

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.

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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 [21,23]. 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 [10,17,19,22]. Although many countries have introduced and stepped up nature protection programs, e.g. the Council Directive 92/43/EEC on the conservation of natural

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habitats and of wild fauna and flora (Habitat Directive) of the European Union, the rate of land conversion for economic purposes is still positive even in countries with shrinking human populations.¹

The principal reason for concerns about declining biodiversity is the positive correlations between the flow of ecosystem services and biodiversity [9,10] 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.

Regarding the link between the size of habitat and biodiversity, the widely accepted and plausible hypothesis is that biodiversity is an increasing function of habitat. There is a long tradition (since [3]) in ecological research to determine species–area relationships through field studies. As an 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. [20]). The insights from such an approach are limited, however, not only because the universality of that relation is questioned (e.g. [7]) but also because to our knowledge there is no formal theory from which that power law is derived.

Another approach with an equally long tradition is population ecology. It was developed initially to describe the dynamics of aquatic species communities and fishery [12,15] but it has also been applied to terrestrial communities [18] which are the exclusive focus of the present paper. Arguing within the population ecology framework, Swanson [22] 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” [22, 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 ...” [22, p. 814]. Swanson’s approach to species–area relationships is richer and more demanding than the power-law concept. Yet it does not 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.²

As reviewed by Chave and Levin [5], 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 [11] acknowledge the desirability, if not need, of such a microfoundation. Yet they do not follow that line finding “... it easier to study the macro-dynamics of an ecosystem directly without peering at microfoundations” [11, 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 [16], Tschirhart [24,25], Eichner and Pethig [14] and Christiaans et al. [6], we 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*

¹In 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 ha every day. The government also announced its goal to reduce that increase in land use to 30 ha per day in the year 2020.

²This is not to say that the differential equation 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.

(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.

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 answer the question as to “... what proportion ... of land must remain relatively undisturbed ... to sustain the delivery of essential ecosystem services” [10, p. 14], a question, whose further investigation would be profitable for society according to Daily et al. [10].

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 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 an exemplary numerical simulation. In Section 4 the focus is on the integrated analysis of both submodels. The optimal land use policy is characterized with full regard of ecosystem dynamics. The optimal habitat is shown to be larger than the *laissez-faire* habitat at each point in time implying that ecosystem services are underprovided in the no-policy scenario making the case for land use restrictions for nature protection. Finally, labor-augmenting technical change is introduced to generate ever increasing pressure toward 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 requires to refrain from using all land for economic purposes despite ever growing labor productivity. Section 5 concludes.

2. The integrated economy–ecosystem model

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 function³

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

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. The time index is suppressed to avoid clutter.

The total endowment of land is denoted \bar{r} . r_y is the land used by humans for economic purposes. This land includes land for business buildings and installations, residential houses, and traffic infrastructure, etc. To simplify, we assume that all land, r_y , set aside for economic uses is lost for use by *all* nonhuman species. 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

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

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.

³Upper-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.

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

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

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) 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. 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.⁴ 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 of biological resources.⁵

The economy submodel is closed by the equations

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

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

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

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

Consider now 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 regulation (*laissez faire*). In that scenario the profits of the consumer good industry and the land development industry are, respectively, $\pi_y = p_y \ell_y^\sigma r_y^{1-\sigma} - p_\ell \ell_y - p_r r_y$ and $\pi_d = p_r [\bar{r} - c / \ell_r] - p_\ell \ell_r$. Maximization of these profits on competitive markets implies

$$\frac{(1-\sigma)y}{r_y} = \frac{p_r}{p_y}, \quad \frac{\sigma y}{\ell_y} = \frac{p_\ell}{p_y} \quad \text{and} \quad \frac{p_r}{p_\ell} = \frac{\ell_r^2}{c}. \quad (7)$$

We combine (7), (2) and (4) to obtain, after some rearrangement of terms,

$$\frac{\sigma \bar{r}}{c(1-\sigma)} \ell_r^2 - \frac{\sigma}{(1-\sigma)} \ell_r - \ell_y = 0. \quad (8)$$

When Eq. (6) is considered in (8) we solve (8) for ℓ_r :

$$\ell_r = -\frac{c(1-2\sigma)}{2\sigma \bar{r}} + \sqrt{\frac{c^2(1-2\sigma)^2}{4\sigma^2 \bar{r}^2} + \frac{c(1-\sigma)\ell}{\sigma \bar{r}}}. \quad (9)$$

Inserting (9) into (2) and accounting for (4) yields the equilibrium value

$$r_d = r_y = \bar{r} - \frac{1}{-\frac{1-2\sigma}{2\sigma \bar{r}} + \sqrt{\frac{c^2(1-2\sigma)^2}{4\sigma^2 \bar{r}^2} + \frac{(1-\sigma)\ell}{c\sigma \bar{r}}}}. \quad (10)$$

As expected, the land 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 (9) and (10) the entire equilibrium allocation $(\ell_r, \ell_y, r_y, r_d, y_c, y)$ and the pertaining market clearing prices $(p_\ell \equiv 1, p_r, p_y)$ can readily be calculated.

⁴There are many measures of biodiversity that could be inserted in (3). See e.g. Armsworth et al. [2].

⁵As described by Daily et al. [10] 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;" [10, p. 13].

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. Consumers 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 .

So far we have characterized the (time-invariant) allocation of resources in the submodel of the laissez-faire market economy specifying, in particular, the size of land, r_y , to be used for economic purposes. Quite realistically, the size of habitat $r_0 := \bar{r} - r_y$ is unilaterally determined by the extent of the humans' economic land use (Eq. (10)). This observation gives rise to the question what the intertemporal impact is on the ecosystem of the land used for economic purposes. To answer this question we now proceed to set up the ecosystem submodel.

2.2. The ecosystem submodel

Building on Eichner and Pethig [14] and Christiaans et al. [6] we consider an ecosystem with three 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

$$b_i = B^i \left(\begin{matrix} x_{i-1}, z_i, n_i \\ + \quad - \quad +, 0 \end{matrix} \right), \quad i = 1, 2, 3 \tag{11}$$

and $D^i := \mathbb{R}_+ \times [0, \bar{z}_i] \times \mathbb{R}_+$. In (11), 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.⁶ 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 [4].⁷

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

$$e_i + p_i z_i \geq p_{i-1} x_{i-1}, \quad i = 1, 2, 3, \tag{12}$$

which is described and interpreted in Christiaans et al. [6].

All individual organisms are assumed to be price takers and to behave as if they solve the maximization problem:

$$\max_{(x_{i-1}, z_i)} B^i(x_{i-1}, z_i, n_i) \quad \text{s.t. (12)}. \tag{13}$$

⁶To avoid clumpy phrases we refer to organism 1's intake of the resource, x_0 , as 'intake of biomass of species 0'.

⁷According 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.

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 if,^{8,9}

$$r_0 = n_1 x_0, \quad (14a)$$

$$n_i z_i = n_{i+1} x_i \quad \text{for } i = 1, 2, \quad (14b)$$

where $r_0 := \bar{r} - r_y$ (with r_y as specified in (10)) denotes the land endowment available as habitat for all nonhuman species.

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 (13), (14a) and (14b) are satisfied. The short-run equilibrium allocation in the ecosystem is linked to the growth of populations as follows: 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:

$$\frac{dn_i}{dt} = \dot{n}_i = n_i b_i, \quad i = 1, 2, 3. \quad (15)$$

To obtain more specific results we replace (11) by the parametric net offspring function

$$B^i(x_{i-1}, z_i, n_i) = A^i(n_i) \cdot x_{i-1}^{\alpha_i} \cdot (\bar{z}_i - z_i)^{1-\alpha_i} - \gamma_i, \quad (16)$$

where

$$A^i(n_i) := \min \left[1, \frac{n_i}{\tilde{n}_i} \right], \quad (17)$$

and where $0 < \alpha_i < 1$ and $\gamma_i > 0$. For this parametric specification we derive in an appendix, which is available from the authors upon request, the differential equations of population growth:

$$\dot{n}_1 = n_1 \cdot G^1(r_0, n_1, n_2, n_3), \quad (18a)$$

$$\dot{n}_2 = n_2 \cdot G^2(n_1, n_2, n_3), \quad (18b)$$

$$\dot{n}_3 = n_3 \cdot G^3(n_2, n_3), \quad (18c)$$

where

$$G^1(\cdot) = A^1(n_1) \cdot \left(\frac{r_0}{n_1} \right)^{\alpha_1} \cdot \left[\bar{z}_1 \cdot \frac{(1 - \alpha_1) \sum_{i=1}^3 n_i e_i}{(1 - \alpha_1) \left(\sum_{i=1}^3 n_i e_i \right) + \alpha_1 \left(\sum_{i=2}^3 n_i e_i \right)} \right]^{1-\alpha_1} - \gamma_1, \quad (19a)$$

$$G^2(\cdot) = A^2(n_2) \cdot \left[\frac{n_1 \alpha_1 \bar{z}_1}{n_2} \cdot \frac{\sum_{i=2}^3 n_i e_i}{\left(\sum_{i=2}^3 n_i e_i \right) + (1 - \alpha_1) n_1 e_1} \right]^{\alpha_2} \cdot \left[\bar{z}_2 \cdot \frac{(1 - \alpha_2) \sum_{i=2}^3 n_i e_i}{(1 - \alpha_2) \left(\sum_{i=2}^3 n_i e_i \right) + \alpha_2 n_3 e_3} \right]^{1-\alpha_2} - \gamma_2, \quad (19b)$$

$$G^3(\cdot) = A^3(n_3) \cdot \left[\frac{n_2 \alpha_2 \bar{z}_2}{n_3} \cdot \frac{e_3}{e_3 + \frac{n_2}{n_3} (1 - \alpha_2) e_2} \right]^{\alpha_3} \cdot (\bar{z}_3)^{1-\alpha_3} - \gamma_3. \quad (19c)$$

Having introduced and analyzed 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

⁸While the equality sign in (14b) is imperative the more general form of (14a) 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 [14].

⁹Taking Eq. (14a) literally, each organism of species 1 is supposed to consume the amount $x_0 = r_0/n_1$ of land. However, following Swanson [22, p. 811], we take the land 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)efficiency of economic land use. However, before doing so it is worthwhile to shed more light on the complex link between the size of habitat and the dynamics of species populations as established in (18). 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 (18) 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 a numerical example, 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 system (18) 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 a numerical simulation.

Closer inspection of (18) and (19) 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 system (18) of differential equations, called ‘system (18)’ hereafter, and a modified version of it which differs from system (18) only in replacing (17) by $A^i(n_i) \equiv 1$ for $i = 1, 2, 3$. We denote this modified version as ‘reference system (18)’. Since the properties of the reference system (18) are less complex than those of the ‘true’ system (18) it will turn out to be very helpful in specifying important characteristics of system (18). We therefore proceed by investigating the reference system (18) 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 (18). Restricting the parameter space as specified in the appendix and assuming that the reference system (18) runs into a stationary point¹⁰ 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 (18), if the initial populations are n_0 and the habitat size is r_0 .¹¹

Closer inspection of the function N^R reveals that the reference system (18) has the following properties¹²:

- (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, $r_0 = 0$. According to property (ii) the carrying capacity of all species is linear in habitat, i.e. $N^R(n_0, \lambda r_0) = \lambda N^R(n_0, r_0)$ for all $\lambda > 0$. To see the rationale of this result suppose $N^R(n_0, r_0)$ is given and then the habitat is doubled. If you double the number of individuals of each species and let them have the equilibrium transactions of the individuals in the initial stationary point $N^R(n_0, r_0)$, one clearly ends up in the stationary state $N^R(n_0, 2r_0) = 2N^R(n_0, r_0)$. It is therefore interesting to explore how properties (i)–(iii) need to be modified when the regeneration efficiency term (17) comes to bear.

¹⁰In case of a predator–prey model the global stability of the stationary point has been proven in Christiaans et al. [6]. For the three species case our numerical analysis shows that there exists a large set of parameters for which this assumption is verified.

¹¹By \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.

¹²Properties (i)–(iii) are proven in the appendix which is available upon request.

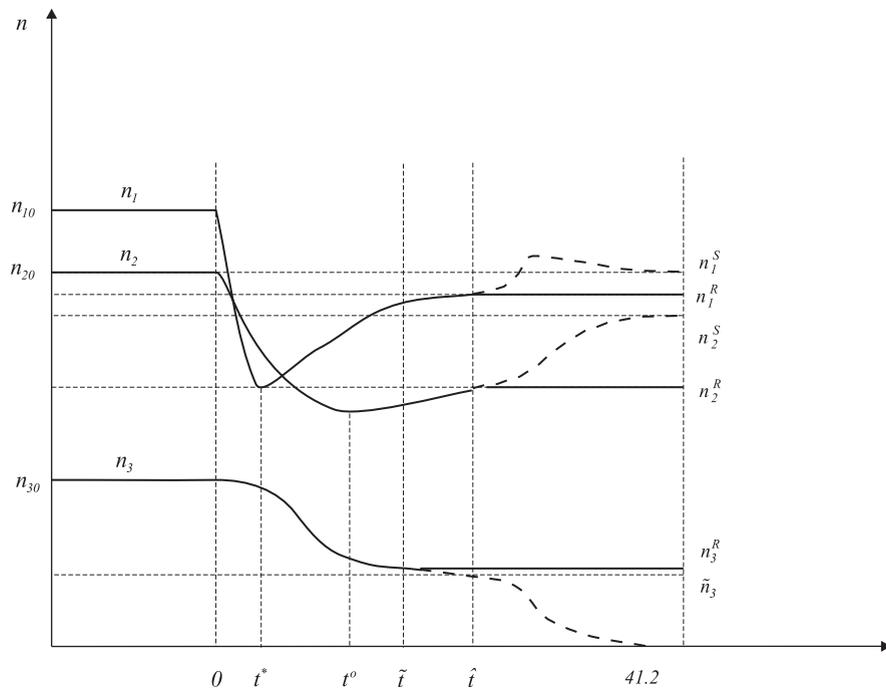


Fig. 1. Population responses to a drastic shock reduction in habitat.

To begin with, the dynamics of the reference system (18) and those of system (18) coincide—and hence properties (i)–(iii) also characterize the ‘true’ system (18)—if and only if the dynamics of the reference system (18) 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).

A full investigation of the dynamics of system (18) 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. Fig. 1 summarizes¹³ the characteristic features of a series of numerical exercises¹⁴ in comparative dynamics. We restrict our attention to the solid curves, first. 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 $t^0 > t^*$ and then also recovers moderately. The top predator species 3 is also bound to decline due to reduced prey abundance but then manages to stabilize its population above its critical level \tilde{n}_3 .

The solid lines in Fig. 1 thus describe an example in which 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 final 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. This is exactly what happens to species 3 when in the right part of Fig. 1 the solid lines are replaced by the dashed lines. In that case, the time paths of the reference system (18)

¹³Fig. 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.

¹⁴The numerical example is calculated with the help of the computer program Mathematica. The program for simulations is available from the authors upon request. The parameter values are set as follows: $\alpha_1 = \alpha_2 = \alpha_3 = 0.5$, $e_1 = 1$, $e_2 = 1.85$, $e_3 = 2.4$, $\gamma_1 = 1.5$, $\gamma_2 = 1.2$, $\gamma_3 = 1.2$, $\tilde{n}_1 = \tilde{n}_2 = \tilde{n}_3 = 2$, $\bar{r} = 832$, $\bar{z}_1 = 2.4$, $\bar{z}_2 = 1.5$, $\bar{z}_3 = 1$. For more detailed description and interpretation of the exercises performed see Eichner and Pethig [13].

and system (18) coincide until $t = \hat{t}$. But at $t = \hat{t}$ the population of species 3 becomes $n_{3t} = \hat{n}_3$ with a tendency of further decline. The term $A^3(n_{3t})$ switches from 1 to n_{3t}/\hat{n}_3 driving species 3 toward extinction while the populations of 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 at which species 3 perishes can be interpreted as a new starting point of the ecosystem dynamics with the populations of the two surviving species.

The principal message of the numerical example underlying Fig. 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. The incorporation into system (18) 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 dynamics (18) diverge from that of the reference system (18) 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

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, due to missing markets (and separability assumptions) the laissez-faire economy does not respond to changes in the supply of ecosystem services indicating an inefficient resource allocation due to an ecosystem service externality in the sense of Crocker and Tschirhart [8].

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.¹⁵ 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 do not offer a comparative policy assessment but rather implicitly assume that land zoning legislation is 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 (10). Hence with time-invariant labor endowment, ℓ , the size of habitat turns out also to be time-invariant, too. To see whether this allocation is efficient consider a Utilitarian social planner solving the problem

$$\max \int_0^\infty n_c U(\cdot) e^{-\delta t} dt \quad \text{s.t. (1)–(6), (18a)–(18c), } r_d \leq \bar{r}_y, \quad r_0 = \bar{r} - \bar{r}_y, \tag{20}$$

where δ is a positive social discount rate and n_c is the constant population of humans. Eq. (20) 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 (20) reads

$$\begin{aligned} \mathcal{L} = n_c U \left\{ \frac{1}{n_c} Y[\ell - \ell_r, R(\ell_r)], \bar{r} - R(\ell_r), n_1, n_2, n_3 \right\} + \lambda_{n_1} n_1 G^1[\bar{r} - R(\ell_r), n_1, n_2, n_3] \\ + \lambda_{n_2} n_2 G^2(n_1, n_2, n_3) + \lambda_{n_3} n_3 G^3(n_2, n_3). \end{aligned} \tag{21}$$

¹⁵In 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 do not follow that approach in the present paper, (20) may be interpreted as a secondbest optimization approach.

An interior solution to (21) satisfies¹⁶

$$Y_r R_\ell - Y_\ell = n_c \cdot \frac{U_r R_\ell}{U_y} + \frac{n_1 \lambda_{n_1} G_r^1 R_\ell}{U_y} > 0, \quad (22)$$

$$\dot{\lambda}_{n_i} = \delta \lambda_{n_i} - \lambda_{n_i} G^i - \sum_{k=1}^3 \lambda_{n_k} n_k G_{n_i}^k - n_c U_{n_i}, \quad i = 1, 2, 3. \quad (23)$$

The first term on the right side of (22), $n_c U_r R_\ell / U_y > 0$, 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 (22), $n_1 \lambda_{n_1} G_r^1 R_\ell / U_y > 0$, 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. Both these marginal social benefits are not accounted for in the laissez-faire market allocation because maximizing profits π_y and π_d implies $Y_r R_\ell = Y_\ell$. Consequently, the market allocation does not satisfy (22).

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 (22). 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 Eqs. (22) and (23) do not provide enough information to fully characterize the time path 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 (21). 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. We do not 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

$$G^1(r_0, n_1, n_2, n_3) = G^2(n_1, n_2, n_3) = G^3(n_2, n_3) = 0. \quad (24)$$

Due to (24), Eqs. (23) simplify to

$$\delta \lambda_{n_i} = \sum_{k=1}^3 \lambda_{n_k} n_k G_{n_i}^k + n_c \theta_i, \quad i = 1, 2, 3, \quad (25)$$

¹⁶Due to (17) and (19), (21) is not differentiable at $n_i = \tilde{n}_i$ for $i = 1, 2, 3$. We restrict our attention to solutions in which this 'complication' does not matter.

where the utility function U employed in (23) is replaced by the parametric function (3). Simple but tedious calculations show that

$$\begin{aligned} n_1 G_r^1 &= \beta_1, & n_1 G_{n_1}^1 &= \beta_2, & n_1 G_{n_2}^1 &= \beta_3, & n_1 G_{n_3}^1 &= \beta_4, & n_2 G_{n_1}^2 &= \beta_5, \\ n_2 G_{n_2}^2 &= \beta_6, & n_2 G_{n_3}^2 &= \beta_7, & n_3 G_{n_2}^3 &= \beta_8, & n_3 G_{n_3}^3 &= \beta_9, \end{aligned} \tag{26}$$

where β_i for $i = 1, \dots, 9$ are parameters. The derivation of (26) and the definition of β_i for $i = 1, \dots, 9$ are provided in the appendix. In the appendix it is also shown that inserting (26) into (25) gives us

$$\lambda_{n_1} = \frac{n_c \theta_1 [(\delta - \beta_6)(\delta - \beta_9) - \beta_7 \beta_8] + n_c \theta_2 \beta_3 \beta_5 (\delta - \beta_9) + n_c \theta_3 \beta_5 \beta_8}{(\delta - \beta_2)[(\delta - \beta_6)(\delta - \beta_9) - \beta_7 \beta_8] - \beta_5 [\beta_3 (\delta - \beta_9) + \beta_4 \beta_8]}. \tag{27}$$

Next we make use of the parametric production function (1) and the parametric utility function (3) to rewrite (22) as

$$\frac{(1 - \sigma)}{r_y} - \frac{\ell_r^2 \sigma}{c \ell_y} = n_c \eta + \lambda_{n_1} \beta_1. \tag{28}$$

Accounting for $r_y = \bar{r} - c/\ell_r$ and $\ell_y = \ell - \ell_r$ in (28) yields

$$\begin{aligned} \ell_r^3 + \frac{(1 - 2\sigma)c - \bar{r}c(n_c \eta + \lambda_{n_1} \beta_1)}{\sigma \bar{r}} \ell_r^2 - \frac{(1 - \sigma)c\ell - c(c + \ell \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)}{\sigma \bar{r}} \ell_r \\ - \frac{(n_c \eta + \lambda_{n_1} \beta_1)c^2 \ell}{\sigma \bar{r}} = 0. \end{aligned} \tag{29}$$

The solution to (29) 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: $\eta = 10^{-5}$, $n_c = 100$, $\sigma = 0.5$, $\theta_1 = \theta_2 = \theta_3 = 10^{-6}$.

Table 1 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 results are not special features of the numerical examples on which the results in Table 1 are based. To support 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

Table 1
Optimal versus laissez-faire habitat for alternative labor endowments

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

n_c of the human species) but we may rather look at it as growth of labor in efficiency units reflecting exogenous labor-saving technical progress.¹⁷

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 Eq. (10) that the economic land use is now ever growing which translates into an ever shrinking size of habitat. In fact we easily infer from (9) 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. Hence the ecosystem with all its species is doomed.

Such a gloomy scenario appears to be considered realistic by many ecologists, e.g. by Daily [9], Daily et al. [10] and Alcamo [1]. If in addition, a minimum provision of ecosystem services is considered indispensable to both human welfare and human existence, humankind is bound to perish along with all other species in the laissez-faire scenario.¹⁸ Having made the point that due to the public-good characteristics of ecosystem services the laissez-faire economy lacks incentives to preserve the ecosystem is not tantamount to saying that humankind is doomed, since the laissez-faire regime can be replaced by a policy regime. To see what an efficient policy should accomplish we now take a closer look at the social planner's partition of land between humans and nonhumans. The planner's optimization calculus is the same as in (21) 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

$$\lim_{t \rightarrow \infty} \ell_{rt} = \ell_r^*. \quad (30)$$

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 (21). 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 (22) we find that the left side of (22) converges to $-\infty$ whereas the right side of (22) converges to 0 such that Eq.(22) is violated. This contradiction proves that $r_0 \rightarrow 0$ is not a solution to (21).

To further specify the upper bound ℓ_r^* observe that the optimal time path is still characterized by (22) and (23), and (24)–(29) apply correspondingly. Following some rearrangement of terms (29) can be turned into

$$H(\ell_t, \ell_{rt}) := \frac{\sigma \bar{r} \ell_{rt}^3}{(1 - \sigma)c\ell_t - c(c + \ell_t \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)} + \frac{[(1 - 2\sigma)c - \bar{r}c(n_c \eta + \lambda_{n_1} \beta_1)]\ell_{rt}^2}{(1 - \sigma)c\ell_t - c(c + \ell_t \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)} - \ell_{rt} - \frac{(n_c \eta + \lambda_{n_1} \beta_1)c^2 \ell_t}{(1 - \sigma)c\ell_t - c(c + \ell_t \bar{r})(n_c \eta + \lambda_{n_1} \beta_1)} = 0. \quad (31)$$

Quite obviously, the term $H(\ell_t, \ell_r^*)$ with function H from (31) is not zero, in general, for any $t \in \mathbb{R}_+$. However, in view of (31) and (30) it is true that

$$\lim_{t \rightarrow \infty} H(\ell_t, \ell_r^*) = 0. \quad (32)$$

In view of $\lim_{t \rightarrow \infty} \ell_t = \infty$ and L'Hopital's rule, (32) can be shown to imply

$$\ell_r^* = \frac{(n_c \eta + \lambda_{n_1} \beta_1)c}{\bar{r}(n_c \eta + \lambda_{n_1} \beta_1) - (1 - \sigma)}. \quad (33)$$

¹⁷Such an approach to technical change is very simple and stylized but it serves well our purpose of modeling the growing pressure on the ecosystem of continuing productivity gains in the real world.

¹⁸There is a simple way to cope with the issue of indispensable ecosystem services in our model by restricting the domain of the utility function in (3) to a set of feasible consumption bundles that is bounded from below. More specifically, a consumption bundle $(y_c, r_0, n_1, n_2, n_3)$ is defined as being feasible, if none of its components drops below some *positive* lower bound. Since in our laissez-faire scenario r_0 , n_1 , n_2 and n_3 cannot be bounded away from zero, humans would eventually be faced with infeasible consumption and then perish.

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 1.

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

$$\hat{y}_t = \sigma \hat{\ell}_{yt} + (1 - \sigma) \eta_{rt} \hat{\ell}_{rt}, \tag{34}$$

$$\hat{\ell}_{yt} = \frac{\hat{\ell}_t}{\rho_t} - \frac{1 - \rho_t}{\rho_t} \hat{\ell}_{rt}, \tag{35}$$

where $\rho_t := \ell_{yt}/\ell_t$, $\hat{x}_t := \dot{x}_t/x_t$ for $x = y, \ell_y, \ell_r, \ell$ and $\eta_{rt} := \ell_{rt} R_\ell / r_{yt}$. Owing to (30) and (2) we find that $\lim_{t \rightarrow \infty} \eta_{rt}$ is positive and constant and that $\lim_{t \rightarrow \infty} \rho_t = 1$. Therefore, (34) and (35) yield

$$\lim_{t \rightarrow \infty} \hat{\ell}_{yt} = \hat{\ell}_t = \omega \quad \text{and} \quad \lim_{t \rightarrow \infty} \hat{y}_t = \sigma \omega. \tag{36}$$

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 microfounded 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 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 does not 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. In our view, environmental-economic modeling should not offer a sophisticated and microfounded analysis of the economic system with the environment being added as a small appendix or a black box. Our ecosystem–economy model avoids such an 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 three-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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