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ECONOMIC LAND USE, ECOSYSTEM SERVICES AND MICROFOUNDED SPECIES DYNAMICS

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Abstract

In an integrated economy-ecosystem model humans choose their land use and leave the residual land as habitat for three species forming a food chain. The size of habitat determines the diversity and abundance of species. That biodiversity generates, in turn, a flow of ecosystem services with public-good characteristics for human consumption. The ecosystem submodel yields (rather than assumes!) population growth functions with each species' growth depending on the size of habitat. First the relationship between habitat and species growth (sustenance, decline and extinction) is explored. The laissez-faire economy is shown to result in an underprovision of habitat, making the case for land use restrictions for nature protection. The optimal land use policy is characterized with full regard of ecosystem dynamics. Finally, labor-augmenting technical change is introduced to generate ever increasing pressure towards further habitat reductions. In the laissez-faire economy the habitat is consequently squeezed to zero in the long-run so that all species are doomed. Social optimality demands, however, to refrain from using all land for economic purposes despite ever-growing labor productivity.

JEL classification: Q24, Q57.

Keywords: land use, ecosystem dynamics, biodiversity, ecosystem services.

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1 Introduction

Observations and predictions of continuing world-wide biodiversity decline have concerned the public and have led, over the last decades, to a fast growing literature on the economic and ecological issues involved (Perrings et al. 1995, Swanson 1995). Undisputedly, a major reason for that biodiversity problem is the pressure from expanding economic activities. The loss of habitat through land conversion to "agrosapes" and urbanization is among the factors that have had the greatest impact on species loss (Swanson 1994, Holling et al. 1995, Moran and Pearce 1997, Dailey et al. 1997). Although many countries have introduced and stepped up nature protection programs¹ the rate of land conversion for economic purposes is still positive even in countries with shrinking human populations.²

The principal reason for concerns about declining biodiversity are the positive correlations between the flow of ecosystem services and biodiversity (Daily et al. 1997, Daily 1997) on the one hand and between biodiversity and habitat on the other hand. It is obvious, therefore, that the analysis of the impact of economic land use on the ecosystem and the feedback effects on ecosystem services calls for an integrated economic-ecological analysis. The *economic* submodel would have to specify (i) the forces for the (continuing expansion of) economic land use and (ii) possible reasons as to why the allocation of ecosystem services might not be appropriately guided by prices and markets. The *ecosystem* submodel would have to establish (i) how reductions in 'wild lands' affect biodiversity and (ii) how these changes translate into quantitative and qualitative variations in the supply of ecosystem services.

Our subsequent integrated economy-ecosystem model will explicitly address all these aspects. We will refrain from following many economic-ecological studies that offer an elaborate economic analysis with a minor ecological appendix. Our economic submodel will rather be kept very simple while priority will be given to the theoretical foundation of the ecosystem with particular emphasis on the link between the size of habitat and biodiversity.

Regarding this link, the widely accepted and plausible hypothesis is that biodiversity is an increasing function of habitat. There is a long tradition (since Arrhenius 1921) in ecological research to determine species-area relationships through field studies. As an

¹A remarkable more recent example of such a program is the Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Habitat Directive) of the European Union.

²In its 'Strategy for a Sustainable Development' presented at the World Economic Summit in September 2002, the German government reports that in Germany the land use for economic purposes is currently expanded by 130 hectare every day. The government also announced its goal to reduce that increase in land use to 30 hectare per day in the year 2020.

empirical generalization from such studies the biogeographical literature suggests species-area curves following a so-called power law: the elasticity of the number of species with respect to the size of habitat is found to be positive but less than one (e.g. Myers and Giller 1988). The insights from such an approach are limited, however, not only because the universality of that relation is questioned (e.g. Crawley and Harral 2001) but also because it lacks a rigorous theoretical basis.

Another approach with an equally long tradition is population ecology. It was developed initially to describe the dynamics of aquatic species communities and fishery (Gordon 1954, Eggert 1998) but it has also been applied to terrestrial communities (Kremer and Morcom 2000) which are the exclusive focus of the present paper. Arguing within the population ecology framework, Swanson (1994) draws his attention directly to the impact of habitat size on the growth of species. He *assumes* that "... the 'natural' growth rate of a biological resource is affected by the allotment of natural habitat" (ibidem, p. 812) and concludes from his study of a simple one-species harvesting model that "... the passive 'undercutting' of species through base resource reallocation [i.e. habitat reduction through land conversion; the authors] probably explains most species endangerment and extinctions ..." (ibidem, p. 814). Swanson's approach to species-area relationships is richer and more demanding than the power-law concept. Yet it doesn't explain exactly how changes in the size of habitat affect species growth and the interactions of *individual* organisms among themselves and their physical and chemical environment are not addressed because population ecology is a macro-approach with species populations being the basic units of analysis.³

As reviewed by Chave and Levin (2003), ecologists developed various methods for providing microfoundations of the macro-properties of ecosystems. However, we are not aware of approaches capable of serving as a microfoundation of population models. In their economic analysis of non-convex ecosystems Dasgupta and Mäler (2003) acknowledge the desirability, if not need, of such a microfoundation. Yet they don't follow that line finding "... it easier to study the macro dynamics of an ecosystem directly without peering at microfoundations" (ibidem, p. 506).

In the present paper we will develop such a microfoundation of population ecology linking in addition, population growth, sustenance and extinction to the size of habitat. Building on Hannon (1976), Tschirhart (2000, 2002) and Eichner and Pethig (2003), we

³This is not to say that the differential equations of populations ecology are arbitrary constructs. On the contrary, they have been modeled and can be calibrated using valuable empirical information from numerous field studies. However, they are not derived from a more basic theory, and in this sense they are not microfounded.

use economic methodology to explain the interactions among organisms of three different species forming a food chain: The top predators (carnivores) feed on herbivores, the latter feed on plants and the plants feed on a vital base resource whose supply is proportional to the size of habitat. In the short-run period of the ecosystem submodel all populations are constant and the representative organisms of all species behave as if they maximize their net offspring as price takers choosing their prey biomass demand and the supply of own biomass subject to a budget constraint. The aggregate net offspring each species has generated in the short-run equilibrium allocation then gives rise to that species' population dynamics over time. Technically, a system of three differential equations is *derived* (rather than *assumed*, as in conventional models of population ecology) that links changes of species populations in time (flows) to populations (stocks) in an interdependent way. Implied in that system of equations there is a link between the size of habitat and population dynamics that will be carefully developed and elaborated because it is an important and the most innovative building block of our approach.

To sum up, the structure of the complete integrated economy-ecosystem model is as follows. Humans and all nonhuman species share the available land which is in fixed supply. Since land used for economic purposes is lost as habitat for nonhuman species the humans determine the size of habitat via their choice of economic land thus making the ecosystem dependent on the economy. Conversely, the economy depends on the ecosystem through the flow of ecosystem services that are non-marketed public goods⁴ and assumed to be positively correlated to the size of habitat and populations.

The principal aim of the present paper is to investigate the interdependence of the economy and the ecosystem constituted by the impact of the economy on the ecosystem through economic land use and by the feedback impact of the ecosystem on the economy through changes in the flow of ecosystem services via changes in species abundance and diversity. We also aim at contributing to answering the question as to "... what proportion ... of land must remain relatively undisturbed ... to sustain the delivery of essential ecosystem services" (Dailey et al. 1997, p. 14); a question, whose further investigation would be profitable for society according to Dailey et al. (1997).

In section 2 the integrated economy-ecosystem model will be set up. A rather brief description of the simple economic submodel in section 2.1 is followed by the introduction and discussion of the more elaborate ecosystem submodel in section 2.2. Section 3 serves to explore essential characteristics of our 'microfounded population ecology approach' derived

⁴In order to sharpen our focus we exclude from the analysis all ecosystem services that are directly related to harvested and marketed ecosystem goods. We don't consider pollution either which is a severe side effect of economic activities with the potential of impairing ecosystems and ecosystem services.

in section 2.2 with a special emphasis on the effects of parametric variations of the size of habitat on species growth, sustenance and extinction. The richness and plausibility of population dynamics implied by the present model is illustrated in several exemplary numerical simulations. While a complete rigorous characterization of the dynamics is clearly beyond the scope of the present paper we will explore a number of important features of the link between size of habitat and species diversity. Our model tends to support the widely accepted view that species diversity and abundance decrease with successive reductions in habitat. Yet the dynamics of the ecosystem render this link much more complex than suggested by the power law referred to above. In section 4 the focus is on the integrated analysis of both submodels. The *laissez-faire* economy is shown to result in an underprovision of habitat making the case for land use restrictions for nature protection. The optimal land use policy is characterized with full regard of ecosystem dynamics. Finally, labor-augmenting technical change is introduced to generate ever increasing pressure towards further habitat reductions. As a consequence, in the *laissez-faire* economy the habitat is squeezed to zero in the long-run so that all species are doomed. In contrast, social optimality demands to refrain from using all land for economic purposes despite ever growing labor productivity. Section 5 concludes.

2 The integrated economy-ecosystem model

The *economy submodel* is populated by a fixed number of consumers who derive utility from a composite consumer good and from ecosystem services. Labor is needed to produce the consumer good and to prepare land for economic use. Since marginal (labor) cost of converting land is strictly increasing some residual land area is left as habitat for all nonhuman species. The *ecosystem submodel* is microfounded, dynamic and links the size of habitat to species growth and species diversity. Ecosystem services are public goods whose flow is assumed to be positively correlated with the size of habitat and the size and number of populations. Thus both submodels are linked as follows: humans unilaterally determine the size of habitat. The latter determines species abundance and diversity over time and with it the flow of ecosystem services which, in turn, affects the well-being of consumers.

Sections 2.1 and 2.2 serve to specify the submodels of the economy and the ecosystem, respectively. The complete integrated economy-ecosystem model will be analyzed in section 4.

2.1 The economy submodel

Consider a simple economy in which the amount y of a composite consumer good is produced by means of the production function⁵

$$y = Y \left(\ell_y, r_y \right)_+ = \ell_y^\sigma r_y^{1-\sigma}, \quad (1)$$

where $\sigma \in [0, 1]$ is a parameter characterizing the Cobb-Douglas technology. In (1), ℓ_y and r_y denote the inputs 'labor' and 'land', respectively. All variables refer to one and the same point in time, but the time index is suppressed to avoid clutter.

The total endowment of land is denoted \bar{r} . r_y is the land area used by humans for economic purposes. This land includes land for business buildings and installations, residential houses, and traffic infrastructure etc. To a large extent those economic land uses consist in sealing the land such that it becomes unsuitable as a habitat for most nonhuman species. Agricultural land is also land used for economic purposes and will thus be included in r_y although it can still serve as a habitat for some nonhuman species. To simplify, we assume that all land, r_y , set aside for economic uses is lost for use by *all* nonhuman species.⁶ As a consequence $\bar{r} - r_y$ is the land available for nonhuman species called habitat, for short.

Claiming land for economic uses is not costless. The land development activity is modeled by the production function

$$r_d = R \left(\ell_r \right)_+ = \bar{r} - \frac{c}{\ell_r}, \quad (2)$$

where r_d is the land claimed for economic uses with the help of labor input ℓ_r and where $c > 0$ is a productivity-reducing technological parameter. Note that in (2) r_d is strictly increasing and strictly concave in ℓ_r with r_d tending toward \bar{r} for ℓ_r becoming very large.

As for the demand side of the economy, there are n_c identical consumers with utility

$$u = U \left(y_c, \bar{r} - r_y, n_1, n_2, n_3 \right)_+ = \ln y_c + \eta \cdot (\bar{r} - r_y) + \sum_{i=1}^3 \theta_i n_i, \quad (3)$$

where η and θ_i for $i = 1, 2, 3$ are positive preference parameters. According to (3) the representative consumer's utility depends on his or her consumption y_c of the (private)

⁵Upper-case letters represent functions. Subscripts assigned to upper-case letters denote partial derivatives. A plus or minus sign underneath an argument of a function denotes the sign of the corresponding partial derivative.

⁶In a more elaborate approach one would want to distinguish 'human-dominated ecosystems' (on economic land) and 'natural ecosystems' (on land not used for economic purposes). The former is ignored in our present model.

consumer good and on ecosystem services which are assumed to be positively correlated with both the size of habitat, $\bar{r} - r_y$, and the populations of all (nonhuman) species, n_1 , n_2 and n_3 , that will be determined later in the ecosystem submodel.⁷ The consumer's appreciation of the size of habitat, $\partial U / \partial (\bar{r} - r_y) > 0$, reflects her benefits accruing from ecosystem services related to the habitat. Likewise, $\partial U / \partial n_i > 0$ (for $i = 1, 2, 3$) is interpreted as the marginal utility from ecosystem services that increase with growing populations. As described by Dailey et al. (1997) in detail, ecosystem services come in a great variety of different forms: "many ecosystem services are not traded or valued in the marketplace; many serve as public good rather than provide direct benefits to individual landowners;" (Dailey et al. 1997, p. 13). Here we restrict our attention to the large subset of *public* ecosystem services and neglect all *private* and marketable ecosystem goods that are supplied through harvesting or mining of biological resources.⁸

The economy submodel is closed by the equations

$$r_y = r_d, \quad (4)$$

$$n_c y_c = y, \quad (5)$$

$$\ell_r + \ell_y = \ell. \quad (6)$$

(4), (5) and (6) represent conventional scarcity constraints accounting for the limited supply of land, the consumer good and labor supply, respectively. The aggregate labor endowment, ℓ , is assumed to be time invariant in the sections 2 and 3 of the present paper. Later in section 4 we will also explore the implications of growing labor supply.

Consider now the economy (1)-(6) with competitive markets for labor, for the consumer good and for land with prices p_ℓ , p_y and p_r , respectively, in the absence of any government intervention or regulation (*laissez faire*). In that scenario the profits of the consumer good industry and the land development industry are, respectively,

$$\pi_y := p_y \ell_y^\sigma r_y^{1-\sigma} - p_\ell \ell_y - p_r r_y, \quad (7)$$

$$\pi_d := p_r \left[\bar{r} - \frac{c}{\ell_r} \right] - p_\ell \ell_r. \quad (8)$$

Maximization of profits on competitive markets implies

$$\frac{(1-\sigma)y}{r_y} = \frac{p_r}{p_y}, \quad \frac{\sigma y}{\ell_y} = \frac{p_\ell}{p_y} \quad \text{and} \quad \frac{p_r}{p_\ell} = \frac{\ell_r^2}{c}. \quad (9)$$

We combine (9), (2) and (4) to obtain, after some rearrangement of terms,

$$\frac{\sigma \bar{r}}{c(1-\sigma)} \ell_r^2 - \frac{\sigma}{(1-\sigma)} \ell_r - \ell_y = 0. \quad (10)$$

⁷According to Dailey et al. (1997, p. 6), "... biodiversity is a direct source of ecosystem goods."

⁸See footnote 4.

When equation (6) is considered in (10) we solve (10) for ℓ_r :

$$\ell_r = -\frac{c(1-2\sigma)}{2\sigma\bar{r}} + \sqrt{\frac{c^2(1-2\sigma)^2}{4\sigma^2\bar{r}^2} + \frac{c(1-\sigma)\ell}{\sigma\bar{r}}}. \quad (11)$$

Inserting (11) into (2) and accounting for (4) yields the equilibrium value

$$r_d = r_y = \bar{r} - \frac{1}{-\frac{1-2\sigma}{2\sigma\bar{r}} + \sqrt{\frac{c^2(1-2\sigma)^2}{4\sigma^2\bar{r}^2} + \frac{c(1-\sigma)\ell}{\sigma\bar{r}}}}. \quad (12)$$

As expected, the land area claimed for economic use is expanded if the land use becomes more productive ($(dr_y/dc) < 0$) and if the economy's labor endowment becomes larger ($(dr_y/d\ell) > 0$). With the help of (11) and (12) the entire equilibrium allocation $(\ell_r, \ell_y, r_d, y_c, y)$ and the pertaining market clearing prices $(p_\ell \equiv 1, p_r, p_y)$ can readily be calculated.

In the laissez-faire market economy, humans are insensitive land claimers responding only to increasing costs of development while ignoring the impact of economic land use on all nonhuman species and denying nonhuman species any 'codetermination' in how to allocate the total land area for economic and ecological uses. To be sure, consumers do benefit from ecosystem services for free as specified in (3) but they are assumed to take as given these services whose supply is determined by the state of the ecosystem, described by $\bar{r} - r_y$, n_1 , n_2 and n_3 . The laissez-faire market mechanism doesn't account for the impact of economic land use on ecosystem services. Although changes in the supply of ecosystem services directly affect the consumers' well-being they leave unchanged the short-run equilibrium of our economy over time.⁹

So far we have characterized the (time-invariant) allocation of resources in the sub-model of the laissez-faire market economy specifying, in particular, the size of land, r_y , to be used for economic purposes. Since the size of habitat is $r_0 := \bar{r} - r_y$, economic land use is the channel through which the economy impacts on the ecosystem. Quite realistically, the size of habitat is unilaterally determined by the extent of the humans' economic land use (equation (12)). This observation gives rise to the question what the intertemporal impact is on the ecosystem of the land area used for economic purposes. To answer this question we now proceed to set up the ecosystem submodel.

⁹In an economic model with more than one consumer good and with non-separable utility functions changes in the state of the ecosystem would change the economy's equilibrium allocation, in general. However these second-order effects are not at the core of the issue of allocative efficiency in an integrated economy-ecosystem world and are therefore ignored in the present model.

2.2 The ecosystem submodel

Building on Eichner and Pethig (2003) we consider an ecosystem with 3 species forming a food chain: Species 3 feeds on species 2, species 2 feeds on species 1 and species 1 feeds on a resource referred to as 'species 0' for analytical convenience. Basic units of analysis are the individual organisms of each species. To simplify, all organisms of the same species are assumed to be identical and the representative organism of species i is called organism i , for short.

In the short-run period the population n_i of each species i is constant. Organism i generates net offspring b_i according to the function $B^i : D^i \rightarrow \mathbb{R}$, where

$$b_i = B^i \left(\begin{matrix} x_{i-1}, z_i, n_i \\ + \quad - \quad +, 0 \end{matrix} \right) \quad i = 1, 2, 3 \quad (13)$$

and $D^i := \mathbb{R}_+ \times [0, \bar{z}_i] \times \mathbb{R}_+$. In (13), x_{i-1} is organism i 's intake of biomass of its prey species $i - 1$, and z_i is organism i 's loss of own biomass to its predator, species $i + 1$. The latter is bounded from above by \bar{z}_i , a positive constant. To avoid clumpy phrases we refer to organism 1's intake of the resource, x_0 , as 'intake of biomass of species 0'. B^i is a concave function satisfying $B^i(0, 0, n_i) < 0$, $B^i(x_{i-1}, \bar{z}_i, n_i) < 0$ and

$$B_{n_i}^i(x_{i-1}, z_i, n_i) \begin{cases} > 0 & \text{if } (x_{i-1}, z_i) \in \tilde{D}^i, \\ = 0 & \text{otherwise,} \end{cases}$$

where $\tilde{D}^i := \{(x_{i-1}, z_i, n_i) \in D^i \mid x_{i-1} > 0, z_i < \bar{z}_i \text{ and } n_i \in [0, \tilde{n}_i]\}$ and where \tilde{n}_i is a positive constant. 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 some critical population level $\tilde{n}_i > 0$. 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 provided in ecological studies and known as Allee's Law (Berryman 2003).¹⁰

In our ecosystem model the biomasses of all species are viewed as commodities traded in a system of virtual 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

¹⁰According to Allee's Law, there is reduced reproduction or reduced survival at low population densities. Since small populations have lower chances to reproduce or survive, Allee's Law is of special interest to ecologists for the study of endangered species.

incomes are denominated in virtual units of account. Organism i 's transactions are constrained by the inequality¹¹

$$e_i + p_i z_i \geq p_{i-1} x_{i-1} \quad i = 1, 2, 3. \quad (14)$$

Obviously, (14) closely resembles the household's budget constraint that economists use to employ for describing the consumer's decision problem. According to (14) organism i has two kinds of incomes for buying prey biomass $p_{i-1} x_{i-1}$: the exogenous 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 therefore interpret e_i as the *predation power* of organism i . e_i is organism i 's only income if i has no enemies - either because i is the top predator ($i = 3$ in our model) or because i 's predator has become extinct.¹²

If the predator species $i + 1$ exists and if the biomass of species $i - 1$ is scarce¹³ ($p_{i-1} > 0$), organism i is able to expand its purchase of prey biomass beyond $x_{i-1} = e_i/p_{i-1}$, if and only if it is willing to earn some biomass income, $p_i z_i > 0$, to pay for the extra food. Hence the extra purchase of prey biomass $p_i z_i/p_{i-1}$ requires a sacrifice of own biomass z_i which readily reflects what ecologists refer to as organism i 's *predation risk*, the risk of being preyed upon while preying (Lima and Dill 1990).

Having specified organism i 's budget constraint we now turn to its decision problem. All individual organisms are assumed to be price takers and to behave as if they solve the maximization problem:

$$\max_{(x_{i-1}, z_i)} B^i(x_{i-1}, z_i, n_i) \quad \text{s.t.} \quad (14). \quad (15)$$

Recalling that in the short run all populations n_i are constant, an ecosystem allocation $(x_0, x_1, x_2, r_0, z_1, z_2)$ is said to be feasible if¹⁴

$$r_0 = n_1 x_0, \quad (16a)$$

$$n_i z_i = n_{i+1} x_i \quad \text{for } i = 1, 2, \quad (16b)$$

¹¹The constraint (14) differs significantly from the constraints the organisms are subjected to in Eichner and Pethig (2003). The present specification is well suited for studying the extinction issue.

¹²In these cases, any positive supply of own biomass ($z_i > 0$) would necessarily be an excess supply, and therefore the market for biomass i doesn't exist ($p_i \equiv 0$).

¹³It will be shown below that all prices are positive in the short-run ecosystem equilibrium.

¹⁴While the equality sign in (16b) is imperative the more general form of (16a) would be $r_0 \geq n_1 x_0$ allowing aggregate demand to fall short of supply. For an analytical treatment of resource abundance see Eichner and Pethig (2003).

where $r_0 := \bar{r} - r_y$ (with r_y as specified in (12)) denotes the land endowment available as habitat for all nonhuman species. Taking the equation (16a) literally, each organism of species 1 is supposed to consume the amount $x_0 = r_0/n_1$ of land. However, following Swanson (1994, p. 811), we take the land area as a proxy for the "... flow of biological services, or base resources or biological necessities for the organisms' sustenance ..." such as water, air, minerals and sunlight. In fact, we assume that there is a composite base resource whose supply is proportional to the size of habitat. Hence we essentially equate the size of habitat, r_0 , with the supply of a composite base resource.¹⁵

Next we specify the coordination of market transactions by prices. A short-run ecosystem equilibrium is said to be constituted by a price vector $(p_0, p_1, p_2, p_3 \equiv 0)$ and transactions $(x_0, x_1, x_2, z_1, z_2, z_3 \equiv 0)$ if (15), (16a) and (16b) are satisfied.

To obtain more specific results we replace (13) by the parametric net offspring function

$$B^i(x_{i-1}, z_i, n_i) = A^i(n_i) \cdot x_{i-1}^{\alpha_i} \cdot (\bar{z}_i - z_i)^{1-\alpha_i} - \gamma_i, \quad (17)$$

where

$$A^i(n_i) := \min \left[1, \frac{n_i}{\bar{n}_i} \right], \quad (18)$$

and where $0 < \alpha_i < 1$ and $\gamma_i > 0$. Solving (15) yields the biomass demands and supplies

$$x_0 = \frac{p_1}{p_0} \alpha_1 \bar{z}_1 + \alpha_1 \frac{e_1}{p_0}, \quad z_1 = \alpha_1 \bar{z}_1 - (1 - \alpha_1) \frac{e_1}{p_1}, \quad (19a)$$

$$x_1 = \frac{p_2}{p_1} \alpha_2 \bar{z}_2 + \alpha_2 \frac{e_2}{p_1}, \quad z_2 = \alpha_2 \bar{z}_2 - (1 - \alpha_2) \frac{e_2}{p_2}, \quad (19b)$$

$$x_2 = \frac{e_3}{p_2}, \quad (19c)$$

whose properties conform to our intuition: The demand curves slope down and the supply curves slope up. Moreover, an increase in an organism's predation power raises its demand for prey biomass but reduces its supply of own biomass.

Inserting (19) in (16) allows us to completely characterize the short-run ecosystem

¹⁵The supply of the resource, r_0 , is a flow defined for each point in time. The resource is perfectly renewable as its supply at each point in time always equals the size of habitat at that point in time. Water and sunlight may be considered approximations of such resources. In a more elaborate analysis one might want to model renewable base resources with stock-flow interdependencies.

equilibrium by

$$p_0 = \frac{n_3 e_3 + n_2 e_2 + n_1 e_1}{r_0}, \quad (20a)$$

$$p_1 = \frac{n_3 e_3 + n_2 e_2 + n_1 (1 - \alpha_1) e_1}{n_1 \alpha_1 \bar{z}_1}, \quad (20b)$$

$$p_2 = \frac{n_3 e_3 + n_2 (1 - \alpha_2) e_2}{n_2 \alpha_2 \bar{z}_2}, \quad (20c)$$

$$x_0 = \frac{r_0}{n_1}, \quad (20d)$$

$$x_1 = \frac{n_1 \alpha_1 \bar{z}_1 (n_3 e_3 + n_2 e_2)}{n_2 [n_3 e_3 + n_2 e_2 + n_1 (1 - \alpha_1) e_1]}, \quad (20e)$$

$$x_2 = \frac{n_2 \alpha_2 e_3 \bar{z}_2}{n_3 e_3 + n_2 (1 - \alpha_2) e_2}, \quad (20f)$$

$$z_1 = \frac{\alpha_1 \bar{z}_1 (n_3 e_3 + n_2 e_2)}{n_3 e_3 + n_2 e_2 + n_1 (1 - \alpha_1) e_1}, \quad (20g)$$

$$z_2 = \frac{\alpha_2 \bar{z}_2 n_3 e_3}{n_3 e_3 + n_2 (1 - \alpha_2) e_2}. \quad (20h)$$

The equations (20) demonstrate that with the parametric functions (17) and (18) a short-run equilibrium exists and is unique with all equilibrium prices being strictly positive. The equilibrium prices (20a)-(20c) are scarcity indicators for the habitat and for the species 1 and 2, respectively. Observe that the supplies of own biomass z_1 and z_2 are positive, too.

Having determined the short-run allocation in the ecosystem we now link that allocation to the growth of populations over time. At the end of the short-run period each organism has acquired a positive or negative amount of net offspring b_i . The adjustment in time of the population of species i is then given by the simple differential equations

$$\frac{dn_i}{dt} =: \dot{n}_i = n_i b_i \quad i = 1, 2, 3. \quad (21)$$

Combining (17), (20) and (21) yields the differential equations of population growth

$$\dot{n}_1 = n_1 \cdot G^1(r_0, n_1, n_2, n_3), \quad (22a)$$

$$\dot{n}_2 = n_2 \cdot G^2(n_1, n_2, n_3), \quad (22b)$$

$$\dot{n}_3 = n_3 \cdot G^3(n_2, n_3), \quad (22c)$$

where

$$G^1(\cdot) = A^1(n_1) \cdot \left(\frac{r_0}{n_1}\right)^{\alpha_1} \cdot \left[\bar{z}_1 \cdot \frac{(1 - \alpha_1) \sum_{i=1}^3 n_i e_i}{(1 - \alpha_1) \left(\sum_{i=1}^3 n_i e_i\right) + \alpha_1 \left(\sum_{i=2}^3 n_i e_i\right)} \right]^{1-\alpha_1} - \gamma_1, \quad (23a)$$

$$G^2(\cdot) = A^2(n_2) \cdot \left[\frac{n_1 \alpha_1 \bar{z}_1}{n_2} \cdot \frac{\sum_{i=2}^3 n_i e_i}{\left(\sum_{i=2}^3 n_i e_i\right) + (1 - \alpha_1) n_1 e_1} \right]^{\alpha_2} \cdot \left[\bar{z}_2 \cdot \frac{(1 - \alpha_2) \sum_{i=2}^3 n_i e_i}{(1 - \alpha_2) \left(\sum_{i=2}^3 n_i e_i\right) + \alpha_2 n_3 e_3} \right]^{1-\alpha_2} - \gamma_2, \quad (23b)$$

$$G^3(\cdot) = A^3(n_3) \cdot \left[\frac{n_2 \alpha_2 \bar{z}_2}{n_3} \cdot \frac{e_3}{e_3 + \frac{n_2}{n_3} (1 - \alpha_2) e_2} \right]^{\alpha_3} \cdot (\bar{z}_3)^{1-\alpha_3} - \gamma_3. \quad (23c)$$

The system (22) of differential equations determines the dynamics of the three-species ecosystem submodel. It is worth noting that while the regeneration efficiency terms $A^i(n_i)$ from (18) don't affect the allocation (20) of the short-run ecosystem equilibrium at all, they do play an important role in the growth functions (22).

Having introduced and analysed the submodels of the economy and the ecosystem in the preceding sections 2.1 and 2.2, we are now in the position to explore the integrated model regarding, in particular, the (in)efficiency of economic land use. However, before doing so it is both worthwhile and necessary to shed more light on the complex link between the size of habitat and the dynamics of species populations as established in (22) and (23). Recall from section 2.1 that the size of habitat is unilaterally determined by humans. Hence changes in economic land use, induced e.g. by changes in the labor endowment of the economy or by technical progress, hit the ecosystem as exogenous shocks and trigger complex repercussions of interdependent population growth until eventually a new long-run ecosystem equilibrium (stationary point) is reached. A full-scale systematic analytical characterization of how the dynamic system (22) depends on the size of habitat, r_0 , is clearly beyond the scope of the present paper. Yet the subsequent section 3 aims at illuminating, with the help of several numerical examples, the complexity and richness of ecosystem adjustment to changes in the size of habitat with a special emphasis on species sustenance and extinction.

3 Dynamic ecosystem responses to the size of habitat

In the first part of the present section we will investigate some general characteristics of the system (22) of differential equations with respect to the size of habitat and after that we will illustrate how the ecosystem reacts to changes in the size of habitat by means of several numerical simulations.

Closer inspection of (22) and (23) shows that the growth of species 1 depends on r_0 directly and that the growth of the other species depends on r_0 in an indirect way, because the population of species 1 enters their growth functions. To further clarify the impact of the size of habitat on population dynamics it is convenient to distinguish between the system (22) of differential equations, called '*system (22)*' hereafter, and a modified version of it which differs from the system (22) only in replacing (18) by $A^i(n_i) \equiv 1$ for $i = 1, 2, 3$. We denote this modified version as '*reference system (22)*'. Of course, the reference system (22) is an auxiliary system of differential equations that coincides with system (22) only partly. However, since its properties are less complex than those of the 'true' system (22) it will turn out to be very helpful in specifying important characteristics of the system (22). We therefore proceed by investigating the reference system (22) first.

We denote by $n_0 := (n_{10}, n_{20}, n_{30}) \in \mathbb{R}_+^3$ the triple of populations at $t = 0$, called the *initial populations*, and by $n^R := (n_1^R, n_2^R, n_3^R) \in \mathbb{R}_+^3$ a stationary point of the reference system (22). Restricting the parameter space as specified in the Appendix and assuming that the reference system (22) runs into a stationary point¹⁶ for each $n_0 \in \mathbb{R}_+^3$ and $r_0 \in \mathbb{R}_{++}$, there exists a function $N^R : \mathbb{R}_+^3 \times \mathbb{R}_{++} \rightarrow \mathbb{R}_+^3$ such that $n^R = N^R(n_0, r_0) = [N^{R1}(n_0, r_0), N^{R2}(n_0, r_0), N^{R3}(n_0, r_0)]$ is the stationary point of the reference system (22), if the initial populations are n_0 and the habitat size is r_0 .¹⁷ Obviously, a predator species is bound to perish if the initial population of its prey species is zero. We therefore have the trivial results

- $N^{R2}(n_0, r_0) = N^{R3}(n_0, r_0) = 0$ for all $n_0 \in \mathbb{R}_+^3$ with $n_{10} = 0$,
- $N^{R3}(n_0, r_0) = 0$ for all $n_0 \in \mathbb{R}_+^3$ with $n_{20} = 0$.

Initial populations exhibiting $n_i > 0$ and $n_{i-1} = 0$ for some $i = 1, 2, 3$ will be disregarded in the sequel. For all other $n_0 \in \mathbb{R}_+^3$, three cases have to be distinguished:

(i) If $n_0 \in \mathbb{R}_{++}^3$, then¹⁸

$$n_1^R = N^{R1}(n_0, r_0) = \frac{r_0}{\bar{z}_1} \cdot \left(\frac{\bar{z}_1}{\gamma_1} \right)^{\frac{1}{\alpha_1}} \cdot M^1(e_1, e_2, e_3), \quad (24a)$$

$$n_2^R = N^{R2}(n_0, r_0) = M^2(e_1, e_2, e_3) \cdot n_1^R, \quad (24b)$$

$$n_3^R = N^{R3}(n_0, r_0) = M^3(e_1, e_2, e_3) \cdot n_2^R. \quad (24c)$$

¹⁶This assumption has to be supported by a global stability analysis which is beyond the scope of the present paper. Our numerical simulations strongly suggest this feature of global stability.

¹⁷By \mathbb{R}_{++} , \mathbb{R}_+ we denote the sets of positive and non-negative real numbers, respectively. \mathbb{R}_+^3 stands for the non-negative Euclidean 3-orthant.

¹⁸The definition of the functions $M^i(\cdot)$ for $i = 1, 2, 3$ is provided in the Appendix.

(ii) If $n_0 \in \mathbb{R}_+^3$ with $n_{10} > 0$, $n_{20} > 0$ and $n_{30} = 0$, then

$$n_1^R = N^{R1}(n_0, r_0) = \frac{r_0}{\bar{z}_1} \cdot \left(\frac{\bar{z}_1}{\gamma_1} \right)^{\frac{1}{\alpha_1}} \cdot M^1(e_1, e_2, 0), \quad (25a)$$

$$n_2^R = N^{R2}(n_0, r_0) = M^2(e_1, e_2, 0) \cdot n_1^R, \quad (25b)$$

$$n_3^R = N^{R3}(n_0, r_0) = 0. \quad (25c)$$

(iii) If $n_0 \in \mathbb{R}_+^3$ with $n_{10} > 0$ and $n_{20} = n_{30} = 0$, then

$$n_1^R = N^{R1}(n_0, r_0) = \frac{r_0}{\bar{z}_1} \cdot \left(\frac{\bar{z}_1}{\gamma_1} \right)^{\frac{1}{\alpha_1}} \cdot M^1(e_1, 0, 0), \quad (26a)$$

$$n_2^R = n_3^R = 0. \quad (26b)$$

Closer inspection of the function N^R reveals that the reference system (22) has the following properties:¹⁹

- (i) Each species that exists in the initial state along with all downstream species never goes extinct in the long run irrespective of how large or small the habitat is.
- (ii) The stationary population of such a species is linear increasing in the size of habitat.
- (iii) The stationary population of such a species depends only on how many more upstream species are present in the initial state but not on the size of its own and the size of the other species' initial populations.

Property (i) characterizes the reference system as an unrealistically robust system: There is no way to endanger and extinguish a species whose initial population is positive (along with the populations of all downstream species) except through deleting the entire habitat, $r_0 = 0$. It is therefore interesting to explore how the properties (i)-(iii) need to be modified when the regeneration efficiency term (18) comes to bear that is incorporated in system (22) and distinguishes it from the reference system (22) discussed so far. To begin with, the dynamics of the reference system (22) and those of the system (22) coincide - and hence properties (i)-(iii) also characterize the 'true' system (22) - if and only if the dynamics of the reference system (22) are such that $n_{it} > \tilde{n}_i$ for all i and for all $t > 0$ (which obviously presupposes $n_{i0} > \tilde{n}_i$ for all i). Although this is an important piece of information the properties (i)-(iii) cannot tell us anything about species endangerment and extinction in our ecosystem submodel. More specifically, even if one sets $n_{i0} > \tilde{n}_i$ for all species that exist initially, the dynamics and the stationary point of the reference system (22) become irrelevant or even misleading as an indicator of the behavior of the system (22) if in case

¹⁹While the properties (ii) and (iii) follow directly from (24)-(26) the property (i) is proven in the Appendix.

of *small* habitats the population dynamics of the reference system (22) exhibit $n_{it} < \tilde{n}_i$ for some $t > 0$ and for some i whose initial population was positive.

A full investigation of the dynamics of the system (22) for small habitats is clearly beyond the scope of the present paper. Nevertheless, in what follows we will offer some interesting and specific information on these dynamics with an emphasis on the impact of the size of habitat by means of numerical analysis. Before we turn to the numerical examples it is convenient to define the function $N^S : \mathbb{R}_+^3 \times \mathbb{R}_{++} \rightarrow \mathbb{R}_+^3$ where $n^S = N^S(n_0, r_0) = [N^{S1}(n_0, r_0), N^{S2}(n_0, r_0), N^{S3}(n_0, r_0)]$ represents the stationary point of the system (22), if the initial populations are n_0 and the habitat size is r_0 . The existence of such a function relies on the assumption that the system (22) reaches a stationary point for any given $n_0 \in \mathbb{R}_+^3$ and $r_0 \in \mathbb{R}_{++}$ (see footnote 16).

Table 1 reports on a series of numerical exercises²⁰ in comparative dynamic analysis. The starting point (example 1) describes an ecosystem with habitat $r_0 = 832$ and initial populations $n_0 = (537.53, 461.00, 62.43)$ which happen to coincide with the stationary populations: $n_0 = N^S(n_0, r_0) = N^R(n_0, r_0)$. The examples 2-9 are generated through successive habitat reductions by 50 percent. In example 2 the habitat is cut to half from 832 to 416. After that the dynamics of system (22) apply until eventually the stationary point $n^R = n^S = (268.77, 230.50, 31.21)$ is reached. The example 3 builds on example 2 through taking the stationary populations from example 2 as initial populations for example 3. This rule applies to all further examples listed in Table 1. As in example 2, the pertaining stationary point $n^S = N^S(n_0, r_0)$ coincides in the following examples 3-5 with the stationary point $n^R = N^R(n_0, r_0)$ of the reference system (22) as noted in the last three columns of Table 1. In the examples 2-5, all species survive in the long run although the stationary populations shrink (linearly) with each habitat reduction.

The solid lines in Figure 1 illustrate the time paths of all populations for an example of type 2-5.²¹ Initially the ecosystem is in a long-run (stationary) equilibrium with populations (n_{10}, n_{20}, n_{30}) . Then, at $t = 0$, the habitat is cut to half with the consequence that the populations of all species start to shrink. Species 1 suffers the steepest decline. After having reached its minimum population at $t = t^*$ species 1 begins to recover due to lower pressure from its predator species 2. The population of species 2 reaches its minimum later at $t^o > t^*$ and then also recovers moderately. The top predator species 3 is also bound

²⁰The numerical examples are calculated with the help of the computer program Mathematica. The program for simulations is available from the authors upon request.

²¹Figure 1 is a freehand drawing emphasizing the main properties of the population time paths in a very stylized way only. The exact plotted graphs can be obtained by the authors upon request.

example no.	habitat	initial populations			stationary point of the system (22)			stationary point of the reference system (22)		
		n_{10}	n_{20}	n_{30}	n_1^S	n_2^S	n_3^S	n_1^R	n_2^R	n_3^R
	r_0									
1	1	2	3	4	5	6	7	8	9	10
1	832	537.53	461.00	62.43	537.53	461.00	62.43	$\left. \begin{array}{c} \\ \\ \\ \\ \\ \end{array} \right\} n^S = n^R$		
2	416	537.53	461.00	62.43	268.77	230.50	31.21			
3	208	268.77	230.50	31.21	134.38	115.25	15.61			
4	104	134.38	115.25	15.61	67.19	57.62	7.80			
5	52	67.19	57.62	7.80	33.60	28.81	3.90			
6	26	33.60	28.81	3.90	16.86	16.52	0	16.80	14.41	1.95
7	13	16.80	16.52	0	8.43	8.26	0	$\left. \begin{array}{c} \\ \\ \\ \\ \\ \end{array} \right\} n^S = n^R$		
8	6.5	8.43	8.26	0	4.22	4.13	0			
9	3.25	4.22	4.13	0	2.11	2.06	0			
10	3.20	2.11	2.06	0	2.07	2.03	0			
11	3.15	2.07	2.03	0	2.04	2.01	0			
12	3.10	2.04	2.01	0	3.31	0	0	2.01	1.97	0
13	3.05	3.31	0	0	3.25	0	0	$\left. \begin{array}{c} \\ \\ \\ \\ \\ \end{array} \right\} n^S = n^R$		
	\vdots	\vdots	\vdots	\vdots	\vdots	\vdots	\vdots			
14	1.90	2.08	0	0	2.03	0	0			
15	1.975	2.03	0	0	2.00	0	0			
16	3.15	8.43	8.26	0	2.04	2.01	0	2.04	2.01	0
17	3.15	16.80	16.52	0	0	0	0	2.04	2.01	0

Table 1: Numerical examples (parameter values: $\alpha_1 = \alpha_2 = \alpha_3 = 0.5$, $e_1 = 1$, $e_2 = 1.85$, $e_3 = 2.4$, $\gamma_1 = 1.5$, $\gamma_2 = 1.2$, $\gamma_3 = 1.2$, $\tilde{n}_1 = \tilde{n}_2 = \tilde{n}_3 = 2$, $\bar{r} = 832$, $\bar{z}_1 = 2.4$, $\bar{z}_2 = 1.5$, $\bar{z}_3 = 1$)

to decline due to reduced prey abundance but then manages to stabilize its population above its critical level \tilde{n}_3 . Figure 1 thus shows that in case of the examples 2-5 the long-run impact of the reduction in habitat is a new stationary state with all populations positive and above their critical levels (of endangerment) but smaller than before the shock. Moreover, during the transition to the new stationary state the populations of the species 1 and 2 take a dip below their later stationary values. Since such dips continue to occur with successive reductions in habitat there is the risk that the population of some species i drops below its threshold value \tilde{n}_i and thus becomes endangered.

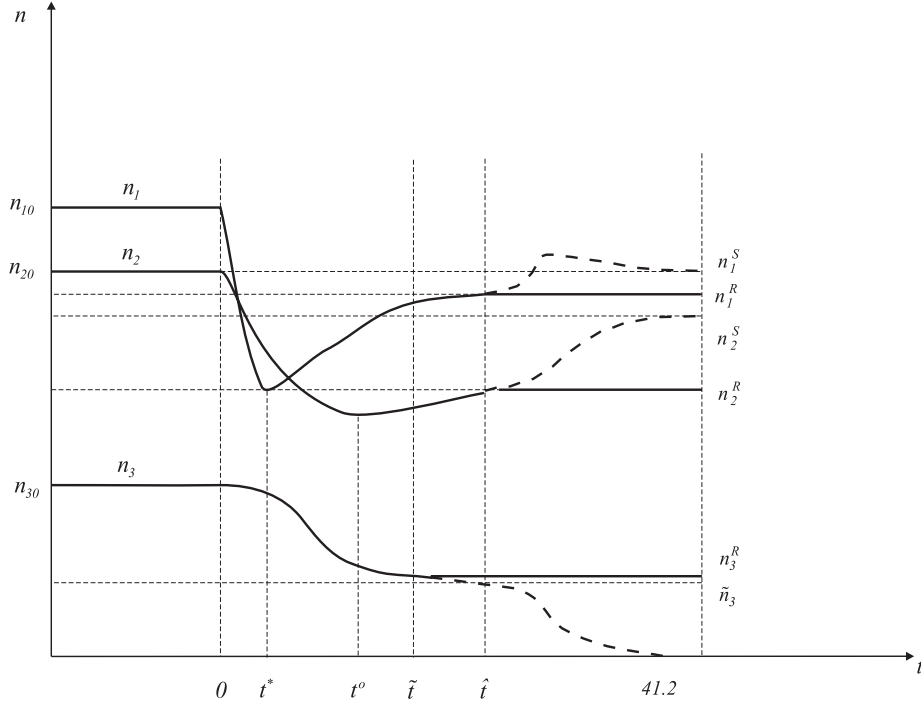


Figure 1: Three-species examples

This is exactly what happens to species 3 in example 6 of Table 1 where the habitat is reduced to 26. The population time paths of example 6 are depicted by the solid lines in the left part of figure 1 and the dashed lines in the right part of it. Until $t = \tilde{t}$ the time paths of the reference system (22) and the system (22) coincide.²² But the population of species 3 becomes $n_{3t} = \tilde{n}_3$ at $t = \hat{t}$ with a tendency of further decline. The term $A^3(n_{3t})$ switches from 1 to n_{3t}/\tilde{n}_3 driving species 3 toward extinction²³ while the populations of

²²This observation does not imply, of course, that the time paths of the example 6 and the examples 2-5 are identical for $t \leq \tilde{t}$. We only make the point (to save on pages) that their main features are the same.

²³If one would incorrectly have continued at $t = \tilde{t}$ to follow the dynamics of the reference system (22) one would have reached the stationary point $n^R = (16.80, 14.41, 1.95)$ as listed in the columns 8, 9 and 10 of row 6 in Table 1.

species 2 and 1 experience a marked recovery. Interestingly, the recovery of species 1 is faster than that of species 2 and even overshoots the stationary population to which it converges eventually. The time $t^* = 41.2$ at which species 3 perishes can be interpreted as a new starting point of the ecosystem dynamics with the populations prevailing at t^* regarded as the associated 'initial' populations: $n_{3t^*} = 0$, $n_{2t^*} > \tilde{n}_2$ and $n_{1t^*} > \tilde{n}_1$. For $t \in [t^*, \infty[$ the dynamics of example 6 are such that $n_{it} > \tilde{n}_i$ for $i = 1, 2$. The stationary state approached satisfies $N^S(n_{t^*}, r_0) = N^R(n_{t^*}, r_0)$ with $N^R(\cdot)$ as specified by (25). To sum up, the long-run impact of the habitat reduction in example 6 is that species 3 goes extinct and the stationary populations of the species 1 and 2 are smaller than they were before that reduction.

The examples 7-11 in Table 1 consider an ecosystem inhabited by the species 1 and 2 only. Their gist is the same as that of the examples 2-5 in the 3-species ecosystem. Although the habitat is further reduced in the examples 7-11 step by step, both species prevail in the long run and the dynamics of both, the system (22) and the reference system (22), coincide. This is no longer true in example 12 which resembles example 6 in that the dynamics of both systems diverge because species 2 hits its critical population level \tilde{n}_2 at some point in time and is then bound to perish. Species 1 is left as the only species in the by now very small habitat. With further reductions of habitat (examples 13, 14 and 15 in Table 1) the stationary population of species 1 (i.e. its carrying capacity) shrinks. Once the size of habitat drops below 1.875, the carrying capacity becomes less than $\tilde{n}_1 = 2$ implying that species 1 cannot survive anymore.

The principal message of the examples 2-15 in Table 1 is that it is the combination of the size of habitat and the initial populations that jointly determine the dynamics and the long-run state of the ecosystem for any given set of all other parameters. If the size of habitat is given, the dynamics and even the stationary point that is eventually reached depend on the initial populations. For an illustration consider the examples 11, 16 and 17 in Table 1. Their common feature is $n_{30} = 0$ and $r_0 = 3.15$ and they differ with respect to the initial populations: in example 16 these populations are about four times and in example 17 about eight times as large as in example 11. As Table 1 shows quadrupling the initial populations of example 11 doesn't change the long-run ecosystem equilibrium: the stationary points of the examples 11 and 16 are the same. Nonetheless, the dynamics differ in an interesting way. While in example 11 both populations stay above their critical levels \tilde{n}_1 and \tilde{n}_2 at all times, in example 16 the population of species 1 declines so sharply that it drops below \tilde{n}_1 temporarily but then manages to recover to $N^{R1}(n_0, r_0) > \tilde{n}_1$ as illustrated by the solid lines in Figure 2. Example 16 thus demonstrates the possibility that after having been exposed to high pressure from a large predator population a prey species

may succeed to prevail in the long run despite temporary severe decline and endangerment. However, if that pressure is further stepped up as in example 17, the population of species 1 declines even more sharply, falls short of the critical level \tilde{n}_1 at some point in time and is not capable to recover anymore. The associated time paths of populations are depicted in Figure 2 by the solid lines for all $t \leq \tilde{t}$ and by the dashed lines for all $t > \tilde{t}$. The monotone decline of species 1 and its eventual extinction deprive the predators of their prey without which they cannot survive either.²⁴

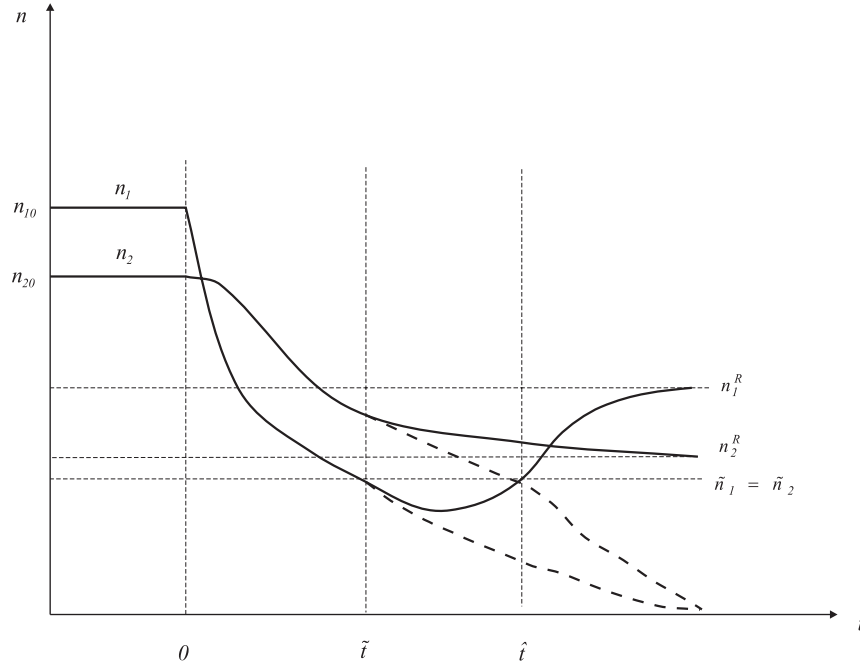


Figure 2: Two-species examples

Although our examples strongly suggest that some features of our examples may be valid far beyond the numerical specifications of those examples, we are aware that nomological insights cannot be gained by way of induction. Nonetheless, we find it worth summarizing some major "suggestive conclusions" (in the sequel denoted as conjectures) from the examples discussed above:

- (i) Let $N^S(n_0, r_0)$ satisfy the condition: For $i = 1, 2, 3$ it is true that $N^{Si}(n_0, r_0) > 0$, if $n_{i0} > 0$. Then $N^S(n_0, r_0) = N^R(n_0, r_0)$.

²⁴Observe that the initial populations in example 16 [17] are the same as those in example 8 [7]. Hence the solid lines [the combined solid and dashed lines] in Figure 2 can alternatively be interpreted as resulting from a massive cut of habitat from $r_0 = 6.5$ [$r_0 = 13$] to $r_0 = 3.15$. The results suggest that the "speed" of habitat reduction matters.

- (ii) If $N^S(n_0, r_0) \neq N^R(n_0, r_0)$, then there exist one or more species i such that $N^{Si}(n_0, r_0) = 0$ and $N^{Ri}(n_0, r_0) > 0$.
- (iii) If $N^S(n_0, r_0) \neq N^R(n_0, r_0)$, then there exists $\tilde{r}_0 > r_0$ such that $N^S(n_0, r'_0) = N^R(n_0, r'_0)$ for all $r'_0 > \tilde{r}_0$.
- (iv) Let $n_0, n'_0 \in \mathbb{R}_+^3$ satisfy $\text{sign } n_{i0} = \text{sign } n'_{i0}$ for $i = 1, 2, 3$. There is $n_0, n'_0 \in \mathbb{R}_+^3$, $n_0 \neq n'_0$ such that $N^S(n_0, r_0) \neq N^S(n'_0, r_0)$ for any given $r_0 > 0$.

Conjecture (i) is straightforward for those time paths of system (22) that satisfy $n_{it} \geq \tilde{n}_i$ for all i and for all $t > 0$ since this condition is necessary and sufficient for the dynamics of both systems to be identical. However, if there is a species i with a positive initial population that drops below the critical level \tilde{n}_i at some point in time $t \geq 0$ we infer from our numerical examples that it either goes extinct or it recovers and eventually reaches its stationary population level $N^{Si}(n_0, r_0) = N^{Ri}(n_0, r_0) > \tilde{n}_i$. Conjecture (i) claims that, under its presuppositions, it is not possible that $N^{Ri}(n_0, r_0) \geq N^{Si}(n_0, r_0)$ for all i and $N^{Si} \in]\tilde{n}_i, 0[$ for some i . Conjecture (ii) formalizes our claim that a species either goes extinct or reaches the stationary point of the reference system (22). Conjecture (iii) asserts a positive correlation between the size of habitat and species diversity. Conjecture (iv) claims that the stationary state reached depends on the initial populations which means, essentially, that the 'speed' of habitat reduction matters with respect to species' diversity.

Leaving these conjectures for future analytical exploration the major validated insight from our preceding investigation is that the incorporation into the system (22) of Allee's law (i.e. the assumption that a species' ability to reproduce is impaired when its population falls short of a critical level), implies that the dynamics (22) diverge from that of the reference system (22) in significant ways and the more so the smaller is the habitat. We showed that a species existing in the initial state may not survive in the long run. Sustainance or extinction depends, *ceteribus paribus*, on both the size of habitat and on initial populations.

4 Economic land use: social optimum versus laissez-faire

As announced at the end of section 2 we now take up the integrated model to explore the issue of efficient economic land use or efficient nature protection, respectively. Recall from section 2.1 that with given technologies and labor endowment the economic land use, r_y , is uniquely determined and time-invariant in the laissez-faire market economy. The economic decision on economic land use makes the ecosystem dependent on the economy. However, fixing the economic land use and, *uno actu*, the size of habitat has an impact on

the supply of ecosystem services through complex intra-ecosystem interactions as shown in section 3. Consumers demand and use ecosystem services and therefore their well-being depends on the state of the ecosystem. However, we have shown that due to missing markets (and separability assumptions) the laissez-faire economy doesn't respond to changes in the supply of ecosystem services (see footnote 9) indicating an inefficient resource allocation.

The present section serves to specify that allocative distortion by invoking a social planner who includes the provision of ecosystem services into her optimization calculus and respects, at the same time, the ecosystem allocation mechanism.²⁵ We aim at determining the optimal economic land use for comparison with the laissez-faire allocation of land. Although various policy instruments are available for implementing the optimal partition of land we don't offer a comparative policy assessment but rather implicitly assume that land use restrictions (land zoning legislation) are directly imposed. In the sequel we will first address the optimality and misallocation issue for the 'static' economy of section 2.1, and after that we explore the consequences of an exogenously growing labor supply.

Recall that in the laissez-faire economy with competitive markets of section 2.1 the land used for economic purposes, r_y , has been determined in (12). Hence with time-invariant labor endowment, ℓ , the size of habitat turns out also to be time-invariant. To see whether this allocation is efficient consider a Utilitarian social planner solving the problem

$$\max \int_0^\infty n_c U(\cdot) e^{-\delta t} dt \quad \text{s.t. (1)-(6), (22a)-(22c), } r_d \leq \bar{r}_y, r_0 = \bar{r} - \bar{r}_y, \quad (27)$$

where δ is a positive social discount rate and n_c is the constant population of humans. (27) is an optimal control problem where n_1 , n_2 and n_3 are state variables and all other variables are controls. By means of substitution, all controls other than the variable ℓ_r can be eliminated such that the Lagrangean associated to (27) reads

$$\begin{aligned} \mathcal{L} = & n_c U \left\{ \frac{1}{n_c} Y[\ell - \ell_r, R(\ell_r)], \bar{r} - R(\ell_r), n_1, n_2, n_3 \right\} + \lambda_{n_1} n_1 G^1[\bar{r} - R(\ell_r), n_1, n_2, n_3] \\ & + \lambda_{n_2} n_2 G^2(n_1, n_2, n_3) + \lambda_{n_3} n_3 G^3(n_2, n_3). \end{aligned} \quad (28)$$

An interior solution to (28) satisfies²⁶

$$Y_r R_\ell - Y_\ell = n_c \cdot \frac{U_r R_\ell}{U_y} + \frac{n_1 \lambda_{n_1} G_r^1 R_\ell}{U_y} > 0, \quad (29)$$

$$\dot{\lambda}_{n_i} = \delta \lambda_{n_i} - \lambda_{n_i} G^i - \sum_{k=1}^3 \lambda_{n_k} n_k G_{n_i}^k - n_c U_{n_i} \quad i = 1, 2, 3. \quad (30)$$

²⁵In principle, the social planner could include in her optimization exercise all biomass transactions which is probably a more realistic procedure for agriculture than for wildlife. Since we don't follow that approach in the present paper, (27) may be interpreted as a secondbest optimization approach.

²⁶Due to (18) and (23), (28) is not differentiable at $n_i = \tilde{n}_i$ for $i = 1, 2, 3$. We restrict our attentions to solutions in which this 'complication' doesn't matter.

The first term on the right side of (29), $n_c U_r R_\ell / U_y > 0$, is the consumers' aggregate marginal willingness-to-pay for increasing the size of habitat through a small decrease in labor input for economic land development. The second term on the right side of (29), $n_1 \lambda_{n_1} G_r^1 R_\ell / U_y > 0$, represents the marginal social value of reducing economic land use that consists of the (present value of the) beneficial effects of the increase in net offspring generation brought about by a small expansion of habitat.²⁷ Both these marginal social benefits are not accounted for in the laissez-faire market allocation because maximizing profits π_y and π_d from (7) and (8) implies $Y_r R_\ell = Y_\ell$. Consequently, the market allocation doesn't satisfy (29).

To obtain more specific information on the nature of the allocative distortion in the market economy consider the function $y = Y[\ell - \ell_r, R(\ell_r)] =: \tilde{Y}(\ell_r)$ whose first derivative is the left side of (29). Assuming that $Y_{\ell_r} \geq 0$ and that Y and R are concave in ℓ_r we find that \tilde{Y} is strictly concave in ℓ_r and attains its maximum at $\tilde{Y}_{\ell_r} = Y_r R_\ell - Y_\ell = 0$. Hence we conclude:

- (i) In each short-run equilibrium of the laissez-faire market economy, $\ell_r = \ell_r^M$ is chosen as to maximize the output of the consumer good. The corresponding size of habitat is $r_0^M := \bar{r} - R(\ell_r^M)$ for all t .
- (ii) For each point in time, the social planner chooses $\ell_{rt} = \ell_{rt}^S$ such that

$$Y_r[\ell - \ell_{rt}^S, R(\ell_{rt}^S)] R_\ell(\ell_{rt}^S) > Y_\ell[\ell - \ell_{rt}^S, R(\ell_{rt}^S)].$$

Since this inequality holds if and only if $\tilde{Y}(\ell_{rt}^S) > 0$, it follows that $\ell_{rt}^S < \ell_r^M$ and hence $r_{0t}^S := \bar{r} - R(\ell_{rt}^S) > r_0^M$ for all $t \geq 0$.

In other words, the optimal habitat is larger than the laissez-faire habitat at each point in time implying that ecosystem services are underprovided in the laissez-faire market economy. Although the equations (29) and (30) don't contain enough information to fully characterize the time sequence of r_{0t}^S , the optimal habitat cannot be expected to be time-invariant, in general.

Our preceding exploration of the social planner's allocation plan has been restricted to interior solutions of (28). The implicit assumption underlying this restriction is that along the entire optimal time path the populations of all species are positive. This, in turn presupposes that the initial populations, i.e. n_{it} for $t = 0$ and $i = 1, 2, 3$, support an optimal long-run ecosystem equilibrium with positive stationary populations of all species.

²⁷One may wonder why the marginal utilities U_{n_i} do not show up in the social planner's solution (29) as some kind of positive externality. The reason is that the beneficial effects of n_1 , n_2 and n_3 for the consumers are captured indirectly only in (30) and in the values of U_r , U_y , G_r^1 and λ_{n_1} in (29).

We don't know how large this subset of initial populations is, but we know that for any pair of different initial populations from this set the associated time paths of habitats will generally differ. In sharp contrast, the laissez-faire habitat r_0^M remains unaffected by variations in initial populations.

In search for further informative results we now restrict our focus to long-run interior ecosystem equilibria defined by $\dot{n}_i = \dot{\lambda}_{n_i} = 0$ for $i = 1, 2, 3$. Quite obviously, a long-run equilibrium requires

$$G^1(r_0, n_1, n_2, n_3) = G^2(n_1, n_2, n_3) = G^3(n_2, n_3) = 0. \quad (31)$$

Due to (31), the equations (30) simplify to

$$\delta \lambda_{n_i} = \sum_{k=1}^3 \lambda_{n_k} n_k G_{n_i}^k + n_c \theta_i \quad i = 1, 2, 3, \quad (32)$$

where the utility function U employed in (30) is replaced by the parametric function (3). Simple but tedious calculations show that

$$\begin{aligned} n_1 G_r^1 &= \beta_1, & n_1 G_{n_1}^1 &= \beta_2, & n_1 G_{n_2}^1 &= \beta_3, & n_1 G_{n_3}^1 &= \beta_4, & n_2 G_{n_1}^2 &= \beta_5, \\ n_2 G_{n_2}^2 &= \beta_6, & n_2 G_{n_3}^2 &= \beta_7, & n_3 G_{n_2}^3 &= \beta_8, & n_3 G_{n_3}^3 &= \beta_9, \end{aligned} \quad (33)$$

where β_i for $i = 1, \dots, 9$ are parameters.²⁸ Inserting (33) into (32) gives us²⁹

$$\lambda_{n_1} = \frac{n_c \theta_1 [(\delta - \beta_6)(\delta - \beta_9) - \beta_7 \beta_8] + n_c \theta_2 \beta_3 \beta_5 (\delta - \beta_9) + n_c \theta_3 \beta_5 \beta_8}{(\delta - \beta_2) [(\delta - \beta_6)(\delta - \beta_9) - \beta_7 \beta_8] - \beta_5 [\beta_3 (\delta - \beta_9) + \beta_4 \beta_8]}. \quad (34)$$

Next we make use of the parametric production function (1) and the parametric utility function (3) to rewrite (29) as

$$\frac{(1 - \sigma)}{r_y} - \frac{\ell_r^2 \sigma}{c \ell_y} = n_c \eta + \lambda_{n_1} \beta_1. \quad (35)$$

The consideration of $r_y = \bar{r} - c/\ell_r$ and $\ell_y = \ell - \ell_r$ in (35) yields

$$\begin{aligned} \ell_r^3 + \frac{(1 - 2\sigma)c - \bar{r}c(n_c \eta + \lambda_{n_1} \beta_1)}{\sigma \bar{r}} \ell_r^2 &- \frac{(1 - \sigma)c\ell - c(c + \ell \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)}{\sigma \bar{r}} \ell_r \\ &- \frac{(n_c \eta + \lambda_{n_1} \beta_1)c^2 \ell}{\sigma \bar{r}} = 0. \end{aligned} \quad (36)$$

The solution to (36) is the labor input $\ell_r = \ell_r^S$ in the long-run ecosystem equilibrium. Since an analytical solution is hard to obtain we will content ourselves with a few numerical examples. For that purpose we reactivate the parameter values employed in section 3: $\alpha_1 = \alpha_2 = \alpha_3 = 0.5$, $e_1 = 1$, $e_2 = 1.85$, $e_3 = 2.4$, $\gamma_1 = 1.5$, $\gamma_2 = 1.2$, $\gamma_3 = 1.2$, $\tilde{n}_1 = \tilde{n}_2 = \tilde{n}_3 = 2$, $\bar{r} = 832$, $\bar{z}_1 = 2.4$, $\bar{z}_2 = 1.5$, $\bar{z}_3 = 1$, and add to them the following economic parameters: $\eta = 10^{-5}$, $n_c = 100$, $\sigma = 0.5$, $\theta_1 = \theta_2 = \theta_3 = 10^{-6}$.

²⁸The derivation of (33) and the definition of β_i for $i = 1, \dots, 9$ is provided in the Appendix.

²⁹For the derivation of (34) we refer to the Appendix.

labor endowment ℓ	0.0013	0.005	0.1	0.3	1	5	10	100
laissez-faire r_0	800.00	407.92	91.42	52.66	28.84	12.90	9.12	2.88
optimal r_0	800.05	527.89	378.40	368.52	364.79	363.47	363.30	363.15

Table 2: Optimal vs. laissez-faire habitat for alternative labor endowments

Table 2 lists the long-run size of habitat in the laissez-faire economy and in the social optimum for alternative labor endowments. Two remarkable features deserve to be emphasized:

- (i) In the laissez-faire economy, increasing economic pressure through successively increasing labor endowments continuously and severely squeezes the habitat until hardly any space for nonhuman species is left.
- (ii) Growing economic pressure renders it optimal to expand economic land use at the expense of habitat since the Utilitarian principle requires to balance benefits and costs at the margin. However, unlike in the laissez-faire economy there appears to be a lower bound for the optimal size of habitat with a significant area of land reserved for the ecosystem. Consequently the allocative bias of the laissez-faire economy from the ecosystem grows with increasing economic pressure.

It is plausible that these observations are not special features of the numerical examples on which the results in Table 2 are based. To substantiate that conjecture we will modify the model of section 2.1 in one point only: the assumption of labor supply being constant and time-invariant is now replaced by assuming that the labor supply grows exponentially in time: $\ell_t = \ell_0 e^{\omega t}$, where ω is a positive and constant growth rate. We need not interpret this labor growth as physical growth (which is implausible when one keeps constant the population n_c of the human species) but we rather look at it as growth of labor in efficiency units reflecting exogenous labor-saving technical progress. Such an approach to technical change is very simple and stylized but it serves well our purpose of modelling the growing pressure on the ecosystem of continuing productivity gains in the real world.

As a first step we will briefly consider the impact of exponential labor growth on the allocation of the otherwise unchanged model of the laissez-faire market economy of section 2.1. It is obvious from equation (12) that the economic land use is now ever growing which translates into an ever shrinking size of habitat. In fact we easily infer from (11) that the labor input, ℓ_r , grows without bounds over time. Correspondingly, the parametric functional form of the production function R from (2) implies that the economic land is continuously expanded over time until it eventually absorbs the entire available land area. Hence the ecosystem with all its species is doomed.

We don't suggest this gloomy scenario as a realistic one regarding the long-run fate of humanity and the ecosystem but rather look at it as a frame of reference for the social planner's partition of land between humans and nonhumans. The planner's optimization calculus is the same as in (28) except that ℓ is not a positive constant anymore but grows autonomously in time according to $\ell_t = \ell_0 e^{\omega t}$.

For this scenario we are able to show that there is $\ell_r^* > 0$ such that the optimal time path satisfies

$$\lim_{t \rightarrow \infty} \ell_{rt} = \ell_r^*. \quad (37)$$

To prove this claim suppose the long-run optimal habitat converges to zero as in laissez-faire or in other words $r_0 \rightarrow 0$ is a long-run solution to the social planner's optimization problem (28). Note first that $\lim_{t \rightarrow \infty} \ell_y = 0$ and $\lim_{t \rightarrow \infty} \ell_r = \infty$ is a necessary condition for $r_0 \rightarrow 0$. Suppose now, contrary to our claim, that $\ell_y \rightarrow 0$ and hence $r_y \rightarrow \bar{r}$ is optimal. Then $\lim_{\ell_y \rightarrow 0, r_y \rightarrow \bar{r}} Y_\ell = \infty$, $\lim_{\ell_y \rightarrow 0, r_y \rightarrow \bar{r}} Y_r = 0$, $\lim_{\ell_r \rightarrow \infty} R_\ell = c$, $\lim_{y \rightarrow 0} U_y = \infty$ and $\lim_{t \rightarrow \infty} n_1 = 0$. When this information is applied to (29) we find that the left side of (29) converges to $-\infty$ whereas the right side of (29) converges to 0 such that the equation (29) is violated. This contradiction proves that $r_0 \rightarrow 0$ is not a solution to (28).

In an effort to further specify the upper bound ℓ_r^* observe that the optimal time path is still characterized by (29) and (30), and (31) through (36) apply correspondingly. Following some rearrangement of terms (36) can be turned into

$$\begin{aligned} H(\ell_t, \ell_{rt}) &:= \frac{\sigma \bar{r} \ell_{rt}^3}{(1 - \sigma) c \ell_t - c(c + \ell_t \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)} + \frac{[(1 - 2\sigma)c - \bar{r}c(n_c \eta + \lambda_{n_1} \beta_1)] \ell_{rt}^2}{(1 - \sigma) c \ell_t - c(c + \ell_t \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)} \\ &\quad - \ell_{rt} - \frac{(n_c \eta + \lambda_{n_1} \beta_1) c^2 \ell_t}{(1 - \sigma) c \ell_t - c(c + \ell_t \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)} = 0. \end{aligned} \quad (38)$$

Quite obviously, the term $H(\ell_t, \ell_r^*)$ with function H from (38) is not zero, in general, for any $t \in \mathbb{R}_+$. However, in view of (38) and (37) it is true that

$$\lim_{t \rightarrow \infty} H(\ell_t, \ell_r^*) = 0. \quad (39)$$

In view of $\lim_{t \rightarrow \infty} \ell_t = \infty$ and L'Hopital's rule, (39) can be shown to imply

$$\ell_r^* = \frac{(n_c \eta + \lambda_{n_1} \beta_1) c}{\bar{r}(n_c \eta + \lambda_{n_1} \beta_1) - (1 - \sigma)}. \quad (40)$$

Clearly, ℓ_r^* is the long-run optimal labor input for economic land development. Via $r_y^* = R(\ell_r^*)$ we calculate $r_0^* := \bar{r} - R(\ell_r^*)$ as the long-run optimal size of habitat. While in laissez-faire the habitat is squeezed toward zero over time it turns out to be optimal to place a lower bound on the size of habitat which reinforces and sharpens the comparative-static results of Table 2.

With the optimal labor input in land development converging to ℓ_r^* in the long run and continuous exponential growth of labor supply it is clear that the growth of labor supply will be absorbed in stepping up the production of the consumer good. In terms of the formal model, observe that (1), (2) and (6) imply

$$\hat{y}_t = \sigma \hat{\ell}_{yt} + (1 - \sigma) \eta_{r\ell t} \hat{\ell}_{rt}, \quad (41)$$

$$\hat{\ell}_{yt} = \frac{\hat{\ell}_t}{\rho_t} - \frac{1 - \rho_t}{\rho_t} \hat{\ell}_{rt}, \quad (42)$$

where $\rho_t := \ell_{yt}/\ell_t$, $\hat{x}_t := \dot{x}_t/x_t$ for $x = y, \ell_y, \ell_r, \ell$ and $\eta_{r\ell t} := \ell_{rt} R_\ell / r_{yt}$. Owing to (37) and (2) we find that $\lim_{t \rightarrow \infty} \eta_{r\ell t}$ is positive and constant and that $\lim_{t \rightarrow \infty} \rho_t = 1$. Therefore, (41) and (42) yield

$$\lim_{t \rightarrow \infty} \hat{\ell}_{yt} = \hat{\ell}_t = \omega \quad \text{and} \quad \lim_{t \rightarrow \infty} \hat{y}_t = \sigma \omega. \quad (43)$$

The conclusion is that while the ecosystem converges to a long-run stationary equilibrium with zero population growth the economy approaches an optimal steady state where the consumer good (representing the national product) grows at the constant positive rate $\sigma \omega$.

Due to our restricted focus on interior solutions in the preceding analysis we were not able to address the question whether long-run optimality may be compatible with the extinction of some or even all species. Our conjecture is that depending on the concrete specification of all functional forms Y , R and U extinction may turn out to be optimal under certain conditions. An exploration of this issue is beyond the scope of the present paper, however.

5 Concluding remarks

The present paper investigates the impact of the economy on the ecosystem through economic land use that deprives species of their habitat and the feedback effects from the ecosystem to the economy through the provision of ecosystem services. This interdependence between the economy and the ecosystem calls for an integrated analysis of both systems. Economists have a good understanding of how to model the allocation of land and ecosystem services in the economy. However, to our knowledge the link between the size of habitat, species diversity and the ecosystem's supply of services to the economy has not yet been modeled in a way that (i) accounts for interdependent species in a dynamic ecosystem and (ii) is, at the same time, compact enough to allow for a tractable integrated economy-ecosystem analysis. The core of the model presented here is a micro-founded ecosystem submodel that is linked to the economy submodel via the allotment of

land for habitat and via the supply of ecosystem services. The size of habitat is shown to be an important factor for the population dynamics of all nonhuman species as well as for their scarcity, abundance and (lack of) sustenance which in turn determines the provision of ecosystem services.

The principal policy implication of our analysis is a rationale for restricting the laissez-faire economic land use. Since ecosystem services have been assumed to be non-exclusive public consumer goods, such a proposition doesn't come too unexpectedly. However, the theoretical foundation of the nature-protection results presented here is novel. Our results are based on a rigorous economy-ecosystem analysis which explicitly specifies the intertemporal interactions and feedbacks within the ecosystem and between both subsystems. All these interactions need to be taken into account in the design of land-use regulations aiming at an efficient partition of total land for economic use and habitat, respectively. Most of the extant environmental-economic modeling tends to offer a sophisticated and microfounded analysis of the economic system whereas the environment is added as a small appendix with the ecosystem as a black box. Our ecosystem-economy model does away with this imbalance and reverses it, in fact.

Predator-prey relations are considered the driving force for intra-ecosystem interactions. Using economic methodology (in particular price-taking maximizing behavior of individual members of all species and the clearing of biomass markets through prices) we *derive* (rather than *assume*) a system of differential equations of population growth that allow to completely specify the intertemporal movement of populations for any given initial populations and size of habitat. Note that although the well-established models of population ecology, notably those of the Lotka-Volterra type and their refinements, also allow to study such population dynamics they are not microfounded and their link, if any, between population dynamics and the size of habitat is ad hoc.

Due to analytical complexity and limited space the dynamics of our 3-species-ecosystem model have not been rigorously characterized in the present paper. However, section 3 revealed important properties of the population dynamics regarding, in particular, the ecosystem's response to changes in initial populations and habitat with special emphasis on biodiversity and extinction. Although we find these dynamic ecosystem interactions appealing and plausible, empirical tests of the model's rich implications are an important item on the future research agenda.

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Appendix

Definition of the functions $M^i(\cdot)$:

$$M^1(e_1, e_2, e_3) := \gamma_1^{-\frac{1}{\alpha_1}} \cdot \left[\frac{e_3\mu_3\mu_2 + e_2\mu_2 + e_1(1 - \alpha_1)}{(1 - \alpha_1)(e_3\mu_3\mu_2 + e_2\mu_2 + e_1)} \right]^{-\frac{1-\alpha_1}{\alpha_1}} =: \mu_1, \quad (44a)$$

$$M^2(e_1, e_2, e_3) := \frac{\alpha_1 \bar{z}_1(e_2 + e_3\mu_3) - \gamma_2^{\frac{1}{\alpha_2}} \left[\frac{e_3\mu_3 + (1-\alpha_2)e_2}{(1-\alpha_2)\bar{z}_2(e_3\mu_3 + e_2)} \right]^{\frac{1-\alpha_2}{\alpha_2}} (1 - \alpha_1)e_1}{\gamma_2^{\frac{1}{\alpha_2}} \left[\frac{e_3\mu_3 + (1-\alpha_2)e_2}{(1-\alpha_2)\bar{z}_2(e_3\mu_3 + e_2)} \right]^{\frac{1-\alpha_2}{\alpha_2}} (e_2 + \mu_3 e_3)} =: \mu_2, \quad (44b)$$

$$M^3(e_1, e_2, e_3) := \frac{\alpha_2 \bar{z}_2}{(\gamma_3/\bar{z}_3^{1-\alpha_3})^{\frac{1}{\alpha_3}}} - \frac{(1 - \alpha_2)e_2}{e_3} =: \mu_3. \quad (44c)$$

We restrict our analysis to parameters satisfying $M^i(\cdot) > 0$.

Proof of property (i) on page 14: To prove (i) we show that the differential system (22) is incompatible with $n_i = 0$ if $n_0 \in \mathbb{R}_{++}^3$. More specifically we show that $\lim_{n_i \rightarrow 0} \dot{n}_i > 0$

which contradicts $n_i = 0$. Observe that

$$\lim_{n_1 \rightarrow 0} G^1(\cdot) = \lim_{n_1 \rightarrow 0} \left(\frac{r_0}{n_1} \right)^{\alpha_1} \cdot [(1 - \alpha_1)\bar{z}_1]^{1-\alpha_1} - \gamma_1, \quad (45a)$$

$$\lim_{n_2 \rightarrow 0} G^2(\cdot) = \lim_{n_2 \rightarrow 0} \left[\frac{n_1 n_3 \alpha_1 e_3 \bar{z}_1}{n_2 (n_3 e_3 + n_1 (1 - \alpha_1) e_1)} \right]^{\alpha_2} \cdot [(1 - \alpha_2)\bar{z}_2]^{1-\alpha_2} - \gamma_2, \quad (45b)$$

$$\lim_{n_3 \rightarrow 0} G^1(\cdot) = \left[\frac{\alpha_2 e_3 \bar{z}_2}{(1 - \alpha_2) e_2} \right]^{\alpha_3} \cdot \bar{z}_3^{1-\alpha_3} - \gamma_3. \quad (45c)$$

From (45a) it is obviously that $\lim_{n_1 \rightarrow 0} \dot{n}_1 > 0$ which establishes that $n_1 = 0$ cannot be reached. Since $n_1 > 0$ we infer from (45b) $\lim_{n_2 \rightarrow 0} \dot{n}_2 > 0$. Finally, $\lim_{n_3 \rightarrow 0} \dot{n}_3 > 0$ follows due to the assumption that $M^3(\cdot) > 0$.

Derivation of (33): Note that $B^i \left[X^{i-1}(\cdot), \bar{z}_i - \tilde{Z}^i(\cdot), n_i \right] \equiv G^i(\cdot)$ for $i = 1, 2, 3$, where

$$X^0(r_0, n_1) := \frac{r_0}{n_1}, \quad (46a)$$

$$X^1(n_1, n_2, n_3) := \frac{n_1 \alpha_1 \bar{z}_1 \sum_{i=2}^3 n_i e_i}{n_2 [n_3 e_3 + n_2 e_2 + n_1 (1 - \alpha_1) e_1]}, \quad (46b)$$

$$X^2(n_2, n_3) := \frac{n_2 \alpha_2 e_3 \bar{z}_2}{n_3 e_3 + n_2 (1 - \alpha_2) e_2}, \quad (46c)$$

$$\tilde{Z}^1(n_1, n_2, n_3) := \frac{(1 - \alpha_1) \bar{z}_1 \sum_{i=1}^3 n_i e_i}{n_3 e_3 + n_2 e_2 + n_1 (1 - \alpha_1) e_1}, \quad (46d)$$

$$\tilde{Z}^2(n_2, n_3) := \frac{(1 - \alpha_2) \bar{z}_2 \sum_{i=2}^3 n_i e_i}{n_3 e_3 + n_2 (1 - \alpha_2) e_2}. \quad (46e)$$

Differentiation of (46a)-(46e) yields:

$$X_{r_0}^0 = \frac{X^0}{r_0}, \quad (47a)$$

$$X_{n_1}^0 = -\frac{X^0}{n_1}, \quad (47b)$$

$$X_{n_1}^1 = X^1 \cdot \frac{\sum_{i=2}^3 n_i e_i}{n_1 [n_1 (1 - \alpha_1) e_1 + n_2 e_2 + n_3 e_3]}, \quad (47c)$$

$$X_{n_2}^1 = -X^1 \cdot \frac{n_2 e_2 (\sum_{i=2}^3 n_i e_i) + n_3 e_3 [n_1 (1 - \alpha_1) e_1 + n_2 e_2 + n_3 e_3]}{n_2 (\sum_{i=2}^3 n_i e_i) [n_1 (1 - \alpha_1) e_1 + n_2 e_2 + n_3 e_3]}, \quad (47d)$$

$$X_{n_3}^1 = X^1 \cdot \frac{n_1 (1 - \alpha_1) e_1 e_3}{(\sum_{i=2}^3 n_i e_i) [n_1 (1 - \alpha_1) e_1 + n_2 e_2 + n_3 e_3]}, \quad (47e)$$

$$X_{n_2}^2 = X^2 \cdot \frac{n_3}{n_2} \cdot \frac{e_3}{n_2 (1 - \alpha_2) e_2 + n_3 e_3}, \quad (47f)$$

$$X_{n_3}^2 = -X^2 \cdot \frac{e_3}{n_2 (1 - \alpha_2) e_2 + n_3 e_3}, \quad (47g)$$

$$\tilde{Z}_{n_1}^1 = \tilde{Z}^1 \cdot \frac{\alpha_1 e_1 \sum_{i=2}^3 n_i e_i}{\left(\sum_{i=1}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \quad (48a)$$

$$\tilde{Z}_{n_2}^1 = -\tilde{Z}^1 \cdot \frac{n_1 \alpha_1 e_1 e_2}{\left(\sum_{i=1}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \quad (48b)$$

$$\tilde{Z}_{n_3}^1 = -\tilde{Z}^1 \cdot \frac{n_1 \alpha_1 e_1 e_3}{\left(\sum_{i=1}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \quad (48c)$$

$$\tilde{Z}_{n_2}^2 = \tilde{Z}^2 \cdot \frac{n_3 \alpha_2 e_2 e_3}{\left(\sum_{i=2}^3 n_i e_i\right) [n_2(1 - \alpha_2)e_2 + n_3 e_3]}, \quad (48d)$$

$$\tilde{Z}_{n_3}^2 = -\tilde{Z}^2 \cdot \frac{n_2 \alpha_2 e_2 e_3}{\left(\sum_{i=2}^3 n_i e_i\right) [n_2(1 - \alpha_2)e_2 + n_3 e_3]}. \quad (48e)$$

Next, the differentiation of G^i and the consideration of (47a)-(48e) as well as the steady state condition $B^i(\cdot) = 0$ yield after tedious rearrangements

$$G_r^1 = \frac{\alpha_1 \gamma_1}{r_0} \quad (49a)$$

$$G_{n_1}^1 = -\alpha_1 \gamma_1 \cdot \frac{\left(\sum_{i=1}^3 n_i e_i\right) \left(\sum_{i=2}^3 n_i e_i\right) - n_1^2 (1 - \alpha_1) e_1^2}{n_1 \left(\sum_{i=1}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \quad (49b)$$

$$G_{n_2}^1 = -(1 - \alpha_1) \gamma_1 \cdot \frac{n_1 \alpha_1 e_1 e_2}{\left(\sum_{i=1}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \quad (49c)$$

$$G_{n_3}^1 = -(1 - \alpha_1) \gamma_1 \cdot \frac{n_1 \alpha_1 e_1 e_3}{\left(\sum_{i=1}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \quad (49d)$$

$$G_{n_1}^2 = \alpha_2 \gamma_2 \cdot \frac{\sum_{i=2}^3 n_i e_i}{n_1 [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \quad (49e)$$

$$\begin{aligned} G_{n_2}^2 &= (1 - \alpha_2) \gamma_2 \cdot \frac{n_3 \alpha_2 e_2 e_3}{\left(\sum_{i=2}^3 n_i e_i\right) [n_2(1 - \alpha_2)e_2 + n_3 e_3]} \\ &- \alpha_2 \gamma_2 \cdot \frac{n_2 e_2 \left(\sum_{i=2}^3 n_i e_i\right) + n_3 e_3 [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}{n_2 \left(\sum_{i=2}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]}, \end{aligned} \quad (49f)$$

$$\begin{aligned} G_{n_3}^2 &= \alpha_2 \gamma_2 \cdot \frac{n_1(1 - \alpha_1)e_1 e_3}{\left(\sum_{i=2}^3 n_i e_i\right) [n_1(1 - \alpha_1)e_1 + n_2 e_2 + n_3 e_3]} \\ &- (1 - \alpha_2) \gamma_2 \cdot \frac{n_2 \alpha_2 e_2 e_3}{\left(\sum_{i=2}^3 n_i e_i\right) [n_2(1 - \alpha_2)e_2 + n_3 e_3]}, \end{aligned} \quad (49g)$$

$$G_{n_2}^3 = \alpha_3 \gamma_3 \cdot \frac{n_3 e_3}{n_2 [n_2(1 - \alpha_2)e_2 + n_3 e_3]}, \quad (49h)$$

$$G_{n_3}^3 = -\alpha_3 \gamma_3 \cdot \frac{e_3}{n_2(1 - \alpha_2)e_2 + n_3 e_3}. \quad (49i)$$

Finally, we apply (23) and (44) to establish

$$n_1 G_r^1 = \alpha_1 \gamma_1 \mu_1 =: \beta_1, \quad (50a)$$

$$n_1 G_{n_1}^1 = -\alpha_1 \gamma_1 \cdot \frac{\beta_{10} \beta_{11} - (1 - \alpha_1) e_1^2}{\beta_{10} \beta_{12}} =: \beta_2, \quad (50b)$$

$$n_1 G_{n_2}^1 = -(1 - \alpha_1) \gamma_1 \cdot \frac{\alpha_1 e_1 e_2}{\beta_{10} \beta_{12}} =: \beta_3, \quad (50c)$$

$$n_1 G_{n_3}^1 = -(1 - \alpha_1) \gamma_1 \cdot \frac{\alpha_1 e_1 e_3}{\beta_{10} \beta_{12}} =: \beta_4, \quad (50d)$$

$$n_2 G_{n_1}^2 = \mu_2 \alpha_2 \gamma_2 \cdot \frac{\beta_{11}}{\beta_{12}} =: \beta_5, \quad (50e)$$

$$n_2 G_{n_2}^2 = \mu_2 (1 - \alpha_2) \gamma_2 \cdot \frac{\mu_2 \mu_3 \alpha_2 e_2 e_3}{\beta_{11} \beta_{13}} - \mu_2 \alpha_2 \gamma_2 \cdot \frac{\mu_2 e_2 \beta_{11} + \mu_2 \mu_3 e_3 \beta_{12}}{\mu_2 \beta_{11} \beta_{12}} =: \beta_6, \quad (50f)$$

$$n_2 G_{n_3}^2 = \mu_2 \alpha_2 \gamma_2 \cdot \frac{(1 - \alpha_1) e_1 e_3}{\beta_{11} \beta_{12}} - \mu_2 (1 - \alpha_2) \gamma_2 \cdot \frac{\mu_2 \alpha_2 e_2 e_3}{\beta_{11} \beta_{13}} =: \beta_7, \quad (50g)$$

$$n_3 G_{n_2}^3 = \mu_2 \mu_3 \alpha_3 \gamma_3 \cdot \frac{\mu_2 \mu_3 e_3}{\mu_2 \beta_{13}} =: \beta_8, \quad (50h)$$

$$n_3 G_{n_3}^3 = -\mu_2 \mu_3 \alpha_3 \gamma_3 \cdot \frac{e_3}{\beta_{13}} =: \beta_9, \quad (50i)$$

where

$$\beta_{10} := e_1 + \mu_2 e_2 + \mu_2 \mu_3 e_3,$$

$$\beta_{11} := \mu_2 e_2 + \mu_2 \mu_3 e_3,$$

$$\beta_{12} := (1 - \alpha_1) e_1 + \mu_2 e_2 + \mu_2 \mu_3 e_3,$$

$$\beta_{13} := \mu_2 (1 - \alpha_2) e_2 + \mu_2 \mu_3 e_3.$$

Derivation of (34): Using (50) in (32) we get

$$\delta \lambda_{n_1} = \beta_2 \lambda_{n_1} + \beta_5 \lambda_{n_2} + n_c \theta_1, \quad (51a)$$

$$\delta \lambda_{n_2} = \beta_3 \lambda_{n_1} + \beta_6 \lambda_{n_2} + \beta_8 \lambda_{n_3} + n_c \theta_2, \quad (51b)$$

$$\delta \lambda_{n_3} = \beta_4 \lambda_{n_1} + \beta_7 \lambda_{n_2} + \beta_9 \lambda_{n_3} + n_c \theta_3. \quad (51c)$$

Finally, the equation system (51) is solved to obtain

$$\lambda_{n_3} = \frac{\beta_4 \lambda_{n_1} + \beta_7 \lambda_{n_2} + n_c \theta_3}{\delta - \beta_9}, \quad (52a)$$

$$\lambda_{n_2} = \frac{(\delta - \beta_9)(\beta_3 \lambda_{n_1} + n_c \theta_2) + \beta_8 (\beta_4 \lambda_{n_1} + n_c \theta_3)}{(\delta - \beta_6)(\delta - \beta_9) - \beta_7 \beta_8}, \quad (52b)$$

$$\lambda_{n_1} = \frac{n_c \theta_1 [(\delta - \beta_6)(\delta - \beta_9) - \beta_7 \beta_8] + n_c \theta_2 \beta_3 \beta_5 (\delta - \beta_9) + n_c \theta_3 \beta_5 \beta_8}{(\delta - \beta_2) [(\delta - \beta_6)(\delta - \beta_9) - \beta_7 \beta_8] - \beta_5 [\beta_3 (\delta - \beta_9) + \beta_4 \beta_8]}. \quad (52c)$$

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