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

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August 19, 2001

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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 attribute biodiversity loss to economic activities related to decisions of private optimizing agents that ignore useful characteristics or services associated with diverse ecosystems. Using a unified model of economic management of an ecosystem under ecological and genetic constraints, we compare the optimal value of the social optimization problem where positive externalities associated with biodiversity are internalized, to that of a private optimization problem. We obtain an endogenous measure of the biodiversity value and relate this measure to ecologically/biologically oriented biodiversity metrics (species richness, Shannon or Simpson indices) that correspond to the equilibrium diversities of the social and private optimization problems.

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1   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] Biodiversity can be regarded as being synonymous to biological diversity, which contains three levels: genetic diversity (within species), species diversity (species numbers) and ecological diversity (richness of processes to which species contribute).[2] In dealing with the concept of biodiversity, important questions arise. First it seems necessary to examine whether biodiversity is measurable and what the appropriate metric is. Second it is important to know whether biodiversity promotes useful properties, or equivalently provides or enhances useful services, such as ecosystem stability, productivity or sustainability.

Measuring biodiversity is a very complicated task given the various aspects and characteristics that the biodiversity metric should cover.[3] 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

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[1] See for example Harper and Hawksworth (1994).
[2] See Norse et al. (1986).
[3] See Harper and Hawksworth (1994).

richness (R), which is simply the number of species in a landscape, to the Shannon (H) or Simpson (D) diversity indices and their modifications.[4]

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),[5] which is defined in terms of pairwise distances among species, with distance being a measure of dissimilarity among species. In biological application 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. Once the diversity function is defined, then its value 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. Although this approach can be used to rank alternative conservation plans and to derive benefit-cost ratios, it is based on the implicit assumption that diversity measured in terms of genetic distances is desirable.[6] 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" can be regarded as an extension of this approach (Weitzman 1998, Metrick and Weitzman 1998). In this problem 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 the diversity metric. Li, Lofgren and Weitzman (2001) examine the implication for optimal harvesting policies in a fishery by introducing an exogenously determined willingness to pay function for species preservation.

In their approach to pricing biodiversity, Montgomery et al. (1999) use an exogenous range of biodiversity values ranging from $0 to $200 million per diversity index point, where the index computes diversity weights based on the taxonomic tree. An approach that attempts to link diversity with a measure of economic value is associated to "biodiversity prospecting" (Simpson et al. 1996, Craft and Simpson 2001), which values biodiversity on the basis of the marginal species' incremental contribution to the probability of making a commercial discovery.

In our approach we feel that the 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

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

[5] See also Nehring and Puppe (2000) for valuation based on evolutionary information through the phylogenetic tree model.

[6] As stated in Weitzman (1992, p. 401), "The most valuable species is the farthest distant from the others - by any reckoning".

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] knowledge[10] and ecosystem services.[11] Ecosystem characteristics or services could range from the more tangible or measurable - such as productivity or stability (resilience) - to the less tangible - such as aesthetic satisfaction, existence values or bequest motives. If we accept for example that the stability of an ecosystem is a desirable state, that more productive ecosystems in terms of useful biomass are more desirable than less productive ecosystems, or that a more diverse system can provide valuable watershed or ecotourism services, then a relationship can be established between a biodiversity metric and the value of these useful characteristics or services. Once this relationship is established, then changes in the stability properties, the productivity, or the value of services of an ecosystem, can be associated with changes in biodiversity metrics. It is clear that this association can be used to value biodiversity *not* in terms of genetic distances but in terms of the value of characteristics or services that it provides or enhances. In a sense this approach can be regarded as connecting ecologically/biologically oriented biodiversity metrics, such as species richness, the Shannon or the Simpson indices, or the diversity function, with a measure of economic value of biodiversity.

The purpose of this paper is, therefore, to approach the problem of valuing biodiversity from an economic perspective. In order, however, to have a meaningful valuation framework, a link should be established between a biodiversity metric and the services or properties that will be used as a basis for the valuation. We need therefore to establish the mechanism through which biodiversity affects productivity, stability, insurance, knowledge, or the flow of services from an ecosystem. Establishing however a link between a biodiversity metric and a wide range of properties or services implies the development of a complex mechanism that relates processes which are not even properly understood yet. In this paper we take a modest step in this

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[7]See also Daily et al. (1997).

[8]This is associated with the fact that more diverse plant systems are more productive than less diverse ones.

[9]Insurance 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).

[10]Biodiversity can be used as a source of knowledge with which to develop new products in 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.

[11]Biodiversity 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, production of "non-timber forest products", is maintained. (See also Daily and Dasgupta (2000)).

direction by trying to establish a link between biodiversity and productivity/stability of an ecosystem using, for the first time to our knowledge, a unified framework based on ecological and genetic mechanisms.

The question regarding the biodiversity-productivity relationship has been studied extensively. Although there is a high degree of uncertainty associated with species diversity, the rate at which diversity is lost and the implications of such loss, there is evidence that declining species diversity may affect the performance of terrestrial ecosystems in such a way that species-poor assemblages are less productive.[12] If changes in a biodiversity metric, such as richness, result in changes in the ecosystem's biomass, then these changes valued at market or social prices can be used to value biodiversity changes. It is also well known that biodiversity has been 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.[13] Thus, for example, if a change in the biodiversity metric results in the loss of an ecosystem's stability, or in a considerable change in the size of the basin of attraction of the ecosystem, then the change in biodiversity can be "valued" in terms of stability characteristics.

It is well documented (e.g. Wilson and Peter 1988) that activities associated with human expansion are a major factor in biodiversity loss.[14] Given therefore the relationship between human activities, loss of biotic diversity and loss of ecosystems' productivity or resilience, the valuation structure we develop contains, as it should, an economic module indicating that species exploitation results in economic benefits, and an ecological/genetic module representing the mechanism through which the management rules of benefit maximizing economic agents are transmitted to the natural system and affect the equilibrium biodiversity. In our model different stability properties, biomass values, and equilibrium biodiversity metrics emerge as a result of different optimizing management rules. In this way we obtain an *endogenous* valuation of biodiversity in terms of resilience and productivity. This valuation framework is consistent with both the genetic and species diversity concepts, but it is also consistent with the ecological diversity concept, since it uses the value of services accruing from the processes to which species

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[12]There are a number of empirical studies relating the number of species in ecosystems to plant productivity (Naeem 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. Vandermeer (1989), 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.

[13]There is an extensive discussion in the ecological literature regarding the question of whether biodiversity promotes stability. An ecological tenet justifying the conservation of biodiversity, is that biodiversity begets stability. Recent field studies (Tilman and Downing 1994, Tilman et al. 1996) provide support for the diversity-stability hypothesis.

[14]It has been estimated that as much as 50% of biotic diversity will be lost in the next century as a result of human expansion (Soule 1991).

contribute.

In developing our model we consider a system of two varieties of species, $i = 1, 2$, which are similar from a functionalist viewpoint. The species 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. We model the evolution of the pest population by Hardy-Weinberg mating and one locus two alleles genetics. One of the two varieties, $i = 1$, is immune to some types of pests; as a matter of fact this variety is lethal to these types of pests, but is not immune to the other types of pests. The second variety, $i = 2$, is not immune to any type of pest. As long as the population of pests includes the type to which variety 1 is lethal, then this variety has a lower death rate and therefore a productivity advantage over variety 2. Management decisions refer to the distribution of land between the two varieties so that 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 land distribution and the implied diversity corresponding to certain optimizing behavior. Associating the optimal value of the management problem, expressed in terms of equilibrium biomass value, with the corresponding biodiversity metric, we can define an endogenous value for biodiversity based on the economic, ecological, and genetic characteristics of the problem, since economic decisions result in some equilibrium diversity through the ecological/genetic mechanism.

This set-up is motivated by genetic engineering literature on Bt-crops and Bt-corn in particular, where a protein that is found in the soil bacterium Bacillus thuringiensis,[15] 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.[16] 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

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[15] More than 30 crop species have been genetically engineered to express Bacillus thuringiensis endotoxin (Ives 1996).

[16] Trial tests reportedly indicate that Bt-corn has an advantage of 8.5 bushels per acre yield over non Bt-corn hybrids (Hurley et al. 1999).

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. Thus if farmers act myopically by not taking into account the development of resistance through natural selection mechanisms, and in the process turn the area into a Bt-corn monoculture, the externality generated will eliminate all the advantage of the new technology and will eventually reduce productivity.

In the Bt-corn metaphor, the creation of a monoculture generates a negative externality, since it eventually causes the reduction of pest resistance and the elimination of the productivity advantage of Bt-corn.[17] In ecosystem management models, when constraints imposed by ecological/genetic factors are not taken into account in a private optimization management model (POMP), then the system is likely to turn into a specialized monoculture. When these constraints are taken into account in a social optimization management model (SOMP), then equilibrium biodiversity in general is different from that of POMP.[18] Then by comparing the value of biomass corresponding to the POMP/SOMP equilibrium diversities, we obtain our endogenous measure of the value of biodiversity.

The rest of the paper is organized as follows. Section 2 presents some elements of population dynamics which we consider necessary for the understanding of the influence of the natural selection mechanism on our model. Section 3 develops the unified economic/ecological/genetic model. In section 4 we describe how population dynamics affect equilibrium biodiversity. In section 5 the unified model is solved for the POMP and the SOMP. Given the highly nonlinear nature of the solution we perform numerical simulations and we determine the loss in biomass value between a monoculture corresponding to the POMP solution, and a polyculture of two species corresponding to the SOMP solution. This comparison provides the endogenous biodiversity valuation. The last section concludes and discusses further extensions of this approach.

2   Elements of Population Genetics[19]

In a genetic model a *chromosome* is a string which is the carrier of *genes* which are considered to be the elementary unit of inheritance. Every chro-

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[17]Externalities generated by monocultures that eventually have an adverse effect on the state of an ecosystem is a more general issue indicating that biodiversity generates services which should be taken into account in ecosystems management. See for example Scott (1998) or Soule and Piper (1992).

[18]Brock and Xepapadeas (2001) analyze conditions under which the POMP results in a monoculture. They show that the SOMP and POMP equilibria in an ecosystem under mechanistic resource-based competition, are in general different from the equilibrium produced by Nature.

[19]The material in this section relies mainly on Feldman (1989), Roughgarden (1998) and Lyubich (1992).

mosome belongs to a class of *homologous* chromosomes. The *locus* of a gene is the spot or the position on a chromosome that is occupied by this gene. In homologous chromosomes there is a one-to-one correspondence between the loci. The genes occupying identical places in homologous chromosomes are called *alleles or allelic.* We consider corresponding loci as identical and we say that allelic genes are alleles of this locus. Thus each locus contains no less than two alleles. For example two alleles at the A-locus are $\{A_1, A_2\}$. Organisms in which the chromosomes form pairs are called *diploids*, with one chromosome contributed by the father and the matching chromosome contributed by the mother. The simplest possible genetic system can be represented by one locus with two alleles $\{A_1, A_2\}$. The three possible pairs of alleles in the locus are $A_1 A_1$, $A_1 A_2 = A_2 A_1$, $A_2 A_2$. These pairs are the *genotype* of the locus. When both alleles are the same, the organism is called *homozygote*, whereas when they are different it is called *heterozygote*. The *phenotype* of the organism is the manifestation of the gene product.

Consider an infinite population of diploid organisms with one locus, two alleles and three genotypes $A_1 A_1$, $A_1 A_2 = A_2 A_1$, $A_2 A_2$. The *gene pool* is the collection of all genes. Let p be the fraction of A_1 alleles in the gene pool and $q = 1 - p$ the fraction of A_2 alleles. Under random mating, the Hardy-Weinberg law states that the fraction of each genotype in the total population is:

$$A_1 A_1 = p^2, \ A_1 A_2 = A_2 A_1 = 2pq, \ A_2 A_2 = q^2$$

Natural selection takes place when "the different genotypes present in the population in a given generation contribute differently to the next generation" (Feldman, 1989, p. 505). The reasons for natural selection are differences in *viability* (*mortality*) and differences in *fertility* among genotypes.

Denote by W_{ij} $(i, j = 1, 2)$ the viability fitness of each genotype. The proportion of A_1 alleles in the gene-pool for a non-overlapping generation population evolves, in discrete time, from generation to generation according to the fundamental equation of evolutionary biology:

$$p_{t+1} = \frac{W_{11} p_t^2 + W_{12} p_t q_t}{W_{11} p_t^2 + 2W_{12} p_t q_t + W_{22} q_t^2} \tag{1}$$

There are three possible equilibria for the above difference equation describing the two allelic system:

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\begin{aligned}
\bar{p}_1 &= 1, \ \bar{p}_2 = 0, \\
\bar{p}_3 &= \frac{W_{12} - W_{22}}{2W_{12} - W_{11} - W_{22}} = \frac{1}{\frac{W_{12} - W_{11}}{W_{12} - W_{22}} + 1}
\end{aligned}
$$

The $\bar{p}_1$ and $\bar{p}_2$ equilibria are called *monomorphisms* while $\bar{p}_3$ is called a *polymorphism*. Admissible values for the polymorphism are $\bar{p}_3 \in (0, 1)$.

This is possible if: (i) $W_{12} > \max\{W_{11}, W_{22}\}$, that is the heterozygote has higher fitness than both homozygotes, or (ii) $W_{12} < \min\{W_{11}, W_{22}\}$, that is the heterozygote has lower fitness than both homozygotes. The stability properties of the three equilibria can be characterized as follows:

1. $W_{11} > W_{12} > W_{22}$. There are only two equilibria, $\bar{p}_1$ and $\bar{p}_2$. $\bar{p}_1$ is stable while $\bar{p}_2$ is unstable. There is *directional selection* for A_1.

2. $W_{22} > W_{12} > W_{11}$. There is directional selection for A_2. $\bar{p}_2$ is stable while $\bar{p}_1$ is unstable.

3. $W_{12} > W_{22}$ and $W_{12} > \max\{W_{11}, W_{22}\}$. The monomorphisms $\bar{p}_1$ and $\bar{p}_2$ are unstable, while the polymorphism $\bar{p}_3$ is stable. The heterozygotic fitness advantage produces a stable polymorphism.

4. $W_{12} < W_{22}$ and $W_{12} < \min\{W_{11}, W_{22}\}$. The monomorphisms $\bar{p}_1$ and $\bar{p}_2$ are stable, while the polymorphism $\bar{p}_3$ is unstable. The directional selection could be A_1 or A_2, depending on the initial conditions.

3   Economic Management of Ecosystems and Natural Selection

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, $i = 1, 2$,[20] while the pest comes in three genotypes, A_1A_1, $A_1A_2 = A_2A_1$, and A_2A_2. Assuming that the three genotypes correspond to three phenotypes for the pest, in the rest of the paper we will identify each genotype with a different type of pest. Plant variety 1 is immune, or to put it in another way, it kills genotypes (pest types) A_1A_1 and A_1A_2 but not genotype (pest type) A_2A_2.

Let the biomass of corn B_i, $i = 1, 2$, in a given area with size normalized to unity evolve according to Tilman's mechanistic resource-based model of species competition (Tilman 1982, 1988; Pacala and Tilman 1994). Thus the equations of the species competition can be written as:

$$\dot{B}_i = B_i\left[gR - d_i\left(p\right)\right] - H_i\,,\ i = 1, 2\,,\ B_i\left(0\right) = B_i^0 \qquad (2)$$

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

Equation (2) describes the growth of the varieties' biomass where: g is the coefficient of the biomass growth function, assumed the same for the

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[20] In the context of the genetically engineered corn, variety 1 = Bt-corn and variety 2 = non-Bt-corn. The pest is the European corn borer.

two types of plants; $d_i(p)$ is the death rate; and H_i is the harvesting of the variety per unit time. The death rate depends on p, which is the proportion of A_1 alleles in the genetic pool of the pest population. It is assumed that:

$$d_2(p) = d_2, \; d_1(p) = pd_1 + (1-p)d_2 \text{ with } d_1 < d_2 \qquad (4)$$

Thus if $p = 1$, only the A_1A_1 genotype exists in the pest gene pool. Variety 1 kills all A_1A_1 genotypes 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 2). Then $d_1(0) = d_2$ and the growth advantage of variety 1 is eliminated. Then, the two varieties are identical.

Equation (3) describes the resource dynamics where $S - aR$ is the net amount of the resource supplied at time t, with S being exogenous natural supply, and aR reflects natural resource removal, where a can be interpreted as an erosion or a leaching rate. Thus $S - aR$ can be regarded as the net flow of nutrients.[21] 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).

Let x be the proportion of the area planted with variety 1. Then the proportion $p = p(t)$ of A_1 alleles in the pest gene-pool evolves, from generation to generation, according to the fundamental equation (1) of evolutionary biology, which in continuous time is written as:

$$\dot{p} = p[G(p,x) - 1], p(0) = p^0 \qquad (5)$$

$$G(p,x) = \frac{W_{11}(x)p + W_{12}(x)(1-p)}{W_{11}(x)p^2 + 2W_{12}(x)p(1-p) + W_{22}(x)(1-p)^2} \qquad (6)$$

$$W_{ij}(x) = xw_{ij}(1) + (1-x)w_{ij}(2), \; i = 1, 2 \qquad (7)$$

where $w_{ij}(1), w_{ij}(2)$ are the viability fitnesses of the ij pest (type) genotype for plant variety 1 or 2 respectively. If we assume that 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 $w_{ij}(2) > 0$, $i = 1, 2$.

Equations (2) - (7) describe the evolution of the natural system. The evolution of this system, however, depends on parameters which can be regarded as choice variables in a management problem. These are the harvesting per unit time H_i, and the proportion of the area x which is planted with variety 1. So formally the management problem, assuming that both varieties sell at the same competitive market price which is normalized to

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[21]Resource 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.

one, can be defined in terms of choosing time paths for harvesting $H_i(t)$, $i = 1, 2$, and the proportion of the area planted with variety 1, $x(t)$ to solve:

$$\max \int_0^\infty e^{-rt} (H_1 + H_2)\, dt \tag{8}$$

$$\text{subject to ,(2) - (7) and}$$

$$0 \leq x \leq 1 \,,\, 0 \leq H_i \leq K^{\max} \tag{9}$$

where $r \geq 0$ is the discount rate.[22] Problem (8) provides, for the first time to our knowledge, an integration of optimal management theory using a Pacala-Tilman resource-based model of species competition, with explicit population genetics to model evolution of resistance.

4   Evolution of Resistance and Biodiversity

In the optimization problem (8), the choice of x will determine the relative sizes of the areas planted with variety 1 which *is* resistant to the pest and variety 2 which *is not* resistant to the pest.[23] This allocation of land will affect the evolution of resistance in the gene pool through the subsystem (4)-(7). 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.

At a first stage of analysis we can obtain, by analyzing a simplified submodel, some useful insight regarding allocation strategies and examine the case where it is not optimal to run down the resistance of the higher-valued species to zero.

Assume that there is a fixed flow of nutrients to support a fixed flow of new plant biomass available for harvesting in each period, before death rates $d_i(p)$ occur. Death rates depend, however, on the distribution of genotypes in the gene pool. If for example $p = 1$, then $d_2 - d_1 = \alpha > 0$ and variety 1 has a productivity advantage over variety 2 in terms of net, after death, harvesting flow. Under these assumptions, alternative allocation strategies can be analyzed by considering only the subsystem (4)-(7), for given steady-state resource level $\overline{R}$, which for the fixed nutrient flow supports a given steady state $\overline{B}$ of total gross (before death) harvest flow.

In the system (4)-(7) the proportion of A_1 alleles depends on the choice of the allocation strategy x. Then using (5) the equilibrium p will depend on the choice of x. The concept of an allocation strategy implies that the

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[22] The constraint $0 \leq H_i \leq K^{\max}$ is required so that the problem is well posed given its linearity in H. Furthermore, if we had allowed for fertilization and $c(F)$ were the cost of augmenting the resource through fertilization, $c(F)$ should have been deducted from the flow of harvesting revenues.

[23] In terms of Bt-corn analysis this constitutes a refuge strategy.

equilibrium for (5) is defined as:

$$p^* : G\left(p^*, x\right) - 1 = 0, \ p^* \neq 0 \tag{10}$$

In a polymorphic equilibrium the polymorphism is defined as:

$$\bar{p}_3\left(x\right) = \frac{W_{12}\left(x\right) - W_{22}\left(x\right)}{2W_{12}\left(x\right) - W_{11}\left(x\right) - W_{22}\left(x\right)} \tag{11}$$

As discussed in section 2, if there is a heterozygotic fitness advantage, or:

$$W_{12}\left(x\right) > W_{22}\left(x\right) \ \text{and} \ W_{12}\left(x\right) > \max\left\{W_{11}\left(x\right), W_{22}\left(x\right)\right\} \tag{12}$$

this polymorphic equilibrium is stable, while the monomorphic equilibria are not stable.

A polymorphic equilibrium for the pest part of the model can be associated with a biodiversity richness metric $R^b \geq 2$, with $R^b = 3$ being the maximum richness,[24] while a monomorphic equilibrium is associated with a biodiversity richness metric $R^b = 1$.

It can easily be seen by combining (6) and (11) that, since $W_{12}\left(x\right) > W_{22}\left(x\right)$ 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 the entire area is planted with variety 1 which kills A_1A_1 and A_1A_2 alleles, we have $W_{12}\left(1\right) = W_{11}\left(1\right) = 0$, while $W_{22}\left(1\right) = w_{22}\left(i = 1\right) > 0$. This implies that for x sufficiently close to 1 the stability condition is most likely to be violated and for $W_{22}\left(x_\varepsilon\right) > W_{12}\left(x_\varepsilon\right) > W_{11}\left(x_\varepsilon\right)$, with $x_\varepsilon = 1 - \varepsilon$, $\varepsilon > 0$, there is a stable monomorphic equilibrium $\bar{p}_2\left(x_\varepsilon\right) = 0$. With $x = 1$ and $W_{12}\left(1\right) = W_{11}\left(1\right) = 0$, and $W_{22} > W_{12} > W_{11}$, there is directional selection for A_2, with $\bar{p}_2$ being the stable monomorphism. In this case the differential equation (5) can be written as:

$$\begin{aligned} \dot{p} &= 0 - p, \text{or} \\ p\left(t\left|_{x=1}\right.\right) &= p_0 e^{-t} \end{aligned}$$

Thus when $x = 1$ the resistance of the system 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 allele. Therefore the natural selection results in a stable monomorphic equilibrium which eliminates the productivity advantage of variety 1, with $\bar{p}_2$ being the stable monomorhism. In essense variety 1 is now identical to variety 2, and the biodiversity richness metric on the plant side is $R^b = 1$.

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[24] In the rest of the paper we assume, to simplify things, that as long as $0 < p < 1$, then all three types, A_1A_1, A_1A_2, A_2A_2, exist and thus $R^b = 3$ for the pest subsystem.

Assume now that $x = 0$, that is the entire area is planted with variety 2. Then the discussion in section 2 suggests that if there is heterozygotic advantage in the sense that

$$W_{12}(0) \; > \; W_{22}(0) \text{ and } W_{12}(0) > \max\{W_{11}(0), W_{22}(0)\}$$
$$\text{where } W_{ij}(0) \; = \; w_{ij}(2)$$

then the polymorphism (11) is stable with

$$\bar{p}_3(0) = \frac{W_{12}(0) - W_{22}(0)}{2W_{12}(0) - W_{11}(0) - W_{22}(0)} \in (0,1) \tag{11a}$$

and the monomorphisms $\bar{p}_1(0) = 1$ and $\bar{p}_2(0) = 0$ are unstable.

These ideas can be easily demonstrated using the following table of fitness values.

Table 1: Possible Fitness Values

	$x = 0$	$x = 1$
W_{11}	w	0
W_{12}	$w(1+s)$, $s \gtrless 0$	0
W_{22}	w	w

For $x = 0$ and $s > 0$ we have that $W_{12} > W_{22}$ and $W_{12} > \max\{W_{11}, W_{22}\}$ and the polymorphism is a stable equilibrium. That is, the heterozygotic fitness advantage produces a stable polymorphism. For $x = 0$ and $s < 0$, $W_{12} < W_{22}$ and $W_{12} < \min\{W_{11}, W_{22}\}$. The monomorphisms $\bar{p}_1$ and $\bar{p}_2$ are stable, while the polymorphism $\bar{p}_3$ is unstable. The directional selection could be A_1 or A_2, depending on the initial conditions. With $x = 1$ and $W_{12}(1) = W_{11}(1) = 0$, we have that $W_{22} > W_{12} > W_{11}$. There is directional selection for A_2, and $\bar{p}_2$ is stable while $\bar{p}_1$ is unstable

This discussion suggests that the choices of the allocation strategy can be regarded as bifurcation parameters. For $x = 0$ and heterozygotic advantage we have polymorphic stability. As x increases towards one there will be a critical value $\bar{x}$ such that for $x > \bar{x}$ the polymorphic stability is replaced by monomorphic stability with directional selection towards A_2 and elimination of the productivity advantage of variety 1. Let

$$\mathcal{X} = \left\{ \begin{array}{c} x : W_{12}(x) > W_{22}(x) \text{ and } W_{12}(x) > \max\{W_{11}(x), W_{22}(x)\} \\ \text{and } \bar{p}_3(x) \in (0,1) \end{array} \right\}$$

For allocation strategies in this set there is a stable polymorphic equilibrium with the equilibrium proportion of the A_1 alleles in the gene pool $\bar{p}_3(x)$ defined by (11).

Denote the fitness of pest type ij when the total area is planted with variety 2 by $W_{ij}(0) = w_{ij}(2)$. Then under heterozygotic advantage, $W_{12}(0) =$

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$w_{12}(2) > W_{22}(0) = w_{22}(2)$. Let $\hat{x}$ solve $\bar{p}_3(\hat{x}) = 0$, or[25]

$$\hat{x} : W_{12}(x) - W_{22}(x) = 0, \text{ with}$$
$$\hat{x} = \frac{W_{12}(0) - W_{22}(0)}{W_{12}(0) - W_{22}(0) + W_{22}(1)} < 1 \qquad (11b)$$

Conditions (11b) imply that the stable polymorphism vanishes before the whole area is planted with variety 1.

The description of the possible equilibria of the subsystem describing the evolution of the gene pool indicates, therefore, two basic results:

1. Planting the whole area with variety 1, the $x = 1$ strategy, eliminates the productivity advantage of variety 1 at the fastest possible rate. This strategy produces a monoculture with richness metric for plants $R^b = 1$, and the richness $R^b = 1$ for pests since only the $A_2 A_2$ pest survives. The polymorphism with plant richness $R^b = 2$ becomes unstable as x approaches 1, while for $x = 1$ the monoculture with the productivity advantage is unstable. The stable state is the one in which the productivity advantage has been eliminated.

2. There is a strategy $x \in [0, \hat{x}), \hat{x} < 1$, which results in a stable polymorphism. This strategy produces a stable equilibrium biodiversity with richness metric for plants $R^b = 2$, and the richness $R^b = 3$ for pests.

With heterozygotic disadvantage $(s < 0)$ we have monomorphic stability towards A_1 or A_2, depending on initial conditions. Suppose that for $x = 0$, the directional selection is towards A_1. Then the discussion above suggests that there will be an $\tilde{x} > 0$ such that for $x > \tilde{x}$ there is directional selection towards A_2 and the productivity advantage of variety 1 is eliminated again.

The emergence of a polymorphic allocation strategy can also be presented by considering the more complex relative fitness values shown in table 2, which are scaled to the fitness value of the $A_1 A_1$ allele when the whole area is planted with variety 1. These values represent a more general formulation where variety 1 might not kill all the $A_1 A_1$ alleles but will reduce their relative fitness and the heterozygote does not have a fitness advantage when $x = 0$.[26]

Table 2: Possible Relative Fitness Values

---

[25]Recall that $W_{ij}(x) = w_{ij}(1)x + w_{ij}(2)(1 - x)$, and that under our assumptions

$$W_{11}(1) = w_{11}(1) = W_{11}(1) = w_{12}(1) = 0 < W_{22}(1) = w_{22}(1)$$

[26]We are grateful to Simon Levin for providing this value structure.

	$x = 0$	$x = 1$
W_{11}	1	$1 - \tau$
W_{12}	$1 - hz$	$1 - hz - (1 - g)\tau$
W_{22}	$1 - z$	$1 - z$

In table 2, τ is the percentage loss in fitness of the $A_1 A_1$ allele when the total area is planted with variety 1. The limiting case where variety 1 kills all $A_1 A_1$ alleles is $\tau = 1$. Furthermore $(1 - g)\tau$ is the percentage loss in fitness of the $A_1 A_2$ allele when the whole area is planted with variety 1. The limiting case where variety 1 kills all $A_1 A_2$ alleles is $(1 - g)\tau = 1 - hz$.

For $x = 0$ and $0 < h < 1$, $0 < z < 1$ we have $W_{11} > W_{12} > W_{22}$. There is directional selection towards A_1 and the monomorphism $\bar{p}_1 = \bar{p}(0) = 1$ is stable. For $x = 1$ and $z < \frac{(1-g)\tau}{1-h}$, $g\tau > hz$ we have $W_{22} > W_{12} > W_{11}$. There is directional selection towards A_2 and the monomorphism $\overline{p}_2 = \overline{p}(1) = 0$ is stable, which implies the elimination of the variety 1 advantage. For a polymorphism it is required that:

$$
\begin{aligned}
(1 - x)hz &< x(g\tau - hz) \\
(1 - x)(1 - h)z &> x[(1 - g)\tau - (1 - h)z]
\end{aligned}
$$

which implies that x should be in the interval $\left(\frac{(1-h)z}{(1-g)\tau}, \frac{hz}{g\tau} \right)$. For the special case $g = \tau = 1$ the polymorphism requires that $x > hz$ and $hz < 1$ which is always true.[27]

Therefore the valuation without heterozygote fitness advantage and without complete elimination of the $A_1 A_1$, $A_1 A_2$ alleles by variety 1 suggests that the polymorphism vanishes as x approaches unity, that is, as the whole area is planted with variety 1, which means that $\bar{p}_3(\hat{x}) = 0$ for some critical value which in general is less than one.

4.1 Optimal allocation strategies for a special case

Given the results derived above, it is natural to ask whether an optimal allocation strategy and an associated optimal composition of the gene pool characterized by p, exist for the subproblem (4)-(7). The optimality criterion for this case with given $\overline{R}$ and the total gross harvest flow $\overline{B}$ is to choose $\{x(t)\}$ to maximize the capitalized value of the net harvest flow. This flow is defined as:

$$
\begin{aligned}
x\left(\overline{B} - d_1(p)\right) + (1 - x)\left(\overline{B} - d_2(p)\right) &= \\
xp\left(d_2(p) - d_1(p)\right) + \overline{B} - d_2(p) &= \\
xp\left(d_2 - d_1\right) + \overline{B} - d_2
\end{aligned}
$$

[27]Furthermore, if we set $\tau = 1$, $W_{12}(x = 0) = 1 - \omega$, $W_{12}(x = 1) = 1 - \omega - (1 - g)$, $\omega = g$, $z = 0$, then the fitness structure of table 2 is reduced to that of table 1 for $w = 1$.

Consider now the subutility

$$U(x, p) = u(p) x, \ u(p) = \alpha p, \ \alpha > 0 \tag{13}$$

This subutility is derived by considering first the case where $p = 1, \ x = 1$. That is, the whole area is planted with variety 1 and resistance is complete. Then $d_2 - d_1 > 0$ is the growth advantage of variety 1 and $u(1) = d_2 - d_1 = \alpha$. Consider second the case where $p = 0, \ x = 0$; that is, no resistance exists. Then the growth advantage is eliminated and $u(0) = 0$. Using (13) as the objective function the optimization problem can be written as:

$$\max_{\{x(t)\}} \int_0^\infty e^{-rt} p(t) x(t) \, dt \tag{14}$$
subject to
$$\dot{p}(t) = p[G(p(t), x(t)) - 1], \ p(0) = p_0 \text{ given}$$

where the maximization in (14) is equivalent to the maximization of the capitalized value of the net harvest flow.

We analyze first the problem with zero discounting, $r = 0$. In the undiscounted infinite horizon problem ($r = 0$) the integral (14) might not converge. Thus we use the concept of overtaking optimality, which holds for $r \geq 0$.[28] The optimal steady state (OSS) (p^*, x^*) for this problem is the solution of the static optimization problem

$$\max_{p,x} px \text{ subject to } 0 = p(G(p, x) - 1) \tag{15}$$

We know however from the analysis above that the solution for p of the constraint will correspond to an equilibrium $\bar{p}(x)$ that could be a polymorphism or a monomorphism. The question is whether or not the OSS determines a stable polymorphism.

Proposition 1 *Under heterozygotic fitness advantage for $x = 0$, or the relative fitness values of table 2, and $r = 0$, the optimal steady-state allocation strategy for the area between variety 1 and variety 2 is $0 < x^* < 1$.*

For proof, see Appendix.

Having established that in the undiscounted problem, it is optimal not to plant the whole area with variety 1, we consider the discounted problem. The current value Hamiltonian for this problem is defined as:

$$\mathcal{H}(p, x, \lambda) = px + \lambda p[G(p, x) - 1] \tag{16}$$

---

[28] The concept of overtaking optimality is defined as follows.

Definition: *A trajectory $\{p^*(t)\}$ emanating from an initial state $p(0)$ and generated by the control $\{x^*(t)\}$ is overtaking optimal, for $r \geq 0$, if:*

$$\lim_{T \to \infty} \inf \int_0^T e^{-rt} \{[p^*(t) x^*(t)] - [p(t) x(t)]\} \, dt \geq 0$$

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

By the maximum principle the short-run optimal strategy is defined as:

$$x\left(p,\lambda\right) = \arg\max_{0 \leq x \leq 1} \mathcal{H}\left(p, x, \lambda\right) \qquad (17)$$

The modified Hamiltonian dynamic system (MHDS) is defined as:

$$\dot{\lambda} = r\lambda - \frac{\partial \mathcal{H}}{\partial p}$$

$$= r\lambda - x\left(p,\lambda\right) - \lambda\left[G\left(p, x\left(p,\lambda\right)\right) - 1\right] - \lambda p \frac{\partial G\left(p, x\left(p,\lambda\right)\right)}{\partial p} \qquad (18)$$

$$\dot{p} = p\left[G\left(p, x\left(p,\lambda\right)\right) - 1\right] \qquad (19)$$

The optimal steady-state equilibrium values for the state, costate and control variables, p^*, λ^*, $x^* = x\left(p^*, \lambda^*\right)$, will be defined by the solution of the system (18) and (19) for $\dot{p} = 0$, $\dot{\lambda} = 0$. If we assume the fitness structure of table 1, or:

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

and $w_{11}\left(1\right) = w_{12}\left(1\right) = 0$ under the assumption that plant variety 1 kills $A_1 A_1$ and $A_1 A_2$ pest types, then the short-run allocation strategy depends only on the fitness differential of the heterozygote and is determined as:

$$x\left(p,\lambda\right) = \frac{\left[1 - p\left[\lambda\left(2 - p\right) + 2s\left(1 - p\right)\left(1 - \lambda\right)\right]\right]^2}{\left(1 + s\right) - p\left(2 - p\right) - ps\left[3\left(1 - p\right) + p^2\right]} \qquad (20)$$

Substituting (20) into the MHDS we obtain the system that determines the evolution of the proportion p and its shadow value λ. A solution of this system, if it exists, will determine the optimal steady state $\left(p^*, \lambda^*, x\left(p^*, \lambda^*\right)\right)$.

The same optimal control problem can be solved for relative fitness values of table 2. The assumptions about W_{ij} imply the following values for w_{ij} :

$$w_{11}\left(2\right) = 1, \ w_{11}\left(1\right) = 1 - \tau, \ w_{12}\left(2\right) = 1 - hz, \ w_{12}\left(1\right) = 1 - hz - \left(1 - g\right)\tau$$
$$w_{22}\left(2\right) = w_{22}\left(1\right) = 1 - z$$

Then, the short-run allocation strategy is defined in terms of the fitness parameters as:

$$x\left(p,\lambda\right) = \frac{\left(1 + \left(p - 1\right)\left(1 + \left(2h - 1\right)p\right)z + p\left(p - 2g\left(p - 1\right) - 2\right)\lambda\tau\right)^2}{\left(p - 1\right)\left(p - 1 + z + p\left(hp - 1\right)z - g\left(2p - 1 + \left(p - 1\right)^2 z\right)\right)\tau} \qquad (21)$$

As before a solution of the MHDS, if it exists, will determine the optimal steady state.

From (18)-(20) it is clear that the optimal steady state is determined as a solution of a nonlinear system, for which an analytical solution is not possible. Thus further characterization of the steady state requires numerical

simulations. Using for example the fitness structure of table 1 and a discount rate of $r = 0.01$, the results for s ranging from $s = 0.5$, that is 50% heterozygotic advantage, to $s = -0.02$, that is 2% heterozygotic disadvantage, are shown in table 3.

Table 3: Optimal Steady States for the Special Case

s	p^*	λ^*	$x\,(p^*, \lambda^*)$	# of eigenvalues with negative real parts	H	D
0.5	0.4473	1.1288	0.0870	1	0.295	0.158
0.4	0.4534	1.1627	0.0638	1	0.237	0.119
0.3	0.4609	1.2003	0.0417	1	0.173	0.780
0.2	0.4700	1.2418	0.0221	1	0.106	0.043
0.1	0.4809	1.2869	0.0073	1	0.043	0.014
-0.01	0.8284	1.0645	0.0368	1	0.158	0.071
-0.015	0.8112	1.0796	0.0473	1	0.190	0.090
-0.02	0.8005	1.0915	0.0568	1	0.218	0.107

Thus, for $s = 0.5$, the optimal proportion of $A_1 A_1$ alleles in the gene pool is 44.7% and it is optimal to plant 8.7% of the area with variety 1 in equilibrium. For $s = -0.01$, the optimal proportion of $A_1 A_1$ alleles in the gene pool is 82.8% and it is optimal to plant 3.7% of the area with variety 1 in equilibrium. Furthermore, as shown by the eigenvalues, the equilibrium point has the saddle point property, with a one-dimensional stable manifold. The richness biodiversity metric is $R^b = 2$ for the plants and $R^b = 3$ for the pests. The Shannon $H = -\sum_{i=1,2} x_i \ln x_i$ and Simpson $D = 1 - \sum_{i=1,2} x_i^2$ diversity indices[29] for the plants are shown in the last two columns of the table.

The results of this subsection suggest that the optimal allocation strategy results in a resilient and diverse system in terms of both plant varieties and pests.

5 Optimal Management and Biodiversity Valuation in the Unified Model

The analysis in the previous section indicates the existence of optimal allocation strategies for the special case in which the ecological variables, that is the resource and the biomasses, are kept constant at some equilibrium values. This analysis does not however allow us to explore the responses of the ecological variables to the management rules and to compare equilibrium biomass values and equilibrium biodiversities in the plant-pest system under monoculture or polyculture.

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[29]For the calculation of the indices, x_1 is the calculated value of x^* from table 3, while $x_2 = 1 - x_1$.

5.1 The General Model

The unified mechanistic resource-based competition - natural selection management model, with the price of the harvested biomass normalized to one, can be written as:

$$\max_{x,H_1,H_2} \int_0^\infty e^{-\rho t} \left(H_1 + H_2 \right) dt \tag{22}$$

$$\text{s.t. } \dot{B}_i = B_i \left[gR - d_i\left(p \right) \right] - H_i \ , \ i = 1, 2 \ , \ B_i\left(0 \right) = B_i^0 \tag{23}$$

$$\dot{R} = S - aR - gwR \sum_{i=1,2} B_i \ , \ R\left(0 \right) = R^0 \tag{24}$$

$$\dot{p} = p[G\left(p, x \right) - 1] \ , \ p\left(0 \right) = p^0 \tag{25}$$

$$0 \leq x \leq 1 \ , \ 0 \leq H_i \leq K^{\max} \tag{26}$$

$$d_1\left(p \right) = pd_1 + \left(1 - p \right) d_2 \ , \ d_2\left(p \right) = d_2 \ , \ d_1 < d_2 \tag{27}$$

with

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

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

where $w_{ij}\left(1 \right)$, $w_{ij}\left(2 \right)$ are the viability fitnesses of the ij pest genotype for plant variety 1 and 2 respectively.[30]

This general model can be used to analyze two cases: the POMP where private agents ignore effects of the natural selection mechanism in the evolution of the pest resistance, and the SOMP where these interactions are taken into account.

5.2 The POMP

In this problem the private agent ignores the genetic interactions described by equations (5)-(7) and treats death rates as fixed with $d_1 < d_2$. Then the POMP problem becomes:

$$\max_{x,H_1,H_2} \int_0^\infty e^{-\rho t} \left(H_1 + H_2 \right) dt \tag{28}$$

$$\text{s.t. } \dot{B}_i = B_i \left[gR - d_i \right] - H_i \ , \ i = 1, 2 \ , \ d_1 < d_2 \tag{29}$$

$$\dot{R} = S - aR - gwR \sum_{i=1,2} B_i \tag{30}$$

$$0 \leq x \leq 1 \ , \ 0 \leq H_i \leq K^{\max} \tag{31}$$

---

[30]Assuming the fitness structure of table 1, we have for example that since variety 1 kills the A_1A_1 and A_1A_2 genotypes but not the A_2A_2, then $w_{11}\left(1 \right) = w_{12}\left(1 \right) = 0$, while $w_{22}\left(1 \right) > 0$. On the other hand $w_{ij}\left(2 \right) > 0$, $i = 1, 2$.

Define

$$x \;=\; \frac{B_1}{B_1 + B_2} \;,\; B = B_1 + B_2 \tag{32}$$

$$B_1 \;=\; xB \;,\; B_2 = (1 - x) B \;,\; H = H_1 + H_2 \tag{33}$$

By adding together the two biomass transition equations the constraints of the POMP become

$$\dot{B} \;=\; B\left(gR + x\left(d_2 - d_1\right) - d_2\right) - H \tag{34}$$

$$\dot{R} \;=\; S - aR - gwRB \tag{35}$$

$$0 \;\leq\; x \leq 1 \;,\; 0 \leq H \leq K^{\max} \tag{36}$$

The current value Hamiltonian for the POMP can be written as:

$$\mathcal{H}^P = H + \lambda\left[B\left(gR + x\left(d_2 - d_1\right) - d_2\right) - H\right] + \mu\left[S - aR - gwRB\right] \tag{37}$$

Maximization of the current value Hamiltonian over H subject to (36) implies that the following conditions of the maximum principle should be satisfied at the OSS:

$$H = \begin{cases} 0 \text{ if } \lambda > 1 \\ K^{\max} \text{ if } \lambda < 1 \end{cases} \tag{38}$$

Furthermore the singular solution implies at the OSS that

$$\lambda \;=\; 1 \;,\; \dot{B} = 0 \;,\; \dot{R} = 0 \tag{39}$$

$$H \;=\; B\left(gR + x\left(d_2 - d_1\right) - d_2\right) \;,\; S - aR = gwRB \tag{40}$$

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

For proof, see Appendix.

For the choice of x at this OSS the maximum principle implies that since $\lambda = 1$, $\left(\overline{B}, \overline{H}\right) > 0$, $d_1 < d_2$, and x should maximize $\lambda x B\left(d_2 - d_1\right)$ in (37), then the optimal choice should be

$$\overline{x} = 1 \tag{41}$$

Thus the POMP plants the total area with plant variety 1 since it is perceived as having a productivity advantage. With $\lambda = 1$, $x = 1$ the maximum principle implies that for the MHDS at the steady state:

$$0 = \left(gR - d_1 - \rho\right) - \mu gwR \tag{42}$$

$$0 = \left(\rho + a + gwB\right)\mu - Bg \tag{43}$$

$$S - aR = gwRB \tag{44}$$

$$H = B\left(gR - d_1\right) \tag{45}$$

From the above system we obtain

$$Q_1(R, \rho, d_1) = \frac{(gR - d_1 - \rho)}{gwR} \tag{46}$$

$$f(R, \rho) = \frac{S - aR}{w(R\rho + S)} \tag{47}$$

Equations (46) and (47) determine the steady state $\overline{R}(d_1)$ from the solution of $Q_1(R, \rho, d_1) = f(R, \rho)$. It can easily be seen that $Q_1(R, \rho, d_1)$ is monotonically increasing and concave in R.[31] Furthermore,

$$\lim_{R \to \infty} Q_1(R, \rho, d_1) = \frac{1}{w}, \; Q_1(R^*, \rho, d_1) = 0, \; R^* = \frac{d_1 + \rho}{g}$$

On the other hand $f(R, \rho)$ is monotonically decreasing and convex in R.[32] Also

$$f(0, \rho) = \frac{1}{w}, \; f\left(\frac{S}{a}, \rho\right) = 0$$

Therefore, the intersection of $Q_1(R, \rho, d_1)$ and $f(R, \rho)$ determines a unique steady-state resource level $\overline{R}$ as shown in figure 1.

[Figure 1]

Then the optimal steady-state biomass level and harvest for the Bt-corn monoculture is defined as:

$$\overline{B}(d_1) = \frac{S - a\overline{R}(d_1)}{gw\overline{R}(d_1)}, \; \overline{H}(d_1) = \overline{B}(d_1)\left(g\overline{R}(d_1) - d_1\right) \tag{48}$$

This steady state is not however sustainable since the genetic constraint (4) implies that $G(p, 1) = 0$ and $p \to 0$ at the most rapid rate as shown in section 4. 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 $\overline{R}(d_2)$ which is defined as:

$$Q_2(R, \rho, d_2) = \frac{(gR - d_2 - \rho)}{gwR} = f(R, \rho) \tag{49}$$

Since $d_2 > d_1$ the locus $Q_2(R, \rho, d_2)$ is to the right of $Q_1(R, \rho, d_1)$ as shown in figure 1 and $\overline{R}(d_2) > \overline{R}(d_1)$.

From (44) we have

$$\frac{\partial \overline{B}}{\partial \overline{R}} = \frac{\partial}{\partial R}\left(\frac{S - aR}{gwR}\right) = -\frac{S}{gwR^2} < 0 \tag{50}$$

---

[31] $\frac{\partial Q_1}{\partial R} = \frac{(d+\rho)}{wgR^2} > 0$, $\frac{\partial^2 Q_1}{\partial R^2} = -\frac{2(d+\rho)}{wgR^3} < 0$

[32] $\frac{\partial f}{\partial R} = -\frac{S(a+\rho)}{w(\rho R + S)^2} < 0$, $\frac{\partial^2 f}{\partial R^2} = \frac{2S\rho(a+\rho)}{w(\rho R + S)^3} > 0$

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Thus

$$\overline{B}(d_2) < \overline{B}(d_1) \tag{51}$$

The difference

$$\overline{B}(d_1) - \overline{B}(d_2) \tag{52}$$

can be regarded as a net loss from ignoring the genetic externality.

5.3 The SOMP

The SOMP is the unified Tilman-natural selection model. By making the transformations (32)-(33) and adding the biomass transition equations we obtain the current value Hamiltonian for the SOMP as

$$
\begin{aligned}
\mathcal{H}^S &= H + \lambda \left[B\left(gR + xp\left(d_2 - d_1\right) - d_2\right) - H \right] + \mu \left(S - aR - gwRB\right) \\
&\quad + qp\left(G\left(x, p\right) - 1\right) + \xi\left(1 - x\right) + \zeta x
\end{aligned} \tag{53}
$$

where ξ and ζ are Lagrangian multipliers associated with the $0 \leq x \leq 1$ constraint. Assuming as before $K^{\max} > \frac{S}{w} + \hat{B}\left(d_2 - d_1\right)$ we obtain for the singular solution at a steady state with positive biomass

$$\lambda = 1 \ , \ H = B\left(gR + xp\left(d_2 - d_1\right) - d_2\right) \tag{54}$$

The maximum principle implies that for the choice of x :

$$Bp\left(d_2 - d_1\right) + qp\frac{\partial G\left(p, x\right)}{\partial x} - \xi + \zeta \leq 0 \ , \ x \geq 0 \tag{55}$$

$$\text{If } 0 < \overline{x} < 1 \text{ then } \xi = \zeta = 0 \tag{56}$$

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

$$0 = \left(gR + xp\left(d_2 - d_1\right) - d_2 - \rho\right) - \mu gwR \tag{57}$$

$$0 = \left(\rho + a + gwB\right)\mu - gB \tag{58}$$

$$0 = \left(\rho - p\frac{\partial G\left(p, x\right)}{\partial p}\right)q - xB\left(d_2 - d_1\right) \tag{59}$$

From (57) and (58) we obtain as in the POMP case

$$Q^S\left(R, \rho\right) = \frac{gR + xp\left(d_2 - d_1\right) - d_2 - \rho}{gwR} \tag{60}$$

$$f^S\left(R, \rho\right) = \frac{S - aR}{w\left(R\rho + S\right)} \tag{61}$$

We know that if $x = 1$ then $p \to 0$ and the SOMP solution is the same as the POMP solution. The same holds for $x = 0$, since as in the POMP equilibrium, we have a plant variety 2 monoculture. Thus we set $\xi = \zeta =$

0 and explore solutions for $0 < \bar{x} < 1$. In this case the OSS equations become:

$$Bp(d_2 - d_1) + qp\frac{\partial G(p, x)}{\partial x} = 0 \tag{62}$$

$$\frac{gR + xp(d_2 - d_1) - d_2 - \rho}{gwR} = \frac{S - aR}{w(R\rho + S)} \tag{63}$$

$$\left(\rho - p\frac{\partial G(p, x)}{\partial p}\right)q = xB(d_2 - d_1) \tag{64}$$

$$G(p, x) - 1 = 0 \tag{65}$$

$$B = \frac{S - aR}{gwR} \tag{66}$$

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

5.3.1   A Most Rapid Approach Path for the SOMP

The dimensionality of the SOMP with respect to the state variables can be reduced by transforming the problem into a Most Rapid Approach Path (MRAP) problem. Substituting H by

$$H = B(gR + xp(d_2 - d_1) - d_2) - \dot{B} \tag{67}$$

into the objective function for the SOMP, integrating by parts and assuming that $\lim_{t\to\infty} e^{-\rho t}B(t) = 0$, we have the following problem:[33]

$$\max_{x,B} \int_0^\infty e^{-\rho t}B(gR + xp(d_2 - d_1) - d_2 - \rho)\,dt \tag{68}$$

$$\text{s.t.}\ \dot{R} = S - aR - gwRB \tag{69}$$

$$\dot{p} = p[G(p, x) - 1] \tag{70}$$

$$0 \leq x \leq 1\,,\ 0 \leq B \leq B^{\max} \tag{71}$$

The current value Hamiltonian for this problem is

$$\mathcal{G} = B(gR + xp(d_2 - d_1) - d_2 - \rho) + \mu_2(S - aR - gwRB) + q_2 p(G(p, x) - 1) \tag{72}$$

For positive biomass at an OSS the singular solution implies

$$gR + xp(d_2 - d_1) - d_2 - \rho = \mu_2 gwR \tag{73}$$

while for $0 < x < 1$

$$Bp(d_2 - d_1) + q_2 p\frac{\partial G(p, x)}{\partial x} = 0 \tag{74}$$

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[33] See Kamien and Schwartz (1991, p. 97).

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

$$0 = (\rho + a + gwB)\mu_2 - gB \tag{75}$$

$$0 = \left(\rho - p\frac{\partial G(p, x)}{\partial p}\right) q_2 - xB(d_2 - d_1) \tag{76}$$

By comparing (73)-(76) with (55) and (57)-(59), it is clear that the OSS of the MRAP is the same as the OSS of the complete SOMP.

Then from (73) and (74) we obtain for the OSS controls

$$x^* = \frac{\mu_2 gwR - gR + d_2 + \rho}{p(d_2 - d_1)} = X(R, \mu_2, p, q_2) \tag{77}$$

$$B^* = -\frac{q_2 \frac{\partial G(p, x^*)}{\partial x}}{(d_2 - d_1)} = \beta(R, \mu_2, p, q_2) \tag{78}$$

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

$$0 = S - aR - gwRB^* \tag{79}$$

$$0 = G(p, x^*) - 1 \tag{80}$$

$$0 = (\rho + a + gwB^*)\mu_2 - gB^* \tag{81}$$

$$0 = \left(\rho - p\frac{\partial G(p, x^*)}{\partial p}\right) q_2 - x^* B^* (d_2 - d_1) = \tag{82}$$

$$\rho - p\frac{\partial G(p, x^*)}{\partial p} + x^*\frac{\partial G(p, x^*)}{\partial x} \tag{83}$$

If a steady state $\left(\overline{R}, \overline{\mu}_2, \overline{p}, \overline{q}_2\right)$ exists, then

$$\overline{x} = X\left(\overline{R}, \overline{\mu}_2, \overline{p}, \overline{q}_2\right) \ , \ \overline{B} = \beta\left(\overline{R}, \overline{\mu}_2, \overline{p}, \overline{q}_2\right) \tag{84}$$

$$\overline{B}_1 = \overline{x}\,\overline{B} \ , \ \overline{B}_2 = (1 - \overline{x})\,\overline{B} \tag{85}$$

$$\overline{H}_1 = \overline{x}\,\overline{B}\left(g\overline{R} + \overline{x}\,\overline{p}(d_2 - d_1) - d_2\right) \tag{86}$$

$$\overline{H}_2 = (1 - \overline{x})\,\overline{B}\left(g\overline{R} + \overline{x}\,\overline{p}(d_2 - d_1) - d_2\right) \tag{87}$$

The difference $\overline{B} - \overline{B}(d_2)$ determines the loss in biomass from ignoring the genetic externality, adopting a monoculture with everything planted with plant variety 1, and eventually reaching a steady state where the productivity advantage of plant variety 1 has been eliminated and there is a monoculture in plant variety 2. Since $\overline{B}$ is the biomass for the optimal polyculture, $\overline{B} - \overline{B}(d_2)$ can be regarded as the value of biodiversity corresponding to the change in the biodiversity metrics (species richness, H, D) from monoculture to polyculture.

5.4 Numerical Approximations to Biodiversity Valuation

System (79)-(82) that determines the OSS for the SOMP is highly nonlinear. Thus in order to obtain some insights into the structure of the solution and verify whether or not biodiversity valuation through the term $\overline{B} - \overline{B}(d_2)$ can be detected, we resort to some numerical simulations.

We start by calculating the OSS resource and biomass levels $\left[\overline{R}(d_1), \overline{R}(d_2)\right]$ and $\left[\overline{B}(d_1), \overline{B}(d_2)\right]$ respectively, for the POMP using the following parameter values:

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

The results are shown in table 4.

Table 4: Steady-State Resource and Biomass Levels at the POMP

d_2	$\overline{R}(d_1)$	$\overline{R}(d_2)$	$\overline{B}(d_1)$	$\overline{B}(d_2)$	% 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

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 when the equilibrium moves away from the unstable variety 1 monoculture to the stable variety 2 monoculture. 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 solving numerically the nonlinear system (79)-(82).[34] In table 5 we present solutions for both heterogygotic advantage ($s > 0$) and disadvantage ($s < 0$) following the fitness structure of table 1 for alternative values of d_2, with the rest of the parameters the same as in the POMP numerical analysis.[35] Table 5 includes the steady states, the percentage gain in biomass of the OSS at the SOMP relative to the variety 2 monoculture which eventually emerges at the POMP, the Shannon and Simpson biodiversity indices, and the number of eigenvalues with negative real parts. It should be noted the the richness metric is $R^b = 2$ for the plant subsystem and $R^b = 3$ for the pest subsystem. Table 6 contains the same information but using the relative fitness structure of table 2.

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[34] The 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.

[35] That is, $\rho = 0.01, S = 2, d_1 = 0.05, a = 0.10, w = 0.05, g = 0.05$.

[Tables 5 and 6 here]

Our numerical simulations indicate that, for $s > -0.02$ in table 5[36] and for all the cases in table 6, the SOMP solution results in a polyculture, and that there is always a gain in terms of biomass relative to the POMP monoculture. This gain 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, or the H, D indices corresponding to the specific parameter constellations. This measure depends not only on the ecological parameters, but also on economic parameters, such as market prices and the discount rate. In our specific case the biodiversity value seems to increase with the difference between the death rates of the two varieties.

In terms of resilience the high biomass steady-state monoculture associated with the POMP, $\overline{B}(d_1)$, is not resilient and the system converges to the low biomass steady state $\overline{B}(d_2)$ with the losses in terms of biomass shown in table 4. On the other hand the polyculture steady state is resilient along a stable manifold whose dimension is determined by the number of negative eigenvalues. Thus the more diverse system is more productive and resilient along the stable manifold.

6   Conclusions and Areas of Further Research

In this paper we develop a conceptual framework for valuing biodiversity from an economic perspective. Our approach is based on two central principles. First that biodiversity is important because of a number of characteristics or services that it provides or enhances. Second that the kind of biodiversity loss that is of interest to us is a result of economic activity, and that this loss occurs because private optimizing agents ignore, to some extent, properties or services that make biodiversity important. Ignoring these services is equivalent to ignoring positive externalities associated with diverse ecosystems. As a result the social return of the diverse system where all characteristics and services are taken into account tends to be less than private returns that ignore positive externalities. This discrepancy leads to less diverse ecosystems under private optimization rules relative to social optimization rules.[37] Thus the creation of monocultures is relatively more likely under private optimization rules.[38] On the other

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[36]For $s = -0.02$ the socially-optimal choice is $x^* = 0$ and the SOMP and POMP solutions coincide.

[37]More generally if there are negative externalities as well, such as diseases or weeds, which are ignored by private agents, then the private and the social optimization rules lead to a system with *different* diversity structures.

[38]Brock and Xepapadeas (2001) derive conditions under which a monoculture can be created in a multispecies ecosystem under mechanistic resource-based competition when

hand, socially-optimizing management that takes into account these externalities and thus the full social return of biodiversity results in general in more diverse ecosystems. By comparing the optimal value of the SOMP with that of the POMP we can obtain an endogenous measure of the biodiversity value and relate this measure to ecologically/biologically oriented biodiversity metrics (species richness, Shannon, Simpson, diversity function) that correspond to the equilibrium diversities of the SOMP and the POMP.

Thus our approach can be regarded as providing a link between the ecologically/biologically oriented biodiversity metrics and economically oriented biodiversity metrics, with all measures being the outcome of optimizing behavior.

To build this link, however, we need to uncover the mechanism through which economic decisions affect the biodiversity of an ecosystem and consequently its resilience, productivity, value of services, and so forth. In this paper we develop such a mechanism which is based on interactions between ecological processes, reflected in mechanistic resource-based species competition, and genetic processes reflected in Hardy-Weinberg mating, to model optimal harvesting decisions in a system where two plant varieties and three pest types interact. We are able to derive the equilibrium productivity and stability characteristics of: (i) the POMP, where the genetic constraint is ignored and the system tends to a monoculture in the plant/pest domain; and (ii) the SOMP, where the genetic constraint is taken into account and the system tends to a polyculture in the plant/pest domain. By comparing the equilibrium biomass values of the two solutions we are able to obtain the endogenous measure of biodiversity value and to associate it with the ecologically/biologically oriented biodiversity metrics species richness, Shannon and Simpson indices. By using numerical simulations we are able to confirm our theoretical results and to obtain numerical measures of changes in biodiversity values between the SOMP and the POMP and the corresponding changes in the ecologically/biologically oriented biodiversity metrics.

We feel that our methodological approach provides a modest step towards solving, with the help of a unifying optimizing model, the puzzle of valuing biodiversity. Although we have concentrated on a specific metaphor inspired by the Bt-crop discussion, it seems that this unifying model should contain two major building blocks. The first should be an objective function that incorporates as far as possible the economic or social values associated with the ecosystem under consideration, such as harvesting values, insurance or knowledge values, or values of ecosystem services. The second building block should be an ecological/biological module, that describes interactions

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the value of ecosystem services are not taken into account. Scott (1998) and Murray (1993) discuss the cases of Norway Spruce in scientific German forestry and the Nile perch respectively, where creating a monoculture and ignoring the externalities associated with interrelations among species, which allow the proper functioning of diverse ecosystems, lead to the collapse of the ecosystems.

among species, and interactions among economic decisions and ecosystem state. Optimizing an objective function defined in terms of economic or social profits, subject to the ecological/biological constraints, will result in a maximal economic or social profit and a corresponding privately-optimal or socially-optimal equilibrium biodiversity. Using the equilibrium ecosystem diversity we can compute ecologically/biologically oriented biodiversity measures for the private or the social equilibrium and then relate changes in these measures to the changes in the maximal value of the objective function, thus obtaining an endogenous valuation of biodiversity. The major obstacles in this approach are: (i) the proper definition of the objective function, since with the exception of harvesting values the rest of the value concepts might be difficult to estimate; and (ii) the development of the appropriate ecological/biological model.[39] In this paper the plant/pest interaction was a useful framework, but not universally applicable, which suggests that apart from the general principles characterizing the unified model, biodiversity valuation from an economic perspective could be a case-by-case issue.

This observation suggests that further research in biodiversity valuation should aim at building and linking realistic economic and ecological/biological models and then trying to work out solutions corresponding to privately- or socially-optimal decisions. For example in hierachical metapopulation models with sites destroyed by human activities (Tilman and Lehman 1997), if an objective function - defined in terms of both the harvesting benefits (possibly including existence values of species) and the economic benefits accruing from activities associated with sites destruction - is added to the ecological module, then the above methodology can be used to value biodiversity loss because human activities destroy sites and species.

Therefore, although our approach does not provide one model that can be used to value biodiversity in different ecosystems, it provides a unifying conceptual framework capable of determining endogenous values of biodiversity. The fact that a single all-purpose model does not seem to exist for this purpose, is most likely to be the consequence of the complexity of the processes that drive the ecosystems whose diversity we are trying to value.

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[39]For example, in relating biodiversity to ecosystem functions, "keystone species" should be identified and the effects of economic decisions on their abundance should be determined.

Appendix

Proof of Proposition 1.

The steady-state objective function for the OSS problem (15) is $g(x) = \bar{p}(x) x$. In this function $\bar{p}(x)$ is defined by the solution for $p(x)$ of the constraint function (15), or

$$\bar{p}(x) = \frac{W_{12}(x) - W_{22}(x)}{2W_{12}(x) - W_{11}(x) - W_{22}(x)}$$

which is obtained by solving the constraint for p. For the function $g(x)$ observe that we have $g(0) = 0$, $g'(0) = \bar{p}'(0)0 + \bar{p}(0) = \bar{p}(0)$. But $\bar{p}(0) \in (0,1]$, since $\bar{p}(0) > 0$ under heterozygotic fitness advantage for $x = 0$ as shown in (11a), or $\bar{p}(0) = 1$ for the fitness values of table 2. Furthermore $g(1) < 0$, since, as shown in the previous section, $\bar{p}(\hat{x}) = 0$ with $\hat{x} < 1$. These observations imply that the $g(x)$ function has a global interior maximum x^* for $x \in [0,1]$, with $p^* = p(x^*)$. $\square$

Proof of Lemma 1.

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

$$wK^{\max} = w\overline{B}(g\overline{R} + x(d_2 - d_1) - d_2) < w\overline{B}(g\overline{R} + x(d_2 - d_1)) =$$
$$S - a\overline{R} + w\overline{B}x(d_2 - d_1) < S + w\overline{B}x(d_2 - d_1) , \ 0 \le x \le 1$$

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

References

Brock, W.A. and Xepapadeas, A. "Optimal Ecosystem Management when Species Compete for Limiting Resources." *Journal of Environmental Economics and Management*, 2001, forthcoming.

Chichilniski, G. and Heal, G. "Economic Returns from the Biosphere." *Nature*, 1998, pp. 629-630.

Craft, A.B. and Simpson, R.D. "The Value of Biodiversity in Pharmaceutical Research with Differentiated Products." *Environmental and Resource Economics*, 2001, 18, pp. 1-17.

Daily, G.C., Alexander, S.E., Ehrlich, P.R., Goulder, L.H., Lubchenco, J., Matson, P.A., Mooney, H.A., Postel, S., Schneider, S.H., Tilman, D. and Woodwell, G.M. "Ecosystem Services: Benefits Supplied to Human Societies by Natural Ecosystems." *Issues in Ecology*, 1997, *2*, pp. 1-18.

Daily, G. C. and Dasgupta, S. "Entry on Ecosystem Services," in S. Levin, G.C. Daily, J. Lubchenco, and D. Tilman, eds., *Encyclopedia of Biodiversity.* Academic Press, 2000.

Feldman, M. "Dynamical Systems from Evolutionary Population Genetics," in D. Stein, ed., *Lectures in the Science of Complexity.* The Santa Fe Institute, Lectures Volume I, Redwood City, California: Addison-Wesley, 1989.

Harper, J.L. and Hawksworth, D.L. "Biodiversity: Measurement and Estimation." *Philosophical Transactions of the Royal Society London*, B, 1994, 345, pp. 5-12.

Heal, G. "Biodiversity as a Commodity", in S. Levin, G.C. Daily, J. Lubchenco, and D. Tilman, eds., *Encyclopedia of Biodiversity.* Academic Press, 2000.

Hooper, D. and Vitousek, P. "The Effects of Plant Composition and Diversity on Ecosystem Processes." *Science*, 1997, 277, pp. 1302-1305.

Hurley, T., Secchi, S., Babcock, B. and Hellmich, R. "Managing the Risk of European Corn Borer Resistance to Transgenic Corn: An Assessment of Refuge Recommendations." CARD, Iowa State University, Staff Report 99 SR 88, 1999.

Ives, A. "Evolution of Insect Resistance to Bacillus Thuringiensis-Transformed Plants." *Science*, 1996, 273, pp. 1412-1413.

Kamien, M.I. and Schwartz, N.L. *Dynamic Optimization: The Calculus of Variations and Optimal Control in Economics and Management*, Second Edition. New York: North-Holland, 1991.

Li, C.Z., Lofgren, K-G. and Weitzman, M.L. "Harvesting versus Biodiversity: An Occam's Razor Version." *Environmental and Resource Economics*, 2001, 18, pp. 355-366.

Lyubich, Y. *Mathematical Structures in Population Genetics.* Berlin: Springer-Verlag, 1992.

Metrick, A. and Weitzman, M.L. "Conflicts and Choices in Biodiversity Preservation." *Journal of Economic Perspectives*, 1998, 12(3), pp. 21-34.

Montgomery, C., Pollak, R.A., Freemark, K. and White, D. "Pricing Biodiversity." *Journal of Environmental Economics and Management*, 1999, 38, pp. 1-19.

Murray, J. D. *Mathematical Biology.* Berlin: Springer-Verlag, 1993.

Naeem, S., Thompson, L.J., Lawlers, S.P., Lawton, J.H. and Woodfin, R.M. "Empirical Evidence that Declining Species Diversity May Alter the Performance of Terrestrial Ecosystems." *Philosophical Transactions of the Royal Society London*, B, 1995, 347, pp. 249-262.

Naeem, S., Hakansson, K., Lawton, J.H., Crawley, M.J. and Thompson, L.J. "Biodiversity and Plant Productivity in a Model Assemblage of Plant Species." *Oikos*, 1996, 76, pp. 259-264.

Nehring, K. and Puppe, C. "A Theory of Diversity." *Econometrica*, 2000, forthcoming.

Norse, E. A., Rosenbaum, K.L., Wilcove, D.S., Wilcox, B.A., Romme, W.H., Johnston, D.W. and Stout, M.L. *Conserving Biological Diversity in our National Forests.* Washington, D.C.: The Wilderness Society, 1986.

Pacala, S. and Tilman, D. "Limiting Similarity in Mechanistic and Spatial Models of Plant Competition in Heterogeneous Environments." *The American Naturalist*, 1994, 143(2), pp. 222-257.

Rausser, G. C. and Small, A.A. "Genetic Resource Libraries: Bioprospecting and Knowledge Assets." NCEAS Workshop on Economics of Biodiversity, Santa Barbara, 2001.

Roughgarden, J. *Primer of Ecological Theory.* New York: Prentice Hall, 1998.

Scott, J. C. *Seeing Like a State.* New Haven: Yale University Press, 1998.

Simpson, R.D., Sedjo, R. and Reid, J. "Valuing Biodiversity for Use in Pharmaceutical Research." *Journal of Political Economy*, 1996, 104, pp. 163-185.

Solow, A., Polasky, R. Stephan and Broadus, J. M. "On the Measurement of Biological Diversity." *Journal of Environmental Economics and Management*, 1993, 24, pp. 60-68.

Soule, J. "Conservation: Tactics for Constant Crisis." *Science*, 1991, 253, pp. 744-750.

Soule, J. and Piper, J. *Farming in Nature's Image: An Ecological Approach to Agriculture.* Washington, D.C.: Island Press, 1992.

Tilman, D. *Resource Competition and Community Structure.* Princeton: Princeton University Press, 1982.

Tilman, D. *Plant Strategies and the Dynamics and Structure of Plant Communities.* Princeton: Princeton University Press, 1988.

Tilman, D. and Downing, J.A. "Biodiversity and Stability in Grasslands." *Nature*, 1994, 367, pp. 363-365.

Tilman, D. and Lehman, C. "Habitat Destruction and Species Extinction", in D. Tilman and P. Kareiva, eds., *Spatial Ecology: The Role of Space*

in Population Dynamics and Interspecific Interactions. Princeton: Princeton University Press, 1997.

Tilman, D., Wedin, D. and Knops, J. "Productivity and Sustainability Influenced by Biodiversity in Grassland Ecosystems." *Nature*, 1996, 379, pp. 718-720.

Vandermeer, J. *The Ecology of Intercropping.* Cambridge University Press, 1989.

Weitzman, M. L. "On Diversity." *Quarterly Journal of Economics*, 1992, *107*, pp. 363-406.

Weitzman, M. L. "What to Preserve? An Application of Diversity Theory to Crane Conservation," *Quarterly Journal of Economics*, 1993, 108, pp. 157-183.

Weitzman, M. L. "The Noah's Ark Problem." *Econometrica*, 1998, 66(6), pp. 1279-1298.

Weitzman, M. L. "Economic Profitability versus Ecological Entropy." *Quarterly Journal of Economics*, 2000, 115, pp. 237-263.

Wilson, E.O. and Peter, F.M. *Biodiversity.* Washington, D.C.: National Academy of Science, 1988.

Wolfram, S. *The Mathematica Book*, Fourth Edition, Wolfram Media/Cambridge University Press, 1999.

Table 5: The OSS of the SOMP for the Fitness Values of Table 1

(s, d_2)	$\overline{R}$	$\overline{\mu}_2$	$\overline{p}$	$\overline{q}_2$	x^*	B^*	$\overline{B}(d_2)$	% gain in biomass	H	D	# of eigenvalues with negative real parts
$(0.5, 0.5)$	13.65	5.94	0.3093	14.49	0.2164	18.593	16.779	10.81	0.522	0.339	1
$(0.4, 0.5)$	13.73	5.87	0.3035	14.43	0.1841	18.282	16.779	8.96	0.478	0.300	1
$(0.3, 0.5)$	13.81	5.79	0.2962	14.34	0.1480	17.949	16.779	6.97	0.419	0.252	1
$(0.2, 0.5)$	13.89	5.71	0.2857	14.13	0.1071	17.588	16.779	4.82	0.340	0.191	1
$(0.1, 0.5)$	13.99	5.62	0.2635	13.52	0.0604	17.195	16.779	2.48	0.228	0.113	1
$(-0.01, 0.5)$	13.35	6.23	0.9358	1684.88	0.1196	19.911	16.779	18.67	0.366	0.211	2
$(-0.015, 0.5)$	14.07	5.54	0.5889	14.10	0.0065	16.878	16.779	0.59	0.039	0.013	2
$(-0.02, 0.5)$	14.09	5.52	0.4975	29.61	0.0000	16.779	16.779	0.00	0.000	0.000	2
$(0.5, 0.4)$	12.21	7.34	0.3093	15.46	0.2164	25.501	23.459	8.70	0.522	0.339	1
$(0.5, 0.3)$	10.70	8.93	0.3093	15.37	0.2164	35.494	33.375	6.35	0.522	0.339	1
$(0.5, 0.2)$	8.71	10.82	0.3094	13.46	0.2164	51.836	49.569	4.57	0.522	0.339	1
$(0.5, 0.1)$	6.32	13.25	0.3993	7.49	0.2164	86.476	84.507	2.33	0.522	0.339	1

Table 6: The OSS of the SOMP for the Relative Fitness Values of Table 2

d_2	$\overline{R}$	$\overline{\mu}_2$	$\overline{p}^1$	$\overline{q}_2$	$x^{*1,2}$	B^*	$\overline{B}(d_2)$	% gain in biomass	H	D	# of eigenvalues with negative real parts
0.5	13.47	6.12	0.7955	170.12	0.1186	19.386	16.779	18.22	0.364	0.209	1
0.4	12.06	7.49	0.7955	179.89	0.1186	26.356	23.459	12.35	0.364	0.209	1
0.3	10.47	9.06	0.7955	177.52	0.1186	36.414	33.375	9.11	0.364	0.209	1
0.2	8.62	10.91	0.7955	154.46	0.1186	52.817	49.569	6.55	0.364	0.209	1
0.1	6.28	13.30	0.7955	85.13	0.1186	87.308	84.507	3.31	0.364	0.209	1

[1]The values of $\overline{p}$ and x^* start becoming different after approximately the 13th decimal place.

[2]The value of x^* lies in the interval defined in section 4, which for the specific numerical values is $(0.099723, 0.210526)$.

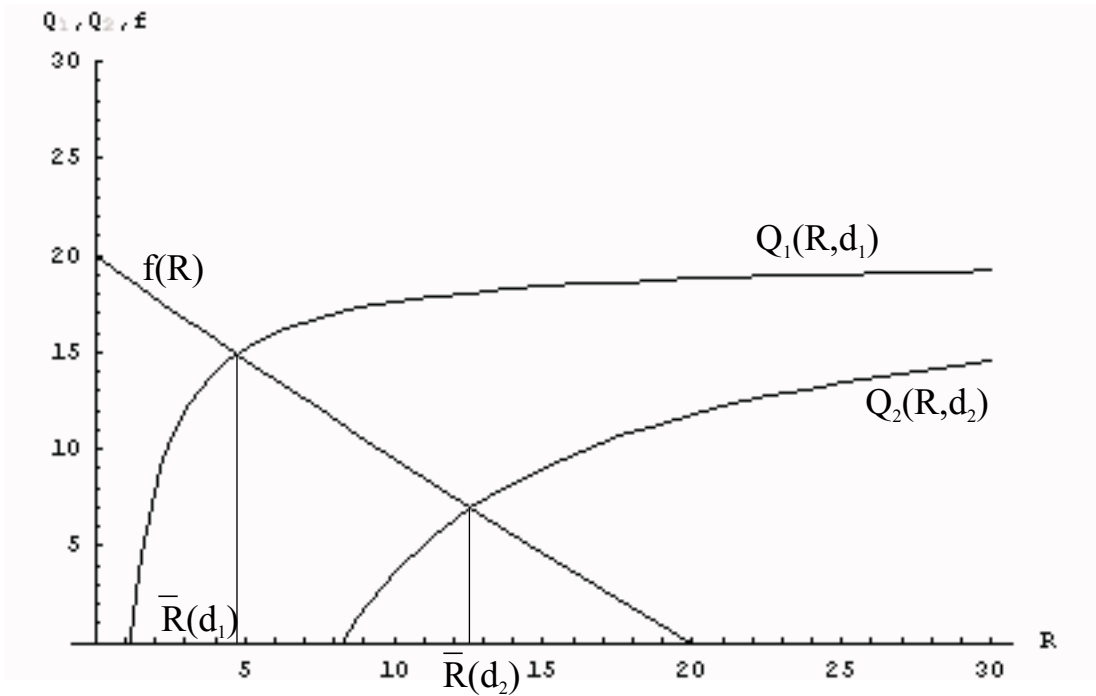S=2, d$_{2}$=0.40, d$_{1}$=0.05, a=0.10,w=0.05, g=0.05

Figure 1: The POMP Solution
(S=2, d$_2$=0.40, d$_1$=0.05, a=0.10,w=0.05, g=0.05)