

**Optimal Management in Tilmania:
A Competitive Species Assembly
Constrained by a Limiting Factor**

William Brock* and Anastasios Xepapadeas**
NOTA DI LAVORO 68.98

NOVEMBER 1998

EM – Environmental Management

*Department of Economics, University of Wisconsin
**Department of Economics, University of Crete

This paper was presented at the 1998 World Congress of Environmental and Resource Economists, Venice, June 25-27, 1998, organised by the Association of Environmental and Resource Economists, European Association of Environmental and Resource Economists and Fondazione Eni Enrico Mattei. Research leading to this paper was undertaken under the Resilience Network for Economic/Ecological modelling. We would like to thank J. Roughgarden for stimulating conversations about ecology and economy, Mark Willinger and the participants of the Economic Theory Seminar at Louis Pasteur University for helpful comments on an earlier draft of this paper. William Brock wishes to thank NSF grant #SBR 94 2267 and the Vilas Trust.

Address for correspondence:

A. Xepapadeas

University of Crete, Department of Economics

University Campus

74 100 Retymno, Crete

Greece

Phone: +831+23680

Fax: +831+54013

E-mail: xepapad@fortezza.cc.ucr.gr

Le opinioni espresse nel presente lavoro non rappresentano necessariamente
la posizione della Fondazione Eni Enrico Mattei

SUMMARY

Resource-based models of species competition predict that when species compete for a limiting resource in a homogeneous habitat, then the equilibrium outcome is a monoculture with the species characterised by the lowest resource requirement outcompeting all the rest. We derive harvesting rules for a habitat that maximise the utility flows generated from consumption activities of the harvested species, and from nonconsumptive activities associated with utility generated from positive species biomass. Under the harvesting rules the maximal desired biodiversity is preserved in the long-run equilibrium assembly. Our harvesting rule at the steady state corresponds to a golden biodiversity rule. The equilibrium assembly is characterised by a 'strong resilience principle' in both deterministic and stochastic environments, indicating that irrespective of the initial state of the assembly, the system tends to the steady state where full biodiversity is preserved.

Keywords: Biodiversity, Monoculture, Optimal harvesting, Resilience

JEL: O20, Q20

NON TECHNICAL SUMMARY

Species competition and the eventual fate of various species once competitive interactions have reached an equilibrium is an issue of fundamental importance to ecology. The phenomenological and descriptive approach of classical theory is based on the Lotca-Volterra competition that describes the interactions between species in terms of summary variables which are the competition coefficients.

In the last few decades a new approach has emerged based on the work of Tilman. This approach is based on a mechanistic resource-based model of competition between species and uses the resource requirements of the competing species to predict the outcome of species competition. As stated in Tilman, the strength of the mechanistic approach when applied to species communities is that it can make explicit predictions about a wide range of patterns and processes in nature. A central feature of the resource-based model is an exclusion principle. This principle states that in the context of a multispecies competition for a limiting factor, in a patch free of disturbance, the species with the lowest resource requirement in equilibrium will competitively displace all other species. Thus the system is driven to a monoculture and the equilibrium outcome of species competition is the survival of the species which is the superior competitor for the limiting resource, that is the species with the lowest resource requirement.

The purpose of this paper is to analyse optimal management strategies in an environment where biodiversity is valued, but the above-described exclusion principle drives the system to a monoculture. The value of biodiversity can be related to 'nonconsumptive' use values or existence values of species.

Biodiversity, however, can also be regarded as promoting the resilience of the ecosystem with resilience characterising the system's ability to withstand perturbations and move back towards its equilibrium state. Another reason for promoting biodiversity lies in the possibility of undertaking intercropping, that is the growing of two or more crops in association with one another. Some advantages of intercropping are considered to be the increased productivity of intercropping, the better use of available human or natural resources, the reduction of damages caused by pests and the greater stability (resilience) of the system.

Our main goal in this paper is to show the existence of optimal resource management rules which, when applied to unified economic/ecological models, can preserve biodiversity and, at the same time, promote the resilience of the ecosystem.

Our results indicate that optimal harvesting practices can mimic disturbances caused by environmental heterogeneities in spatial models, like spatial differences in temperature or abundance of herbivores, which lead to species coexistence, and secure the desired biodiversity in homogeneous habitats constrained by a limiting factor. In addition optimal harvesting practices attribute to the habitat a strong resilience property, in the sense that equilibrium biodiversity is preserved irrespective of the types of shocks affecting the system. Furthermore the management rules ensure sustainable harvesting of the assembly since biodiversity is preserved for the future generations.

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1 Introduction

Species competition and the eventual fate of various species once competitive interactions have reached an equilibrium is an issue of fundamental importance to ecology. The phenomenological and descriptive approach of classical theory is based on the Lotca-Volterra competition. These equations, which have been the major descriptor of competition in the ecological literature since the 1920s (Lotca [8], Volterra [20]), describe the interactions between species in terms of summary variables which are the competition coefficients.

In the last few decades a new approach has emerged based on the work of Tilman ([14], [15], Pacala and Tilman [11], Roughgarden [13]). This approach is based on a mechanistic resource-based model of competition between species and uses the resource requirements of the competing species to predict the outcome of species competition. As stated in Tilman ([15]), the strength of the mechanistic approach when applied to species communities is that it can make explicit predictions about a wide range of patterns and processes in nature. A central feature of the resource-based model is an exclusion principle. This principle states that in the context of a multispecies competition for a limiting factor, in a patch free of disturbance, the species with the lowest resource requirement in equilibrium will competitively displace all other species. Thus the system is driven to a monoculture and the equilibrium outcome of species competition is the survival of the species which is the superior competitor for the limiting resource, that is the species with the lowest resource requirement.

The purpose of this paper is to analyze optimal management strategies in an environment where biodiversity is valued, but the above-described exclusion principle drives the system to a monoculture. The value of biodiversity can be related to 'nonconsumptive' use values or existence values of species. Biodiversity, however, can also be regarded as promoting the resilience of the ecosystem with resilience characterizing the system's ability to withstand perturbations and move back towards its equilibrium state.¹ Another reason for promoting biodiversity lies in the possibility of undertaking intercropping, that is the growing of two or more crops in association with one another. Some advantages of intercropping are considered to be the increased productivity of intercropping, the better use of available human or natural resources, the reduction of damages caused by pests and the greater stability (resilience) of the system (Vandermeer [19]).

Our main goal in this paper is to show the existence of optimal resource

¹An ecological tenet justifying the conservation of biodiversity, is that biodiversity begets stability. Recent field studies (Tilman and Downing [16], Tilman, Wedin and Knops [17]) provide support for the diversity-stability hypothesis.

management rules which, when applied to unified economic/ecological models, can preserve biodiversity and, at the same time, promote the resilience of the ecosystem.

In particular, we consider a number of species competing for a limiting resource in a given patch. In the absence of any disturbances, the resource-based model predicts that in the steady-state equilibrium the assembly tends to a monoculture with the species with the lowest resource requirement in equilibrium outcompeting the rest. This is Tilman's R^* rule, indicating that species can be ranked according to their equilibrium resource requirement R^* , where R^* is the resource level at which the net rate of population change of the species is zero.² According to the resource-based model, the species with the lowest R^* is the superior competitor. Coexistence of species in mechanistic models of competition is mainly explained by introducing disturbances and heterogeneities when species inhabit spatially and temporally variable environments. As analyzed in Pacala and Tilman [11], in mechanistic and spatial models of competition, plant species can coexist in heterogeneous environments because they could have sufficient differences in optimal temperature, or root-shoot ratio, or palatability when there is local abundance of herbivores.

In this paper we consider a homogeneous habitat in which optimal management takes the form of harvesting rules to maximize the utility flow from the assembly. Utility flow is generated from consumption activities of the harvested species, but also from nonconsumptive activities associated with utility generated from positive species biomass. Thus society derives 'consumptive' utility from biodiversity through harvesting, and 'nonconsumptive' utility from biodiversity itself.

We model 'consumptive' utility by a concave function of harvest flow, while 'nonconsumptive' utility may be modeled by a CES function of the utilities derived from the biomass of each species, since this function can provide a premium for biodiversity. We furthermore assume concave species dynamics in the sense that the biomass dynamics can be represented by density dependent functions which are concave in the biomass and the limiting resource.

When the objective is to maximize the undiscounted flow of utilities over an infinite time horizon, we derive an 'inverse R^* ' harvesting rule, by which species are harvested in an inverse ranking as compared to their R^* ranking. This management rule supports a maximal desired biodiversity maintenance principle. By this principle a unique steady-state exists with the assembly

²This equilibrium occurs when the growth and the reproduction of the species equals the loss rate of the species in the given habitat.

that maximizes consumptive and nonconsumptive utility preserved in the long-run equilibrium. The 'inverse R^* ' harvesting rule at the steady-state can be interpreted as a golden biodiversity rule. Furthermore, since this rule can be applied to functional groups evolving at different time scales, we provide a conceptual framework for management in more than one time scale. We show that a 'strong resilience principle' is satisfied at the steady state. That is, irrespective of the initial state of the assembly, 'inverse R^* ' harvesting will drive the system to the steady-state where the maximal desired biodiversity is preserved. This resilience principle is also satisfied for sufficiently small positive discount rates. We also show that the 'strong resilience principle' is preserved in a stochastic environment, in the sense of the system converging to a steady-state distribution of species' biomasses.

Our results indicate that optimal harvesting practices can mimic disturbances caused by environmental heterogeneities in spatial models, like spatial differences in temperature or abundance of herbivores, which lead to species coexistence, and secure the desired biodiversity in homogeneous habitats constrained by a limiting factor. In addition optimal harvesting practices attribute to the habitat a strong resilience property, in the sense that equilibrium biodiversity is preserved irrespective of the types of shocks affecting the system. Furthermore the management rules ensure sustainable harvesting of the assembly since biodiversity is preserved for the future generations.

2 Species Competition for a Limiting Resource

Assume that $i = 1, \dots, n$ species exist in a given habitat and that all species are limited by the same single resource. In this context a resource is defined following Tilman [14] (Chapter 2, page 11), as: "any substance or factor which can lead to increased growth rate [of an organism] as its availability in the environment is increased, and which is consumed by the organism."³

Let $R(t)$ denote the amount of the available limiting resource at time t and $B_i(t)$ the biomass of species i at the same time. The competition among species can be described by the following system of differential equations.

$$\frac{\dot{B}_i}{B_i} = l_i(B_i)[g_i(R) - d_i], B_i(0) = B_i^0 > 0, i = 1, \dots, n \quad (1)$$

$$\dot{R} = S(R) - aR - \sum_{i=1}^n w_i B_i l_i(B_i) g_i(R), R(0) = R^0 > 0 \quad (2)$$

³For example the growth rate of a plant measured as the rate of weight gain may be increased by the addition of nitrate which is consumed by the plant.

Equation (1) describes the rate of growth of the biomass of species i where $g_i(R)$ reflects the resource rate growth for this species. This function is increasing by the definition of a resource given above, and is furthermore assumed to be concave reflecting 'diminishing returns' in the resource use. Thus $g'_i(R) > 0$ and $g''_i(R) < 0$ for all $R \geq 0$. The function $l_i(B_i)$ reflects the underlying assumption that the rate of growth depends on the existing density of the species. This is an empirically-relevant formulation since empirical evidence suggests that relative growth rates and weight per plant decrease with initial plant density in both poor and rich soils (Tilman [14]). This observation suggests that $l'_i(B_i) < 0$ for all $B_i > 0$.⁴ Using (1) the biomass dynamics can be defined as:

$$\dot{B}_i = f_i(B_i)[g_i(R) - d_i], \text{ where } f_i(B_i) = B_i l_i(B_i) \quad (3)$$

It is assumed that the biomass dynamics are concave in the sense that $f''_i(B_i) < 0$ and $f_i(B_i)[g_i(R) - d_i]$ is concave in B_i and R .⁵

Equation (2) describes the resource dynamics where $S(R) - aR$ is the amount of the resource supplied at time t as a function of the resource (Tilman [14], page 14), with a being a rate constant for resource supply. This rate could reflect the natural rate of the resource removal, for example, the leaching rate. We assume that an \bar{R} exists such that:

$$s(\bar{R}) = S(\bar{R}) - a\bar{R} = 0, \quad s(R) \leq 0 \text{ as } R \geq \bar{R}$$

The last term on the right-hand side of (2), $\sum_{i=1}^n w_i f_i(B_i) g_i(R)$, is the consumption of the resource by all species, with w_i being a constant reflecting the concentration of the resource in the tissues of the i th species (Pacala and Tilman [11]).

In the competitive process among species described by (1) and (2), an equilibrium is defined as a situation where the net growths of the species and the resource are zero, or equivalently $\dot{B}_i = \dot{R} = 0$. Define by R_i^* the resource level at which the net growth rate for species i is zero. From (3), R_i^* is defined as the solution of:

$$g_i(R) - d_i = 0 \quad (4)$$

Let all species be ranked, by relabelling if necessary, according to their R_i^* as:

$$R_1^* < R_2^* < \dots < R_n^*$$

⁴The growth rate of the species biomass is density independent when $l_i(B_i) \equiv 1$.

⁵Concavity for example holds in the case where $g_i(R) = R^\eta$, $f_i(B_i) = B_i^{1-\theta}$ with $\eta, \theta \in (0, 1)$, $\theta > \eta$, and $R^\eta(\theta - \eta) + \theta(\eta - 1)d_i > 0, \forall R > 0$.

According to the competitive displacement mechanism, species 1 with the lowest R^* is expected to displace all other species in equilibrium (Tilman [14], [15]). This result can be shown for the density dependent growth described by equation (1) as follows:

Theorem 1 (Tilman R^* rule) Assume that: (i) for all functions $g_i(R)$ there is a solution $R_i^* > 0$ to $\frac{g_i(R)}{d_i} - 1 = 0$, and (ii) $\frac{g_1(R)}{d_1} > \frac{g_2(R)}{d_2} > \dots > \frac{g_n(R)}{d_n}$ for all $R \geq 0$. Then species 1 will competitively displace all other species in equilibrium.

Proof: By the assumption about the $g_i(R)$ functions, all $\frac{g_i(R)}{d_i}$ functions are increasing in R and concave. Then all sets $P_i(y) \equiv \left\{ R : \frac{g_i(R)}{d_i} \geq y \right\}$ are convex and by the ranking defined by assumption (ii), $P_1 \supset P_2 \supset \dots \supset P_{n-1} \supset P_n$. This can be shown in figure 1 where $y = 1$. Assuming that $R^0 > R_1^*$, the value R^0 can not be an equilibrium since the biomass of at least one species is growing. Thus values of $R > R_1^*$ can not be an equilibrium. On the other hand for values of $R < R_1^*$ all species shrink in biomass. For $R = R_1^*$, the species 1 biomass is at a steady-state while all other species shrink in biomass. Thus R_1^* is a steady-state equilibrium. Eventually the biomasses of all species except the first one will tend to zero, while the species 1 biomass will remain constant at the steady-state level B_1^* defined by the solution for B_1 of equation (2) in equilibrium, or $0 = S(R_1^*) - aR_1^* - w_1 B_1 l_1(B_1) g_1(R_1^*)$. ■

[Figure 1]

The mechanism driving this result is resource consumption. The biomass of species 1 will keep increasing until it drives the amount of the resource to its R^* , at which point there will be an insufficient amount of the resource for the survival of the other species.

The competitive displacement of species according to the R^* occurs in the long-run equilibrium. The transition dynamics of the system, which may include species from different functional groups, towards steady-state equilibrium are most likely to evolve in terms of fast and slow time scales.

In particular species with relatively high R^* show an initial period of relatively rapid growth with larger population than low R^* species. However, as time goes by, the low R^* species reduces the resource to levels insufficient for the survival of the high R^* species. The high R^* species is eventually displaced and its population approaches zero in the long run.⁶ Thus high R^*

⁶See Tilman [14], page 45; Tilman [12], page 22.

species tend to grow relative faster than low R^* species, but they are eventually displaced in equilibrium by the slow growing species. In an ecosystem with species belonging to different functional groups, the time scale of evolution might be quite different, including very fast growing species and very slow growing species. In such a case the competitive displacement principle will operate in the very long run and management rules for preserving the maximal biodiversity will be hard to interpret since some type of biodiversity is preserved for a long period of transitional dynamics.

Therefore, management rules for biodiversity preservation will be operational if applied to species evolving at approximately similar time scales. In this case the competitive displacement principle will tend to operate in one time scale within the same functional group.

In view of the above, and since our interest is in providing operational management rules, we interpret the system of (1) and (2) as representing a specific functional group in which the different species evolve in approximately the same time scale. For example consider a system of four functional groups ($j = 1, \dots, 4$), with $j = 1$ representing, say, trees, $j = 2$ representing woody shrubs, $j = 3$ representing perennials and $j = 4$ representing annuals. Each group consists of $i = 1, \dots, n_j$ species that evolve in the same time scale which is different from the time scale of the other groups. In this context the R^* rule can be interpreted as operating at different time scales that correspond to the time scales of the functional groups. Consider the case where the system (1) and (2) refers to the functional group $j = 1, \dots, 4$, and define $l_{j,i}(B_i) = \lambda_j l_i(B_i)$, with $\lambda_1 = 1$, $\lambda_2 = 1 + \varepsilon_2$, $\lambda_3 = \lambda_2 + \varepsilon_3$, $\lambda_4 = \lambda_3 + \varepsilon_4$, $\varepsilon_k > 0$, $k = 2, 3, 4$. Then there will be one R^* for each group and competitive displacement will take place at approximately the same time scale for the whole group, which means that one species of the group - the one with lowest $R_{j,i}^*$ - will competitively displace the other species, as shown in figure 2 for species $j = 1, 4$. The timing of the displacement will be different for each functional group.

[Figure 2]

The purpose of management in this context is to provide rules for each functional group. Thus the use of model (1) and (2) can be regarded as a metaphor in order to design management in more than one time scale, with these rules applied to functional groups evolving at different time scales. In view of this interpretation of the model, our subsequent analysis will refer to a specific functional group whose species evolve at the same time scale, with the index j dropped to simplify the notation.

3 Optimal Harvesting under Species Competition and the Golden Biodiversity Rule

In the optimal management problem we examine a situation where utility is derived both from the consumption of species and the existence of biodiversity within the functional group. That is, harvesting of the species generates consumptive utility, but utility is additionally derived from the existence of positive biomasses of species, which is nonconsumptive utility. We also assume that the limiting resource for which the species are competing has a negligible existence value and that no harvesting utility is derived by harvesting this resource.

Total consumptive and nonconsumptive utility derived at each instant of time $t \in [0, \infty)$ can be defined as:

$$v(\mathbf{H}(t), \mathbf{B}(t)) = V(\mathbf{H}(t)) + U(\mathbf{B}(t)) \quad (5)$$

$$\text{where } \mathbf{H}(t) = (H_1(t), \dots, H_n(t)), \mathbf{H} \in \mathcal{U} \subset \mathcal{R}^n$$

$$\mathbf{B}(t) = (B_1(t), \dots, B_n(t)), \mathbf{B} \in \mathcal{B} \subset \mathcal{R}^n \quad (6)$$

are the harvest and biomass vectors respectively with $\mathbf{H}, \mathbf{B} \geq 0$. We assume that $V(\cdot)$ is strictly increasing and concave with bounded first derivative, and that $U(\cdot)$ is strictly concave⁷ with $\frac{\partial U}{\partial B_i} = m_i \geq 0$ as $B \rightarrow 0^+$. If m_i is assumed to be very large ($m_i \rightarrow \infty$), then the assumption that the marginal utility of the biomass of a group of species becomes very large as the biomass becomes very small, reflects the fact that the specific species provides ecoservices which are essential at the margin when extinction of the species is near. Alternatively if we measure biomasses by using consumables as the numeraire, then if technological progress makes consumables such as computers and TV sets more plentiful,⁸ but it does not make environmental

⁷Since biodiversity is valued, the function $U(\cdot)$ can be specified by a Dixit-Stiglitz type utility function which defines a utility index from biodiversity as:

$$U(\mathbf{B}) = \left\{ \sum_{i=1}^n (u_i(B_i))^\gamma \right\}^{\frac{1}{\gamma}}, \quad \gamma \in (0, 1]$$

where $u_i(B_i)$ are concave utility functions with $\gamma(u_i'(B_i))^{\gamma-1} \rightarrow \infty$ for $B_i \rightarrow 0^+$ for all i . This specific utility index $U(\mathbf{B})$ puts a premium on biodiversity since aggregate utility increases when one more species with positive biomass is added. Furthermore γ parametrizes the substitutability among species regarding tastes for them, since the elasticity of substitution between the utility derived from any two species is $\frac{1}{1-\gamma} > 1$, if $\gamma = 1$ species are considered as perfect substitutes regarding individuals' tastes.

⁸This relates to Weitzman's [21] recombinant growth concept.

goods such as prairies more plentiful, then the marginal utility of a species near extinction becomes very high in terms of consumable units. On the other hand if $m_i = 0$ then the services of the specific species are not valued even if the species is close to extinction. This species can for example be regarded as a 'weed'.

The objective of management is to choose piecewise continuously differentiable harvesting functions $\{H_1(t), \dots, H_n(t)\}$ of time t on $[0, \infty)$ to maximize:

$$J = \int_0^{\infty} e^{-\rho t} [V(\mathbf{H}) + U(\mathbf{B})] dt \quad (7)$$

where $\rho \geq 0$ is the discount rate for future consumptive and nonconsumptive utilities. The constraint to the above maximization problem is the growth rate of the biomasses adjusted to take into account the reduction in the growth rate due to harvesting and the death rates d_i . Thus the biomass constraints can be written as:

$$\dot{B}_i = f_i(B_i) [g_i(R) - d_i - h_i], \quad H_i = f_i(B_i) h_i \quad (8)$$

In the optimal control problem (7) and (8) the resource is treated as a parameter since it is neither a control nor a source that generates utility.

In analyzing the optimal management problem (7) and (8) we distinguish two cases regarding the value of the discount rate ρ . One is the case where $\rho = 0$ and the other is the case where $\rho > 0$. In the first case a justification for a low discount rate $\rho \simeq 0$ can be given along two different lines. The first is the well-known Ramsey argument (Ramsey [12]) according to which discounting future utilities is 'ethically indefensible and arises mainly from weakness of the imagination'. Therefore according to this argument the utility derived from the existence of biodiversity by future generations should not be weighted less than the corresponding utility of the present generations. The second approach (Brock [1]) suggests that the observed real rates of interest, which are determined by the observed marginal physical product of capital and can be used as a discount rate for future utilities, are low - around 1% to 2% - and may be biased upwards. The upward bias arises when unpriced environmental services enter the aggregate production function as an input, along with aggregate capital, and the marginal product of capital is increasing in the unpriced environmental services. In this case the observed marginal product of capital is priced upwards. Thus not only are observed real rates of interest low, but if the above-described upward bias is taken into account, the discount rate chosen for future utilities could be close to zero.

When the undiscounted infinite horizon optimal control problem is analyzed, the integral (7) might not converge for $\rho = 0$, therefore an optimality concept needs to be introduced. We use the concept of overtaking optimality defined as follows:

Definition: A trajectory $\{\mathbf{B}^*(t)\}$ emanating from an initial state $\mathbf{B}(0)$ and generated by the control $\{\mathbf{H}^*(t)\}$ is overtaking optimal if:

$$\liminf_{T \rightarrow \infty} \int_0^T \{[V(\mathbf{H}^*) + U(\mathbf{B}^*)] - [V(\mathbf{H}) + U(\mathbf{B})]\} dt \geq 0$$

for any other trajectory $\{\mathbf{B}(t)\}$ emanating from $\mathbf{B}(0)$ and generated by the control $\{\mathbf{H}(t)\}$.

Having defined the optimality concept we now turn to the analysis of the control problem. According to the maximum principle if $\{\mathbf{B}^*(t)\}$ and $\{\mathbf{H}^*(t)\}$ are optimal according to the overtaking optimality criterion, the following conditions are satisfied for all i :

$$\frac{\partial \mathcal{H}}{\partial H_i} = \frac{\partial V}{\partial H_i} - q_i \leq 0 \text{ with equality if } H_i^* > 0 \quad (9)$$

$$\dot{q}_i = -\frac{\partial \mathcal{H}}{\partial B_i} = -\frac{\partial U}{\partial B_i} - q_i f'_i(B_i) [g_i(R) - d_i - h_i] \quad (10)$$

$$\dot{B}_i = f_i(B_i) [g_i(R) - d_i - h_i] \quad (11)$$

where $\mathcal{H}(\mathbf{B}, \mathbf{H}, \mathbf{q})$ is the Hamiltonian function defined as:

$$\mathcal{H}(\mathbf{B}, \mathbf{H}, \mathbf{q}) = [V(\mathbf{H}) + U(\mathbf{B})] + \sum_{i=1}^n q_i f_i(B_i) [g_i(R) - d_i - h_i] \quad (12)$$

and the costate variables q_i reflect the shadow value (price) of the biomass of species i .

Solving (7) we obtain, for interior solutions,

$$H_i^* = G(\mathbf{q}), \quad \mathbf{q} = (q_1, \dots, q_n) \text{ with } \frac{\partial G}{\partial q_i} < 0 \quad (13)$$

This is a short-run demand for harvesting as a function of the shadow cost of the biomass.

Substituting (13) into (10) and (11) we obtain the Hamiltonian Dynamic System (HDS):

$$\dot{q}_i = -\frac{\partial U}{\partial B_i} - q_i f'_i(B_i) [g_i(R) - d_i - G(\mathbf{q})] \quad (14)$$

$$\dot{B}_i = f_i(B_i) [g_i(R) - d_i - G(\mathbf{q}) h_i] \quad (15)$$

By the concavity assumptions of the objective function $V(\mathbf{H}) + U(\mathbf{B})$, and the functions $f_i(B_i)[g_i(R) - d_i - h_i]$, a bounded trajectory $\mathbf{B}^*(t)$ satisfying the maximum principle with a bounded associated trajectory $\mathbf{q}^*(t)$ is overtaking optimal.⁹

The steady-state for this system, defined as $(\bar{\mathbf{B}}, \bar{\mathbf{q}}) : \dot{B}_i = \dot{q}_i = 0 \forall i$, determines the equilibrium biomasses and their corresponding shadow values. We examine the properties of this steady-state in association with the optimal steady-state (OSS) of the optimal management problem (7) and (8) which defines the optimal equilibrium values of the biomasses and harvesting. For this problem the OSS $(\bar{\mathbf{B}}, \bar{\mathbf{H}})$ can be obtained as the solution of the concave programming problem:

$$\begin{aligned} & \max_{\mathbf{B}, \mathbf{H} \geq 0} V(\mathbf{H}) + U(\mathbf{B}) & (16) \\ \text{s.t. } & 0 \leq f_i(B_i)[g_i(R) - d_i - h_i], \forall i \end{aligned}$$

The OSS problem depends parametrically on the resource level R . We consider the case where the resource supply rate, $S(R) - aR$, in (2) acts as a 'homeostatic sink' at \bar{R} . This means that if $D(R) = \sum_{i=1}^n w_i f_i(B_i) g(R)$ is the demand for the resource which comes from the consumption by species, then for a wide range of demand values,¹⁰ the dynamics of (2) can move rapidly to \bar{R} . In such a case the OSS problem can be solved for fixed \bar{R} as a useful approximation of the 'true problem'.

⁹The existence of an overtaking optimal trajectory follows from theorem 4.5 of Carlson et al. [5].

¹⁰If we specify, for example, the resource supply rate as $S(R) - aR = A \left(1 - \frac{R}{\bar{R}}\right) - aR$, then (2) can be written as:

$$\dot{R} = \left[A \left(1 - \frac{R}{\bar{R}}\right) - aR \right] - D(R) = A \left[\left(1 - \frac{R}{\bar{R}}\right) - \frac{aR}{A} - \frac{D(R)}{A} \right] \quad (2')$$

For sufficiently large A , the rest point of (2') is sufficiently close to \bar{R} , and furthermore by sufficiently increasing A , the speed of relaxation towards the rest point can become very fast. Alternatively a constant level \bar{R} for the resource can be achieved by assuming external feeding to the system, without cost, so that the resource is kept at a constant level. For example, feeding intensity determining nutrient supply rates can produce nutrient poor, or nutrient rich, soils in which morphologically different but otherwise identical species compete (Tilman [15], Ch. 6). Since feeding does not impose any costs, the objective is reduced in optimizing the 'rest' of the system that reflects harvesting and biomass utility. The simplification of free feeding allows us to focus more clearly on biodiversity preservation management rules in more than one time scale. Costly feeding can be introduced into the model by allowing for a convex cost of feeding function. This can be regarded as a future research area for extensions of the present paper.

Solution of problem (16) determines the optimal steady-state harvesting and biomass vector. We call this equilibrium harvesting rule the maximal desired biodiversity maintenance (MDBM) principle, since it maintains the biodiversity that maximizes steady-state consumptive and nonconsumptive utility.

Theorem 2 (Biodiversity preservation) If $m_i > 0$, then with zero discount rate the MDBM principle preserves all species at the OSS. That is, all species have positive biomasses in equilibrium, irrespective of their R^* .

Proof: The biomass sets $\mathcal{B} \subset \mathfrak{R}^n$ are bounded below by zero and above by some B_i^{\max} since the limiting resource level is fixed at \bar{R} , the natural rate growth function $g_i(R)$ exhibits diminishing returns and the function $l_i(B_i)$ that describes density dependent growth is decreasing. Since biomasses are bounded the harvest sets $\mathcal{U} \subset \mathfrak{R}^n$ are bounded below by zero and above by H_i^{\max} . Thus the sets $\mathcal{B} \subset \mathfrak{R}^n$ and $\mathcal{U} \subset \mathfrak{R}^n$ of biomasses and harvesting respectively can be considered closed and bounded. Thus the constraint set of problem (16) is compact. The constraint set is furthermore convex by the concavity assumption on the constraint function. Since the objective function is strictly concave, a unique OSS exists. This OSS is defined parametrically for $R = \bar{R}$, thus in general $\bar{B}_i = \bar{B}_i(\bar{R})$ and $\bar{H}_i = \bar{H}_i(\bar{R})$. The OSS is characterized by the Kuhn-Tucker conditions as:

$$\frac{\partial \mathcal{L}}{\partial B_i} \leq 0 \text{ or } \frac{\partial U(\bar{\mathbf{B}})}{\partial B_i} + \bar{q}_i f'_i(\bar{B}_i) [g_i(R) - d_i - \bar{h}_i] \leq 0 \quad (17)$$

$$\text{with equality if } \bar{B}_i > 0 \quad (18)$$

$$\frac{\partial \mathcal{L}}{\partial H_i} \leq 0 \text{ or } \frac{\partial V(\bar{\mathbf{H}})}{\partial H_i} \leq \bar{q}_i \text{ with equality if } \bar{H}_i > 0 \quad (19)$$

$$\bar{q}_i f_i(\bar{B}_i) [g_i(R) - d_i - \bar{h}_i] = 0, \bar{q}_i \geq 0 \quad (20)$$

where \mathcal{L} is the Lagrangian function

$$\mathcal{L} = V(\mathbf{H}) + U(\mathbf{B}) + \sum_{i=1}^n q_i f_i(B_i) [g_i(R) - d_i - h_i]$$

From (19), $q_i > 0$. Thus from (20), $[g_i(R) - d_i - \bar{h}_i] = 0$, or $f_i(\bar{B}_i) = 0$. Take the case where $[g_i(R) - d_i - \bar{h}_i] = 0$, then (17) becomes $\frac{\partial U}{\partial B_i} \leq 0$, $\bar{B}_i \geq 0$. But since $\lim_{B_i \rightarrow 0} \frac{\partial U}{\partial B_i} = m_i > 0$, $\bar{B}_i = 0$ can not be a solution to the OSS problem. If $f_i(\bar{B}_i) = 0$ with $\bar{B}_i = 0$, then by the definition of the OSS, equilibrium for equation (1) implies $[g_i(R) - d_i - \bar{h}_i] = 0$, and as shown

before, $\bar{B}_i = 0$ can not be a solution. Therefore in equilibrium $\bar{B}_i > 0 \forall i$ and biodiversity is preserved irrespective of the species R^* . ■

Corollary 1 If $m_i = 0$ for some species, say ζ , then the species could be extinct at the steady state.

This follows directly from the proof of theorem 2. If $m_\zeta = 0$, then $\bar{B}_\zeta = 0$, could be a solution of (18). In this case the MDBM principle does not preserve all species in equilibrium.

Corollary 2 The Lagrangian multiplier \bar{q} of the OSS problem is the steady-state biomass shadow value (costate variable) for the HDS. That is, (\bar{B}, \bar{q}) is the unique steady-state of the HDS.

This corollary follows directly from the implicit programming theorem for optimal control with zero discounting (Carlson et al., [5], Theorem 6.6). The costate variable is also a function of the resource $\bar{q}_i = \bar{q}_i(R)$.

At the steady-state of the HDS, we obtain from (15)

$$g_i(R) - d_i - \bar{h}_i = 0 \quad (21)$$

Thus the optimal equilibrium harvesting rate is defined as $\bar{h}_i = g_i(R) - d_i$, where $\bar{h}_i = \frac{H_i}{f_i(\bar{B}_i)}$ is the effective rate of the equilibrium 'depreciation-equivalent' harvest. The relative size of this optimal harvesting rate among the different species is determined as follows:

Theorem 3 (Inverse R^* harvesting rule) The MDBM principle implies that the size of the effective harvest rate for each species is in reverse order to the species R^* . The species with lower R^* are harvested more heavily.

Proof. For preservation of biodiversity we must have $\bar{R} \geq R_n^*$ with strict inequality if the harvest rate of the n th species is positive. The level of \bar{R} is shown in figure 1. From (21) equilibrium requires

$$\frac{g_i(\bar{R}) - \bar{h}_i}{d_i} - 1 = 0 \quad (22)$$

With the ranking of $\frac{g_i(R)}{d_i}$ functions as in theorem 1, condition (22) implies that $\frac{\bar{h}_1}{d_1} > \frac{\bar{h}_2}{d_2} > \dots > \frac{\bar{h}_n}{d_n}$, as shown in figure 1, which is an inverse R^* harvesting rule. ■

The above theorem implies that to preserve the maximal desired biodiversity, the optimal rule is to harvest more aggressively the species that in

the unmanaged-undisturbed habitat would have competitively displaced all other species in the long-run equilibrium. In order to support all species indicated by the MDBM principle in equilibrium, \bar{R} must be large enough to exceed R_n^* (see figure 1).¹¹

Since the inverse R^* rule can be applied to different functional groups, the MDBM principle implies management in more than one time scale. Therefore there could be distinct management rules for annuals, for perennials, for woody shrubs and for trees. Harvesting will take place at different time scales, but the combined application of the four management rules will ensure MDBM for the ecosystem containing all four functional groups.

Having established the characteristics of the steady-state regarding the biodiversity and harvesting rules, we turn now to an examination of its stability properties. Stability relates to the ability of the system to return to the OSS and is closely related to the system's resilience.

Theorem 4 (Strong resilience property) The OSS of the biomass vector $\bar{\mathbf{B}}$ is globally asymptotically stable for all bounded biomass trajectories.

Proof. By the concavity of the $U(\mathbf{B})$ and $V(\mathbf{H})$ functions we have

$$\begin{aligned} & \int_0^T \{ [V(\mathbf{H}) - V(\bar{\mathbf{H}})] + [U(\mathbf{B}) - U(\bar{\mathbf{B}})] \} dt = \\ & \int_0^T V'_H(\bar{\mathbf{H}}) (\mathbf{H} - \bar{\mathbf{H}}) dt + \int_0^T U'_B(\bar{\mathbf{B}}) (\mathbf{B} - \bar{\mathbf{B}}) dt \\ & - \int_0^T \delta(t) dt - \int_0^T \beta(t) dt \end{aligned} \quad (23)$$

where $V'_H(\bar{\mathbf{H}})$ and $U'_B(\bar{\mathbf{B}})$ are the gradient vectors evaluated at $(\bar{\mathbf{H}}, \bar{\mathbf{B}})$. From the maximum principle we have:

$$V'_H(\mathbf{H}) = \mathbf{q} \text{ and } \dot{\mathbf{H}} = f(\mathbf{B}) [g(R) - \mathbf{d}] - \dot{\mathbf{B}}$$

Substituting above, the first term of the RHS of (23) becomes:

$$\int_0^T \bar{\mathbf{q}} \left\{ \left[\dot{\mathbf{B}} - f(\mathbf{B}) [g(R) - \mathbf{d}] \right] - \left[\dot{\bar{\mathbf{B}}} - f(\bar{\mathbf{B}}) [g(R) - \mathbf{d}] \right] \right\} dt$$

¹¹ If the MDBM principle indicates extinction of a species, say ζ , in equilibrium, then the harvesting rule should be $h_\zeta > g_\zeta(\bar{R}) - d_\zeta$. Then, $\dot{B}_\zeta < 0$, and eventually the species biomass is driven to zero. In terms of figure 1, this implies that for species ζ we move below the unit line. The same harvesting rule can also be applied in the case where there is no consumptive or nonconsumptive utility from a species. This species can be regarded as a 'weed'. If the weed, ξ , is harvested according to the 'weeding rule' $h_\xi > g_\xi(\bar{R}) - d_\xi$, then it is not preserved at the steady-state.

$$\begin{aligned}
&= \int_0^T \bar{q} (\dot{\bar{\mathbf{B}}} - \dot{\mathbf{B}}) dt + \\
&\quad \int_0^T \bar{q} \{f(\mathbf{B}) [g(R) - d] - f(\bar{\mathbf{B}}) [g(R) - d]\} dt
\end{aligned} \tag{24}$$

Integrating by parts the first term of (24) we obtain:

$$\begin{aligned}
&\int_0^T \bar{q} (\dot{\bar{\mathbf{B}}} - \dot{\mathbf{B}}) dt = \bar{q} (\bar{\mathbf{B}} - \mathbf{B}) \Big|_0^T - \int_0^T \dot{\bar{q}} (\bar{\mathbf{B}} - \mathbf{B}) dt \\
&= \bar{q}(T) (\bar{\mathbf{B}}(T) - \mathbf{B}(T)) \\
&\quad - \bar{q}(0) (\bar{\mathbf{B}}(0) - \mathbf{B}(0)) - \int_0^T \dot{\bar{q}} (\bar{\mathbf{B}} - \mathbf{B}) dt
\end{aligned} \tag{25}$$

Assuming that $(\bar{\mathbf{B}}, \bar{\mathbf{H}}, \bar{q})$ is the OSS, then we have $\dot{\bar{\mathbf{B}}} = \dot{\bar{q}} = 0$, $U'_{\mathbf{B}}(\bar{\mathbf{B}}) = 0$, and also $\bar{\mathbf{B}}(0) = \mathbf{B}(0)$. Then the RHS of (24) becomes

$$\bar{q} (\bar{\mathbf{B}} - \mathbf{B}(T)) + [g(R) - d] \int_0^T \bar{q} [f(\mathbf{B}) - f(\bar{\mathbf{B}})] dt \tag{26}$$

After substitutions (23) becomes:

$$\begin{aligned}
&\int_0^T \delta(t) dt + \int_0^T \beta(t) dt = \bar{q} (\bar{\mathbf{B}} - \mathbf{B}(T)) \\
&+ [g(R) - d] \int_0^T \bar{q} [f(\mathbf{B}) - f(\bar{\mathbf{B}})] dt \\
&- \int_0^T \{ [V(\mathbf{H}) - V(\bar{\mathbf{H}})] + [U(\mathbf{B}) - U(\bar{\mathbf{B}})] \} dt
\end{aligned} \tag{27}$$

with $[g(R) - d] > 0$ at the OSS since $\bar{\mathbf{H}} > 0$. For the LHS of (27) we have

$$- \int_0^T \delta(t) dt \Big\{_{\text{finite}}^{-\infty}, - \int_0^T \beta(t) dt \Big\}_{\text{finite}}^{-\infty}$$

For good programs the above integrals are finite, under appropriate regularity conditions.¹² This implies that

$$\lim_{T \rightarrow \infty} \delta(T) = 0, \quad \lim_{T \rightarrow \infty} \beta(T) = 0$$

From (27) we obtain for $t = T$:

$$\begin{aligned}
&\delta(T) + \beta(T) = \bar{q} (\bar{\mathbf{B}} - \mathbf{B}(T)) + \bar{q} [g(R) - d] [f(\mathbf{B}(T)) - f(\bar{\mathbf{B}})] \\
&- \{ [V(\mathbf{H}(T)) - V(\bar{\mathbf{H}})] + [U(\mathbf{B}(T)) - U(\bar{\mathbf{B}})] \} = 0
\end{aligned} \tag{28}$$

¹² See Carlson et al. [5], Chapter 4.

In (28) $\delta(T) + \beta(T)$ is a concave function of \mathbf{B} and \mathbf{H} , and the function $V(\mathbf{H}(T)) + U(\mathbf{B}(T))$ attains a unique maximum at the OSS at $(\bar{\mathbf{H}}, \bar{\mathbf{B}})$. Therefore as $T \rightarrow \infty$, $\mathbf{H} \rightarrow \bar{\mathbf{H}}$ and $\mathbf{B} \rightarrow \bar{\mathbf{B}}$. ■

The strong resilience property of the equilibrium biomass vector implies that as long as the habitat is optimally managed by using the inverse R^* harvesting rule, then optimal equilibrium biodiversity can be preserved irrespective of the initial biodiversity state. Also and perhaps more importantly, no matter how the initial conditions are shocked, the system always returns to the OSS and biodiversity is preserved.

The results obtained in theorems 2-4 above introduce a concept of sustainable harvesting strategy because, by following the inverse R^* harvesting rule, biomasses are preserved for future generations. Furthermore, since the inverse R^* harvesting rule is obtained at the optimal steady-state by maximizing utility subject to the steady-state condition, and by the strong resilience property the system converges to the OSS with zero discounting, the inverse R^* harvesting rule can be regarded as a golden biodiversity rule. This definition of the golden biodiversity rule is similar to other approaches defining golden rules in relation to the environment. In particular, Brock [1] defines a polluted golden age as the maximizing of utility from consumption and environmental goods subject to steady-state conditions, while Chichilnisky et al. [6] define a green golden rule as maximizing the undiscounted very long-run utility from consumption of a single renewable resource.

3.1 Biodiversity Preservation and the Resilience Principle under Discounting

In this section we relax the assumption of zero discounting and examine the implications of discounting consumptive and nonconsumptive utility at a positive discount rate, $\rho > 0$. For this problem, (12) determines now the current value Hamiltonian, and the conditions of the maximum principle include (9), (11) and

$$\dot{q}_i = \rho q_i - \frac{\partial U}{\partial B_i} - q_i f'_i(B_i) [g_i(R) - d_i - h_i] \quad (29)$$

The Modified Hamiltonian Dynamic System (MHDS) is defined in this case by (11) and (29) for solutions for H_i^* given by (13).

The OSS for \mathbf{B} , \mathbf{H} and \mathbf{q} is the triplet $(\bar{\mathbf{B}}, \bar{\mathbf{H}}, \bar{\mathbf{q}})$ defined by the solution of the implicit programming problem (Carlson et al., [5]):

$$\max_{\mathbf{B}, \mathbf{H} \geq 0} V(\mathbf{H}) + U(\mathbf{B}) \quad (30)$$

$$\text{s.t. } 0 = f_i(B_i) [g_i(R) - d_i - h_i] - \rho (B_i - \bar{B}_i), \forall i$$

where \mathbf{q} is the vector of the Lagrangian multipliers associated with the above problem. In this case $(\bar{\mathbf{B}}, \bar{\mathbf{q}})$ is the steady state of the MHDS (11), (29).

One implication of discounting at a positive rate is that all species with $m_i > 0$ are not necessarily included in the maximal desired biomass if m_i is sufficiently small and ρ is sufficiently large.

Theorem 5 (Biodiversity preservation under discounting) Let \bar{q}_i be
the steady-state biomass shadow value as defined by the solution of the implicit programming problem (30). If $\frac{m_i}{\bar{q}_i} < \rho$, then $\bar{B}_i = 0$.

Proof. The proof follows theorem 2. The Lagrangian function for the implicit programming problem is:

$$\mathcal{L} = V(\mathbf{H}) + U(\mathbf{B}) + \sum_{i=1}^n q_i [f_i(B_i) [g_i(R) - d_i - h_i] - \rho (B_i - \bar{B}_i)]$$

The Kuhn Tucker conditions are (19), and

$$\frac{\partial \mathcal{L}}{\partial B_i} \leq 0 \text{ or } \frac{\partial U(\bar{\mathbf{B}})}{\partial B_i} + \bar{q}_i [f'_i(\bar{B}_i) [g_i(R) - d_i - \bar{h}_i] - \rho] \leq 0 \quad (17')$$

with equality if $B_i > 0$

At the steady-state we have $[g_i(R) - d_i - \bar{h}_i] = 0$ with $\bar{q}_i > 0$. Then for $\bar{B}_i = 0$ to be a steady-state equilibrium for species i , condition (17') requires $\frac{m_i}{\bar{q}_i} < \rho$. ■

Since m_i can be interpreted as the marginal nonconsumptive value for a species near extinction and \bar{q}_i can be interpreted, by using (19), as the marginal consumptive value of the same species near extinction, then the above theorem implies that the species does not enter the maximal desired biomass if the ratio of the nonconsumptive to the consumptive marginal utility near extinction is less than the discount rate.¹³

A strong resilience property can also be shown in the discounted management problem, $\rho > 0$. The strong resilience principle defined above still holds for the discounted case, provided that the discount rate is sufficiently small.

¹³It should also be noted that discounting may have significant effects when moving from one time scale to another. For example using a specific rate for a functional group with short lived species, at the time scale of a functional group with long lived species, will result in heavy discounting on the long lived species time scale. In such a case only a portion of these species' lives will get any weight at the short lived species discount rate. Thus we regard the issue of choosing a discount rate as relevant for a functional group at the same time scale.

Theorem 6 (Resilience under light discounting) If the discount rate ρ
 is sufficiently small, then the OSS of the biomass vector $\bar{\mathbf{B}}$ is globally asymptotically stable (GAS) for all bounded biomass trajectories.

Proof. We prove that the steady-state of the MHDS $(\bar{\mathbf{B}}, \bar{\mathbf{q}})$ is GAS for bounded solutions $\phi_t(\mathbf{B}(0), \mathbf{q}(0))$ of the MHDS following the Brock and Scheinkman [4]¹⁴ approach to the stability of optimal control.

Define the maximized current value Hamiltonian:

$$\mathcal{H}^o(\mathbf{B}, \mathbf{q}) = V(\mathbf{G}(\mathbf{q})) + U(\mathbf{B}) + \mathbf{q}f(\mathbf{B})[g(R) - \mathbf{d} - \mathbf{G}(\mathbf{q})]$$

which is concave in \mathbf{B} and convex in \mathbf{q} , and the curvature matrix

$$Q(\mathbf{B}, \mathbf{q}) = \begin{bmatrix} \mathcal{H}_{\mathbf{q}\mathbf{q}}^o & \frac{\rho}{2}I \\ \frac{\rho}{2}I & -\mathcal{H}_{\mathbf{B}\mathbf{B}}^o \end{bmatrix} \quad (31)$$

where I is an $(n \times n)$ identity matrix and the matrices of second derivatives are positive semidefinite matrices, since \mathcal{H}^o is concave in \mathbf{B} and convex in \mathbf{q} .

Let the discount rate be sufficiently small so that

$$\lambda_q \lambda_B > 4\rho^2 \quad (32)$$

where λ_q is the smallest eigenvalue of the positive definite matrix $\mathcal{H}_{\mathbf{q}\mathbf{q}}^o$ and λ_B is the smallest eigenvalue of the positive definite matrix $-\mathcal{H}_{\mathbf{B}\mathbf{B}}^o$. Since $\mathcal{H}_{\mathbf{q}\mathbf{q}}^o$ and $-\mathcal{H}_{\mathbf{B}\mathbf{B}}^o$ are positive semidefinite matrices, they will be positive definite except in hairline cases. When (32) is satisfied, the curvature matrix is positive definite and all bounded solutions of the MHDS converge to the steady state $(\bar{\mathbf{B}}, \bar{\mathbf{q}})$ as $t \rightarrow \infty$. ■

Thus if the discount rate for future utilities is not very large, the inverse R^* harvesting rules attribute a strong resilience property to the system. Thus on the stable n -dimensional manifold for any initial biomass vector, an initial biomass shadow value vector exists, such that the system converges to the OSS with the maximal desired biodiversity preserved.

Our results on the resilience principle with zero or light discounting, can be compared to the results obtained by Chichilnisky et al. [6], who found that low discounting is required in order to achieve saddle point stability for the problem of maximizing discounted utility plus very long-run utility in a growth model, where a single renewable resource is used for output production and its stock generates utility. As mentioned above the maximization of the undiscounted very long-run utility is used to derive the green golden rule.

¹⁴ See also Brock and Malliaris [3] for a review of these results.

It is important to note that the inverse R^* harvesting rule that ensures biodiversity in equilibrium also attributes global stability to the habitat. It can therefore be claimed that under optimal management and light discounting, biodiversity begets stability.

4 Biodiversity preservation under uncertainty

The previous section analyzed the optimal management problem when the growth rates of the species biomasses were deterministic. In this section we extend our results to a stochastic environment.

Let (Ω, \mathcal{F}, P) be a complete probability space, and let $\mathbf{B}(\omega, t)$ and $\mathbf{H}(\omega, t)$ be the stochastic processes for the species biomasses and harvesting respectively and let $\mathbf{z}(\omega, t)$ be an $(n \times 1)$ vector Wiener process, $\mathcal{E}(dz) = 0$, $\text{var}(dz) = dt$. To simplify things we assume that the Wiener processes are uncorrelated.

The stochastic management problem can be defined as the choice of a nonanticipating harvesting process $\mathbf{H}(\omega, t)$ that maximizes the expected value of the consumptive and nonconsumptive utility, subject to the constraints imposed by species growth rates:

$$\max_{\mathbf{H}(\omega, t)} \mathcal{E}_0 \int_0^\infty e^{-\rho t} [V(\mathbf{H}(\omega, t)) + U(\mathbf{B}(\omega, t))] dt \quad (33)$$

$$\text{s.t. } dB_i = [f_i(B_i(\omega, t)) [g(R) - d_i] - H_i(\omega, t)] dt + \sigma_i B_i(\omega, t) dz_i(\omega, t) \quad (34)$$

$$i = 1, \dots, n, \quad B_i(0) = B_i^0 \text{ nonrandom.}$$

with $\mathbf{B} = \mathbf{B}(t) = \mathbf{B}(\omega, t)$ the state variable and $\mathbf{H} = \mathbf{H}(t) = \mathbf{H}(\omega, t)$ the control variable of the stochastic control problem. In equation (34) the term $[f_i(B_i) [g(R) - d_i] - H_i]$ represents the expected change in the biomass of species i at any given point in time, while the term $\sigma_i B_i dz_i$ is the random amount of biomass change, with zero mean and variance $(\sigma_i B_i)^2$.

To determine the optimal harvesting process we introduce the generalized current value Hamiltonian

$$\begin{aligned} \mathcal{M}(\mathbf{B}, \mathbf{H}, \mathbf{p}, \boldsymbol{\pi}) &= V(\mathbf{H}) + U(\mathbf{B}) \\ &+ \sum_{i=1}^n p_i [f_i(B_i) [g(R) - d_i] - H_i] + \sum_{i=1}^n \pi_i \sigma_i B_i \end{aligned} \quad (35)$$

where π_i is the risk associated with the adjustments induced by the disturbances $(\sigma_i B_i)$.

Optimal harvesting is obtained by maximizing the generalized Hamiltonian. For interior solutions we have:

$$\frac{\partial \mathcal{M}}{\partial H_i} = 0 \text{ or } \hat{H}_i^* = s_i(\mathbf{p}) \quad (36)$$

The costate variable \mathbf{p} of the generalized Hamiltonian (35) is defined as:

$$p_i(t) = \frac{\partial W(\mathbf{B}(t))}{\partial B_i} \quad (37)$$

where $W(\mathbf{B}(t))$ is the current value function defined as:

$$W(\mathbf{B}(t)) = \max_{\mathbf{H}} \mathcal{E}_t \int_0^{\infty} e^{-\rho(\tau-t)} [V(\mathbf{H}(\omega, \tau)) + U(\mathbf{B}(\omega, \tau))] d\tau \quad (38)$$

and where $\mathbf{B}(\omega, t)$ is determined through (34). The current value function solves the following Hamilton-Bellman-Jacobi equation (Malliaris and Brock [9]):

$$\begin{aligned} \rho W = \max_{\mathbf{H}} [V(\mathbf{H}) + U(\mathbf{B}) + \\ \sum_{i=1}^n W'_{B_i} [f_i(B_i) [g(R) - d_i] - H_i] + \frac{1}{2} \sum_{i=1}^n W''_{B_i B_i} (\sigma_i B_i)^2] \end{aligned} \quad (39)$$

Therefore $\frac{\partial p_i(t)}{\partial B_i} = \frac{\partial^2 W(\mathbf{B}(t))}{\partial B_i^2} = W''_{B_i B_i}$. Using (35), (36) and (39) the maximized generalized Hamiltonian is defined as:

$$\mathcal{M}^o(\mathbf{B}, \mathbf{p}, \pi, \mathbf{s}(\mathbf{p})) = \max_{\mathbf{H}} \mathcal{M}(\mathbf{B}, \mathbf{p}, \pi, \mathbf{H}) = \rho W$$

and $\pi_i = \frac{1}{2} \frac{\partial^2 W(\mathbf{B}(t))}{\partial B_i^2} (\sigma_i B_i) < 0$ for a concave value function, reflecting risk premiums associated with random biomass growth rates. Using (37) optimal harvesting can be defined as:

$$\hat{H}_i^* = s_i(\mathbf{p}) = \left(\frac{\partial W(\mathbf{B}(t))}{\partial B_1}, \dots, \frac{\partial W(\mathbf{B}(t))}{\partial B_n} \right) = \psi_i^*(\mathbf{B}) \quad (40)$$

since optimal harvesting depends on current biomasses and $\psi_i^*(\mathbf{B})$ is called an optimal policy function (Brock and Magill [2]).

If the functions

$$\phi_{i1}^*(\mathbf{B}) = [f_i(B_i) [g(R) - d_i] - \psi_i^*(\mathbf{B})], \quad \phi_{i2}^*(\mathbf{B}) = \sigma_i B_i$$

satisfy a Lipschitz condition then the optimal biomass process that solves the stochastic optimal management problem, defined as

$$B_i^*(\omega, t) = B_i^o + \int_0^t \phi_{i1}^*(\mathbf{B}(\omega, \tau)) d\tau + \int_0^t \phi_{i2}^*(\mathbf{B}(\omega, \tau)) d\tau$$

is a continuous Markov process (Brock and Magill [2]).

The optimal biomass processes and the corresponding costate variables \mathbf{p} are determined by the stochastic Hamiltonian system (SHS):

$$dB_i = [f_i(B_i^*) [g(R) - d_i] - s_i(\mathbf{p})] dt + \sigma_i B_i^* dz_i \quad (41)$$

$$dp_i = \left[\rho p_i - \frac{\partial U(\mathbf{B}^*)}{\partial B_i} - f_i'(B_i) [g(R) - d_i] + s_i(\mathbf{p}) - 2\pi_i \sigma_i \right] dt + 2\pi_i dz_i \quad (42)$$

The SHS defined above can be used to analyze the equilibrium mean biomasses as well as the equilibrium distribution of the biomasses.

Denote by $\mathbf{B}^m(t) = \mathcal{E}[\mathbf{B}^*(t)]$, $\mathbf{H}^m(t) = \mathcal{E}[\hat{\mathbf{H}}^*(t)]$ and $\mathbf{p}^m(t) = \mathcal{E}[\mathbf{p}(t)]$ the mean biomasses, harvesting and the corresponding shadow values respectively and assume that $\lim_{B_i^m \rightarrow 0} \frac{\partial U(\mathbf{B}^*)}{\partial B_i} = +\infty$ and that $U'''(\mathbf{B}^m)$ is sufficiently small. By taking expected values in the integral form of equations (41), (42) and assuming $\rho = 0$, we obtain the following system of ordinary differential equations:

$$\dot{B}_i^m = \mathcal{E}[f_i(B_i^*)] [g(R) - d_i] - \mathbf{H}^m, \quad \mathbf{H}^m = h_i \mathcal{E}[f_i(B_i^*)] \quad (43)$$

$$\dot{p}_i^m = \mathcal{E} \left[-\frac{\partial U(\mathbf{B}^*)}{\partial B_i} \right] - \left\{ \mathcal{E}[f_i'(B_i)] [g(R) - d_i] - \mathbf{H}^m \right\} - 2\sigma_i \mathcal{E}[\pi_i] \quad (44)$$

Theorem 7 When optimal management as defined above is undertaken in the stochastic environment, then: (i) all species have positive mean biomasses in equilibrium irrespective of their R^* , and (ii) biodiversity preservation in equilibrium in terms of means, implies that the size of the mean effective harvest rate for each species is in reverse order to the species R^* .

Proof. From (43) equilibrium in terms of mean biomasses implies

$$[g(R) - d_i] - \mathbf{H}^m = 0$$

Then from (44), $\mathcal{E} \left[\frac{\partial U(\mathbf{B}^*)}{\partial B_i} \right] = -2\sigma_i \mathcal{E} [\pi_i]$, but by Jensen's inequality

$$\mathcal{E} \left[\frac{\partial U(\mathbf{B}^*)}{\partial B_i} \right] = \frac{\partial U(\mathbf{B}^m)}{\partial B_i} + \gamma,$$

$$\gamma \begin{matrix} \geq \\ \leq \end{matrix} 0 \text{ according to whether } U'''(\mathbf{B}) \begin{matrix} \geq \\ \leq \end{matrix} 0$$

Then according to the assumptions about the marginal utility of the mean biomass, we have that $\mathbf{B}^m > 0$ for all i , which proves the first part of the theorem. The second part follows from (43) after dividing throughout by $\mathcal{E} [f_i(B_i^*)]$. ■

According to the above theorem, inverse R^* harvesting preserves biodiversity in expected value terms which is a result similar to the one obtained for the deterministic case. Also in a way similar to the deterministic case a resilience principle can be associated with the inverse R^* harvesting of the stochastic model. In order to prove the stochastic resilience principle the following assumptions are made:¹⁵

- A1 The optimal stochastic processes $\mathbf{B}^*(\omega, \tau)$, $\mathbf{p}(\omega, \tau)$ that solve the SHS satisfy the transversality condition:

$$\lim_{T \rightarrow \infty} \sup \mathcal{E}_0 [\mathbf{p}(\omega, \tau) \mathbf{B}^*(\omega, \tau)] \leq 0$$

- A2 $\mathbf{B}^*(\omega, \tau) \in \mathcal{A}$, $\mathbf{p}(\omega, \tau) \in \mathcal{P} \forall (\omega, \tau)$, where \mathcal{A} and \mathcal{P} are compact and convex sets.

- A3 The value function is strictly concave.

Theorem 8 (Stochastic resilience principle) Assume that A1 - A3 are satisfied and let $F_t(\mathbf{B}) = F_t(B_1, \dots, B_n)$ be the distribution function of the species biomasses at time t as determined by the optimal process $\mathbf{B}^*(\omega, \tau)$, generated by the optimal harvesting policy function $\psi_i^*(\mathbf{B})$. Then under light discounting, a stationary distribution function exists. $F(\mathbf{B}) = F(B_1, \dots, B_n)$ for the n species such that F_t converges to F as $t \rightarrow \infty$, or $F_t(\mathbf{B}) - F(\mathbf{B}) \rightarrow 0$ as $t \rightarrow \infty$.

Proof. Define the Hamiltonian curvature condition as:

- (i) $\tilde{Q}(\mathbf{B}, \mathbf{p}) = \begin{bmatrix} \mathcal{M}_{\mathbf{p}\mathbf{p}}^o & \frac{\rho}{2} I \\ \frac{\rho}{2} I & -\mathcal{M}_{\mathbf{B}\mathbf{B}}^o \end{bmatrix}$, uniformly positive definite
- (ii) $\mathcal{M}_{\pi_i \pi_i}^o, \forall i$ are non-negative definite

¹⁵ See Brock and Magill [2] for a detailed presentation of these assumptions.

This condition is satisfied since $\tilde{Q}(\mathbf{B}, \mathbf{p})$ is positive definite by the same arguments as in the proof of theorem 4 above and $\mathcal{M}_{\pi, \pi_t}^o = 0$. Since the curvature condition is satisfied it follows from Brock and Magill([2], Theorem 4) that if ϕ_t denotes the probability measure for the process $\mathbf{B}^*(\omega, \tau)$ that starts from a nonrandom initial condition $\mathbf{B}^o \in \mathcal{A}$, then ϕ_t converges weakly to a unique invariant probability measure ϕ as $t \rightarrow \infty$ for all nonrandom initial conditions $\mathbf{B}^o \in \mathcal{A}$, or $\phi_t \rightarrow \phi$ as $t \rightarrow \infty$. Since convergence in probability implies convergence in distribution, $F_t - F \rightarrow 0$ as $t \rightarrow \infty$. ■

The stochastic resilience principle implies that irrespective of how the system's initial conditions are shocked, the optimally-managed habitat will converge to the equilibrium species distribution.

The analysis of the management problem under uncertainty also suggests that the model can be used as a basis for further extensions along the lines of the capital assets pricing model (CAPM) developed in the theory of finance. In the context of economic/ecological modelling this could relate to the concept of a portfolio of species.¹⁶ One way of approaching the 'ecological CAPM' problem is to determine the allocation of biomasses for different species in a functional group, given an initial total biomass of all the species in the group and stochastic growth rates, in order to maximize utility defined over the expected mean of total biomass and its variance. In the same context the allocation (portfolio) of biomasses that determines a minimum variance locus for a given mean biomass can be obtained. An alternative way of approaching the problem is to consider it as an intercropping problem where the objective is defined in terms of the harvest from the polyculture. The target would be to determine harvesting rules for different species, in order to maximize utility from harvesting, defined in mean - variance terms, or determine the minimum variance locus for a given mean harvesting.¹⁷

5 Conclusions

When species compete for a limiting resource in a homogeneous habitat, then the equilibrium outcome, according to the resource-based model, is a monoculture with the species characterized by the lowest resource requirement (the lowest R^*) outcompeting all the rest. Species coexistence and biodiversity, in this context, is explained by spatial and temporal heterogeneities of the

¹⁶There are a number of empirical studies relating the number of species in ecosystems to plant productivity (Naeem et al.[10], Tilman et al.[18], Hooper and Vitousek [7]) which have found that functional diversity is a principal factor explaining plant productivity.

¹⁷Vandermeer [19], in a similar type of problem, seeks to allocate a given area to different plants so as to minimize the variance of the sum of crops from all plants.

habitats, differences among species and disturbances with spatially and possibly temporally differentiated incidences. Therefore the extent to which a given habitat undisturbed by human action will end up as a monoculture or a multispecies assembly depends upon natural characteristics and stochastic shocks in the habitat.

Biodiversity, however, can be regarded as valuable to a society for two reasons. The first is the presence of existence values for the species of the habitat. The second is that biodiversity promotes the functioning and the sustainability of an ecosystem and thus can prevent the system from collapsing when random shocks affect it. As shown for example by Tilman and Downing [16], diverse plant communities are more resistant to and recover more fully from a major drought.

In this paper we examined the management of ecosystems which are valued not only in terms of the amounts of species harvested, but also in terms of the number of species existing as a result of positive existence values. The main result is that when the objective is to maximize aggregate utility from harvesting and from existence of biodiversity, then by following the inverse R^* harvesting rule, that is, harvesting more aggressively the species with relatively lower resource requirements, the maximal desired biodiversity is preserved in equilibrium. The harvesting rule can be applied to functional groups evolving at different time scales, providing therefore a framework for management in more than one time scales. Furthermore the equilibrium biodiversity is globally stable, indicating that the optimally-managed system possesses a strong resilience property. This property holds under light discounting and in both the deterministic and stochastic cases.

Our results indicate that the inverse R^* harvesting rule can be regarded as an optimal disturbance from the society to the ecosystem, optimal in the sense of preserving species diversity and at the same time promoting the resilience of the system. It should be further noted that our optimal management rule provides a sustainable harvesting strategy for the harvested habitat, since its biodiversity is preserved intact for future generations and the habitat acquires resilience to external shocks.

The sustainable harvesting concept can be related to Chichilnisky et al.'s [6] green golden rule, obtained by maximizing the very long-run utility from consumption and a single renewable resource. Our harvesting rule at the OSS with zero discounting can be regarded as characterizing the maximum utility level, both consumptive and nonconsumptive, that can be maintained indefinitely. In this sense our inverse R^* rule can be interpreted as a golden biodiversity rule. An area of future research could be to derive the optimal harvesting rules in a multi-species context under a limiting resource, when preferences are represented, as in Chichilnisky et al. [6], by the sum of

discounted utilities plus the very long-run utility value.

The results of this paper can also be related to intercropping. As suggested by Vandermeer [19], Chapter 2, if the land equivalent ratio (which is the amount of land that would be needed to produce as much in a monoculture as produced in one hectare of polyculture) exceeds one, then intercropping is more efficient than monoculture. By appropriate redefinition of the objective function, our results can be interpreted in the context of optimal cropping theory as determining the optimal polyculture, in the sense of securing the largest relative yield of the intercrop, with diversity among species chosen in an optimal way.

Finally, our analysis under uncertainty suggests that the model can be used as a basis for deriving optimal species portfolios in the context of a CAPM approach in ecological modeling.

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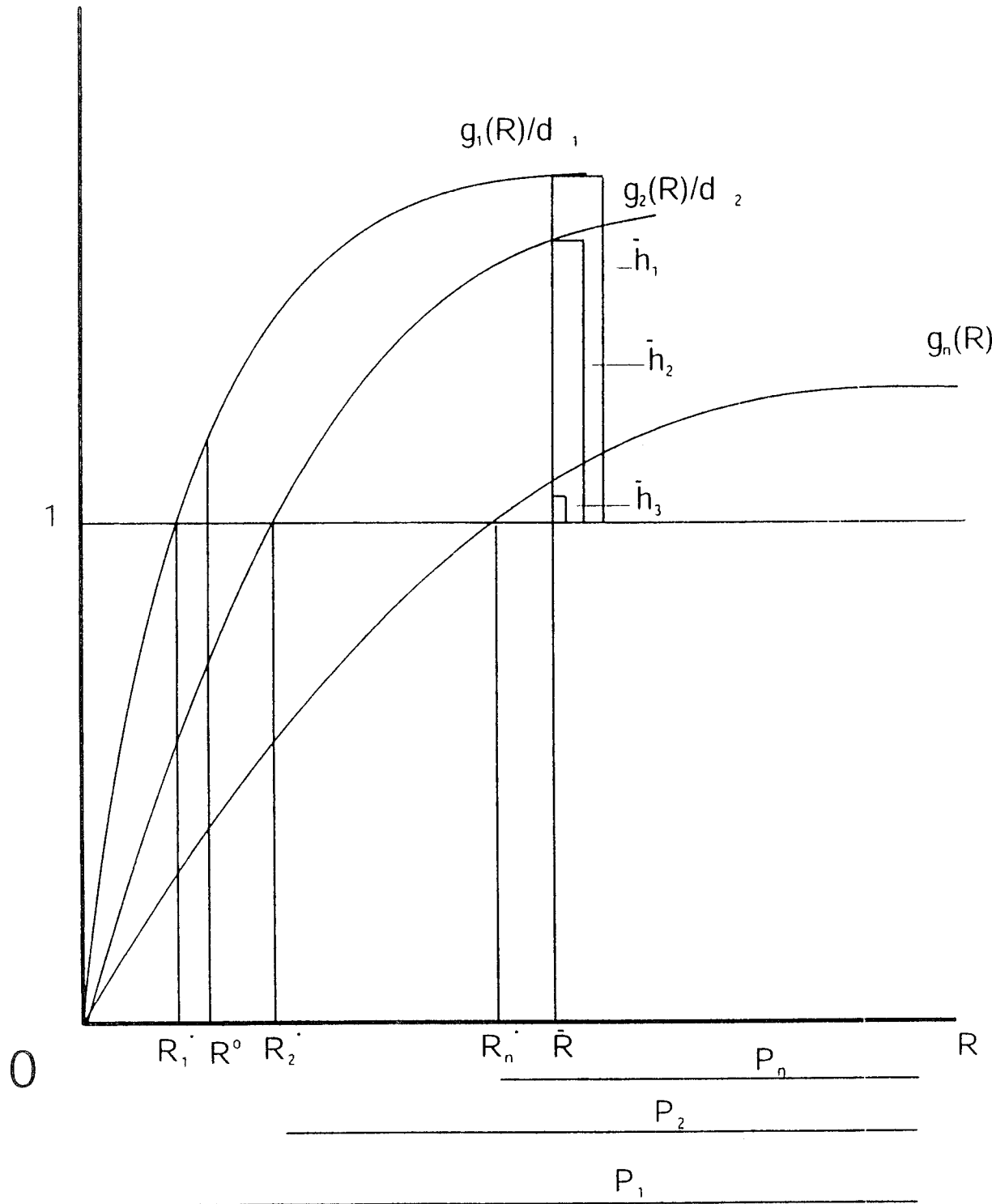


Figure 1: Tilman R^* rule and optimal harvesting

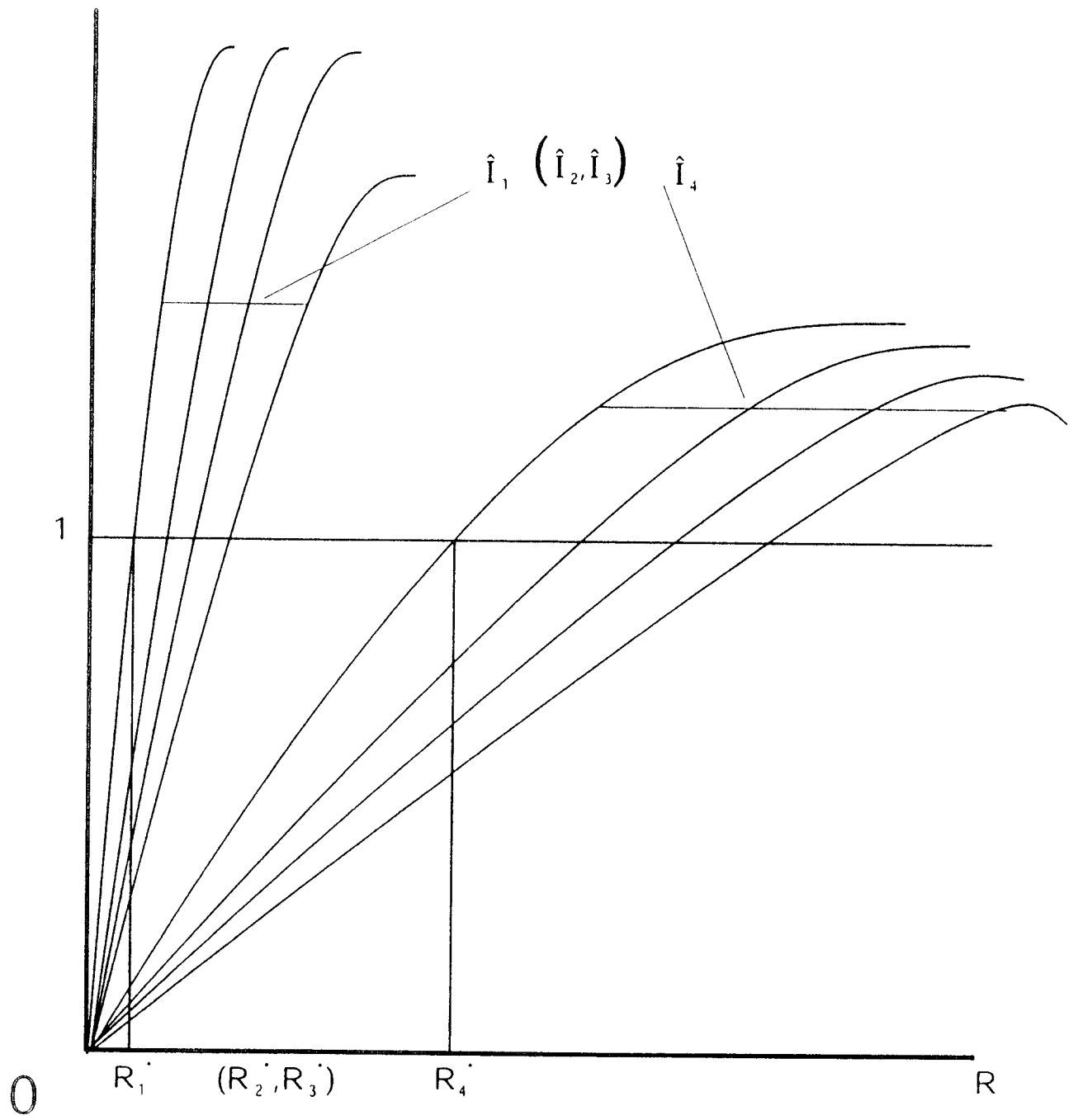


Figure 2: Tilman R^* rule at more than one time scale

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- (xix) This paper was presented at the International Workshop on "Environment and Transport in Economic Modelling" organized by the Department of Economics - Ca' Foscari University, Venice for the "Progetto Finalizzato Trasporti 2" CNR and in cooperation with Fondazione Eni Enrico Mattei, Venice, November 9-10, 1995
- (xx) This paper was presented at the Conference on "Technology, Employment and Labour Markets" organized by the Athens University of Economics and Business and Fondazione Eni Enrico Mattei, Athens, May 16-18, 1996
- (xxi) This paper was presented at the Conference on "Applications of Environmental Accounting", sponsored by the Fondazione Eni Enrico Mattei and the State Science and Technology Commission of the People's Republic of China, Beijing China, March 11-13, 1996
- (xxii) This paper was presented at the Conference on "Economics of Tourism", Fondazione Eni Enrico Mattei and University of Crete, Crete, October 13-14, 1995
- (xxiii) This paper was presented at the Conference on "The Economics and Law of Voluntary Approaches in Environmental Policy", Fondazione Eni Enrico Mattei and CERNA (Ecole des Mines de Paris), Venice, November 18-19, 1996
- (xxiv) This paper was presented at the Conference on "Pressure Groups, Self-Regulation and Enforcement Mechanisms", Fondazione Eni Enrico Mattei, Milan, January 10-11, 1997
- (xxv) This paper was presented at the Conference on "Plotting our Future. Technology, Environment, Economy and Society: a World Outlook", Fondazione Eni Enrico Mattei, Milan, October 24-26, 1996
- (xxvi) This paper was presented at the Conference on "International Environmental Agreements on Climate Change", Fondazione Eni Enrico Mattei, Venice, May 6-7, 1997
- (xxvii) This paper was presented at the "First European Corporate Governance Network Conference", Fondazione Eni Enrico Mattei, Directorate General for Industry of the Commission of the European Communities and the Politecnico of Milan, Milan, March 7-8, 1997

(xxviii) This paper was presented at the Conference on "Trade and Technology Diffusion: The Evidence with Implications for Developing Countries", Fondazione Eni Enrico Mattei and The World Bank - International Trade Division, Milan, April 18-19, 1997

(xxix) This paper was presented at the 2nd Toulouse Conference on "Environment and Resource Economics" organised by Fondazione Eni Enrico Mattei, Institut d'Economie Industrielle and INRA, Toulouse, May 14-16, 1997

(xxx) This paper was presented at the Conference on "Coalition Formation: Applications to Economic Issues" organised by Fondazione Eni Enrico Mattei, the CORE of Louvain-La-Neuve and the Johnson Center for Economic Studies at SMU, Dallas, in co-operation with the Istituto Veneto di Scienze Lettere ed Arti, Venice, January 8-10, 1998

(xxxii) This paper was presented at the Second Coalition Formation Workshop organised by Fondazione Eni Enrico Mattei and the CORE of Louvain-La-Neuve, Louvain-La-Neuve, June 13-14, 1997

(xxxiii) This paper was presented at the Conference on "Colloquia on Economic Research", AIDEI (International Association of Italian Economists), IGER (Innocenzo Gasparini Institute for Economic Research) and Fondazione Eni Enrico Mattei with the contribution of Banca Monte dei Paschi di Siena and CNR (Consiglio Nazionale di Ricerca), Milan, June 18-19, 1998

(xxxiv) This paper was presented at the 1998 World Congress of Environmental and Resource Economists, organised by the Association of Environmental and Resource Economists, European Association of Environmental and Resource Economists and Fondazione Eni Enrico Mattei, Venice, June 25-27, 1998

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