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**Working Paper**

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Volkswirtschaftliche Diskussionsbeiträge, No. 123-05

**Provided in Cooperation with:**

Fakultät III: Wirtschaftswissenschaften, Wirtschaftsinformatik und Wirtschaftsrecht, Universität Siegen

*Suggested Citation:* Christiaans, Thomas; Eichner, Thomas; Pethig, Rüdiger (2005) : A micro-level 'consumer approach' to species population dynamics, Volkswirtschaftliche Diskussionsbeiträge, No. 123-05, Universität Siegen, Fakultät III, Wirtschaftswissenschaften, Wirtschaftsinformatik und Wirtschaftsrecht, Siegen

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# A micro-level 'consumer approach' to species population dynamics\*

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## Abstract

In this paper we develop a micro ecosystem model whose basic entities are representative organisms which behave as if maximizing their net offspring under constraints. Net offspring is increasing in prey biomass intake, declining in the loss of own biomass to predators and Allee's Law applies. The organism's constraint reflects its perception of how scarce its own biomass and the biomass of its prey is. In the short-run periods prices (scarcity indicators) coordinate and determine all biomass transactions and net offspring which directly translates into population growth functions. We are able to explicitly determine these growth functions for a simple food web when specific parametric net offspring functions are chosen in the micro-level ecosystem model. For the case of a single species our model is shown to yield the well-known Verhulst-Pearl logistic growth function. With two species in predator-prey relationship, we derive differential equations whose dynamics are completely characterized and turn out to be similar to the predator-prey model with Michaelis-Menten type functional response. With two species competing for a single resource we find that coexistence is a knife-edge feature confirming Tschirhart's (2002) result in a different but related model.

Key words: species, growth, extinction, predator-prey relations, resource competition

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\*Helpful comments by two anonymous referees and the participants at the DIVERSITAS Workshop "Integrated Modeling of Economies and Ecosystems" held in Paris in November 2004 are gratefully acknowledged. Remaining errors are the authors' responsibility.

# 1 Introduction

The theory of dynamic interactions of species has a long tradition in population biology. The study of dynamic predator-prey relations dates back to the seminal works of Lotka (1925) and Volterra (1926). Various generalizations and refinements have since been suggested, e.g. by May (1981), Kuang and Beretta (1998), Cantrell and Cosner (2001), Hsu et al. (2001). The dynamics of resource competition among species has also been a major research focus over the last decades (Tilman 1980, 1982, 1985 and Pacala and Tilman 1994). The basic building blocks of all these ecological population models are difference or differential equations of population growth and decline. Each species is represented by a single equation containing as variables its own population and, in general, also populations of other species.

There is an ongoing effort to choose the functional forms of those differential equations in line with theoretical and empirical insights from ecological research. In that sense the population models have a firm conceptual foundation. And yet, by taking populations or densities (and their change in time) as their basic endogenous variables these models are macro approaches which, by construction, cannot explain the development of species communities over time as a result of various kinds of interactions of individual organisms inhabiting the ecosystem. These interactions take the form of transfers of resources and (prey) biomasses. We will take on the theoretical challenge to link the population dynamics that can be observed at the macro level of an ecosystem with those continuous activities of organisms at the micro level.

The interactions of individual organisms with other organisms that are characteristic of ecosystems at the micro level resemble the interactions of consumers and producers in an economic system in several important ways: Using the notion of resources in a very broad sense we observe that in both systems

- (i) production, consumption and transfers of resources take place;
- (ii) resource scarcity is a central feature; it is therefore important to understand how the system's agents cope with that scarcity;
- (iii) the allocation of resources is determined by the system's agents in a decentralized and uncoordinated way.

Economists have a good understanding of the market system as the principal decentralized mechanism of allocating scarce resources in an economy. They use to explain the working of that mechanism by recurring to the micro level of the economy, more specifically, to the economic agents' optimizing behavior under appropriate constraints. In that sense the economic allocation theory can be said to be microfounded. As for the resource

allocation in ecosystems, we are not aware of ecological approaches to explain the allocation of resources in ecosystems which are microfounded in a similar way as economic systems are. In the present paper we set up a microfounded theory of resource allocation in an ecosystem that makes use of economic methodology and aims at explaining the dynamics of species populations.<sup>1</sup>

To our knowledge, Hannon (1973, 1976) was the first to apply economic concepts such as prices and optimizing behavior of individual organisms to theoretical ecosystem analysis. His basic ideas have eventually been taken up by environmental economists, notably by Crocker and Tschirhart (1992), Tschirhart (2000, 2002, 2003, 2004), Pethig and Tschirhart (2001), Finnoff and Tschirhart (2003a, 2003b) and Eichner and Pethig (2003, 2004). The present paper shares the conceptual basis of all these contributions, but it will offer the most uncompromizing approach of transplanting the perfectly competitive allocation mechanism from economic theory into the realm of ecosystem analysis. In our ecosystem model organisms of each species will be modeled isomorphic to consumers in economic textbooks.

The starting point of our analysis is the short-run period in which populations are constant. Representative individual organisms of all species are assumed to behave as if they maximize their net offspring subject to a budget constraint. Net offspring is increasing in prey biomass intake, declining in the loss of own biomass to predators, and it satisfies Allee's law. The organism's 'budget constraint' reflects its perception of how scarce its own biomass and the biomass of its prey are. This constraint can readily be related to ecological concepts such as predation power of an organism vis-à-vis its prey and predation risk. The allocation mechanism that coordinates the supply of each species' biomass and all predators' demand for that biomass is analogous to the general perfectly competitive mechanism, borrowed again from economics methodology. In the context of the ecosystem model, the only decisive role of this allocation mechanism is to make consistent all organisms' perceptions of biomass scarcity. The general ecosystem equilibrium attained in the short-run period determines all biomass transfers and thus the net offspring of all species. The latter constitutes the (positive or negative) population growth in time. In that way, a system of population growth functions is generated rather than assumed. We are able to explicitly determine these functions for a simple food web in continuous time when suitable parametric functional forms are chosen in the corresponding micro-level ecosystem model.

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<sup>1</sup>There is a long tradition in ecology and related sciences to provide so-called mechanistic approaches to community ecology, i.e. to explain population dynamics by modelling behavior at the individual level. An early review is provided by Schoener (1986), and more recent developments are summarized by Persson and de Roos (2003). The defining difference between this literature and the approach of the present paper is that we focus on a micro-level ecosystem approach based on economic methodology.

In the paper such analytical solutions are derived and characterized.

We are aware that using terms like income, prices and markets may be considered grossly misplaced in ecological analysis if not provocative. In fact, non-human species definitively don't use money. It is interesting to note, however, that the neoclassical economic market system of perfect competition as it is set up e.g. in Debreu's (1959) "Theory of Value" does not describe a monetized economy with real (fiat or commodity) money and real institutionalized markets. That theory can readily be interpreted (i) to deal with assigning 'values' or shadow prices to scarce resources, (ii) to consider rational agents coping with these scarcities under some appropriate constraints and (iii) to envisage an equilibrium state of 'market clearing' that essentially expresses the idea of an allocation process reaching a state in which all agents' perceptions of scarcities are consistent.

We believe that with appropriate modifications economic neoclassical allocation theory can be fruitfully applied to theoretical ecosystem analysis. The main purpose of the present paper is to substantiate that claim. The approach suggested here is flexible, rich in (testable) implications, and is well suited for its ultimate purpose to form a central building block of an integrated theory of the ecosystem and the economy.

The paper is organized as follows: Section 2 presents the short-run ecosystem model. First we introduce the representative organism's net offspring function, then its budget constraint and after solving the organism's optimization problem we explain the allocation mechanism which equilibrates all biomass demands and supplies. In addition, we perform a comparative static analysis to answer the question how the organism's biomass demand and supply is affected by changes in its predation power and in prices. At the end of section 2 we establish the link between the organism's net offspring generated in the short-run period and the growth of species population.

In section 3 we focus on a food web consisting of two prey species and one predator species and parametrize the model by Cobb-Douglas functions. After presenting three numerical examples in section 3.1 we turn to special cases. In section 3.2 we investigate the growth function of a single species, in section 3.3 we rigorously analyze the dynamics of a two-species predator-prey model. Finally we turn to resource competition when two species compete for a resource in section 3.4.

## 2 The general model

Following the methodology of models explaining economic growth in time, the focus is first on an ecosystem equilibrium of flow variables in a short-run period, where all stocks (here:

populations) are kept constant. In our approach the short-run period is a point in time, in fact, since we take time to be continuous.<sup>2</sup> After the equilibrium allocation of the short-run period is determined, the implied changes (or updates) of populations are accounted for. They give rise to a system of differential equations that describes the motion of populations in time. The time path of ecosystem variables (including populations) is thus constituted by a sequence of (moving) short-run ecosystem equilibria. Owing to this structure, the short-run, or rather instantaneous, ecosystem model clearly is at the core of the present approach. It is therefore important to describe the building blocks of the short-run ecosystem model in great detail. All variables introduced below relate to a specific point in time,  $t \geq 0$ . However, all time indexes are suppressed to avoid clutter.

The ecosystem to be modeled consists of a habitat conceived of as an area of land and/or water, that is endowed with non-biomass resources and that is inhabited by  $N$  species in a food web. The habitat has no spatial structure, i.e. the model is confined to a single patch.<sup>3</sup> No species interacts with any organisms or resources outside the habitat. Resources are substances or factors other than species which can promote the growth of some species when consumed by its organisms.<sup>4</sup> There is a great variety of such resources in real world ecosystems, some of them being renewable and some non-renewable. Since our present main focus is on the interaction of species we simplify the resource part of the model as follows: The ecosystem is assumed to be endowed with a single renewable resource whose supply  $r > 0$  is time invariant.

In the analysis of species, basic units are individual organisms. To simplify, all organisms of the same species are assumed to be identical, and the representative member of species  $i$  is called organism  $i$ , for short. In the short-run period under consideration the population  $n_i$  of each species  $i$  is assumed to be constant. Organism  $i$  generates net offspring  $b_i$  that is modeled by a strictly concave function  $B^i : D^i \rightarrow \mathbb{R}$  such that  $D^i := \mathbb{R}_+^N \times [0, \bar{z}_i] \times \mathbb{R}_+$  and

$$b_i = B^i \begin{pmatrix} \mathbf{x}_i \\ +,0 & - & +,0 \end{pmatrix} \quad z_i, n_i \quad i = 1, \dots, N. \quad (1)$$

In (1),  $\mathbf{x}_i^\top := (x_{i0}, x_{i1}, \dots, x_{i,i-1}, x_{i,i+1}, \dots, x_{iN}) \in \mathbb{R}_+^{N-1}$ , is a vector of organism  $i$ 's biomass intake and  $z_i$  is organism  $i$ 's loss of own biomass to its predators. The latter is bounded from above by  $\bar{z}_i$ , a constant positive real number. We denote by  $x_{i0}$  organism  $i$ 's intake of the resource which is also referred to as biomass of species 0, for notational convenience.

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<sup>2</sup>For discrete time frameworks see e.g. Tschirhart (2000, 2002, 2004).

<sup>3</sup>At the end of the present section some discussion is offered on the changes that would have to be made for multiple patches.

<sup>4</sup>Essentially, this definition is Tilman's (1982) notion of resources except that we exclude biomass resources because these biological resources are explicitly modeled as species in the present approach.

For  $j \neq 0$  and  $j \neq i$ ,  $x_{ij}$  is organism  $i$ 's intake of biomass of (prey) species  $j$ . Obviously,<sup>5</sup>  $B_{z_i}^i < 0$  means that organism  $i$ 's net offspring generation is hampered by losses of own biomass  $z_i$ . On the other hand the derivatives  $B_{x_{ij}}^i > 0$  for  $j \neq i$  indicate that organism  $i$ 's net offspring is fostered by the intake of biomass of prey species. Since organism  $i$  cannot survive without resource or biomass intake we set<sup>6</sup>  $B^i(\mathbf{0}^N, 0, n_i) < 0$ . As a consequence,  $B^i(\cdot) = 0$  requires some food intake. The special case  $B^i(\cdot) = 0$  characterizes a situation where the birth rate of species  $i$  equals its death rate such that its population is constant. Some partial derivatives of function  $B^i$  may be zero, of course. If organism  $i$  belongs to a plant species, one would expect  $B_{x_{i0}}^i > 0$  and  $B_{z_i}^i < 0$  but  $B_{x_{ij}}^i = 0$  for all  $j \neq 0, j \neq i$ . In case of an animal species we certainly have  $B_{x_{ij}}^i > 0$  for some  $j \neq i$  but perhaps  $B_{x_{i0}}^i = 0$ .

The net offspring function (1) also has the property

$$B_{n_i}^i(\mathbf{x}_i, z_i, n_i) \begin{cases} > 0 & \text{if } (\mathbf{x}_i, z_i, n_i) \in \tilde{D}^i \\ = 0 & \text{otherwise,} \end{cases}$$

where  $\tilde{D}^i := \{(\mathbf{x}_i, z_i, n_i) \mid \mathbf{x}_i \neq \mathbf{0}^N, z_i < \bar{z}_i \text{ and } n_i \in [0, \tilde{n}_i]\}$  and where  $\tilde{n}_i$  is a constant positive real number referred to as the critical population level of species  $i$ . The idea behind including  $n_i$  as an argument of the function  $B^i$  is that the representative organism's generation of net offspring is the more hampered, the further  $n_i$  drops below the critical level  $\tilde{n}_i$ . Due to reduced ability and/or opportunity to reproduce species  $i$  is an endangered species, if  $n_i < \tilde{n}_i$ . This hypothesis is in line with empirical evidence from ecological studies known as Allee's Law (Berryman 2003).<sup>7</sup>

The next step is to specify the allocation mechanism that determines all short-run biomass transactions in the ecosystem. Central features of ecosystems and economies alike are scarcity and competition for resources (broadly conceived). In economic models of resource allocation the perfectly competitive mechanism is a device to deal with scarcities in an efficient way. It is described in terms of prices, price-taking agents and markets and is, in our view, appropriate to solve the (short-run) allocation problem in multi-species ecosystems. This adaptation does not imply at all to suggest the introduction of real money and real markets into the ecosystem. After all, the neoclassical allocation theory (with Debreu's (1959) "Theory of Value" as its outstanding if not defining contribution) does *not* describe a monetized economy with real markets. That theory can readily be interpreted (i) to deal with assigning 'values' or shadow prices to scarce resources, (ii) to consider rational agents coping with these scarcities under some appropriate constraints and (iii) to

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<sup>5</sup>Subscripts assigned to upper-case letters representing functions denote partial derivatives.

<sup>6</sup> $\mathbf{0}^N$  is the  $N$ -dimensional vector consisting of  $N$  zeros.

<sup>7</sup>According to Allee's Law, reproduction is reduced at low population densities. This is why small populations have lower chances to survive, and therefore Allee's Law is of special interest to ecologists studying endangered species.

envisage a short-run equilibrium state of 'market clearing' that essentially expresses the idea of the allocation process reaching a state in which all agents' perceptions of scarcities are consistent. Such a mechanism will now be specified for the problem of resource allocation in the ecosystem.

In our ecosystem model the biomasses of all species are viewed as commodities traded in a system of competitive markets, where 'intake of prey biomass' translates into 'demand for prey biomass' and 'loss of own biomass' is interpreted as 'supply of own biomass'. To further specify this 'economic approach' to the ecosystem, denote by  $p_i$  the price of biomass of species  $i$  and by  $e_i$  organism  $i$ 's (exogenous) lumpsum income. Prices and incomes are denominated in virtual units of account. Organism  $i$ 's transactions are constrained by the inequality

$$e_i + p_i z_i \geq \mathbf{p}_{-i}^\top \cdot \mathbf{x}_i \quad i = 1, \dots, N, \quad (2)$$

where  $\mathbf{p}_{-i}^\top := (p_0, p_1, \dots, p_{i-1}, p_{i+1}, \dots, p_N) \in \mathbb{R}_+^N$ . Obviously, (2) closely resembles the household's budget constraint that economists use to employ for describing the consumer's decision problem. According to (2) organism  $i$  has two kinds of incomes for purchasing prey biomass  $\mathbf{p}_{-i}^\top \cdot \mathbf{x}_i$ : the lumpsum income  $e_i > 0$  and the receipts from selling own biomass  $p_i z_i$ . The lumpsum income is a species-specific parameter reflecting organism  $i$ 's status or power as a predator, i.e. its 'entitlement' to feed on its prey without being forced to sacrifice own biomass to its predators. We will therefore refer to  $e_i$  as the *predation power* of organism  $i$ .  $e_i$  is organism  $i$ 's only income if  $i$  has no enemies because  $i$  is - or has become - a top predator.

If a predator species exists for species  $i$ , organism  $i$  can expand its expenditure on prey biomass beyond  $e_i$  if and only if it is willing to earn some biomass income,  $p_i z_i > 0$ , to pay for the extra food. The observation that purchasing extra prey biomass requires a sacrifice of own biomass<sup>8</sup>  $z_i$  readily reflects what ecologists refer to as organism  $i$ 's *predation risk*, the risk of being preyed upon while preying (Lima and Dill 1990): During the process of foraging ('purchasing  $\mathbf{x}_i$ ') organism  $i$  exposes itself to its predators, and the more prey biomass organism  $i$  demands the greater is the risk of being devoured by predators. Thus equation (2) combines the forces of predation power and predation risk: To secure some given amount of prey biomass, at given prices, organism  $i$  needs to sacrifice the more own biomass the lower is its predation power.

Having specified organism  $i$ 's budget constraint we now turn to its decision problem. It is assumed that all individual organisms are price takers and behave as if they solve the

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<sup>8</sup>The obvious analogy to the economic consumer theory is the correspondence between biomass income and the consumer's labor income: The supply of labor reduces utility, the supply of own biomass reduces net offspring.



maximization problem:

$$\max_{(\mathbf{x}_i, z_i)} B^i(\mathbf{x}_i, z_i, n_i) \quad \text{s.t.} \quad (2). \quad (3)$$

The first-order conditions of the solution to (3) can be rearranged to read

$$\frac{B_{x_{ij}}^i}{B_{x_{ik}}^i} = \frac{p_j}{p_k} \quad i = 1, \dots, N; j, k = 0, 1, \dots, N; i \neq j, k, \quad (4a)$$

$$-\frac{B_{x_{ij}}^i}{B_{z_i}^i} = \frac{p_j}{p_i} \quad i = 1, \dots, N; j = 0, 1, \dots, N; i \neq j. \quad (4b)$$

As known from textbook consumer theory, (4a) requires the organism  $i$  to expand its intake of prey biomass  $j$  to the point at which the marginal rate of substitution  $B_{x_{ij}}^i/B_{x_{ik}}^i$  of prey biomass  $j$  for prey biomass  $k$  equals the prevailing (price) ratio  $p_j/p_k$  of exchanging each unit of biomass  $j$  for biomass  $k$ . Similarly, (4b) requires organism  $i$  to expand its intake of prey biomass  $j$  to the point at which the marginal rate of substituting prey biomass  $j$  for own biomass,  $-B_{x_{ij}}^i/B_{z_i}^i$ , equals the rate of exchanging each unit of prey biomass  $j$  for own biomass,  $p_j/p_i$ . Combined with (2), (4a) and (4b) implicitly determine the Marshallian demand and supply functions

$$\mathbf{x}_i = \mathbf{X}^i(\mathbf{p}, e_i, \mathbf{n}) := (X^{i0}(\mathbf{p}, e_i, \mathbf{n}), \dots, X^{iN}(\mathbf{p}, e_i, \mathbf{n})) \quad i = 1, \dots, N, \quad (5a)$$

$$z_i = Z^i(\mathbf{p}, e_i, \mathbf{n}) \quad i = 1, \dots, N, \quad (5b)$$

where  $\mathbf{p} := (p_0, \dots, p_N) \in \mathbb{R}_+^{N+1}$  is the vector of prices and  $\mathbf{n} := (n_1, \dots, n_N) \in \mathbb{R}_+^N$  is the vector of populations.

In the following we are interested in how an organism's feeding choice varies with changes in its predation power and in prices. Let us begin with changes in the parameter  $e_i$ . For any given  $(\mathbf{p}, e_i, \mathbf{n})$ , the derivative  $X_{e_i}^{i\ell}(\mathbf{p}, e_i, \mathbf{n})$  represents the increment in its demand for biomass of species  $\ell$  induced by a small change of its predation power. Whether this derivative is positive or negative is an empirical matter whose investigation is beyond the scope of the present paper. Another important piece of information is how organism  $i$  adjusts its demand for biomass  $\ell$  to a small change in the price of biomass  $k$ ,  $p_k$ . The derivative  $X_{p_k}^{i\ell}(\mathbf{p}, e_i, \mathbf{n})$  represents that price effect of  $p_k$  on organism  $i$ 's demand for biomass  $\ell$ . Like in the economic consumer theory one may want to refer to biomass  $\ell$  and biomass  $k$  as substitutes [complements] for organism  $i$ , if  $X_{p_k}^{i\ell} > 0$  [ $X_{p_k}^{i\ell} < 0$ ].

In fact, due to the isomorphism between (5) and the demand and supply function of consumers we can tap on the well elaborated comparative-static analysis of consumer behavior to further scrutinize the price effects  $X_{p_k}^{i\ell}$  with the help of the expenditure function and deriving the Hicksian demand and supply functions (see e.g. Mas-Colell et al. 1995, p. 67). To that end recall that we have envisaged the organism as maximizing its net

offspring for given prices and predation power. It is easy to see that net offspring will be maximized for given expenditure only if the level of net offspring realized is being achieved in the cheapest possible way: expenditure must be minimized for any given level of net offspring. Formally, the expenditure minimization problem is

$$\min_{(\mathbf{x}_i, z_i)} \quad \mathbf{p}_{-i}^\top \cdot \mathbf{x}_i - p_i z_i \quad \text{s.t.} \quad b_i \geq \bar{b}_i. \quad (6)$$

The solution to (6) gives the so called Hicksian demand and supply functions

$$\mathbf{x}_i = \mathbf{H}^i(\mathbf{p}, b_i, \mathbf{n}) := (H^{i0}(\mathbf{p}, b_i, \mathbf{n}), \dots, H^{iN}(\mathbf{p}, b_i, \mathbf{n})) \quad i = 1, \dots, N, \quad (7a)$$

$$z_i = K^i(\mathbf{p}, b_i, \mathbf{n}) \quad i = 1, \dots, N. \quad (7b)$$

Combining (5) and (7) and considering their relation yields the Slutsky equation<sup>9</sup>

$$X_{p_k}^{i\ell}(\mathbf{p}, e_i, \mathbf{n}) = H_{p_k}^{i\ell}(\mathbf{p}, b_i, \mathbf{n}) - X_{e_i}^{i\ell}(\mathbf{p}, e_i, \mathbf{n}) \cdot X^{ik}(\mathbf{p}, e_i, \mathbf{n}). \quad (8)$$

That equation decomposes the change in demand induced by a price change into two separate effects: the substitution effect  $H_{p_k}^{i\ell}$  and the income effect  $X_{e_i}^{i\ell} \cdot X^{ik}$ . The substitution effect indicates how the organism  $i$  substitutes one prey for another when the price  $p_k$  changes but purchasing power  $e_i/p_k$  remains constant. The idea is that the organism is being compensated for a price rise by increasing its predation power such that it is able to purchase the initial feeding bundle. The substitution effect is negative, since the change in demand due to this effect is always opposite to the change in price. If the price of a good increases, the substitution effect causes a reduction in the demand for that good. The second partial effect of the price change is the income effect. Here the purchasing power  $e_i/p_k$  has changed upon the price change and the term  $X_{e_i}^{i\ell} \cdot X^{ik}$  measures the impact of this change on demand. The basic insight is that implicit in each price change is a change in 'real predation power' (exogenous income). Depending on the sign of  $X_{e_i}^{i\ell}$  (see above) the income and substitution effects in (8) can exhibit the same sign - in which case  $X_{p_k}^{i\ell}$  is unambiguously negative - or can be opposite in sign - in which case  $X_{p_k}^{i\ell}$  becomes positive if and only if, in absolute terms, the income effect overcompensates the substitution effect.

At the present stage of conceptual analysis it is difficult to predict how useful this analytical Slutsky decomposition will turn out to be in future (applied) ecosystem studies. The main purpose of having discussed the properties of the demand functions (5a) here in some depth is to point out that our short-run ecosystem theory can fall back on a wealth of theoretical results well established in the economic consumer theory.

Our basic hypothesis elaborated above is that organisms maximize net offspring under constraints. While individual optimizing behavior appears to be a fairly accepted hypothesis

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<sup>9</sup>For a proof of the Slutsky equation see e.g. Mas-Colell et al. (1995, p. 71).

in the ecological literature, taking net offspring (i.e. the function  $B^i$  from (1)) as the objective function is less common. Alternatives are net energy (Tschirhart 2000) or utility (Anderson 2002). All these objective functions may be interpreted as indicators of fitness which is a much broader concept that is hard to operationalize. Given the rather high level of abstraction of the present model it is possible to reinterpret net offspring  $B^i(\cdot)$  as net energy, utility or even fitness without changing the implications of the ecosystem model. The only additional hypothesis necessary to proceed with the model as it stands is to assume that net energy, utility or fitness is positively correlated to net offspring.<sup>10</sup>

As the above outline of our approach demonstrates, its central focus is to explain population dynamics as emerging from micro-level interactions of individual organisms. Another, quite different route to establish a link between population dynamics and processes acting at the individual is taken by the so called individual-based models surveyed in Grimm (1999).<sup>11</sup> Although the objective of both bottom-up approaches is very similar they differ vastly in methodology and analytical structure. We model an allocation mechanism for the ecosystem with optimizing behavior of individual organisms, with scarcity indicators and with a concept of short-run ("market clearing") equilibrium for the ecosystem. All these features are absent in most individual-based models although it is important to emphasize that individual-based models do not follow uniform standards in micro-level modeling. For example, Anderson (2002) models individual organisms seeking to maximize expected utility where the probability of enhancing utility by some action may vary. In spirit, such an approach is quite close to the model of the present paper. Another distinguishing feature is the complexity in modeling the micro-level processes:<sup>12</sup> While we assume that all individuals of a species are alike (but differ across species) individual-based models deal with species made up of heterogeneous individuals; heterogeneous by age class, size or weight. Moreover, in the present paper, the ecosystem consists of a single patch.<sup>13</sup> In contrast, individual-based models are spatially explicit considering, e.g. a collection of two-dimensional cells in space (Railsback et al. 2002). Another important difference in complexity is that our approach does not model uncertainty explicitly, while individual-based models often incorporate stochastic processes.

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<sup>10</sup>With such a reinterpretation, equation (12) below would then imply the assumption that net energy, utility or fitness is proportional to net offspring. But (12) could be relaxed to reflect positive correlation only. See, for example, the procedure chosen by Tschirhart (2000).

<sup>11</sup>See also the special issue on 'advancing the individual-based modeling approach' of the journal *Natural Resource Modeling*, Volume 15, Number 1, Spring 2002.

<sup>12</sup>On the one hand, complexity is desirable since it promises realistic modeling. Yet as Adami (2002, p. 134) notes "... to some extent, the modeling of complex systems defeats its purpose if the complexity cannot be *reduced*."

<sup>13</sup>The changes that would have to be made for multiple patches in the present approach are outlined at the end of section 2.

We will now complete the description of the ecosystem allocation mechanism. The demand and supply functions (5) are defined for alternative price vectors  $\mathbf{p}$  taken as given by all organisms. It is now necessary to determine that particular price vector which renders compatible all (decentralized) plans of demanding and supplying biomass. In terms of the formal model we introduce the following *definition of short-run ecosystem equilibrium*:

Let the vector of predation power,  $\mathbf{e} := (e_1, \dots, e_N) \in \mathbb{R}_+^N$  and the ecosystem's resource endowment  $r \in \mathbb{R}_{++}$  be given. For any given vector of populations  $\mathbf{n}$  the ecosystem exhibits a short-run equilibrium at the price vector  $\mathbf{p}^*$ , if  $\mathbf{p}^*$  satisfies

$$r \geq \sum_i n_i X^{i0}(\mathbf{p}^*, e_i, \mathbf{n}), \quad (9a)$$

$$n_i Z^i(\mathbf{p}^*, e_i, \mathbf{n}) = \sum_{j \neq i} n_j X^{ji}(\mathbf{p}^*, e_j, \mathbf{n}) \quad \text{for } i = 1, \dots, N. \quad (9b)$$

Conceptually, this notion of short-run ecosystem equilibrium is the same as the Debreu-type general perfectly competitive equilibrium from neoclassical economic theory. (9a) and (9b) are market clearing conditions in economics. Yet in the present context, the 'market clearing' price vector  $\mathbf{p}^*$  is interpreted as a vector of scarcity indicators which, if perceived correctly by all organisms, make all biomass transactions compatible. This compatibility, in turn, is indispensable for characterizing a vector of biomass transactions  $((\mathbf{x}_1, z_1), \dots, (\mathbf{x}_N, z_N))$  as being feasible. In that perspective, assuming that a short-run ecosystem equilibrium is reached (as we will do) amounts to suggesting that all organisms have rational expectations concerning the 'prevailing' scarcity of their own and their prey species' biomass.<sup>14</sup>

Whether a price vector  $\mathbf{p}^*$  exists that solves the formidable coordination problem (9) is not a trivial issue. Although it is not the purpose of the present paper to tackle the mathematical-technical intricacies of existence rigorously, a few remarks on that issue are in order indicating some differences of the existence issue between economic models and the present ecosystem model. Observe first that in (9b) the strict equality sign is used rather than the  $\geq$  sign as is common in economic models with 'free disposal'. In the ecosystem the resource may be abundant but biomass transactions are such that the intake of biomass by the predator is always equal to the prey's loss of own biomass. Hence abundance cannot mean that in short-run equilibrium demand falls short of supply. Consequently we have  $p_i^* > 0$  for all  $i > 0$  with positive short-run equilibrium demand. Nonetheless, under certain conditions  $p_i^* = 0$  for  $i > 0$  is feasible. To see that suppose species  $i$  is a top predator, i.e. a species that is not preyed upon by any other species (hence  $x_{ji} = 0$  for all  $j$ ). If  $p_i > 0$  would prevail,  $z_i > 0$  might be optimal for organism  $i$  resulting in the excess supply

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<sup>14</sup>The model doesn't offer an explanation as to how such a short-run equilibrium is brought about at each point in time. But it shares this feature with all economic general equilibrium models that represent an important and widely undisputed part of the mainstream body of economic theory.

$z_i - \sum_{j \neq i} x_{ji} = z_i > 0$ . Such an excess supply is effectively avoided only if  $p_i^* = 0$  since in that case organism  $i$  cannot earn an income by supplying own biomass and hence will not offer own biomass.<sup>15</sup>

Another interesting point is whether the nonsatiation assumption in (1), i.e.  $B_{x_{ij}}^i > 0$  for all  $x_{ij} \geq 0$ , can be considered realistic.<sup>16</sup> If it is dropped as in Eichner and Pethig (2003) serious existence problems arise (and such problems would also arise in economic models) even in an ecosystem model with a simple food chain. In Eichner and Pethig (2004) as well as in the subsequent parametric models the nonsatiation assumption is applied such that all short-run equilibrium prices are positive except those for top predators.

The short-run equilibrium definition also allows for an interesting interpretation of the parameters  $e_i$  which we have referred to as organism  $i$ 's predation power. Consider (2) as an equality and rearrange it as follows

$$\begin{aligned}
& p_i z_i - \sum_{j \neq i} p_j x_{ij} = p_0 x_{i0} - e_i \\
\iff & p_i n_i z_i - \sum_{j \neq i} p_j n_i x_{ij} = p_0 n_i x_{i0} - e_i n_i \\
\iff & \sum_i p_i n_i z_i - \sum_i \sum_{j \neq i} p_j n_i x_{ij} = \sum_i p_0 n_i x_{i0} - \sum_i e_i n_i \\
\iff & \sum_i p_i \left( n_i z_i - \sum_{h \neq i} n_h x_{hi} \right) = p_0 \sum_i n_i x_{i0} - \sum_i e_i n_i. \tag{10}
\end{aligned}$$

In view of (9b) the right side of (10) is zero in short-run equilibrium. Moreover, (9a) yields  $\sum_i n_i x_{i0} = r$ , and therefore

$$p_0 r = \sum_i e_i n_i \tag{11}$$

follows from (10). According to (11) the resource rent is equal to total exogenous income. This rent represents an indicator of the value of the entire ecosystem since all species depend on the resource in a direct or indirect way. A somewhat unconventional way of looking at that result is to suggest that the resource is owned by all organisms with organism  $i$  being entitled to the share  $\theta_i := e_i / \sum_j e_j n_j$  of the resource rent. From that definition of  $\theta_i$  and (11) we readily infer  $e_i = \theta_i \sum_j e_j n_j = \theta_i p_0 r$ . This equation suggests to interpret the predation power  $e_i$  as a (natural) capital income accruing to organism  $i$  owing to its property rights in the resource. The greater its ownership share is the more powerful organism  $i$  is relative to organisms of other species. Note also, that the share  $\theta_i$  is homogeneous of degree zero in the parameters  $e_1, \dots, e_N$  and is strictly decreasing in all populations.

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<sup>15</sup>Owing to this observation one can also assume (as we do in section 3) that a market for the biomass of top predator species doesn't exist.

<sup>16</sup>With respect to his net energy function, Tschirhart (2000, 2002, 2004) assumes satiation.

Solving (9) with respect to prices and inserting the resulting short-run equilibrium prices into the demand and supply functions (5) we obtain the short-run equilibrium demands and supplies,  $(\mathbf{x}_i, z_i)$  all  $i$ , as functions of species populations. In formal terms we write  $x_i = \tilde{X}^i(\mathbf{n})$  and  $z_i = \tilde{Z}^i(\mathbf{n})$  for  $i = 1, \dots, N$ . At the end of each short-run period, each organism has generated the positive or negative net offspring  $B^i [\tilde{\mathbf{X}}^{i-1}(\mathbf{n}), \tilde{Z}^i(\mathbf{n}), n_i]$ . If positive, the net offspring generated by the representative organism can be identified as offspring. If negative, the net offspring indicates the organism's probability to survive the period. We normalize each organism as consisting of one unit of (own) biomass and write

$$\dot{n}_i = \frac{dn_i}{dt} = n_i B^i [\tilde{\mathbf{X}}^{i-1}(\mathbf{n}), \tilde{Z}^i(\mathbf{n}), n_i] \quad i = 1, \dots, N. \quad (12)$$

The differential equations (12) form the decisive link between the short-run equilibrium allocations and the populations updates. They describe the interdependent development of all populations over time as determined by micro-level intra-ecosystem biomass transactions at each point in time. It is crucial to emphasize that the population dynamics in (12) are not *assumed* ad hoc but rather *derived* from the underlying ecosystem model of the short-run period. That ecosystem model provides a theoretical microfoundation for (12) with the consequence that the properties of (12) depend on the assumptions regarding offspring generation, behavior and allocation rules in the short-run ecosystem model.

The system of differential equations (12) is too general to provide specific information on the growth or decline of species populations in time. The rest of the paper (section 3) will aim at making progress by reducing the number of species to three and introducing simple parametric forms for the net offspring functions. But before we proceed along these lines some further discussion is in order on the short-run ecosystem model developed above regarding the assumption that this model is confined to a single patch.

In the real world, ecosystems are patchy, of course, and that patchiness has an important impact on predator-prey relations which is similar, in principle, to the impact of heterogeneous regions or countries on interregional or international economic activities under a free-trade regime. Hence, conceptually, our single-patch ecosystem model can be extended to a multiple-patch habitat in a similar way as the economic model of a closed (and spaceless) economy is extended to an economic model with many regions or countries which is extensively done in the economic subdisciplines of regional science and international economics. Following this line of analogy in modeling a multi-patch framework one obviously needs to introduce a price vector for every patch and along with that an appropriate modification of the transactions constraint (2). Mobile organisms develop demand for some prey biomass across regions and optimize by comparing regional prices of the prey as well as regional predation risks. Whether equilibrium prices will equalize or differ between regions depends on the mobility or immobility of species and hence on whether markets

are regional or global. For example, if a mobile animal demands some prey across regions, arbitrage purchases will induce a tendency toward interregional equalization of both the price of that prey and predation risk. On the other hand, plants are territorial (i.e. not mobile) and hence a plant located in patch 1 cannot tap into a resource (e.g. sunlight) in patch 2. Hence regional resource prices will likely differ at least until a steady state is reached (in which case we conjecture the interregional equalization of all equilibrium prices). Some further qualifications apply in case of imperfect or costly mobility. As these sketchy remarks show, the methodology of our short-run ecosystem model can be readily extended to a multiple-patch framework and promises, moreover, interesting if not provoking implications. To elaborate and explore such an approach in a systematic way is, however, beyond the scope of the present paper.

### 3 A parametric specification of a three-species ecosystem model

To obtain additional information on the characteristics of population growth we proceed by introducing a parametric net-offspring function of the Cobb-Douglas type.<sup>17</sup> To further simplify we restrict our attention to a food web with three species. Species 1 and 2 feed on the resource,  $r$ , and species 3 feeds on both species 1 and 2. The corresponding net offspring functions are

$$B^1(x_{10}, z_1, n_1) = A^1(n_1) \cdot x_{10}^{\alpha_1} \cdot (\bar{z}_1 - z_1)^{\beta_1} - \gamma_1, \quad (13a)$$

$$B^2(x_{20}, z_2, n_2) = A^2(n_2) \cdot x_{20}^{\alpha_2} \cdot (\bar{z}_2 - z_2)^{\beta_2} - \gamma_2, \quad (13b)$$

$$B^3(x_{31}, x_{32}, z_3, n_3) = A^3(n_3) \cdot x_{31}^{\alpha_3} \cdot x_{32}^{\phi_3} \cdot (\bar{z}_3 - z_3)^{\beta_3} - \gamma_3, \quad (13c)$$

where

$$A^i(n_i) := \min \left[ 1, \frac{n_i}{\tilde{n}_i} \right], \quad (14)$$

and where  $\alpha_i, \beta_i, \phi_3 \in ]0, 1[$ ,  $\tilde{n}_i > 0$ , and  $\gamma_i > 0$ .

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<sup>17</sup>This parametric functional form had been introduced into the economic literature by Cobb and Douglas (1928) who employed it as an aggregate production function in empirical studies. Since then it plays a prominent role in microeconomic research and textbooks representing production functions or even utility functions. If the model presented here will be used for large-scale numerical simulations one may want to replace the Cobb-Douglas functions by its generalized form, the so called CES functions (with CES for constant elasticity of substitution), which allow for more parametric flexibility. But analytical convenience is not the only reason for choosing here the simpler Cobb-Douglas form. We are going to demonstrate below that the population dynamics *induced* by our ecosystem model with Cobb-Douglas are very close to those which are *assumed* in conventional macro models of population ecology.

To describe the parameters of the net offspring functions, we restrict our focus on (13a).  $\tilde{n}_1$  has been specified above as the critical population level of species 1. If  $n_1$  drops below  $\tilde{n}_1$ , reproduction is hampered (Allee's Effect).  $\gamma_1$  is the death rate. Without any food intake  $x_{10} = 0$  or with maximum possible loss of own biomass ( $z_1 = \bar{z}_1$ ) net offspring would be negative:  $B^1(\cdot) = -\gamma_1$ . The role of  $\alpha_1$  is further clarified as follows:

$$\begin{aligned}\frac{\partial B^1}{\partial x_{10}} &= \alpha_1 \cdot \frac{B^1(\cdot) + \gamma_1}{x_{10}} > 0, & \frac{\partial^2 B^1}{\partial x_{10}^2} &= \alpha_1 \cdot (\alpha_1 - 1) \cdot \frac{B^1(\cdot) + \gamma_1}{x_{10}^2} < 0, \\ \frac{\partial B^1}{\partial \alpha_1} &= [B^1(\cdot) + \gamma_1] \cdot \ln x_{10} > 0.\end{aligned}$$

An increase in prey biomass intake increases net offspring but less than proportionate. Moreover, an increase in the parameter  $\alpha_1$  also increases net offspring. Along the same lines we obtain

$$\frac{\partial B^1}{\partial z_1} < 0, \quad \frac{\partial^2 B^1}{\partial z_1^2} < 0, \quad \frac{\partial B^1}{\partial \beta_1} > 0.$$

An increase in the loss of own biomass to predators reduces reproduction more than proportionate. An increase in the parameter  $\beta_1$  increases net offspring.

Solving (3) for the functions (13) yields the biomass demands and supplies

$$x_{10} = \frac{\alpha_1 e_1 + \alpha_1 p_1 \bar{z}_1}{(\alpha_1 + \beta_1) p_0}, \quad z_1 = \frac{\alpha_1 \bar{z}_1 p_1 - \beta_1 e_1}{(\alpha_1 + \beta_1) p_1}, \quad (15a)$$

$$x_{20} = \frac{\alpha_2 e_2 + \alpha_2 p_2 \bar{z}_2}{(\alpha_2 + \beta_2) p_0}, \quad z_2 = \frac{\alpha_2 \bar{z}_2 p_2 - \beta_2 e_2}{(\alpha_2 + \beta_2) p_2}, \quad (15b)$$

$$x_{31} = \frac{\alpha_3 e_3}{(\alpha_3 + \phi_3) p_1}, \quad x_{32} = \frac{\phi_3 e_3}{(\alpha_3 + \phi_3) p_2}. \quad (15c)$$

The properties of these functions conform to intuition: The demand curves slope down and the supply curves slope up.<sup>18</sup> Moreover, an increase in an organism's predation power raises its demand for prey biomass but reduces its supply of own biomass.

Inserting (15) in (5) enables us to completely characterize the short-run ecosystem

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<sup>18</sup>These properties of demand and supply functions are due, of course, to the Cobb-Douglas specification (13) of the net offspring functions. Other parametric functional forms, e.g. CES-functions, would allow for downward sloping supply functions that would correspond to the 'backward bending labor supply curves' discussed in the economic consumer theory.



equilibrium:

$$p_0 = P^0 \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ + + + + + + - \end{pmatrix} := \frac{n_1 e_1 + n_2 e_2 + n_3 e_3}{r}, \quad (16a)$$

$$p_1 = P^1 \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ + 0 + - 0 + 0 \end{pmatrix} := \frac{n_1 \beta_1 (\alpha_3 + \phi_3) e_1 + n_3 \alpha_3 (\alpha_1 + \beta_1) e_3}{n_1 \alpha_1 (\alpha_3 + \phi_3) \bar{z}_1}, \quad (16b)$$

$$p_2 = P^2 \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ 0 + + 0 - + 0 \end{pmatrix} := \frac{n_2 \beta_2 (\alpha_3 + \phi_3) e_2 + n_3 \phi_3 (\alpha_2 + \beta_2) e_3}{n_2 \alpha_2 (\alpha_3 + \phi_3) \bar{z}_2}, \quad (16c)$$

$$x_{10} = \tilde{X}^{10} \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ + - ? ? - ? + \end{pmatrix} := \frac{r}{n_1} \cdot \frac{n_1 (\alpha_3 + \phi_3) e_1 + n_3 \alpha_3 e_3}{(\alpha_3 + \phi_3) (n_1 e_1 + n_2 e_2 + n_3 e_3)}, \quad (16d)$$

$$x_{20} = \tilde{X}^{20} \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ - + ? - ? ? + \end{pmatrix} := \frac{r}{n_2} \cdot \frac{n_2 (\alpha_3 + \phi_3) e_2 + n_3 \phi_3 e_3}{(\alpha_3 + \phi_3) (n_1 e_1 + n_2 e_2 + n_3 e_3)}, \quad (16e)$$

$$x_{31} = \tilde{X}^{31} \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ - 0 + + 0 - 0 \end{pmatrix} := \frac{n_1 \alpha_1 \alpha_3 e_3 \bar{z}_1}{n_1 \beta_1 (\alpha_3 + \phi_3) e_1 + n_3 \alpha_3 (\alpha_1 + \beta_1) e_3}, \quad (16f)$$

$$x_{32} = \tilde{X}^{32} \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ 0 - + 0 0 + - 0 \end{pmatrix} := \frac{n_2 \alpha_2 \phi_3 e_3 \bar{z}_2}{n_2 \beta_2 (\alpha_3 + \phi_3) e_2 + n_3 \phi_3 (\alpha_2 + \beta_2) e_3}, \quad (16g)$$

$$z_1 = \tilde{Z}^1 \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ - 0 + - 0 + 0 \end{pmatrix} := \frac{n_3 \alpha_1 \alpha_3 e_3 \bar{z}_1}{n_1 \beta_1 (\alpha_3 + \phi_3) e_1 + n_3 \alpha_3 (\alpha_1 + \beta_1) e_3}, \quad (16h)$$

$$z_2 = \tilde{Z}^2 \begin{pmatrix} e_1, e_2, e_3, n_1, n_2, n_3, r \\ 0 - + 0 - + 0 \end{pmatrix} := \frac{n_3 \alpha_2 \phi_3 e_3 \bar{z}_2}{n_2 \beta_2 (\alpha_3 + \phi_3) e_2 + n_3 \phi_3 (\alpha_2 + \beta_2) e_3}. \quad (16i)$$

The equations (16) demonstrate that with the parametric functions (13) and (14) a short-run equilibrium of the parametric three-species ecosystem model exists and is unique with all short-run equilibrium prices being strictly positive. Observe that the supplies of own biomass,  $z_1$  and  $z_2$ , are positive, too, which means that in short-run equilibrium the organisms 1 and 2 prefer to expand their intake of prey biomass by sacrificing some own biomass rather than being satisfied with the amount of food they are able to secure by exclusively relying on their predation power. The short-run equilibrium prices (16a)-(16c) are scarcity indicators for the resource and for the species 1 and 2, respectively. We have marked in (16) by plus and minus signs how short-run equilibrium prices and transactions react to parametric changes in predation power and population sizes to indicate how rich our (short-run) ecosystem model is with respect to testable hypotheses. For example, it conforms to one's intuition that an organism's short-run equilibrium intake of prey biomass rises [sacrifice of own biomass shrinks] with own predation power and declines [increases] with growing predation power of its predator. Further discussions of these comparative-static effects are left to the reader.

Combining (16), (13) and (12) yields the differential equations of population growth

$$\dot{n}_1 = n_1 \cdot G^1(r, n_1, n_2, n_3), \quad (17a)$$

$$\dot{n}_2 = n_2 \cdot G^2(r, n_1, n_2, n_3), \quad (17b)$$

$$\dot{n}_3 = n_3 \cdot G^3(n_1, n_2, n_3), \quad (17c)$$

where

$$G^1(\cdot) = A^1(n_1) \cdot \left[ \frac{r}{n_1} \cdot \frac{n_1(\alpha_3 + \phi_3)e_1 + n_3\alpha_3e_3}{(\alpha_3 + \phi_3)(n_1e_1 + n_2e_2 + n_3e_3)} \right]^{\alpha_1} \cdot \left[ \bar{z}_1 \cdot \frac{n_1\beta_1(\alpha_3 + \phi_3)e_1 + n_3\beta_1\alpha_3e_3}{n_1\beta_1(\alpha_3 + \phi_3)e_1 + n_3\alpha_3(\alpha_1 + \beta_1)e_3} \right]^{\beta_1} - \gamma_1, \quad (18a)$$

$$G^2(\cdot) = A^2(n_2) \cdot \left[ \frac{r}{n_2} \cdot \frac{n_2(\alpha_3 + \phi_3)e_2 + n_3\phi_3e_3}{(\alpha_3 + \phi_3)(n_1e_1 + n_2e_2 + n_3e_3)} \right]^{\alpha_2} \cdot \left[ \bar{z}_2 \cdot \frac{n_2\beta_2(\alpha_3 + \phi_3)e_2 + n_3\beta_2\phi_3e_3}{n_2\beta_2(\alpha_3 + \phi_3)e_2 + n_3\phi_3(\alpha_2 + \beta_2)e_3} \right]^{\beta_2} - \gamma_2, \quad (18b)$$

$$G^3(\cdot) = A^3(n_3) \cdot \left[ \frac{n_1\alpha_1\alpha_3e_3\bar{z}_1}{n_1\beta_1(\alpha_3 + \phi_3)e_1 + n_3\alpha_3(\alpha_1 + \beta_1)e_3} \right]^{\alpha_3} \cdot \left[ \frac{n_2\alpha_2\phi_3e_3\bar{z}_2}{n_2\beta_2(\alpha_3 + \phi_3)e_2 + n_3\phi_3(\alpha_2 + \beta_2)e_3} \right]^{\phi_3} \cdot \bar{z}_3^{\beta_3} - \gamma_3. \quad (18c)$$

The system (17) of differential equations fully determines the dynamics of the three-species model. It is worth noting that while the Allee's Law terms  $A^i(n_i)$  from (9a) have not affected the allocation (16) of the short-run ecosystem equilibrium at all they do play an important role in the growth functions (17).

A full investigation of the system (17) is clearly beyond the scope of the present paper. To shed more light on the development of populations we proceed by presenting three numerical examples (section 3.1). Next we consider the simplest case where species 2 and 3 are absent (section 3.2). After that we turn our attention to the case where species 2 is absent (section 3.3) which turns our food web model into a predator-prey model. Finally we consider the case where species 3 is absent which amounts to modelling resource competition.

### 3.1 Numerical simulations

In this section we present three numerical examples which are calculated with the help of the computer program Mathematica.<sup>19</sup> In these examples the initial populations are assumed to be  $n_i(t) = 20$  for  $i = 1, 2, 3$  and the critical population levels are set equal to  $\tilde{n}_i = 1$  for  $i = 1, 2, 3$ .

**Example 1:** In example 1 the parameters are chosen as follows:  $\alpha_1 = 0.4$ ,  $\alpha_2 = 0.5$ ,  $\alpha_3 = 0.5$ ,  $\beta_1 = \beta_2 = \beta_3 = 0.5$ ,  $\phi_3 = 0.1$ ,  $\gamma_1 = 2$ ,  $\gamma_2 = 1.5$ ,  $\gamma_3 = 1.5$ ,  $e_1 = 4$ ,  $e_2 = 1$ ,  $e_3 = 8$ ,  $r = 100$ ,  $\bar{z}_1 = 4$ ,  $\bar{z}_2 = 9$  and  $\bar{z}_3 = 4$ .

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<sup>19</sup>The program for simulations is available from the authors upon request.

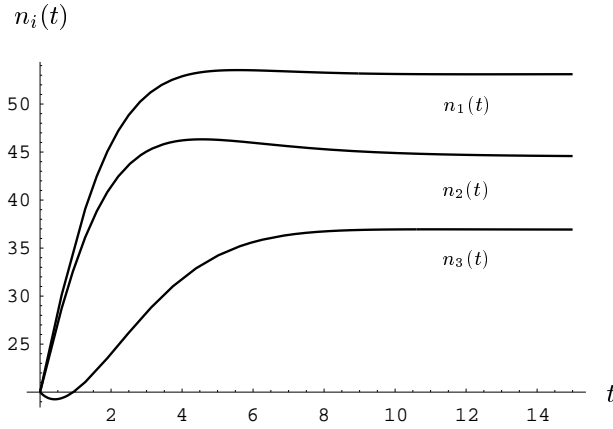


Figure 1: Coexistence of three species

Figure 1 illustrates the population growth in example 1. Initially the populations of species 1 and 2 grow rapidly while the population of species 3 declines from  $t = 0$  to  $t = 0.5$ . Obviously, in that first time period the populations of species 1 and 2 are too low to provide enough food for species 3 but with increasing prey populations food becomes more abundant such that the predator population recovers and increases as of  $t \geq 0.5$ . It is also interesting to observe that the growth of the predator population levels (that levels off eventually) increases predation pressure which, in turn, causes a slight decline in both prey populations after  $t = 3$ . All populations converge to their equilibrium<sup>20</sup> levels

$$n_1 = 53.13, n_2 = 44.50 \quad \text{and} \quad n_3 = 36.93.$$

The populations of species 1 and 2 reach their equilibrium level from above and the population of species 3 from below.

**Example 2:** This example serves to demonstrate the case where the predator species goes extinct. We use the same parameter values as in example 1 except for the death rate of the predator species 3 which is now raised from  $\gamma_3 = 1.5$  to  $\gamma_3 = 3$ .

As shown in figure 2 raising the predator death rate results in a decline of the predator population while both prey populations increase. At  $t = 10.2$  the predator population hits its critical level  $\tilde{n}_3 = 1$  and from that time on Allee's law applies to species 3. The associated time paths for  $t > 10.2$  are depicted in figure 3. The predator population becomes extinct while the prey populations grow and converge to their equilibrium levels

$$n_1 = 81.45 \quad \text{and} \quad n_2 = 74.20.$$

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<sup>20</sup>When we say equilibrium without the prefix short-run it is a steady state (stationary point).

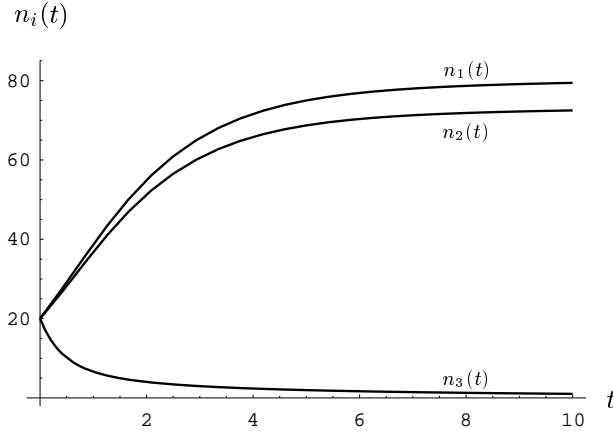


Figure 2: Predator extinction

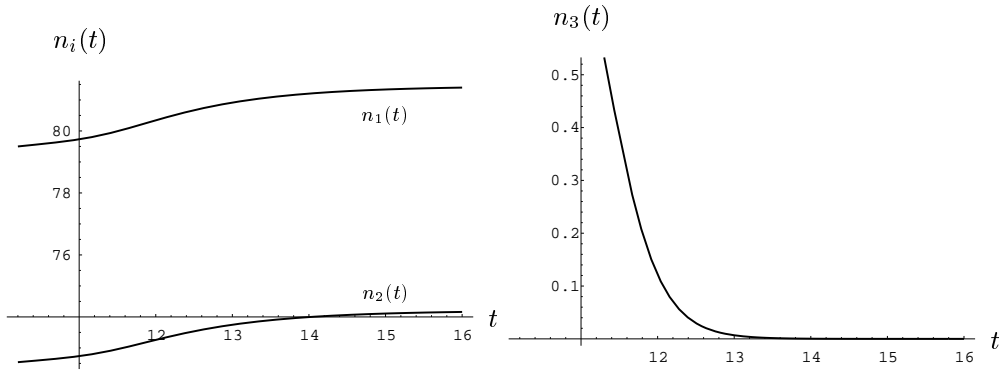


Figure 3: Predator extinction,  $n_3 \leq \tilde{n}_3$

**Example 3:** In our last example we construct the case of prey extinction. Here we use the same parameter values as in example 1 but change species 2's death rate from  $\gamma_2 = 1.5$  in example 1 to  $\gamma_2 = 6$ . The corresponding population growth paths are illustrated in figures 4-7. In figure 4 the population of species 1 increases, the population of species 2 decreases rapidly and the population of species 3 decreases slowly. At  $t = 1.755$  the population of species 2 hits its critical level  $\tilde{n}_2 = 1$ . In the next time period  $1.755 \leq t \leq 6.098$  shown in figure 5 the population of species 3 shrinks rapidly and hits its critical level  $\tilde{n}_3 = 1$  at  $t = 6.098$  in the left panel of figure 5 while the population of species 2 is still positive (as can be seen in right panel of figure 5). Figures 6 and 7 characterize the population growth for the time periods  $6.098 \leq t \leq 9.52$  and  $t \geq 9.52$ , respectively. They show that species 2 is the first to perish and then species 3 goes extinct while species 1 approaches its equilibrium population  $n_1 = 100$ .

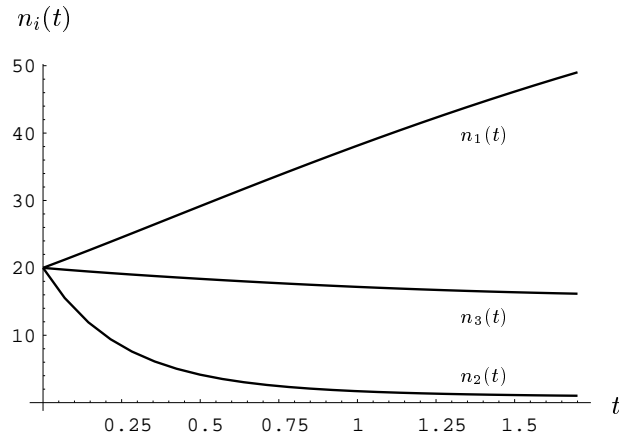


Figure 4: Prey extinction

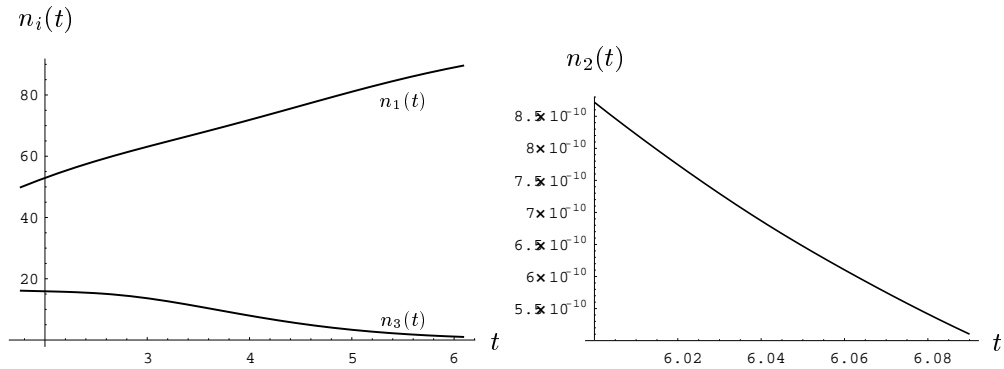


Figure 5: Prey extinction,  $n_2 < \tilde{n}_2$

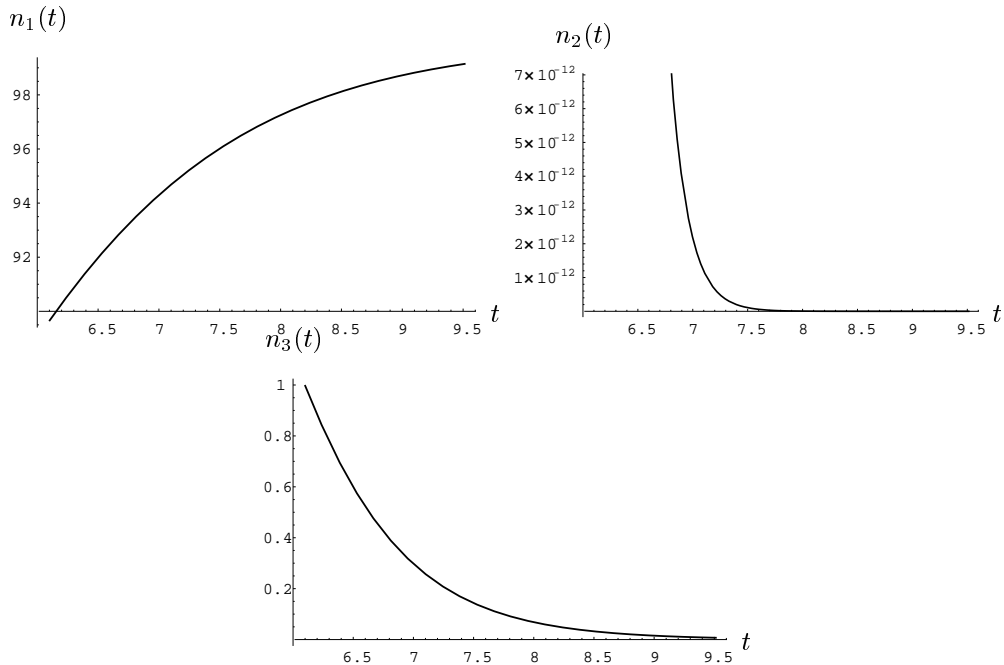


Figure 6: Prey extinction,  $n_2 < \tilde{n}_2$ ,  $n_3 < \tilde{n}_3$

It is a general feature of our model that if one of the prey species becomes extinct then the predator species cannot survive either. To see that consider the case where species

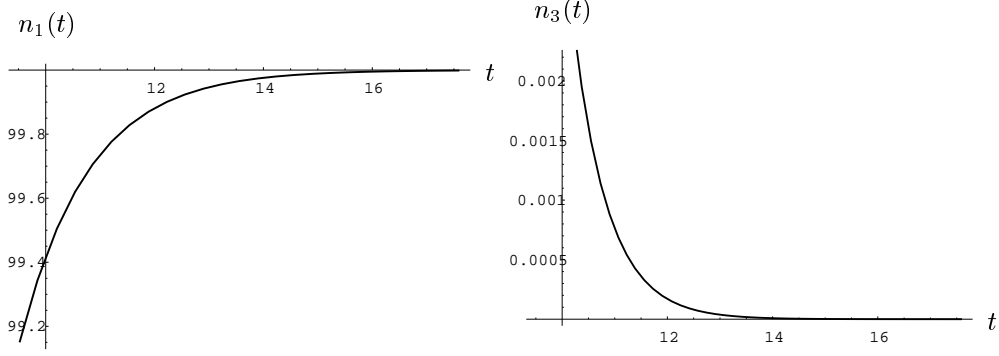


Figure 7: Prey extinction,  $n_2 = 0$ ,  $n_3 < \tilde{n}_3$

1 goes extinct ( $n_1 = 0$ ). Then owing to (16f) the predator's demand for biomass of species 1 is  $x_{31} = 0$  and the predator's population growth simplifies to  $\dot{n}_3 = -n_3\gamma_3$  with the consequence that the predator goes extinct, too. The simple reason for that feature is the Cobb-Douglas specification of organism 3's net offspring function. With Cobb-Douglas, both prey biomass intakes are *essential* inputs for the survival of species 3. If one would replace the Cobb-Douglas function by a CES function with an elasticity of substitution unequal to one it would be possible to generate a scenario in which species 2 perishes while species 1 and 3 prevail.

### 3.2 Microfounded dynamics of a single species: the logistic growth function

If the ecosystem is inhabited by species 1 only, its population growth is obtained by setting  $n_2 = n_3 = 0$  in equation (18a):

$$\dot{n}_1 = \tilde{F}(n_1) := n_1 \cdot \left[ \frac{n_1}{\tilde{n}_1} \cdot \left( \frac{r}{n_1} \right)^{\alpha_1} \cdot (\bar{z}_1)^{\beta_1} - \gamma_1 \right] \quad \text{for } n_1 \in [0, \tilde{n}_1], \quad (19a)$$

$$\dot{n}_1 = F(n_1) := n_1 \cdot \left[ \left( \frac{r}{n_1} \right)^{\alpha_1} \cdot (\bar{z}_1)^{\beta_1} - \gamma_1 \right] \quad \text{for } n_1 \geq \tilde{n}_1. \quad (19b)$$

Consider first the function  $F$  from (19b) and ignore temporarily the constraint  $n_1 \geq \tilde{n}_1$  on its domain. Closer inspection of (19b) shows that

$$F_{n_1 n_1} = -\frac{(1 - \alpha_1)\alpha_1 r^{\alpha_1} \bar{z}_1^{\beta_1}}{n_1^{1+\alpha_1}} < 0, \quad (20a)$$

$$F_{n_1} \geq 0 \iff n_1 \leq r \cdot \left( \frac{(1 - \alpha_1)\bar{z}_1^{\beta_1}}{\gamma_1} \right)^{\frac{1}{\alpha_1}} =: \hat{n}_1, \quad (20b)$$

$$F(n_1) = 0 \iff \left[ n_1 = 0 \quad \text{or} \quad r \cdot \frac{\bar{z}_1^{\beta_1/\alpha_1}}{\gamma_1^{1/\alpha_1}} =: \bar{n}_1 \right]. \quad (20c)$$

The properties (20) of the function  $F$  reveal that  $F$  is a logistic growth function of the Verhulst-Pearl type (Verhulst (1838)):  $F$  is strictly concave and attains its unique maximum

at  $\hat{n}_1 := r \cdot \left[ (1 - \alpha_1) \bar{z}_1^{\beta_1} / \gamma_1 \right]^{\frac{1}{\alpha_1}}$ .  $F(n_1) = 0$  is satisfied at  $n_1 = 0$  and  $n_1 = \bar{n}_1 > 0$  where  $\bar{n}_1$  is known as the carrying capacity of species 1. As (20c) reveals, the carrying capacity is increasing in  $r$  which is exactly what the extant, more recent literature emphasizes. For example, Swanson (1994, p. 811) argues that on land, "... the amount of habitat available to a given species ... is probably the single most important factor determining species viability in the short and the medium run" and he sets up a model of resource harvesting where the 'natural' growth rate of a biological resource is assumed to be affected by the allotment of natural habitat in the same way as in (19b). Note, however, that the dependence of the carrying capacity on the size of the resource (or size of habitat, respectively) is not *assumed* in the model of the present paper but rather is *derived* from more basic assumptions.

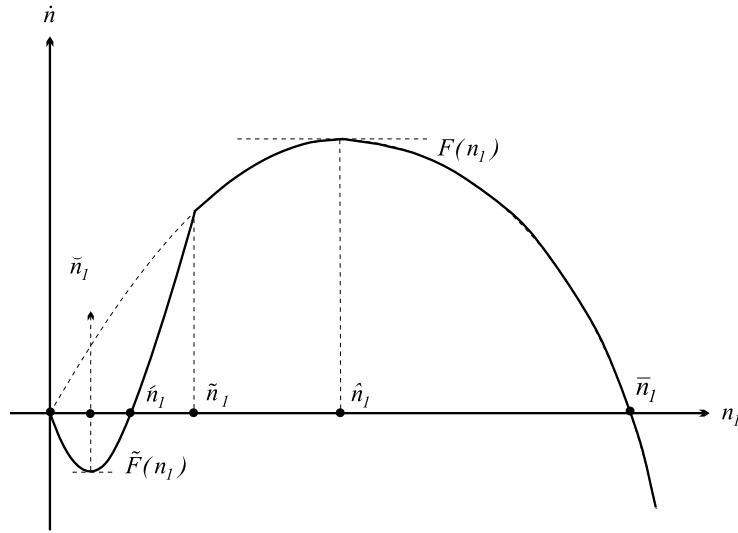


Figure 8: The logistic growth function for species

We now reintroduce the constraint  $n_1 \geq \tilde{n}_1$  on the domain of the function  $F$ . In function  $\tilde{F}$  from (19a)  $\tilde{n}_1 > 0$  can arbitrarily be chosen, in principle, although setting  $\tilde{n}_1 \geq \hat{n}_1$  would seem to be an implausible specification. Obviously we have  $F(\tilde{n}_1) = \tilde{F}(\tilde{n}_1)$  which implies that the differential equation (17a) is continuous on  $n_1 \in [0, \infty[$ . Differentiation of  $\tilde{F}$  with respect to  $n_1$  yields

$$\tilde{F}_{n_1} = \frac{(2 - \alpha_1)r^{\alpha_1} \bar{z}_1^{\beta_1}}{\tilde{n}_1} n_1^{1-\alpha_1} - \gamma_1 < 0, \quad (21a)$$

$$\tilde{F}_{n_1 n_1} = \frac{(2 - \alpha_1)r^{\alpha_1} \bar{z}_1^{\beta_1}}{\tilde{n}_1 n_1^{\alpha_1}} > 0. \quad (21b)$$

Hence the function  $\tilde{F}$  is strictly convex and attains its unique minimum at

$$\check{n}_1 := \frac{\gamma_1 \tilde{n}_1}{(2 - \alpha_1)r^{\alpha_1} \bar{z}_1^{\beta_1}} > 0.$$

From  $\tilde{F}(n_1) = 0$  at  $n_1 = 0$  and  $\tilde{F}_{n_1} \leq 0$  for  $n_1 \leq \tilde{n}_1$  follows  $\tilde{F}(\tilde{n}_1) < 0$ . Moreover, since  $\tilde{F}(\tilde{n}_1) > 0$  there exists  $\hat{n}_1 \in [\tilde{n}_1, \tilde{n}_1]$  such that  $\tilde{F}(\hat{n}_1) = 0$ . Invoking (19b) we readily calculate  $\hat{n}_1 = \left( \gamma_1 \tilde{n}_1 / (r^{\alpha_1} \bar{z}_1^{\beta_1}) \right)^{1/(1-\alpha_1)}$ . Summing up, the growth function (19) exhibits three equilibria:  $n_1 = 0$ ,  $\hat{n}_1 > 0$  and  $\bar{n}_1 > \hat{n}_1$  where  $[0, \hat{n}_1[$  and  $] \hat{n}_1, \infty[$  are the basins of attraction for  $n_1 = 0$  and  $\bar{n}_1$ , respectively. Figure 8 illustrates the growth function (19) where the dashed line represents the graph of the function  $F$  from (19a) on the interval  $[0, \tilde{n}_1]$  on which  $F$  is not defined.

### 3.3 Microfounded population dynamics of a predator-prey system

Suppose now the initial situation is characterized by positive  $n_1$  and  $n_3$  and  $n_2 = 0$ . In this case the equations (18a) and (18c) yield<sup>21</sup>

$$\dot{n}_1 = n_1 \cdot \left[ A^1(n_1) \cdot \left( \frac{r}{n_1} \right)^{\alpha_1} \cdot \left( \bar{z}_1 \cdot \frac{\beta_1(n_1 e_1 + n_3 e_3)}{\beta_1(n_1 e_1 + n_3 e_3) + \alpha_1 n_3 e_3} \right)^{\beta_1} - \gamma_1 \right], \quad (22a)$$

$$\dot{n}_3 = n_3 \cdot \left[ A^3(n_3) \cdot \left( \frac{n_1 \alpha_1 e_3 \bar{z}_1}{\beta_1(n_1 e_1 + n_3 e_3) + n_3 \alpha_1 e_3} \right)^{\alpha_3} \cdot \bar{z}_3^{\beta_3} - \gamma_3 \right]. \quad (22b)$$

We normalize the constant  $\bar{z}_3^{\beta_3}$  by setting  $\beta_3 = 0$ . This assumption simplifies the analysis without substantially altering the results ( $\beta_3 > 0$  would merely require to modify some assumptions on parameters). Moreover, we define the new parameters

$$m := \frac{\alpha_1 + \beta_1}{\beta_1} \frac{e_3}{e_1}, \quad f := \frac{\alpha_1 e_3}{\beta_1}, \quad c := \frac{\bar{z}_1}{e_1}.$$

With these qualifications, equations (22a) and (22b) take the form

$$\dot{n}_1 = n_1 \left[ A^1(n_1) \left( \frac{r}{n_1} \right)^{\alpha_1} \left( \frac{c[n_1 e_1 + n_3 e_3]}{n_1 + m n_3} \right)^{\beta_1} - \gamma_1 \right], \quad (23a)$$

$$\dot{n}_3 = n_3 \left[ A^2(n_3) \left( \frac{f c n_1}{n_1 + m n_3} \right)^{\alpha_3} - \gamma_3 \right]. \quad (23b)$$

As the right sides of (23a) and (23b) are not defined at  $(n_1, n_3) = (0, 0)$ , it will be assumed that  $\dot{n}_1 = \dot{n}_3 = 0$  if  $n_1 = n_3 = 0$  by definition. Calculating the limit for  $\lim_{(n_1, n_3) \rightarrow (0, 0)}$  shows that under this assumption both  $\dot{n}_1$  and  $\dot{n}_3$  are continuous on  $\mathbb{R}_+^2$  if  $0 < \alpha_1 < 1$ , although not differentiable at  $(0, 0)$  as shown in appendix A. The following assumptions are supposed to be met in the sequel.

<sup>21</sup>In addition, we have to set  $\phi_3 = 0$  which follows from (15c). Observe that in case of  $n_2 = 0$ , the demand of organism 3 for biomass of species 1 is directly determined by organism 3's budget constraint  $e_3 = p_1 x_{31}$  which yields  $x_{31} = e_3/p_1$ . To be consistent with (15c) we thus have to require  $\alpha_3/(\alpha_3 + \phi_3) = 1$  or equivalently  $\phi_3 = 0$ .



**Assumptions:** The parameters in the equations (23a) and (23b) satisfy  $fc > \gamma_3^{1/\alpha_3}$ . In addition, the initial values of  $n_1$  and  $n_3$  are non-negative. If  $n_1 = n_3 = 0$ , then  $\dot{n}_1 = \dot{n}_3 = 0$ .

We begin with an analysis of system<sup>22</sup> (23) for the special case where  $A^i(n_i) \equiv 1$ ,  $i = 1, 2$ . That is, we temporarily neglect Allee's Law as formulated in equation (14) but we will reintroduce it in section 3.3.2.

### 3.3.1 Neglecting Allee's Law

If  $A^i(n_i) \equiv 1$  in system (23), we refer to (23) as the *simplified system* (23). This system has three equilibria. To begin with, set  $n_1 = 0$  and  $n_3 > 0$ , implying  $\dot{n}_1 = 0$  and  $\dot{n}_3 = -\gamma_3 n_3$ . Thus, there is a first (trivial) equilibrium  $E_0 = (0, 0)$  and there can be no other equilibrium where  $n_1 = 0$ . It is obvious that  $(0, 0)$  is stable along the  $n_3$ -axis. Thus, if there is no prey, the predator will become extinct.

Setting  $n_3 = 0$  and  $n_1 > 0$  implies  $\dot{n}_3 = 0$  and

$$\dot{n}_1 = r^{\alpha_1} \bar{z}_1^{\beta_1} n_1^{1-\alpha_1} - \gamma_1 n_1.$$

It is straightforward that there is a second equilibrium  $E_1$  at<sup>23</sup>

$$(n_1, n_3) = (\bar{n}_1, 0)$$

that is stable along the  $n_1$ -axis. Thus, if there is no predator, the prey population reaches a steady state that is directly proportional to the size of the basic resource,  $r$  (see also section 3.2).

A third equilibrium,  $E_2$ , entails positive populations of both species. If  $n_1 > 0$  and  $n_3 > 0$ , setting  $\dot{n}_3 = 0$  yields

$$n_3 = \underbrace{\frac{fc - \gamma_3^{1/\alpha_3}}{m\gamma_3^{1/\alpha_3}}}_{=:q} n_1 = qn_1. \quad (24)$$

Hence, a positive equilibrium exists if and only if the condition

$$fc > \gamma_3^{1/\alpha_3} \quad (25)$$

holds, which has already been assumed. Since  $\gamma_3^{1/\alpha_3}$  can be expected to be a small number in relation to  $fc$ , this assumption doesn't appear to be restrictive. Upon substitution of (24) into  $\dot{n}_1 = 0$  one gets

$$n_1 = \frac{r}{\gamma_1^{1/\alpha_1}} \left( \frac{c(e_1 + qe_3)}{1 + mq} \right)^{\beta_1/\alpha_1},$$

---

<sup>22</sup>The equations (23a) and (23b) constitute a system of two differential equations. To avoid clumpy phrases we refer to (23a) and (23b) as system (23).

<sup>23</sup>For the definition of  $\bar{n}_1$  we refer to (20c).

which together with (24) describes the positive equilibrium  $E_2$ . Observe that for all equilibria it is true that if an equilibrium population is positive, it is proportional to the size of the basic resource,  $r$ .

As for the stability of the positive steady state, the Jacobian of the simplified system (23) evaluated at  $E_2$  can be shown to have the following pattern of signs (cf. appendix B):

$$\text{sgn}(J) = \text{sgn} \begin{pmatrix} \partial \dot{n}_1 / \partial n_1 & \partial \dot{n}_1 / \partial n_3 \\ \partial \dot{n}_3 / \partial n_1 & \partial \dot{n}_3 / \partial n_3 \end{pmatrix} = \begin{pmatrix} - & - \\ + & - \end{pmatrix}. \quad (26)$$

Therefore,  $\text{Tr}(J) < 0$  and  $|J| > 0$ , implying that the equilibrium  $E_2$  is locally asymptotically stable by the Routh-Hurwitz criterion. These results are summarized as follows:

*There are three equilibria.  $E_0 = (0, 0)$  is locally asymptotically stable along the  $n_3$ -axis,  $E_1 = (\bar{n}_1, 0)$  is locally asymptotically stable along the  $n_1$ -axis, and*

$$E_2 = \left( \frac{r}{\gamma_1^{1/\alpha_1}} \left( \frac{c(e_1 + qe_3)}{1 + mq} \right)^{\beta_1/\alpha_1}, q \frac{r}{\gamma_1^{1/\alpha_1}} \left( \frac{c(e_1 + qe_3)}{1 + mq} \right)^{\beta_1/\alpha_1} \right)$$

*is locally asymptotically stable.*

The global dynamic behavior of solutions can be determined using the phase diagram of figure 9, whose derivation is as follows. From (24), the isocline  $\dot{n}_3 = 0$  is a positively sloped straight line through the origin (unionized with the  $n_1$ -axis) in  $(n_1, n_3)$ -space if condition (25) holds. Setting  $\dot{n}_1 = 0$  and solving for  $n_3$  yields the following expression (unionized with the  $n_3$ -axis) for the isocline  $\dot{n}_1 = 0$ :

$$n_3 = \frac{\beta_1 e_1 n_1 \left[ \bar{z}_1 - \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right]}{e_3 (\alpha_1 + \beta_1) \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} - \beta_1 \bar{z}_1 e_3}. \quad (27)$$

As for the denominator, it is straightforward that

$$\text{denominator} \gtrless 0 \iff n_1 \gtrless r \left( \frac{\beta_1}{\alpha_1 + \beta_1} \bar{z}_1 \right)^{\beta_1/\alpha_1} \frac{1}{\gamma_1^{1/\alpha_1}} =: \underline{n}_1. \quad (28)$$

Thus, there is a vertical asymptote at  $\underline{n}_1$ . Similarly, under the condition  $n_1 > 0$ ,

$$\text{numerator} \gtrless 0 \iff n_1 \gtrless \bar{n}_1. \quad (29)$$

Therefore, the isocline cuts the  $n_1$ -axis at the equilibrium  $E_1$  where  $n_1 = \bar{n}_1 > \underline{n}_1$  (and at the equilibrium  $E_0$ , where  $n_1 = 0$ ). Comparing the sign patterns of the numerator and the denominator shows that the isocline lies below the  $n_1$ -axis for  $0 < n_1 < \underline{n}_1$  and  $n_1 > \bar{n}_1$ , while it lies above the axis if  $\underline{n}_1 < n_1 < \bar{n}_1$ .

As shown in appendix B, the cross partial derivatives are

$$\frac{\partial \dot{n}_1}{\partial n_3} < 0 \quad \text{and} \quad \frac{\partial \dot{n}_3}{\partial n_1} > 0,$$

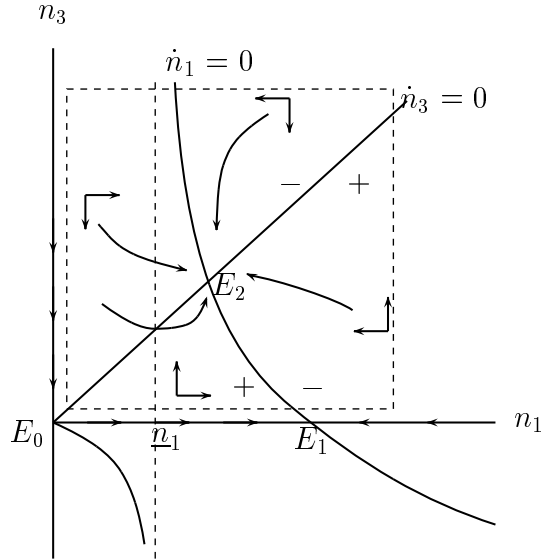


Figure 9: Phase diagram of the simplified system (23)

respectively. These partial derivatives give rise to the + and – signs indicating the directions of motion of the zero isoclines.<sup>24</sup> Putting all this information together yields the phase diagram in figure 9. For the sake of completeness, it is shown in appendix C that the slope of the isocline  $\dot{n}_1 = 0$  is negative if  $\underline{n}_1 < n_1 < \bar{n}_1$ .

The phase diagram reveals that the equilibrium  $E_2$  is globally asymptotically stable for strictly positive initial values. The proof relies on the fact that it is always possible to draw a rectangular closed region from which the trajectories cannot escape (e.g. the dashed rectangle in figure 9). Therefore the differential equations have a solution defined for all  $t \geq 0$  (Hirsch and Smale, 1974, p. 172). According to the Generalized Poincaré-Bendixson Theorem (cf. Perko, 1996, p. 243), any limit point of trajectories must be an equilibrium if there exists neither a closed orbit nor a separatrix cycle. As the region under consideration contains just one equilibrium which is locally asymptotically stable, there is no separatrix cycle. Closed orbits are ruled out by the direction of movements in the four regions separated by the zero-isoclines, or, more rigorously, by Dulac’s criterion (cf. appendix D). It follows that there is just one possible limit point of trajectories if  $t \rightarrow \infty$ , the equilibrium  $E_2$ . This proves global stability. The analysis is summarized as follows:

*Each trajectory of the simplified system (23) converges to an equilibrium. If  $n_1(0) = 0 <$*

<sup>24</sup>Due to the existence of the vertical asymptote, there is one specialty to be taken care of. Above but near the isocline  $\dot{n}_1 = 0$  in the region where  $n_3$  is negative,  $\dot{n}_1 < 0$ . As  $\dot{n}_1 > 0$  below  $\dot{n}_1 = 0$  in the positive region, the question arises where the sign of  $\dot{n}_1$  changes. Inspection of the simplified equation (23a) shows that a sign change of the isocline  $\dot{n}_1 = 0$  derived from (27) (or from  $n_1 = 0$ ) is possible only if the simplified equation (23a) has a vertical asymptote at  $n_1 + mn_3 = 0$ . Thus, if  $n_1 > 0$  the sign change must occur in the irrelevant region where  $n_3 < 0$ .

$n_3(0)$ ,  $\lim_{t \rightarrow \infty} (n_1(t), n_3(t)) = E_0$ . If  $n_1(0) > 0 = n_3(0)$ ,  $\lim_{t \rightarrow \infty} (n_1(t), n_3(t)) = E_1$ . If  $n_1(0) > 0$  and  $n_3(0) > 0$ ,  $\lim_{t \rightarrow \infty} (n_1(t), n_3(t)) = E_2$ .

It is worthwhile to compare the simplified system (23) with the following ratio-dependent predator-prey model recently extensively analyzed in mathematical biology, e.g. by Kuang and Beretta (1998):

$$\dot{n}_1 = n_1 \left[ a \left( 1 - \frac{n_1}{K} \right) - \frac{hn_3}{n_1 + mn_3} \right], \quad (30a)$$

$$\dot{n}_3 = n_3 \left[ \frac{fn_1}{n_1 + mn_3} - d \right]. \quad (30b)$$

Remarkably that the simplified equation (23b) is qualitatively equivalent to (30b). Although (30a) is rather distinct from the simplified equation (23a), the dynamics of both systems are similar if  $fc > \gamma_3^{1/\alpha_3}$  and  $0 < \alpha_1 < 1$  in the microfounded model (23) and  $f > d$  and  $am \geq h$  in the conventional model (30), respectively. Kuang and Beretta (1998) have shown that the latter system possesses a unique and globally stable positive equilibrium if  $f > d$  and  $am \geq h$ . In fact, the phase diagram of (30) can be shown to look exactly like in figure 9 if  $f > d$  and  $am \geq h$ . Empirically, it would be impossible to distinguish whether a given set of observations was generated by model (30) or by the simplified system (23), respectively.

The condition  $fc > \gamma_3^{1/\alpha_3}$  is necessary and (given other assumptions about parameters following from the micro approach) sufficient for the existence of a positive equilibrium in the microfounded model. In contrast,  $f > d$  is just a necessary condition in the biological model (30). If  $am < h$ , such an equilibrium exists only if  $f$  is suitably bounded from above (Kuang and Beretta, 1998, p. 392). In that case, the equations (30) can generate completely different dynamics. E.g., it is possible that the positive equilibrium  $E_2$  is locally but not globally asymptotically stable, and one or both species could become extinct. Moreover, even limit cycles or heteroclinic cycles are possible (cf. Hsu et al. 2001). All these cases are excluded in the microfounded model.

If  $f \leq d$  (or  $fc \leq \gamma_3^{1/\alpha_3}$ , respectively), the positive equilibrium disappears in both models. However, this case is rather irrelevant in the microfounded model. Note that  $fc = \alpha_1 \bar{z}_1 e_3 / (\beta_1 e_1)$  and that  $e_1$ ,  $e_3$  and  $\alpha_1$ ,  $\beta_1$  should reasonably be of comparable magnitude, respectively, while  $\bar{z}_1$ , the maximum amount of biomass that the prey could offer for transactions, should reasonably exceed the natural death rate of the predator,  $\gamma_3 < 1$ , raised to the power  $1/\alpha_3 \geq 1$ . Thus, the analysis of this case doesn't appear to be empirically relevant.

In conclusion, while the biological model (30) is capable of explaining species extinction for  $am < h$  even if  $f > d$ , in the simplified system (23) all species with positive initial populations will survive and coexist in the long run. In other words, if Allee's Law is neglected (as it is by assumption in the simplified system (23)) the approach of the present

paper partly reproduces the dynamics of conventional population models but adds more stability by excluding extinction. As will be shown in the next section, the phenomenon of extinction can be reintroduced by taking Allee's Law into account.

### 3.3.2 Reintroducing Allee's Law

Reintroducing Allee's Law amounts to accounting in (23) for  $A^i(n_i)$  as defined in (14). As a first step, observe that the phase diagram can now be partitioned into three regions depending on the values of  $\tilde{n}_i$ . As long as  $n_i \geq \tilde{n}_i$  for  $i = 1, 3$ , the phase diagram in figure 9 applies as before, because we know from figure 9 that the vector field generated by the simplified system (23) always points inwards in any closed rectangular region lying in the positive quadrant. If  $n_i < \tilde{n}_i$  for  $i = 1$  and/or  $i = 2$ , the dynamics will change. The result will depend on the relative position of the equilibrium  $E_2$ . Figure 10 illustrates the situation for the case where the equilibrium values of  $n_1$  and  $n_3$  both exceed  $\tilde{n}_1$  and  $\tilde{n}_3$ , respectively. Note that the differential equations are continuous at  $(n_1, n_3) = (\tilde{n}_1, \tilde{n}_3)$ . It remains to determine the shape of the isoclines in the regions to the left of  $\tilde{n}_1$  and below  $\tilde{n}_3$ .

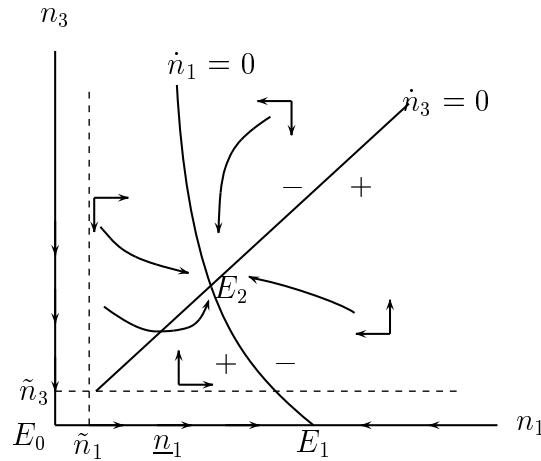


Figure 10: Partitioning the phase diagram

As there is a large set of feasible parameter configurations giving rise to various dynamics, this section solely offers an analysis of representative phase diagrams without analytically investigating the local stability or instability of equilibria, which is straightforward in most cases. Also, whether closed orbits can be excluded is not explicitly investigated as the phase diagrams reveal that trajectories are always trapped in either the basin of attraction of the positive equilibrium or in a region where at least one species eventually becomes extinct.

We begin with the case of a small predator population, that is, in the region below  $\tilde{n}_3$ . The shape of the isocline  $\dot{n}_1 = 0$  is left unchanged, while  $\dot{n}_3 = 0$  can be solved for  $n_1$  to

yield

$$n_1 = \frac{(\gamma_3 \tilde{n}_3)^{1/\alpha_3} m n_3}{f c n_3^{1/\alpha_3} - (\gamma_3 \tilde{n}_3)^{1/\alpha_3}}, \quad (31)$$

which is positive at  $n_3 = \tilde{n}_3$  due to (25). At  $n_3^a := \gamma_3 \tilde{n}_3 / (f c)^{\alpha_3} < \tilde{n}_3$ , there is a horizontal asymptote. As  $n_3$  declines further,  $n_1$  in (31) becomes negative. In addition, it is shown in appendix E that  $\alpha_3 \leq 1$  is a sufficient condition for the slope to be negative. Thus, the relevant part of the isocline has the shape shown in figure 11.

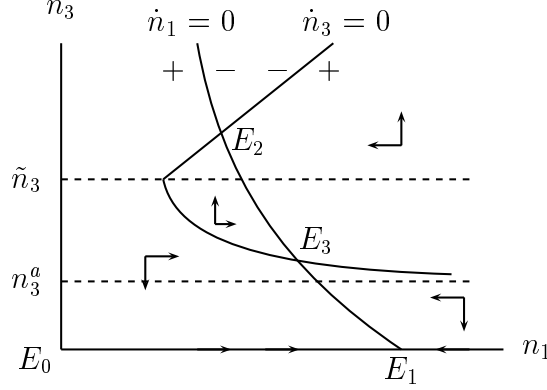


Figure 11: Dynamics in case of  $n_3 < \tilde{n}_3$

There emerges a new equilibrium  $E_3$ , which is unstable. As the direction arrows indicate, the equilibrium  $E_2$  may even be approached if  $n_3 < \tilde{n}_3$ , that is, if the predator is an endangered species. Extinction of the endangered species is certain, however, if  $n_3 \leq n_3^a$ . The system then approaches the equilibrium  $E_1$  on the  $n_1$ -axis, where only the prey survives.

At this point it is worthwhile to consider the consequences of varying the size of the basic resource,  $r$ , as studied more broadly in Eichner and Pethig (2004). While the isocline  $\dot{n}_3 = 0$  is independent of  $r$ , the  $\dot{n}_1 = 0$  locus will shift to the left as  $r$  is parametrically reduced. Figure 12 shows a case, where the equilibrium  $E_2$  as well as the equilibrium  $E_3$  have vanished. As the direction arrows indicate, the equilibrium  $E_1$  will be approached. Note, however, that this result presupposes  $n_1 \geq \tilde{n}_1$ , as the modifications of the dynamics arising from  $n_1 < \tilde{n}_1$  have not yet been taken into account.

We now turn to the case of a small prey population, that is, to the region left of  $\tilde{n}_1$ . In that case the shape of the isocline  $\dot{n}_3 = 0$  remains unchanged, while  $\dot{n}_1 = 0$  from (23a) can be solved for  $n_3$  to yield

$$n_3 = \frac{\beta_1 e_1 n_1 \left[ \bar{z}_1 n_1^{1/\beta_1} - (\gamma_1 \tilde{n}_1)^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right]}{e_3 (\alpha_1 + \beta_1) (\gamma_1 \tilde{n}_1)^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} - \beta_1 \bar{z}_1 e_3 n_1^{1/\beta_1}}. \quad (32)$$

Recall that  $0 < \alpha_1 < 1$  and  $\beta_1 > 0$ . As to the denominator, it is straightforward that

$$\text{denominator} \geq 0 \iff n_1 \leq r^{\alpha_1/(\alpha_1-1)} \left( \frac{\beta_1}{\alpha_1 + \beta_1} \bar{z}_1 \right)^{\beta_1/(\alpha_1-1)} \frac{1}{(\gamma_1 \tilde{n}_1)^{1/(\alpha_1-1)}} =: n_1^a. \quad (33)$$

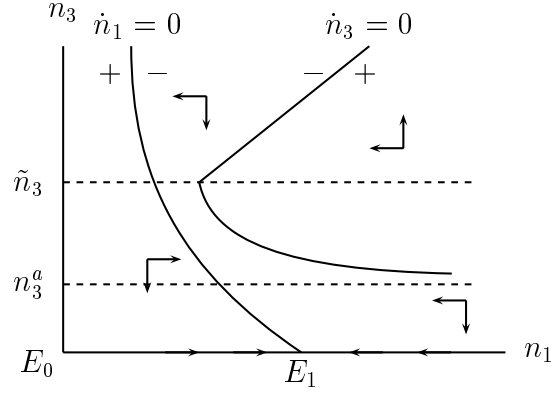


Figure 12: Dynamics in case of  $n_3 < \tilde{n}_3$  if  $E_2$  and  $E_3$  have vanished

Thus, there is a vertical asymptote at  $n_1^a$ . Similarly,

$$\text{numerator} \gtrless 0 \iff n_1 \gtrless r^{\alpha_1/(\alpha_1-1)} \bar{z}_1^{\beta_1/(\alpha_1-1)} \frac{1}{(\gamma_1 \tilde{n}_1)^{1/(\alpha_1-1)}} \equiv \acute{n}_1. \quad (34)$$

Thus, the isocline cuts the  $n_1$ -axis at  $\acute{n}_1 < n_1^a$ . Similar considerations to those employed to rationalize the isocline  $\dot{n}_1 = 0$  in figure 9 lead to the graph of the isocline shown in figure 13. As for the + and - signs beneath the isocline, the remarks in footnote 24 apply analogously.

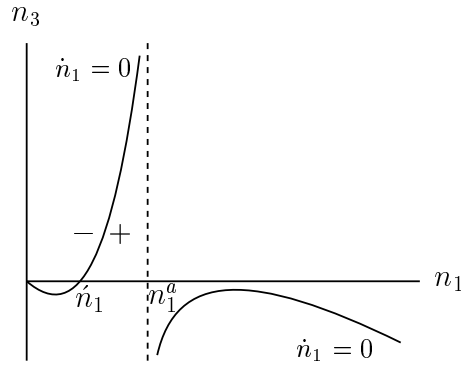


Figure 13: The isocline  $\dot{n}_1 = 0$  if  $n_1 < \tilde{n}_1$

For the dynamics it is important whether a part of the isocline (32) in the positive region lies to the left of  $\tilde{n}_1$ . Closer inspection shows that

$$\acute{n}_1 \gtrless \tilde{n}_1 \iff \tilde{n}_1 \gtrless \bar{n}_1.$$

Thus, if  $\tilde{n}_1 < \bar{n}_1$ , there is a relevant positive part of (32) lying to the left of  $\tilde{n}_1$ . Similarly, we find that

$$n_1^a \gtrless \tilde{n}_1 \iff \tilde{n}_1 \gtrless \underline{n}_1.$$

Therefore, the vertical asymptote of (32) lies to the left of  $\tilde{n}_1$  if and only if  $\tilde{n}_1$  lies to the left of the asymptote at  $\underline{n}_1$  of equation (27). Proceeding under the reasonable assumption  $\tilde{n}_1 < \bar{n}_1$ , it follows that there are essentially two cases to be considered.

First, suppose  $\tilde{n}_1 \leq \underline{n}_1$ . Figure 14 depicts a possible configuration in this case. Other configurations are feasible, depending on the relative position of  $\tilde{n}_1$ . In case of figure 14, the predator will go extinct if the initial values of  $n_1$  and  $n_3$  are such that the system starts below the isocline  $\dot{n}_3 = 0$  or sufficiently far to the left of the  $\dot{n}_1 = 0$  isocline. Even the prey may perish as the equilibrium at  $n_1 = \hat{n}_1$  is unstable.

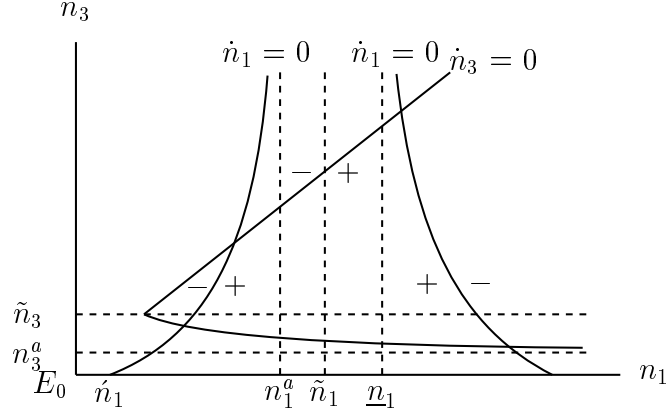


Figure 14: Dynamics in case of  $n_1 < \tilde{n}_1$  if  $\tilde{n}_1 \leq \underline{n}_1$

Second, let  $\underline{n}_1 < \tilde{n}_1 < \bar{n}_1$ . This constellation implies that the right part and the left part of  $\dot{n}_1 = 0$  are both valid only up to the point where  $n_1 = \tilde{n}_1$ . Moreover, as (23a) is continuous at  $n_1 = \tilde{n}_1$ , the isocline is also continuous here. One possible configuration is shown in figure 15, where the positive equilibrium  $E_2$  vanishes. Depending on parameter values, this equilibrium could as well remain in existence. In case of figure 15, the predator cannot survive in the long run.

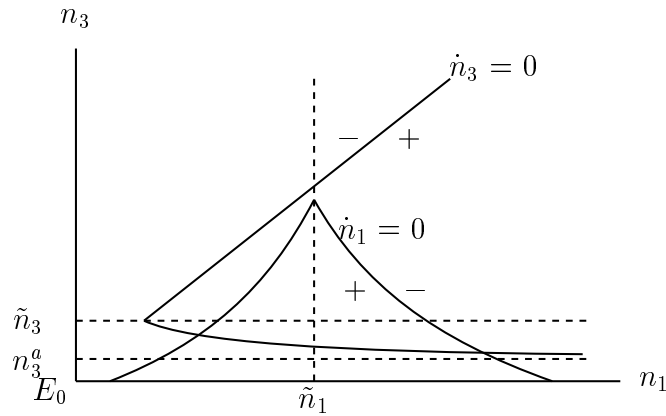


Figure 15: Dynamics in case of  $n_1 < \tilde{n}_1$  if  $\underline{n}_1 < \tilde{n}_1 < \bar{n}_1$

Putting that all information together yields the complete phase diagram, whose shape depends on the specific values of  $\tilde{n}_1$  and  $\tilde{n}_3$ . Figure 16 provides an example.

Although not all possible configurations have been analyzed in detail in this section, it is straightforward to consider the principle shapes of alternative (complete) phase diagrams. As our examples demonstrated, it is fairly obvious that the only possible limit points for



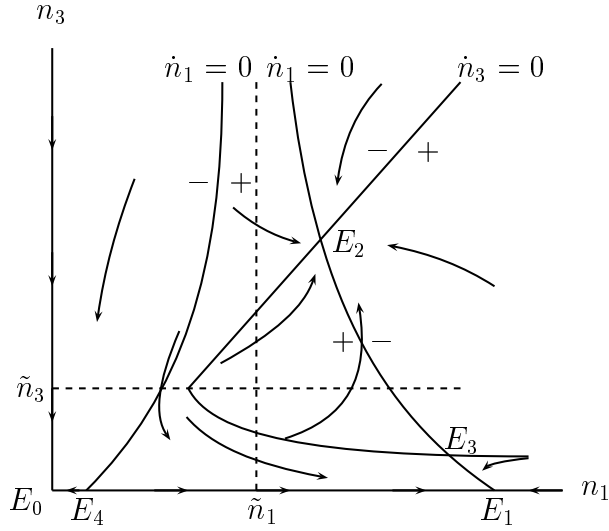


Figure 16: A complete phase diagram

$t \rightarrow \infty$  are equilibria. Exact proofs could be given along the lines in section 3.3.1. We now summarize the main results:

*Let  $(0, 0) < (\tilde{n}_1, \tilde{n}_3) < E_2$ . Then each trajectory of system (23) converges to an equilibrium. The positive equilibrium  $E_2$  is asymptotically stable and its basin of attraction covers at least  $(n_1, n_3) \in \mathbb{R}_+^2$ . There exist initial values  $n_1 \in ]0, \tilde{n}_1[$  and  $n_3 \in ]0, \tilde{n}_3[$ , respectively, such that the predator or both species eventually become extinct.*

### 3.4 Microfounded population dynamics in case of resource competition

A model of resource competition is easily derived from the three-species model (17) by assuming that the top predator is absent ( $n_3 = 0$ ). In that case the equations (17) simplify to

$$\dot{n}_1 = n_1 \cdot \left[ A^1(n_1) \cdot \left( \frac{r e_1}{n_1 e_1 + n_2 e_2} \right)^{\alpha_1} \cdot \bar{z}_1^{\beta_1} - \gamma_1 \right], \quad (35a)$$

$$\dot{n}_2 = n_2 \cdot \left[ A^2(n_2) \cdot \left( \frac{r e_2}{n_1 e_1 + n_2 e_2} \right)^{\alpha_2} \cdot \bar{z}_2^{\beta_2} - \gamma_2 \right]. \quad (35b)$$

As in the last section we require

**Assumptions.** *The initial values of  $n_1$  and  $n_2$  are non-negative. If  $n_1 = n_2 = 0$ , then  $\dot{n}_1 = \dot{n}_2 = 0$ .*

As shown in appendix F  $\dot{n}_1$  and  $\dot{n}_2$  are continuous on  $\mathbb{R}_+^2$ .

### 3.4.1 Neglecting Allee's Law

In this subsection we neglect Allee's Law, i.e.  $A^1(n_1) \equiv A^2(n_2) \equiv 1$ . We infer from  $\dot{n}_1 = \dot{n}_2 = 0$  and (35) that a positive steady state will exist if and only if the condition

$$\underbrace{\left(\frac{e_1^{\alpha_1} \bar{z}_1^{\beta_1}}{\gamma_1}\right)^{1/\alpha_1}}_{=:u_1} = \underbrace{\left(\frac{e_2^{\alpha_2} \bar{z}_2^{\beta_2}}{\gamma_2}\right)^{1/\alpha_2}}_{=:u_2} \quad (36)$$

is satisfied.<sup>25</sup> The zero isoclines of (35) are given by

$$n_2 = \frac{r}{e_2}u_1 - \frac{e_1}{e_2}n_1 \quad \text{or} \quad n_1 = 0 \quad \text{for} \quad \dot{n}_1 = 0, \quad (37a)$$

$$n_1 = \frac{r}{e_1}u_2 - \frac{e_2}{e_1}n_2 \quad \text{or} \quad n_2 = 0 \quad \text{for} \quad \dot{n}_2 = 0. \quad (37b)$$

Thus, the interior segments of the zero isoclines are negatively sloped straight lines which coincide if condition (36) holds. Otherwise they are parallels. Taking into account that all partial derivatives of (35) with respect to  $n_1$  and  $n_2$  evaluated at  $\dot{n}_1 = 0$  and  $\dot{n}_2 = 0$ , respectively, are negative, yields the phase diagrams shown in figure 17. Observe that the phase diagram in case of  $u_1 < u_2$  can be obtained by simply interchanging the axes in the diagram for  $u_1 > u_2$ .

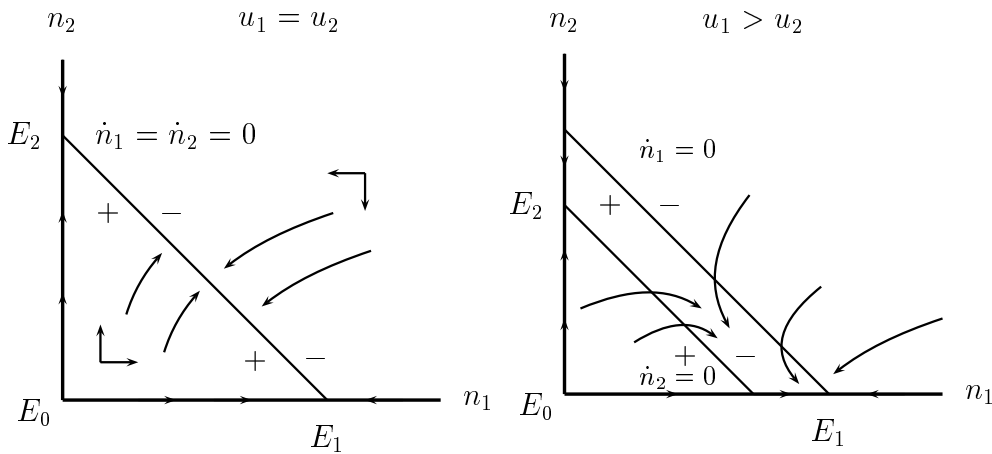


Figure 17: Phase diagrams of system (35)

If  $u_1 = u_2$ , there is a continuum of equilibria in the positive orthant given by the straight line  $n_2 = ru_1/e_2 - e_1n_1/e_2$ . As each trajectory converges to one of these non-isolated equilibria (or stays at the origin), the dynamic system (35) is quasi-globally stable in the sense of Uzawa (1961). If  $u_1 > u_2$  ( $u_1 < u_2$ , resp.), the equilibrium  $E_1$  ( $E_2$ , resp.) is globally stable, while  $E_2$  ( $E_1$ , resp.) is stable along the  $n_2$ -axis ( $n_1$ -axis, resp.).  $E_0$  is unstable in any case. Observe that there is no need to analytically exclude closed orbits or graphics as the trajectories are always trapped in a positive invariant region.

<sup>25</sup>A similar result has been established by Tschirhart (2002) in a somewhat different model.

Summarizing, if Allee's Law is neglected in the population dynamics, a stationary equilibrium where both species coexist represents a knife-edge case whose existence has been established in the numerical example 2 of section 3.1. Usually only one of the species will survive in the long run, depending on the relative magnitudes of  $u_1$  and  $u_2$ . Thus,  $u_1$  and  $u_2$  may be considered as measures of competitiveness in our microfounded model.

We conclude this subsection with a brief comparison of the model explored here with Gause's model as put forward in Clark (1976, p. 311 - 314). In both models the  $\dot{n} = 0$  isoclines are straight downward sloping lines. But while in our model both isoclines are parallel, in Gause's model these slopes differ, in general. As a consequence, both models predict the survival of only one species as the generic case and both imply long-run coexistence for some subset of parameter values. That subset is larger in Gause's than in our model, however, because in the former the  $\dot{n} = 0$  isoclines may exhibit a unique interior point of intersection. In conclusion, both models imply similar population dynamics but our microfounded resource competition model does not exactly reproduce Gause's model.

### 3.4.2 Reintroducing Allee's Law

We now aim at answering the question whether our results go through when Allee's Law is reintroduced. For that purpose we drop the assumption  $A^i(n_i) \equiv 1$ ,  $i = 1, 2$ , and proceed with the analysis of the zero isoclines. If  $n_1 < \tilde{n}_1$  and  $n_2 < \tilde{n}_2$ , respectively, the zero-isoclines of system (35) are given by

$$n_2 = \frac{r}{e_2} u_1 \left( \frac{n_1}{\tilde{n}_1} \right)^{1/\alpha_1} - \frac{e_1}{e_2} n_1 \quad \text{or} \quad n_1 = 0 \quad \text{for} \quad \dot{n}_1 = 0, \quad (38a)$$

$$n_1 = \frac{r}{e_1} u_2 \left( \frac{n_2}{\tilde{n}_2} \right)^{1/\alpha_2} - \frac{e_2}{e_1} n_2 \quad \text{or} \quad n_2 = 0 \quad \text{for} \quad \dot{n}_2 = 0. \quad (38b)$$

Due to  $\alpha_1 \in ]0, 1[$  equation (38a) is a convex function intercepting with the  $n_1$ -axis at 0 and

$$\left( \frac{e_1}{ru_1} \right)^{\alpha_1/(1-\alpha_1)} \tilde{n}_1^{1/(1-\alpha_1)} \equiv \hat{n}_1. \quad (39)$$

As (38a) has the same value at  $n_1 = \tilde{n}_1$  as equation (37a), the isocline is continuous at  $n_1 = \tilde{n}_1$ .

The shape of the complete  $\dot{n}_1 = 0$  isocline depends on the value of  $\tilde{n}_1$ . Note that (37a) hits the  $n_1$ -axis at  $n_1 = ru_1/e_1$ . Comparing  $\hat{n}_1$  from (39) with  $\tilde{n}_1$  shows that

$$\hat{n}_1 \lesseqgtr \tilde{n}_1 \iff \tilde{n}_1 \lesseqgtr ru_1/e_1 \equiv \bar{n}_1.$$

From the  $\dot{n}_1 = 0$  isocline which is illustrated in figure 18 we conclude that there are no equilibria in  $\mathbb{R}_{++}^2$  unless  $\tilde{n}_1 < ru_1/e_1$ . If  $\tilde{n}_1 = ru_1/e_1$ ,  $\dot{n}_1 = 0$  only if  $n_1 = 0$  or

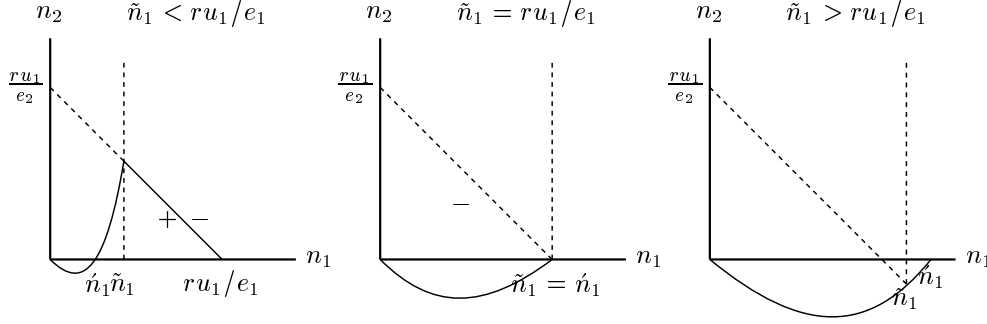


Figure 18: The isocline  $\dot{n}_1 = 0$

$(n_1, n_2) = (\tilde{n}_1, 0)$ . Otherwise,  $\dot{n}_1 < 0$ . If  $\tilde{n}_1 > ru_1/e_1$ ,  $\dot{n}_1 = 0$  only if  $n_1 = 0$ , while  $\dot{n}_1 < 0$  otherwise.

The shape of the complete  $\dot{n}_2 = 0$  isocline can be determined along the same lines. Using the information that (37b) cuts the  $n_2$ -axis at  $n_2 = ru_2/e_2$  and defining

$$\acute{n}_2 := \left( \frac{e_2}{ru_2} \right)^{\alpha_2/(1-\alpha_2)} \tilde{n}_2^{1/(1-\alpha_2)},$$

as the positive interception with the  $n_2$  axis, it follows that

$$\acute{n}_2 \lesseqgtr \tilde{n}_2 \iff \tilde{n}_2 \lesseqgtr ru_2/e_2.$$

If  $\tilde{n}_1 \geq ru_1/e_1$ , then  $\dot{n}_1 < 0$  whenever  $n_1 > 0$  (and  $n_1 \neq \tilde{n}_1$  in case of  $\tilde{n}_1 = ru_1/e_1$ ), irrespective of the state of competitor 2. The immediate consequence is that species 1 cannot survive in the long run. An analogous argument applies to species 2. We thus focus on the more interesting case where  $\tilde{n}_1 < ru_1/e_1$  and  $\tilde{n}_2 < ru_2/e_2$ .

Suppose first  $u_1 = u_2$ . In that case the linear parts of both zero isoclines coincide. The resulting phase diagram is shown in figure 19. The lower (upper) linear part which is drawn solid as well as dotted belongs to  $\dot{n}_1 = 0$  ( $\dot{n}_2 = 0$ ) but not to  $\dot{n}_2 = 0$  ( $\dot{n}_1 = 0$ ).

As the phase diagram reveals, a new equilibrium  $E_3$  emerges, which is unstable. If both species start with sufficiently similar initial values greater than  $\tilde{n}_i$ ,  $i = 1, 2$ , Allee's Law does not change the dynamics. A species can become extinct, however, if its initial value is below the respective  $\tilde{n}_i$  or if the initial value of the respective other species is sufficiently large in relation to the own initial value.

Next, let  $u_1 > u_2$ , implying that the linear part of the  $\dot{n}_1 = 0$  isocline lies above the linear part of the isocline  $\dot{n}_2 = 0$ . The resulting phase diagram is shown in figure 20. Note

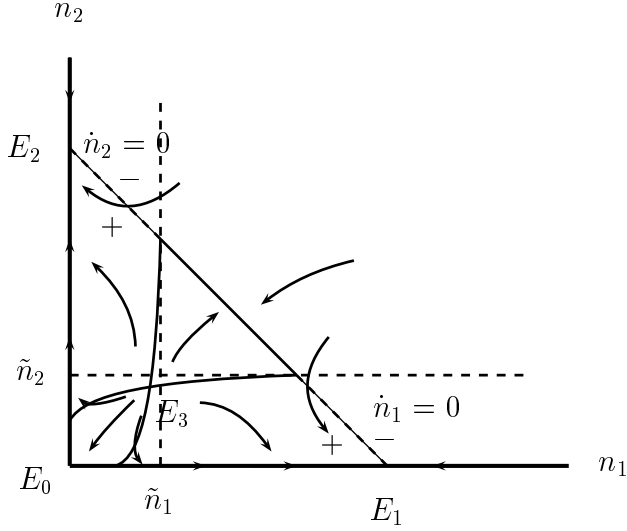


Figure 19: Phase diagram if  $u_1 = u_2$

that equilibrium  $E_4$  is a saddle, as

$$\begin{aligned} \left. \frac{\partial \dot{n}_1}{\partial n_1} \right|_{\dot{n}_1=0} &= n_1 \tilde{z}_1^{\beta_1} \left[ \frac{1}{\tilde{n}_1} \left( \frac{re_1}{n_1 e_1 + n_2 e_2} \right)^{\alpha_1} - \alpha_1 \frac{n_1}{\tilde{n}_1} \left( \frac{re_1}{n_1 e_1 + n_2 e_2} \right)^{\alpha_1 - 1} \frac{re_1^2}{(n_1 e_1 + n_2 e_2)^2} \right] \\ &= \frac{n_1}{\tilde{n}_1} \tilde{z}_1^{\beta_1} \left( \frac{re_1}{n_1 e_1 + n_2 e_2} \right)^{\alpha_1} \left( 1 - \frac{\alpha_1 n_1 e_1}{n_1 e_1 + n_2 e_2} \right) > 0. \end{aligned}$$

All remaining partial derivatives of  $\dot{n}_1$  and  $\dot{n}_2$  evaluated at  $E_4$  are negative. Thus, the determinant of the Jacobian is negative:

$$|J|_{E_4} = \frac{\partial \dot{n}_1}{\partial n_1} \frac{\partial \dot{n}_2}{\partial n_2} - \frac{\partial \dot{n}_1}{\partial n_2} \frac{\partial \dot{n}_2}{\partial n_1} < 0,$$

confirming that  $E_4$  is a saddle. In case of  $u_1 < u_2$  the corresponding phase diagram would look like figure 20 with interchanged axes.

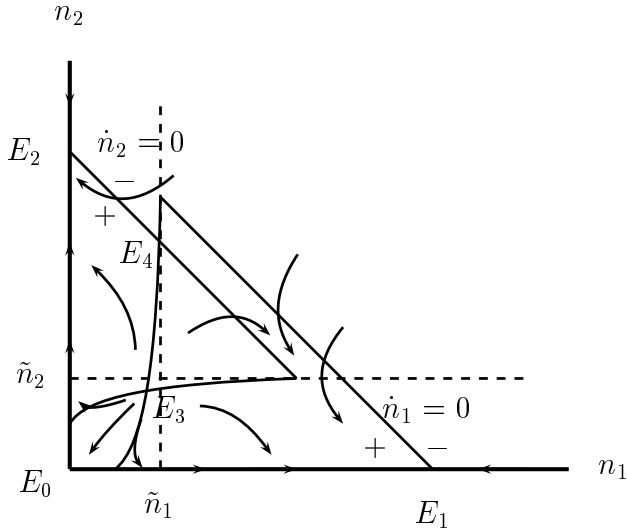


Figure 20: Phase diagram if  $u_1 > u_2$

As the condition  $u_1 = u_2$  represents a knife-edge case, the situation in figure 20 where  $u_1 > u_2$  is most interesting. Comparing that constellation with the case  $u_1 < u_2$  in figure

17 shows that reintroducing Allee's Law in the formulation of the differential equations has no consequences for the qualitative behavior of solutions as long as the initial value of the more competitive species 1 exceeds  $\tilde{n}_1$ . If, however, the initial value falls short of  $\tilde{n}_1$ , Allee's Law implies that the less competitive species 2 survives while species 1 becomes extinct.

## 4 Concluding remarks

This paper provides a microfoundation of population growth based on economic methodology. To that end, we assume that representative individuals of species behave as if they maximize their net offspring subject to a budget constraint which reflects scarcity of its own biomass and scarcity of prey biomass. For a parametric class of net offspring functions we obtain differential equations which are comparable to those suggested in the ecological literature. More specifically, for the case of a single species our model is shown to yield the well-known Verhulst-Pearl logistic growth function. With two species in predator-prey relationship, we derive differential equations whose dynamics are similar to the predator-prey model with Michaelis-Menten type functional response. With two species competing for a single resource we prove that coexistence is feasible but our analysis shows that coexistence is a knife-edge case.

The primary focus of the present paper is on methodology and conceptual analysis. But empirical applications in case studies ought to be an important end once the theoretical foundations are well understood. Tschirhart (2000, 2002, 2004) points to various possibilities of tapping available relevant data to find realistic parameter values and to test various hypotheses implied by the formal model.

## Appendix

### A Continuity of (23a) and (23b) at the Origin

We begin with the special case where  $A^i(n_i) \equiv 1$ . Using the definition of  $m$ , it is obvious that  $n_1e_1 + n_3e_3 \leq e_1(n_1 + mn_3)$  which can be rearranged to

$$0 \leq \frac{n_1e_1 + n_3e_3}{n_1 + mn_3} \leq e_1.$$

Applying some transformations yields

$$-\gamma_1 n_1 \leq n_1 \left[ \left( \frac{r_0}{n_1} \right)^{\alpha_1} \left( \frac{c[n_1e_1 + n_3e_3]}{n_1 + mn_3} \right)^{\beta_1} - \gamma_1 \right] \leq n_1 \left( \frac{r_0}{n_1} \right)^{\alpha_1} (ce_1)^{\beta_1} - \gamma_1 n_1.$$

As  $n_1 \rightarrow 0$ , both interval boundaries converge to zero if  $0 < \alpha_1 < 1$ . Thus,

$$\lim_{(n_1, n_3) \rightarrow (0, 0)} n_1 \left[ \left( \frac{r_0}{n_1} \right)^{\alpha_1} \left( \frac{c[n_1 e_1 + n_3 e_3]}{n_1 + m n_3} \right)^{\beta_1} - \gamma_1 \right] = 0.$$

Given that  $A^1(n_1) \equiv 1$ , this proves continuity of (23a) on  $\mathbb{R}_+^2$  if  $\dot{n}_1 = 0$  for  $n_1 = n_3 = 0$  by definition. If  $A^1(n_1)$  according to the definition in (14) is used, the argument is even simpler. Continuity of equation (23b) is proven similarly.

## B Derivation of (26)

The partial derivative of the simplified (23a) with respect to  $n_1$  evaluated at  $\dot{n}_1 = 0$  is

$$\left. \frac{\partial \dot{n}_1}{\partial n_1} \right|_{\dot{n}_1=0} = \left( \beta_1 \frac{n_1 n_3 (m e_1 - e_3)}{(n_1 + m n_3)(n_1 e_1 + n_3 e_3)} - \alpha_1 \right) \left( \frac{r}{n_1} \right)^{\alpha_1} \left( \frac{c[n_1 e_1 + n_3 e_3]}{n_1 + m n_3} \right)^{\beta_1}. \quad (\text{A1})$$

Using the definition of  $m$ , it follows that  $m e_1 - e_3 = (\alpha_1 + \beta_1) e_3 / \beta_1 - e_3 = \alpha_1 e_3 / \beta_1 > 0$ . Substituting into (A1) shows that the first term in parentheses and therefore the entire expression is negative.

The partial derivative of the simplified (23a) with respect to  $n_3$ ,

$$\frac{\partial \dot{n}_1}{\partial n_3} = \beta_1 \frac{n_1^2 (e_3 - m e_1)}{(n_1 + m n_3)(n_1 e_1 + n_3 e_3)} \left( \frac{r}{n_1} \right)^{\alpha_1} \left( \frac{c[n_1 e_1 + n_3 e_3]}{n_1 + m n_3} \right)^{\beta_1},$$

is negative since  $e_3 - m e_1 < 0$ .

Finally, it is straightforward that the partial derivatives of the simplified (23b) are

$$\frac{\partial \dot{n}_3}{\partial n_1} = \frac{\alpha_3 m n_3^2}{n_1 (n_1 + m n_3)} \left( \frac{f c n_1}{n_1 + m n_3} \right)^{\alpha_3} > 0$$

and

$$\left. \frac{\partial \dot{n}_3}{\partial n_3} \right|_{\dot{n}_3=0} = - \frac{\alpha_3 m n_3}{n_1 + m n_3} \left( \frac{f c n_1}{n_1 + m n_3} \right)^{\alpha_3} < 0, \quad (\text{A2})$$

proving (26). Note that the signs of the cross partials are determined even off the isoclines.

## C The slope of (27)

Differentiation of

$$n_3 = \frac{\beta_1 e_1 n_1 \left[ \bar{z}_1 - \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right]}{e_3 (\alpha_1 + \beta_1) \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} - \beta_1 \bar{z}_1 e_3}$$

with respect to  $n_1$ , letting  $D$  be an abbreviation for the denominator, yields:

$$\left. \frac{\partial n_3}{\partial n_1} \right|_{\dot{n}_1=0} = \frac{\left( \beta_1 e_1 \left[ \bar{z}_1 - \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right] - \alpha_1 e_1 \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right) D}{D^2} - \frac{e_1 e_3 \alpha_1 (\alpha_1 + \beta_1) \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \left[ \bar{z}_1 - \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right]}{D^2}.$$

Recall relations (28) and (29). As the denominator is positive if  $n_1 > \underline{n}_1$ , this expression is negative if

$$\begin{aligned} & \left( \beta_1 \left[ \bar{z}_1 - \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right] - \alpha_1 \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right) D \\ & < e_3 \alpha_1 (\alpha_1 + \beta_1) \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \left[ \bar{z}_1 - \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} \right]. \end{aligned}$$

The right-hand side of this inequality is positive as  $\bar{z}_1 > \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1}$  if  $n_1 < \bar{n}_1$ . The left-hand side is negative as  $n_1 > \underline{n}_1$  implies that  $D > 0$  and  $\beta_1 \bar{z}_1 - (\alpha_1 + \beta_1) \gamma_1^{1/\beta_1} (n_1/r)^{\alpha_1/\beta_1} < 0$ , respectively. This proves that the isocline  $\dot{n}_1 = 0$  is negatively sloped if  $\underline{n}_1 < n_1 < \bar{n}_1$ .

## D Exclusion of closed orbits

Applying Dulac's criterion (cf. Perko, 1996, p. 262) to the simplified system (23), there is no closed orbit lying entirely in  $\mathbb{R}_{++}^2$  if there exists a function  $B \in \mathbb{R}_{++}^2$  such that the trace of the Jacobian of  $(B\dot{n}_1, B\dot{n}_3)$  is not identically zero and does not change sign in  $\mathbb{R}_{++}^2$ . Now consider the function  $B = 1/(n_1 n_3)$ . The partial derivative (A1) has been calculated under the assumption that  $\dot{n}_1 = 0$ , which has had just the effect that the term in square brackets in (23a) has been omitted in (A1). Thus, it is straightforward that

$$\frac{\partial(B\dot{n}_1)}{\partial n_1} = \frac{1}{n_1 n_3} \frac{\partial \dot{n}_1}{\partial n_1} \Big|_{\dot{n}_1=0}$$

for all  $(n_1, n_3) \in \mathbb{R}_{++}^2$ . An analogous argument shows that, using (A2),

$$\frac{\partial(B\dot{n}_3)}{\partial n_3} = \frac{1}{n_1 n_3} \frac{\partial \dot{n}_3}{\partial n_3} \Big|_{\dot{n}_3=0}$$

for all  $(n_1, n_3) \in \mathbb{R}_{++}^2$ . As it follows from appendix B that both expressions are negative, the trace of the Jacobian of  $(B\dot{n}_1, B\dot{n}_3)$  is negative for all  $(n_1, n_3) \in \mathbb{R}_{++}^2$ , proving that there are no closed orbits lying entirely in  $\mathbb{R}_{++}^2$ .

## E The slope of (31)

Consider the region where  $n_3^a < n_3 < \tilde{n}_3$ . As the denominator of the derivative of (31) with respect to  $n_3$  is positive, it suffices to consider the numerator, which is

$$(\gamma_3 \tilde{n}_3)^{1/\alpha_3} m \left[ f c n_3^{1/\alpha_3} - (\gamma_3 \tilde{n}_3)^{1/\alpha_3} \right] - \frac{1}{\alpha_3} f c n_3^{1/\alpha_3} m (\gamma_3 \tilde{n}_3)^{1/\alpha_3}.$$

A sufficient condition for this expression to be negative is  $\alpha_3 \leq 1$ :

$$\begin{aligned} & \alpha_3 (\gamma_3 \tilde{n}_3)^{1/\alpha_3} m \left[ f c n_3^{1/\alpha_3} - (\gamma_3 \tilde{n}_3)^{1/\alpha_3} \right] - f c n_3^{1/\alpha_3} m (\gamma_3 \tilde{n}_3)^{1/\alpha_3} < 0 \\ & \iff (\alpha_3 - 1) f c n_3^{1/\alpha_3} - \alpha_3 (\gamma_3 \tilde{n}_3)^{1/\alpha_3} < 0. \end{aligned}$$



## F Continuity of (35a) and (35b)

In this appendix we prove that both  $\dot{n}_1$  and  $\dot{n}_2$  are continuous on  $\mathbb{R}_+^2$ , although the right-hand sides of (35a) and (35b) are not defined at  $(n_1, n_2) = (0, 0)$ . Observe that  $rn_1e_1 \leq r(n_1e_1 + n_2e_2)$  can be rearranged to

$$0 \leq \frac{re_1}{n_1e_1 + n_2e_2} \leq \frac{r}{n_1}.$$

Applying some transformations we obtain

$$-\gamma_1 n_1 \leq n_1 \left[ \left( \frac{re_1}{n_1e_1 + n_2e_2} \right)^{\alpha_1} \bar{z}_1^{\beta_1} - \gamma_1 \right] \leq r^{\alpha_1} n_1^{1-\alpha_1} \bar{z}_1^{\beta_1} - \gamma_1 n_1.$$

As  $n_1 \rightarrow 0$ , both interval boundaries converge to zero if  $\alpha_1 \in ]0, 1[$ . Thus,

$$\lim_{(n_1, n_2) \rightarrow (0, 0)} n_1 \left[ \left( \frac{re_1}{n_1e_1 + n_2e_2} \right)^{\alpha_1} \bar{z}_1^{\beta_1} - \gamma_1 \right] = 0.$$

Given that  $A^1(n_1) \equiv 1$ , this proves the continuity of (35a) on  $\mathbb{R}_+^2$  if  $\dot{n}_1 = 0$  for  $n_1 = n_2 = 0$  by definition. If  $A^1(n_1)$  is set as in (14), the result would hold all the more. Continuity of equation (35b) is proven similarly.

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