

Valuing Biodiversity from an Economic Perspective: A Unified Economic, Ecological and Genetic Approach¹

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Abstract

We develop a conceptual framework for valuing biodiversity from an economic perspective. We consider biodiversity important because of a number of characteristics or services that it provides or enhances. We argue for a dynamic economic welfare measure of biodiversity that complements the existing literature on benefit-cost approaches and genetic distance/phylogenetic tree approaches, which to date have been more static. Using a unified model of optimal economic management of an ecosystem under ecological and genetic constraints, we identify gains realized by management policies leading to a more diverse system, using the Bellman state valuation function of the problem. We show that a more diverse system could attain a higher value even though the genetic distance of the species in the more diverse system could be almost zero. We relate this endogenous measure of the biodiversity value to ecologically/biologically oriented biodiversity metrics (species richness, Shannon or Simpson indices).

I. INTRODUCTION

In recent years there has been a dramatic increase in the use of the term “biodiversity” in fora such as governmental and intergovernmental groups, the popular press and the scientific community.¹ In this context biodiversity is a term which has acquired a positive connotation but which is difficult to conceptualize and measure. Diversity measures that have been extensively employed in biological and ecological applications are influenced by two components: (i) richness, which refers to the number of species present; and (ii) evenness, which refers to the distribution of species. The most commonly used diversity metrics range from richness (R), which is simply the number of species in a landscape, to the Shannon (H) or Simpson

¹See for example Harper and Hawksworth (1994).

(*D*) diversity indices and their modifications.²

In the environmental and resource economics literature, the measuring and valuing of biodiversity has been approached through the diversity function (Weitzman 1992, 1993; Solow et al. 1993),³ which is defined in terms of pairwise distances among species, with distance being a measure of dissimilarity among species. In biological applications this distance is based on the DNA-DNA hybridization. As shown by Weitzman (1992) for ecological applications, this diversity function is 50% of the Shannon index. The diversity function can be used to rank conservation alternatives, with the most desirable alternative being the one showing the relatively highest value for the ecological diversity function. The diversity function approach is based on the implicit assumption that diversity measured in terms of genetic distances is desirable.⁴ It does not make clear, however, why it is desirable, or establish a mechanism linking the size of genetic distances and some well-defined concept of usefulness or desirability. The so-called “Noah’s ark problem” is an extension of this approach (Weitzman 1998, Metrick and Weitzman 1998), where species are valued according to both the genetic distances and direct utility associated with the species which is taken to reflect aesthetic or existence values. The direct utility is, however, exogenously determined and not linked to

² $H = -\sum_{i=1}^n (P_i \ln P_i)$, $D = 1 - \sum_{i=1}^n P_i^2$, where P_i is the proportion of individuals or biomass of species i in the landscape.

³Polasky et al. (1993) and Polasky and Solow (1995) value a collection of species, assuming either that species providing the same type of benefit are perfect substitutes or allowing for imperfect substitution and dependence between species, with dependence related to genetic distance. Nehring and Puppe (2002) develop a valuation approach based on evolutionary information through the phylogenetic tree model. This approach, based on genetic diversity, is the more recent one. The traditional cost-benefit analysis approach to biodiversity stemming from Krutilla (1967), identifies “use values”, “existence value” and “option value” as sources of value. See Goulder and Kennedy (1997) for the pros and cons of the cost-benefit approach, and Brown and Shogren (1998).

⁴As stated in Weitzman (1992, p. 401), “The most valuable species is the farthest distant from the others - by any reckoning.”

the diversity metric.^{5, 6}

In our approach we feel that a basic principle for valuing biodiversity should be the association of diversity with some useful characteristics that it possesses or useful services that it provides or enhances, since if biodiversity is desirable it should be desirable because of these characteristics or services.⁷ This approach is directly related to Heal's idea (Heal 2000) of regarding biodiversity as a commodity. Heal suggests that biodiversity is important from an economic perspective because it provides or enhances ecosystem productivity,⁸ insurance,⁹ knowledge¹⁰ and ecosystem services.¹¹ Thus, since in this context biodiversity acquires a positive connotation, our paper will argue for an economic welfare measure of biodiversity in the following sense: Given two ecosystems A and B , with A being more diverse than B in terms of the ecologically/biologically oriented biodiversity metrics (species richness,

⁵Li, Lofgren and Weitzman (2001) follow this approach to characterize optimal harvesting policies in a fishery.

⁶See also Montgomery et al. (1999) for an approach based on the taxonomic tree and Simpson et al. (1996) and Craft and Simpson (2001) for an approach that links diversity to a measure of economic value associated with "biodiversity prospecting."

⁷See also Daily et al. (1997).

⁸This is associated with the fact that more diverse plant systems are more productive than less diverse ones. There are a number of empirical studies relating the number of species in ecosystems to plant productivity (Naem et al. 1995, 1996; Tilman et al. 1996; Tilman and Lehman 1997; Hooper and Vitousek 1997) which have found that functional diversity is a principal factor explaining plant productivity.

⁹Insurance is associated with the possibility of finding genes in non-commercially used species that can be used to build resistance against lethal diseases affecting other species. Thus genetic diversity can be used as insurance against catastrophic events or infections. See also Weitzman (2000).

¹⁰Biodiversity can be used as a source of knowledge with which to develop new products in the biotechnology industry or pharmaceuticals. Rausser and Small (2001) stress the complementarity between genetic resources and knowledge resources and the incentives for data collection and resource conservation.

¹¹Biodiversity is essential for the proper functioning of an ecosystem so that its ability to provide economically important services, such as watershed benefits (Chichilnisky and Heal 1998), ecotourism, carbon sequestration services of forests, or production of "non-timber forest products", is maintained. (See also Daily and Dasgupta (2000).)

Shannon or Simpson indices), the value of biodiversity is determined by the difference between the Bellman state valuation functions of optimal management, $V_A - V_B$. Thus, we value biodiversity *not* based on genetic distances but in terms of the value of characteristics or services that an ecosystem provides or enhances when managed optimally, obtaining in this way an *endogenous* measure for biodiversity valuation.¹²

The purpose of this paper is to make the above intuitive idea of biodiversity valuation more precise. We do it in the context of two species whose “genetic distance” is almost zero in the sense of Weitzman (1992) and Solow et al. (1993), but where the economic value of the optimally-managed system with one of the species extinct is less than the economic value of the optimally-managed system with both species present.

In order to have a very precise context for clear exposition, we consider an agroecological example where the general service provided by the ecosystem is food and the value of crop diversity stems from its role in producing food. In this example optimal management of crop diversity involves trading off the gains from specialization to the most desirable crop today against facing a less desirable gene pool of threats to the system as a whole tomorrow. As we shall see, this framing of the problem exposes which dynamic feedback loops and which system parameters must be properly understood in order to manage the system properly. More specifically in our example the dynamics of the species mix of threats to the system’s ability to provide valuable services is controlled indirectly by controlling the dynamics of the gene pool of threatening species by directly controlling the dynamics of the crop mix over time. More precisely the crop mix dynamics are controlled to maintain a desirable gene pool equilibrium. In this way we reveal which models need to be built of which parts of the ecosystem, which parameters need to be measured, and which uncertainties are most worthwhile to resolve, in order to properly manage the system to maximize its output of

¹²This approach can also be regarded as connecting the ecologically/biologically oriented biodiversity metrics, with an endogenous measure of economic value of biodiversity.

services. While an agroecological example appears somewhat special (even though food is of key importance to human survival), the trade-off between managing some part of an ecosystem to achieve better services in the short term and the longer term objective of maintenance of the whole system's ability to deliver service flow in the future seems quite general.¹³

More specifically, the two varieties of species, $i = 1, 2$, in our model, which are similar from a functionalist viewpoint, are harvested on a fixed area and the harvest has a market value. On the ecological side, the species compete for a limiting resource in the context of a Pacala-Tilman mechanistic resource-based model (Tilman 1982, 1988; Pacala and Tilman 1994). The system also contains more than one type of pest, with the mortality rate of the species depending on the relative abundance of a certain type of pest. Management decisions refer

¹³For example, a common complaint of ecologists is that humans too often manage an ecosystem to optimize some short term goal, e.g. crop, forest, or animal yield, or landscape appearance, but this sets off unobserved or ignored interaction dynamics, which ultimately lead to a degradation or collapse of the system (Gunderson and Holling 2001). We illustrate how this complaint can be approached by explicit modelling in our example which is general enough to reveal dynamic links of interaction between parameters such as degree of assortative mating of pests, genetic fitness values of different pest genotypes, and crop mix, which play a key role in maintenance of the system's ability to deliver the desired service flow. Our type of modelling and analysis immediately suggest generalizations to deal with practical issues of model uncertainty such as "robust control". For example Bernhard (2002) shows how one should react to using control channels to control the system dynamics as a function of "degree" of trust in linking parameters of each part of the system with its other parts, and he shows how this "degree" of trust can be viewed by using parameter uncertainties. Our ultimate goal is to contribute to a quantitative approach to key problems of management of increasingly human dominated ecosystems. In particular, our type of approach can lead to quantitative formulations of precautionary principles and a theory of who should bear the burden of proof in environmental disputes. In other words, the explicit modelling of the embedded dynamic linkage of the ecosystem part of primary interest with the rest of the ecosystem that we illustrate here can be viewed as a quantitative approach to the "eco-pragmatism" view advocated by Farber (1999). Of course we will barely make a dent in this formidable problem within the scope of one paper. More will be said about this in our concluding section.

to the optimal distribution of land between the two varieties, or equivalently the crop mix, when total harvest benefits are maximized subject to the constraints imposed by the ecological and genetic mechanisms. If the land is divided between the two varieties, then the richness biodiversity metric is $R^b = 2$ for the subsystem of the plants, while the Shannon or Simpson indices depend on the relative amount of land devoted to each variety. If the management decisions lead to a monoculture then $R^b = 1$, while $H = D = 0$. Thus this framework can be used to determine the equilibrium diversity corresponding to certain optimizing behavior and the corresponding state valuation function. The value of genetic diversity is the *extra economic value*, measured by the Bellman value function, that is realized by a management policy that attains a *more diverse* species base. We show that in our model, while genetic distance can go to zero, the value function difference of the two assemblies can go to plus infinity, depending on the shape of the demand curve, in the case where a resistant pest kills both varieties.

A plausible generalization of our model could be towards a more general model of antagonistic co-evolution of many species and parasites or pests,¹⁴ in which management decisions leading to a less diverse group of species could increase the effectiveness of pests in attacking the less diverse group of species. More generally our model focuses attention on the dynamic links between the set, S , of species of primary interest, i.e. the set of service-providing species and the rest of the ecosystem in which S is embedded. While we used the example of $S = \{\text{service providing plants}\}$ and “rest of ecosystem” = {gene pool of pests}, the point we make is far more general than this particular example. To put it another way, in our example, the gene pool is part of the “natural capital” “state vector” that one needs to put into the Bellman state valuation function in order to properly value the whole ecosystem. Our analysis will show how reduction of the size of set S can easily lead to collapse of the

¹⁴This co-evolution refers to the so-called “red queen” hypothesis. See our concluding section for a more detailed exposition.

ability of S to provide essential services because of the interaction dynamics with the rest of the ecosystem in which S is embedded.

The rest of the paper is organized as follows. Section II develops the unified economic/ecological/genetic model. Section III defines the economic welfare measure of biodiversity. In section IV the unified model is solved. Given the highly nonlinear nature of the solution we perform numerical simulations and we determine the gain in value from a more diverse system, which provides the endogenous value of biodiversity. The last section concludes.

II. ECONOMIC MANAGEMENT OF ECOSYSTEMS UNDER ECOLOGICAL AND GENETIC CONSTRAINTS

In order to develop an integrated model of management of an ecosystem when natural selection occurs, we consider an ecosystem with plant - pest interactions. To put the problem in the context described in the Introduction, we assume that the plant comes in two varieties, $i = 1, 2$, while the pest comes in three types (genotypes), A_1A_1 , $A_1A_2 = A_2A_1$, and A_2A_2 , where A_1 and A_2 denote distinct genes. Plant variety 1 kills pest types A_1A_1 and A_1A_2 but not pest type A_2A_2 , while plant variety 2 is not immune to any type of pest.¹⁵

¹⁵This set-up is motivated by genetic engineering literature on *Bt*-crops (e.g. Ives 1996, Ives and Andow 2002) like *Bt*-corn, where variety 1 = *Bt*-corn and variety 2 = non-*Bt*-corn. The pest is the European corn borer. A protein that is found in the soil bacterium *Bacillus thuringiensis*, and is engineered into the corn tissues, is lethal to the European corn borer when ingested. The advantages of using *Bt*-corn hybrids include improved standability and plant health, higher yields, and fewer insecticide applications (e.g. Hurley et al. 1999). Given these advantages of *Bt*-corn, it seems most likely that profit-maximizing farmers will be willing to plant only *Bt*-corn in a given area. This however might create an externality due to the operation of natural selection mechanisms. When the whole area is planted with *Bt*-corn, borers remaining from the first generation will be those which are resistant to the protein. These borers will produce a predominantly resistant second generation of borers and the advantage of the *Bt*-corn will disappear. The high-dose/refuge strategy for resistance management is thought to delay resistance, because the refuge provides a source for

The objective of economic management for the ecosystem is the maximization of the present value of harvesting. Consider a given area, with size normalized to unity, and let $H_i(t)$, $i = 1, 2$ denote harvest of plant variety i at time t , and $x(t) \in [0, 1]$ denote the proportion of the land planted with variety 1. Let $D(H(t))$, $H(t) = H_1(t) + H_2(t)$ be the inverse demand function and let $v(H) = \int_{z_0}^H D(z) dz$ be the benefit function. Assuming, for simplicity, zero harvesting cost, and a discount rate $\rho > 0$, the objective of economic management can be stated as choosing time paths for $H_i(t)$ and $x(t)$ to maximize

$$\int_0^{\infty} e^{-\rho t} v(H) dt \quad (1)$$

Maximization problem (1) is, however, subject to additional constraints imposed by the underlying biological and ecological factors. On the ecological side we assume that the two plants compete for a limiting resource (e.g. nitrates), thus, the growth of biomass for each plant is affected by the availability of this resource. On the other hand resource consumption by the plants affects the availability of the resource. In this set up, the rate of growth of the plant biomass depends on the difference between the biomass reproduction rate, which is resource dependent, and the death rate, and the harvest rate, while the rate of change of the resource depends on the difference between its supply and its consumption by the plants.¹⁶ Formally the equations characterizing biomass and resource evolution which describe the ecological side of our model can be stated as:

$$\dot{B}_i = B_i [gR - m_i] - H_i, \quad i = 1, 2, \quad B_i(0) = B_i^0 \quad (2)$$

$$\dot{R} = S - aR - gw \sum_{i=1,2} B_i, \quad R(0) = R^0 \quad (3)$$

where

$$x = \frac{B_1}{B_1 + B_2}, \quad B = B_1 + B_2 \quad (4)$$

susceptible borers to mate with resistant ones, so that their offspring can be killed by *Bt*-corn.

¹⁶This set up for the ecological model corresponds to Tilman's mechanistic resource-based model of species competition (Tilman 1982, 1988; Pacala and Tilman 1994).

$$B_1 = xB, B_2 = (1-x)B, H = H_1 + H_2 \quad (5)$$

Equation (2) describes the growth of the varieties' biomass B_i where: g is the coefficient of the biomass growth function, assumed to be the same for the two types of plants; R is the resource; m_i is the death rate; and H_i is the harvesting of the variety per unit time. Equation (3) describes the resource dynamics where $S - aR$ is the net amount of the resource (such as nutrients) supplied at time t , with S being exogenous natural supply and aR reflecting natural resource removal, where a can be interpreted as an erosion or a leaching rate.¹⁷ The term $wg \sum_{i=1,2} B_i$ is the consumption of the resource by the two varieties, with w being a constant reflecting the concentration of the resource in the tissues of corn (Pacala and Tilman 1994).

The fact, however, that plant variety 1 is immune to pest types A_1A_1 and A_1A_2 but not to A_2A_2 , while plant variety 2 is not immune to any type of pest, makes it necessary to take into account the evolution of the pest population. This is because the death rate of each plant variety depends on the relative abundance of genes A_1 and A_2 in the pest gene pool. Thus in (2) the death rate depends on the proportion, p , of A_1 genes in the genetic pool of the pest population, with the proportion of A_2 genes being $(1-p)$. Thus, the death rate for each plant is a function of p or $m_i = d_i(p)$. Given the relative immunities of plants 1 and 2, it follows that the *higher* the proportion of gene types A_1 in the gene pool, the *lower* the death rate of plant variety 1, and the *higher its productivity advantage* over plant variety 2. This can be stated as:

$$d_2(p) = d_2, d_1(p) = pd_1 + (1-p)d_2 \text{ with } d_1 < d_2 \quad (6)$$

Thus if $p = 1$, only the A_1A_1 type exists in the pest gene pool. Variety 1 kills all A_1A_1 types

¹⁷Resource supply could be modelled more realistically by introducing the possibility of augmenting it through fertilization. In this case the net flow of nutrients would be $S + h(F) - aR$, where $h(F)$ is additional resource supply through fertilization F . Although it is relatively straightforward to introduce fertilization, we choose not to, in the interests of simplicity. Our basic results do not depend on the presence of fertilization.

and has a growth advantage over variety 2, since $d_1(1) = d_1 < d_2$. On the other hand, if $p = 0$, only the A_2A_2 genotype exists in the pest gene pool which is resistant to variety 1 (as well as variety 2). Then $d_1(0) = d_2$ and the growth advantage of variety 1 is eliminated. Then, the two varieties are identical.

Since genetics affects productivity we need to explain how the different pest types spread in the population relative to each other. This is essentially determined by the evolution of p from generation to generation, assuming random mating and fixed survival probabilities for the different types. To set out the genetic part of our model, let x be the proportion of the area planted with variety 1. Then the proportion $p = p(t)$ of A_1 genes in the pest gene-pool evolves, from generation to generation, according to the fundamental equation of evolutionary biology, as:¹⁸

$$\dot{p} = p[G(p, x) - 1], p(0) = p^0 \quad (7)$$

$$G(p, x) = \frac{W_{11}(x)p + W_{12}(x)(1-p)}{W_{11}(x)p^2 + 2W_{12}(x)p(1-p) + W_{22}(x)(1-p)^2} \quad (8)$$

$$W_{ij}(x) = xw_{ij}(1) + (1-x)w_{ij}(2), i = 1, 2 \quad (9)$$

where $w_{ij}(1)$, $w_{ij}(2)$ are the viability fitness of the ij pest type for plant variety 1 or 2 respectively. When plant variety 1 kills the A_1A_1 and A_1A_2 genotypes but not the A_2A_2 , we have that $w_{11}(1) = w_{12}(1) = 0$, while $w_{22}(1) > 0$. On the other hand $w_{ij}(2) > 0$, $i = 1, 2$.

The maximization of (1) subject to (2) - (9) provides, for the first time to our knowledge, an integration of optimal management theory using a Pacala-Tilman resource-based model of

¹⁸In population genetics terminology we model the evolution of the pest population by Hardy-Weinberg mating and one locus, two alleles genetics. See, for example, Feldman (1989) or Roughgarden (1998). Localization effects where spatially nearby pests are more likely to mate with each other than spatially more distant pests, as well as assortative mating effects, can lead to more complicated evolution dynamics than those based upon Hardy-Weinberg mating (Ives 1996, Ives and Andow 2002) and even make existence of a steady-state reserve strategy problematic. We ignore such complications in the current piece which is only intended to serve as a metaphorical model of gene-pool-specific functional services of biodiversity and not as a realistic model of resistance management.

species competition to model the ecological side, with explicit population genetics to model natural selection. In this optimization problem, the choice of x will determine the relative sizes of the areas planted with variety 1 and variety 2.¹⁹ This allocation of land will affect the evolution of pest population in the gene pool through the subsystem (6)-(9). The value of p determined through this subsystem affects in turn the evolution of the biomasses for each variety through the growth equations (2) and eventually the equilibrium biodiversity.

III. AN ECONOMIC WELFARE MEASURE OF BIODIVERSITY

In order to derive an economic welfare measure of biodiversity, we use the value function associated with dynamic programming representation of the ecosystem planning problem (1).²⁰ Let $\mathbf{s} = (B_1, B_2, R, p)$ and $\mathbf{u} = (H_1, H_2, x)$ be the state and control vectors respectively, associated with the maximization of (1) subject to (2) - (9), and let $\mathbf{f}(\mathbf{s}, \mathbf{u})$ be the vector of transition equations (2),(3) and (7). Then the value function for this problem is defined as:

$$V(\mathbf{s}) = \max_{\mathbf{u} \in \mathcal{U}_s} J(\mathbf{s}; \mathbf{u}) \quad (10)$$

while the dynamic programming equation is obtained as:

$$\rho V(\mathbf{s}) = \mathcal{H}(\mathbf{s}, \partial_{\mathbf{s}} V(\mathbf{s})) \quad , \quad \mathcal{H}(\mathbf{s}, \boldsymbol{\lambda}) = \max_{\mathbf{u} \in \mathcal{U}_s} \{v(H) + \boldsymbol{\lambda} \cdot \mathbf{f}(\mathbf{s}, \mathbf{u})\} \quad (11)$$

where \mathcal{H} is the maximized Hamiltonian for problem (1), $\partial_{\mathbf{s}} V(\mathbf{s})$ is the vector of the first derivatives of the value function with respect to the state variable, $\boldsymbol{\lambda} = \partial_{\mathbf{s}} V(\mathbf{s})$ is the vector of costate variables and \mathcal{U}_s is a compact control space. Since (11) is fundamental in intertemporal welfare economics, showing that the optimized Hamiltonian equals the return on social well-being,²¹ our formulation of social well-being extends previous discussions by including

¹⁹In terms of *Bt*-corn analysis this constitutes a refuge strategy.

²⁰This approach has been used in welfare considerations of National Accounting and in particular for the definition of the Net National Product and the evaluation of policy reforms. See, for example, Weitzman (1976), Dasgupta and Maler (2000) or Hartwick (2000).

²¹See Dasgupta and Maler (2000), where they show that the result holds even for non-optimizing economies. They also show that if $v(H)$ is linear then Weitzman's interpretation of Net National Product as the constant-

through (11) the value of the gene pool as part of society's total capital base.

From (11) the optimal stationary feedback policy functions $H_i^* = H_i^*(\mathbf{s})$, $i = 1, 2$, $x^* = x^*(\mathbf{s})$ can be derived. Then, at a corresponding optimal steady state (OSS), $\bar{\mathbf{s}} = (\bar{B}_1, \bar{B}_2, \bar{R}, \bar{p})$, the value of the ecosystem is

$$V(\bar{\mathbf{s}}) = \frac{v(\bar{H}^*)}{\rho}, \quad \bar{H}^* = \bar{H}_1^* + \bar{H}_2^* \quad (12)$$

This argument implies that for any two stationary feedback policy functions resulting from different structures of the optimization problem,²² and leading to differing biodiversity metrics (e.g. number of species), the value function (12) can be used to evaluate biodiversity. This can be accomplished by comparing the value functions of the two optimization problems.

If for our specific problem we consider the value functions associated with a two-species system and a one-species system, $V^2(\bar{\mathbf{s}}^2)$ and $V^1(\bar{\mathbf{s}}^1)$ respectively, then the OSS economic welfare measure of biodiversity can be defined as:

$$V^2(\bar{\mathbf{s}}^2) - V^1(\bar{\mathbf{s}}^1) = \frac{v(\bar{H}^{*2}) - v(\bar{H}^{*1})}{\rho} \quad (13)$$

where $\bar{H}^{*j} = H^{*j}(\bar{\mathbf{s}})$, $j = 1, 2$ is the OSS stationary feedback policy function associated with each system. The right hand side of (13) can be obtained by solving the optimal control representation of the problem, determining the OSS, and then evaluating the controls $H^{*j}(\mathbf{s})$, and $x^*(\mathbf{s})$ at the OSS.

We consider, therefore, two alternative policy functions which are associated with different property rights to the gene pool. When there is a system of full property rights to the gene pool, then optimal management maximizes (1) subject to (2) - (9). We call this problem the equivalent consumption holds.

²²For example, if death rates d_1 and d_2 are regarded as fixed parameters, we have an optimization problem where the genetic constraints (7) - (9) are *not* taken into account. The feedback policy function for this problem will differ from the corresponding policy function when d_1 and d_2 are *not* regarded as fixed parameters, and the genetic constraints *are* taken into account.

socially-optimal management problem (SOMP), since its solution corresponds to the first best solution.

When there is a lack of property rights then the genetic constraints (7) -(9) are ignored. We call this solution the privately-optimal management problem (POMP) since it corresponds to a situation where private optimizing agents are “small” and they ignore the impact of their decisions regarding the species variety mix on the gene pool. The implications of the lack of property rights to the gene pool can be further analyzed by considering the genetic subsystem (7) -(9).

For any fixed land allocation strategy x , pest fitness is determined through (9) and the evolution of the pest population is determined through (7). Then, equilibrium for (7) is defined, for any given x , as:

$$p^* : G(p^*, x) - 1 = 0, p^* \neq 0 \quad (14)$$

In general (14) has three possible equilibria, which depend on the choice of land allocation x : (i) $\bar{p}_1 = 1$, (ii) $\bar{p}_2 = 0$, and (iii) $\bar{p}_3 \in (0, 1)$. In \bar{p}_1 only the A_1 gene type exists in the gene pool, in \bar{p}_2 only the A_2 gene type exists, while in \bar{p}_3 both A_1 and A_2 exist. In population genetics terminology \bar{p}_1 and \bar{p}_2 are monomorphic equilibria, while \bar{p}_3 is a polymorphic equilibrium. It is a standard result of population genetics²³ that if

$$W_{12}(x) > W_{22}(x) \text{ and } W_{12}(x) > \max \{W_{11}(x), W_{22}(x)\} \quad (15)$$

the polymorphic equilibrium \bar{p}_3 is stable, while if $W_{22}(x) > W_{12}(x)$ the monomorphic equilibrium $\bar{p}_2 = 0$ is stable.

It can easily be seen from (9) that, since $W_{12}(x) > W_{22}(x)$ cannot hold for all $x \in [0, 1]$, the polymorphic stability condition will be satisfied for small x but it will be violated for x close to 1. In the limiting case of $x = 1$, that is when the entire area is planted with variety 1 which kills A_1A_1 and A_1A_2 genes, we have $W_{12}(1) = W_{11}(1) = 0$, while $W_{22}(1) =$

²³See for example Feldman (1989) or Roughgarden (1998).

$w_{22} (i = 1) > 0$. This implies that for x sufficiently close to 1 the stability condition is most likely to be violated. With $x = 1$ and $W_{12} (1) = W_{11} (1) = 0$, and $W_{22} > W_{12} > W_{11}$, and x close to one, or $x \in (1 - \varepsilon]$, $\varepsilon > 0$, we say that there is directional selection for A_2 , with \bar{p}_2 being the stable monomorphism. In this case $G(p, x) = 0$ in (8) and the differential equation (7) can be written as:

$$\dot{p} = 0 - p, \text{ or } p(t|_{x=1}) = p_0 e^{-t} \quad (16)$$

Thus when $x = 1$ the resistance of the system to the pest is reduced at the most rapid rate. This means that by planting the area with only variety 1, the system generates directional selection toward the A_2A_2 pest type. Therefore, when the genetic constraint is ignored, the natural selection mechanism results in a stable monomorphic equilibrium which eliminates the productivity advantage of variety 1, since when $\bar{p}_2 = 0$, only the pest type A_2A_2 is present and neither variety 1 nor variety 2 is immune to this type of pest.²⁴ That is, variety 1 is now identical to variety 2, and the biodiversity richness metric on the plant side is $R^b = 1$.

IV. OPTIMAL MANAGEMENT AND BIODIVERSITY VALUATION

We start by analyzing the solution for the SOMP. This solution involves choosing time paths for the controls $H_i(t)$, $i = 1, 2$ and $x(t)$ to maximize (1) subject to (2)-(9). To simplify things we assume that both plant varieties sell at the same competitive price which is normalized to one, so that $v(H) = H_1 + H_2$. The maximization problem includes four state variables $(B_1(t), B_2(t), R(t), p(t))$ and it is linear with respect to harvesting $H_i(t)$.²⁵ This linearity

²⁴In Nature the tiny genotypic difference in two “apparently same” species might not be detectable by human managers, so the “resistance” species is eliminated and this serves as a “slow variable” to create an unpleasant “Holling surprise” when the pests evolve to eliminate the remaining species upon which some important ecosystem function depends. This insight suggests future extensions of our work to managing systems where the role of some species in maintaining resistance to pests is unobservable because the phenotypic distance upon which management strategies are based appears to be zero, even though the genotypic distance while “small” is still positive—yet it is critical.

²⁵Linearity in H requires the additional constraint $0 \leq H_i \leq K^{\max}$ so that the optimization problem is

allows the reduction of the problem's dimensionality with respect to the state variables, by a transformation into a Most Rapid Approach Path (MRAP) problem. Let $B = B_1 + B_2$ denote total biomass and μ, q denote the costate variables associated with the state variables R and p respectively. The OSS for the SOMP, as determined by the solution of the corresponding MRAP problem, is characterized in the following proposition.

Proposition 1: *If an OSS for the MRAP exists, then it is determined for the state-costate vector (R, μ, p, q) by the solution of the modified Hamiltonian dynamic system (MHDS)*

$$0 = S - aR - gwRB^* \quad (17)$$

$$0 = G(p, x^*) - 1 \quad (18)$$

$$0 = (\rho + a + gwB^*)\mu - gB^* \quad (19)$$

$$0 = \rho - p \frac{\partial G(p, x^*)}{\partial p} + x^* \frac{\partial G(p, x^*)}{\partial x} \quad (20)$$

In this system x^* and B^* , which are the optimal stationary feedback policy functions for the MRAP problem, are defined as:

$$x^* = \frac{\mu gwR - gR + d_2 + \rho}{p(d_2 - d_1)} = X(R, \mu, p, q) \quad (21)$$

$$B^* = -\frac{q \frac{\partial G(p, x^*)}{\partial x}}{(d_2 - d_1)} = \beta(R, \mu, p, q) \quad (22)$$

Then, the OSS, land allocation strategy \bar{x}^* , total biomass \bar{B}^* , and harvesting for varieties 1 and 2, \bar{H}_1^* and \bar{H}_2^* respectively, are defined as

$$\bar{x}^* = X(\bar{R}, \bar{\mu}, \bar{p}, \bar{q}), \quad \bar{B}^* = \beta(\bar{R}, \bar{\mu}, \bar{p}, \bar{q}) \quad (23)$$

$$\bar{B}_1^* = \bar{x}^* \bar{B}^*, \quad \bar{B}_2^* = (1 - \bar{x}^*) \bar{B}^* \quad (24)$$

$$\bar{H}_1^* = \bar{x}^* \bar{B}^* (g\bar{R} + \bar{x}^* \bar{p} (d_2 - d_1) - d_2) \quad (25)$$

$$\bar{H}_2^* = (1 - \bar{x}^*) \bar{B}^* (g\bar{R} + \bar{x}^* \bar{p} (d_2 - d_1) - d_2) \quad (26)$$

well posed.

For proof see Appendix.

The OSS levels \bar{B}^* and \bar{H}^* for the biomass and the flow of harvesting respectively, determine the value of the ecosystem's output at the social maximum when diversity is preserved and all the ecological and genetic constraints have been taken into account. Then from the dynamic programming equation, the OSS value of the two-species system is

$$V^2 = \frac{\bar{H}_1^* + \bar{H}_2^*}{\rho} = \frac{\bar{H}^*}{\rho} = \frac{\bar{B}^* (g\bar{R} + \bar{x}\bar{p} (d_2 - d_1) - d_2)}{\rho} \quad (27)$$

We turn now to the case where there are no property rights at all to the gene pool and we analyze the POMP which ignores the genetic constraint. In cases where the decision-making farmers operate on a small scale and do not take into account the effects of their actions on diversity, the genetic constraint and thus potential gains from diversity could be ignored. We expect reality to be between the two polar cases of the SOMP and the POMP, since there is evidence that farmers take into effect potential gains from diversity if they are operating on a large scale. Thus we would like to consider the POMP solution as a metaphor for providing a yardstick in order to more precisely measure gains from the continuation of diversity.

Proposition 2: *If the genetic constraint is ignored at the POMP, then at the OSS for this problem $\bar{x} = 1$, $\bar{p} = 0$, $\bar{B}(d_2) = \frac{S - a\bar{R}(d_2)}{gw\bar{R}(d_2)}$, $\bar{H}(d_2) = \bar{B}(d_2) (g\bar{R}(d_2) - d_2)$ where $\bar{R}(d_2)$ is the solution of $\frac{(gR - d_2 - \rho)}{gwR} = \frac{S - aR}{w(R\rho + S)}$.*

For proof, see Appendix.

This implies that the variety 1 monoculture with equilibrium biomass $\bar{B}(d_1)$ and corresponding resource level $\bar{R}(d_1)$ is not stable. The stable equilibrium is a variety 2 monoculture where the productivity advantage of variety 1 has been eliminated. The difference $\bar{B}^* - \bar{B}(d_2)$ determines the biomass gain in the social maximand as a result of keeping a more diverse system. From the dynamic programming equation the OSS value of the one-species system is $V^1 = \frac{\bar{H}(d_2)}{\rho}$. Then from (13) the OSS economic welfare measure of biodiversity is determined by $V^2 - V^1$. This value corresponds to the change in the biodiversity metrics (species

richness, H , D) from a homogenous system to a diverse system.

A. Numerical Approximations to Biodiversity Valuation

System (17)-(20) that determines the OSS for the unified model is highly nonlinear. Thus in order to obtain some insights into the structure of the solution and verify whether or not biodiversity valuation through $V^2 - V^1$ can be detected, we resort to some numerical simulations.

We start by calculating the OSS resource and biomass levels $[\bar{R}(d_1), \bar{R}(d_2)]$ and $[\bar{B}(d_1), \bar{B}(d_2)]$ for the yardstick case of the POMP, with fitness structure:

$$w_{11}(2) = w_{22}(1) = w_{22}(2) = w \text{ and } w_{12}(2) = (1 + s)w, \quad s \geq 0$$

with $w_{11}(1) = w_{12}(1) = 0$ under the assumption that plant variety 1 kills A_1A_1 and A_1A_2 pest types, and parameter values:

$$\rho = 0.01, S = 2, d_1 = 0.05; a = 0.10; w = 0.05; g = 0.05, d_2 = \{0.1, 0.2, 0.3, 0.4, 0.5\}$$

When $s > 0$ we say that there is heterozygotic fitness advantage. The results are shown in table 1.

Table 1: Steady-State Resource and Biomass Levels when the Genetic Constraint is Ignored

d_2	$\bar{R}(d_1)$	$\bar{R}(d_2)$	$\bar{B}(d_1)$	$\bar{B}(d_2)$	% loss in biomass
0.5	4.72586	14.0897	129.281	16.779	87.02
0.4	4.72586	12.5887	129.281	23.549	81.78
0.3	4.72586	10.9029	129.281	33.375	74.18
0.2	4.72586	8.93162	129.281	49.569	61.66
0.1	4.72586	6.4253	129.281	84.507	34.63

The $\bar{R}(d_1), \bar{B}(d_1)$ are the unstable equilibria, while the $\bar{R}(d_2), \bar{B}(d_2)$ are the stable equilibria where the productivity advantage of variety 1 has been eliminated. The loss in biomass

is the result of pest adaptation due to the natural selection mechanism. As anticipated, the smaller the deviation between the two death rates (that is, the smaller the productivity advantage of variety 1), the smaller the percentage loss in biomass. The richness metric for both the plant and the pest subsystems are $R^b = 1$, while for the plant subsystem $H = D = 0$.

At the next step we calculate the OSS for the SOMP by numerically solving the nonlinear system (17)-(20).²⁶ In table 2 we present solutions for different values of the fitness differential s and d_2 , with the rest of the parameters the same as those used for table 1. Table 2 includes the steady states, the percentage gain in biomass and harvesting of the OSS at the social optimum, relative to the variety 2 monoculture which eventually emerges when the genetic constraint is ignored, the value of biodiversity determined by $V^2 - V^1$, and the Shannon and Simpson biodiversity indices. It should be noted that the richness metric is $R^b = 2$ for the plant subsystem and $R^b = 3$ for the pest subsystem.

[Table 2]

Our numerical simulations indicate that the socially-optimal solution results in a diverse system with two species present,²⁷ and that there is always a percentage gain in equilibrium, harvesting, biomass and a positive biodiversity value relative to the homogeneous one-species system. The gain in value can be regarded as an *endogenous* measure of the value of biodiversity which corresponds to a change from the monoculture biodiversity metrics, $R^b = 1$, $H = D = 0$, to the polyculture biodiversity metrics $R^b = 2$, $R^b = 3$ for the plant/pest subsystems respectively, and the H, D indices corresponding to the specific parameter constellations. The results indicate that the higher the advantage of the heterozygote, that is the value of s , for a given death rate d_2 , the higher the harvesting, biomass and biodiversity value.²⁸ Our results also indicate that for varying s , increased diversity at the social

²⁶The numerical solutions were obtained using Mathematica 4.0 (Wolfram 1999) using both Newton's method and the secant method with accuracy goal set at 10.

²⁷For $s = -0.02$ the socially-optimal choice is $x^* = 0$.

²⁸A similar pattern holds for $s < 0$.

optimum, as indicated by an increase in the H, D indices, is associated with a higher biodiversity value.²⁹ Thus, for our simulations, the social maximand increases with diversity, and our measure of diversity value depends not only on the ecological parameters, but also on economic parameters, such as market prices and the discount rate. Finally, it should be noted that a biodiversity value emerges for the more diverse system, even though the genetic distance between the two varieties is almost zero.

V. CONCLUDING REMARKS

In this paper we develop a conceptual framework for valuing biodiversity from an economic perspective. Our approach is based on the principle that biodiversity is important because of a number of characteristics or services that it provides or enhances. We develop an economic welfare measure of biodiversity by comparing the Bellman state valuation functions which are associated with feedback policy functions of alternative optimization problems. The optimization problems are characterized by the existence or not of property rights to the gene pool, which is part of the state vector of the ecosystem. We thus obtain an endogenous measure of the biodiversity value and link this measure to ecologically/biologically oriented biodiversity metrics (species richness, Shannon, Simpson, diversity function) that correspond to the equilibrium diversities of the optimizing models.

By taking into account ecological and genetic constraints implying that crop diversity reduces pest effectiveness, we determine the socially-optimal harvesting rules and crop mix when there is a system of full property rights to the gene pool. Our results indicate that there is a gain at the social optimum from having a more diverse system, relative to the polar case of a homogenous system emerging from private optimizing decisions with no property

²⁹For fixed $s = 0.5$ the H and D indices are approximately constant for varying death rates. There is always, however, a positive biodiversity value relative to the homogenous system, which is inversely related to the death rate d_2 .

rights to the gene pool. This gain - which is defined by the extra value, measured in terms of the OSS Bellman state valuation function, which is attained by a more diverse system - is the value of genetic diversity. By using numerical simulations, we are able to confirm our theoretical results and to obtain numerical measures of the value of biodiversity and the corresponding ecologically/biologically oriented biodiversity metrics.³⁰

In relation to the four sources of economic value for biodiversity - productivity, insurance, knowledge and services - mentioned in the introduction (Heal 2000), it seems that since in our model biodiversity increases productivity by protecting the group from lethal pests, the productivity and the insurance value sources are captured together. In a sense, biodiversity increases productivity through an insurance mechanism that is produced by the role of biodiversity in controlling the dynamics of natural selection of pest species.

If the shape of the demand curve $D(H)$ is more general than the one used in this paper, the loss of variety 2 (non *Bt* crop) could generate a huge loss in value because it leads to all resistant pests (borers). If we assume resistant borers are totally fatal to corn, then crop yields are ultimately zero. In this case if the harvest is “essential” in demand in the sense that $D(0) \rightarrow \infty$, then the losses are huge. Therefore, the “true” economic value of biodiversity in this example of almost zero “DNA distance”³¹ could be huge depending upon the shape of the demand curve.

Although we use a two-species system, the main point of our paper can be regarded as quite general, on the basis of the following argument. Suppose that we have an ecosystem

³⁰Tilman et al. (2002), using a similar mechanistic resource-based model of species competition, without stressing the impact of the genetic subsystem or introducing optimal economic management, show that ecosystem simplification resulting from selective harvesting, replanting harvested ecosystems with one or few species and habitat fragmentation, can lead to decreased productivity and increased year-to-year variation of productivity.

³¹For example only one gene was changed in the maize genome to produce *Bt*-corn and the maize genome, like any real genome, is huge.

that consists of a set of “similar” varieties (or species), the collection of which is essential to providing a valued ecosystem service. Call this set $S = \{s_1, s_2, \dots, s_n\}$ where s denotes species. Each member s_i of the collection S can do an essentially equal job of providing that service. So it looks (on the surface) that there is no reason to preserve all of these similar species. However, there is a collection of species such as predator or parasite that endangers each member of S . Call this set $P = \{p_1, p_2, \dots, p_m\}$. Rank the P 's as $p_1 < p_2 < \dots < p_m$, with p_m the most lethal to all the members of S and p_1 the least harmful to members of S . The ability to deflect members of P varies across the s_i . Rank the s_i from $s_1 < s_2 < \dots < s_n$ from most vulnerable to members of P to least vulnerable to members of P . If s_1 is the only member of S present, the population distribution across p_i in P evolves to a wide distribution. If s_n is the only member of S present, the population distribution of p_i in P evolves to only the most lethal type p_m . This is so because s_n is the least vulnerable, so only the most effective member of P , i.e. p_m , can deal with the “defenses” of s_n .

A plant can use resources to put up defenses against members of P (e.g. produce toxins in its root system to fight pathogens) but if it uses more resources to do this, it has less resources for other functions like roots, shoots, and leaves. So it might be natural for humans to think that they can delete s_n to open space in the ecosystem for some other s_i , say s_1 , because s_n 's bigger assignment to defense resources leaves it with less production of the visible ecosystem services that interests the humans. This thinking suggests that humans might selectively delete the plants that are providing the most useful (but “invisible”) ecosystem “service” of maintaining a P -diversity, that supports sustainable production of S -services. That is, the most desirable plant to humans may be the least desirable for the objective of maintaining a desirable biodiversity of the set P , thus the selective narrowing by humans of S -diversity leads to a malevolent narrowing of P -diversity that ultimately threatens existence of the service S .

In the context of the discussion regarding social well-being, our work not only shows that

when we want to correct the Net National Product for ecosystem services, the complete gene pool should be shadow priced, but also that this shadow pricing should not always be done based on “genetic distance” diversity measures.

In the context of externalities associated with genetic engineering, one might view the tactics of “re-engineering” genetically modified plants as an attempt by humans to simulate the adaptation mechanism of “sex” in Nature, where sex enables a slow-moving genetic dynamics host to survive a fast-moving genetic dynamics pest (Axelrod 1997). However the incentive of farmers to always use the most productive variety contributes a negative externality in the form of narrowing the population of crop genotypes which “speeds up” the evolution of the pest population towards the most lethal pest genotype. Our current model can be viewed as a tractible compromise that attempts to abstract out the essential forces in a way that hopefully contributes to an understanding of the more complex reality dynamics.

Of course more realistic genetic and mating assumptions can be used. Ives and Andow (2002) use more realistic genetics and mating dynamics in modeling evolution of resistance to *Bt* crops, by allowing non assortative (non-random) mating, and limited dispersal of pests from their natal fields. We are using this example, however, only as a parable to communicate the usefulness of an economic-valuation-based definition of “increased biodiversity.” In general there are always likely to be unobserved services provided by extra biodiversity.

The conceptual model developed in this paper can also be generalized to a multi-variety set up, which involves antagonistic co-evolution of the species of a functional group and pest or parasites according to the so-called “Red Queen” hypothesis.³² According to this hypothesis, parasites evolve ceaselessly in response to perpetual evolution of species’ (or hosts’) resistance. The co-evolution of the parasites’ ability to attack (virulence) and the hosts’ resistance is expected to indicate persistent fluctuations of resistance and virulence.

³²See for example Van Valen (1973), May and Anderson (1983), Ebert and Hamilton (1996) and Kawecki (1998).

In this context the Red Queen hypothesis generates a continuous need for variation, and a common clone will be wiped out by parasites that have adapted to parasitize it.³³

The economic optimization developed in this paper basically argues that if we monoculturalize group G to the “most desirable” species s^* in G , we speed up evolution of a pest genotype that can destroy the group. A fuller model would have a “genetic arms race” of a group $P = \{p_1, p_2, \dots, p_m\}$ of pests co-evolving in a Red Queen-type race against the target functional group G . When private profit-optimization incentives ignore Red Queen co-evolution and reduce the diversity of the group, or even monoculturalize the G side of this Red Queen race, the speed of the pest side increases and might wipe out the less diverse group, with a consequent welfare loss.

Another more general mechanism associated with the plant-pest interactions developed in this paper, which could cover multiple-species, multiple-pest cases, can be found in the hypothesis that a more diverse system is less susceptible to pest attacks because of: (i) the disruptive-crop hypothesis, (ii) the trap-crop hypothesis, and (iii) the enemies hypothesis.³⁴

Finally, regarding generalizations, it should be pointed out that since ecosystem services of different types are delivered by functional groups of different types, we expect to find in each functional group-ecosystem service type pair, a particular member of that functional group that is “most efficient” at delivering the services that humans desire. Relevant examples of most desirable species could be green lawn grass for lawn services, a most desirable corn species for corn food services, a most desirable wheat species for wheat food services, and so

³³There are empirical studies documenting the presence of genetic variation for resistance against plant pathogens or against animal parasites. See, for example, Carius et al. (2001) or Lively and Dybdahl (2000) for an empirical verification of the Red Queen hypothesis for fresh water snails in New Zealand.

³⁴In the disruptive-crop hypothesis a new species disrupts the ability of the pest to attack the proper host, in the trap-crop hypothesis a new species attracts pests that would be detrimental to a main species, while in the enemies case a diverse system attracts more predators than a monoculture and reduces pests through predation. For details, see Vandermeer (1989).

on. If, for example, we narrow the lawn grass species distribution down to one, the genetics Red Queen race for pathogens (e.g. leaf spot, necrotic ring spot, anthracnose) might speed up and could eliminate the single species.

The idea of associating reduction of diversity within a functional group with increased ability of pests to attack the remaining host and reduce the value of the system could also be associated with the genetic distance-based approach to biodiversity (Weitzman 1993, Solow et al. 1993) in the following way. Assume that a pest has already optimally evolved its genotype to attack species s_i in G . If it is easier for the s_i -specific pest to evolve into an s_{i+1} specific pest when s_{i+1} is the closest to s_i in terms of a phenotypic measure, then there is a link between the phenotypic-distance-based biodiversity valuation and welfare losses which could be established, since in this case Red Queen dynamics might work towards eliminating the less diverse system. Of course this is largely an empirical issue, but if such a relationship exists it could provide a more precise link between the diversity function and welfare changes.

The above discussion suggests that our model could be generalized towards models attempting to unify the economic optimization problem with more general models of hosts-pests co-evolution, or multi-species models incorporating trap-crop type mechanisms. As in our simple two-species model, biodiversity could increase welfare relative to a less diverse group, through an insurance mechanism that prevents the evolution of pests that might wipe out the whole group. Undoubtedly this is much more difficult to model, but it seems an interesting area for future research. At a more abstract level the general point of our paper is this. Proper valuation of the biodiversity of a set S of species requires identification of a “sufficient” state vector, call it x_S , which reflects the full interaction of S with the ecosystem in which S is embedded to yield a workable approximation of the “true” state vector, call it $x_S\{true\}$. The quality of this approximation can be measured in terms of the deviation of any approximation valuation from the “true” Bellman state valuation function”, call it $V_{true}(x_S\{true\})$. In this way we point towards identification and proper measurement of

some of the necessary ingredients that would go into a practical implementation of the general approach to computation of “full value” advanced by, for example, Dasgupta and Maler (2000).

Appendix

Proof of Proposition 1:

By adding together the two biomass transition equations, the constraints regarding the biomass and resource become:

$$\dot{B} = B(gR + x(d_2 - d_1) - d_2) - H \quad (28)$$

$$\dot{R} = S - aR - gwRB \quad (29)$$

$$\dot{p} = p[G(p, x) - 1] \quad (30)$$

$$0 \leq x \leq 1, 0 \leq H \leq K^{\max} \quad (31)$$

The current value Hamiltonian for this problem can be written as:

$$\begin{aligned} \mathcal{H}^U = & H + \lambda [B(gR + xp(d_2 - d_1) - d_2) - H] + \mu (S - aR - gwRB) \\ & + qp(G(x, p) - 1) + \xi(1 - x) + \zeta x \end{aligned} \quad (32)$$

where ξ and ζ are Lagrangian multipliers associated with the $0 \leq x \leq 1$ constraint. Maximization of the current value Hamiltonian over H subject to (31) implies that the following conditions of the maximum principle should be satisfied at the OSS:

$$H = \begin{cases} 0 & \text{if } \lambda > 1 \\ K^{\max} & \text{if } \lambda < 1 \end{cases} \quad (33)$$

Furthermore the singular solution implies at the OSS that

$$\lambda = 1, \dot{B} = 0, \dot{R} = 0, \dot{p} = 0 \quad (34)$$

$$H = B(gR + x(d_2 - d_1) - d_2), S - aR = gwRB, G(p, x) = 1 \quad (35)$$

We further analyze the singular solution, which represents the most interesting case, with the help of the following lemma.

Lemma 1 *Assume that an OSS with $(\bar{B}, \bar{H}, \bar{R}, \bar{p}) > 0$ exists for the POMP and let \hat{B} sufficiently high such that $\hat{B} > \bar{B}$. If $K^{\max} > \frac{S}{w} + \hat{B}(d_2 - d_1)$, then $\lambda = 1$.*

P roof. Let $(\bar{B}, \bar{H}, \bar{R}, \bar{p}) > 0$ be an OSS. Then $gw\bar{R}\bar{B} = S - a\bar{R}$. If at this OSS $\lambda < 1$, then $K^{\max} = \bar{B}(g\bar{R} + x(d_2 - d_1) - d_2)$ and we have:

$$\begin{aligned} wK^{\max} &= w\bar{B}(g\bar{R} + x(d_2 - d_1) - d_2) < w\bar{B}(g\bar{R} + x(d_2 - d_1)) = \\ &S - a\bar{R} + w\bar{B}x(d_2 - d_1) < S + w\bar{B}x(d_2 - d_1), \quad 0 \leq x \leq 1 \end{aligned}$$

Therefore $K^{\max} < \frac{S}{w} + \bar{B}x(d_2 - d_1)$ for $\lambda < 1$. Thus if $K^{\max} > \frac{S}{w} + \hat{B}(d_2 - d_1)$ then $\lambda = 1$.

■

Assuming $K^{\max} > \frac{S}{w} + \hat{B}(d_2 - d_1)$ we obtain at a steady state with positive biomass

$$\lambda = 1, \quad H = B(gR + xp(d_2 - d_1) - d_2) \quad (36)$$

The maximum principle implies for the choice of x that:

$$Bp(d_2 - d_1) + qp \frac{\partial G(p, x)}{\partial x} - \xi + \zeta \leq 0, \quad x \geq 0 \quad (37)$$

If $0 < \bar{x} < 1$ then $\xi = \zeta = 0$

Furthermore the system for the costate variables at the steady state becomes

$$0 = (gR + xp(d_2 - d_1) - d_2 - \rho) - \mu gwR \quad (38)$$

$$0 = (\rho + a + gwB)\mu - gB \quad (39)$$

$$0 = \left(\rho - p \frac{\partial G(p, x)}{\partial p} \right) q - xB(d_2 - d_1) \quad (40)$$

From (38) and by combining (39) and (40) we obtain the following equations which determine the OSS resource level

$$Q^S(R, \rho) = \frac{gR + xp(d_2 - d_1) - d_2 - \rho}{gwR} \quad (41)$$

$$f^S(R, \rho) = \frac{S - aR}{w(R\rho + S)} \quad (42)$$

To further characterize the OSS we note that if $x = 1$ at the OSS then $p \rightarrow 0$ as shown by (16) and the solution tends to a homogeneous system of variety 2. The same holds for $x = 0$.

Thus we set $\xi = \zeta = 0$ and explore solutions for $0 < \bar{x} < 1$. In this case the OSS equations become:

$$Bp(d_2 - d_1) + qp \frac{\partial G(p, x)}{\partial x} = 0 \quad (43)$$

$$\frac{gR + xp(d_2 - d_1) - d_2 - \rho}{gwR} = \frac{S - aR}{w(R\rho + S)} \quad (44)$$

$$\left(\rho - p \frac{\partial G(p, x)}{\partial p} \right) q = xB(d_2 - d_1) \quad (45)$$

$$G(p, x) - 1 = 0 \quad (46)$$

$$B = \frac{S - aR}{gwR} \quad (47)$$

which determine the five unknowns (B, x, R, p, q) at the OSS.

A Most Rapid Approach Path for the Unified Model

The dimensionality of the unified model with respect to the state variables can be reduced by transforming the problem into a MRAP problem. Substituting H by

$$H = B(gR + xp(d_2 - d_1) - d_2) - \dot{B} \quad (48)$$

into the objective function for the unified model, integrating by parts and assuming that $\lim_{t \rightarrow \infty} e^{-\rho t} B(t) = 0$, we have the following problem:³⁵

$$\begin{aligned} & \max_{x, B} \int_0^{\infty} e^{-\rho t} B(gR + xp(d_2 - d_1) - d_2 - \rho) dt & (49) \\ \text{s.t. } & \dot{R} = S - aR - gwRB \\ & \dot{p} = p[G(p, x) - 1] \\ & 0 \leq x \leq 1, 0 \leq B \leq B^{\max} \end{aligned}$$

The current value Hamiltonian for this problem is

$$\begin{aligned} \mathcal{G} &= B(gR + xp(d_2 - d_1) - d_2 - \rho) + \mu(S - aR - gwRB) \\ & \quad + qp(G(p, x) - 1) \end{aligned} \quad (50)$$

³⁵See Kamien and Schwartz (1991, p. 97).

For positive biomass at an OSS the singular solution implies

$$gR + xp(d_2 - d_1) - d_2 - \rho = \mu gwR \quad (51)$$

while for $0 < x < 1$

$$Bp(d_2 - d_1) + qp \frac{\partial G(p, x)}{\partial x} = 0 \quad (52)$$

The maximum principle also implies that for the costate variables at the OSS

$$0 = (\rho + a + gwB)\mu - gB \quad (53)$$

$$0 = \left(\rho - p \frac{\partial G(p, x)}{\partial p} \right) q - xB(d_2 - d_1) \quad (54)$$

By comparing (51)-(54) with (37) and (38)-(40), it is clear that the OSS of the MRAP is the same as the OSS of the complete unified model.

Then from (51) and (52) we obtain for the OSS controls

$$x^* = \frac{\mu gwR - gR + d_2 + \rho}{p(d_2 - d_1)} = X(R, \mu, p, q) \quad (55)$$

$$B^* = -\frac{q \frac{\partial G(p, x^*)}{\partial x}}{(d_2 - d_1)} = \beta(R, \mu, p, q) \quad (56)$$

Therefore, the MHDS for the MRAP problem at an OSS is defined as:

$$0 = S - aR - gwRB^* \quad (57)$$

$$0 = G(p, x^*) - 1 \quad (58)$$

$$0 = (\rho + a + gwB^*)\mu - gB^* \quad (59)$$

$$0 = \left(\rho - p \frac{\partial G(p, x^*)}{\partial p} \right) q - x^* B^* (d_2 - d_1) = \quad (60)$$

$$\rho - p \frac{\partial G(p, x^*)}{\partial p} + x^* \frac{\partial G(p, x^*)}{\partial x} \quad (61)$$

If a steady state $(\bar{R}, \bar{\mu}, \bar{p}, \bar{q})$ exists, then

$$\bar{x} = X(\bar{R}, \bar{\mu}, \bar{p}, \bar{q}), \quad \bar{B} = \beta(\bar{R}, \bar{\mu}, \bar{p}, \bar{q}) \quad (62)$$

$$\bar{B}_1 = \bar{x}\bar{B}, \quad \bar{B}_2 = (1 - \bar{x})\bar{B} \quad (63)$$

$$\overline{H}_1 = \overline{x}\overline{B}(g\overline{R} + \overline{x}\overline{p}(d_2 - d_1) - d_2) \quad (64)$$

$$\overline{H}_2 = (1 - \overline{x})\overline{B}(g\overline{R} + \overline{x}\overline{p}(d_2 - d_1) - d_2) \quad (65)$$

□

Proof of Proposition 2:

By making the transformations (4)-(5) and adding the biomass transition equations we obtain the current value Hamiltonian for this problem as:

$$\mathcal{H}^P = H + \lambda [B(gR + x(d_2 - d_1) - d_2) - H] + \mu [S - aR - gwRB] \quad (66)$$

Assuming as before $K^{\max} > \frac{S}{w} + \hat{B}(d_2 - d_1)$ we obtain

$$\lambda = 1, \dot{B} = 0, \dot{R} = 0 \quad (67)$$

$$H = B(gR + x(d_2 - d_1) - d_2), S - aR = gwRB \quad (68)$$

For the choice of x at this OSS, the maximum principle implies that since $\lambda = 1$, $(\overline{B}, \overline{H}) > 0$, $d_1 < d_2$, and x should maximize $\lambda x B(d_2 - d_1)$ in (66), then the optimal choice should be

$$\overline{x} = 1 \quad (69)$$

With $\lambda = 1$, $x = 1$ the maximum principle implies that for the MHDS at the steady state:

$$0 = (gR - d_1 - \rho) - \mu gwR \quad (70)$$

$$0 = (\rho + a + gwB)\mu - Bg \quad (71)$$

$$S - aR = gwRB \quad (72)$$

$$H = B(gR - d_1) \quad (73)$$

From the above system we obtain

$$Q_1(R, \rho, d_1) = \frac{(gR - d_1 - \rho)}{gwR} \quad (74)$$

$$f(R, \rho) = \frac{S - aR}{w(R\rho + S)} \quad (75)$$

Equations (74) and (75) determine the steady state $\bar{R}(d_1)$ from the solution of $Q_1(R, \rho, d_1) = f(R, \rho)$. This steady state is not however sustainable since the genetic constraint (16) implies that $G(p, 1) = 0$ and $p \rightarrow 0$ at the most rapid rate as shown in section III. Then the death rate of plant variety 1, which is not exogenous as perceived by the private agents, tends to d_2 or $d_1(0) = d_2$. This means that eventually equilibrium is reached at the resource level $\bar{R}(d_2)$ which is defined by:

$$\frac{(gR - d_2 - \rho)}{gwR} = \frac{S - aR}{w(R\rho + S)} \text{ with } \bar{B}(d_2) = \frac{S - a\bar{R}(d_2)}{gw\bar{R}(d_2)} \quad (76)$$

□

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Table 2: Value of Biodiversity

s, d_2	\bar{R}	$-$	\bar{p}	\bar{q}	x	B	$\bar{B} d_2$	% gain in biomass	H	$\bar{H} d_2$	% gain in harvesting	Biodiversity Value V^2 V^1	Shannon Index, H	Simpson Index, D
0.5,0.5	13.65	5.94	0.3093	14.49	0.2164	18.593	16.779	10.81	3.953	3.431	15.22	52.218	0.522	0.339
0.4,0.5	13.73	5.87	0.3035	14.43	0.1841	18.282	16.779	8.96	3.869	3.431	12.77	43.821	0.478	0.300
0.3,0.5	13.81	5.79	0.2962	14.34	0.1480	17.949	16.779	6.97	3.773	3.431	9.98	34.231	0.419	0.252
0.2,0.5	13.89	5.71	0.2857	14.13	0.1071	17.588	16.779	4.82	3.663	3.431	6.76	23.199	0.340	0.191
0.1,0.5	13.99	5.62	0.2635	13.52	0.0604	17.195	16.779	2.48	3.554	3.431	3.57	12.250	0.228	0.113
0.01,0.5	13.35	6.23	0.9358	1684.88	0.1196	19.911	16.779	18.67	4.338	3.431	26.43	90.685	0.366	0.211
0.015,0.5	14.07	5.54	0.5889	14.10	0.0065	16.878	16.779	0.59	3.464	3.431	0.95	3.269	0.039	0.013
0.5,0.4	12.21	7.34	0.3093	15.46	0.2164	25.501	23.459	8.70	6.136	5.403	13.57	73.308	0.522	0.339
0.5,0.3	10.70	8.93	0.3093	15.37	0.2164	35.494	33.375	6.35	9.410	8.182	15.01	122.844	0.522	0.339
0.5,0.2	8.71	10.82	0.3094	13.46	0.2164	51.836	49.569	4.57	13.650	12.223	11.67	142.691	0.522	0.339
0.5,0.1	6.32	13.25	0.3993	7.49	0.2164	86.476	84.507	2.33	22.041	18.698	17.88	334.289	0.522	0.339