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Working Paper

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Kiel Working Paper, No. 1662

Provided in Cooperation with:
Kiel Institute for the World Economy – Leibniz Center for Research on Global Economic Challenges

Suggested Citation: Bertram, Christine (2010) : Integrating biodiversity indices into a multi-species optimal control model, Kiel Working Paper, No. 1662, Kiel Institute for the World Economy (IfW), Kiel

This Version is available at:
https://hdl.handle.net/10419/43118

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No. 1662 | November 2010

Web: www.ifw-kiel.de

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Integrating biodiversity indices into a multi-species optimal control model

Christine Bertram

Abstract:
Biodiversity is often adversely affected by human activities. This reduces social welfare but may be external to private economic decisions. Consequently, these external effects on biodiversity need to be considered explicitly in economic models, which is only partly reflected in the literature. So far, biodiversity is mostly treated only implicitly in multiple renewable resource models, or it is considered in terms of (genetic) variability or species richness only, but not in terms of indices that simultaneously account for species richness and evenness. However, both constitute important dimensions of biodiversity. This paper integrates such biodiversity indices into an optimal control model, thus accounting for non-use values derived from the existence of multiple living resources.
Main findings include that a unique equilibrium satisfying sufficient optimality conditions can be determined although the biodiversity index is non-concave. Compared to a model set-up with a monotonically increasing, concave utility function, steady state stocks are distributed more evenly and biodiversity is higher but the total number of individuals is lower when the biodiversity index is applied.

Keywords: Biodiversity, Renewable Resources, Optimal Control, Non-Concavity

JEL classification: Q20, Q29, Q57

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1 Introduction

Human activities and economic development pose a continuous threat to biodiversity, which has given rise to calls for biodiversity conservation. Heal (2004) unequivocally makes clear that biodiversity creates and contributes to economic values. He distinguishes four categories to which biodiversity positively contributes: ecosystem productivity, insurance, genetic knowledge, and ecosystem services. Consequently, biodiversity does increase social welfare though it might be external to individual considerations of profit maximization. This has to be taken into account when determining efficient management strategies for the use of renewable and non-renewable resources. Not accounting for the adverse effects of economic activities on biodiversity would imply attaching a value of zero to it.

Biodiversity is a complex concept for which different definitions exist. According to the United Nations Convention on Biological Diversity (CBD, 1992) it is "...the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part [which] includes diversity within species, between species and of ecosystems." This definition illustrates that biodiversity concepts can be applied to different organizational levels, i.e. the species-level or the community-level, and to different spatial scales (see Armswoth et al. (2004) for an overview of biodiversity concepts). This paper applies the concept of species-level biodiversity because it is concerned with the damage that economic activities like the extraction of non-renewable resources, agricultural activities or soil sealing resulting from construction activities inflict upon certain living species in a confined area.[1]

Two general concepts are used to determine species-level biodiversity (Purvis and Hector, 2000). The first concept takes into account certain features of different species and calculates pairwise differences between the attributes of these species (Weitzmann, 1992). This concept can for example be applied to phylogenetic diversity, which would be larger the more the genetic features of the species differ.

[1] In the following, the term biodiversity will be used to indicate species-level biodiversity throughout the paper although this will not always be explicitly mentioned.

The second concept defines a biodiversity index that takes into account the total number of species as well as the abundances of the different species. This paper follows the second approach because it investigates the direct impacts of economic activities on relative species abundances. Moreover, this approach is also widely used by ecologists.

Species-level biodiversity in this second sense has several dimensions. One dimension is species richness, which means the number of species within a certain area. This term was coined by McIntosh (1967) and represents the oldest and most common measure of biodiversity. The second dimension of species-level biodiversity is species evenness, which means the variability in the distribution of species abundances within a certain area (Magurran, 2004). While the role of species richness for biodiversity is intuitively clear, the role of evenness is subtler. From an ecological point of view, more abundant species usually have a larger influence on the functioning of ecosystems than rare species do. Consequently, considering an ecosystem with the same number of species, diversity increases the more evenly the species abundances are distributed. On the contrary, diversity decreases the more the ecosystem is dominated by few species (Duelli and Obrist, 2003; Armsworth et al., 2004).

The importance of species evenness for ecosystems is exemplified by the following issue which has also been addressed in an economic context. Consider the case of farming. Increasing the abundance of a highly profitable crop is likely to increase the individual profits for a farmer. However, the increasing dominance of this crop might also induce the development of parasites and pests specialized on that crop. Consequently, an even distribution of crops can work as an insurance against pest outbreaks. Thus, the socially optimal decision should balance the farmer‘s profit considerations with the insurance considerations of society as a whole, as the individual decision of the farmer might not be socially optimal if he does not take the "disease externality" into account (Weitzman, 2000).

The two dimensions, species richness and species evenness, can be incorporated into a single measure by calculating so-called diversity indices.[2] A large number

[2]Following Good (1953), these indices are also called heterogeneity measures. However, throughout this paper they will be referred to as diversity or biodiversity indices.

of these indices exist and they are widely used in ecology to measure species-level biodiversity (see Magurran (2004) for an overview). Weitzman (2000) highlights that a diversity index could be used in the objective function of economic models to capture external effects on biodiversity. However, the explicit integration of biodiversity into economic models is still rare and diversity indices that also account for species evenness had not been incorporated into economic models (Eppink and van den Berg (2007)) until very recently (Noack et al., 2010). In most cases in which biodiversity is considered in economic models, it is either covered only implicitly in multi-species renewable resource models (e.g. Clark, 1976 or Swanson, 1994), or it is considered in terms of species richness (Li et al., 2001) or (genetic) variability (Brock and Xepapadeas, 2003).

This paper integrates a biodiversity index that simultaneously accounts for species richness and evenness into an optimal control model. The inclusion of such a biodiversity index allows for interesting insights into the question of how economic activities have to be adjusted when they affect relative species abundances. This would not be possible if species richness was used to measure biodiversity. Moreover, the paper explores how a biodiversity index that may induce non-concavity of the current-value Hamiltonian influences optimal steady state solutions and illustrates how the characteristics of the steady state change compared to the case where the utility derived from the existence of the living resources is monotonically increasing and concave in absolute stock sizes and independent of relative stock sizes. In addition, the index used provides a direct measure for biodiversity and no evaluation technique is necessary to infer the utility derived from biodiversity from empirical surveys.

The paper is organized as follows. Section 2 provides a brief review of the relevant literature, mainly in the field of the economics of renewable resources and biodiversity. Section 3 introduces different biodiversity indices and explores their properties. Section 4 develops an optimal control model that incorporates these indices, describes its analytical features, provides a numerical example and compares steady state results to a model with a monotonically increasing, concave utility function. Section 5 discusses the model set-up and results before concluding.

2 Literature review

This paper introduces biodiversity indices into a multi-species optimal control model, where living resources are damaged by some kind of human-induced economic activity. The approach is similar to traditional harvesting models, where optimal harvesting of fish resources, for example, is determined by taking into account trade-offs between possible profits and harvesting costs. Living resources, such as fish or other animals, usually do not grow linearly but e.g. according to a logistic growth function and face natural carrying capacities. The literature on renewable resources considers these biological constraints and investigates among other things optimal harvesting programs or efficient management techniques.

Seminal papers on renewable resources include Gordon (1954), who highlights that the common property character of fish resources can lead to socially inefficient harvest. Clark and Munro (1975) use an optimal control approach to determine optimality conditions for harvest and resource stocks. Clark (1979) determines optimal harvesting of a common property resource and compares it to the case of privately owned fisheries. The standard one-species models of optimal fisheries have been extended to multiple-species models, where the species interact in different ways (see e.g. Clark, 1976). These interactions can be competing (Flaaten, 1991), mutualistic (Wacker, 1999) or predator-prey relationships (Hannesson, 1983).

The second strand of research important to this paper is that of biodiversity in economic models. Eppink and van den Bergh (2007) provide an extensive review of how biodiversity has been integrated into economic models, including those considering the optimal extraction of renewable resources. In these models, a value is typically attached to renewable resources due to the possibility of harvesting them. Non-use values have also been captured in these models, e.g. as opportunity costs of land conservation where agricultural production yields positive returns but impacts negatively on the species abundances (Skonhoft, 1999; Bulte and Horan, 2003). In addition, biodiversity can be a determinant for the resilience of an ecosystem against exogenous events. Perrings and Walker (1997) investigate the optimal management of ecosystems, where biodiversity and resilience are influenced by human interfer-

ence. Biodiversity is thus often implicitly accounted for but only few papers include explicit indices to reflect direct or indirect values of biodiversity.

One way to consider biodiversity explicitly is to follow Weitzman (1992), who defines biodiversity in terms of pairwise differences between several features of different species. Brock and Xepapadeas (2003) build on this approach and establish an endogenous measure for biodiversity that accounts for the economic value derived from an ecosystem with genetic diversity. In an earlier paper, they set up a model where two species compete for the same resource and derive optimal management rules when considering the economic value derived from ecosystem functions (Brock and Xepapadeas, 2002). Another way to consider biodiversity explicitly is to integrate biodiversity indices in terms of species richness into optimal control models. Li and Loefgren (1998) as well as Li et al. (2001) include information on species richness in their models to determine optimal paths for the number of species as well as for single resource stocks. In addition, Eichner and Tschirrhart (2007) use a biodiversity measure that is based on species abundances and constructed such that divergences from the natural level of biodiversity affect utility negatively. They integrate this measure into a CGE modeling framework. Moreover, Eppink and Withagen (2009) integrate spatial patterns of biodiversity conservation into a multiregional CGE model by considering a species-area curve, where the number of species is a concave function of habitat size.

Two recent papers apply the concept of diversity indices in their considerations. Noack et al. (2010) integrate a biodiversity index into the objective function of an optimal control model. They consider the optimal management of timber production, livestock and biodiversity in the Caspian Forest. However, they use absolute instead of relative abundances to compute the biodiversity index. Given their parameter choice, this results in using a strictly increasing, concave utility function for resource stocks. Consequently, problems of non-concavity, which arise when using relative abundances, are avoided. Another recent paper by Brock, Kinzig and Perrings (2010) investigates the effect of land-use change on environmental hetero-

geneity, and thereby on biodiversity.[3] They assume that land-use decisions can either increase or decrease environmental heterogeneity, thus applying the concepts of relative abundances, evenness and dominance to landscape types. However, they do not model the heterogeneity index in detail but only state that it might be non-monotonic (Brock, Kinzig and Perrings, 2010). This paper adds to the literature by integrating an explicit biodiversity index that uses relative species abundances and thus is non-monotonic and accounts for both species richness and evenness in a multi-species optimal control model.

In fact, the construction of the biodiversity index using relative abundances implies that the marginal utility derived from an increase in the stock of one species may be positive or negative, depending on relative stock sizes. This could induce non-concavity of the Hamiltonian so that the usual sufficient optimality conditions would not apply. Qualitatively, this is similar to considering living renewable resources that may create both benefits and damages. One example for such a framework in a one-species model is presented by Rondeau (2001), who examines an optimal control model where the reintroduction of a harvested species may induce benefits e.g. from recreational opportunities but may also induce damages e.g. on human health, while harvesting this species creates benefits through consumptive use. Another example is presented by Horan and Bulte (2004), who consider living resources that may either create an economic benefit via tourism revenues or that induce a stock-dependent damage via agricultural damage or human mortality. Both frameworks allow for shadow prices that may either be positive or negative even in an optimal program in a one-species framework. This can give rise to non-concavity of the Hamiltonian and multiple equilibrium candidates. A related case is presented by Tahvonen and Salo (1996) who present a dynamic optimal pollution control model with a concave-convex decay function. They also find that multiple equilibrium candidates may exist but that the globally optimal solution may be determined independently of initial stock levels.

[3]Note that in the example by Brock, Kinzig and Perrings (2010), heterogeneity refers to land-use types and not to species abundances. In terms of species, they consider biodiversity to be reflected by species richness.

3 Biodiversity indices

The biodiversity indices that are used in this paper build on three basic assumptions. Firstly, all species are assumed to be equal. Species with different conservation values or with different contributions to ecosystem functions are not discriminated but treated equally. Only the relative abundance of a species indicates its ecological importance. Secondly, all individuals of the same species are assumed to be equal. And thirdly, it is assumed that all species abundances are measured and recorded using appropriate and comparable units (Magurran, 2004).

The group of diversity indices used to represent biodiversity in this paper is based on an entropy measure that had originally been used in information theory (Renyi, 1961; Hill, 1973). This measure is constructed using the (relative) abundances of the species and thus (usually) accounts for species richness and species evenness. See Baumgärtner (2007) for a detailed discussion, part of which is briefly laid out in the following. The general biodiversity index is constructed as follows:[4]

$$B_\omega(x_1, ..., x_n) = B_\omega(\mathbf{x}) = (\sum_{i=1}^{n} {r_i}^\omega)^{\frac{1}{1-\omega}} \quad \text{with} \quad \omega \geq 0 \tag{1}$$

and

$$r_i = \frac{x_i}{\sum_{i=1}^{n} x_i} \quad \text{for} \quad i = 1, ..., n \tag{2}$$

The number of species under consideration is n. The relative abundance of each species $i = 1, ..., n$ is given by r_i. This relative abundance is given by the absolute abundance, x_i, of each species i relative to the sum of the absolute abundances of all species. As outlined in the introduction, the relative abundances of the species are important for their role within an ecosystem. All else being equal, the index value increases with increasing species richness but also with increasing evenness in the distribution of the relative abundances.

The importance attached to species richness and evenness is determined by setting the parameter ω. The higher ω the higher the value attached to evenness be-

[4] In the following, the variables $(x_1, ..., x_n)$ will be collected in the vector $(\mathbf{x})$.

tween the species. Neglecting evenness puts a relatively large weight on rare species. For different values of ω, different biodiversity indices emerge (Baumgärtner, 2007). There are two extreme cases. For $\omega = 0$, only species richness will be measured, but not evenness. Consequently, the resulting measure is just called Species Richness (following McIntosh, 1967). It always assumes the value n, reflecting the total number of species. Biodiversity loss only occurs if a species becomes extinct. For $\omega \to \infty$, only species evenness will be measured, but not richness. This measure is called Berger-Parker-Index (Berger and Parker, 1970). It only accounts for the species that is relatively most abundant. Biodiversity is given by the inverse of the relative abundance of this species.

All cases in between take into account both species richness and evenness but vary with respect to the degree of importance attached to either. However, the qualitative characteristics of these indices are similar as long as $0 < \omega < \infty$. One case that receives special attention in ecology and which will be applied in section 4 of this paper is the Simpson-Index for $\omega = 2$ (Simpson, 1949). The Simpson-Index is popular among ecologists because it has a meaningful ecological interpretation. It is computed as follows:

$$B_2(\mathbf{x}) = (\sum_{i=1}^{n} r_i^2)^{-1} \tag{3}$$

The sum of the squared relative abundances present in the Simpson-Index reflects the probability that any two individuals drawn randomly from an infinitely large ecosystem belong to different species. Biodiversity is represented by the inverse of this expression, so that the Simpson-Index increases with increasing evenness in the distribution of relative species abundances (Baumgärtner, 2007).

For a given number of species, i.e. for a given value of n, the values of all indices are larger than 1 and smaller or equal to n, depending on the relative abundances r_i. For a given n and for $\omega > 0$, the value of $B_\omega(\mathbf{x})$ decreases with increasing unevenness in the distribution of relative abundances between the species. The maximum value n is reached for $\omega > 0$ only if all species in an ecosystem have equal relative abundances, i.e. if $r_i = \frac{1}{n}$ for all i. This is a very important and interesting feature of these biodiversity indices, which will be further discussed below. Consider,

for example, an ecosystem with two species. The biodiversity index then only takes on the maximum value 2 if both species account for 50% of all individuals. But it does not matter how large their absolute abundance is. This also implies that increasing the absolute abundance of one species may lead to an increase in diversity or to a decrease of diversity, depending on whether this species had been underrepresented or overrepresented in the sample prior to the change.

In terms of economic thinking, this may seem counterintuitive. Usually, economists assume jointly concave utility functions where an increase in the availability of each good has a positive marginal utility.[5] The basic assumption underlying this is that of substitutability. Economic reasoning mostly assumes that goods are substitutes for one another, which results in convex indifference curves. Transferring this concept to living species would imply that increasing the abundance of one species would always increase utility, no matter how strongly it might already dominate a sample. From an ecological point of view, however, biological species are different from normal economic goods. Direct interactions between individuals and species within ecosystems influence survival probabilities and ecosystem dynamics. Consequently, the distribution of abundances matters for the functioning of ecosystems and the provision of ecosystem services. This also implies that treating species as substitutes may not be appropriate (Baumgärtner, 2007; Baumgärtner et al., 2006). Thus, it seems worthwhile to also explore the role of diversity indices in economic models where external effects on relative species abundances and biodiversity occur.

[5]However, one can also think of backward-bending indifference curves where e.g. an increase in income has a negative marginal utility given that a high level of working hours has been reached. This would be an example for a case in which the balance between income and leisure as the two goods under consideration becomes important.

4 Biodiversity in an optimal control model

4.1 General modeling framework

In this subsection, the general biodiversity index as described in section 3 is incorporated into an optimal control model. The model is set up as follows:

$$max \quad W = \int_0^\infty e^{-\rho t}[U(y_{1t}, ..., y_{nt}) + B(x_{1t}, ..., x_{nt})]dt \tag{4}$$

s.t.

$$\dot{x}_{it} = G_i(x_{1t}, ..., x_{nt}) - \phi_i y_{it} \quad \text{and} \quad x_{i0} = X_i \quad \text{for} \quad i = 1, ..., n \tag{5}$$

and

$$G_i(x_{1t}, ..., x_{nt}) = \psi_i x_{it}(1 - \frac{\sum_{j=1}^n x_{jt}}{\kappa}) \quad \text{with} \quad 0 < \sum_{j=1}^n x_{jt} \leq \kappa \quad \forall\, i, t \tag{6}$$

In this model, the instantaneous utility function $U(y_{1t}, ...y_{nt}) = U(\mathbf{y}_t)$ expresses the net benefit generated by economic activities, such as the extraction of non-renewable resources, construction activities or agricultural activities, at time t. Vector $\mathbf{y}_t = (y_{1t}, ..., y_{nt})$ describes the level or intensity of this economic activity but it is not further specified. In particular, there is no explicit modeling of the costs related to this activity. This simple modeling approach has been chosen to clearly identify the effects of the second factor contributing to social welfare, the biodiversity index, on the model solutions. The instantaneous utility function $U(\mathbf{y}_t)$ is separable in the components of $\mathbf{y}_t$ and satisfies the following properties: $\frac{\partial U(\mathbf{y}_t)}{\partial y_{it}} = U_{y_{it}} > 0 \quad \forall \quad i, t$; $U_{y_{it}y_{it}} < 0 \ \forall \ i, t$ and $U_{y_{it}y_{jt}} = 0 \ \forall \ i \neq j, t$.

Vector $\mathbf{x}_t = (x_{1t}, ..., x_{nt})$ contains the stocks of the n renewable or living resources at time t. The utility derived from their existence is expressed by the biodiversity index $B(x_{1t}, ..., x_{nt}) = B(\mathbf{x}_t)$. The properties of this biodiversity index are crucial for the model's solutions and are discussed below in more detail. Inserting the biodiversity index directly into the objective function implies that the relationship between biodiversity, ecosystem services and human well-being is not explicitly considered. This would require more explicit modeling, e.g. by integrating the biodiversity index into a production function. However, whenever a biodiversity index will be used in

more detailed economic models, its properties are likely to influence the results, as they do in this paper. Consequently, exploring the effects of integrating a biodiversity index into this relatively simple model framework is also useful when integrating it into more complex models.

In this paper it is therefore assumed that biodiversity will directly contribute to social welfare. This could, on the one hand, be the case because preserving biodiversity has become a widely acknowledged societal goal. Consequently, all external effects of economic activities on biodiversity should be considered in optimization frameworks. On the other hand, biodiversity can also be seen as an insurance e.g. against the outbreak of diseases. The structure of the model reflects the approach suggested by Weitzman (2000), who derives an objective function similar to that used in this paper. He considers the trade-off between increasing economic profits by growing predominantly high-yield crops versus maintaining a mixture of sufficiently diverse crops to lower the risks of infection with endogenously evolving lethal pathogens. He derives an additively separable objective function that contains both the profit from growing crops and the ecosystem‘s resistance to internalize the external effects of agriculture on biodiversity. Moreover, he shows that this resistance can be expressed as an ecological entropy measure[6], which is closely related to the biodiversity index that will be employed in the following.

The case that n may change is not considered here, which implies that no species becomes extinct and that the number of species cannot be increased. This is reasonable because the economic activity takes place in an environment with a given ecosystem and thus with a given number of species. It is assumed that a social planner intends to maximize social welfare by integrating the discounted utility functions over time. In this partial equilibrium model, $U(\mathbf{y}_t)$ and $B(\mathbf{x}_t)$ are both given in money metrics and therefore enter the social welfare function separably.

Conditions (5) and (6) together define the equations of motion for the stocks of the living resources x_i. Note that the growth of each living resource does not only

[6]Weitzman (2000) derives the Shannon entropy as a measure for resistance. Referring to the discussion in section 3, the Shannon entropy is the natural logarithm of the biodiversity index for $\omega = 1$, the Shannon-Wiener index.

depend on its own stock size but also on the stock sizes of all other living resources. In this specification, all living resources compete for the same external resource, which may be food supply.[7] In the absence of the other living resources, the biomass stock of one living resource x_i would grow according to a logistic growth function. The growth function $G_i(\mathbf{x})$ defined in (5) would then take on the form of a concave quadratic function dependent only on x_i with $G_i(0) = 0$ and $G_i(\kappa) = 0 \ \forall \ i$. The maximum growth rate would be reached when the stock is equal to $\frac{\kappa}{2}$. The parameter ψ_i represents the intrinsic growth rate of the stock x_i, and κ represents the carrying capacity of the stock.

In addition, it is assumed that the economic activity expressed by $\mathbf{y}$ reduces the stock of the living resource according to the damage coefficient ϕ_i. Note that there is one separate control variable y_i for each living resource stock x_i. This implies that the damage caused by the economic activity can be controlled separately for each living resource, which is similar to fishery models with selective harvesting (see e.g. Clark, 1976). Assuming that the damage was non-selective would impose rigidities on the model, inducing the possibility of negative shadow prices and the existence of multiple equilibrium candidates. The more flexible approach has been chosen here to deliver clear insights into the behavior of the biodiversity index in the model. Moreover, it is quite possible that economic activities can be executed such that the damage inflicted upon different living species can be controlled separately.

Moreover, note that this is only one way in which the negative impact of economic activities upon living resources could be modeled. Another possibility would be that these activities damage the habitat of the living resources, so that the carrying capacity κ would decrease. However, here the impact occurs in the form of a flow externality, reducing the biomass stock of the renewable resource whenever the economic activity is carried out.

[7] The specification is a modified version of the Gause model (Gause, 1935) as described by Clark (1976). For simplicity, here it is assumed that $\kappa_i = \kappa \ \forall \ i$.

The current-value Hamiltonian reads as follows:[8]

$$H^c = U(\mathbf{y}) + B(\mathbf{x}) + \sum_{i=1}^{n} \lambda_i (G_i(\mathbf{x}) - \phi_i y_i) \tag{7}$$

The necessary first order conditions are given by expressions (8) and (9):

$$\frac{\partial H^c}{\partial y_i} = 0 \quad \Rightarrow \quad U_{y_i} = \phi_i \lambda_i \qquad \forall\, i \tag{8}$$

$$-\frac{\partial H^c}{\partial x_i} = \dot{\lambda}_i - \rho\lambda_i \quad \Rightarrow \quad \rho = G_{ix_i} + \sum_{j \neq i} \frac{\lambda_j}{\lambda_i} G_{jx_i} + \frac{\dot{\lambda}_i}{\lambda_i} + \frac{B_{x_i}}{\lambda_i} \quad \forall\, i \tag{9}$$

The conditions given by (8) represent the static optimality conditions for the optimal level of the economic activity at each point in time. The marginal utility of this activity has to be equal to its marginal costs. As the costs are not explicitly considered here, the right-hand-sides of the equations only include the damage on the living resources caused by the economic activity, evaluated with the corresponding shadow price, λ_i, of the living resource x_i. With each unit of the economic activity carried out, a certain share of the stocks of the living resources is destroyed. This implies opportunity costs because this share of the living resources will not be present in the future to contribute to reproduction, thus diminishing the living resources' own rate of interest. Based on the assumptions that $U_{y_i} > 0$ and $\phi_i > 0$, the optimality conditions in (8) imply that $\lambda_i > 0 \; \forall\, i$.

The conditions in (9) describe the optimal allocation of each stock of the living resources over time. The social discount rate ρ has to be equal to the own rate of interest of each living resource stock. This own interest rate consists of the growth rate of the resource stock x_i (G_{ix_i}), the impact of the resource stock on the growth rate of all other living resource stocks evaluated with the corresponding shadow prices ($\sum_{j \neq i} \frac{\lambda_j}{\lambda_i} G_{jx_i}$), the increase of its own shadow price ($\frac{\dot{\lambda}_i}{\lambda_i}$) and the change of the existence value derived from this stock, i.e. the change of the biodiversity index divided by the shadow price ($\frac{B_{x_i}}{\lambda_i}$).

[8] Time subscripts are dropped for convenience where this does not lead to confusion. The variables $(x_1, ..., x_n)$ and $(y_1, ..., y_n)$ are collected in the vectors $(\mathbf{x})$ and $(\mathbf{y})$ respectively.

4.2 Implications of the properties of the biodiversity indices

In this subsection, the properties of the biodiversity indices, especially their reaction to changes in the stock size of a living resource, and the resulting impacts on the optimal control model are traced analytically in more detail for different values of ω.

Suppose first that $\omega = 0$ so that only species richness matters for biodiversity. This implies that biodiversity will solely be measured by means of the total number of species n and $B_0(\mathbf{x}) = n$. So, as long as n remains constant, i.e. as long as no species is driven to extinction by the economic activity, $\frac{\partial B_0(\mathbf{x})}{\partial x_i} = 0$ for $i = 1, ..., n$, and the conditions in (9) reduce to:

$$\rho = G_{ix_i} + \sum_{j \neq i} \frac{\lambda_j}{\lambda_i} G_{jx_i} + \frac{\dot{\lambda}_i}{\lambda_i} \quad \forall \quad i \tag{10}$$

At first sight, this suggests that the stocks of the living resources are not important for the optimal path of the economic activity over time. However, the opportunity costs of destroying shares of the stocks of the living resources are still present in equations (8), implying that the damage inflicted upon the living resources does still matter for the optimal path of the economic activity $\mathbf{y}$. This is because decreasing the stock of the living resources still induces reduced opportunities for future stock growth.

Suppose now that $\omega = \infty$ so that biodiversity is represented by the Berger-Parker-Index, which only takes into account species evenness. Denote the relatively most abundant living resource stock by x_m, so that $B_\infty(\mathbf{x}) = r_m^{-1} = \frac{\sum_{i=1}^n x_i}{x_m}$. From this it follows that:

$$\frac{\partial B_\infty(\mathbf{x})}{\partial x_m} = \frac{x_m - \sum_{i=1}^n x_i}{x_m^2} = \frac{-\sum_{i \neq m} x_i}{x_m^2} \; < 0 \tag{11}$$

Note that this partial derivative is negative as long as more species than just the species m exist with a positive number of individuals each. This implies that an increase in the stock of the most abundant species necessarily leads to a reduction of biodiversity and thus to a decrease in utility derived from this stock increase. The reason for this is obvious: Increasing the stock size of the species that is already

dominant in the sample increases the unevenness and thus decreases diversity. On the other hand, an increase in the abundance of any non-dominant species x_i with $i \neq m$ will necessarily increase biodiversity:

$$\frac{\partial B_\infty(\mathbf{x})}{\partial x_i} = \frac{1}{x_m} > 0 \quad \forall \quad i \neq m \tag{12}$$

As it is the aim of the paper to consider species richness and evenness simultaneously, it will be assumed from now on that $B(\mathbf{x})$ is given by the Simpson-Index with $\omega = 2$. This is sensible because the Simpson-Index has a meaningful ecological interpretation. In addition, the Simpson-Index is "one of the most meaningful and robust diversity measures available" (Magurran, 2004).[9] Moreover, the Simpson-Index is representative for all cases in which $0 < \omega < \infty$. The derivatives presented below have also been derived for the general case. Qualitative features, in particular the results derived from equation (15), also hold in general. Consequently, the assumption $\omega = 2$ does not entail any loss of generality. Note also that for illustrative purposes, the number of species will from now on be reduced to $n = 2$. It follows that:

$$B_2(x_1, x_2) = B_2(\mathbf{x}) = (r_1^2 + r_2^2)^{-1} \tag{13}$$

with

$$r_i = \frac{x_i}{x_1 + x_2} \quad \text{for} \quad i = 1, 2 \tag{14}$$

Partially differentiating $B_2(\mathbf{x})$ with respect to x_1 yields the following derivative:[10]

$$B_{x_1} = -2 * B_2(\mathbf{x})^2 * (x_1 + x_2)^{-3} * [x_2(x_1 - x_2)] \begin{cases} < 0, & x_1 > x_2; \\ = 0, & x_1 = x_2; \\ > 0, & x_1 < x_2. \end{cases} \tag{15}$$

It is obvious that the effect of an increase in the abundance of one species does not necessarily lead to an increase in the value of the biodiversity index. If x_1 is

[9] It should be noted here that the Simpson-Index puts a relatively large emphasis on evenness compared to richness. However, this is appropriate here because the model considers an environment with a fixed number of species.

[10] The partial derivative B_{x_2} can be constructed analogously.

underrepresented in the sample, i.e. $x_1 < x_2$, an increase in its stock size will lead to higher biodiversity. But if it is overrepresented in the sample, i.e. $x_1 > x_2$, an increase in its stock size will lead to lower biodiversity. This is the main difference to other renewable resource models where the marginal utility of the stock usually is positive for all stock sizes.[11]

If all species are equally abundant, i.e. $x_i = x' \; \forall \; i$, the derivative of $B_2(\mathbf{x})$ with respect to each x_i is zero. That is, diversity has reached its maximum value, n, and will increase no further with an increase in the relative abundance of any species because all species are equally abundant. (Sufficient conditions for a maximum are verified below.) However, biodiversity will decline whenever the size of any stock diverges from x' because evenness is no longer fully satisfied. This holds for all ω.

Constructing the general Hessian matrix composed of the second partial derivatives of $B_2(\mathbf{x})$, one receives the following:

$$He(B_2(\mathbf{x})) = \begin{pmatrix} B_{x_1x_1} & B_{x_1x_2} \\ B_{x_2x_1} & B_{x_2x_1} \end{pmatrix} = \begin{pmatrix} \frac{4x_1x_2(x_1^2-3x_2^2)}{(x_1^2+x_2^2)^3} & \frac{-2(x_1^4-6x_1^2x_2^2+x_2^4)}{(x_1^2+x_2^2)^3} \\ \frac{-2(x_1^4-6x_1^2x_2^2+x_2^4)}{(x_1^2+x_2^2)^3} & \frac{4x_1x_2(-3x_1^2+x_2^2)}{(x_1^2+x_2^2)^3} \end{pmatrix} \tag{16}$$

The eigenvalues and the determinant of this Hessian are as follows:

$$EV_1(He) = \frac{2(x_1 - x_2)^2}{(x_1^2 + x_2^2)^2} \geq 0 \tag{17}$$

$$EV_2(He) = \frac{-2(x_1 + x_2)^2}{(x_1^2 + x_2^2)^2} \leq 0 \tag{18}$$

$$Det(He) = \frac{-4(x_1^2 - x_2^2)^2}{(x_1^2 + x_2^2)^4} \leq 0 \tag{19}$$

This allows important conclusions for the curvature of the biodiversity index $B_2(\mathbf{x})$. Two cases can be distinguished:

Case 1: $x_1 = x_2$**.** In this case, the first partial derivatives of the biodiversity index, B_{x_1} and B_{x_2}, are zero and $B_2(\mathbf{x})$ assumes the critical value $n = 2$. Moreover, it now

[11] Two exceptions are Rondeau (2001) and Horan and Bulte (2004), who account for the possibility of negative marginal utility in a one-species framework.

holds that the first eigenvalue $EV_1(He)$ is zero while the second one is negative. In addition, the determinant of He is zero. From this it follows that He is negatively semi-definite and thus $B_2(\mathbf{x})$ is locally concave for $x_1 = x_2$. Consequently, the critical value $n = 2$ is proven to be a maximum.

Case 2: $x_1 \neq x_2$**.** In this case, the eigenvalues of He are necessarily of different signs and the determinant of He is negative, so that He is indefinite and no conclusions can be drawn for the curvature properties of $B_2(\mathbf{x})$.

As the Simpson-Index is locally concave in x_i only for $x_1 = x_2$ and not for all combinations of x_1 and x_2, the Hamiltonian will also not necessarily be jointly concave in the control and state variables on the whole domain. This makes a specific analysis of the equilibrium candidates necessary. A concave Hamiltonian (together with the condition of non-negative shadow prices) would ensure that a unique equilibrium exists that would necessarily be a maximum and thus part of an optimal solution. However, the non-concavity of the Hamiltonian requires a more subtle analysis here.

4.3 Analytical features of the model

When rearranging equations (8), one receives the value of y_i as the following function:

$$y_i = U_{y_i}^{-1}(\phi_i \lambda_i) = Y_i(\lambda_i) \quad \forall\, i = 1, 2 \tag{20}$$

Note that equation (8) requires that the shadow prices λ_i have to be positive in an optimal solution for all i. Inserting $y_i = Y_i(\lambda_i)$ into the growth functions in (6) and rearranging the terms of the conditions in (9), the equations of motion for the two state variables x_1 and x_2 and the two co-state variables λ_1 and λ_2 can be derived:

$$\dot{x_i} = G_i(\mathbf{x}) - \phi_i Y_i(\lambda_i) = \psi_i x_i (1 - \frac{\sum_{j=1}^{n} x_j}{\kappa}) - \phi_i U_{y_i}^{-1}(\phi_i \lambda_i) \quad \forall\, i \tag{21}$$

$$\dot{\lambda_i} = \lambda_i(\rho - G_{ix_i}) - B_{x_i} - \sum_{j \neq i} \lambda_j G_{jx_i} \quad \forall\, i \tag{22}$$

Conditions (21) and (22) describe the optimal dynamics of the system in state co-state space. To complete the necessary conditions for optimal solutions, the following transversality conditions are needed in addition to the initial conditions given in (5):

$$\lim_{t\to\infty} \lambda_{it} x_{it} e^{-\rho t} \geq 0 \quad \forall\, i \tag{23}$$

Setting $\dot{\lambda_1} = \dot{\lambda_2} = \dot{x_1} = \dot{x_2} = 0$, the general steady state conditions of the system read as follows:

$$\bar{x_i} = \frac{\phi_i Y_i(\bar{\lambda_i})}{\psi_i(1 - \frac{\sum_{j=1}^{n} \bar{x_j}}{\kappa})} \quad \forall\, i \tag{24}$$

$$\bar{\lambda_i} = \frac{B_{\bar{x_i}} + \sum_{j\neq i} \bar{\lambda_j} G_{j\bar{x_i}}}{\rho - G_{i\bar{x_i}}} \quad \forall\, i \tag{25}$$

To be able to solve these conditions analytically, it is assumed that the instantaneous utility function $U(\mathbf{y})$ takes on the form of the isoelastic function $U(\mathbf{y}) = ln(y_1) + ln(y_2)$. It follows that $Y_i(\lambda_i) = U_{y_i}^{-1}(\phi_i \lambda_i) = \frac{1}{\phi_i \lambda_i}$ for $i = 1, 2$. The steady state conditions then are given by:

$$\bar{x_1} = \frac{\phi_1 Y_1(\bar{\lambda_1})}{\psi_1(1 - \frac{\bar{x_1}+\bar{x_2}}{\kappa})} = \frac{1}{\bar{\lambda_1}\psi_1(1 - \frac{\bar{x_1}+\bar{x_2}}{\kappa})} \quad \Leftrightarrow \quad \bar{\lambda_1} = \frac{1}{G_1(\mathbf{x})} \tag{26}$$

$$\bar{x_2} = \frac{\phi_2 Y_2(\bar{\lambda_2})}{\psi_2(1 - \frac{\bar{x_1}+\bar{x_2}}{\kappa})} = \frac{1}{\bar{\lambda_2}\psi_2(1 - \frac{\bar{x_1}+\bar{x_2}}{\kappa})} \quad \Leftrightarrow \quad \bar{\lambda_2} = \frac{1}{G_2(\mathbf{x})} \tag{27}$$

$$\bar{\lambda_1} = \frac{B_{\bar{x_1}} + \bar{\lambda_2} G_{2\bar{x_1}}}{\rho - G_{1\bar{x_1}}} \tag{28}$$

$$\bar{\lambda_2} = \frac{B_{\bar{x_2}} + \bar{\lambda_1} G_{1\bar{x_2}}}{\rho - G_{2\bar{x_2}}} \tag{29}$$

Considering the system $(26 - 29)$, one can plug $\bar{\lambda_2}$ from equation (27) into equations (28) and (29) and solve the remaining three equations for $\bar{\lambda_1}$, each then depending only on $\bar{x_1}$ and $\bar{x_2}$. These functions can then be plotted as surfaces in a 3D diagram. The intersection of all three surfaces constitutes the equilibrium of the

system. The three resulting steady state conditions read as follows:

$$F_1 = \bar{\lambda_1} = \frac{1}{G_1(\mathbf{x})} \tag{30}$$

$$F_2 = \bar{\lambda_1} = \frac{B_{\bar{x_1}} + \frac{G_{2\bar{x_1}}}{G_2(\mathbf{x})}}{\rho - G_{1\bar{x_1}}} \tag{31}$$

$$F_3 = \bar{\lambda_1} = \frac{\frac{\rho - G_{2\bar{x_2}}}{G_2(\mathbf{x})} - B_{\bar{x_2}}}{G_{1\bar{x_2}}} \tag{32}$$

These equations represent isoclines in three dimensions. Note that an increase in λ_2 would shift the two isoclines (31) and (32) down, when depicting the isoclines in a 3D diagram with x_1 and x_2 at the base and λ_1 on the vertical axis. Equation (30) gives the combinations of x_1 and x_2 for which $\dot{x}_1 = 0$. Equation (31) gives the combinations for which $\dot{x}_2 = 0$ and $\dot{\lambda}_1 = 0$. Equation (32) gives the combinations for which $\dot{x}_2 = 0$ and $\dot{\lambda}_2 = 0$. The equilibria of the system are determined by the intersection of all three surfaces. As all three functions are non-linear, a graphical illustration of all three surfaces in a 3D diagram is not very clear. However, it is possible to depict the intersections of all three surfaces with one another in a contour plot in x_1-x_2 space. Equilibria occur where all three contours intersect. This is illustrated by a numerical example below.

4.4 Numerical example

This subsection presents a numerical example for a two-species renewable resource model with a biodiversity index. Parameter values used are presented in Table 1. Species 2 features a higher intrinsic growth rate than species 1 but the same carrying capacity. Moreover, species 2 is damaged less by the same level of economic activity than species 1.

Figure 1 depicts the intersections of the three isoclines in x_1-x_2 space. The red lines depict the intersections of the surfaces described by equations (31) and (32). The green and the blue lines depict the intersections of the surface described by equation (30) with the ones described by (31) and (32) respectively. The illustration

Parameter values					
ρ	0.01	ψ_1	0.04	ϕ_1	0.2
κ	100	ψ_2	0.10	ϕ_2	0.1

Table 1: Parameter values for Model 1 with $\omega = 2$ and $n = 2$.

shows that only one real-valued equilibrium exists. The corresponding steady state values are given in Table 2. The eigenvalues of the Jacobian of the dynamic system evaluated at the steady state values have been computed. Two eigenvalues are positive while the other two are negative, which reveals that the determinant of the Jacobian is negative and shows that the steady state is a saddle.

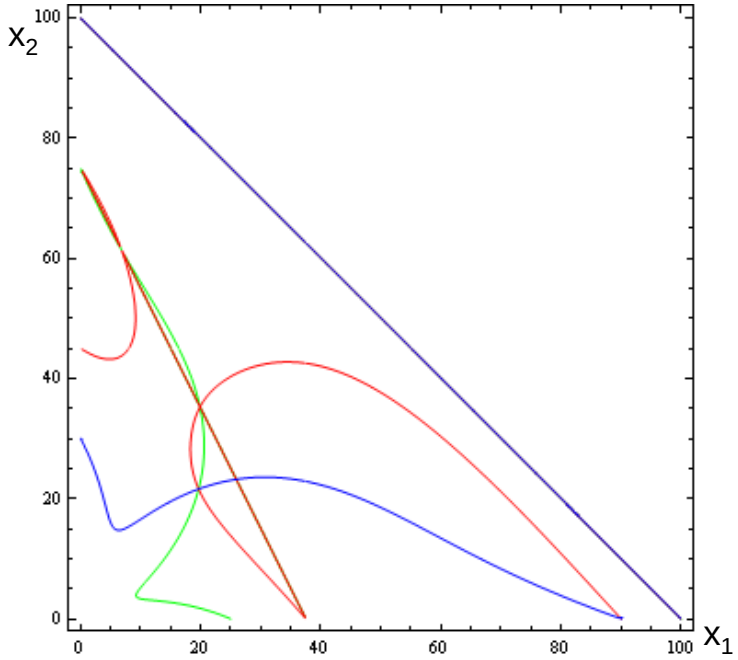

Figure 1: Contour plot: Intersections of the three isoclines in x_1-x_2 space.

Note that the steady state stock $\bar{x}_2$ is larger than $\bar{x}_1$, but that the two stocks are very evenly distributed. This results in a high steady state value of the biodiversity index, $\bar{B}_2$. Note also that $\bar{y}_2$ is much higher than $\bar{y}_1$, which is due to the fact that the damage coefficient ϕ_2 and the steady state shadow price $\bar{\lambda}_2$ are smaller than ϕ_1 and $\bar{\lambda}_1$ respectively. The shadow prices depend among other things on the marginal value of the biodiversity index $B_{\bar{x}_i}$. As $\bar{x}_1 < \bar{x}_2$, it directly follows that $B_{\bar{x}_1} > 0$ while

Steady state values			
$\bar{x}_1$	19.6457	$\bar{y_1}$	2.3084
$\bar{x}_2$	21.6043	$\bar{y_2}$	12.6925
$\bar{\lambda}_1$	2.1660	$\bar{B}_2$	1.9955
$\bar{\lambda}_2$	0.7879		

Table 2: Steady State values for Model 1 with $\omega = 2$ and $n = 2$.

$B_{\bar{x}_2} < 0$, which influences the shadow prices in the way that $\bar{\lambda}_1 > \bar{\lambda}_2$.

As the biodiversity index is not concave for all combinations of x_1 and x_2, it is necessary to explicitly check the sufficient conditions for the steady state to be a maximum. In order to do so, the Hessian matrix of the current-value Hamiltonian evaluated at the steady state values is analyzed in the following:

$$Hessian(H^c) \mid_{stst} = \begin{pmatrix} -0.1877 & 0 & 0 & 0 \\ 0 & -0.0062 & 0 & 0 \\ 0 & 0 & -0.0045 & 0.0006 \\ 0 & 0 & 0.0006 & -0.0035 \end{pmatrix} \tag{33}$$

The four eigenvalues of this Hessian are: $(-0.1877, -0.0062, -0.0048, -0.0032)$. The determinants of the leading principal minors are: $Det_1 = -0.1877$, $Det_2 = 0.0012$, $Det_3 = -5.25 \times 10^{-6}$, and $Det_4 = 1.77 \times 10^{-8}$. It can be observed that all four eigenvalues of the Hessian are negative and that the signs of the leading principal minors alternate, starting with a negative sign of Det_1. Consequently, the current-value Hamiltonian is concave at the steady state. Moreover, both shadow prices are necessarily positive in steady state. As a result, sufficient optimality conditions are fulfilled, which proves that there is a unique optimal steady state that solves the dynamic system. Also note that the off-diagonal elements of the Hessian are very close to zero, while all diagonal elements of the Hessian are negative. Sufficient optimality conditions will be fulfilled as long as this is the case and the off-diagonal elements of the Hessian are sufficiently close to zero.

4.5 Comparison to a model with a strictly increasing, concave utility function

This subsection compares the results derived in subsection 4.4 with those derived in a model where increases in the stocks of the living resources always positively add to the value derived from the existence of these resources. That is, it compares the results derived so far to the case where $B_{x_i} > 0$ holds for both living resources at all times and independently of relative stock sizes and where $B(\mathbf{x})$ is strictly concave in x_1 and x_2. To exemplify this, consider the following utility function:

$$B_{new}(x_1, x_2) = \frac{ln(x_1) + ln(x_2)}{8} + \frac{3}{4} \tag{34}$$

The first partial derivatives of $B(\mathbf{x})$ with respect to both stock sizes are now positive for all possible combinations of stock sizes. Moreover, the function is strictly concave for all x_1 and x_2. This concrete functional form of the utility function has been chosen to make it comparable to the biodiversity index. Its values are confined to the interval $[1, 2]$, which also holds for the biodiversity indices for $n = 2$.

The utility function (34) has been substituted into the maximization problem (4-6) instead of the biodiversity index in order to compare results. For comparison, the model presented in subsection 4.4, which incorporates the biodiversity index, is referred to as the first or the "non-concave" model while the model presented in this subsection is referred to as the second or the "concave" model. Solutions for the real-valued equilibrium values of the concave model are given in Table 3. The arrows indicate the change with respect to the results derived in the non-concave model. The value given in the last row of Table 3, $\bar{B}_2$, is the steady state value of the Simpson-Index. Note that this biodiversity index had not been considered in the welfare maximization problem here, so $\bar{B}_2$ represents ex-post biodiversity, observed after the maximization with the new utility function. Applying the new utility function implies that both parts of the welfare function, i.e. $U(\mathbf{y})$ and $B_{new}(\mathbf{x})$, are now strictly concave on the whole domain so that the current-value Hamiltonian is also jointly concave in the control and state variables. Moreover, optimality conditions require

that both shadow prices are positive in equilibrium. The properties of the Hessian matrix of the current-value Hamiltonian have also been analyzed. As expected, all eigenvalues of the Hessian are negative. Consequently, the steady state fulfills the usual sufficient optimality conditions.

Steady state values					
$\bar{x}_1$	18.6029	$\downarrow$	$\bar{y}_1$	2.0573	$\downarrow$
$\bar{x}_2$	26.1029	$\uparrow$	$\bar{y}_2$	14.4334	$\uparrow$
$\bar{\lambda}_1$	2.4304	$\uparrow$	$\bar{B}_2$	1.52317	$\downarrow$
$\bar{\lambda}_2$	0.6928	$\downarrow$			

Table 3: Steady State values for Model 2 with $B_{new}(x_1, x_2)$ and n=2

Comparing the steady values of concave model presented here to that of the non-concave model, one can see that the steady state stock of the more abundant species, $\bar{x}_2$, increased, while that of the less abundant species, $\bar{x}_1$, decreased. This implies that the distribution of species abundances has become more uneven. In both model settings, restrictions on the shadow prices imply that both $\bar{\lambda}_1$ and $\bar{\lambda}_2$ have to be greater than zero in steady state. In the second model setting, the shadow price of the more abundant species, $\bar{\lambda}_2$, decreased and the corresponding control variable, $\bar{y}_2$, increased. The increase in $\bar{y}_2$ directly follows from the decrease in $\bar{\lambda}_2$ as $\bar{y}_2 = \frac{1}{\phi_2 \bar{\lambda}_2}$. The inverse holds in analogy for the shadow price and the control variable corresponding to the less abundant steady state stock, $\bar{x}_1$.

Most importantly, the solution in the second model setting does no longer depend on *relative* stock sizes. This implies that the evenness of the distribution of species abundances no longer matters for optimization. Instead, now the absolute abundances of the living resources are important. The result is that the ex-post value of the Simpson-Index decreases considerably. While the Simpson-Index takes on a value of nearly 2 in the first example, it now declines to approximately 1.5. On the other hand, it can be observed that the total number of individuals in steady state, i.e. $\bar{x}_1 + \bar{x}_2$, increases by 8.5% from 41.2 to 44.7. This result confirms expectations that the choice of the utility function influences the degree of evenness in the distribution of relative species abundances in steady state. Choosing a strictly

increasing, concave utility function induces steady states with lower evenness and thus with lower biodiversity in a setting with a given number of species n.

5 Discussion and conclusion

Biodiversity is often only considered in terms of species richness. Doing so implies that biodiversity loss only occurs when a species becomes extinct (Baumgärtner, 2007). This decline in species richness tends to receive special attention because species extinction is irreversible. Conserving species therefore means preserving a real option value in the sense that the function of a certain species and its contribution to ecosystem services, which might not be known today, will still be available in the future (Heal, 2004). However, Chapin et al. (2000) point out that "human activities influence the relative abundances of species more frequently than the presence or absence of species". They emphasize that changes in species evenness respond more quickly to human interference than changes in species richness do and that changes in species evenness have a vital impact on ecosystems and their functioning long before a species is threatened by extinction (Chapin et al., 2000). So, more generally, biodiversity loss can also occur when relative species abundances change.

Consequently, the aim of this paper is to set up a model that introduces a biodiversity index that accounts for both species richness and evenness in an optimal control model. The model includes two living resources which grow according to a logistic growth function but which compete with one another for the same external resource that sustains their growth. Moreover, both living resources are damaged by an economic activity according to a damage parameter. The economic activity yields a net benefit represented by a utility function that is strictly increasing and jointly concave in the controls. Biodiversity is introduced into the model by using a function that reflects the utility derived from the existence of the two living resources. In a first setting, this utility is represented by the Simpson-Index, a biodiversity index widely accepted by ecologists. In a second setting, this utility is represented by a monotonically increasing, concave utility function. Thus, the application of an ecological concept that accounts for the role of evenness in ecosystems can be compared

to that of an economic concept that emphasizes the role of absolute abundances for utility. To my knowledge, this is the first paper that studies the effects of introducing such a biodiversity index into an optimal control model and compares its application to that of a monotonically increasing, concave utility function.

When using the biodiversity index, the signs of the marginal utilities of the resource stocks are necessarily of opposite signs as long as $x_1 \neq x_2$. As a consequence, the marginal utility of the less abundant species is positive, while that of the more abundant species is negative. Moreover, the biodiversity index is locally concave only for $x_1 = x_2$ but not on the whole domain. This could induce non-concavity of the current-value Hamiltonian. However, this paper shows that it is possible to derive a unique equilibrium that satisfies sufficient conditions for a welfare maximum in spite of using a non-concave function to express the utility derived from the existence of the living resources. In addition, the analysis presented indicates that the properties of the biodiversity index crucially influence the equilibrium of the model. Once biodiversity is considered in the optimization problem, the stock sizes are distributed more evenly in steady state. This in turn implies that using a monotonically increasing, concave function to express the utility of the living resources induces an equilibrium with lower species evenness and thus with lower biodiversity.

Several limitations apply to the simple model presented in this paper. Firstly, the economic activity that yields utility via the utility function $U(\mathbf{y})$ is not modeled in much detail. A natural extension of the model would be to consider benefits and costs of this activity separately. One would then also be able to contrast the decision of a private economic agent, say a company, that does not care for biodiversity, with the decision of a social planner who takes biodiversity into account. Consequently, such a set-up would allow us to determine efficient policy measures, e.g. an optimal tax on the economic activity, in order to internalize external damages.

Secondly, one could argue that the flexible control approach presented in this paper is not fully realistic because damages caused by economic activities and inflicted upon living resources cannot be controlled separately. However, a more rigid control approach with only one control variable would complicate the analysis and cause problems that would divert attention from the effects of introducing the biodi-

versity index to the model. In a setting with two species, using a more rigid control approach would allow for one shadow price to be negative as long as the other one is positive and sufficiently large. This leads to the appearance of several steady states, no matter whether one uses the biodiversity index or the concave, monotonically increasing utility function in the maximization framework. Moreover, it would be harder to prove sufficient optimality conditions. Consequently, the more flexible control approach has been chosen here to show in a relatively simple but clear setting that the biodiversity index can be used to express the non-use values derived from the existence of living resources in order to determine a unique and optimal steady state of the system.

Thirdly, the model in this paper does not include spatial aspects. Living resources are not static but continuously change their location. In particular, they can wander between sites affected by the economic activity and e.g. protection sites. Consequently, possible extensions include the consideration of site selection and site preservation. All this is deferred to future research.

In spite of these limitations, the paper presents important insights into how considering biodiversity indices influences the optimal solution of multiple-species optimal control models. It can be seen as a starting point for further research building richer models and addressing the mentioned limitations.

Acknowledgements: I thank Stefan Baumgärtner, Thomas Lontzek, Daiju Narita, Martin Quaas and Katrin Rehdanz for helpful comments and discussion. The German Research Foundation (DFG) provided welcome financial support through the Cluster of Excellence "The Future Ocean". All errors and opinions are mine.

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