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## Efficient Nonanthropocentric Nature Protection

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# Efficient nonanthropocentric nature protection\*

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## Abstract

This paper analyzes nature protection by a social planner under different 'utilitarian' social welfare functions. For that purpose we construct an integrated model of the economy and the ecosystem with explicit consideration of nonhuman species and with competition between human and nonhuman species for land and prey biomass. We characterize and compare the efficient allocations when social welfare is anthropocentric (only consumers have positive welfare weights), when social welfare is biocentric (only nonhuman species have positive welfare weights) and when social welfare is nonanthropocentric (all species have positive welfare weights). Not surprisingly, biocentric social welfare calls for suspending all economic activities. It is more important, however, that both anthropocentrism and nonanthropocentrism make the case for nature protection through different channels, though. Our analysis suggests that one may dispense with the concept of nonanthropocentric social welfare provided that in the anthropocentric framework the consumers' intrinsic valuation of nature is properly accounted for.

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Key words: anthropocentrism, biocentrism, welfare, nature protection

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## 1 Introduction

Environmental economists not only borrowed from economics methodological individualism but also the paradigm that *all* value originates in some consumer's valuation. Focusing on the interface of the economy and the environment they maintain that all *environmental* value is ultimately based on some or all consumers' valuation of natural objects or ecosystem services. In other words, ecosystems, natural resources and species communities are valuable only because and so far as they are valuable for consumers. Yet, this anthropocentric perspective is not tantamount to making the case against nature protection. It rather implies that nature protection ought to be derived from and confined to nature's instrumental value for humans.

This instrumental role of nature is quite well understood. For example, the efficient intertemporal extraction and harvesting of nonrenewable and renewable resources can be interpreted as a normative rule for optimal nature protection. Overharvesting as well as underharvesting are 'wasteful' deviations from the optimum. Moreover, in environmental economic analysis consumers are usually assumed to 'care about nature' in the sense that they suffer from 'environmental degradation' which is often interpreted as suffering from deteriorating life-supporting ecosystem services (Dailey 1997). In terms of formal modeling such ecosystem services come as positive consumption externalities to the effect that taking them properly into account provides a rationale for nature protection in addition to the extraction/harvesting rationale.

The major part of normative environmental economics has been and still is committed to this anthropocentric paradigm of efficient nature protection. Yet in sharp contrast, many environmental ethicists embrace nonanthropocentrism and the concept of intrinsic value in nature, e.g. in individual animals, species and/or ecosystems, and they call for these natural objects' moral consideration in human decision making on environmental issues (Routley 1973, Rolston 1988, Callicott 1989). Such an intrinsic-value argument seems to suggest that nature protection should be stepped up beyond the level which is efficient under the anthropocentric paradigm.

Summarizing, two separate rationales for nature protection can be distinguished: (i) the anthropocentric argument calling for a restrained use of nature out of the consumers'

self-interest in order to take the best possible (long-term) advantage of nature's resources and ecosystem services and (ii) the nonanthropocentric argument calling for nature protection for its own sake, i.e. independent of its instrumental value to consumers.<sup>1</sup> As mentioned above, the extant literature provides useful insights into the logic of optimal anthropocentric nature protection even though important impacts of human activities on species, habitats and ecosystems are rarely addressed in formal models. On the other hand, we know very little about the analytics of nonanthropocentric nature protection. In fact, we are not aware of any formal analyses investigating the consequences of values intrinsic to nature itself.

When the focus is on intrinsic value and *social* welfare which may or may not include nonhuman components, one can hardly avoid taking notice of the differences and linkages between the concepts of utility, preferences, informed preferences, well-being, happiness and welfare regarding both human and nonhuman organisms as scrutinized, e.g. by Ng (1995, 1999, 2003) and the literature quoted there. Following that literature, we take the view that social welfare ought to be based on individual welfare rather than on preferences. This methodological decision raises the questions (i) whether it is sensible to attribute welfare to nonhuman species, and if so, to which, and (ii) what the appropriate determinants of welfare are in theoretical analysis. In the present paper we do introduce and specify individual welfare functions for both human and nonhuman species without claiming, however, to provide an innovative let alone comprehensive contribution to the formation of welfare.

It may be considered a plausible proposition that under nonanthropocentrism the optimal human use of (and strain on) nature will be less than under anthropocentrism. But how should that be made precise and how exactly differs nature protection under both paradigms? With the focus on the intrinsic value to nature, will there be larger species populations, habitats, ecosystems and/or, perhaps lower resource extraction and biomass harvesting by humans? Do we need to sacrifice human welfare and material well-being for greater ecosystem health? Interestingly, even the strongest proponents of nonanthropocentrism, mainly environmental ethicists, have no clear conception of the consequences of attaching intrinsic value to nature. Norton (1991) even proposed a 'convergence hypothesis' suggesting "... that, if one takes all human interests into account (including the full breadth of human values in the present and in the future), and if one defines nonanthropocentric interests reasonably, then the policies required to comply with anthropocentric and nonanthropocentric values will converge". Since the difference between both approaches on the

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<sup>1</sup>This line of reasoning already has significant impacts on the real world. In a recent amendment to the German constitution the intrinsic value of nature has been recognized. Almost ninety percent of the German population believe that the plants' and animals' right to live ought to be respected.

conceptual level can hardly be denied we take 'convergence' to mean that the approaches become closer rather than the same.

The present paper aims at scrutinizing in rigorous analysis the consequences for nature protection of the social planner's choice between accounting for human welfare, nonhuman welfare and a combination of both. To that end two principal prerequisites are needed. First, we need to construct an integrated model of the economy and the ecosystem with an explicit consideration of nonhuman species and their constituent individuals. Second the conventional anthropocentric concept of social welfare has to be modified to encompass the welfare of nonhuman organisms.

As for the integrated model we follow the lines of Hannon (1976), Tschirhart (2000) and Eichner and Pethig (2003) conceiving of the ecosystem as a community of species the individuals of which engage in intra-ecosystem transactions competing for prey biomass and natural resources (here: land for habitat). Humans are additional competitors for prey biomass and for land which they annex at the expense of the nonhuman species' habitat. Since humans are unchallenged usurpers of land and top predators, the species communities have to content themselves with the residual land for habitat and the residual biomass for foraging. (Recall, however, that even if humans have their way, some level of nature protection is in their self-interest.)

Conventional welfare economics is based on the proposition that individual consumers' welfare is to count, and the conventional (utilitarian) concept of social welfare defines social welfare as the sum of all consumers' welfare with positive welfare weights attached to all individual welfares. We will call this concept *anthropocentric* social welfare, since positive welfare weights are assigned to all consumers and to nobody else or nothing but consumers. In the present paper we wish to generalize the (utilitarian) notion of social welfare to include the welfare of nonhuman organisms. Nonanthropocentrists have suggested divergent views on the exact nature of natural objects that could be said to have intrinsic value. Some authors attribute intrinsic values to composites such as species, communities or ecosystems (Callicott 1989), others to nonhuman individual organisms (Regan 1983). Ng (1995) also argues in favor of recognizing the welfare values of nonhuman individual organisms but he maintains that only a subset of them, the set of organisms he characterizes as 'affective sentients' ought to be considered as morally relevant. For the purpose of our subsequent exploration we need not provide an ultimate answer for what the appropriate natural object is to be endowed with intrinsic value, because any natural entity that enters the social planner's objective function in addition to or instead of human welfare will serve our conceptual analysis. We choose to allow nonhuman organisms, possibly only a subset of them, to be 'morally considerable' individuals in the sense that their welfare is to count. To this

end we need to assign welfare to nonhuman organisms and we introduce a generalized concept of (utilitarian) social welfare that allows for attaching positive welfare weights to the welfare of nonhuman organisms. If positive welfare weights are placed only on nonhuman organisms, we call the resultant social welfare concept *biocentric*. Combining biocentric and anthropocentric social welfare yields *nonanthropocentric* social welfare defined by a (generalized utilitarian) social welfare function with positive welfare weights attached to both consumers and nonhuman organisms.

Within this framework of analysis we are interested in characterizing the efficient intertemporal allocation under biocentric, anthropocentric and nonanthropocentric social welfare. Not unexpectedly, the biocentric social welfare optimum will turn out to require shutting down all economic activities thus extinguishing the human species. In contrast, with anthropocentric social welfare, optimal nature protection implies to maintain the ecosystem in operation because humans depend on nature but nature doesn't depend on humans. The comparison of the marginal efficiency rules under anthropocentric and nonanthropocentric social welfare turns out to yield interesting general but limited specific information about differences in optimal nature protection. We therefore proceed by focusing our attention on optimal steady states in simplified models to explore the allocative displacement effects of parametric changes in (i) the welfare weights of organisms belonging to a nonhuman species and (ii) the marginal welfare consumers derive from nature's ecosystem services. In both cases stepping up nature protection tends to be optimal, although the results do not conform to one's intuition in all details. Of particular interest is a special case where optimal protection of nature under anthropocentric and nonanthropocentric social welfare coincides.

Section 2 outlines the general intertemporal integrated model of the economy and the ecosystem. For that model the efficient time paths of resource allocation are characterized in Section 3, when the social welfare is either biocentric, anthropocentric or nonanthropocentric. In Section 4 the focus is on steady states of two different, substantially simplified models to elicit additional information on optimal nature protection by means of comparative dynamic analysis. Section 5 concludes.

## 2 The general model

Suppose the amount  $y \geq 0$  of the composite *consumption good*  $Y$  is supplied by the production sector according to the concave production function  $Y : \mathbb{R}_+ \times \mathbb{R}_+^N \rightarrow \mathbb{R}_+$  satisfying

$$y \leq Y \left( \begin{matrix} r_y & \mathbf{z}_y \\ + & + \end{matrix} \right). \quad (1)$$

Good  $Y$  is produced with a *non-biomass natural resource*,  $r_y \geq 0$ , and with the biomass of  $N$  species,  $\mathbf{z}_y := (z_{y1}, \dots, z_{yN}) \in \mathbb{R}_+^N$ , where  $z_{yj}$  is the *biomass of species  $j$* . We assume that<sup>2</sup>  $Y_{rz} \geq 0$  and that all inputs are essential in production, i.e.<sup>3</sup>  $Y(0, \mathbf{z}_y) = Y(r_y, \mathbf{0}^N) = 0$ .

In the real world, the production sector uses as inputs a variety of renewable and non-renewable (non-biomass) natural resources, e.g. minerals, fossil fuels, water, sunlight or land. In the present model we focus on a single natural resource for which humans compete along with organisms of (other) species. Among such resources, we select land as a particularly important life-supporting resource for species. Land cannot only be used for economic activities,  $r_y$ , but it also accommodates the ecosystem. Focusing on land is also convenient on analytical grounds because its total endowment,  $\bar{r}$ , is fixed and time invariant. Since economic uses of land supersede ecological uses quite often we confine the ecosystem to the segment of land,  $\bar{r} - r_y$ , referred to as the *habitat* of the community of  $N$  species. To further simplify, all organisms of the same species are assumed to be identical. We denote by *organism  $i$*  the representative organism of species  $i$ , for short. In the period under consideration, organism  $i$  generates *net offspring  $b_i$*  that is modeled<sup>4</sup> by the concave function  $B^i : \mathbb{R}_+ \times \mathbb{R}^N \rightarrow \mathbb{R}$  such that

$$b_i \leq B^i \left( r_i, \mathbf{z}_i \right), \quad i = 1, \dots, N. \quad (2)$$

In (2),  $r_i$  is the input of land used exclusively by organism  $i$  and  $\mathbf{z}_i := (z_{i1}, \dots, z_{ii}, \dots, z_{iN}) \in \mathbb{R}^N$  is a vector of organism  $i$ 's biomass transactions.  $z_{ij} \geq 0$  is interpreted as organism  $i$ 's *intake of biomass* of (prey) species  $j \neq i$  and  $z_{ii} \leq 0$  is organism  $i$ 's *loss of own biomass* to its predators. Obviously,  $B_{z_{ii}}^i > 0$  means that organism  $i$ 's net offspring generation is hampered by losses of own biomass  $z_{ii}$ . On the other hand, the derivatives  $B_{z_{ij}}^i \geq 0$  for  $i \neq j$  and  $B_r^i > 0$ , respectively, indicate that organism  $i$ 's net offspring is fostered by the intake of biomass of (prey) species  $j$ , and by land available for its own use. We assume  $B_{rz} \leq 0$ , and since organism  $i$  cannot survive without prey biomass intake or space for living (land), we set  $B^i(0, 0) < 0$ . As a consequence,  $B^i(\cdot) = 0$  presupposes some food intake or some land use since this special case characterizes a situation where the birth rate of species  $i$  equals its death rate such that the population of species  $i$  is constant. Some partial derivatives of function  $B^i$  may be zero, of course. If organism  $i$  belongs to a plant species, one would expect  $B_r^i > 0$  and  $B_{z_{ii}}^i > 0$  but  $B_{z_{ij}}^i = 0$  for all  $j \neq i$ . In case of an animal species we certainly have  $B_{z_{ij}}^i > 0$  for some  $j \neq i$  but perhaps  $B_r^i = 0$ .

<sup>2</sup>If letters denote functions, subscripts attached to them indicate derivatives.

<sup>3</sup> $\mathbf{0}^N$  is the  $N$ -dimensional vector consisting of  $N$  zeros.

<sup>4</sup>The conceptual origin of (2) is Hannon (1976) whose approach has been further elaborated by Tschirhart (2000). Our approach differs from theirs mainly in that these authors focused on the generation of net energy rather than net offspring.

A more realistic description of the process of offspring generation would require to include as arguments of function  $B^i$  many more variables such as nutrients, minerals, fresh water etc. or perhaps even populations or individuals of own and/or other species. Yet space for living ( $r_i$ ) and intake of prey biomass ( $z_{ij}$  for  $j \neq i$ ) as well as loss of own biomass to predators ( $z_{ii}$ ) appear to be the central and most important determinants of offspring generation. Therefore suppressing other variables in (2) is warranted in view of both Occam's razor and the quest for tractability.

As indicated in the introduction, various approaches to nonanthropocentrism support the idea of recognizing the welfare of nonhuman organisms as morally relevant. Taking up this line of reasoning we will endow nonhuman organisms with welfare. However, the question as to what the appropriate determinants of these organisms' welfare are is difficult to answer, since 'welfare biology' is a discipline in its infancy (Ng 1995). We will employ a simple hypothesis that we find quite plausible and appealing: Nonhuman organisms enjoy both their offspring and their own population.<sup>5</sup> In terms of the formal model we therefore represent organism  $i$ 's welfare by the concave function  $V^i : \mathbb{R} \times \mathbb{R} \rightarrow \mathbb{R}$  satisfying

$$v_i \leq V^i \left( \begin{matrix} b_i, n_i \\ +, 0 \quad +, 0 \end{matrix} \right), \quad i = 1, \dots, N. \quad (3)$$

Endowing nonhuman organisms with welfare is certainly an unusual feature of our approach. Yet it is necessary to prepare for an analysis reaching beyond the conventional view that the entire ecosystem (similar as the producers' activities) is evaluated by means of its instrumental contribution to human welfare. Even if one accepts that nonhuman species are capable of enjoyment and suffering (as captured in  $V^i$  in (3)) one may not agree that this is true for *all* such organisms. Ng (1995) scrutinizes this issue and concludes that welfare and hence moral relevance is attached only to individuals of that (proper) subset of animal species whose members are *affective sentients*. For the purpose of the present paper we need not make a decision in favor or against particular concepts of nonhuman welfare or moral irrelevance of species. In the formal model, we may readily adopt Ng's (1995) approach to welfare biology by specifying (3) as strictly increasing in its arguments, if species  $i$  consists of affective sentients and by setting  $V^i(b_i, n_i) \equiv 0$  in case that the organisms of species  $i$  are not affective sentients. However, the model is flexible enough to accomodate other concepts of nonhuman welfare.

The human species consists of  $n_h$  identical consumers. The representative consumer's

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<sup>5</sup>One might think about different specifications of the function  $V^i$  in (3) depending on (future) insights of welfare biology. Note, however, that the main contribution of the present paper is conceptual rather than an inquiry into which are the most appropriate variables determining the nonhuman organisms' welfare.



welfare is specified by the concave function  $U : \mathbb{R}^N \times \mathbb{R}_+ \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$  such that

$$u \leq U \left( \underset{+}{\mathbf{n}}, \underset{+}{\bar{r}} - \underset{+}{r_y}, \underset{+}{y_h} \right). \quad (4)$$

According to (4), the consumer derives welfare from consuming the amount  $y_h$  of good  $Y$  and from the *state of the ecosystem* as described by the variables  $\mathbf{n} := (n_1, \dots, n_N)$ , and  $\bar{r} - r_y$ . These variables are interpreted to be indicators of ecological functions or ecosystem services whose significance for consumers range from esthetic to life-supporting. According to Dailey (1997, 3) ecosystem services are "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life".  $U_{n_i} > 0$  for all  $i$  reflects the consumer's satisfaction from ecosystem services which are assumed to be positively correlated to species populations;<sup>6</sup> the consumer also benefits from ecosystem services whose flow increases with an expanding habitat,  $U_r := \partial U / \partial (\bar{r} - r_y) > 0$ .

In the short-run period of our model the allocation of resources is constrained by

$$n_h y_h \leq y, \quad (5)$$

$$\sum_i n_i r_i + r_y \leq \bar{r}, \quad (6)$$

$$\sum_{i \neq j} n_i z_{ij} + z_{yj} = -n_j z_{jj} \quad \forall j. \quad (7)$$

While (5) and (6) represent conventional scarcity constraints accounting for the limited supply of good  $Y$  and total land, respectively, (7) sees to it that, for all  $j$ , total demand for biomass of species  $j$  equals<sup>7</sup> total supply of biomass of species  $j$ .

To sum up, we envisage a model with two integrated subsystems: an economy with consumers and an aggregate producer *and* an ecosystem populated by organisms belonging to a variety of species. The economy and the ecosystem are interrelated in important ways:

- The total endowment of land needs to be shared by individuals of both subsystems; land used for economic activities is lost as habitat for nonhuman species.
- The producer harvests biomass to provide consumers with food (implicit in the composite consumption good) and thus competes with nonhuman species for prey.
- The net offspring of all nonhuman organisms is hampered when their habitat shrinks due to increasing demand for land put aside for economic activities, and net offspring is also impaired when organisms yield own biomass to the producer.<sup>8</sup>

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<sup>6</sup> $U_{n_i} > 0$  for all  $i$  is a stylized assumption, of course, since negative partial derivatives can be considered plausible for viruses and bacteria, e.g.

<sup>7</sup>Note that in contrast to (5) and (6), in (7) the strict equality sign is indispensable; see Eichner and Pethig (2003).

<sup>8</sup>They also suffer from losing own biomass to their predators, but this is an intra-system interdependence.

- The consumers receive positively valued ecosystem services from the ecosystem that are increasing in the health of the ecosystem which in turn is assumed to improve with the population size of all species and with the size of their habitat.

All these channels of 'cross-system activities' highlight the heavy interdependence of both subsystems. Of particular importance are the effects of economic activities on the ecosystem through the variables  $r_y$  and  $\mathbf{z}_y$ , and the effects of the ecosystem on the economy through the variables  $\mathbf{n}$  and  $\bar{r} - r_y$ .

All variables of the model, i.e.  $y$ ,  $r_y$ ,  $\mathbf{z}_y$ ,  $u$  and  $b_i$ ,  $n_i$ ,  $r_i$ ,  $v_i$ ,  $\mathbf{z}_i$  for  $i = 1, \dots, N$ , relate to one and the same short-run period (point in time), and there is a set of such variables for each short-run period. The populations,  $\mathbf{n}$ , are stock variables while all others are flow variables. It remains to be specified, how the stocks of population change in time. To establish that intertemporal link, recall that  $b_i$  is the net offspring of organism  $i$ . Hence the adjustment in time of the population of species  $i$ ,  $dn_i/dt =: \dot{n}_i$ , is given by the simple differential equation

$$\dot{n}_i = n_i b_i \quad i = 1, \dots, N. \quad (8)$$

According to (8), the (positive) population of species  $i$  increases, iff  $b_i > 0$ , and it decreases, iff  $b_i < 0$ .

### 3 Optimal intertemporal allocations for alternative sets of welfare weights

Consider a social planner who maximizes an individualistic social welfare function. Social welfare is non-negatively related to each and every consumer's and each and every organism's welfare. For simplicity, we restrict our attention to the class of additive separable generalized utilitarian social welfare indexes

$$\delta_h a_h n_h U(\cdot) + \delta_s \sum_i a_i n_i V^i(\cdot) \quad (9)$$

defined for each point in time. In (9),  $a_h, a_1, \dots, a_N \in \mathbb{R}_{++}$  are positive constant welfare weights,  $n_h, n_1, \dots, n_N \in \mathbb{R}_{++}$  are positive populations of humans and nonhuman species,<sup>9</sup> and  $\delta_h, \delta_s$  are jump variables taking on either the value one or zero. The specification (9) is convenient for distinguishing three different sub-classes of social welfare functions as

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<sup>9</sup>The issue of species extinction ( $n_i = 0$ ) is in the realm of our analytical framework but beyond the scope of the present paper.

follows:

For any vector  $(a_h, a_1, \dots, a_N) \in \mathbb{R}_{++}^{1+N}$  the social welfare index (9) is said to be

- (i) *anthropocentric*, if  $\delta_h = 1$  and  $\delta_s = 0$ ;
- (ii) *biocentric*, if  $\delta_h = 0$  and  $\delta_s = 1$ ;
- (iii) *nonanthropocentric*, if  $\delta_h = \delta_s = 1$ .

The anthropocentric social welfare function clearly represents the conventional welfare-economic approach. The biocentric social welfare function ignores human welfare altogether while the nonanthropocentric social welfare function obviously combines the polar cases (i) and (ii): it takes up the principle of the established individualistic social welfare concept that 'individuals are to count' and extends that principle from individual consumers to the organisms of all (other) species.

To determine an efficient allocation for the integrated model of the ecosystem and the economy, the social planner seeks to maximize

$$\int_0^\infty \left[ \delta_h a_h n_h U(\cdot) + \delta_s \sum_i a_i n_i V^i(\cdot) \right] e^{-\rho t} dt \quad \text{s.t. (1)-(8)}, \quad (10)$$

where  $\rho$  is a positive constant discount rate. (10) is an optimal control problem where  $\mathbf{n}$  is a vector of state variables and all other variables are controls. The solution to (10) is an allocation that will be said to exhibit *anthropocentric*, *biocentric* or *nonanthropocentric efficiency*, respectively, depending on whether the social planner employs an anthropocentric, biocentric or nonanthropocentric social welfare function.<sup>10</sup>

Efficient allocations are characterized by solving the Lagrangean

$$\begin{aligned} \mathcal{L} = & \delta_h a_h n_h U(\mathbf{n}, \bar{r} - r_y, y_h) + \delta_s \sum_i a_i n_i V^i(b_i, n_i) + \sum_i \mu_{n_i} n_i b_i \\ & + \sum_i n_i \lambda_{b_i} [B^i(r_i, \mathbf{z}_i) - b_i] + \lambda_y (y - n_h y_h) + \lambda_Y [Y(r_y, \mathbf{z}_y) - y] \\ & + \lambda_r \left( \bar{r} - r_y - \sum_i n_i r_i \right) - \sum_j \lambda_{z_j} \left( \sum_{i \neq j} n_i z_{ij} + z_{yj} + n_j z_{jj} \right). \end{aligned} \quad (11)$$

To simplify the subsequent characterization of solutions to (11), we restrict our attention to interior solutions except for the case of a biocentric social welfare function where zero solution values of the variables  $r_y$ ,  $\mathbf{z}_y$ ,  $y$ ,  $y_h$  are not excluded.

**Proposition 1.** *(Properties of efficient allocations)*

*Consider a solution to (10).*

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<sup>10</sup>Note that the notion of *anthropocentric* efficiency is equivalent to the conventional concept of Pareto efficiency.

(i) The intertemporal allocation exhibiting biocentric efficiency is characterized by  $r_y = y = y_h = 0$ ,  $z_y = \mathbf{0}^N$  and

$$\frac{B_{z_{ij}}^i}{B_{z_{ik}}^i} = \frac{B_{z_{mj}}^m}{B_{z_{mk}}^m} \quad \forall i, j, k, m, \quad (12)$$

$$\frac{B_r^i}{B_{z_{ik}}^i} = \frac{B_r^m}{B_{z_{mk}}^m} \quad \forall i, k, m, \quad (13)$$

$$\frac{\mu_{n_i}}{\lambda_r} = \frac{1}{B_r^i} - \frac{a_i V_b^i}{\lambda_r} \quad \forall i, \quad (14)$$

$$\begin{aligned} \dot{\mu}_{n_i} = & \mu_{n_i} \cdot \left[ \rho - b_i + \sum_j z_{ij} B_{z_{ij}}^i + r_i B_r^i \right] + a_i V_b^i \cdot \left( \sum_j z_{ij} B_{z_{ij}}^i + r_i B_r^i \right) \\ & - a_i \cdot (V^i + n_i V_n^i) \quad \forall i. \end{aligned} \quad (15)$$

(ii) The intertemporal allocation exhibiting anthropocentric efficiency is characterized by

$$\frac{B_{z_{ij}}^i}{B_{z_{ik}}^i} = \frac{B_{z_{mj}}^m}{B_{z_{mk}}^m} = \frac{Y_{zyj}}{Y_{zyk}} \quad \forall i, j, k, m, \quad (16)$$

$$\frac{B_r^i}{B_{z_{ik}}^i} = \frac{B_r^m}{B_{z_{mk}}^m} = \frac{Y_r}{Y_{zyk}} - \frac{n_h U_r}{U_y Y_{zyk}} \quad \forall i, k, m, \quad (17)$$

$$\frac{\mu_{n_i}}{\lambda_r} = \frac{1}{B_r^i} \quad \forall i, \quad (18)$$

$$\dot{\mu}_{n_i} = \mu_{n_i} \cdot \left[ \rho - b_i + \sum_j z_{ij} B_{z_{ij}}^i + r_i B_r^i \right] - a_h n_h U_{n_i} \quad \forall i. \quad (19)$$

(iii) The intertemporal allocation exhibiting nonanthropocentric efficiency is characterized by

$$\frac{B_{z_{ij}}^i}{B_{z_{ik}}^i} = \frac{B_{z_{mj}}^m}{B_{z_{mk}}^m} = \frac{Y_{zyj}}{Y_{zyk}} \quad \forall i, j, k, m, \quad (20)$$

$$\frac{B_r^i}{B_{z_{ik}}^i} = \frac{B_r^m}{B_{z_{mk}}^m} = \frac{Y_r}{Y_{zyk}} - \frac{n_h U_r}{U_y Y_{zyk}} \quad \forall i, k, m, \quad (21)$$

$$\frac{\mu_{n_i}}{\lambda_r} = \frac{1}{B_r^i} - \frac{a_i V_b^i}{\lambda_y Y_r - a_h n_h U_r} \quad \forall i, \quad (22)$$

$$\begin{aligned} \dot{\mu}_{n_i} = & \mu_{n_i} \cdot \left[ \rho - b_i + \sum_j z_{ij} B_{z_{ij}}^i + r_i B_r^i \right] - a_h n_h U_{n_i} \\ & + a_i V_b^i \cdot \left( \sum_j z_{ij} B_{z_{ij}}^i + r_i B_r^i \right) - a_i \cdot (V^i + n_i V_n^i). \quad \forall i. \end{aligned} \quad (23)$$

Proposition 1 is proved in Appendix A. As expected, the marginal conditions governing efficiency depend on which kind of social welfare function is applied. A major principal message of Proposition 1 is that it is efficient in the anthropocentric as well as in the

nonanthropocentric sense to have positive transactions in both the economy and the ecosystem while, in contrast, the biocentrically efficient allocation requires to reduce all economic activities to zero. This result confirms the common sense proposition that nature can do without humans (and would do so if it had its way) but that the latter cannot do without the ecosystem, even if the anthropocentric social welfare concept is applied. In terms of the formal model this result is due to the premises that nature provides humans with land and biomass and with life-supporting ecosystem services that take the form of positive consumption externalities in (4).

It is interesting to observe that in Proposition 1 the equations (12) and (13) constitute a common feature of all three social welfare regimes. According to (12) optimality requires that in generating net offspring the marginal rate of technical substitution of biomass  $j$  for biomass  $k$ ,  $B_{z_{ij}}^i/B_{z_{ik}}^i$ , is the same for the organisms of all species. Likewise, (13) requires the marginal rate of technical substitution of land for biomass  $k$ ,  $B_r^i/B_{z_{ik}}^i$ , to be the same for the organisms of all species. Hence (12) and (13) are conditions for the non-wasteful allocation of land and prey biomass *within* the ecosystem.<sup>11</sup> It doesn't come as a surprise, therefore, that if it is optimal to produce good  $Y$  (Proposition 1ii and 1iii), efficiency in production requires the marginal rate of technical substitution of biomass  $j$  for biomass  $k$ ,  $Y_{z_{yj}}/Y_{z_{yk}}$ , to be the same as  $B_{z_{ij}}^i/B_{z_{ik}}^i$ . This inter-system efficiency requirement is spelled out in (16) and (20). The equations (17) and (21) exhibit a similar rule for allocating land and biomass transactions within and across both subsystems. However, the socially efficient marginal rate of substituting land for biomass  $k$  in producing good  $Y$  is not  $Y_r/Y_{z_{yk}}$  but rather  $Y_r/Y_{z_{yj}}$  corrected for the consumption externality  $n_h U_r/(U_y Y_{z_{yj}})$ . This externality term represents the consumer's willingness to pay for habitat protection. Hence at the margin, the social value (in terms of biomass of species  $k$ ) of land for economic uses is less than its marginal value in producing the consumption good. This is so because land input in production diminishes the habitat available to all species which negatively affects consumers, in turn. To sum up, the instantaneous efficiency conditions in case of anthropocentric social welfare, (16) and (17), equal those in case of nonanthropocentric social welfare, (20) and (21). If social welfare is biocentric, the corresponding conditions are (12) and (13) which are implied, in turn, by (16)-(17) and (20)-(21), respectively.

The equations (14), (18) and (22) specify the shadow price of the population of species  $i$  measured in terms of the resource. In case of anthropocentric social welfare (18), that price equals the marginal resource costs of net offspring,  $1/B_r^i$ . When social welfare is not anthropocentric, (14) and (22), the shadow price  $\mu_{n_i}/\lambda_r$  is the difference between the

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<sup>11</sup>These conditions are analogous to the efficiency conditions governing the efficient production in disaggregated models of the economy.

marginal resource costs of net offspring and the marginal benefit of net offspring in terms of the resource. Although we were unable to formally establish  $\mu_{n_i}/\lambda_r > 0$  in (14) and (18), there are compelling reasons why these optimal shadow prices of populations are also positive, and will be assumed to be positive, henceforth, when the optimal control problem (10) is well-behaved. To see that recall that by the construction of the welfare index (9) all populations positively affect the social planner's objective function. Yet with  $\mu_{n_i} \leq 0$  the optimal  $b_i$  would be smaller, *ceteribus paribus*, than with  $\mu_{n_i} > 0$  (since  $a_i V_b^i = \lambda_{b_i} - \mu_{n_i}$ ). That would be necessarily suboptimal since offspring  $b_i$  needs to be encouraged in view of the positive social value of species populations beyond its short-period value  $\lambda_{b_i}$ . It deserves to be emphasized that unless social welfare is anthropocentric, the welfare weights that are positive in the social welfare regime under consideration impact on the size of the shadow prices of species populations. Since these shadow prices direct the socially optimal allocation over time, it becomes obvious at this point that the optimal time paths of the three social welfare regimes depend on the magnitude of all welfare weights (including zero weights, of course).

Finally, comparing (15), (19) and (23) shows that the change in time of the shadow price of the population of species  $i$  differs among all three social welfare regimes reinforcing our conclusion in the last paragraph that these regimes' optimal time paths differ. A rigorous comparison of these three equations is not feasible, since the time paths of the endogenous variables differ in all these regimes. It is worth pointing out, yet, that the change in time of the shadow price of populations depends on all welfare weights that are non-zero in the respective regime.

It is certainly quite intriguing to learn (in Proposition 1i) that placing zero welfare weights on all consumers renders it optimal to wipe out the species of humans. Yet (being humans ourselves) we will disregard biocentric social welfare in what follows and focus, instead, on the concept of nonanthropocentric social welfare with anthropocentric social welfare as a limiting case.

Recall that looking at anthropocentric social welfare (Proposition 1ii) from a nature protection perspective two routes linking the ecosystem to the economy can be distinguished: (i) the resource-competition link as specified by  $Y_r > 0$  and  $Y_{z_{yj}} > 0$  (all  $j$ ) and (ii) the ecosystem-services link as formalized by  $U_r > 0$  and  $U_{n_i} > 0$ , all  $i$ . Concerning the resource-competition link we deal with the conventional problem of the optimal intertemporal consumption of non-renewable and renewable resources where it is irrelevant whether the (aggregate) firm's competitors are other firms or organisms. Nature protection is an issue here as one needs to avoid both inefficient overharvesting/overextraction and inefficient underharvesting/underextraction. The ecosystem-services link takes the form of positive

consumption externalities suggesting that it is desirable for the social planner to expand species populations and the habitat beyond what would be optimal for efficient harvesting of renewable resources. Hence the ecosystem-services link appears to be an important rationale for nature protection beyond the postulate of efficient intertemporal harvesting. Note, however, that in case of an anthropocentric social welfare function (Proposition 1ii) the forces working in favor of nature protection are entirely in the human species' self-interest. Nature is then assumed to be of instrumental value only for all humans.

When turning from anthropocentric social welfare to nonanthropocentric social welfare, the resource-competition link and the ecosystem-services link are still active since consumers continue to carry positive welfare weights. Comparing the efficiency conditions of the Propositions 1ii and 1iii reveals that they differ only with respect to the shadow prices of species populations and their change in time. In the nonanthropocentric regime these shadow prices tend to be smaller than under anthropocentrism and the more so, the greater is the welfare weight placed on nonhuman organisms. Clearly, assigning positive welfare weights to nonhuman organisms amounts to placing some intrinsic (as opposed to instrumental) value on them. Consequently the social planner is likely to support the growth of species populations beyond what she would deem desirable in case of an anthropocentric social welfare function which then appears to constitute a rationale in its own right for stepping up nature protection.

To sum up, with social welfare being nonanthropocentric, there seem to be two separate arguments for making the case for nature protection (reaching beyond the quest for efficient harvesting or extraction of resources): First, due to the ecosystem services rendered to consumers nature protection is in the consumers' self-interest. Second, with assigning intrinsic value to nonhuman organisms through positive welfare weights these organisms' 'interests' count along with those of consumers suggesting that additional attention ought to be placed on nature protection.

In principle, the model of the present paper is capable of investigating these conjectures on optimal nature protection in a rigorous way. Yet the specification of the model and the characterization of efficient time paths in Proposition 1 are far too general to answer the question as to how exactly (i) nature's ecosystem services and (ii) intrinsic values on species translate into nature protection. To obtain more informative results we will simplify our model substantially and restrict, moreover, our attention to the comparative dynamics of long-run steady states. We aim at checking the conjecture that the more essential the ecosystem services are that are rendered to consumers by nature, or technically speaking, the larger the marginal welfare  $U_r > 0$  and/or  $U_{n_i} > 0$  is, the greater are the habitat and the populations in the optimal long-run steady state. Similarly, to explore the impact

on optimal nature protection of assigning positive welfare weights to nonhuman species we will introduce exogenous small changes of these weights, to determine their impact on the steady-state allocation. We aim at checking the conjecture that the greater a species' welfare weight the larger will be its optimal population and its habitat.

## 4 Protection of nature in the steady states of simplified models

### 4.1 Nature protection in a one-species model

Suppose there is only a single species ( $N = 1$ ) and set  $n_h = 1$  to avoid clutter. Carrying over the notation from the general model of Section 2 with a few self-explanatory adaptations, the simplified model to be studied in the present section is given by the following equations:

$$u = U(n, \bar{r} - r_y, y) = \beta W(n) + y, \quad (24)$$

$$b = B(r, z) \quad \text{with } B_{rz} \leq 0, \quad (25)$$

$$v = V(b, n) \quad \text{with } V_{bn} = 0, \quad (26)$$

$$y = Y(r_y, z_y) \quad \text{with } Y_{rz} \geq 0, \quad (27)$$

$$y_h = y, \quad (28)$$

$$\bar{r} = nr + r_y, \quad (29)$$

$$nz = z_y, \quad (30)$$

$$\dot{n} = bn, \quad (31)$$

$$a_h U(n, \bar{r} - r_y, y_h) + anV(b, n). \quad (32)$$

In (24)  $\beta$  is an exogenous positive constant. The specification (24) of the consumer's appreciation of ecosystem services enables us to explore the allocative impacts of changes in the appreciation of those services through (small) parametric changes in  $\beta$ . Assuming quasi-linear welfare in (24) is quite restrictive. This specification of human welfare may be criticized on the grounds that it overdoes the substitution possibilities between ecosystem services and consumption goods. We therefore also explore the consequences of replacing (24) by

$$u = \min[\beta n, y] \quad (24a)$$

which expresses the opposite polar assumption of complementarity between ecosystem services and manufactured goods.<sup>12</sup> In the subsequent analysis we will also modify the model

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<sup>12</sup>The specification (24a) is reminiscent of the concept of strong sustainability where substitutability between natural and man-made capital is denied.



(24)-(32) by replacing (25) by

$$b = \min[r, c(\bar{z} - z)] - e, \quad (25a)$$

where  $c$ ,  $\bar{z}$  and  $e$  are positive constants.<sup>13</sup>

In what follows we will focus on optimal steady states of the model (24)-(32) or one of its variants and investigate the impacts of parametric changes in  $\beta$  (in equation (24) or (24a)) and in the species welfare weight  $a$  (in (32)) in comparative-dynamic analysis. We will describe our procedure in its principal aspects for the model (24)-(32), and we delegate all other technical details and calculations to Appendix B.

An efficient allocation of the model (24)-(32) is characterized by solving the Lagrangean<sup>14</sup>

$$\mathcal{L} = \beta W(n) + Y(\bar{r} - nr, nz) + anV(b, n) + \mu nb + \lambda n[B(r, z) - b]. \quad (33)$$

The first-order conditions for an interior maximum of (33) are

$$\mathcal{L}_r = -nY_r + \lambda nB_r = 0, \quad (34a)$$

$$\mathcal{L}_z = nY_z + \lambda nB_z = 0, \quad (34b)$$

$$\mathcal{L}_b = anV_b + \mu n - \lambda n = 0, \quad (34c)$$

$$\dot{\mu} = \rho\mu - \mathcal{L}_n = \rho\mu - \beta W_n - a(V + nV_n) + rY_r - zY_z - \mu b. \quad (34d)$$

We set  $\dot{n} = \dot{\mu} = 0$  and use (31) and (34a)-(34d) to determine the optimal long-run levels of  $r$ ,  $z$  and  $n$  implicitly by

$$nB(r, z) = 0, \quad (35a)$$

$$-Y_r + \left( \frac{\beta W_n + a(V + nV_n + \rho V_b) - rY_r + zY_z}{\rho} \right) B_r = 0, \quad (35b)$$

$$Y_z + \left( \frac{\beta W_n + a(V + nV_n + \rho V_b) - rY_r + zY_z}{\rho} \right) B_z = 0. \quad (35c)$$

To find out how the optimal long-run allocation responds to changes in  $\beta$  and  $a$  we totally

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<sup>13</sup>We don't aim at defending either specification (24), (24a), or (25), (25a) regarding its empirical relevance. The main reason for introducing the quite restrictive functions (24), (24a), (25) and (25a) is clearly analytical tractability, and the main reason for employing *alternative* specifications of human welfare and species net offspring generation is to examine the robustness of our results.

<sup>14</sup>To explore the impact of changing welfare weights it suffices to change the parameter  $a$  while keeping  $a_h$  constant. This allows us to further simplify the notation by setting  $a_h \equiv 1$ .

differentiate (35a)-(35c) to obtain (see Appendix B)

$$\text{sgn} \frac{dr}{d\beta} = \text{sgn} \frac{dr}{da} = \text{sgn} \frac{B_z \cdot [(zY_{zz} - zY_{rz}) B_r - (rY_{rr} - zY_{zr}) B_z]}{|J|}, \quad (36a)$$

$$\text{sgn} \frac{dz}{d\beta} = \text{sgn} \frac{dz}{da} = \text{sgn} \frac{B_r \cdot [(zY_{rz} - zY_{zz}) B_r - (zY_{zr} - rY_{rr}) B_z]}{|J|}, \quad (36b)$$

$$\text{sgn} \frac{dn}{d\beta} = \text{sgn} \frac{dn}{da} = \text{sgn} \frac{B_r^2 (nY_{zz} + \lambda B_{zz}) + B_z^2 (nY_{rr} + \lambda B_{zr})}{|J|} - \frac{2B_r B_z (-nY_{rz} + \lambda B_{rz})}{|J|}, \quad (36c)$$

where  $|J|$  is the determinant of the pertinent Jacobian matrix. The equilibria are assumed to be 'stable' so that the sign of  $|J|$  is the same as that of the determinant of the Hessian matrix associated to the Hamiltonian. Consequently,  $J$  is negative definite ( $|J| < 0$ ).

We are also interested in the changes of  $u$ ,  $y$ ,  $nr$  and  $nz$  which are easily determined as (see Appendix B),

$$du = W d\beta + \beta W_n dn + dy, \quad (37a)$$

$$dy = (zY_z - rY_r) dn, \quad (37b)$$

$$d(nr) = rdn + ndr, \quad (37c)$$

$$d(nz) = zdn + ndz. \quad (37d)$$

shock	line	model	$du$	$dy$	$\text{sgn } dv = \text{sgn } dn$	$dr$	$dz$	$d(nr)$	$d(nz)$
$d\beta > 0$	1	Model A	?	?	+	-	-	?	?
	2	Model B	?	?	+	0	0	+	+
	3	Model C	+	+	+	-	-	?	?
	4	Model D	+	+	+	0	0	+	+
$da > 0$	5	Model A	?	?	+	-	-	?	?
	6	Model B	?	?	+	0	0	+	+
	7	Model C	0	0	0	0	0	0	0
	8	Model D	0	0	0	0	0	0	0

Table 1: Comparative dynamics of simplified one-species models

Accounting for  $|J| < 0$ , (36a)-(36c) and (37a)-(37d) yield the comparative dynamic results for the model (24)-(32). These results along with those obtained when the model (24)-(32) is modified by replacing (24) by (24a) and/or (25) by (25a) are now summarized in

**Proposition 2.**

*Denote by Model A the equations (24)-(32), by Model B the equations (24), (25a) and (26)-(32), by Model C the equations (24a) and (25)-(32) and by Model D the equations (24a), (25a) and (26)-(32). If an optimal steady state of these models is disturbed, alternatively, by a small increase in the parameter  $\beta$  or in the parameter  $a$ , the direction of change in the steady state values of  $n$ ,  $r$ ,  $u$ ,  $y$ ,  $z$ ,  $nr$  and  $nz$  is as shown in Table 1.*

The lines 7 and 8 of Table 1 contain the rather unexpected result that if consumers consider ecosystem services and the composite consumption good to be strictly complementary, changing the welfare weight of the species ( $da \neq 0$ ) leaves the optimal steady state unchanged. In this special case the anthropocentric and nonanthropocentric social welfare optima coincide, and the level of nature protection depends solely on how essential the ecosystem services are for consumers.

Except for the (zero) responses to changing parameter  $a$  in the models C and D Table 1 shows somewhat mixed results depending on which model is applied and whether  $\beta$  or  $a$  is increased. Quite obviously, consumers benefit from an increase in  $\beta$  or in  $a$  if and only if  $du > 0$  and likewise, nonhuman organisms benefit if and only if  $dv > 0$ . According to Table 1 nonhuman organisms gain unambiguously in both cases, i.e. when  $\beta$  or  $a$  is raised (excluding the case discussed above of increasing  $a$  in the Models C and D). In that sense the parameters  $\beta$  and  $a$  are alternative sources of nature protection whose impact on nature is similar in qualitative terms. Rather than taking the nonhuman organism's welfare,  $v$ , as the relevant indicator for nature protection one may want to argue that nature protection is enhanced, in a comprehensive (and more demanding) sense, only if in addition to  $\text{sgn } dv = \text{sgn } dn > 0$  we also have  $dr \geq 0$  (and hence  $d(nr) > 0$ ) as well as  $dz \leq 0$ . Table 1 confirms  $dz \leq 0$ , but in the Models A and C we find  $dr < 0$  and  $d(nr)$  ambiguous in sign. Observe that both  $dr$  and  $dz$  are either zero or negative. In fact, since the differential of (35a) yields  $B_r dr = -B_z dz$  it follows that  $\text{sgn } dr = \text{sgn } dz$  owing to  $B_r > 0$  and  $B_z < 0$ , which implies, in turn, either  $\text{sgn } dr = \text{sgn } dz < 0$  or  $\text{sgn } dr = \text{sgn } dz > 0$ . The reason for  $\text{sgn } dr = \text{sgn } dz < 0$  is not clear. In case of  $\text{sgn } dr = \text{sgn } dz > 0$  the producer would have harvested more biomass ( $dz_y > 0$ ) and used less land ( $dr_y < 0$ ) thus changing the factor input ratio significantly. Yet with  $\text{sgn } dr = \text{sgn } dz < 0$ , the signs of  $dz_y$  and  $dr_y$  are ambiguous.

Table 1 also shows a slight tendency across all models for consumers to benefit from changes in  $\beta$  or  $a$  although ambiguities are prevalent. The sign of the change in economic production activity,  $\text{sgn } dy$ , is the same as  $\text{sgn } du$  in all lines of Table 1. Despite some indeterminacies one may draw the tentative conclusion that enhancing nature protection

by raising  $\beta$  or  $a$  doesn't come at the expense of consumers and their economy.

## 4.2 Nature protection in a two-species model

To gain further insight into the rationale for nature protection consider now a simple model consisting of one consumer and two species:  $n_h = 1$  and  $N = 2$ . The model is specified by the following equations:

$$u = U(n_1, n_2, \bar{r} - r_y, y_h) = \beta W(n_1, n_2) + y_h \quad \text{with } W_{n_1 n_2} = 0, \quad (38)$$

$$b_1 = B^1(r, z_{11}), \quad b_2 = B^2(z_{21}) \quad \text{with } B_{rz}^1 = 0, \quad (39)$$

$$v_1 = V^1(b_1, n_1), \quad v_2 = V^2(b_2, n_2) \quad \text{with } V_{bn}^1 = V_{bn}^2 = 0, \quad (40)$$

$$y = Y(r_y, z_{y1}, z_{y2}) = \gamma \cdot r_y \quad \text{with } \gamma > 0 \text{ and const.}, \quad (41)$$

$$y_h = y, \quad (42)$$

$$\bar{r} = n_1 r + r_y, \quad (43)$$

$$n_1 z_{11} = n_2 z_{21}, \quad (44)$$

$$\dot{n}_1 = n_1 b_1, \quad \dot{n}_2 = n_2 b_2, \quad (45)$$

$$\beta W(n_1, n_2) + y_h + a_1 n_1 V^1(n_1, b_1) + a_2 n_2 V^2(n_2, b_2). \quad (46)$$

According to (39) and (44) species 2 feeds on species 1 and species 1 feeds on the resource. Humans don't harvest any biomass ( $z_{y1} = z_{y2} = 0$  due to (41)) but they compete for the resource along with the organisms of species 1 ((39), (41) and (43)).

The efficient allocation of the model (38)-(46) is characterized by maximizing the Lagrangean

$$\begin{aligned} \mathcal{L} = & \beta W(n_1, n_2) + \gamma(\bar{r} - n_1 r) + a_1 n_1 V^1(b_1, n_1) + a_2 n_2 V^2(b_2, n_2) \\ & + \mu_{n_1} n_1 b_1 + \mu_{n_2} n_2 b_2 + \lambda_{b_1} n_1 [B^1(r, z_{11}) - b_1] \\ & + \mu_{n_2} n_2 [B^2(z_{21}) - b_2] + \lambda_n (n_1 z_{11} - n_2 z_{21}). \end{aligned} \quad (47)$$

The first-order conditions read

$$\mathcal{L}_r = -\gamma n_1 + \lambda_{b_1} n_1 B_r^1 = 0, \quad (48a)$$

$$\mathcal{L}_{z_{11}} = \lambda_{b_1} n_1 B_z^1 + \lambda_n n_1 = 0, \quad (48b)$$

$$\mathcal{L}_{z_{21}} = \lambda_{b_2} n_2 B_z^2 - \lambda_n n_2 = 0, \quad (48c)$$

$$\mathcal{L}_{b_1} = a_1 n_1 V_b^1 + \mu_{n_1} n_1 - \lambda_{b_1} n_1 = 0, \quad (48d)$$

$$\mathcal{L}_{b_2} = a_2 n_2 V_b^2 + \mu_{n_2} n_2 - \lambda_{b_2} n_2 = 0, \quad (48e)$$

$$\dot{\mu}_{n_1} = \rho \mu_{n_1} - \beta W_{n_1} - a_1 (V^1 + n_1 V_n^1) + \gamma r - \mu_{n_1} b_1 - \lambda_n z_{11}, \quad (48f)$$

$$\dot{\mu}_{n_2} = \rho \mu_{n_2} - \beta W_{n_2} - a_2 (V^2 + n_2 V_n^2) - \mu_{n_2} b_2 + \lambda_n z_{21}. \quad (48g)$$

From (48a)-(48g) we obtain the optimal steady-state allocation by setting  $\dot{n}_1 = \dot{n}_2 = \dot{\mu}_{n_1} = \dot{\mu}_{n_2} = 0$ :

$$n_1 B^1(r, z_{11}) = 0, \quad (49a)$$

$$n_2 B^2(z_{21}) = 0, \quad (49b)$$

$$n_1 z_{11} - n_2 z_{21} = 0, \quad (49c)$$

$$[\beta W_{n_1} + a_1 (V^1 + n_1 V_n^1 + \rho V_b^1) - \gamma r] B_r^1 - \gamma (\rho + z_{11} B_z^1) = 0, \quad (49d)$$

$$[\beta W_{n_2} + a_2 (V^2 + n_2 V_n^2 + \rho V_b^2)] B_r^1 + \gamma B_z^1 \left( z_{21} + \frac{\rho}{B_z^2} \right) = 0. \quad (49e)$$

	dr	dz <sub>11</sub>	dz <sub>21</sub>	sgn dv <sub>1</sub> = sgn dn <sub>1</sub>	sgn dv <sub>2</sub> = sgn dn <sub>2</sub>
dβ > 0	?	?	0	+	+
da <sub>1</sub> > 0	−	−	0	+	+
da <sub>2</sub> > 0	+	+	0	+	+
dγ > 0	?	?	0	−	−

Table 2: Comparative dynamics of a simple two-species model

Total differentiation of (49a)-(49e) yields the comparative dynamic results summarized in

**Proposition 3.**

*Consider the model (38)-(46). If an optimal steady state of this model is disturbed, alternatively, by a small increase in the parameter  $\beta$ ,  $a_1$ ,  $a_2$  or  $\gamma$ , the direction of change in the steady state values of  $r$ ,  $z_{11}$ ,  $z_{21}$ ,  $n_1$ ,  $n_2$ ,  $v_1$  and  $v_2$  is as shown in Table 2. The direction of change in all other variables is ambiguous.*

Proposition 3 reinforces our findings in the one-species model that nonhuman organisms gain unambiguously when either  $\beta$ ,  $a_1$  or  $a_2$  is raised. Again, increasing the consumers' appreciation of ecosystem services ( $d\beta > 0$ ) and raising some species' welfare weight ( $da_i > 0$  for  $i = 1, 2$ ) are alternative sources of nature protection whose impact on nature is similar in qualitative terms. The invariance of  $z_{21}$  ( $dz_{21} = 0$ ) is no general feature since it is due to the steady state condition  $db_2 = 0$  combined with the simplifying assumption in (39) that  $b_2$  is completely determined by  $z_{21}$ . More significant, and more intuitively appealing at the same time, are the differential effects on  $z_{11}$  of increasing the welfare weights  $a_1$  and  $a_2$ . When organism 1's [organism 2's] welfare weight is raised, it is optimal to reduce [increase] organism 1's sacrifice of own biomass to its predator species 2.

Table 2 also reports a dynamic exercise that was not carried out in the one-species

model of the previous section. It is about an exogenous technical progress in producing the consumer good brought about by an increase in the parameter  $\gamma$  which represents the productivity of using land for economic purposes. As shown in Table 2, the clearcut result of such a technical improvement is a reduction in both species populations and hence, via (40), a decline in all nonhuman organism's welfare. In other words technical progress in manufacturing renders it optimal to reduce nature protection for any given set of weights in a nonanthropocentric social welfare function.

## 5 Concluding remarks: nonanthropocentrism and double-counting

Environmental economics, an anthropocentric discipline, and environmental ethics, based on nonanthropocentrism, are "... trapped in a bifurcated discourse, each rejecting the other's ontological position ..." (Norton and Minter 2002, p. 377). The present paper focused on investigating and comparing the consequences of both paradigms regarding the appropriate level of nature protection. Interpreting 'intrinsic values in individuals' as attaching positive welfare weights on the welfare of human and/or nonhuman individuals our finding is that nonanthropocentrism tends to be a rationale for nature protection in addition and above the level of protection warranted to serve the humans' welfare. Roughly speaking, increasing the welfare weights on nonhuman organisms turned out to call for intensifying nature protection in much the same way as increases in the marginal welfare consumers derive from ecosystem services.

In our formal model ecosystem services take the form of positive consumption externalities induced by the variables 'populations of nonhuman species' and 'habitat of all species'. Throughout the paper we interpreted these variables as indicators of ecosystem functions that consumers perceive as ecosystem services (as specified by a quote from Dailey (1997) in Section 2) for which their willingness-to-pay is positive. Note, however, that these arguments in the consumers' welfare functions may also (and additionally!) be interpreted as reflecting the individual consumers 'intrinsic' valuation of these ecosystem components. According to Johannson-Stenman (1998) some consumers tend to value nature intrinsically. He links this observation to the discussion of existence values and non-use values in the context of contingent valuation studies and argues that individual motivations such as paternalistic, impure and genuine altruism as well as altruism towards nonhuman organisms need to be accounted for to attain good estimates of the social value of public goods. According to Spash (2000) there is strong empirical "... evidence in people's words and

practices that they do indeed value nature intrinsically ...".<sup>15</sup> In light of these considerations our comparative-dynamic exercise of raising the parameter  $\beta$  in Section 4 can be reinterpreted as accounting for an increase in the consumers' intrinsic valuation of nature. Since the impacts on nature protection of raising either the parameter  $\alpha$  or  $\beta$  are qualitatively similar, the chasm between anthropocentrism and nonanthropocentrism appears to be reduced, from a pragmatic point of view, at least. In other words, environmental economists may stick to their conventional concept of anthropocentric social welfare (setting the welfare weights of all nonhuman individuals zero) provided that they pay due attention to the intrinsic values of natural components as perceived by the consumers. Apparently, Norton and Minter (2002, p. 399) also endorse such an approach maintaining that it is consistent with 'nonanthropocentrism in the broader sense'. In any case, all who are willing to accept the route of capturing intrinsic values in nature through the consumers' perception of these values will have no reasons to reject Norton's 'convergence hypothesis' alluded to in the introduction of the present paper.

Those who wish to pursue a nonanthropocentric approach need to make sure that the arguments 'populations of nonhuman species' and 'habitat of all species' in the consumers' welfare functions capture nothing but ecosystem services. However, if these variables are interpreted to value nature intrinsically along with valuing ecosystem services proponents of nonanthropocentric social welfare run into the risk of double-counting. Suppose each member of the human society increases her intrinsic valuation of nonhuman organisms by increasing  $\beta$ . If the social planner notices that shift of individual welfare and reacts by raising  $\alpha$  in addition to raising  $\beta$  we are clearly confronted with a problem of double-counting implying an excessive protection of nature even according to the standards of nonanthropocentric social welfare.

The issue of intrinsic values in nature is highly reminiscent of the old and rather sterile debate on Musgrave's concept of merit goods that dragged on for decades and is still a source of confusion in some textbooks and applied work. It seems to us that mainstream public finance discarded this concept due to its inconsistency with methodological individualism. The issue at hand can also be resolved convincingly and conveniently without abandoning this methodology simply by accounting for the fact that consumers attach values to and articulate them for natural composites like ecosystems, habitats, natural amenities, species communities and/or individual organisms. With continuously improving methods of measuring the individuals' willingness-to-pay for nature protection with an eye

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<sup>15</sup>Similarly, Norton (1991) recommends the indicator 'percentage of ground area with pervious surfaces' as representing values of advocates of green space, of biological diversity, of water quality, and of anti-sprawl. One might consider the habitat variable  $\bar{r} - r_y$  from our model as a proxy for such an indicator.

on both instrumental and intrinsic value the prospects seem to be quite favorable for obtaining reliable estimates for the individuals' intrinsic valuation of nature. In contrast, the social planner's welfare weights placed on nonhuman organisms (or natural objects) appear to be a concept difficult to operationalize and open to arbitrary specifications.

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## Appendix A

**Proof of Proposition 1:** The associated first-order conditions to the Lagrangean (11) are

$$\mathcal{L}_y = \lambda_y - \lambda_Y \leq 0, \quad y\mathcal{L}_y = 0, \quad (50a)$$

$$\mathcal{L}_{y_h} = \delta_h a_h n_h U_y - \lambda_y n_h \leq 0, \quad y_h \mathcal{L}_{y_h} = 0, \quad (50b)$$

$$\mathcal{L}_{r_y} = -\delta_h a_h n_h U_r + \lambda_Y Y_r - \lambda_r \leq 0, \quad r_y \mathcal{L}_{r_y} = 0, \quad (50c)$$

$$\mathcal{L}_{z_{yj}} = \lambda_Y Y_{z_{yj}} - \lambda_{z_j} \leq 0, \quad z_{yj} \mathcal{L}_{z_{yj}} = 0, \quad (50d)$$

$$\mathcal{L}_{r_i} = n_i \lambda_{b_i} B_r^i - \lambda_r n_i \leq 0, \quad r_i \mathcal{L}_{r_i} = 0, \quad (50e)$$

$$\mathcal{L}_{z_{ij}} = n_i \lambda_{b_i} B_{z_{ij}}^i - n_i \lambda_{z_j} \leq 0, \quad z_{ij} \mathcal{L}_{z_{ij}} = 0, \quad (50f)$$

$$\mathcal{L}_{b_i} = \delta_s a_i n_i V_b^i + \mu_{n_i} n_i - n_i \lambda_{b_i} = 0, \quad (50g)$$

$$\begin{aligned} \dot{\mu}_{n_i} = & \rho \mu_{n_i} - \mathcal{L}_{n_i} = \rho \mu_{n_i} - \mu_{n_i} b_i + \lambda_r r_i + \sum_j \lambda_{z_j} z_{ij} - \delta_h a_h n_h U_{n_i} \\ & - \delta_s a_i (V^i + n_i V_n^i), \end{aligned} \quad (50h)$$

$$\mathcal{L}_{\lambda_{b_i}} \geq 0, \lambda_{b_i} \mathcal{L}_{\lambda_{b_i}} = 0, \quad \mathcal{L}_{\lambda_y} \geq 0, \lambda_y \mathcal{L}_{\lambda_y} = 0, \quad \mathcal{L}_{\lambda_Y} \geq 0, \lambda_Y \mathcal{L}_{\lambda_Y} = 0,$$

$$\mathcal{L}_{\lambda_r} \geq 0, \lambda_r \mathcal{L}_{\lambda_r} = 0, \quad \mathcal{L}_{\lambda_{z_j}} \geq 0, \lambda_{z_j} \mathcal{L}_{\lambda_{z_j}} = 0. \quad (50i)$$

- (i) Set  $\delta_h = 0$  and  $\delta_s = 1$  in (50a)-(50i) and consider a maximum of (10) in which  $r_i > 0$  for all  $i$ ,  $z_{ij} > 0$  for all  $i, j$ ,  $i \neq j$ , and (hence)  $z_{jj} < 0$  for all  $i$ . In view of (50e) and (50f) it is straightforward that either (a)  $\lambda_r > 0$  and therefore  $\lambda_{b_i} > 0$  and  $\lambda_{z_j} > 0$  or (b)  $\lambda_r = 0$  and therefore  $\lambda_{b_i} = \lambda_{z_j} = 0$ . Consider first the case (b). Raise  $\bar{r}$  by  $d\bar{r} > 0$  and set  $n_i dr_i = d\bar{r}$  and  $db_i = B_r^i dr_i > 0$ . The impact of  $db_i > 0$  on social welfare is given by (50g)  $\lambda_{b_i} = 0$  is the marginal welfare cost of offspring, where  $a_i n_i V_b^i > 0$  is the direct impact on instantaneous welfare and where  $\mu_{n_i}$  captures the shadow price of the population of species  $i$  or, more technically, the present value of the marginal future welfare induced by  $d\dot{n}_i = n_i db_i > 0$ . Since the welfare index (9) is strictly increasing in  $n_i$  (for all  $i$ )  $\mu_{n_i} > 0$  follows cogently. Yet  $\lambda_{b_i} = 0$  and (50g) imply  $\mu_{n_i} = -a_i V_b^i < 0$  which is incompatible with a maximum of (10). This leads us to conclude that case

(a) applies with  $\mu_{n_i} = \lambda_{b_i} - a_i V_b^i > 0$ .

Suppose now case (a) holds but  $y > 0$ , contrary to the assertion in Proposition 1i. Then  $\lambda_y = \lambda_Y \geq 0$  follows via (50a). If  $\lambda_y > 0$  then  $y_h = 0$  from (50b) and therefore  $\mathcal{L}_{\lambda_y} > 0$ . However,  $\lambda_y \mathcal{L}_{\lambda_y} = 0$  implies  $\lambda_y = 0$ . This contradiction establishes  $\lambda_y = \lambda_Y = 0$ . Moreover, (50c) yields  $\lambda_Y Y_r - \lambda_r = -\lambda_r < 0$  and therefore  $r_y = 0$  via  $r_y \mathcal{L}_{r_y} = 0$ . Since  $Y(0, \mathbf{z}_y) = 0$  by assumption,  $y = 0$  follows from  $r_y = 0$ . This contradiction proves that  $y = 0$  when (10) is maximized.  $y = 0$  and (6) yield  $y_h = 0$  for all  $h$ . Finally,  $r_y = 0$  and  $z_{yj} = 0$  for all  $j$  is the unique efficient way to produce  $y = 0$ .

In the remaining proof of (i) we establish (12)-(15). (12) follows from (50f). More precisely

$$\frac{n_i \lambda_{b_i} B_{z_{ij}}^i}{n_i \lambda_{b_i} B_{z_{ik}}^i} = \frac{\lambda_{z_j}}{\lambda_{z_k}} = \frac{n_m \lambda_{b_m} B_{z_{mj}}^m}{n_m \lambda_{b_m} B_{z_{mk}}^m} \quad \text{for } i, j, k, m = 1, \dots, N. \quad (51)$$

Eq. (13) is derived from (50e) and (50f):

$$\frac{n_i \lambda_{b_i} B_r^i}{n_i \lambda_{b_i} B_{z_{ik}}^i} = \frac{\lambda_r}{\lambda_{z_k}} = \frac{n_m \lambda_{b_m} B_r^m}{n_m \lambda_{b_m} B_{z_{mk}}^m} \quad \text{for } i, j, k, m = 1, \dots, N. \quad (52)$$

Eq. (14) follows from (50e) and (50g), and finally, using (50c), (50e) and (50g) in (50h) we obtain (15).

(ii) Set  $\delta_s = 0$  and  $\delta_h = 1$  in (50a)-(50i). Now we restrict our attention to an interior solution such that all inequalities (50a)-(50i) hold as equalities. Equation (16) follows from (50d) and (50f). To establish (17) we combine (50c)-(50f). To obtain (18) we combine (50e) and (50g), and using (50c), (50e) and (50g) in (50h) we get (19).

(iii) Here we set  $\delta_h = \delta_s = 1$  and make use of the same manipulations as in the derivation of equations (16)-(19).

## Appendix B: Comparative dynamics in the one-species model

**Derivation of (36a)-(36c):** Total differentiation of (35a)-(35c) yields:

$$J \cdot \begin{pmatrix} dr \\ dz \\ dn \end{pmatrix} = \begin{pmatrix} 0 \\ -(\mathrm{d}\beta W_n + \mathrm{d}a(V + nV_n + \rho V_b)) B_r \\ -(\mathrm{d}\beta W_n + \mathrm{d}a(V + nV_n + \rho V_b)) B_z \end{pmatrix} \quad (53)$$

where

$$J := \begin{pmatrix} B_r & B_z & 0 \\ nY_{rr} + \lambda B_{rr} + \phi_1 B_r & -nY_{rz} + \lambda B_{rz} + \phi_2 B_r & -zY_{rz} + rY_{rr} + \phi_3 B_r \\ -nY_{zr} + \lambda B_{zr} + \phi_1 B_z & nY_{zz} + \lambda B_{zz} + \phi_2 B_z & -zY_{rz} + zY_{zz} + \phi_3 B_z \end{pmatrix}$$

and

$$\begin{aligned}
\lambda &= (\beta W_n + a(V + nV_n + \rho V_b) - rY_r + zY_z) / \rho, \\
\phi_1 &:= (-Y_r + nrY_{rr} - nzY_{zr}) / \rho, \\
\phi_2 &:= (Y_z - nrY_{zr} + nzY_{zz}) / \rho, \\
\phi_3 &:= (\beta W_{nn} + a(2V_n + nV_{nn}) + r^2Y_{rr} + z^2Y_{zz} - 2rzY_{rz}) / \rho.
\end{aligned}$$

Solving the equation system (53) by using Cramer's rule we obtain

$$dr = \frac{d\beta W_n + da(V + nV_n + \rho V_b)}{|J|} \cdot B_z \cdot [(zY_{zz} - zY_{rz}) B_r - (rY_{rr} - zY_{zr}) B_z], \quad (54a)$$

$$dz = \frac{d\beta W_n + da(V + nV_n + \rho V_b)}{|J|} \cdot B_r \cdot [(zY_{rz} - zY_{zz}) B_r - (zY_{zr} - rY_{rr}) B_z], \quad (54b)$$

$$\begin{aligned}
dn &= \frac{d\beta W_n + da(V + nV_n + \rho V_b)}{|J|} \cdot \left[ B_r^2 (nY_{zz} + \lambda B_{zz}) + B_z^2 (nY_{rr} + \lambda B_{zr}) \right. \\
&\quad \left. - 2B_r B_z (-nY_{rz} + \lambda B_{rz}) \right]. \quad (54c)
\end{aligned}$$

**Derivation of (37a)-(37d):** While (37a), (37c) and (37d) follow directly from total differentiation of (24),  $nr$  and  $nz$ , respectively, totally differentiating  $Y(\bar{r} - nr, nz)$  yields

$$dy = nY_z dz - nY_r dr + (zY_z - rY_r) dn. \quad (55)$$

$B_r = Y_r/\lambda$  and  $B_z = -Y_z/\lambda$  from (34a) and (34b), respectively, inserted into  $B_r dr + B_z dz = 0$  yields  $Y_r dr - Y_z dz = 0$  such that (55) simplifies to (37b).

### Proof of Proposition 2:

**Model A:** The results in lines 1 and 5 of table 1 follow directly from (36a)-(36c) and (37a)-(37d) by taking into account that  $|J| < 0$ ,  $B_r > 0$ ,  $B_z < 0$ ,  $Y_{rr} < 0$ ,  $Y_{zz} < 0$ ,  $B_{rz} \leq 0$ ,  $Y_{rz} \geq 0$  and  $\lambda > 0$ .

**Model B:** In case of the Leontief net offspring function  $b = \min[r, c(\bar{z} - z)] - \varepsilon$  efficiency requires  $r = c(\bar{z} - z)$  such that (33) turns into

$$\mathcal{H} = \beta W(n) + Y \left[ \bar{r} - nr, n \left( \bar{z} - \frac{r}{c} \right) \right] + anV(n, r - \varepsilon) + \mu n(r - \varepsilon) \quad (56)$$

and we obtain the first-order conditions

$$\mathcal{H}_r = -nY_r - n \frac{Y_z}{c} + anV_b + n\mu = 0, \quad (57a)$$

$$\dot{\mu} = \rho\mu - \beta W_n - a(V + nV_n) + rY_r - \left( \bar{z} - \frac{r}{c} \right) Y_z - \mu(r - \varepsilon). \quad (57b)$$

Then the long-run equilibrium is characterized by  $nb = 0$  which implies  $r = c(\bar{z} - z) = \varepsilon$  and by

$$\beta W_n + a(V + nV_n + \rho V_b) - (r + \rho)Y_r + \left( z - \frac{\rho}{c} \right) Y_z = 0. \quad (58)$$

Since the long-run levels of  $r$  and  $z$  are constant (58) determines the long-run level of  $n$ . Implicit differentiation of (58) yields

$$\frac{dn}{d\beta} = -\frac{W_n}{\tilde{J}} \quad \text{and} \quad \frac{dn}{da} = -\frac{V + nV_n + \rho V_b}{\tilde{J}} \quad (59)$$

where  $\tilde{J} := \beta W_{nn} + a(2V_n + nV_{nn}) + r(r + \rho)Y_{rr} + z(z - \frac{\rho}{c})Y_{zz} - (2rz + \rho z - \frac{\rho r}{c})Y_{rz}$  is assumed to be negative (stability of the equilibrium) implying that  $dn/d\beta > 0$  and  $dn/da > 0$ . Since  $dr/d\beta = dr/da = dz/d\beta = dz/da = 0$ , the results in lines 2 and 6 are straightforward.

**Model C:** In case of  $u = \min[\beta W(n), Y(\bar{r} - nr, nz)]$  the social planner's objective is to maximize

$$\mathcal{L} = \beta W(n) + anV(n, b) + \mu nb + \lambda[\beta W(n) - Y(\bar{r} - nr, nz)] + \lambda_b n[B(r, z) - b] \quad (60)$$

and the first-order conditions read

$$\mathcal{L}_r = \lambda_b n B_r + \lambda n Y_r = 0, \quad (61a)$$

$$\mathcal{L}_z = \lambda_b n B_z - \lambda n Y_z = 0, \quad (61b)$$

$$\mathcal{L}_b = anV_b + n\mu - n\lambda_b = 0, \quad (61c)$$

$$\mathcal{L}_\lambda = \beta W(n) - Y(\bar{r} - nr, nz) = 0, \quad (61d)$$

$$\dot{\mu} = \rho\mu - \beta W_n - a(V + nV_n) + \lambda(zY_z - rY_r - \beta W_n) - \mu b. \quad (61e)$$

Observe that the efficient long-run allocation  $(r, z, n)$  is characterized by

$$nB(r, z) = 0, \quad (62a)$$

$$\beta W(n) - Y(\bar{r} - nr, nz) = 0, \quad (62b)$$

$$B_r Y_z + B_z Y_r = 0. \quad (62c)$$

It is interesting to note that equations (62a)-(62c) are independent of the parameter  $a$ . Total differentiation of (62a)-(62c) yields<sup>16</sup>

$$\begin{pmatrix} B_r & B_z & 0 \\ 0 & 0 & \beta W_n - rY_r + zY_z \\ \phi_4 & \phi_5 & \phi_6 \end{pmatrix} \cdot \begin{pmatrix} dr \\ dz \\ dn \end{pmatrix} = \begin{pmatrix} 0 \\ -d\beta W \\ 0 \end{pmatrix} \quad (63)$$

where

$$\phi_4 := B_{rr}Y_z - B_rY_{zr}n + B_{zr}Y_r - B_zY_{rr}n < 0,$$

$$\phi_5 := B_{rz}Y_z + B_rY_{zz}n + B_{zz}Y_r + B_zY_{zr}n < 0,$$

$$\phi_6 := B_r(zY_{zz} - rY_{zr}) + B_z(zY_{rz} - rY_{rr}) < 0.$$

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<sup>16</sup>Total differentiating (62b) one gets  $(\beta W_n - rY_r + zY_z)dn + Wd\beta + Y_r ndr - Y_z ndz$ . In (63) we have taken into account that (61a), (61b) and  $B_r dr + B_z dz = 0$  imply  $Y_r ndr - Y_z ndz = 0$ .

Solving the equation system (63) we obtain

$$\frac{dr}{d\beta} = \frac{B_z W \phi_6}{|\check{J}|} < 0, \quad \frac{dz}{d\beta} = -\frac{B_r W \phi_6}{|\check{J}|} < 0, \quad \frac{dn}{d\beta} = \frac{W (B_r \phi_5 - B_z \phi_4)}{|\check{J}|} > 0, \quad (64)$$

where  $|\check{J}|$  is assumed to be negative. Finally we differentiate  $u = \beta W(n) = y$  to get

$$du = W d\beta + \beta W_n dn = dy \quad (65)$$

which establishes  $du/d\beta > 0$  and  $dy/d\beta > 0$ .

**Model D:** Now suppose  $u$  and  $b$  are specified as  $b = \min[r, c(\bar{z} - z)] - \varepsilon$  and  $u = \min[\beta W(n), Y(\bar{r} - nr, nz)]$ . Then it is easy to see that the long-run allocation is determined by  $r = c(\bar{z} - z) = \varepsilon$  and

$$\beta W(n) - Y(\bar{r} - nr, nz) = 0. \quad (66)$$

Implicit differentiation of (66) yields

$$\frac{dn}{d\beta} = -\frac{W}{\beta W_n + r Y_r - z Y_z} > 0, \quad (67)$$

since  $\beta W_n + r Y_r - z Y_z$  is assumed to be negative. Summarizing, we have  $dr/d\beta = 0$ ,  $dz/d\beta = 0$ ,  $d(rn)/d\beta > 0$ ,  $d(zn)/d\beta > 0$ , and  $du/d\beta = dy/d\beta = W + \beta W_n (dn/d\beta) > 0$ .

## Appendix C: Comparative dynamics in the two-species model

First, observe that

$$B_z^2 dz_{21} = 0. \quad (68)$$

Next, total differentiation of (49a), (49c)-(49e) leads to

$$\hat{J} \cdot \begin{pmatrix} dr \\ dz_{11} \\ dn_1 \\ dn_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ -d\beta W_{n_1} B_r^1 - da_1(V^1 + n_1 V_n^1 + \rho V_b^1) B_r^1 + d\gamma(\tau B_r^1 + \rho + z_{11} B_z^1) \\ -d\beta W_{n_2} B_r^1 - da_2(V^2 + n_2 V_n^2 + \rho V_b^2) B_r^1 + d\gamma\left(z_{21} + \frac{\rho}{B_z^2}\right) \end{pmatrix} \quad (69)$$

where

$$\hat{J} := \begin{pmatrix} B_r^1 & B_z^1 & 0 & 0 \\ 0 & n_1 & z_{11} & -z_{21} \\ \phi_\tau B_{rr}^1 - \gamma B_r^1 & -\gamma B_z^1 - \gamma z_{11} B_{zz}^1 & [\beta W_{n_1 n_1} + a_1(2V_n^1 + n_1 V_{nn}^1)] B_r^1 & 0 \\ \phi_8 B_{rr}^1 & \gamma B_{zz}^1 \left(z_{21} + \frac{\rho}{B_z^2}\right) & 0 & [\beta W_{n_2 n_2} + a_2(2V_n^2 + n_2 V_{nn}^2)] B_r^1 \end{pmatrix}$$

and

$$\phi_7 := \beta W_{n_1} + a_1(V^1 + n_1 V_n + \rho V_b^1) - \gamma r < 0 \quad \text{and} \quad \phi_8 := \beta W_{n_2} + a_2(V^2 + n_2 V_n + \rho V_b^2) > 0.$$

Then solving (69) by Cramer's rule gives

$$\frac{dr}{da_1} = -\frac{1}{|\hat{J}|} z_{11} (B_r^1)^2 B_z^1 (V^1 + n_1 V_n^1) [\beta W_{n_2 n_2} + a_2(2V_n^2 + n_2 V_{nn}^2)] , \quad (70)$$

$$\frac{dz_{11}}{da_1} = \frac{1}{|\hat{J}|} z_{11} (B_r^1)^3 (V^1 + n_1 V_n^1) [\beta W_{n_2 n_2} + a_2(2V_n^2 + n_2 V_{nn}^2)] , \quad (71)$$

$$\frac{dn_1}{da_1} = -\frac{(V^1 + n_1 V_n^1) B_r^1}{|\hat{J}|} \left[ (B_r^1)^2 n_1 [\beta W_{n_2 n_2} + a_2(2V_n^2 + n_2 V_{nn}^2)] + z_{21} \gamma B_r^1 B_{zz}^1 \left(z_{21} + \frac{\rho}{B_z^2}\right) - z_{21} \phi_8 B_z^1 B_{rr}^1 \right] , \quad (72)$$

$$\frac{dn_2}{da_1} = \frac{(V^1 + n_1 V_n^1) B_r^1}{|\hat{J}|} \left[ -z_{11} \gamma B_r^1 B_{zz}^1 \left(z_{21} + \frac{\rho}{B_z^2}\right) + z_{11} \phi_8 B_z^1 B_{rr}^1 \right] , \quad (73)$$

$$\frac{dr}{da_2} = \frac{1}{|\hat{J}|} z_{21} (B_r^1)^2 B_z^1 (V^2 + n_2 V_n^2) [\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)], \quad (74)$$

$$\frac{dz_{11}}{da_2} = -\frac{1}{|\hat{J}|} z_{21} (B_r^1)^3 (V^2 + n_2 V_n^2) [\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)], \quad (75)$$

$$\frac{dn_1}{da_2} = -\frac{(V^2 + n_2 V_n^2) B_r^1}{|\hat{J}|} [\gamma z_{11} B_{zz}^1 + z_{21} \phi_7 B_z^1 B_{rr}^1], \quad (76)$$

$$\frac{dn_2}{da_2} = -\frac{(V^2 + n_2 V_n^2) B_r^1}{|\hat{J}|} n_1 (\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)) + \gamma (z_{11})^2 B_{zz}^1 + z_{11} \phi_7 B_z^1 B_{rr}^1, \quad (77)$$

$$\frac{dr}{d\beta} = -\frac{(B_r^1)^2 B_z^1}{|\hat{J}|} [W_{n_1} z_{11} (\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)) - W_{n_2} z_{21} (\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1))], \quad (78)$$

$$\frac{dz_{11}}{d\beta} = \frac{(B_r^1)^3}{|\hat{J}|} [W_{n_1} z_{11} (\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)) - W_{n_2} z_{21} (\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1))], \quad (79)$$

$$\begin{aligned} \frac{dn_1}{d\beta} &= \frac{B_r^1}{|\hat{J}|} \left[ -W_{n_1} \left\{ (B_r^1)^2 n_1 [\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)] + z_{21} \gamma B_r^1 B_{zz}^1 \left( z_{21} + \frac{\rho}{B_z^2} \right) - z_{21} \phi_8 B_z^1 B_{rr}^1 \right\} \right. \\ &\quad \left. - W_{n_2} \left\{ z_{11} \gamma B_r^1 B_{zz}^1 + z_{21} \phi_7 B_z^1 B_{rr}^1 \right\} \right], \end{aligned} \quad (80)$$

$$\begin{aligned} \frac{dn_2}{d\beta} &= -\frac{B_r^1}{|\hat{J}|} \left[ W_{n_1} \left\{ z_{11} \gamma B_r^1 B_{zz}^1 \left( z_{21} + \frac{\rho}{B_z^2} \right) - z_{11} \phi_8 B_z^1 B_{rr}^1 \right\} \right. \\ &\quad \left. + W_{n_2} \left\{ (B_r^1)^2 n_1 [\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)] + (z_{11})^2 \gamma B_r^1 B_{zz}^1 + z_{11} \phi_7 B_z^1 B_{rr}^1 \right\} \right], \end{aligned} \quad (81)$$

$$\frac{dr}{d\gamma} = \frac{B_r^1 B_z^1}{|\hat{J}|} \left[ (r B_r^1 + \rho + z_{11} B_z^1) z_{11} (\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)) - \left( z_{21} + \frac{\rho}{B_z^2} \right) z_{21} (\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)) \right], \quad (82)$$

$$\frac{dz_{11}}{d\gamma} = \frac{(B_r^1)^2}{|\hat{J}|} \left[ - (rB_r^1 + \rho + z_{11}B_z^1) z_{11} (\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)) + \left( z_{21} + \frac{\rho}{B_z^2} \right) z_{21} (\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)) \right], \quad (83)$$

$$\begin{aligned} \frac{dn_1}{d\gamma} &= \frac{1}{|\hat{J}|} \left[ (rB_r^1 + \rho + z_{11}B_z^1) \left\{ n_1 (B_r^1)^2 (\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)) + z_{21} \gamma B_r^1 B_{zz}^1 \left( z_{21} + \frac{\rho}{B_z^2} \right) - z_{21} \phi_8 B_z^1 B_{rr}^1 \right\} \right. \\ &\quad \left. + \left( z_{21} + \frac{\rho}{B_z^2} \right) (z_{11} z_{21} \gamma B_r^1 B_{zz}^1 + z_{21} \phi_7 B_z^1 B_{rr}^1) \right], \end{aligned} \quad (84)$$

$$\begin{aligned} \frac{dn_2}{d\gamma} &= \frac{1}{|\hat{J}|} \left[ (rB_r^1 + \rho + z_{11}B_z^1) \left\{ z_{11} \gamma B_r^1 B_{zz}^1 \left( z_{21} + \frac{\rho}{B_z^2} \right) - z_{11} \phi_8 B_z^1 B_{rr}^1 \right\} \right. \\ &\quad \left. + \left( z_{21} + \frac{\rho}{B_z^2} \right) \left\{ n_1 (B_r^1)^2 (\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)) + (z_{11})^2 \gamma B_r^1 B_{zz}^1 + z_{11} \phi_7 B_z^1 B_{rr}^1 \right\} \right], \end{aligned} \quad (85)$$

$$\begin{aligned} \text{where } |\hat{J}| &= B_r^1 \left\{ n_1 [\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)] [\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)] (B_r^1)^2 + \left[ z_{11} (\gamma B_z^1 + \gamma z_{11} B_{zz}^1) \right. \right. \\ &\quad \left. \left. + z_{21} \gamma B_{zz}^1 \left( z_{21} + \frac{\rho}{B_z^2} \right) \right] [\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)] B_r^1 \right\} - B_z^1 \left\{ - z_{11} (\phi_7 B_{rr}^1 - \gamma B_r^1) \right. \\ &\quad \left. [\beta W_{n_2 n_2} + a_2 (2V_n^2 + n_2 V_{nn}^2)] B_r^1 + z_{21} \phi_8 B_{rr}^1 [\beta W_{n_1 n_1} + a_1 (2V_n^1 + n_1 V_{nn}^1)] B_r^1 \right\}. \end{aligned} \quad (86)$$

The results of Table 2 follow from (70)-(86) and the properties of the functions  $W$ ,  $B^1$ ,  $B^2$ ,  $V^1$  and  $V^2$ . In addition, we assume  $\beta W_{n_i n_i} + a_i (2V_n^i + V_{nn}^i) < 0$  for  $i = 1, 2$  and  $\phi_7 B_{rr}^1 - \gamma B_r^1 < 0$  which are sufficient for the negative definiteness of  $\hat{J}$  ( $|\hat{J}| > 0$ ).