative organism of a species maximizes its net biomass subject to the budget constraint. In this framework the organisms' optimal demands and supplies can be thought of as being coordinated by prices. Thus a concept of a general short-run ecosystem equilibrium is put forward which is equivalent, in spirit, to the notion of a general perfectly competitive economic equilibrium.

Although the idea of providing a microfoundation for population dynamics is not new and some important contributions have already been made, notably Tschirhart (2000) and Pethig and Tschirhart (2001), the derivation of concrete differential equations based on the short-run optimization problems of representative organisms turns out to be difficult. To our knowledge, Pethig and Tschirhart (2001) is the only paper in which such a differential equation is derived.[3] Their differential equation relates to a single species for the special case that the populations of all other species are constant. In contrast, our present approach exhibits a number of generalizations and differences that will be detailed below. The most substantial deviation from earlier studies consists in treating representative organisms similar to economic consumers. While Hannon (1976), Tschirhart (2000, 2002) and Finnoff and Tschirhart (2003) model organisms as economic (production) firms, Pethig and Tschirhart (2001) apply the economic concept of congestion, well known from the public goods literature. This concept is well suited for resource competition but appears to be less appropriate for explaining predator-prey relations.

The present paper is organized as follows. Section 2 presents the short-run ecosystem model, derives the short-run ecosystem equilibrium and proves its existence thus assuring

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[3]Eichner and Pethig (2003) also derive differential population equations but their basic unit of analysis are species rather than representative organisms of species.

that our results are not vacuous. At the end of section 2 we perform a comparative static analysis to answer the question as to how the ecosystem equilibria are affected by changes in resource endowments and populations. In section 3 we turn to the growth of populations and derive the differential equations which characterize the predator-prey dynamics. In section 4 we parametrize the model by Cobb-Douglas functions and provide three different numerical specifications yielding more concrete information about the development of the predator-prey system in time. The population dynamics *derived* here turn out to differ significantly from those *assumed* in the standard Lotka-Volterra model.

# 2  The ecosystem in the short term

## 2.1  Organisms as decision makers

Consider an ecosystem of fixed size (or space) in which $m$ species form a one-directional non-circular food chain: Species $m$ feeds on species $m-1$, species $m-1$ feeds on species $m-2$, ..., species 2 feeds on species 1, and species 1 feeds on a resource referred to as 'species 0' in the formal model. Basic units of analysis are the individual organisms of each species. To simplify, all organisms of one and the same species are assumed alike. Hence it suffices to focus on a representative individual of each species $i$, $i = 1, \ldots, m$ which we call organism $i$, for short.

In the short-run period the population $n_i$ of each species $i$ is assumed to be constant. Denote by $x_{i-1}$ organism $i$'s intake of biomass of species $i-1$ (demand) and by $y_i$ organism $i$'s loss (or sacrifice) of own biomass[4] to its predators (supply) during the period under consideration. If organism $i = 1, \ldots, m$ carries out the transaction $(x_{i-1}, y_i)$, its net biomass acquired is

$$b_i = B^i \left( \underset{+}{x_{i-1}}, \underset{-}{y_i} \right), \tag{1}$$

where the function $B^i$ is a concave mapping from $\mathbb{R}_+ \times [0, \bar{y}_i]$ into $\mathbb{R}$. Since organism $i$ transforms the prey biomass $x_{i-1}$ into own biomass, we have $B^i_x > 0$. Moreover, $B^i_{xx} < 0$ reflects decreasing marginal returns. On the other hand, $B^i_y < 0$ because own biomass built up by foraging is conceded to predators. $B^i_{yy} < 0$ is plausible, because growing losses of own biomass have an increasingly serious negative impact on the organism's rate of reproduction. The upper bound $\bar{y}_i$ on the domain of $B^i$ is introduced because the representative organism cannot sustain the loss of own biomass beyond some threshold, say $\bar{y}_i$. More formally,

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[4]For $i = 1$, $x_{i-1}$ is organism 1's intake of the resource.

$B^i$ is assumed to satisfy $B^i(0, y_i) = B^i(x_{i-1}, \bar{y}_i) = -1$ which implies, by assumption, the extinction of species $i$. $B^i$ is a physiological function, similar to that employed by Hannon (1976), Crocker and Tschirhart (1992) and Tschirhart (2000). It accounts for maintenance, respiration and metabolism which depends partly on transactions and is partly independent of transactions.

From an economist's perspective, $B^i$ is a production function since (for $y_i = 0$) the input 'biomass of $i-1$' is transformed into the output 'biomass of $i$'. But rather than making the entire output available to other agents, as economic firms do, only part of it, namely $y_i$, is offered for that purpose. The rest, $B^i(x_{i-1}, y_i)$, is transferred to the next period (to be specified further below).

Another striking similarity between ecosystems and economies is the existence and the role of commodities and transactions. In ecosystems the biomass of each species can be viewed as a commodity and so can resources (nutrients, sunlight, water etc.). The latter are used as primary inputs and the former as intermediate products. Transactions take place via predator-prey interactions which one might also describe as trade. As in economic models, traders can be identified: there are those who demand biomass of other species (predators) and those who supply own biomass (preys). All organisms (other than the top predator; see below) trade own biomass for prey biomass. The total supply of some species' (prey) biomass must equal the total demand for that biomass on the part of predators. Since most ecosystem commodities are in short supply, demanders compete for their use implying that shadow prices are attached to all of these commodities.

Our approach is even more explicit about those prices. We assume that ecosystem transactions are guided and ultimately coordinated by prices in much the same way as transactions are guided by prices in perfectly competitive economies. Denote by $p_i$ the price of the biomass of species $i = 0, 1, \ldots, m$. Organism $i$'s transactions are constrained by the inequality

$$p_i y_i \geq p_{i-1} x_{i-1} \qquad i = 1, \ldots, m. \tag{2}$$

Obviously, (2) is isomorphic to a standard household budget constraint in economic models. The expenditure $p_{i-1} x_{i-1}$ on prey biomass must be financed out of the organism's income earned by supplying own biomass, $p_i y_i$.

The prices $p_i$ and $p_{i-1}$ determine how much own biomass organism $i$ needs to offer to its predators to purchase a given amount $x_{i-1}$ of prey biomass. The budget constraint (2) reflects in a simple but straightforward way what ecologists refer to as organism $i$'s predation risk, the risk of being preyed upon while preying (Lima and Dik 1990). During the process of foraging ("purchasing $x_{i-1}$") organism $i$ exposes itself to its predators, and

the more prey biomass organism $i$ demands the greater is the risk of being devoured by preditors. Although our model is deterministic, (2) captures the notion that at a given state of scarcity (prices) organism $i$ must sacrifice the more own biomass the greater the amount of prey biomass it wants to take in. Moreover, (2) also offers the remarkable and well-fitting interpretation that organism $i$'s cost of some given amount $x_{i-1}$ of prey biomass, in terms of own biomass sacrificed, is the higher, the lower priced is its own biomass relative to that of prey species $i-1$. In other words, $i$'s cost of $x_{i-1}$ rises when prey species $i-1$ becomes scarcer relative to predator species $i$. The scarcer the prey the more time is spent for foraging a given amount of prey biomass and the longer is the exposure to predators. The prices reflect relative scarcities of the species involved and hence (2) expresses the hypothesis that organism $i$'s predation risk depends on both the amount of prey biomass intake, $x_{i-1}$, and the relative abundance of its prey species as measured by the price ratio $p_{i-1}/p_i$.

Obviously there is a complete analogy between (2) and the household's budget constraint. Yet a counter factual implication emerges when $p_i \geq 0$ and $p_{i-1} = 0$. In that case organism $i$ is in the land of Cockaign with respect to its prey and, moreover, it can satisfy (2) without any supply of own biomass. As shown below organism $i$ would then choose $y_i = 0$, in fact, irrespective of its exposure to risk through foraging and irrespective of its own scarcity ($p_i$). To prevent the predation risk from vanishing in situations of abundant prey we will complement (2) by the assumption that there is always a minimum predation risk that increases with the intake of prey biomass independent of prices. The simplest possible formalization of this assumption is

$$y_i \geq c_i x_{i-1} \qquad i = 1, \ldots, m \qquad (3)$$

where $c_i$ is interpreted as the loss (= supply) of $i$'s own biomass per unit of prey biomass caught (= demand), and this loss occurs irrespective of whether $p_{i-1} = 0$ or $p_{i-1} > 0$. Hence $c_i > 0$ expresses the extent to which organism $i$ is exposed to price-independent predation risk. From the organism's point of view $c_i$ is a constant like all prices. But as will be discussed in the next section, $c_i$ will be endogenously determined in equilibrium.

Obviously, members of the highest ranking predator species, $m$, do not face any predation risk since they do not have natural enemies by assumption. In our formal model, members of the highest ranking predator species $m$ require special treatment because at this element the food chain is arbitrarily cut off. Although the model contains no demand for biomass of species $m$ we will extend the constraint (3) to $i = m$ implying $y_m > 0$ whenever $x_{m-1} > 0$.[5] Moreover, we assume $p_m \geq 0$ and constant and interprete $p_m y_m$

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[5]In real ecosystems organisms of the species at the top of the food chain do die, are eaten by the

as organism $m$'s income from "exporting" $y_m$ at "world market price" $p_m$. Intuitively, $c_i$ tends to decrease with increasing $i$ since the higher a species in the food chain the less it is challenged by preditors. Hence $c_m$ will probably be small, $p_m y_m$ will be small and so will be the prey intake $x_{m-1}$. Arguably, this is not a fully satisfactory description of the powerful position of a high ranking predator.[6]

Having specified organism $i$'s constraints we now turn to its decision problem. We assume that all individual organisms behave as if they solve the maximization problem:[7]

$$\max_{(x_{i-1}, y_i)} \quad B^i(x_{i-1}, y_i) \quad \text{s.t.} \quad (2) \text{ and } (3). \tag{4}$$

To our knowledge, the hypothesis of 'as if' maximization in an ecosystem has first been suggested and employed in formal analysis by Hannon (1976) and has since been used in several other studies. For its motivation and rationalization see, e.g., Hirshleifer (1977), Finnoff and Tschirhart (2003) and Tschirhart (2000, 2002). Our approach deviates significantly from previous studies regarding the constraints (2) and (3). As we have outlined above the organism's optimization problem (4) is very similar to the economic household's problem of maximizing utility subject to his or her budget constraint. In analogy, $B^i(\cdot)$ corresponds to the consumer's utility derived from the amount $x_{i-1}$ of a consumer good demanded and the amount $y_i$ of labor supplied. Note, however, that in consumer choice models lower bounds on labor supply such as (3) are unknown and that in the present paper $B^i(\cdot)$ is physical biomass *produced* rather than intangible utility generated in the consumer's mind. Organisms are therefore treated as 'hermaphrodites' in the sense that they are consumers regarding their budget constraint but producers regarding their production of net biomass according to biological (rather than engineering) blueprints.

The solution to the individual optimization problem (4) yields demand and supply functions that will turn out to depend on prices. More specifically, we infer

**Proposition 1.** *(Biomass demand and supply)*
*For given non-negative prices $p_{i-1}$ and $p_i$ and $i = 1, \ldots, m$ the demand and supply of organism $i$ are*

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decomposers and in that sense they too are prey.

[6] An attractive way out is to endow organism $m$ with some extra purchasing power, namely the revenues from selling the resource, $p_0 \bar{y}_0 / n_m$, so that organism $m$'s budget constraint would be given by $(p_0 \bar{y}_0 / n_m) + p_m y_m \geq p_{m-1} x_{m-1}$. With this budget constraint one could assume $p_m \equiv 0$ and $c_m \equiv 0$ to the effect that with $p_0 > 0$ organism $m$ would be able to purchase prey without supplying own biomass. However, to ease the exposition, we will stick to the assumption that (i) $p_m > 0$ and constant and (ii) that organism $m$ cannot dispose of any resource income.

[7] Since $B^i(x_{i-1}, 0) = B^i(x_{i-1}, \bar{y}_i) = -1$ the solution will satisfy $y_i < \bar{y}_i$.

*(i)* $x_{i-1}^* = x_{i-1}^c := \arg\max_{x_{i-1}} B^i\left(x_{i-1}, c_i x_{i-1}\right)$ *and* $y_i^* = c_i x_{i-1}^c$ *for all prices that do not satisfy* $p_{i-1} > p_i c_i > 0$.

*(ii)* $x_{i-1}^* = x_{i-1}^\pi := \arg\max_{x_{i-1}} B^i\left(x_{i-1}, \frac{p_{i-1}}{p_i} x_{i-1}\right)$ *and* $y_i^* = (p_{i-1}/p_i)x_{i-1}^\pi$, *if* $p_{i-1} \geq p_i c_i > 0$.

All propositions are proved in the appendix. According to proposition 1 for any constellation of prices the demand $x_{i-1}^*$ is equal to either $x_{i-1}^c$ or $x_{i-1}^\pi$. In fact, we have $x_{i-1}^* = \min\left[x_{i-1}^c, x_{i-1}^\pi\right]$. To see the reason for this result suppose first that all prices are strictly positive. Then organism $i$ faces the constraint $y_i \geq \pi_{i-1}x_{i-1}$ and $y_i \geq c_i x_{i-1}$ where $\pi_{i-1} := p_{i-1}/p_i$ are the terms of trade. Clearly, the constraint (2) [constraint (3)] is not binding if $\pi_{i-1} < c_i$ $[\pi_{i-1} > c_i]$ since for any $(x_{i-1}, y_i)$ with $x_{i-1} > 0$ satisfying $y_i = c_i x_{i-1}$ $[y_i = \pi_{i-1}x_{i-1}]$ we necessarily get $y_i > \pi_{i-1}x_{i-1}$ $[y_i > c_i x_{i-1}]$. Figure 1 illustrates the consequences for organism $i$'s optimal plan. The straight lines $0\pi_{i-1}^b$, $0c_i$ and $0\pi_{i-1}^a$ are the graphs of the linear functions $y_i = \pi_{i-1}^b x_{i-1}$, $y_i = c_i x_{i-1}$ and $y_i = \pi_{i-1}^a x_{i-1}$, respectively, satisfying $\pi_{i-1}^b > c_i > \pi_{i-1}^a$. If the relative price $\pi_{i-1}^a$ prevails, the organism would like to choose point $A$ in figure 1 but is forced to choose point $B$ since (3) is more restrictive than (2) and hence (3) is the only binding constraint. Conversely, at relative price $\pi_{i-1}^b$, $y_i \geq \pi_{i-1}^b x_{i-1}$ is the binding constraint and consequently the organism is forced to choose point $C$ (rather than $B$).

In terms of predation risk, the interpretation is straightforward. If organism $i$'s prey species $i-1$ is relatively abundant $(\pi_{i-1} \leq c_i)$, $i$'s exposure to its own predators during foraging increases with the amount of prey intake. But when $\pi_{i-1} > c_i$ organism $i$ needs more time to search for (each unit of) prey and hence carries a greater risk of being preyed upon during foraging.

The argument of (2) and (3) being mutually exclusive constraints can be easily extended to cover zero prices. If, for example, $\pi_{i-1} = 0$, the line $y_i = \pi_{i-1}x_{i-1}$ coincides with the abscissa in figure 1. Since $c_i > \pi_{i-1} = 0$, the organism's best choice is the point $B$. In other words, $i$ chooses $x_{i-1}^c$ (point $B$) for any $\pi_{i-1} \in [0, c_i]$, that is, $i$ is indifferent with respect to price changes within that interval. Due to this observation one could take $c_i > 0$ as a lower bound of $\pi_{i-1}$ for all $i = 1, \ldots, m-1$. Note, however, that by definition of $\pi_0 = (p_0/p_1)$, $\pi_1 = (p_1/p_2)$ etc., $\pi_{i-1} \geq c_i$ simultaneously establishes an upper bound on all $\pi_{i-1}$. These bounds constitute additional barriers to the smooth working of the price mechanism creating problems in establishing the existence of equilibrium. This is why we refrain from introducing the constraints $\pi_{i-1} \geq c_i$ for all $i = 1, \ldots, m-1$.

Consider now the case that $x_{i-1}^* = x_{i-1}^\pi = \arg\max_{x_{i-1}} B^i\left(x_{i-1}, \pi_{i-1}x_{i-1}\right)$ and $y_i^* = \pi_{i-1}x_{i-1}^c$. Then the maximum of $B^i(\cdot)$ with respect to $x_{i-1}$ is obviously characterized by
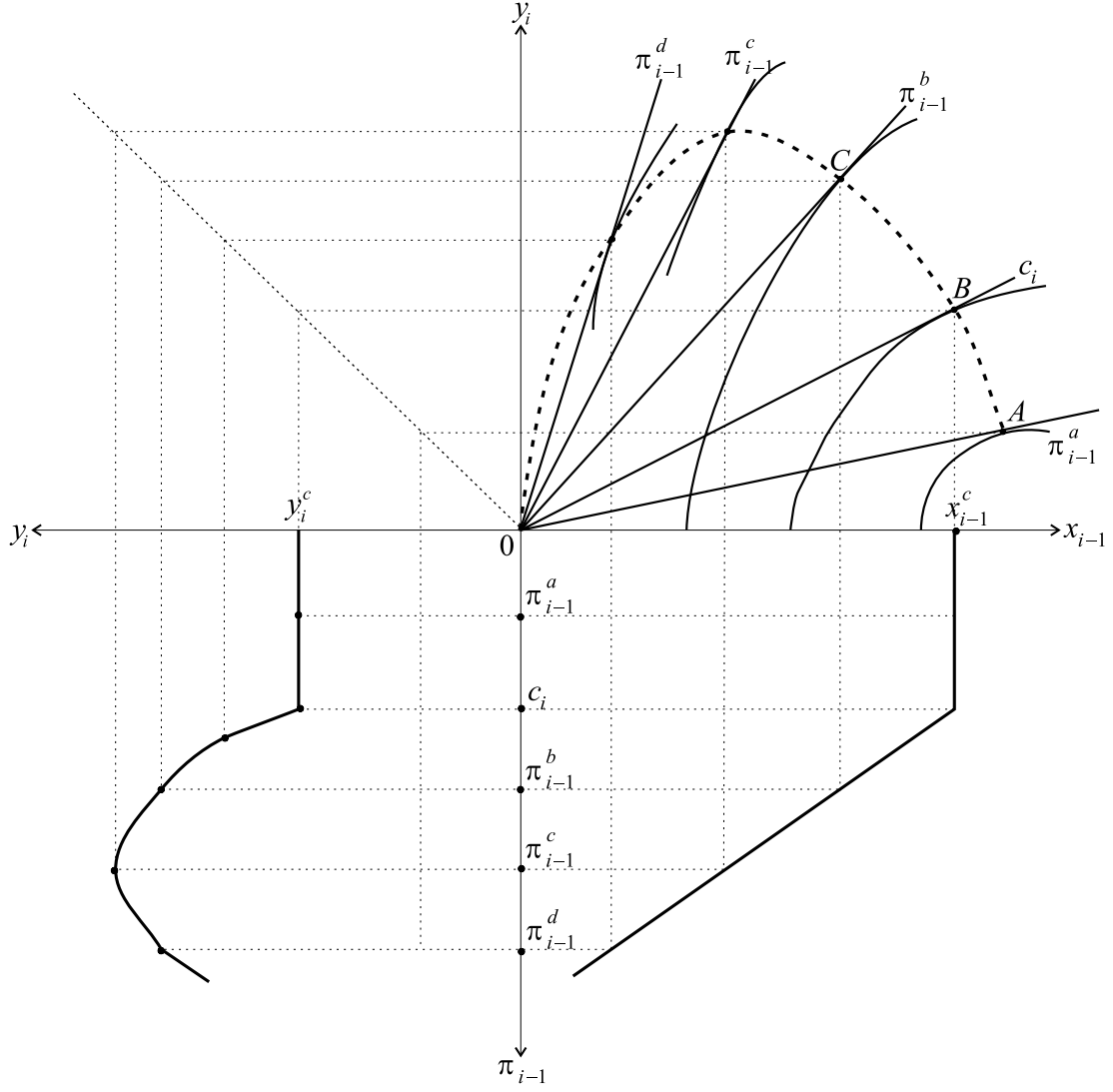
Figure 1: Organism $i$'s optimal demand and supply

the first-order condition

$$-\frac{B_x^i\left(x_{i-1}^*, y_i^*\right)}{B_y^i\left(x_{i-1}^*, y_i^*\right)} = \pi_{i-1} \qquad \text{for } i = 1, \ldots, m.$$

As known from textbook consumer theory this equation requires organism $i$ to expand the intake of prey biomass, $x_{i-1}$, to the point at which $-B_x^i/B_y^i$, the marginal rate of substituting own biomass for prey biomass, equals the (external) rate of exchanging own biomass for each unit of prey biomass. If $x_{i-1}^* = x_{i-1}^c$, we get $\left(-B_x^i/B_y^i\right) = c_i$ with an interpretation analogous to that given above.

## 2.2 Short-run ecosystem equilibrium

So far our focus has been the representative individual organism as a price taker. Now we turn to the coordination of market transactions by suitable (market clearing) prices. Since in the short-run all populations $n_i$ for $i = 1, \ldots, m$ are constant, an ecosystem allocation $(x_0, \ldots, x_{m-1}, \bar{y}_0, y_1, \ldots, y_{m-1})$ is *feasible* if

$$\bar{y}_0 \geq n_1 x_0, \tag{5a}$$

$$n_i y_i = n_{i+1} x_i \qquad \text{for all } i = 1, \ldots, m-1. \tag{5b}$$

The inequality sign in (5a) corresponds to the conventional view in economic equilibrium analysis that an excess supply may be, but an excess demand is not, compatible with equilibrium. This notion fits well for the resource. However, biomass transactions between predators and preys require the equality sign as imposed in (5b), since in that case, an excess supply constitutes an infeasibility. As argued in more detail in Eichner and Pethig (2003), $n_i y_i > n_{i+1} x_i$ implies that each organism $i$ would lose more own biomass than their predators actually consume. This is clearly a disequilibrium feature, since organism $i$ would certainly be eager to reclaim the excess supply of its own biomass. This observation highlights the principal difference between resource constraints in economic models and (5b). In an equilibrium of a competitive economy a market good is in excess supply if and only if its price is zero. No agent is interested in claiming the excess supply since everybody has already come forward with his or her satiation demand. Hence economic goods in (equilibrium) excess supply are free goods, and the excess supply vanishes by virtue of the assumption of free disposal. Yet biomass of prey species always "hurts" the prey and hence cannot be a free good in the sense of economic theory. Neither is free disposal of excess supplies of prey biomass a sensible concept in ecosystem analysis.

Unlike (5b), (5a) is very much in the spirit of economic resource constraints and the resource can rightly be called abundant in case of $\bar{y}_0 > n_1 x_0$. Yet we will show that $p_0 = 0$ is only sufficient but not necessary for this inequality to hold in equilibrium. Having rationalized the equality signs in (5b) it should be added that securing these equality signs will turn out to be a non-trivial issue in establishing an equilibrium. The difficulties stem from the implications of proposition 1 that with demand prices approaching zero finite "satiation demands" are attained for all species' biomass.

To make this point rigorously consider the following

**Equilibrium definition I:** *For any given $\bar{y}_0 > 0$, $p_m > 0$, $n_i > 0$ and $c_i > 0$ for $i = 1, \ldots, m$ an ecosystem allocation of transactions $(x_0^*, \ldots, x_{m-1}^*, y_1^*, \ldots, y_m^*)$ and prices $(p_0, \ldots, p_{m-1})$ is said to constitute a short-run ecosystem equilibrium I, if*

*(i)* $(x_{i-1}^*, y_i^*)$ *solves (4) for all* $i = 1, \ldots, m,$

*(ii) (5a) and (5b) hold.*

**Proposition 2.** *(Failure of existence of equilibrium I)*
*Let* $\bar{y}_0 > 0$, $p_m > 0$, $n_i > 0$ *and* $c_i > 0$ *for* $i = 1, \ldots, m$ *be given. A short-run ecosystem equilibrium I does not exist, in general.*

Proposition 2 is easily proved with the help of figure 2 that illustrates various scenarios for $m = 3$ in which a short-run ecosystem does not exist. Consider first the demand and supply curves in the panels I-IV of figure 2 that are drawn as solid lines. Clearly, the prices $(\pi_0^a, \pi_1^a, \pi_{20}^a)$ and $(\pi_0^b, \pi_1^b, \pi_{20}^b)$ determine a (unique) equilibrium if the resource endowment is $\bar{y}_0^a$ and $\bar{y}_0^b$, respectively. The equilibrium with superscript $a$ (equilibrium $a$, for short) differs from equilibrium $b$ in that the resource is abundant in equilibrium $b$ but scarce in $a$.[8] Suppose now the graph of the aggregate supply function $n_1 Y^1(\pi_0)$ is not given by the solid line in panel II of figure 2 but rather by the dashed line. Then an equilibrium fails to exist in case of either resource endowment, $\bar{y}_0^a$ or $\bar{y}_0^b$, since for $c = a, b$

$$n_1 Y^1(\pi_0^c) > n_2 X^1(\pi_1) \qquad \text{for all } \pi_1 \geq 0.$$

The reason for that 'structural' excess supply is the boundedness (or satiation) of demand $X^1(\pi_1)$ for all $\pi_1 \in [0, c_2]$. Figure 2 illustrates another failure of an equilibrium to exist. As a point of departure consider again the solidly drawn lines and the prices $(\pi_0^b, \pi_1^b, \pi_{20}^b)$. We know that this is an equilibrium scenario. But if the aggregate supply function $n_2 Y^2(\pi_1)$ in panel IV (solid line) is replaced by the dashed line we end up with an excess supply on the market for biomass of species 2. Again, an equilibrium cannot be established.

As drawn in figure 2 it is the predation risk constraint (3) that is responsible for the bounds on demand. But in general, demand satiation (at zero price) is of course implied by many functional forms $B^i$ even if (3) would not apply. Moreover, demand satiation must be considered a realistic feature in ecosystem analysis, since all organisms' capacity of taking in and digest food is limited in the short-run period (which applies to humans as well). Therefore demand satiation combined with the equality (!) (5b) poses a persistent existence problem. Even if an equilibrium can be shown to exist in a given period, it may not exist in some future period depending on how species populations grow or shrink.

These considerations suggest that in order to provide a general proof of equilibrium without abandoning the constraints (3) entirely one needs two ingredients. First, in the

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[8]We note in passing that in figure 1 we assigned $\pi_0^b = c_1$, but all prices $(\pi_0^B, \pi_1^b, \pi_{20}^b)$ with $\pi_0^B \in [0, c_1]$ constitute an equilibrium, too, each of which exhibiting the same equilibrium allocation.
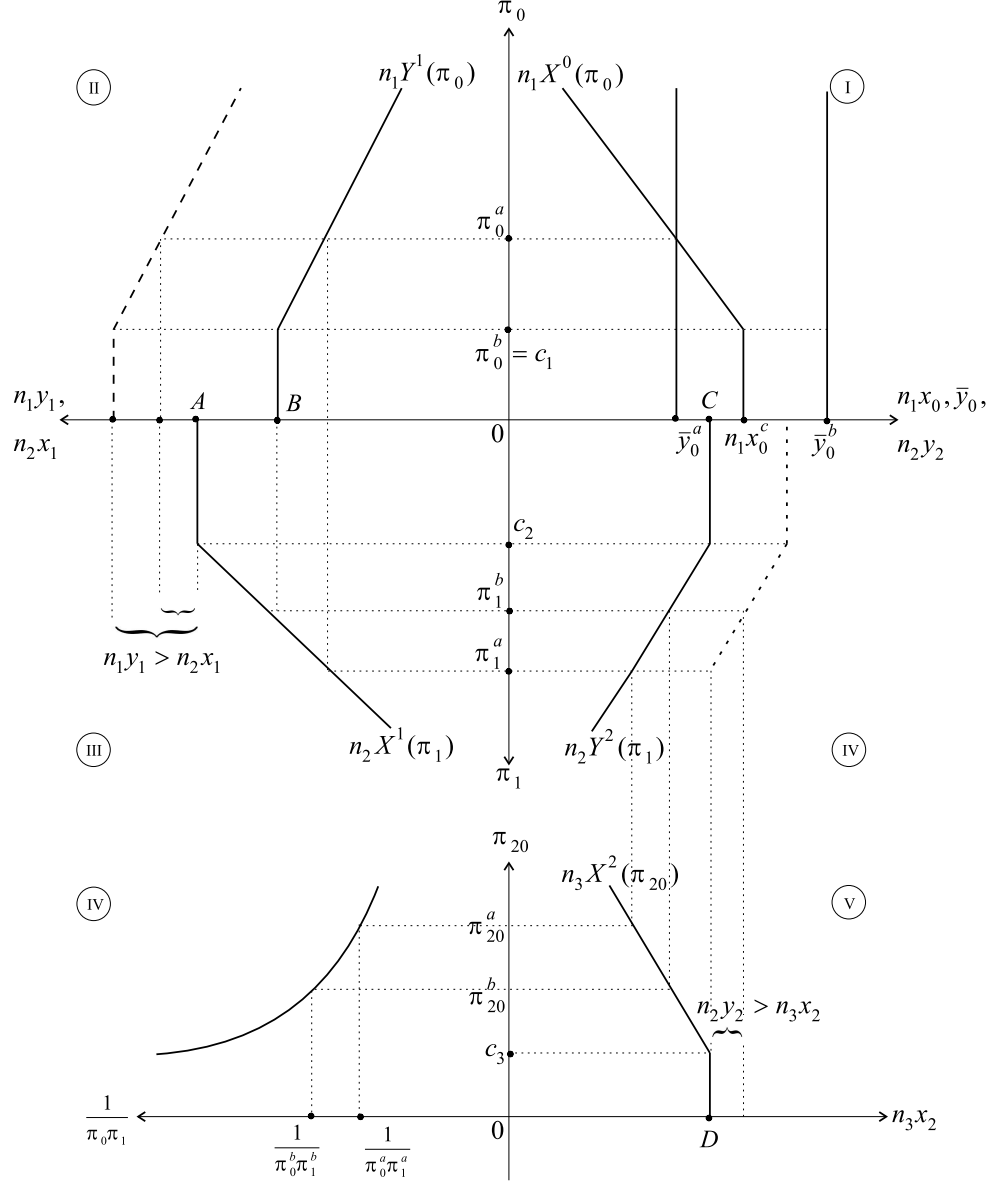
Figure 2: The existence problem

absence of (3) demand satiation at prices tending to zero must be ruled out[9], and second, though positive $c_i$ render demands bounded at low prices, the parameters $c_i$ must be determined endogenously to allow for more flexibility of demands and supplies at low prices.

To make progress, we base our subsequent analysis on net biomass functions yielding demand and supply functions with the following properties:

**Assumption 1:** *Denote by $\tilde{X}^{i-1}$ and $\tilde{Y}^i$ the demand and supply function of organism i in the absence of constraint (3).*

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[9]A non-satiation assumption of this type is needed in existence proofs in all Debreu-type general equilibrium models (Debreu 1959).

(i) $\tilde{X}_\pi^{i-1} < 0$ and $\lim_{\pi_{i-1} \to 0} \tilde{X}^{i-1}(\pi_{i-1}) = \infty$ for $i = 1, \ldots, m$.

(ii) There is $\breve{\pi}_{i-1} \geq 0$ such that $\tilde{Y}_\pi^i(\pi_{i-1}) \leq 0$ for all $\pi_{i-1} \geq \breve{\pi}_{i-1}$.

Assumption 1 is a mild restriction only. It is satisfied, e.g., by net biomass functions of Cobb-Douglas type. The signs of the partials of the functions $\tilde{X}^{i-1}$ and $\tilde{Y}^i$ depend on the signs of the income and substitution effect. Suppose the income effect is positive with respect to $x_{i-1}$ and negative with respect to $y_i$ (which would be considered the typical case in consumer theory). It follows then unambiguously that $\tilde{X}_\pi^{i-1} < 0$. $\tilde{Y}_\pi^i$ is still indeterminate in sign because the negative income effect is accompanied by a positive substitution effect. Following again the prevailing proposition in consumer theory that the labor supply curve is upward sloping we assume here that the negative income effect does not overcompensate the positive substitution effect. Hence $\tilde{Y}_\pi^i \leq 0$.

Prior to checking whether the existence problem of proposition 2 can be overcome by Assumption 1 and the parameters $c_i$ it is necessary to modify the equilibrium definition as follows:

**Equilibrium definition II:**     For any given $\bar{y}_0 > 0$, $p_m > 0$ and $n_i > 0$ for $i = 1, \ldots, m$ an ecosystem allocation of transactions $(x_0^*, \ldots, x_{m-1}^*, y_1^*, \ldots, y_m^*)$, prices $(p_0, \ldots, p_{m-1})$ and parameters $(c_1, \ldots, c_m)$ is said to constitute a short-run ecosystem equilibrium II, if

(i) $(x_{i-1}^*, y_i^*)$ solves (4) for all $i = 1, \ldots, m$,

(ii) (5a) and (5b) hold.

**Proposition 3.**     (Existence and properties of equilibrium II)
Let $\bar{y}_0 > 0$, $c_1 > 0$, $p_m > 0$ and $n_i > 0$ for $i = 1, \ldots, m$ be given and suppose that Assumption 1 holds.

(i) There exists an ecosystem equilibrium II.

(ii) In equilibrium the resource is abundant if and only if $n_1 < \bar{y}_0/X^1(c_1)$.

(iii) If the resource is abundant in an equilibrium then all species are abundant in the sense that the price vector $(p_0 = 0, p_1 = 0, \ldots, p_{m-1} = 0)$ along with the cost parameters[10] $c_{i+1} = \hat{X}^i \left[ \dfrac{c_i n_i}{n_{i+1}} X^{i-1}(c_i) \right]$ for $i = 1, \ldots, m-1$ constitute an equilibrium.

(iv) If the resource is not abundant in an equilibrium all species are scarce in the sense that all equilibrium prices are positive.

----

[10]$\hat{X}^i$ denotes the inverse of the demand function $X^i(c_{i+1})$. For more details we refer to the proof of proposition 3 in the Appendix.

As the proof of proposition 3 in the Appendix shows the parameters $c_i$ are endogenously chosen in such a way that in figure 2 the points $A$ and $B$ coincide and the line segment $0C$ becomes equal to $0D$. Drawing an appropriately modified diagram, one can easily check that under these conditions (and with Assumption 1) the existence of an equilibrium is secured. It turns out that depending on the abundance or scarcity of the resource the entire ecosystem is either abundant (proposition 3 iii) or scarce (proposition 3 iv). Scarcity of the resource and the species is reflected in all relative equilibrium prices being strictly positive (proposition 3 iv). On the other hand, abundance can be associated with all prices being zero (proposition 3 iii). It is important to note, however, that arbitrary prices $\pi_i \in ]0, c_{i+1}]$ for $i = 0, 1, \ldots, m-1$ are also compatible with an equilibrium of an abundant ecosystem. So long as the resource is abundant, prices do not guide the ecosystem allocation.

## 2.3   Comparative statics of short-run ecosystem equilibria

In this subsection we explore how ecosystem equilibria are affected by changes in environmental parameters. To be concrete, we restrict our attention to an ecosystem in which the resource is scarce, and we suppose that Assumption 1, i.e.

$$x_{i-1} = \tilde{X}^{i-1}\left(\underset{-}{\pi_{i-1}}\right) \quad \text{and} \quad y_i = \tilde{Y}^i\left(\underset{-,0}{\pi_{i-1}}\right) \quad i = 1, \ldots, m, \tag{6}$$

is satisfied.

It is easy to see that the system of equations (5a) and (5b) can be solved buttom up: $\bar{y}_0 = x_0^*$ determines $\pi_0^*$ and $y_1^*$, $y_1^* = x_1^*$ implies $\pi_1^*$ and gives us $y_2^*$, and finally $y_2^* = x_2^*$ is attained for $\pi_2 = \pi_2^*$. The observation that the equilibrium can be determined stepwise from species 0 to species $m$ is clearly due to our modeling the ecosystem as a unidirectional food chain whose principal attribute is dependence rather than interdependence. As a consequence, shocks (i.e. parameter changes) in this ecosystem induce repercussions bottom up but not top down. To make this feature more precise and to show, at the same time, the richness in implications of our model of short-run ecosystem equilibrium we now proceed with a comparative static analysis. Without loss of generality we simplify the exposition by setting[11] $m = 3$ and hence we start out with an initial short-run ecosystem equilibrium

---

[11] In unidirectional food chains three types of species need to be distinguished: the species 0 (buttom), the species $m$ (top) and all other species in between. All species $i$ between are clearly alike in the sense that they prey on species $i-1$ and are preyed upon by species $i+1$. In case of $m = 3$ species 2 is the only non-boundary species but it is clearly representative for all intermediate species in food chains longer than $m = 3$.

that is fully characterized by the equations

$$\bar{y}_0 = n_1 x_0, \quad n_1 y_1 = n_2 x_1, \quad n_2 y_2 = n_3 x_2,$$
$$x_{i-1} = \tilde{X}^{i-1}(\pi_{i-1}) \quad \text{and} \quad y_i = \tilde{Y}^i(\pi_{i-1}) \quad i = 1, 2, 3. \tag{7}$$

We now introduce parametric changes (shocks), one at a time, in the parameters $\bar{y}_0$, $n_1$, $n_2$ and $n_3$ and determine the changes induced in the endogenous variables $\pi_0$, $\pi_1$, $\pi_2$, $x_0$, $x_1$, $x_2$, $y_1$, $y_2$, $y_3$, $b_1$, $b_2$ and $b_3$. As shown in the appendix, total differentiation of the set of equations (7) yields the results summarized in table I where "hats" above letters denote relative changes (e.g. $\hat{x} = dx/x$). The signs in brackets indicate the special case $\tilde{Y}^i_\pi = 0$.

| | $\hat{\pi}_0$ | $\hat{\pi}_1$ | $\hat{\pi}_2$ | $\hat{x}_0$ | $\hat{y}_1$ | $\hat{x}_1$ | $\hat{y}_2$ | $\hat{x}_2$ | $\hat{y}_3$ | $\hat{b}_1$ | $\hat{b}_2$ | $\hat{b}_3$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $\hat{\bar{y}}_0 > 0$ | − | − | − | + | + | + | + | + | + | ?, (+) | ?, (0) | ?, (0) |
| $\hat{n}_1 > 0$ | + | ?, (−) | ?, (0) | − | − | ?, (+) | ?, (0) | ?, (0) | ?, (0) | ?, (−) | ?, (+) | ?, (0) |
| $\hat{n}_2 > 0$ | 0 | + | ?, (0) | 0 | 0 | − | − | ?, (+) | ?, (0) | 0 | ?, (−) | ?, (+) |
| $\hat{n}_3 > 0$ | 0 | 0 | + | 0 | 0 | 0 | 0 | − | − | 0 | 0 | ?, (−) |

Table I: Comparative statics of the short-run ecosystem equilibrium

Leaving out some details and special features of table I the principal results of the exercise in comparative statics are:

(i) If the resource endowment of the ecosystem (alias the 'supply of biomass of species 0') increases, then all species' terms of trade improve[12] and all market transactions expand.

(ii) If the population of species $i$ increases, then organism $i$

- faces worse terms of trade, while the other species' terms of trade tend to be non-deteriorating;

- reduces its market transactions;

- reduces its offspring, while the offspring of the other species tend to be non-decreasing.

(iii) If for $i = 2, 3$ species $i$ experiences a change in its population, species $j < i$ is not at all affected by this change: its terms of trade, its transactions and its net biomass remain unchanged.

---

[12]Observe that $\pi_{i-1} = p_{i-1}/p_i < 0$ implies that species $i$ is able to purchase more biomass of prey species $i - 1$.

The last observation (iii) is intriguing, if not counterintuitive, but only to the extent that we let our intuition rely on partial equilibrium arguments. To see that, consider an equilibrium of the market for biomass of species 2 given by

$$n_3 \tilde{X}^2 \left( \underset{-}{p_2}, \underset{+}{p_3} \right) = n_2 \tilde{Y}^2 \left( \underset{+}{p_2}, \underset{-}{p_1} \right),$$ (8)

where $p_1$, $p_2$ and $p_3$ are assumed to be general equilibrium prices. Suppose now, $n_3$ is slightly increased to $n_3' > n_3$ while everything else is kept constant except the price $p_2$. Clearly, the new market equilibrium is then characterized by an increase in $p_2$ and an increase in both $n_2 y_2$ and $n_3' x_2$ implying that the predator species 3 does have an impact on species 2. But this conclusion depends on our partial analysis assumption of keeping $p_1$ and $p_3$ constant. Yet our general equilibrium analysis shows that the market prices change as well so that the new equilibrium on the market under consideration is reached by keeping $\pi_1 = p_1/p_2$ unchanged and by an increase in $\pi_3 = p_2/p_3$ which reduces $x_2$ to $x_2'$ such that $n_3 x_2 = n_3' x_2'$.

# 3  Population dynamics

## 3.1  Some general observations

At the end of the short-run period, each organism acquired a positive or negative amount of net biomass $B^i \left[ X^{i-1}(n), Y^i(n) \right]$ where $n$ is the vector of populations. If positive, the net biomass generated by the representative organism can be identified as offspring. If negative, the net biomass indicates the organism's chance to survive the period. We normalize each organism as consisting of one unit of (own) biomass and can therefore write

$$\dot{n}_i = \frac{dn_i}{dt} = n_i B^i \left[ X^{i-1}(n), Y^i(n) \right] \qquad \text{for } i = 1, \dots, m.$$ (9)

It is interesting to further specify the differential equations of population growth. Some general useful insight is provided by

**Proposition 4.** *(Population growth)*

*(i) If the resource is abundant, then the population growth takes the functional form*

$$
\begin{aligned}
\dot{n}_1 &= n_1 \bar{e}, \\
\dot{n}_2 &= n_2 E^2 \left( n_1, n_2 \right), \\
&\vdots \qquad \vdots \\
\dot{n}_i &= n_i E^i \left( n_1, n_2, \dots, n_i \right), \\
&\vdots \qquad \vdots \\
\dot{n}_m &= n_m E^m \left( n_1, n_2, \dots, n_{m-1}, n_m \right),
\end{aligned}
$$ (10)

*where $\bar{e}$ is a constant and $E^i : \mathbb{R}_+^i \longrightarrow \mathbb{R}$.*

*(ii) If the resource is scarce, then the population growth takes the functional form*

$$
\begin{aligned}
\dot{n}_1 &= n_1 F^1 (n_1), \\
\dot{n}_2 &= n_2 F^2 (n_1, n_2), \\
&\vdots \qquad \vdots \\
\dot{n}_i &= n_i F^i (n_1, n_2, \ldots, n_i), \\
&\vdots \qquad \vdots \\
\dot{n}_m &= n_m F^m (n_1, n_2, \ldots, n_{m-1}, n_m).
\end{aligned}
\tag{11}
$$

*where $F^i : \mathbb{R}_+^i \longrightarrow \mathbb{R}$.*

The functional form of the population growth reflects our modelling of the ecosystem as a unidirectional food chain. The population growth of species $i$ is affected by all populations of species $j$ with $j < i$, but it is independent of all populations of species $k$ with $k > i$.

## 3.2   Analytical population dynamics (Cobb-Douglas)

To obtain additional information on the characteristics of population growth we proceed by introducing a parametric net biomass function, namely the Cobb-Douglas function. Our aim is rather to clarify the potential of our approach as compared to the models of the Verhulst-Pearl type (growth of a single species) and of the Lotka-Volterra type (growth in a predator-prey context). To further simplify we restrict our attention to food chains consisting of a resource and three species.

Consider now the net biomass function

$$
B^i (x_{i-1}, y_i) = x_{i-1}^{\alpha_i} \cdot (\bar{y}_i - y_i)^{\beta_i} - \gamma_i,
\tag{12}
$$

where $0 < \alpha_i < 1$, $0 < \beta_i < 1$ and $\gamma_i > 0$. To investigate how the ecosystem develops over time, it is convenient to start with an abundant resource to see if and how the ecosystem becomes crowded. Then according to proposition 1 (i) biomass demands and supplies are given by

$$
x_{i-1} = \frac{\alpha_i \bar{y}_i}{(\alpha_i + \beta_i) c_i} \quad \text{and} \quad y_i = \frac{\alpha_i \bar{y}_i}{\alpha_i + \beta_i} \quad i = 1, 2, 3.
\tag{13}
$$

Equilibrating demand and supply for biomass of species 1 and 2 yields parameters $(c_2, c_3)$ satisfying

$$
c_2 = \frac{n_2 \alpha_2 (\alpha_1 + \beta_1) \bar{y}_2}{n_1 \alpha_1 (\alpha_2 + \beta_2) \bar{y}_1} \quad \text{and} \quad c_3 = \frac{n_3 \alpha_3 (\alpha_2 + \beta_2) \bar{y}_3}{n_2 \alpha_2 (\alpha_3 + \beta_3) \bar{y}_2}.
\tag{14}
$$

The associated equilibrium demands and supplies are:

$$x_0 = \frac{\alpha_1 \bar{y}_1}{(\alpha_1 + \beta_1)c_1}, \qquad y_1 = \frac{\alpha_1 \bar{y}_1}{\alpha_1 + \beta_1}, \tag{15a}$$

$$x_1 = \frac{n_1 \alpha_1 \bar{y}_1}{n_2(\alpha_1 + \beta_1)}, \qquad y_2 = \frac{\alpha_2 \bar{y}_2}{\alpha_2 + \beta_2}, \tag{15b}$$

$$x_2 = \frac{n_2 \alpha_2 \bar{y}_2}{n_3(\alpha_2 + \beta_2)}, \qquad y_3 = \frac{\alpha_3 \bar{y}_3}{\alpha_3 + \beta_3}. \tag{15c}$$

Combining (15), (12) and (9) yields the differential equations of population growth

$$\dot{n}_1 = n_1 \left[ \mu_0^{\alpha_1} - \gamma_1 \right], \tag{16a}$$

$$\dot{n}_2 = n_2 \left[ \left( \frac{n_1}{n_2} \mu_2 \right)^{\alpha_2} - \gamma_2 \right], \tag{16b}$$

$$\dot{n}_3 = n_3 \left[ \left( \frac{n_2}{n_3} \mu_3 \right)^{\alpha_3} - \gamma_3 \right], \tag{16c}$$

where $\mu_0 := \frac{\alpha_1 \bar{y}_1}{(\alpha_1+\beta_1)c_1} \cdot \left( \frac{\beta_1 \bar{y}_1}{\alpha_1+\beta_1} \right)^{\frac{\beta_1}{\alpha_1}}$, $\mu_2 := \frac{\alpha_1 \bar{y}_1}{\alpha_1+\beta_1} \cdot \left( \frac{\beta_2 \bar{y}_2}{\alpha_2+\beta_2} \right)^{\frac{\beta_2}{\alpha_2}}$, $\mu_3 := \frac{\alpha_2 \bar{y}_2}{\alpha_2+\beta_2} \cdot \left( \frac{\beta_3 \bar{y}_3}{\alpha_3+\beta_3} \right)^{\frac{\beta_3}{\alpha_3}}$.

Suppose now $n_1 = \bar{y}_0/x_0 = (\alpha_1 + \beta_1)c_1\bar{y}_0/(\alpha_1\bar{y}_1)$ is reached and the resource gets scarce. Then ecosystem prices are binding and according to proposition 1 (ii) biomass demands and supplies are now given by:

$$x_{i-1} = \frac{\alpha_i \bar{y}_i}{(\alpha_i + \beta_i)\pi_{i-1}} \quad \text{and} \quad y_i = \frac{\alpha_i \bar{y}_i}{\alpha_i + \beta_i} \quad i = 1, 2, 3. \tag{17}$$

A general short-run equilibrium of the ecosystem is attained at strictly positive prices $(p_0, p_1, p_2)$ satisfying

$$\pi_0 = \frac{n_1 \alpha_1 \bar{y}_1}{(\alpha_1 + \beta_1)\bar{y}_0}, \quad \pi_1 = \frac{n_2 \alpha_2 (\alpha_1 + \beta_1)\bar{y}_2}{n_1 \alpha_1 (\alpha_2 + \beta_2)\bar{y}_1} \quad \text{and} \quad \pi_2 = \frac{n_3 \alpha_3 (\alpha_2 + \beta_2)\bar{y}_3}{n_2 \alpha_2 (\alpha_3 + \beta_3)\bar{y}_2}. \tag{18}$$

The associated equilibrium demands and supplies are

$$x_0 = \frac{\bar{y}_0}{n_1}, \qquad y_1 = \frac{\alpha_1 \bar{y}_1}{\alpha_1 + \beta_1}, \tag{19a}$$

$$x_1 = \frac{n_1 \alpha_1 \bar{y}_1}{n_2(\alpha_1 + \beta_1)}, \qquad y_2 = \frac{\alpha_2 \bar{y}_2}{\alpha_2 + \beta_2}, \tag{19b}$$

$$x_2 = \frac{n_2 \alpha_2 \bar{y}_2}{n_3(\alpha_2 + \beta_2)}, \qquad y_3 = \frac{\alpha_3 \bar{y}_3}{\alpha_3 + \beta_3}, \tag{19c}$$

and the populations grow according to the differential equations[13] (16b), (16c) and

$$\dot{n}_1 = n_1 \cdot \left[ \left( \frac{\mu_1}{n_1} \right)^{\alpha_1} - \gamma_1 \right] \tag{20}$$

where $\mu_1 := \bar{y}_0 \left( \frac{\beta_1 \bar{y}_1}{\alpha_1+\beta_1} \right)^{\frac{\beta_1}{\alpha_1}}$.

---

[13]It should be noted that $c_2 = \pi_1$, $c_3 = \pi_2$, (15b) coincides with (19b) and (15c) is equivalent to (19c). These correspondences are caused by the constant supply functions, formally $\bar{Y}_c^i = Y_\pi^i = 0$ for all $i$.

(16a) and (20), combined with (16b) and (16c), completely describe the dynamics of the three-species food chain. To compare these differential equations to the standard Lotka-Volterra population equations we ignore species 1 and rewrite (16b) and (16c) as

$$\dot{n}_i = \mu_i n_{i-1}^{\alpha_i} n_i^{1-\alpha_i} - \gamma_i n_i \qquad i = 2, 3. \tag{21}$$

The corresponding Lotka-Volterra equations would read[14]

$$\dot{n}_2 = \delta_{21} n_2 - \delta_{22} n_2 n_3 \qquad \text{and} \qquad \dot{n}_3 = \delta_{31} n_2 n_3 - \delta_{32} n_3, \tag{22}$$

where the $\delta$'s are positive parameters. The comparison of (21) and (22) readily reveals a substantial structural asymmetry between both models. In the present model, the population growth of the two species is structurally the same and qualitatively similar to the predator species 3's growth in the Lotka-Volterra model. But the growth of the prey species 2 differs significantly in both models.[15] We therefore conclude that we have suggested here an explanation of predator-prey population dynamics that is incompatible - and hence competes - with the standard Lotka-Volterra approach. It remains to be seen in future empirical work how well our approach describes developments in real-world ecosystems.

Several interesting features[16] of the growth dynamics can be derived from (16b), (16c) and (20). Consider first (20). Differentiation with respect to $n_1$ yields

$$\frac{\mathrm{d}\dot{n}_1}{\mathrm{d}n_1} = \mu_1^{\alpha_1} \cdot (1 - \alpha_1) \cdot n_1^{-\alpha_1} - \gamma_1 \qquad \text{and} \qquad \frac{\mathrm{d}^2 \dot{n}_1}{\mathrm{d}n_1^2} = -\mu_1^{\alpha_1} \cdot \alpha_1 \cdot (1 - \alpha_1) \cdot n_1^{-(1+\alpha_1)} < 0.$$

Clearly, $\dot{n}_1$ from (20) is strictly concave in $n_1$. Hence we calculate

$$\hat{n}_1 := \mu_1 \cdot \left( \frac{1 - \alpha_1}{\gamma_1} \right)^{\frac{1}{\alpha_1}} \qquad \text{and} \qquad n_1^* := \mu_1 \cdot \left( \frac{1}{\gamma_1} \right)^{\frac{1}{\alpha_1}}$$

where $\hat{n}_1 = \arg\max_{n_1} \dot{n}_1$ and where $n_1^*$ solves (20) for $\dot{n}_1 = 0$, i.e. the population of species 1 reaches a long-run equilibrium (steady state). Recall, however, that (20) is only valid for $\bar{y}_0 \geq n_1 x_0$ which is equivalent to $n_1 \geq (\alpha_1 + \beta_1) c_1 \bar{y}_0 / (\alpha_1 \bar{y}_1)$. To determine how $\dot{n}_1$ depends on $n_1$ over the entire domain of non-negative $n_1$ we need to combine (16a) and (20), as illustrated in figure 3. The $\dot{n}_1$-function is inversely u-shaped with a linear segment over the interval $[0, (\alpha_1 + \beta_1) c_1 \bar{y}_0 / (\alpha_1 \bar{y}_1)]$. This linear segment notwithstanding the growth curve in

---

[14] A textbook treatment of the Lotka-Volterra model can be found in Murray (1993).

[15] The first equation in (22) is implausible for $n_3$ since unbounded population growth is infeasible. Note also that the parameters $\delta_{21}$, $\delta_{22}$, $\delta_{31}$ and $\delta_{32}$ are ad hoc whereas the parameters $\alpha_i$, $\gamma_i$ and $\mu_i$ ($i = 2,3$) describe testable properties of the individual organisms (with $\mu_i$ being composed of various other parameters).

[16] A rigorous characterization of the time path and the conditions for convergence are beyond the scope of the present paper.

figure 3 is essentially the Verhulst-Pearl growth curve giving rise to a logistic population curve. Note, however that the Verhulst-Pearl curve is an ad hoc approach for a single isolated species. In contrast, here the equations (16a) and (20) are derived rather than assumed in a three-species model.[17]
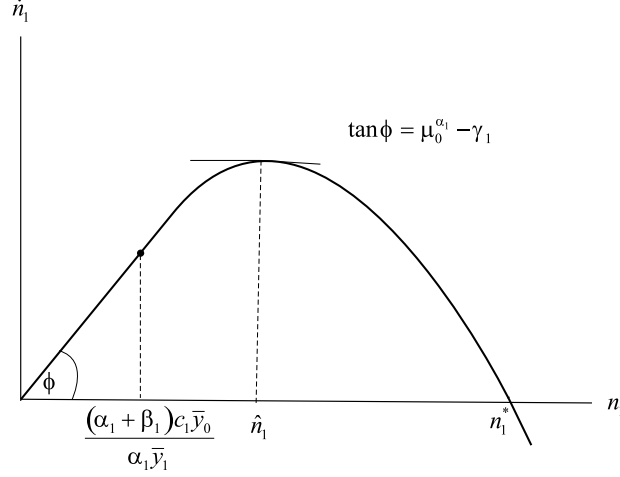


Figure 3: Population growth of species 1

With $n_1$ set constant in (16b) $\dot{n}_2$ can be readily seen to depend on $n_2$ in a similar way as $\dot{n}_1$ depends on $n_1$. The same holds for $\dot{n}_3$ when $n_2$ is assumed to be constant. Differentiation of (16b) and (16c), respectively, yields

$$
\begin{aligned}
\frac{\partial \dot{n}_i}{\partial n_i} &= (n_{i-1}\mu_i)^{\alpha_i} \cdot (1-\alpha_i) \cdot n_i^{-\alpha_i} - \gamma_i \qquad i = 2,3, \\
\frac{\partial^2 \dot{n}_i}{\partial n_i^2} &= -(n_{i-1}\mu_i)^{\rho_i} \cdot \alpha_i \cdot (1-\alpha_i) \cdot n_i^{-(1+\alpha_i)} < 0 \qquad i = 2,3,
\end{aligned}
$$

which shows that $\dot{n}_i$ is a strictly concave function of $n_i$. For any given $n_{i-1}$ the maximum is

$$
\hat{n}_i\left(n_{i-1}\right) = n_{i-1} \cdot \mu_i \cdot \left(\frac{1-\alpha_i}{\gamma_i}\right)^{\frac{1}{\alpha_i}} \qquad i = 2,3,
$$

and the long-run equilibrium of species 2 and 3 $(\dot{n}_2 = \dot{n}_3 = 0)$ is reached at

$$
n_i^*\left(n_{i-1}\right) = n_{i-1} \cdot \mu_i \cdot \left(\frac{1}{\gamma_i}\right)^{\frac{1}{\alpha_i}} \qquad i = 2,3.
$$

Clearly, the carrying capacity of species $i$ is proportional to the population of species $i-1$.

---

[17]Pethig and Tschirhart (2001) also derive a population growth curve of a single species shaped exactly as that in figure 3. But in their one-species model the allocation is driven by congestion rather than by prices.

## 3.3 Numerical population dynamics (Cobb-Douglas)

Now we turn to three numerical examples which are calculated with the help of the computer program Mathematica.[18] In these examples the parameters are chosen as follows: $c_1 = 1$, $\bar{y}_0 = 20000000$, $\bar{y}_1 = 100$, $\bar{y}_2 = 10$, $\bar{y}_3 = 1$, $\alpha_i = \beta_i = 0.5$ for all $i = 1, 2, 3$, $\gamma_1 = 10$, $\gamma_2 = 17$ and $\gamma_3 = 2$.

**Example 1:** We set the initial population stocks at $n_1(0) = 100$, $n_2(0) = 10$ and $n_3(0) = 1$. Since $n_1 < \frac{(\alpha_1 + \beta_1)c_1 \bar{y}_0}{\alpha_1 \bar{y}_1} = 400000$ the resource is abundant and the population growth is given by

$$\dot{n}_1 = 40n_1, \tag{23a}$$

$$\dot{n}_2 = n_2 \left[ 15.8114 \left( \frac{n_1}{n_2} \right)^{0.5} - 17 \right], \tag{23b}$$

$$\dot{n}_3 = n_3 \left[ 1.58114 \left( \frac{n_2}{n_3} \right)^{0.5} - 2 \right]. \tag{23c}$$

The left panels of figures 4-6 illustrate the growth during the time interval $[0, 0.20735]$. Initially all populations grow slowly and then we observe an approximately exponential rapid growth. From $t = 0$ to $\tilde{t} = 0.20735$ the population of species 1 has increased from 100 to 400000. Since $n_1 = 400000$ is a boundary point of the regime at which the resource is abundant, prices take over the control of ecosystem allocation shifting the ecosystem from abundance to scarcity. It is interesting to observe that in our example 1 the populations of species 1 and 2 grow faster than the population of species 3. At $t = \tilde{t}$ we have:

$$n_1\left(\tilde{t}\right) = 400000 \ > \ n_2\left(\tilde{t}\right) = 30802.1 \ > \ n_3\left(\tilde{t}\right) = 54.1504.$$
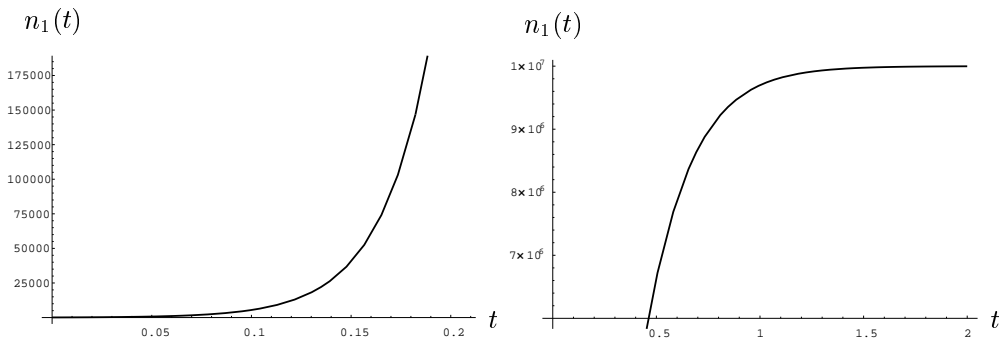


Figure 4: Population growth of species 1 in example 1

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[18]The program for simulations is available from the authors upon request.
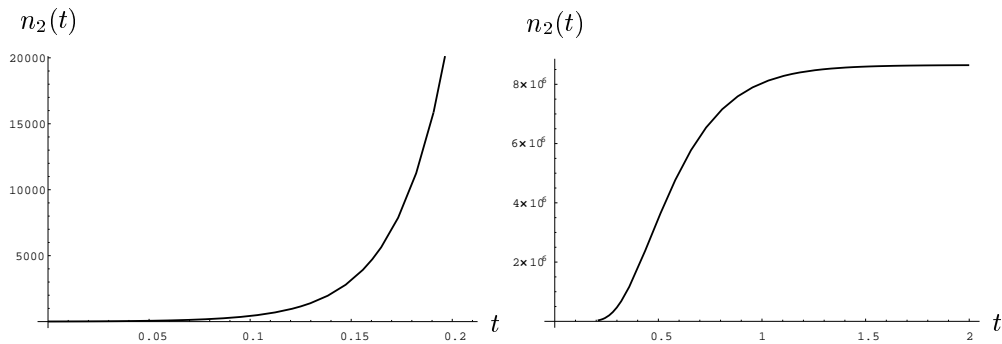
Figure 5: Population growth of species 2 in example 1
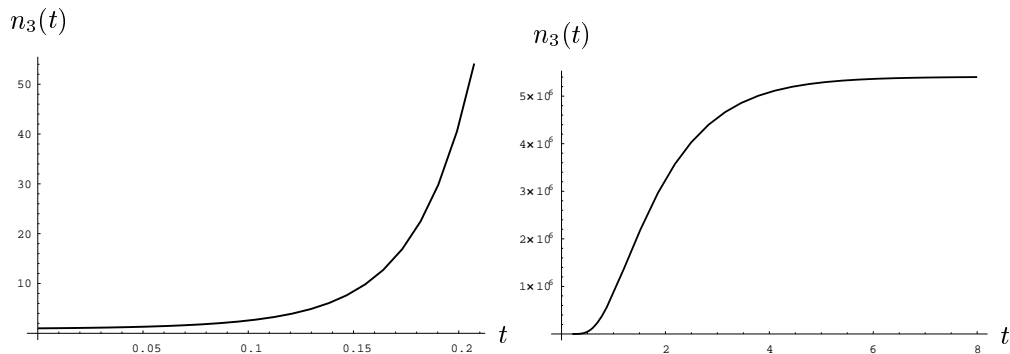


Figure 6: Population growth of species 3 in example 1

When the ecosystem is scarce, the population of species 1 grows according to the differential equation

$$\dot{n}_1 = n_1 \left[ 31622.8 \left( \frac{1}{n_1} \right)^{0.5} - 10 \right]. \tag{24}$$

For the other species the differential equations (23b) and (23c) still apply.

The right panels of figures 4 through 6 illustrate the continuing growth of the populations of all species in the state of scarcity and they show the populations converging to their steady state levels

$$n_1^* = 1 \cdot 10^7 \quad > \quad n_2^* = 8.65052 \cdot 10^6 \quad > \quad n_3^* = 5.40657 \cdot 10^6.$$

Conceptually the left and right panels of figure 4 are segments of a single diagram and the same is true for the two diagrams contained in figures 5 and 6. The reason for presenting that single diagram in two parts is to employ different scales on both axes for improving the illustration of the single diagram's curvature. But even without putting the parts together it is easy to see that our growth curves in example 1 are logistic curves quite similar to the curve implied by the generalized Verhulst-Pearl equation in a one-species-model (Rosen 1984) and all curves together represent the case of coexistence.
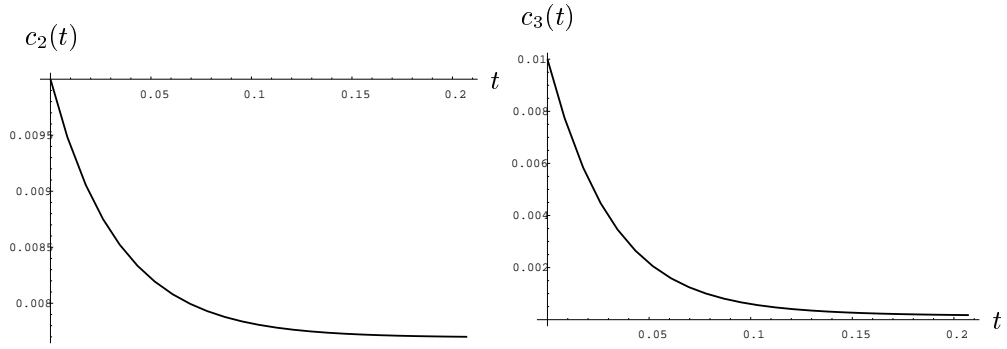
Figure 7: Changes of the parameters $c_2$ and $c_3$
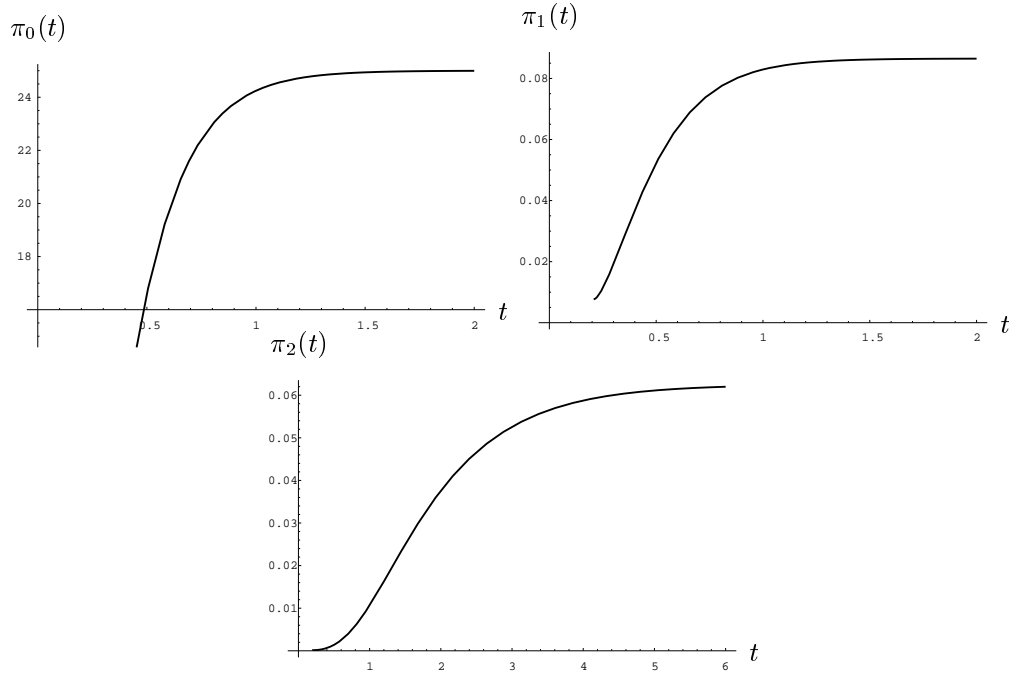


Figure 8: Changes of the terms of trade $\pi_0$, $\pi_1$ and $\pi_2$

Associated to the growth scenarios of the figures 4 through 6 are the figures 7 and 8 that provide information about the change in time of the endogenous parameters $c_2$, $c_3$ and the terms of trade $\pi_0$, $\pi_1$, $\pi_2$, respectively, which can be interpreted as measuring the predation risk (see above). Formally the predation risk variables are specified as

$$\pi_0 = \frac{n_1}{400000}, \quad \pi_1 = c_2 = \frac{n_2}{10n_1} \quad \text{and} \quad \pi_2 = c_3 = \frac{n_3}{10n_2}. \tag{25}$$

It is interesting to observe that both $c_2$ and $c_3$ are decreasing in time implying that the population of species 1 grows more rapidly than the population of species 2 which in turn grows more rapidly than the population of species 3. When the resource is scarce the terms of trade reflect scarcity and abundance of species biomass. Figure 8 shows that all terms of trade increase progressively at first, then they grow at declining rates until they eventually reach their steady state levels. Comparing figure 7 and 8 in combination with (25) we conclude that the speed of population growth depends on whether the ecosystem is

abundant or scarce. In case the resource is scarce the population of species 3 grows faster then the population of species 2 which in turn grows more rapidly than the population of species 1.

**Example 2 and 3:** In example 1 all populations turned out to be strictly increasing on their path towards the steady state. It seems natural to ask whether this feature is generic for the model at hand. Intuitively, one might expect a predator population to be stressed and hence to decline, over some time interval, at least whenever its prey population is sufficiently small. To explore this conjecture we provide two more examples that differ from eaxample 1 in that (i) the ecosystem is already scarce in the initial situation (which serves only to simplify the exposition) and that (ii) one or both predator species have large populations relative to their preys.

In example 2 the populations at $t = 0$ are set $n_1(0) = 400000$, $n_2(0) = 10000$ and $n_3(0) = 100000$. Obviously the population of species 2 is very small in comparison to those of species 1 and 3. Owing to its small population, species 2 will supply only little biomass in the aggregate while the demand of species 3 is high due to its large population. As a consequence the equilibrium price $p_2$ is high and the ecosystem attains an equilibrium at which little biomass of species 2 is traded. Figures 9-11 illustrate the implications on the population dynamics. While the populations of species 1 and 2 exhibit a logistic growth, as in example 1, the population of species 3 drops sharply from $n_3(0) = 400000$ to $n_3(0.05) = 95824.1$ but it recovers after $t = 0.05$. The biomass of species 2 has become less scarce and the representative organism of species 3 can afford to demand more biomass of species 2 due to a lower price $p_2$ with the consequence that the population of species 3 increases for $t > 0.05$.
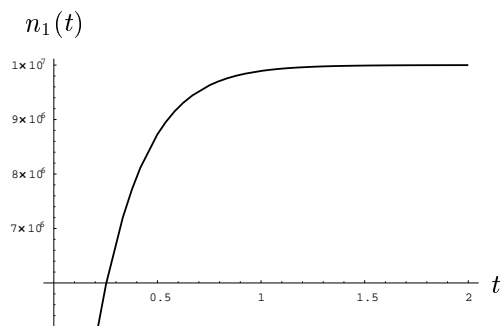


Figure 9: Population growth of species 1 in example 2

In our final example the population of species 1 is relatively low as compared to the populations of species 2 and 3. We have set $n_1(0) = 400000$, $n_2(0) = 4000000$ and $n_3(0) = 3000000$. Induced by biomass demands and supplies responding to the appropriate price
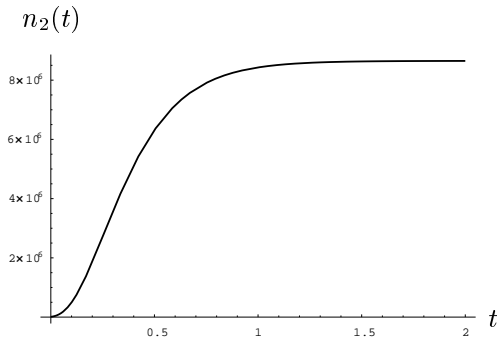
Figure 10: Population growth of species 2 in example 2
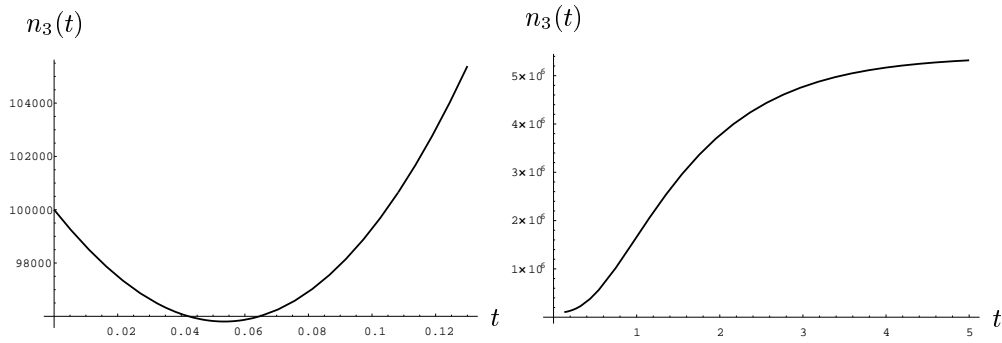


Figure 11: Population growth of species 3 in example 2

signals, the small population of species 1 triggers downward adjustments of the populations of species 2 and 3 as illustrated in the left panels of figures 13 and 14. The population of species 2 recovers after $t = 0.1$ and the population of species 3 also recovers, with some time delay, after $t = 0.3$.
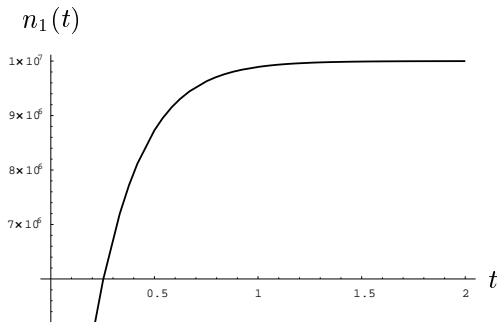


Figure 12: Population growth of species 1 in example 3

To sum up, examples 2 and 3 confirmed our conjecture that predator populations may decline (temporarily) when little prey biomass is available for feeding. In example 2 we observed that the predator species 3 takes a dip owing to the sparse supply of prey biomass (species 2). But the great appetite of the populous species 3 doesn't result in overharvesting its prey species 2. The latter exhibits monotonous population growth. Example 3 is different in that species 2 is under stress of a small supply of prey biomass (species 1) which results in a temporary decline of population 2. As a result of this decline, species 3's population

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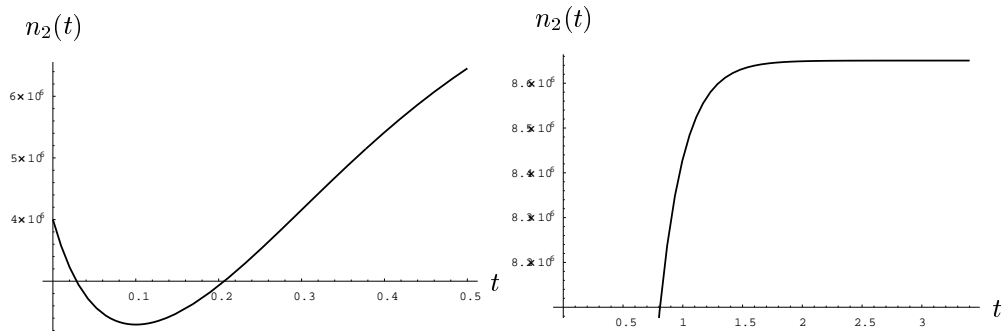
Figure 13: Population growth of species 2 in example 3
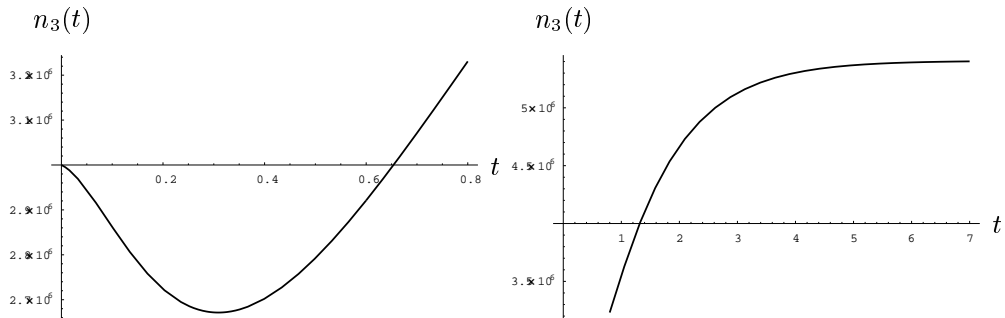


Figure 14: Population growth of species 3 in example 3

also shrinks with a small time lag and exhibits positive growth rates again after recovery of its prey species 2. The time lag gives a clear indication regarding cause and effect. The decline of prey species 2 induces species 3 to shrink. The reverse causation can be rejected: The prey species 2 is not overharvested in an effort of species 3 to prevent the decline of its own population.

# 4    Concluding remarks

This paper provides a microfoundation of intertemporal predator-prey relations in a food chain. Changes in species populations over time are modeled through a sequence of short-run ecosystem equilibria where endogenous scarcity indicators equilibrate demands of biomass by predators and the preys' demand of own biomass. In a parametric version of the model (Cobb-Douglas) we are able to completely derive the population dynamics. Although the time path of interacting populations, convergence and stability are not fully characterized analytically, our three numerical examples are very informative. All of them exhibit convergence to a unique steady state, in stark contrast to the oszillations typical of the standard Lotka-Volterra model. The main reason for the divergent dynamic behavior of both systems are structurally different prey species' growth equations in both models (which are ad hoc in the Lotka-Volterra model but derived from more basic assumptions

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in the present approach). In our model the population growth of each species turns out to have a positive impact on the population of its predator but no prey population is negatively affected by the population of its predator species as in the Lotka-Volterra model. This property is not a special feature of the parametrization chosen but is generic for all food chains. We conjecture, though, that this property doesn't carry over to more complex food webs. Being confronted with competing incompatible explanatory approaches, future empirical research is needed to investigate the merits of the present approach as compared to the Lotka-Volterra model and its refinements. But notwithstanding empirical testing yet to be undertaken, we have shown that the microfoundation suggested here cannot serve as a theoretical basis for generating the Lotka-Volterra population growth functions. It remains an open question whether there is at all a model capable to serve as a theoretical underpinning of these functions.

As the preceding analysis has demmonstrated our modeling of ecosystem transactions and equilibrium is quite involved. But it is simple enough, on the other hand, to serve as a framework for tackling a wide range of relevant issues. Among other things, deviations from unidirectional food chains could be studied and alternative property rights of the resource may be assumed including schemes where all species own shares of the resource. The most promising extension is probably to link a (standard perfectly competitive) economy with the ecosystem to analyze the impacts of human activities on the ecosystem and its repercussions on the economy.

# References

Cantrell R. S. and C. Cosner (2001), On the dynamics of predator-prey models with the Beddington-DeAngelis functional response, *Journal of Mathematical Analysis and Applications* **257**, 206-222.

Clark C. W. (1976), *Mathematical bioeconomics: the optimal management of renewable resources*, Wiley, New York.

Crocker T. D. and J. Tschirhart (1992), Ecosystems, externalities and economies, *Environmental and Resource Economics* **2**, 551-567.

Debreu G. (1959), *Theory of value*, Wiley, New York.

Eichner T. and R. Pethig (2003), The impact of scarcity and abundance in food chains on species population dynamics, *Natural Resource Modeling*, forthcoming.

Finnoff D. and J. Tschirhart (2003), Harvesting in an eight-species ecosystem, *Journal of Environmental Economics and Management*, forthcoming.

Hannon B. (1976), Marginal product pricing in the ecosystem, *Journal of Theoretical Biology* **56**, 253-267.

Hirshleifer J. (1977), Economics from a biological viewpoint, *Journal of Law and Economics* **20**, 1-52.

Kuang Y. and E. Beretta (1998), Global qualitative analysis of a ratio-dependent predator-prey system, *Journal of Mathematical Biology* **36**, 389-406.

Lima S. L. and L. M. Dik (1990), Behavioral decisions made under the risk of predation: a review and prospectus, *Canadian Journal of Zoology* **68**, 619-640.

Lotka A. J. (1925), *Elements of physical biology*, Williams und Wilkins, Baltimore.

May R. M. (1973), *Stability and complexity in model ecosystems*, Monographs in Population Biology VI, Princeton University Press, Princeton.

May R. M. (1981), *Theoretical ecology: principles and applications*, 2nd edn. Blackwell, Oxford.

Murray J. D. (1993), *Mathematical biology*, 2nd edn. Springer, Berlin.

Pethig R. (2003), Agriculture, pesticides and the ecosystem, *Agricultural Economics*, forthcoming.

Pethig R. and J. Tschirhart (2001), Microfoundations of population dynamics, *Journal of Bioeconomics*, **3**, 27-49.

Rosen G. (1984), Characterizing conditions for generalized Verhulst logistic growth of a biological population, *Bulletin of Mathematical Biology* **46**, 963-965.

Tschirhart J. (2000), General equilibrium of an ecosystem, *Journal of Theoretical Biology* **203**, 13-32.

Tschirhart J. (2002), Resource competition among plants: from optimizing to community structure, *Ecological Modelling* **148**, 191-212.

Volterra V. (1926), Variazionie fluttuazioni del numero d'individui in specie animali con-viventi, *Mem. Acad. Lincei.* **2**, 31-113 (Variations and Fluctuations of a Number of Individuals in Animal Species Living Together, Translation In Chapman R. N. (1931), *Animal Ecology*, 409-448, Mc Graw Hill, New York.

# Appendix A: Proofs

**Proof of proposition 1:** The Lagrangean associated to the optimization problem (4) for $i = 1, \ldots, m$ is given by

$$\mathcal{L}^i (x_{i-1}, y_i, \lambda_i, \lambda_{ci}) = B^i (x_{i-1}, y_i) + \lambda_i (p_i y_i - p_{i-1} x_{i-1}) + \lambda_{ci} (y_i - c_i x_{i-1})$$

and the corresponding Kuhn-Tucker conditions are

$$\mathcal{L}^i_{x_{i-1}} = B^i_x - \lambda_i p_{i-1} - \lambda_{ci} c_i \le 0, \qquad x_{i-1} \mathcal{L}^i_{x_{i-1}} = 0, \tag{26a}$$

$$\mathcal{L}^i_{y_i} = B^i_y + \lambda_i p_i + \lambda_{ci} \le 0, \qquad y_i \mathcal{L}^i_{y_i} = 0, \tag{26b}$$

$$\mathcal{L}^i_{\lambda_i} = p_i y_i - p_{i-1} x_{i-1} \ge 0, \qquad \lambda_i \mathcal{L}^i_{\lambda_i} = 0, \tag{26c}$$

$$\mathcal{L}^i_{\lambda_{ci}} = y_i - c_i x_{i-1} \ge 0, \qquad \lambda_{ci} \mathcal{L}^i_{\lambda_{ci}} = 0. \tag{26d}$$

(a) Suppose $p_{i-1} = p_i = 0$. Then $x_{i-1} > 0$, since $B^i_x > 0$ evaluated at $x_{i-1} = 0$. Due to (3) $x_{i-1} > 0$ implies $y_i > 0$. Therefore $-\left(B^i_x / B^i_y\right) = c_i$ follows from (26a) and (26b) which is satisfied iff $x_{i-1} = x^c_{i-1}$.

(b) Suppose next $p_i > 0$ and $p_{i-1} = 0$. As in point (a) above, $x_{i-1} > 0$ and $y_i > 0$. With $p_i > 0$ and $p_{i-1} = 0$ (2) becomes $p_i y_i - p_{i-1} x_{i-1} = p_i y_i > 0$. Hence $\lambda_i = 0$. The implication $x^*_{i-1} = x^c_{i-1}$ follows as in point (a).

(c) Suppose $p_i > 0$, $p_{i-1} > 0$ and $\pi_{i-1} := p_{i-1} / p_i < c_i$. Then for all $\tilde{x}_{i-1} > 0$ it is true that $\pi_{i-1} \tilde{x}_{i-1} < c_i \tilde{x}_{i-1}$. Hence all $(x_{i-1}, y_i)$ satisfying (3) imply $y_i > \pi_{i-1} x_{i-1}$ and therefore $\lambda_i = 0$. Again, $-\left(B^i_x / B^i_y\right) = c_i$ follows from (26a) and (26b) yielding $x^*_{i-1} = x^c_{i-1}$.

(d) If $p_i > 0$, $p_{i-1} > 0$ and $\pi_{i-1} = c_i$ both constraints (2) and (3) coincide, and therefore $x^*_{i-1} = x^c_{i-1}$.

(e) Suppose $p_i > 0$, $p_{i-1} > 0$ and $\pi_{i-1} > c_i$. Then $\pi_{i-1} \tilde{x}_{i-1} > c_i \tilde{x}_{i-1}$ for all $\tilde{x}_{i-1} > 0$. Hence all $(x_{i-1}, y_i)$ satisfying (2) imply $y_i > c_i x_{i-1}$ and therefore $\lambda_{c_i} = 0$. Therefore $-\left(B^i_x / B^i_y\right) = \pi_{i-1}$ follows from (26a) and (26b) which is satisfied iff $x_{i-1} = x^\pi_{i-1}$. ■

**Proof of proposition 3:** In the market for the resource $(i = 0)$ an equilibrium exists for any $c_1 > 0$. Hence $c_1$ can be fixed autonomously. For the markets $i = 1, \ldots, m-1$ the equations $n_i Y^i(c_i) = n_{i+1} X^i(c_{i+1})$ or $n_i c_i X^{i-1}(c_i) = n_{i+1} X^i(c_{i+1})$ for $i = 1, \ldots, m-1$ are sufficient to prevent an excess supply on market $i$. Due to Assumption 1 it is possible to establish these equations by a suitable choice of $c_{i+1}$ for any given $c_i > 0$.

We denote by $\hat{X}^i$ the inverse function to $X^i$ and solve for $c_{i+1}$:

$$c_{i+1} = \hat{X}^i \left[ \frac{c_i n_i}{n_{i+1}} X^{i-1}(c_i) \right] \qquad i = 1, \ldots, m-1. \tag{27}$$

Since $c_1$ can be choosen freely the equations (27) uniquely determine all $c_i$ for $i = 2, \ldots, m - 1$. Moreover, on the market for the resource $(i = 0)$ a unique bounded equilibrium price $\pi_0^* \geq 0$ always exist. If the parameter $c_2$ is chosen as determined in (27) then there is $\pi_1^* \geq 0$ such that $n_1 c_1 X^0(\pi_0^*) = n_2 X^1(\pi_1^*)$ because the definition of $c_2$ implies $n_2 X^1(c_2) \geq n_1 c_1 X^0(\pi_0)$ for all $\pi_0 \geq 0$ and because Assumption 1 secures that for any $z \in ]0, n_1 c_1 X^0(c_1)[$ one can find $\pi_1 \geq 0$ such that $n_2 X^1(\pi_1) = z$. The same argument applies to all subsequent markets $i = 2, \ldots, m - 1$. ∎

**Proof of proposition 4:** The first-order conditions of the optimization problem (4) are either $-B_x^i/B_y^i = c_i$, $y_i = c_i x_{i-1}$ or $-B_x^i/B_y^i = \pi_{i-1}$, $y_i = \pi_{i-1} x_{i-1}$ which imply demand and supply functions

$$x_{i-1} = X^{i-1}(c_i), y_i = Y^i(c_i) \quad \text{or} \quad x_{i-1} = \tilde{X}^{i-1}(\pi_{i-1}), y_i = \tilde{Y}^i(\pi_{i-1}). \tag{28}$$

Let us first consider the case of an abundant resource. $c_1$ can be choosen freely and the equilibrium conditions (5b) can be solved bottom up and the equilibrating parameters have the functional form

$$c_i = C^i(n_1, \ldots, n_i) \qquad i = 2, \ldots, m, \tag{29}$$

which in turn yields equilibrium demands and supplies

$$x_0 = X^0(c_1), y_1 = Y^1(c_1) \tag{30a}$$
$$x_{i-1} = X^{i-1}[C^i(n_1, \ldots, n_i)], y_i = Y^i[C^i(n_1, \ldots, n_i)] \qquad i = 2, \ldots, m. \tag{30b}$$

Now we turn to an ecosystem with a scarce resource. The equilibrium conditions (5a) with equality and (5b) can be solved bottom up with the consequence that the equilibrium terms of trade have the functional form

$$\pi_{i-1} = \Pi^{i-1}(n_1, \ldots, n_i) \qquad i = 1, \ldots, m. \tag{31}$$

Inserting the equilibrium terms of trade (31) into the demand and supply functions (28) we obtain

$$x_{i-1} = \tilde{X}^{i-1}[\Pi^{i-1}(n_1, \ldots, n_i)] \qquad \text{and} \qquad y_i = \tilde{Y}^i[\Pi^{i-1}(n_1, \ldots, n_i)]. \tag{32}$$

Finally plugging (30a)-(30b) and (32), respectively, into the net biomass function (1) which in turn is inserted into (9) establishes proposition 4. ∎

# Appendix B: The comparative statics

Before we turn to the differentiation of the equilibrium equations

$$\bar{y}_0 \;=\; n_1 x_0, \tag{33a}$$

$$n_1 y_1 \;=\; n_2 x_1, \tag{33b}$$

$$n_2 y_2 \;=\; n_3 x_2, \tag{33c}$$

it is convenient to define the following terms used below to avoid clutter:
$$\eta_{i-1} = \frac{\tilde{X}_\pi^{i-1}\pi_{i-1}}{\tilde{X}^{i-1}} < 0,\ \varepsilon_i = \frac{\tilde{Y}_\pi^i \pi_{i-1}}{\tilde{Y}^i} \le 0,\ \delta_{bx}^i = \frac{B_x^i x_{i-1}}{B^i} > 0,\ \delta_{by}^i = \frac{B_y^i y_i}{B^i} < 0.$$
Differentiation of (33a) - (33c) yields:[19]

$$\hat{\bar{y}}_0 \;=\; \hat{n}_1 + \hat{x}_0, \tag{34a}$$

$$\hat{n}_1 + \hat{y}_1 \;=\; \hat{n}_2 + \hat{x}_1, \tag{34b}$$

$$\hat{n}_2 + \hat{y}_2 \;=\; \hat{n}_3 + \hat{x}_2. \tag{34c}$$

Next we differentiate $x_{i-1} = \tilde{X}^{i-1}\left(\pi_{i-1}\right)$ and $y_i = \tilde{Y}^i\left(\pi_{i-1}\right)$ to obtain:

$$\hat{x}_{i-1} = \eta_{i-1}\hat{\pi}_{i-1} \qquad \text{and} \qquad \hat{y}_i = \varepsilon_i \hat{\pi}_{i-1}. \tag{35}$$

It is easy to show that (35) for $i=1$ and (34a) result in:

$$\hat{\pi}_0 = \frac{\hat{\bar{y}}_0}{\eta_0} - \frac{\hat{n}_1}{\eta_0}. \tag{36}$$

Next, we combine (34b), (35) for $i = 1, 2$ and (36) to derive:

$$\hat{\pi}_1 = \frac{\varepsilon_1}{\eta_1\eta_0}\hat{\bar{y}}_0 + \frac{\eta_0 - \varepsilon_1}{\eta_1\eta_0}\hat{n}_1 - \frac{\hat{n}_2}{\eta_1}. \tag{37}$$

We now insert (35) for $i = 2, 3$ combined with $\hat{\pi}_1$ from (37) into (34c) to get:

$$\hat{\pi}_2 = \frac{\varepsilon_2\varepsilon_1}{\eta_2\eta_1\eta_0}\hat{\bar{y}}_0 + \frac{\varepsilon_2\left(\eta_0 - \varepsilon_1\right)}{\eta_2\eta_1\eta_0}\hat{n}_1 + \frac{\eta_1 - \varepsilon_2}{\eta_2\eta_1}\hat{n}_2 - \frac{\hat{n}_3}{\eta_2}. \tag{38}$$

The next step is to insert (36) - (38) into (35) to derive:

$$\hat{x}_0 \;=\; \hat{\bar{y}}_0 - \hat{n}_1, \tag{39a}$$

$$\hat{x}_1 \;=\; \frac{\varepsilon_1}{\eta_0}\hat{\bar{y}}_0 + \frac{\eta_0 - \varepsilon_1}{\eta_0}\hat{n}_1 - \hat{n}_2, \tag{39b}$$

$$\hat{x}_2 \;=\; \frac{\varepsilon_2\varepsilon_1}{\eta_1\eta_0}\hat{\bar{y}}_0 + \frac{\varepsilon_2\left(\eta_0 - \varepsilon_1\right)}{\eta_1\eta_0}\hat{n}_1 + \frac{\eta_1 - \varepsilon_2}{\eta_1}\hat{n}_2 - \hat{n}_3, \tag{39c}$$

$$\hat{y}_1 \;=\; \frac{\varepsilon_1}{\eta_0}\hat{\bar{y}}_0 - \frac{\varepsilon_1}{\eta_0}\hat{n}_1, \tag{39d}$$

$$\hat{y}_2 \;=\; \frac{\varepsilon_2\varepsilon_1}{\eta_1\eta_0}\hat{\bar{y}}_0 + \frac{\varepsilon_2\left(\eta_0 - \varepsilon_1\right)}{\eta_1\eta_0}\hat{n}_1 - \frac{\varepsilon_2}{\eta_1}\hat{n}_2, \tag{39e}$$

$$\hat{y}_3 \;=\; \frac{\varepsilon_3\varepsilon_2\varepsilon_1}{\eta_2\eta_1\eta_0}\hat{\bar{y}}_0 + \frac{\varepsilon_3\varepsilon_2\left(\eta_0 - \varepsilon_1\right)}{\eta_2\eta_1\eta_0}\hat{n}_1 + \frac{\varepsilon_3\left(\eta_1 - \varepsilon_2\right)}{\eta_2\eta_1}\hat{n}_2 - \frac{\varepsilon_3}{\eta_2}\hat{n}_3. \tag{39f}$$

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[19]In what follows we denote by $\hat{a} := \dfrac{da}{a}$ the marginal relative changes of all variables $a$.

We now complete the comparative statics by differentiating $b_i = B^i(x_{i-1}, y_i)$ for $i = 1, 2, 3$:

$$\hat{b}_1 = \delta^1_{bx}\hat{x}_0 + \delta^1_{by}\hat{y}_1, \tag{40a}$$

$$\hat{b}_2 = \delta^2_{bx}\hat{x}_1 + \delta^2_{by}\hat{y}_2, \tag{40b}$$

$$\hat{b}_3 = \delta^3_{bx}\hat{x}_2 + \delta^3_{by}\hat{y}_3, \tag{40c}$$

and then plugging (39a) - (39f) into (40a) - (40c) establishes:

$$\hat{b}_1 = \frac{\delta^1_{bx}\eta_0 + \delta^1_{by}\varepsilon_1}{\eta_0}\hat{\bar{y}}_0 - \frac{\delta^1_{bx}\eta_0 + \delta^1_{by}\varepsilon_1}{\eta_0}\hat{n}_1, \tag{41a}$$

$$\hat{b}_2 = \frac{\delta^2_{bx}\eta_1\varepsilon_1 + \delta^2_{by}\varepsilon_2\varepsilon_1}{\eta_1\eta_0}\hat{\bar{y}}_0 + (\eta_0 - \varepsilon_1)\frac{\delta^2_{bx}\eta_1 + \delta^2_{by}\varepsilon_2}{\eta_1\eta_0}\hat{n}_1 - \frac{\delta^2_{bx}\eta_1 + \delta^2_{by}\varepsilon_2}{\eta_1}\hat{n}_2, \tag{41b}$$

$$\hat{b}_3 = \varepsilon_2\varepsilon_1\frac{\delta^3_{bx}\eta_2 + \delta^3_{by}\varepsilon_3}{\eta_2\eta_1\eta_0}\hat{\bar{y}}_0 + \varepsilon_2(\eta_0 - \varepsilon_2)\frac{\delta^3_{bx}\eta_2 + \delta^3_{by}\varepsilon_3}{\eta_2\eta_1\eta_0}\hat{n}_1 + (\eta_1 - \varepsilon_2)\frac{\delta^3_{bx}\eta_2 + \delta^3_{by}\varepsilon_3}{\eta_2\eta_1}\hat{n}_2$$
$$- \frac{\delta^3_{bx}\eta_2 + \delta^3_{by}\varepsilon_3}{\eta_2}\hat{n}_3. \tag{41c}$$

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