Environment and Development Economics 2 (1997): 145–172
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Wildlife, biodiversity and trade*

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ABSTRACT. This article develops a model of wild-resource exploitation that includes both the standard bioeconomic properties of growth and harvesting and a species–area relationship linked to habitat conversion. The model is developed for both a closed and an open economy. In the closed-economy model the characteristics of the long-run equilibrium are analysed in three versions of the model: the basic bioeconomic model, the inclusion of habitat conversion and the addition of biodiversity value. In the case of the open-economy model, we also examine the potential effects of trade interventions on the optimal exploitation of species and habitat conversion in the long run. The results confirm that the inclusion of habitat conversion as well as biodiversity value in a model of wild-resource exploitation yields significantly different outcomes than a basic bioeconomic model.

1. Introduction

The world's remaining natural areas and habitats for wild species are believed to be located mainly in the developing regions of the world. However, the demand for resources and land to meet the needs of growing populations and developing economies has resulted in many of these wild resources and wildlands coming under threat. At the same time, it is economically feasible and worthwhile to maintain some natural areas broadly in their original state and to conserve wildlife species while allowing important human uses of these resources (Swanson and Barbier, 1992). Sustainable management regimes can be extremely diverse, ranging from commercial wildlife ranching and harvesting to non-timber forest product extraction to community-based wildlife and wildlands development to tourism and recreation, and so on. They may take the form of traditional uses of wild resources by local communities (IIED, 1994). Alternatively, they may be deliberate attempts to reconcile conservation and development aspirations through integrated community-based development projects (Wells and Brandon, 1992) or through major international

* Paper prepared for the European Association for Environmental and Resource Economics Sixth Annual Conference, Umeå, Sweden, 17–20 June 1995. We are grateful for comments by Rögnvaldur Hannesson, Charles Perrings and three anonymous referees; however, the usual disclaimer applies.

https://doi.org/10.1017/S1355770X97000144 Published online by Cambridge University Press

aid programmes such as biodiversity reserves funded by the Global Environmental Facility (Munasinghe, 1993).

Economics clearly has an important role to play in the assessment of the 'sustainable' exploitation and management of wildlife and wildlands. However, it is important to recognize two facets to the economic analysis of optimal exploitation of wildlife species. First there is the familiar bio-economic problem of determining the long-run optimal harvest or use rate, given certain characteristics of the population dynamics of wild species, such as their growth or regeneration rates. This approach does not include any cost for land (or sea) used as habitat, and is particularly appropriate in the analysis of intertemporal allocation of marine resources for which it was originally developed (Clark, 1976). It is less applicable to allocation decisions involving terrestrial wildlife resources, which require determination of not only the optimal stock and harvesting rate of species biomass but also the optimal size or area of the natural habitat that maintains the species (Swanson, 1994).

Thus a second important facet to the economics of wildlife use or exploitation is the optimal allocation of natural habitat. To determine the optimal size or area of habitat, it is necessary to compare the benefits of maintaining habitat with its opportunity costs, which are none other than the forgone economic activities dependent on the conversion of natural habitat to other uses (Swanson and Barbier, 1992; Barrett, 1993). However, knowledge of the optimal area to be preserved as natural habitat alone still gives us only half the story; it tells us nothing about the optimal rate of exploitation of those species found within the preserves. Thus, if we are interested in the possibility of sustainable utilization of species beyond either their complete preservation in a biosphere reserve or only their non-consumptive uses such as for tourist viewing, then we must consider the problem of optimal habitat provision and species exploitation together.

There are two additional dimensions to the problem that are worth considering: the role of trade interventions to promote sustainable management, and the wider social values of biodiversity as a public good for humankind. Although many wild resources are used locally, some products of natural areas are important traded goods, e.g. wildlife products (skins, horns, ivory and even the animals themselves), timber logs and products (tropical hardwoods) and non-timber products (rattan, honey, resins, etc.). In recent years, trade interventions imposed either unilaterally or through multilateral agreements have been proposed to control overexploitation of the traded products derived from wild resources and thus to encourage their sustainable management within developing countries (Barbier *et al*., 1990; Burgess, 1994). Environmental pressure groups in major importing countries are also advocating sanctions and interventions in the tropical timber trade as a means of coercing producer countries into reducing tropical deforestation and the consequent loss of environmental values (Barbier *et al*., 1994).

However, in addition to their direct use or exploitation, the wild species and resources contained in the natural areas of developing countries are also considered to have wider social values that are usually linked to stock size, not the harvesting size. These values are diverse, and could include

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Table 1. *Various valuation estimates for non-consumptive uses of wild resources in developing countries (US$)*

Activity	*Estimated net present value*
Viewing value of elephants, Kenya (Brown and Henry, 1993)	$25,000,000/year
Ecotourism, Costa Rica (Tobias and Mendelsohn, 1990)	$1,250/ha
Tourism, Thailand Research/education, Thailand (Dixon and Sherman, 1990)	$385,000–860,000/year $38,000–77,000/year
Tourism, Cameroon Genetic value, Cameroon (Ruitenbeek, 1989)	$19/ha $7/ha
Eco-tourism, Madagascar (Kramer, 1993)	$800,000–2,160,000
Net private return to pharmaceutical prospecting, Costa Rica (Barbier and Aylward, 1996)	$4,810,000/product
Impact on crop productivity of pest control by Anolis lizard, Greater and Lesser Antilles (Narain and Fisher, 1994)	$670,000/year in lost output per 1% decline in population

the non-consumptive uses of species (e.g. for tourism, recreation and scientific study); their ecological functional role that may indirectly support or protect economic activity (control of pests, genetic diversity, improving productivity); their potential future use values (option and quasi-option values); and their non-use or pure 'existence' value. Various studies indicate that non-consumptive use and ecological values of wild species and resources can be significant and, if captured by a developing country, could make an important contribution to overall welfare (see Table 1). Some of these values are attributed to a single species, but in many cases it is the entire stock of species in a wild area and its inherent diversity, or biodiversity, that are the source of value. Moreover, many important social values of biodiversity may be underestimated at present, as there is a lot we still do not know about the potential ecological role of species and biodiversity in supporting ecosystem functioning and 'resilience' (Holling *et al*., 1995).

This article attempts to integrate some of these concerns by developing a model of wild or natural species exploitation that extends the traditional bioeconomic model for renewable resources to include conversion of habitat and the wider social value of biodiversity. The model is developed for both a closed and an open economy. In the case of the closed economy we demonstrate how extending the bioeconomic model of species exploitation to account explicitly for the opportunity costs of habitat conservation plus any non-consumptive biodiversity values produces a different optimal extraction for wild species than if only the harvesting problem were considered. The open-economy model is an extension of this model, and is

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used to examine the potential effects of trade interventions on the optimal exploitation of species and habitat conversion in the long run, as a means of determining whether such interventions can encourage less exploitation of wild resources.

2. Basic model of species exploitation and habitat conversion

In the following model we assume that the key allocation problem is to determine the optimal stock and rate of exploitation of wild species or resources, given that this total resource stock is a function of a natural rate of population growth or regeneration, harvesting and the total area of natural habitat or 'wildlands'. To do this, we combine a standard bioeconomic model of species exploitation with an approach developed by Barrett (1993), which was used principally to determine the optimal allocation of habitat between preservation and conversion to other economic uses.[1] Our approach requires setting up the problem so that both the biological growth of populations and changes in habitat area affect the aggregate stock of species.

For example, let $S(t)$ be the total stock of species (wild resources) comprising the various populations or species found in a given area, aggregated in some appropriate way.[2] This aggregate stock will consist of many animal and plant populations with the capacity for reproduction and growth. As these populations regenerate and grow, so must the aggregate stock of these populations, $S(t)$. However, the size of $S(t)$ will also be affected by the total number of species comprising this aggregate stock, and as research from island biogeography indicates, the total number of species should be related to the total area of habitat available to these species. For our model, this implies that changes in habitat area will affect the total number of species, and hence determine changes in the total species stock, $S(t)$. We therefore introduce an important modification to the standard bioeconomic model: changes in the total species stock are not only determined by the aggregate biological growth rate across these species, but are also affected by the expansion in the number of species as the size of the natural area or habitat changes. Finally, we assume that changes in the total species stock, $S(t)$, must be net of any such harvesting offtake.

Thus, defining $A(t)$ as the total area of natural habitat or wildlands, and $y(t)$ as the aggregate rate of harvest of species or 'wild' resources, then the change in total species stock, $dS(t)/dt$, can be depicted as

$$\frac{dS(t)}{dt} = \dot{S} = G(S(t),A(t)) - y(t) = G_1(S(t)) + G_2(A(t)) - y(t). \qquad (1)$$

That is, change in the total species stock is determined by a growth func-

[1] Barrett (1993) does not include the bioeconomic growth of the species stock or harvesting from this stock in his habitat allocation model.

[2] For example, the stock of species could be aggregated by the number of individuals in each distinct population or species. Alternatively, the total 'biomass' of each population or species could be aggregated across all species. Some form of 'weighted average' combination of the two approaches could also be employed.

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tion, G, which is in turn a function of the size of the stock, $S(t)$, and the total habitat area, $A(t)$, as well as the total offtake, $y(t)$. We assume that the growth function G is additively separable into subcomponents G_1 and G_2. This separability condition facilitates our ability to depict our results graphically in a two-dimensional (S,y) space. The assumption of separability is not essential to our main results, however. In Appendix 2 we illustrate this with an alternative formulation of the allocation problem that includes a non-separable version of the growth function, G.

In Equation (1) $G_1(S(t))$ can be defined as the aggregate growth or regeneration function of the total species stock.[3] This function is assumed to display the standard bioeconomic properties: G_1 is defined over the interval $S(t) \geq 0$, and there exist values $\underline{S} < S_{max}$ such that $G_1(\underline{S}) = G_1(S_{max}) = 0$ and $d^2G_1(S(t))/dS(t)^2 < 0$.

However, $G_2(A(t))$ is an additional component to the standard bioeconomic properties of a renewable-resource growth function. G_2 represents the growth in total species stock that is attributable to an expansion in the number of species based on a species–area relationship. The basic premise of this relationship is that the total number of species found in a given habitat will increase with the size or area of the habitat. Originally developed through the study of island biogeography, species–area relationships were initially employed to estimate the number of species in biologically diverse habitats such as tropical forests. Now, however, such curves are being used to forecast the extent of species loss associated with current trends in tropical deforestation. As noted by Barrett (1993), a typical species–area relationship employed by ecologists is

$$S(t) = \alpha A(t)^{\beta} \quad \text{or} \quad A(t) = \alpha^{-1/\beta} S(t)^{1/\beta}, \quad 0 < \beta < 1. \tag{2}$$

The parameter α may depend on the type of species, its population density and the biogeographic region. The parameter β determines the shape of the species–area curve, and for most regions of the world has been estimated to range between 0.16 and 0.39 (Lugo *et al.*, 1993). Although β has been observed to increase as habitat area becomes smaller, in the following model we assume it to be fixed.[4] As shown in Equation (2), by inverting the species–area relationship one can also determine the habitat area required to maintain a given number of species.

[3] It is possible that G_1 is aggregated from individual species' growth rates in some meaningful way, such as taking the weighted average of growth rates across all the species comprising the total species stock at time t. Alternatively, G_1 could be simply the observed aggregate growth rate of the total species stock at time t.

[4] Precise estimation of the species–area curve has become an important and controversial issue in ecology, given the tendency to use such curves to predict species extinction associated with tropical deforestation. In particular, the value of β can have a significant impact on such estimates. For example, if β is assumed to be low ($<$20%), then the relationship predicts that more than 50% of the land area can be deforested before additional deforestation results in rising rates of extinction. Conversely, at high values for β ($>$60%), extinction rates are almost proportional to deforestation rates. For further discussion see Lugo *et al.* (1993).

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Ignoring G_1 in Equation (1) for the moment, following Barrett's approach we can determine from (2) the growth in the total species stock that is attributable to the effect of a change in habitat area on the species–area relationship.

$$\begin{aligned} G_2(A(t)) &= \beta\alpha A(t)^{\beta-1} r(t), \quad \text{where } r(t) = dA(t)/dt = \dot{A} \\ &= \beta\alpha^{1/\beta} S(t)^{(\beta-1)/\beta} r(t) \\ &= aS(t)^{-b} r(t), \quad \text{where } a = \beta\alpha^{1/\beta} \quad \text{and } b = (1-\beta)/\beta > 0. \end{aligned} \tag{3}$$

Thus Equation (3) suggests that the growth in total species stock attributed to the species–area relationship can be expressed in terms of the rate of change in habitat area, $r(t)$, and the size of the total stock, $S(t)$. It therefore follows that (1) can be rewritten as

$$\dot{S} = G(S(t),A(t)) - y(t) = G_1(S(t)) + aS(t)^{-b} r(t) - y(t). \tag{1'}$$

Equation (1′) is the basic equation of motion of our model, which links changes in the total stock of species, or wild resources, to biological growth, habitat area, and harvesting offtake.

As noted in the previous section, in developing countries the main threat to natural habitat is conversion to other economic activities. Again, following Barrett (1993) this can be incorporated in our model. Let $D(t)$ be defined as the total developed area arising from conversion of natural habitat, then

$$D(t) = D_0 + \int_0^t r(\tau)d\tau = D_0 + A_0 - A(t), \tag{4}$$

if the total land area is fixed and $r(t) \leq 0$. That is, natural habitat is converted into land used for other activities at the rate $r(t)$ over time. This implies that $r(t)$ is non-positive in Equation (1′). Conversion of habitat occurs because the resulting economic activities produce goods and services for consumption, which in turn contributes to economic welfare.[5] Let $F(D(t))$ be the aggregate production function for economic activities dependent on converted land, which is assumed to have the normal properties $dF(D(t))/dD(t) > 0$ and $d^2F/dD(t)^2 < 0$. It therefore follows that from (2) and (4)

$$F(D(t)) = F(D_0 + A_0 - \alpha^{-1/\beta} S(t)^{1/\beta}) = f(S(t)), \tag{5}$$

with $df/dS(t) < 0$ and $d^2f/dS(t)^2 < 0$ for $0 < \beta < 1$. That is, an increase in the total species stock due to an expansion in the number of species has an increasingly negative impact on aggregate production of output from converted habitat land. This is not surprising, given that the species–area relationship suggests that the number of species can increase only if there

[5] We ignore any windfall gain from the conversion.

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is more habitat area, which of course implies less converted land and a corresponding fall in aggregate output from this land.

Finally, if we assume that all output is consumed and that total consumption, $c(t)$, can be defined as $c(t) = F(D(t)) = f(S(t))$, then we can take into account explicitly in the social utility function of the country the trade-off between, on the one hand, the harvesting or utilization of wild species from their conserved natural habitat and, on the other, the conversion of habitat land to produce other commodities. This trade-off can be further elaborated if we assume also that any positive stock externalities, or biodiversity values, associated with $S(t)$ enter directly into our utility function. Defining the latter as U, then

$$U = U(y(t),c(t),S(t)), \tag{6}$$

which is assumed to be additively separable and to have the standard properties with respect to its partial derivatives, $\partial U/\partial i > 0$, $\partial^2 U/\partial i^2 < 0$ and $\lim_{i\to 0} \partial U/\partial i \to \infty$, $i = y(t)$, $c(t)$, $S(t)$. It is clear from all the above relationships (1)–(6) that an increase in consumption and its consequent social benefits must occur at the expense of the gains from additional harvesting of wild species and biodiversity values.

Equations (1)–(6) represent the basic relationships of the model. In the next two sections we analyse formally the intertemporal allocation problem assuming closed and open economy conditions respectively. In the following optimal control problems, notation is simplified by omitting the argument of time-dependent variables, by representing a derivative of a function by its prime, by employing numbered subscripts to indicate partial derivatives of a function, and by denoting the time derivatives of a variable by a dot.

3. Closed-economy model

We initially assume a closed-economy model. This may be a realistic representation of the problem if all consumption from converted land and harvesting of wild species are non-tradable commodities. We relax this assumption in the next section. Our principal aim in developing the closed-economy model is to demonstrate explicitly how the inclusion of the opportunity costs of habitat conversion plus any non-consumptive value of biodiversity in a bioeconomic model of species exploitation affects the equilibrium stock and thus the optimal harvesting path.

The developing country is assumed to maximize the present value of future welfare, W,

$$Max_y\ W = \int_0^\infty [U(y,c,S) - w(S)y]e^{-\delta t}dt, \tag{7}$$

subject to (1′) and (5). Let $w(S)$ be defined as the unit social cost of harvesting, with $w' \leq 0$ and $w'' \geq 0$, and $\delta > 0$ be the social discount rate. For simplicity, we assume that the rate of land conversion, $r(t) \leq 0$, is a constant which we define as $-r$. Finally, the initial and terminal boundaries of

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the state variable, S, are respectively $S(0) = S_0$ and $\lim_{t\to\infty} S(t) \geq 0$. We exclude the situation with total conversion of the habitat.[6]

The current-value Hamiltonian of the above problem is

$$H = U(y, f(S), S) - w(S)y + \lambda [G_1(S) - aS^{-b} r - y], \tag{8}$$

where the co-state variable λ can be interpreted as the shadow price of the total species stock, S. Assuming an interior solution, the first-order conditions of the control problem are

$$dH/dy = U_y - w(S) - \lambda = 0 \quad \text{or} \quad U_y = w(S) + \lambda \tag{9}$$

$$-dH/dS = \dot{\lambda} - \delta\lambda \quad \text{or} \quad \dot{\lambda} = (\delta - G_1' - baS^{-(b+1)}r)\lambda + yw' - U_c f' - U_S \tag{10}$$

$$dH/d\lambda = \dot{S} = G_1(S) - aS^{-b}r - y. \tag{11}$$

Condition (9) indicates that, along the optimal trajectory, the marginal benefit of harvesting or utilizing wild species for domestic consumption, U_y, must equal its marginal cost, which consists of marginal harvesting costs, $w(S)$, as well as the marginal costs of stock depletion, λ. Condition (11) simply recovers Equation (1′) for determining the change in the total species stock, which we have discussed above. Finally, condition (10) resembles the standard renewable resource dynamic condition for denoting the change in the value of the stock of wild resources, S, but it includes not only the standard (net) marginal bioeconomic costs for retaining species, $(\delta - G_1')\lambda + yw'$, but also the net marginal benefits of 'holding on' to land as habitat, $-baS^{-(b+1)}r\lambda - U_c f'$, and the marginal social value of an additional unit of the total species stock, U_S. As this condition is important for the analytical results of our model, we state its interpretation formally as

PROPOSITION 1. *Along the optimal path the rate of change in the shadow price of the total species stock,* $d\lambda/dt$, *equals the difference between the marginal 'bioeconomic' costs of holding on to an additional unit of the total species stock,* $(\delta - G_1')\lambda + yw'$, *less both the marginal net benefits of holding on to natural habitat for that additional unit of total stock,* $-baS^{-(b+1)}r\lambda - U_c f'$, *and the marginal social value of that additional unit,* U_S.

The long-run equilibrium for the closed economy can be determined by assuming that in the steady state the shadow price of the stock of wild resources, the rates of harvesting and land conversion, and the total species stock are constant: $d\lambda/dt = dy/dt = r = dS/dt = 0$. From the first-order conditions, the long-run equilibrium can be characterized as

[6] Equation (7) includes the opportunity cost of land in the developed sector, and additionally the assumption that the unit cost function, $w(S)$, represents the contribution of harvest to costs.

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$$\delta = G_1' + \frac{[-yw' + U_c f' + U_S]}{[U_y - w(S)]} \quad \text{for} \quad \dot{\lambda} = \dot{y} = r = \dot{S} = 0 \tag{12}$$

$$y = G_1(S) \quad \text{for} \quad \dot{S} = r = 0. \tag{13}$$

Equation (12) is the standard long-run equilibrium for holding on to renewable resources, but in this case with some important modifications. This is best seen by interpreting the different components on the right-hand side of (12). Let

$$R_1(S,y) \equiv G_1' + \frac{-yw'}{[U_y - w(S)]} > 0 \tag{14}$$

$$R_2(S,y) \equiv \frac{U_c f'}{[U_y - w(S)]} < 0 \tag{15}$$

$$R_3(S,y) \equiv \frac{U_S}{[U_y - w(S)]} > 0. \tag{16}$$

Then it follows that R_1 is the standard marginal net 'bioeconomic' return for holding on to species, R_2 is the (relative) marginal opportunity cost of holding on to land as natural habitat for wild species, and R_3 is the (relative) marginal non-consumptive value of biodiversity. If a solution exists for the long-run equilibrium, then it suggests

PROPOSITION 2. *In a closed economy, the equilibrium total species stock,* S*, *is determined by equating the social discount rate,* δ, *and bioeconomic returns net of the opportunity cost of natural habitat plus the non-consumptive value of biodiversity,* $R_1 + R_2 + R_3$.

To verify Proposition 2 it is necessary to determine whether an optimal saddle path and solution exist for the long-run equilibrium characterized by Equations (12) and (13). For our purposes, it is useful to conduct this analysis of the long-run equilibrium in stages, using three versions of the model: the basic bioeconomic model, the inclusion of habitat conversion, and the addition of biodiversity value. As will become evident, each version has different implications for the optimal long-run stock of wildlife species and harvesting rates in the closed economy. The derivation of the results is shown in Appendix 1, and the results are summarized below.

Case 1. Bioeconomic model ($\delta = R_1$*)*

We begin with the basic bioeconomic model with no costs of holding onto land as habitat and no positive stock externalities associated with biodiversity, i.e. $R_2 = R_3 = 0$. As indicated in Appendix 1, the result is a standard modification of the conventional bioeconomic harvesting model, where

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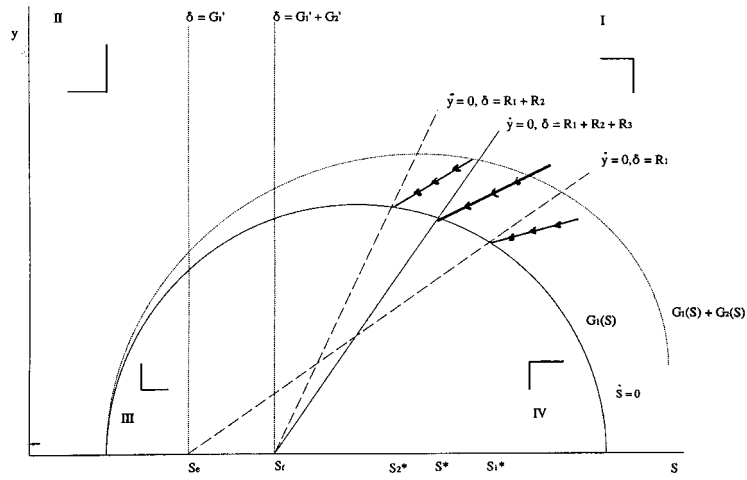


Figure 1. *The long-run equilibrium of the closed economy.*

the optimal steady-state species stock is determined by equating the social discount rate and bioeconomic returns net of harvesting costs that vary with stock size.

The locally stable equilibrium (S_1^*, y_1^*) for case 1 is depicted in Figure 1. An optimal trajectory is represented graphically, assuming $G_1' < 0$ and $S_0 > S_1^*$. Note that for any $y_1^* > 0$ it follows that $S_1^* > S_e$, i.e. the equilibrium level of wild-species stock in case 1 must lie to the right of the vertical $\delta = G_1'$ curve in Figure 1. This result is caused by the decreasing unit costs as the stock increases. We therefore note that if in our closed-economy model there is no opportunity cost of holding on to land as natural habitat and if there is non-consumptive value of biodiversity, then we obtain

PROPOSITION 2.1. *In a closed economy if* $R_2 = R_3 = 0$, *there exists an equilibrium harvesting rate* $y_1^* > 0$ *such that equilibrium total species biomass stock occurs to the right of* $\delta = G_1' > 0$, *i.e.* $S_1^* > S_e$.

Case 2. Habitat conversion model ($\delta = R_1 + R_2$)

In this version the basic bioeconomic model is extended to include the costs of habitat conversion, i.e. R_2 of Equation (15). As shown in Figure 1 and demonstrated in Appendix 1, S_2^* and y_2^* are the new equilibrium levels of total species biomass and harvesting respectively. Corresponding to these values must be an equilibrium level of natural habitat area, A_2^*. Appendix 1 indicates that the equilibrium of case 2 is a saddle point for an upward-sloping $dy/dt = 0$ curve. In Figure 1, the optimal trajectory assuming $G_1' < 0$ and $S_0 > S_2^*$ is shown.

In Appendix 1 the equilibria of cases 1 and 2 are compared, and the result suggests that $S_1^* > S_2^* > S_f > S_e$, i.e. the equilibrium level of wild-species stock in case 2 must be less than that derived in case 1. Intuitively, the reasoning is fairly straightforward: now that there is an opportunity

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cost for holding on to land as natural habitat, in the long run a smaller total stock of species will be maintained.

This result is an important modification of the standard bioeconomic model of renewable resource utilization. We have suggested that the growth in total species stock is dependent not only on the natural biological regeneration rate of species, but also on the total number of species in a given habitat area. However, holding land as a natural habitat also implies an opportunity cost, which in our case 2 version of the model is represented by forgone consumption from development activities that use converted habitat land. Because conventional bioeconomic models do not take explicitly into account the opportunity of maintaining 'wild' lands as habitat for species, the equilibrium level of species stock—and thus implicitly habitat area—is higher than if the opportunity cost of maintaining habitat were included. Consequently, this outcome can be stated more formally as

PROPOSITION 2.2. *In a closed economy if* $R_3 = 0$, *there exists an equilibrium harvesting rate* $y_2^* > 0$ *such that equilibrium total species stock occurs to the right of* $\delta = G_1' + G_2' > 0$ *but is less than the equilibrium stock of the bioeconomic model, i.e.* $S_1^* > S_2^* > S_f > S_e$.

Case 3. Inclusion of biodiversity value ($\delta = R_1 + R_2 + R_3$)

Finally, we extend the model to include $S(t)$ in the social utility function to represent the stock externalities associated with non-consumptive biodiversity values, thus arriving at the original optimal control problem and corresponding first-order conditions (9), (10) and (11). As shown in Figure 1 and demonstrated in Appendix 1, S^* and y^* are the new equilibrium levels of total species stock and harvesting respectively, which in turn imply a new equilibrium level of natural habitat area, A^*. Appendix 1 confirms that the equilibrium of the full version of the model (case 3) is a saddle point for an upward-sloping $dy/dt = 0$ curve, thus verifying Proposition 2. The optimal trajectory is depicted in Figure 1 assuming $G_1' < 0$, $S_0 > S^*$ and $S_1^* > S^* > S_2^*$.

As indicated in Appendix 1, comparison of the results of case 3 with those of cases 1 and 2 yields two interesting conclusions. First, comparing cases 2 and 3, the inclusion of non-consumptive biodiversity values in the model will tend to offset the opportunity costs of holding on to habitat, resulting in a higher long-run equilibrium level of species stock and habitat area. That is, in the full version of the model with biodiversity values included (case 3), the equilibrium wildlife stock and habitat area will always exceed that of case 2 which excludes these values. Second, comparing cases 1 and 3, it is not clear whether the equilibrium level of species stock (and habitat area) in the full model will be less or greater than the equilibrium stock determined by the simple bioeconomic model. The outcome will depend on whether in the long run the marginal value of biodiversity, U_S, compensates sufficiently for the marginal opportunity cost of maintaining habitat, $-U_c f'$. Only under special conditions will the bioeconomic model (case 1) actually be able to predict the long-run equilibrium of the full model (case 3), i.e. when $U_S = -U_c f'$.

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It is worth summarizing these results with a further addition to Proposition 2:

PROPOSITION 2.3. *In a closed economy if the* $\dot{y} = 0$ *curve is defined by* $\delta = R_1 + R_2 + R_3$, *there exists an equilibrium harvesting rate* $\dot{y}^* > 0$ *such that equilibrium total species biomass stock occurs to the right of* $\delta = G_1' = G_2' > 0$ *and exceeds the equilibrium stock of the habitat conversion model, i.e.* $S^* > S_2^* > S_f > S_e$; *however, whether* S^* *is less than, equals or exceeds the equilibrium species stock of the bioeconomic model,* S_1^*, *will depend on whether* U_S *is less than, equals or exceeds* $-U_c f'$.

4. Open-economy model

In this section we develop the model to allow for trade. The basic assumption is that some wildlife products are exported, which in turn allows the importation of consumption goods in addition to domestic production from converted habitat land. As noted in the introduction, if wildlife or natural products enter international markets then the possibility exists that trade interventions may be used to influence the optimal level of harvesting and species biomass stocks. The likely scenario is that importing nations may use such interventions to control exploitation of wildlife stocks and conversion of habitat land. Following the approach of Barbier and Rauscher (1994), we extend the full version of our model to examine the likely implications of such trade interventions, and compare them to the impacts of an alternative policy, such as international transfer.

We assume the following additional relationships for the open-economy model: $x(t)$ is exports of wildlife or natural resource products (in terms of biomass); $m(t)$ is consumption of imported goods; $y(t) - x(t)$ is the domestic consumption of wildlife or natural resource products; and p is the terms of trade, p_x/p_m.

As before, two outputs are produced domestically, $f(S(t))$ from converted habitat land and $y(t)$ from harvesting wildlife resources. By assumption, habitat land is a net exporter of resource products: $x(t) > 0$. All domestic products and imports are assumed to be homogeneous. Consequently, the open-economy model includes a trade balance equation and a new definition of total domestic consumption, c:

$$px(t) = m(t) \tag{17}$$

$$c(t) = f(S(t)) + m(t). \tag{18}$$

From substituting (17) and (18) into (7), the open-economy welfare-maximizing problem for the developing country is now

$$Max_{y,\,x}\ W = \int_0^\infty [U(y - x, f(S) + px, S) - w(S)y]e^{-\delta t}\,dt \tag{19}$$

subject to (1′) and (5) and the initial and terminal conditions as defined before. Thus the open-economy problem contains an additional dimension

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beyond the social decision to trade off wildlife utilization with habitat conversion: on the one hand, holding on to natural habitat implies an opportunity cost of forgone consumption from less habitat conversion; on the other hand, trade in wildlife and natural resource products allows consumption of imported goods which can substitute for commodities produced from converted habitat.

The current-value Hamiltonian of the problem is

$$H = U(y - x, f(S) + px, S) - w(S)y + \lambda[G_1(S) - aS^{-b}r - y], \tag{20}$$

which yields the following first-order conditions, assuming an interior solution:

$$dH/dy = U_1 - w(S) - \lambda = 0 \quad \text{or} \quad U_1 = w(S) + \lambda \tag{21}$$

$$dH/dx = -U_1 + pU_2 = 0 \quad \text{or} \quad U_1 = pU_2 \tag{22}$$

$$-dH/dS = \dot{\lambda} - \delta\lambda \quad \text{or} \quad \dot{\lambda} = (\delta - G_1' - baS^{-(b+1)}r)\lambda + yw' - U_2 f' - U_3 \tag{23}$$

$$dH/d\lambda = \dot{S} = G_1(S) - aS^{-b}r - y \tag{11}$$

where $U_1 = \partial U/\partial(y - x) > 0$, $U_2 = \partial U/\partial(c + m) > 0$ and $U_3 = \partial U/\partial S > 0$. We assume as before that these marginal utilities are subject to diminishing returns and will tend to infinity as their arguments approach zero.

Condition (21) indicates that, along the optimal trajectory, the marginal benefit of harvesting or utilizing wild species for domestic consumption, U_1, must equal its marginal cost, which consists of marginal harvesting costs, $w(S)$, as well as the marginal costs of stock depletion, λ. However, the only difference with condition (9) of the closed economy is that domestic consumption is now defined as harvested output net of exports, $y - x$. Condition (22) is entirely new, and it indicates that, if the developing country is a price-taker in international trade, then the relative marginal value of domestic consumption of wildlife and natural resource products to imported-good consumption must be equated with the terms of trade, p. Finally, condition (23) is almost identical with the renewable-resource dynamic condition (10) for denoting the change in the value of the total species stock in the closed economy, and it includes not only the standard (net) marginal bioeconomic costs for holding on to species, $(\delta - G_1')\lambda + yw'$, but also the net marginal benefits of 'holding on' to land as habitat, $-baS^{-(b+1)}r\lambda - U_2 f'$, and the marginal social value of an additional unit of biodiversity, U_3.

By combining (21) and (23) we obtain

$$\dot{y} - \dot{x} = \frac{[(\delta - G_1' + baS^{-(b+1)}r)(U_1 - w(S)) + w'(G_1(S) - aS^{-b}r) - U_2 f' - U_3]}{U_{11}}. \tag{24}$$

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Utilizing (24) and the first-order conditions (21), (22), (23) and (11), one can solve for the following system of equations describing an equilibrium where $dy/dt = dx/dt = dS/dt = r = 0$

$$U_1(y^\dagger, x^\dagger) = pU_2(S^\dagger, x^\dagger) \tag{25}$$

$$\delta - G_1'(S^\dagger) = \frac{-y^\dagger w'(S^\dagger) + U_2(S^\dagger, x^\dagger) f'(S^\dagger) + U_3(S^\dagger)}{(U_1(y^\dagger) - w(S^\dagger))} > 0, \dot{y} = \dot{x} = \dot{S} = r = 0 \tag{26}$$

$$\text{or} \quad \delta = V_1(S^\dagger, y^\dagger, x^\dagger) + V_2(S^\dagger, y^\dagger, x^\dagger) + V_3(S^\dagger, y^\dagger, x^\dagger)$$

$$G_1(S^\dagger) = y^\dagger, \qquad \dot{S} = r = 0, \tag{27}$$

where the equilibrium values of y, x and S are denoted by obelisks (†), and $V_1 = G_1'(S^\dagger) - y^\dagger w'(S^\dagger)/[U_1(y^\dagger, x^\dagger) - w(S^\dagger)]$, $V_2 = U_2(S^\dagger, x^\dagger) f'(S^\dagger)/[U_1(y^\dagger, x^\dagger) - w(S^\dagger)]$ and $V_3(S^\dagger)/[U_1(y^\dagger, x^\dagger) - w(S^\dagger)]$.

Total differentiation of the system of Equations (25)–(27) can lead to characterization of the equilibrium state and trajectories leading to the equilibrium. As shown in Appendix 1, the equilibrium is a saddle point, and the saddle path is positively sloped. Using these results, the optimal solution is represented graphically in Figure 2 for $S_0 > S^\dagger$ and $G_1' < 0$. This solution suggests

PROPOSITION 3. *In an open economy if the* $\mathrm{dy/dt} = \mathrm{dx/dt} = 0$ *curve is defined by* $\delta = V_1 + V_2 + V_3$ *there exists an equilibrium harvesting rate* $y^\dagger > 0$ *such that equilibrium total species stock,* $S^\dagger$, *occurs to the right of* $\delta = G_1' + G_2' > 0$.

It is useful to compare the equilibrium (S^*, y^*) of the full (case 3) version of the closed-economy model with the new equilibrium ($S^\dagger$, $y^\dagger$) obtained in the open economy. If we assume that the marginal utilities of consumption and biodiversity values are the same in the two models, then $x = 0$ implies that $U_2(f(S^\dagger)) = U_c(f(S^*))$, $U_1(y^\dagger) = U_y(y^*)$ and $U_3(S^\dagger) = U_s(S^*)$. Consequently, equilibrium in the closed and open economy will be the same: $S^\dagger = S^*$ and $y^\dagger = y^*$. However, for any $x > 0$ then $U_2(f(S^*) + x) < U_2(f(S^*))$ and $U_1(y^* - x) > U_1(y^*)$. From inspection of Equation (26), it is unclear in which direction S must change in order to maintain the equilibrium condition. This is because, on the one hand, exports of wildlife products reduce the need for domestic consumption from habitat conversion activities, but on the other hand, increased wildlife exports mean less domestic consumption of these products. If the marginal utility of the latter effect outweighs that of the former, then the right-hand side of (26) may increase, and S must therefore also increase to keep the equilibrium condition. However, if the increase in U_1 is the more powerful effect, then the right-hand side of (26) could decrease and S would have to rise correspondingly. Thus it is unclear

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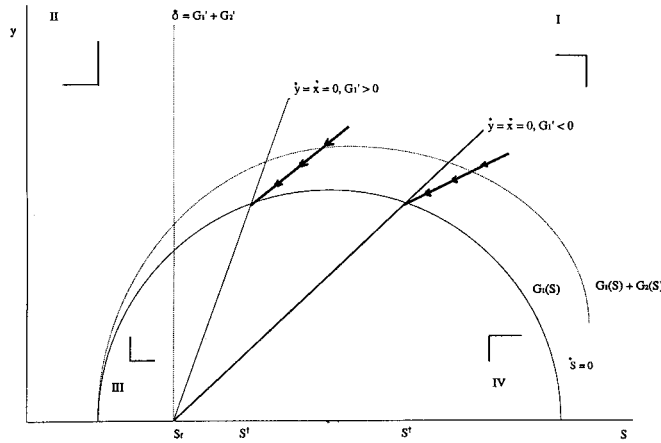


Figure 2. *The long-run equilibrium of the open economy.*

whether the open-economy equilibrium for $x^{\dagger} > 0$ will yield a long-run equilibrium species stock, $S^{\dagger}$, that will be less than, equal to or greater than the equilibrium, S^*, under the closed economy.

There is also an intuitive explanation of this ambiguous result. For the economy to begin trading in wildlife products, p must rise sufficiently high to make exports worthwhile. Starting from autarky this has two effects. First, the development of an external market means that it is more profitable to harvest from wildlife resources, as the external terms of trade with respect to consumption goods are now higher than the domestic terms of trade. This may increase exploitation of the resource base to produce wildlife exports. On the other hand, as noted above, there is less pressure for conversion of land to other uses, as it is now less expensive to obtain consumption goods from world markets. We shall evaluate these effects in the next section.

5. Global biodiversity values: trade interventions vs. transfers

Comparative static analysis of the long-run equilibrium can be employed to determine the impacts of trade interventions in influencing the developing country's decision on how much wildlife species to maintain. Our model already includes positive *domestic* biodiversity values, such as the non-consumptive values that the developing country may capture from maintaining species and natural habitat. However, it is unlikely that the developing country will take into account any positive *global* biodiversity values associated with wildlife and habitat conservation, for example the values that the rest of the world attaches to 'conserving' genetic material for future unknown uses; the global educational and scientific research value of biodiversity; and the 'existence' value of living creatures and natural systems.[7] If the global values of biodiversity are being ignored by domestic policy-makers, then it is likely that the international community

[7] See WCMC (1992) for further discussion and summary of such global values.

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would want the developing country to conserve more species and habitat in the long run than the country would do on its own.

There are essentially two broad approaches that the international community could take to achieve this objective. As described in the introduction, it could through trade interventions such as import bans, tariffs or other controls on wildlife and natural resource products trade try to influence the developing country's decision to 'hold on' to species and habitat. The alternative policy would be to encourage the developing country to 'internalize' any global biodiversity values through an international transfer of funds to reduce the need to exploit and convert wild lands. The effects of both approaches can be characterized through comparative static analysis of our open-economy model.

Following Barbier and Rauscher (1994), we assume that import bans, controls and restrictions have the effect of reducing the terms of trade for the wildlife trade of the developing country. In our open-economy model, a change in the terms of trade, p, has the following impacts on the long-run equilibrium of total species biomass stock:

$$\frac{dS^{\dagger}}{dp} = -\frac{[\Psi(1+\eta_2)U_2 - f'U_{22}x(U_{11}+p^2U_{22})]}{\Delta} \tag{28}$$

where $\eta_2 < 0$ is the elasticity of marginal utility, U_2, with respect to imported consumption goods, m and $\psi = (\delta - G_1')\ U_{11} + f'U_{22}p$. If the absolute value of η_2 is large, i.e. $|\eta_2| > 1$, then marginal welfare in the developing country is highly responsive to a change in imported commodities. The situation with $|\eta_2| > 1$ occurs only when the export supply curve of the developing country is backward-bending. Hence $|\eta_2| < 1$ is the normal case in the trade sector of the model.

From (28) it follows that

$$\frac{dS^{\dagger}}{dp} < 0 \text{ when } |\eta_2| < 1 \text{ and } \psi < \frac{f'U_{22}x(U_{11}+p^2U_{22})}{(1+\eta_2)U_2} < 0, \text{ or}$$

$$\frac{dS^{\dagger}}{dp} < 0 \text{ when } |\eta_2| > 1 \text{ and } \psi > \frac{f'U_{22}x(U_{11}+p^2U_{22})}{(1+\eta_2)U_2} > 0.$$

These conditions are not necessarily fulfilled. For example, if $\psi(1+\eta_2)U_2 > f'U_{22}x(U_{11}+p^2U_{22})$, we get $dS/dp > 0$, quite contrary to the results of standard bioeconomic models (Clark, 1976). A situation with $dS/dp > 0$ will always occur for a positive ψ when $|\eta_2| < 1$, and for a negative ψ when $|\eta_2| > 1$. Under these conditions, trade interventions are counterproductive to conserving species and habitat, and therefore are the wrong strategy for persuading the developing country to 'internalize' global biodiversity values. Thus, without further information on the value of η_2 or the sign of ψ it is impossible to determine whether trade interventions that reduce the terms of trade, p, will increase or decrease the equilibrium value of species stock, $S^{\dagger}$. The ambiguous stock effects make trade inter-

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ventions a poor policy instrument for securing biodiversity conservation.

A large transfer of international funds to the developing country, perhaps through the provisions of the international Convention of Biodiversity or the Global Environmental Facility (GEF), could assist the country in wildlife and habitat conservation. For example, the GEF has a mandate to fund biodiversity conservation projects in developing countries that yield global values but not sufficient domestic net benefits to be funded by these countries. Such international transfers have the effect of 'freeing up' domestic financial resources for other purposes. The developing country is essentially receiving a subsidy from the rest of the world to 'internalize' global biodiversity values. In our model, these transfers can be represented by an increase in foreign exchange available for consumption of imported goods. This has a double benefit in terms of species and habitat conservation: it not only supplements wildlife export earnings, but also reduces consumption from habitat conversion activities. Thus from (17) and (18) consumption now becomes

$$c = f(S) + px + i, \tag{29}$$

where i is the amount of international transfer. An increase in the subsidy has the following effect on the long-run equilibrium of total species biomass stock:

$$\frac{dS^{\dagger}}{di} = -\frac{[\Psi p U_{22} - f' U_{22}(U_{22} + p^2 U_{22})]}{\Delta}. \tag{30}$$

A transfer of funds will increase the long-run stock, $dS^{\dagger}/di > 0$, if $(\delta - G_1') > f'/p$. This is always the case if the equilibrium is to the right of $\delta = G_1'$ as shown in Figure 2, and assuming no impact of the transfer on p. The effect of the international transfer is therefore to make the receiving country better off, with increased income to import from abroad. The subsidy not only replaces wildlife exports as a means of importing consumption goods but also puts less pressure on the species stock through increased harvesting for domestic consumption. Consequently, an increased international transfer leads to a greater long-run equilibrium total species stock.[8]

From the discussion of the effects of trade interventions and a direct international transfer it is worth stating that:

PROPOSITION 4. *In an open economy, if* $(\delta - G_1') > f'/p$ *then a direct international transfer,* i, *will increase the long-run equilibrium total species stock,* $S^{\dagger}$, *unambiguously; however, the effect of a trade intervention is ambiguous.*

[8] Note that if $\psi < 0$ and $|\eta_2| < 1$ then (30) and (32) suggest that an international subsidy will still be preferred to a trade intervention so long as $pU_{22} > -(1 + \eta_2)U_2$. However, it is not necessary for ψ to be negative in order for a subsidy to be preferred to a trade intervention. For example, letting $\omega = f' U_{22}(-U_{11} - p^2 U_{22})$, if $\psi > 0$ and $|\eta_2| > 1$ then a subsidy is still preferred if $\omega \geq \psi(1 + \eta_2)U_2$ and $\omega > \psi p U_{22}$. Similarly, if $\psi > 0$ and $|\eta_2| < 1$ then a subsidy is preferred if $\omega > \psi p U_{22}$.

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6. Conclusion

We have attempted to explore two issues in this article. First, by developing several versions of a closed-economy model of optimal species utilization, we have examined the extent to which the long-run equilibrium of the basic bioeconomic model is affected by the inclusion of habitat conversion and then additionally biodiversity value as a positive externality. Second, by developing an open-economy version of the full model we were able to compare the likely impacts of trade interventions as opposed to international transfers on the developing country's long-run decision to conserve wildlife species and habitat. Several important results emerged from this analysis.

The inclusion of habitat conversion proves to be an important modification of the standard bioeconomic model of renewable resource utilization. We have suggested that the growth in total species stock is dependent not only on the natural biological regeneration rate of species but also on the total number of species contained in a given habitat area. However, holding land as natural habitat also implies an opportunity cost, which is represented by forgone consumption from development activities that use converted habitat land. Because conventional bioeconomic models do not take explicitly into account the opportunity cost of maintaining 'wild' lands as habitat for species, the equilibrium level of species stock—and thus implicity habitat area—is higher than if the opportunity cost of maintaining habitat were included. Consequently, when applied to wildlife utilization problems, conventional bioeconomic models may overestimate the optimal long-run levels of wildlife species and habitat.

Our analysis shows that the additional inclusion of biodiversity values as a positive stock externality will counteract, to some extent, the effects of the opportunity cost of maintaining habitat for species. If the marginal value of biodiversity is sufficiently high, then despite the marginal opportunity cost of maintaining habitat, the optimal equilibrium levels of species and habitat can equal or even exceed the levels determined by the conventional bioeconomic model.

These results for the closed-economy model highlight the importance of extending the conventional bioeconomic model for wild species and resource utilization to include both the opportunity costs of maintaining species habitat and positive biodiversity values if these costs and values are considered significant. If they are instead excluded, the conventional bioeconomic model will predict the 'correct' long-run equilibrium level of species stock (and habitat area) only under very special conditions.

The open-economy model provides an additional dimension to the social decision to trade off wildlife utilization with development benefits from converted habitat land: on the one hand, holding on to natural habitat implies an opportunity cost of forgone consumption from less habitat conversion; on the other hand, trade in wildlife and natural resource products allows consumption of imported goods which can substitute for commodities produced from converted habitat. However, it is unclear, when compared to the closed-economy equilibrium, whether the open economy leads to a higher long-run optimal level of species and habitat conservation. Exports of wildlife products appear to reduce the need for domestic

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consumption from habitat conversion activities, but exports also mean less domestic consumption of these products.

Comparative static analysis of the long-run equilibrium of the open-economy model suggests caution in the use of trade interventions as an international policy for forcing a developing country to internalize externality values of biodiversity. Under certain conditions, trade interventions may be unambiguously counterproductive, whereas the alternative policy of an international transfer of funds would lead to greater long-run conservation of species and habitat. Although in our model it is possible for trade interventions (trade bans, tariffs or trade subsidies) to have the desired effect of increasing long-run equilibrium species stock and habitat area, we need to know the specific conditions underlying the bioeconomic, habitat conversion and trade sectors of the model in order to determine the precise influence of trade policy interventions. Hence, we conclude that trade intervention is a second-best approach for global biodiversity conservation.

Finally, it is worth commenting that the results of the open-economy model might be affected if it were extended to reflect other aspects of trade–environment dimensions to resource exploitation problems in developing countries. For example, Chichilnisky (1994) examines the interactions of ill-defined property rights regimes and international trade in resource products from developing countries; Barbier and Rauscher (1994) expand their basic model of trade and tropical deforestation to allow for market power and foreign asset accumulation (or debt); and Schulz (1994) examines the effects of trade on wildlife utilization in developing countries by explicitly accounting for species interactions, such as predator–prey relationships. Extensions to our model along these lines may further increase its applicability to resource utilization problems in developing countries.

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APPENDIX 1

Solutions of the closed- and open-economy models

This appendix derives the long-run equilibrium solutions and stability conditions for the various versions of the model developed in this paper.

Case 1. Bioeconomic model ($\delta = R_1$)

We begin with the basic bioeconomic model of the closed economy with no costs of holding on to land as habitat and no positive stock externalities associated with biodiversity: $R_2 = R_3 = 0$. Thus the following equations of motion can be derived from the first-order conditions (9), (10) and (11):

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$$\dot{y} = \frac{(\delta - G_1')(U_y - w(S)) + yw' + w'\dot{S}]}{U_{yy}}$$

$$= \frac{(\delta - G_1')(U_y - w(S)) + w'G_1(S)}{U_{yy}}$$

$$\dot{S} = G_1(S) - y,$$

which yield the following long-run equilibrium condition for $dy/dt = dS/dt = 0$:

$$\delta - G_1'(S_1^*) = \frac{-y_1^* w'(S_1^*)}{(U_y(y_1^*) - w(S_1^*))} > 0, \qquad \dot{y} = \dot{S} = 0$$

$$G_1(S_1^*) = y_1^*, \qquad \dot{S} = 0,$$

where S_1^* and y_1^* are the equilibrium levels of the total species stock and harvesting respectively. This equilibrium for case 1 is depicted in Figure 1. Note that from the above equations $y_1^* = 0$ results in $\delta = G_1'$, which means that the origin of the $dy/dt = 0$ curve for case 1 in Figure 1 is $(S_e, 0)$. Therefore, for any $y_1^* > 0$ it follows that $S_1^* > S_e$, i.e. the equilibrium level of wild-species stock in case 1 must lie to the right of the vertical $\delta = G_1'$ curve in Figure 1. This result is caused by the decreasing unit costs as the stock increases.

Through linearizing the above two equations of motion and evaluating the resulting matrix of coefficients at the equilibrium (S_1^*, y_1^*), it can be shown that the equilibrium is a saddle point if the determinant of the matrix is negative, and the curve $dy/dt = 0$ is positively sloped and cuts the curve $dS/dt = 0$ from below. Through linearizing we obtain

$$\dot{S} = G_1'(S - S_1^*) - (y - y_1^*)$$

$$\dot{y} = \frac{X(S - S_1^*) + Z(y - y_1^*)}{U_{yy}},$$

where $X = -(\delta - G_1')w' - (Uy - w(S))G'' + G_1'w'' > 0$, $Z = (\delta - G_1')U_{yy} + w' < 0$ and U_{yy} is assumed to be constant.[9] The determinant Δ of the matrix of coefficients of the above equations is

[9] We take advantage of the fact that at the equilibrium $G_1' dS_1^* = dy_1^*$.

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$$\Delta = \frac{G_1' Z = X}{U_{yy}}.$$

It follows that $\Delta < 0$ if $G_1' < 0$ or if $G_1' > 0$ and $-X/U_{yy} > Z/U_{yy}$. However, if these conditions hold, then comparing the $dy/dt = 0$ and $dS/dt = 0$ curves shows that

$$\frac{dy}{dS} \mid_{\dot{y}=0} = -\frac{X}{Z} > G_1' = \frac{dy}{dS} \mid_{\dot{S}=0}.$$

Consequently, the requirement that $dy/dt = 0$ is upward-sloping and cuts the $dS/dt = 0$ curve from below is a necessary condition for $\Delta < 0$. The equilibrium (S_1*, y_1*) is therefore locally stable (a saddle point). Thus, as shown in Figure 1, for case 1 isosectors I and II are convergent and contain optimal trajectories to the locally stable equilibrium (S_1*, y_1*). An optimal trajectory is represented graphically, assuming $G_1' < 0$ and $S_0 > S_1$*.

Case 2. Habitat conversion model ($\delta = R_1 + R_2$)

In this version the basic bioeconomic model is extended to include the costs of habitat conversion, i.e. R_2 of Equation (15). The equations of motion for the closed economy are now modified to

$$\dot{y} = \frac{(\delta - G_1' - G_2')(U_y - w(S)) + yw' + w'\dot{S} - U_c f']}{U_{yy}}$$

$$= \frac{(\delta - G_1' + baS^{-(b+1)})(U_y - w(S)) + w'(G_1(S) - aS^{-b}r) - U_c f'}{U_{yy}}$$

$$\dot{S} = G_1(S) + G_2(S) = G_1(S) - aS^{-b}r - y.$$

This leads to the following long-run equilibrium conditions for $dy/dt = dS/dt = r = 0$

$$\delta - G_1'(S_2^*) = \frac{-y_2^* w'(S_2^*) + U_c f'(S_2^*)}{(U_y(y_2^*) - w(S_2^*))} > 0, \qquad \dot{y} = \dot{S} = r = 0$$

$$G_1(S_2^*) = y_2^*, \qquad \dot{S} = r = 0,$$

where S_2* and y_2* are the new equilibrium levels of the total species stock and harvesting respectively, as depicted for case 2 in Figure 2. From Equation (2) in the text it is clear that corresponding to these values must be an equilibrium level of natural habitat area, A_2*. Since we have added $G_2(S)$ to the growth function, we must change the origin ($y_2^* = 0$) of the $dy/dt = 0$ curve to S_f, such that $\delta = G_1'(S_f) + G_2'(S_f)$ and $S_f > S_e$. Therefore, as

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shown for case 2 in Figure 1, if the $dy/dt = 0$ curve is upward-sloping, then for any $y_2^* > 0$ it follows that $S_2^* > S_f$; i.e. the equilibrium level of wild-species stock will be to the right of the point S_f.

By linearizing the above equations of motion and evaluating them at the equilibrium point (S_2^*, y_2^*) it is possible to prove that the above condition holds for case 2. Given that at this equilibrium $r = 0$, we obtain through linearizing

$$\dot{S} = G_1'(S - S_2') - (y - y_2^*)$$

$$\dot{y} = \frac{[X - U_{cc}(f')^2 - U_c f^*](S - S_2^*) + Z(y - y_2^*)}{U_{yy}}$$

where $X > 0$ and $Z < 0$ as before and $-U_{cc}(f')^2 - U_c f'' > 0$. The determinant Δ of the matrix of coefficients of the above linearized equations is

$$\Delta = \frac{G_1' Z + (X - U_{cc}(f')^2 - U_c f'')}{U_{yy}}.$$

It follows that $\Delta < 0$ for $G_1' < 0$. If $G_1' > 0$, then $\Delta < 0$ requires $-(X - U_{cc}(f')^2 - U_c f'')/Z > G_1'$. The result of such conditions is

$$\frac{dy}{dS}\Big|_{\dot{y}=0} = -\frac{(Z - U_{cc}(f')^2 - U_c f'')}{Z} > G_1' = \frac{dy}{dS}\Big|_{\dot{S}=0}.$$

Thus for case 2 the requirement that $dy/dt = 0$ is upward-sloping and cuts the $dS/dt = 0$ curve from below is a necessary condition for $\Delta < 0$. The equilibrium (S_2^*, y_2^*) is therefore locally stable (a saddle point). In Figure 1, the optimal trajectory assuming $G_1' < 0$ and $S_0 > S_2^*$ is shown.

In comparing the equilibria of cases 1 and 2, note that in case 2 if in equilibrium $-w'G_1(S) > -U_c f'$, then $(\delta - G_1') > 0$ and the $dy/dt = 0$ curve is upward-sloping. This result suggests that $S_1^* > S_2^* > S_f > S_e$, i.e. the equilibrium level of wild-species stock in case 2 must be less than the equilibrium level derived in case 1.[10] That is, because in case 2 there is an opportunity cost for holding on to land as natural habitat, in the long run a smaller total stock of species and habitat will be maintained.

[10] It is fairly easy to show why this equilibrium condition for case 2 is necessary to yield an upward-sloping $dy/dt = 0$ curve. In case 2 if $-w'G_1(S) = -U_c f'$, then $\delta = G_1'$. It follows that $y_2^* = y_f = G_1(S_f)$. Alternatively, if $-w'G_1(S) < -U_c f'$, then $\delta < G_1'$ and $S_2^* < S_f$ and $y_2^* < y_f$. However, the result would be $-U_c f' \to \infty$, $S_2^* \to \underline{S}$ and $G_1(\underline{S}) = y = 0$. That is, there is complete conversion of habitat in the initial time period $t = 0$. Thus a necessary condition for an upward-sloping $dy/dt = 0$ curve is $-w'G_1(S) > -U_c f'$.

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Case 3. Inclusion of biodiversity value ($\delta = R_1 + R_2 + R_3$)
Incorporating $S(t)$ in the social utility function to represent the stock externalities associated with non-consumptive biodiversity values yields the original optimal control problem and corresponding first-order conditions (9), (10) and (11). The equation of motion for optimal harvesting derived in case 2 now becomes

$$\dot{y} = \frac{(\delta - G_1' - G_2')(U_y - w(S)) + yw' + w'\dot{S} - U_c f' - U_S}{U_{yy}}$$

and the long-run equilibrium conditions for $dy/dt = dS/dt = r = 0$ are the same as (12) and (13) in the text

$$\delta - G_1'(S^*) = \frac{-y^* w'(S^*) + U_c f'(S^*) + U_S(S^*)}{(U_y(y^*) - w(S^*))} > 0, \qquad \dot{y} = \dot{S} = r = 0$$

$$\text{or} \qquad \delta = R_1(S^*, y^*) + R_2(S^*, y^*) + R_3(S^*, y^*)$$

$$G_1(S^*) = y, \qquad \dot{S} = r = 0,$$

where S^* and y^* are the new equilibrium levels of total species stock and harvesting respectively, which in turn imply an equilibrium level of natural habitat area, A^*. Note that once again $y^* = 0$ results in $\delta = G_1'(S_f) + G_2'(S_f)$; i.e., as shown in Figure 1 for case 3 the $dy/dt = 0$ curve originates at S_f, and the equilibrium level of wild-species stock will lie to the right of this point.

The stability condition for this case is similar to that of case 2. That is, the inclusion of biodiversity value means that the determinant Δ of the matrix of coefficients of the linearized equations of motion evaluated at the equilibrium (S^*, y^*) is

$$\Delta = \frac{G_1' Z + (X - U_{cc}(f')^2 - U_c f'' - U_{SS})}{U_{yy}}.$$

It follows that $\Delta < 0$ for $G_1' < 0$. If $G_1' > 0$, then $\Delta < 0$ requires $-(X - U_{cc}(f')^2 - U_c f'' - U_{SS})/Z > G_1'$. The result of such conditions is

$$\frac{dy}{dS}\Big|_{\dot{y}=0} = \frac{-(X - U_{cc}(f')^2 - U_c f'' - U_{SS})}{Z} > G_1' = \frac{dy}{dS}\Big|_{\dot{S}=0}.$$

Thus, for case 3 the requirement that $dy/dt = 0$ is upward-sloping and cuts the $dS/dt = 0$ curve from below is a necessary condition for $\Delta < 0$. The equilibrium (S^*, y^*) is therefore locally stable (a saddle point). In Figure 1, the optimal trajectory assuming $G_1' < 0$ and $S_0 > S^*$ is shown.

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It is useful to compare the equilibrium species stock derived in case 3 with that resulting from cases 1 and 2. In case 3 if $-w'G_1(S) + U_S > -U_c f'$, then $(\delta - G_1') > 0$ and the $dy/dt = 0$ curve is upward-sloping.[11] An immediate result of this condition must be that $G_1'(S_2^*) > G_1'(S^*)$, which in turn implies $S^* > S_2^*$. That is, in the full version of the model with biodiversity values included (case 3), the equilibrium wildlife stock exceeds that of case 2 which excludes biodiversity values. However, the relationship between S^* and S_1^* is more ambiguous and is governed by the following condition:

$$\text{if } U_S \lessgtr -U_c f' \text{ then } S^* \lessgtr S_1^*.$$

That is, if the marginal value of biodiversity is sufficiently high relative to the marginal opportunity cost of maintaining natural habitat, then the optimal equilibrium level of species, S^*, can equal or even exceed the equilibrium level of the bioeconomic model. In Figure 1, the optimal trajectory assumes that $S^* < S_1^*$ which implies $U_S < U_c f'$.

The open-economy model

The stability conditions for the open-economy model can be derived in the following manner. Total differentiation of the simultaneous equation system (25)–(27) characterizing the equilibrium $(S^\dagger, y^\dagger, x^\dagger)$ yields

$$U_{11}dy - (U_{11} + p^2U_{22})dx - (pU_{22}f')dS - (U_2 + pU_{22}x)dp = 0$$

$$[(\delta - G_1')U_{11} + w']dy - \psi dx + \phi dS - f'U_{22}xdp = 0$$

$$-dy + G_1'dS = 0,$$

where $\psi = (\delta - G_1')U_{11} + f'U_{22}p$ and $\phi = -(U_1 - w(S))G_1'' - (\delta - G_1')w' + yw'' - U_{22}(f')^2 - U_2f'' - U_{33} > 0$. The determinant of the Hessian matrix of coefficients for dy, dx and dS in the above system of equations is

$$\Delta = G_1'[((\delta - G_1)U_{11} + w')(U_{11} + p^2U_{22}) - \psi U_{11}] + [\psi pU_{22}f' + \phi(U_{11} + p^2U_{22})].$$

Signing Δ again requires comparing the slopes of the $dy/dt = dx/dt = 0$ and $dS/dt = 0$ curves. Substituting for dx in the above system of equations yields

[11] As in the previous note, for case 3 if $-w'G_1(S) + U_S = -U_c f'$, then $\delta = G_1'$ and $y^* = y_f = G_1(S_f)$. Similarly, if $-w'G_1(S) + U_S < -U_c f'$, then $\delta < G_1'$, $S^* < S_f$ and $y^* < y_f$. However, as $-U_c f' \to \infty$, $S^* \to \underline{S}$ and $G_1(\underline{S}) = y = 0$, which again suggests complete conversion in the initial time period $t = 0$. Thus for case 3 a necessary condition for an upward-sloping $dy/dt = 0$ curve is $-w'G_1(S) + U_S > -U_c f'$.

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$$\frac{dy}{dS} \mid_{\dot{S}=0} = G_1'$$

$$\frac{dy}{dS} \mid_{\dot{y}=\dot{x}=0} = -\frac{\psi p U_{22} f' + \phi(U_{11} + p^2 U_{22})}{((\delta - G_1')U_{11} + w')(U_{11} + p^2 U_{22}) - \psi U_{11}}.$$

It follows that if $G_1' < 0$ and the $dy/dt = dx/dt = 0$ curve is upward-sloping, then $\Delta < 0$. However, if $G_1' > 0$ then not only must the $dy/dt = dx/dt = 0$ curve be upward-sloping, but also the slope of this curve must exceed the slope of the $dS/dt = 0$ curve.[12] If these conditions are met, then the equilibrium ($S^\dagger$, $y^\dagger$, $x^\dagger$) is locally stable (a saddle point). Finally, from Equation (26) in the text it is clear that $y^\dagger = 0$ implies that the $dy/dt = dx/dt = 0$ curve originates at S_f, which was derived for case 2 of the closed-economy model. Using all these results, the optimal solution is depicted graphically in Figure 2 for $S_0 > S^\dagger$ and $G_1' < 0$.

APPENDIX 2

An alternative formulation of the allocation problem

Equation (1) in the text specifies a growth function for the total species stock, S, which is additively separable into subcomponents, $G_1(S)$ and $G_2(A)$, that indicate the influence respectively of stock size and total habitat area, A, on growth. This appendix demonstrates that it is possible to specify a non-separable version of the growth function, $G(S,A)$, and an alternative formulation of the biodiversity and habitat allocation problem without affecting significantly the main results.[13]

For example, following more conventional bioeconomic models, if total habitat area, A, is effectively interpreted as the maximum carrying capacity of the total stock of species, S, then (1) could reasonably be specified as a non-separable logistic function, i.e.

$$\frac{dS(t)}{dt} = \dot{S} = G(S(t),A(t)) - y(t) = \alpha S(t)(A(t) - S(t)) - y(t).$$

Similarly, if it is assumed that land is still allocated through conversion, r, from habitat area and developed land, D, used to produce consumption goods, c, then the optimal allocation problem for the closed economy can be re-specified as

[12] However, an additional restriction in both cases is that the numerator of the slope of the $dy/dt = dx/dt = 0$ curve must be negative and the denominator positive.

[13] We are grateful to an anonymous referee for suggesting the following logistic function as an alternative non-separable version of the growth function $G(S,A)$. This referee raised doubts about the empirical relevance of the original specification of Equation (1) in the text as a separable function, but also noted that 'this assumption does not materially affect the subsequent results'. We hope that this appendix goes some way towards illustrating this latter point.

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$$Max_{y,r}\ W = \int_0^{\infty} [U(y,c,S) - w(S)y]e^{-\delta t}dt$$

subject to $\dot{S} = \alpha S(t)(A(t) - S(t)) - y(t),\ S(0) = S_0,\ \lim_{t\to\infty} S(t) \geq 0$

$$\dot{A} = -r,\ A(0) = A_0$$

$$\dot{D} = r,\ D(0) = D_0$$

$$c = F(D),\ F' > 0,\ F'' < 0,$$

where r is now a control variable in the problem. Specifying μ and ξ as the co-state variables for habitat area and developed land respectively, the following current-value Hamiltonian and first-order conditions result:

$$H = U(y,F(D),S) - w(S)y + \lambda[\alpha S(A - S) - y] - \mu r + \xi r$$

$$dH/dy = U_y - w(S) - \lambda = 0 \quad \text{or} \quad U_y = w(S) + \lambda$$

$$-dH/dS = \dot{\lambda} - \delta\lambda \quad \text{or} \quad \dot{\lambda} = (\delta + 2\alpha S)\lambda - U_S + w'y$$

$$dH/dr = \xi - \mu = 0 \quad \text{or} \quad \xi = \mu$$

$$-dH/dA = \dot{\mu} - \delta\mu \quad \text{or} \quad \dot{\mu} = \delta\mu - \lambda\alpha S$$

$$-dH/dD = \dot{\xi} - \delta\xi \quad \text{or} \quad \dot{\xi} = \delta\xi - U_c F'.$$

The last three conditions can be combined with the first to derive $\lambda = U_y - w(S) = U_c F'/\alpha S$, i.e. along the optimal trajectory the marginal net benefits of harvesting an additional unit of the species stock must equal the net marginal costs of maintaining that unit. Utilizing this relationship and the remaining first-order conditions, the equations of motion for the system are

$$\dot{y} = \frac{\delta(U_y - w(S)) + 2U_c F' + w'(\alpha S(A - S)) - U_S}{U_{yy}}$$

$$\dot{S} = \alpha S(A - S) - y$$

$$\dot{A} = -\dot{D} = -r.$$

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Assuming as before that in equilibrium $dy/dt = dS/dt = r = 0$, the long-run steady-state conditions are

$$\delta = \frac{-y^*w'(S^*) - 2U_cF'(D^*) + U_S(S^*)}{U_y(y^*) - w(S^*)} \quad \text{for } \dot{y} = \dot{S} = r = 0$$

$$G(S^*,A^*) = \alpha S^*(A^* - S^*) = y^* \quad \text{for } \dot{S} = r = 0.$$

Comparison with the equilibrium conditions (12) and (13) derived for the version of the model presented in the text indicates the similarity between the two sets of conditions. That is, Proposition 2 also holds for the above steady state; i.e., in the closed economy the equilibrium total species stock, S^*, is determined by equating the social discount rate, δ, and bioeconomic returns net of the opportunity cost of habitat plus the non-consumptive value of biodiversity. Although not shown here, it is possible to demonstrate that the above equilibrium is locally stable in (S,y) space, and that a necessary requirement for stability is that the $dy/dt = 0$ curve is upward-sloping and cuts the $dS/dt = 0$ from below. Similarly, it is also fairly straightforward to extend the above version of the model to verify Propositions 3 and 4 derived for the open-economy model, although this is not attempted here.[14]

[14] For example, it is clear that the open-economy model would simply add another equilibrium condition, $U_1(y^*,x^*) = pU_2(D^*,x^*)$, to those already derived in this appendix. The similarity with equilibrium conditions (25)–(27) is readily apparent.

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