Modeling the Economics of Biodiversity and Environmental Heterogeneity

William Brock · Ann Kinzig · Charles Perrings

Abstract   It has long been recognized that major drivers of biodiversity loss include both the harvest of wild species and the conversion of habitat for productive purposes. Land that is converted may or may not be lost as habitat for many species. In some cases, monoculture production for example, land conversion reduces the number niches and hence the level of biodiversity. In other cases, it has the opposite effect. We address the problem of anthropogenic biodiversity change due to the effects of both harvest rates and land use decisions on landscape heterogeneity. If the optimal structure of the landscape is extremely homogeneous, forces of competitive exclusion will lead to a single surviving species. If it is extremely heterogeneous, multiple species will coexist, with each species exclusively dominating the patch type to which it is best suited. Where changes in biodiversity due to changes in landscape heterogeneity are not taken into account in land use decisions, they are external effects of those decisions. We identify measures of these effects.

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1 Posing the Problem

The impact of economic activity on biodiversity has been evaluated from two main perspectives. One is the direct effect of depletion. The other is the indirect effect of land use change on habitats. Direct depletion through 'harvesting' is currently the primary cause of biodiversity change in most marine systems (e.g. Worm et al. 2006). Land use change is currently the primary cause of biodiversity change in terrestrial systems (e.g. Barbier and Schulz 1997; Wilcove et al. 1998; Polasky et al. 2004). While harvesting affects abundance of species directly, land use change works through the impact it has on habitat—generally modeled using some variant of the species-area relationship (MacArthur and Wilson 1967). The impact of economic activity on biodiversity in this approach depends on the proportion of the land area converted for agriculture or forestry, and hence on the balance between 'wild' and 'managed' landscapes (e.g. Pereira and Daily 2006; Polasky et al. 2005). The two proximate drivers—harvest and habitat structure—are clearly not independent. Deforestation, for example, is at once the depletion of timber stocks and the fragmentation of forest habitat. In this paper we model the joint effect of overharvesting and land use change, focusing on the impact of land use change that most affects biodiversity—environmental heterogeneity (the niche structure) of managed landscapes.

We are particularly interested in the fact that while land use change reduces the size of existing habitats, it also creates new habitats. Depending on the land use decision involved this may either increase or decrease the number of niches available to species, and so may either increase or decrease the level of biodiversity in the landscape. Industrial monocultures are at one end of a spectrum of land uses. At the other end are land uses that lead to extreme spatial heterogeneity—a very 'patchy' structure to the landscape. Examples of this include many urban and peri-urban environments, or small-scale, highly differentiated mixed arable and pastoral agro-ecosystems. Industrial monocultures would be expected to be biologically depauperate, heterogeneous environments would be expected to be biologically rich.

The relation between environmental heterogeneity and biodiversity is the following. Competitive exclusion of species by the dominant species always reduces diversity, and this is true within each niche. However, a high degree of heterogeneity between patches or niches within a landscape leads to a high level of species diversity at the landscape level (Kinzig et al. 1999). Within each habitat type, a reduction in the size of the habitat leads to declining biodiversity by the species area relationship (Kinzig and Harte 2000; May et al. 1995). But the creation of new habitats, and niches within those habitats, increases the opportunities open to specialist species.

The number and relative abundance of species within managed landscapes are accordingly affected both by direct anthropogenic impacts on abundance and by land uses that change environmental heterogeneity. So biodiversity loss is affected both directly through 'harvest' and indirectly through changes in the structure of the landscape. While this addresses the same pair of drivers that inform the existing literature (harvest and habitat change), the mechanisms involved are quite different. 'Harvest' comprises both the extraction of desirable species and the control or removal of undesirable species. Land use change affects the heterogeneity or niche structure of the landscape. Activities that make the landscape less heterogeneous, cause habitats for specialist species to decline, and so reduce species richness. Activities that make the landscape more heterogeneous have the opposite effect.

This paper develops a model of the relationship between species richness, harvest and landscape heterogeneity. We first consider the problem in the absence of harvest, and then identify the optimal harvest strategy without taking the impact of environmental heterogeneity on biodiversity into account. Finally, we consider the socially optimal harvest strategy

when there are both direct effects on species abundance and indirect effects on landscape structure. We show that where the dual impact of effort is ignored, privately optimal levels of harvest will diverge from socially optimal levels, and that this will be reflected in both landscape structure and species richness. A discussion section then relates these findings to current approaches to conservation in managed landscapes, and the arguments being made for recognizing the multiple services provided by agricultural or forest ecosystems. We consider that the model architecture developed here provides a better (and more neutral) theoretical foundation for the analysis and management of biodiversity change in terrestrial systems, than models that treat all land use change associated with agricultural or forest development as habitat destruction.

2 The Relationship Between Species Richness and Environmental Heterogeneity: The Ecological Problem

To capture the joint effect of 'harvest' and landscape structure on species richness, we first model the impact of these phenomena on the growth potential of each species. Our starting point is a density-dependent growth function for each of m species. We assume a logistic function here, but the choice of functional form is not critical. We could just as well have chosen any other density dependent function. We modify the density-dependent function in two important ways. First, we include density independent additive terms to capture direct anthropogenic changes in the biomass of species. One of these terms is the net effect of harvest. This is the usual additive term found in bioeconomic renewable resource models. The second term captures the net effect of exogenous drivers of biomass change—'imports' from outside the system or direct losses due to 'imports' (*sensu* Norberg et al. 2001). 'Imports', in this context, include both deliberate and accidental additions to the abundance of species. Deliberate additions can be thought of as imported seed, live plants or live animals. Accidental additions can be thought of as invasive species, accidentally introduced through trade, transport or travel. The main impact of 'imports' is to introduce new species to the system, but they can also directly change the abundance and hence the growth rate of existing species. 'Imports' that drove abundance above local carrying capacity would, for example, induce negative growth rates for the species concerned.

The second important modification we make is to the density dependent growth term in the logistic equation. This modification captures the effect of environmental heterogeneity on the growth potential of each species in the system. For an individual species, increasing environmental heterogeneity in the system reduces carrying capacity and hence the potential abundance of that species. At the same time, however, it increases the number of niches in the system and hence the number of species that can coexist.

Suppressing time subscripts, the growth of the ith of m species that can potentially exist in the system is described by the equation of motion:

$$\frac{ds_i}{dt} = s_i \left[r_i \left(1 - \left(\frac{e(L)^2 s_i}{K/\varphi_i(m_0)} + \left(\frac{(1 - e(L))S}{K} \right) \right) \right) - d_i - a_i \ell_i \right] \qquad (1)$$

where s_i denotes biomass of the ith species at time t; $\sum_{i=1}^{m} s_i = S$ denotes aggregate biomass of the m species that define the natural resource base of the economy; r_i denotes the intrinsic rate of growth of the ith species; d_i the density independent mortality rate and $a_i \ell_i$ the rate of 'harvest' or depletion due to exploitation—a product of the share of available labor committed to that activity, ℓ_i, and a measure of the effectiveness of 'harvest' effort,

a_i. $\sum_{i=1}^{m} \ell_i = L, 0 \leq L \leq 1$ is the share of the labor force committed to exploitation of the natural resource base. K is the maximum carrying capacity of the ecosystem in terms of biomass, and $0 \leq e(L) \leq 1$ is an index of environmental heterogeneity.

Access to system-level carrying capacity is a function of environmental heterogeneity. If the system is perfectly homogeneous, then $e = 0$ and the equation of motion collapses to a standard logistic model in which the competitive dominant excludes all other species. If it is perfectly heterogeneous, then $e = 1$ and the ith species accesses $K/\varphi_i(m)$ of the system-level carrying capacity. In general, the expression $\varphi_i(m)e(L)$ determines the share of carrying capacity accessed by the ith species as a function of both the degree of heterogeneity of the landscape and the number of competing species in the system.

In this first section we consider the system without human exploitation (indexing the problem '0'). In this case (1) takes the form,

$$\frac{ds_i}{dt} = s_i \left[r_i \left(1 - \left(\frac{e_0^2 s_i}{K/\varphi_i(m_0)} + \left(\frac{(1-e_0)S}{K} \right) \right) \right) - d_i \right] \tag{2}$$

That is, there is no harvest and the level of heterogeneity is the 'natural' level, e_0. The number of species in the system, m_0, is defined by the set $\{s_i\}$ for which the right hand side of (2) is positive given the natural level of environmental heterogeneity, e_0. Let A be the set of species that exist in these conditions. We suppose initially that $\varphi(m_0) = |A|$, where $|A|$ is just the cardinality of set A. It then follows that for the set of species that exists in the 'natural' steady state, A^*:

$$A^* e_0 s_i + (1 - e_0) S\left(A^*\right) = K \left(\frac{r_i - d_i}{r_i} \right) \tag{3}$$

To see the implications of environmental heterogeneity for the existence and abundance of species in the system, we first define the RHS of (3)

$$g_i := K \left(\frac{r_i - d_i}{r_i} \right) \tag{4}$$

to be the maximum potential biomass of the ith species in the 'natural' state, and rank the m_0 potential species in the system such that $g_1 > g_2 > \cdots > g_{m_0-1} > g_{m_0} > 0$ (Brock and Xepapadeas 2002). Ecologically, this says that the m_0 potential species are competitively ranked by their equilibrium abundance, implying that they are K-selected (K-strategists out-compete r-strategists). A necessary though not generally sufficient condition for the existence of the ith species is that $g_i 0$—it's net growth rate is positive. A sufficient condition is that:

$$g_i > (1 - e_0) \bar{g}_i, \bar{g}_i = \sum_{k=1}^{i} \frac{g_k}{\varphi([1,i])e_0 + i(1-e_0)} \tag{5}$$

where $[1, i]$ is the interval of indices between 1 and i. The sum in (5) is over the set of species whose equilibrium abundance is not less than that of the ith species, and $\varphi([1, i])$ is evaluated on this set of species. For our leading special case $\varphi([1, i]) = i$ and $\bar{g}_i$ is the average for that case. Note that (5) holds *a fortiori* for any set of m species, where $m_0 \geq m \geq i$.

For the intuition behind this, consider Fig. 1, which graphs g_i, $(1 - e)\bar{g}_i$ against $i = 1, 2, \ldots$, assuming continuous species, and shows the set of points, i, for which $g_i > (1-e)\bar{g}_i$. The set, A^*, for which this inequality holds is the set of all living species in the system. Panel (a) illustrates a case where $g(i)$ is linear, and panel (b) a case where $g(i)$ is non-linear. In panel (a) A^* is the interval $[0, m]$. In panel (b) A^* is the union of a set of disjoint intervals, $\{[0, i], [j, m]\}$.
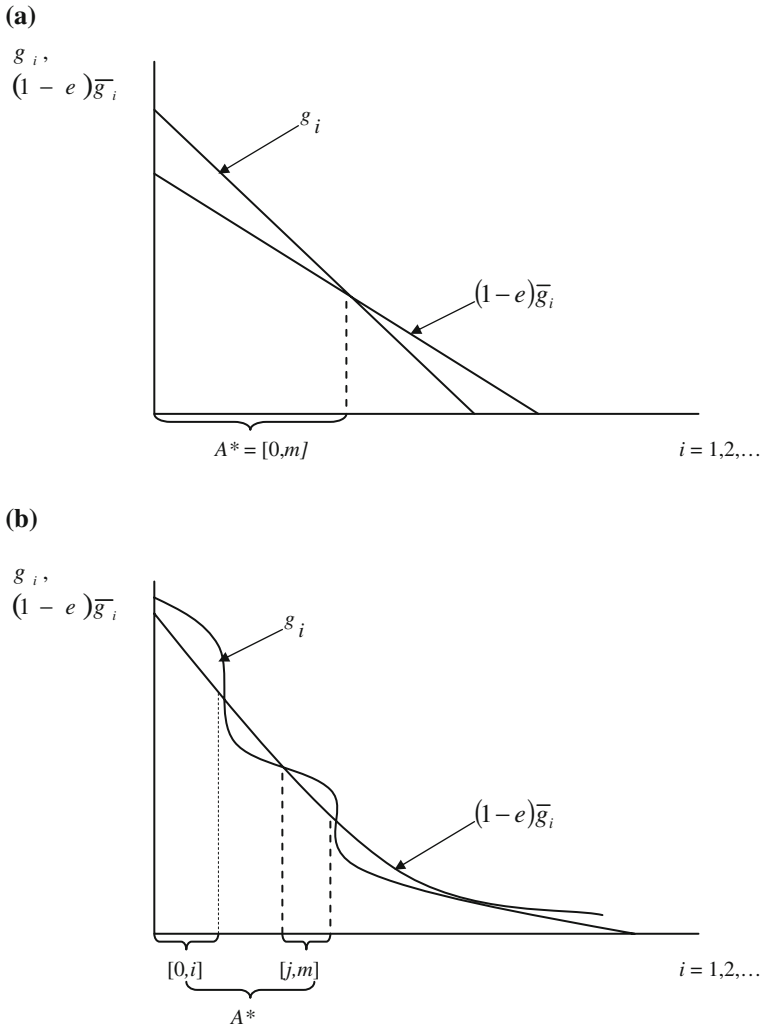
(a)

(b)

Fig. 1 The set of existing species. **a** g_i Linear, A^* is the interval $[0, m]$. **b** g_i Non-linear, A^* is the union of disjoint intervals $[0, i]$ and $[j, m]$

In the perfectly heterogeneous case ($e_0 = 1$), i.e. where the system is perfectly partitioned, (12) collapses to a condition that the net growth rate of the competitive dominant species in each niche is positive. In the perfectly homogeneous case ($e_0 = 0$) the requirement implies that $g_i > \frac{\sum_{j=1}^{i} g_j}{i}$ which, given the ranking of the g_i, is satisfied only for species s_1. That is, in the perfectly homogeneous case, competitive exclusion leaves only the first ranked species in the system. The forgoing is summarized in the following proposition:

Proposition 1 *Species existence in the natural system. In a physically closed system in which the dynamics of the ith of m_0 potential species are described by* (2), *where species are competitively ranked by their equilibrium abundance, and where φ is evaluated at $\varphi([1, m])$, a necessary and sufficient condition for the existence of the ith species in the steady state is*

that: $g_i > (1-e)K \left(\frac{i-\sum_{j=1}^{i} d_j/r_j}{\varphi([1,m])e+i(1-e)} \right) > 0$, where $g_i := K \left(\frac{r_i - d_i}{r_i} \right)$. For proof, see Appendix.

We can then show that the number of species that may coexist in the system is increasing in the degree of environmental heterogeneity. Specifically:

Proposition 2 *Species number and environmental heterogeneity. In a physically closed system in which (a) $A = [0, m]$ is the set of living species, (b) the least productive of surviving species solves $g(m) = (1 - e_0)S(m)$, and (c) m is the Lebesgue measure of the set $A = [0, m]$, m solves $\left(g(m)m - (1-e) \int_0^m g(i) \, di \right) = 0$. Since $\frac{dm}{de} > 0$ the number of species is increasing in the level of environmental heterogeneity. For proof, see Appendix.*

3 The Economic Problem: The Privately Optimal Solution

Now consider the economic problem posed by the exploitation of this system. We assume that the representative of k consumers, endowed with $1/k$ share of total available labor, derives utility from consuming manufactures, $q = Q/k$, plus a primary commodity, $h = H/k$. We suppose that H is produced through the Schaefer function, $H = \int_0^m s(i)a(i)\ell(i) \, di$, in which a measures the effectiveness of harvesting effort and L is the share of total labor committed to harvesting S. One unit of Q is produced with $1/k$ share of labor, and the price of Q is taken as the numeraire. Since the value of the marginal physical product of labor in manufacturing is also equal to 1, the wage, $w = 1$. It follows that $Q = 1 - L$.

The representative consumer solves the following problem: $Max \, u(h, q)$ subject (a) to a budget constraint, $1/k = PH/k + q$, where PH is the domestic value of the aggregate harvested natural resources, and (b) to the dynamics of S. Since both q and h are 'essential' it follows that $u(0, q) = u(h, 0) = 0$ and the partial derivatives with respect to h, q are infinite, i.e. Inada conditions hold. Aggregating across consumers, we have the following 'social' problem:

$$Max_L \int_{t=0}^{\infty} \{U(H, Q)\} e^{-\rho t} \, dt \qquad (6)$$

This is subject to the equations of motion for the set of all species, (1), and to the structure of property rights. Following Brander and Taylor (1997) we assume that the social utility function takes the specific form $U \left(H^{\beta} Q^{1-\beta} \right)$, $U' > 0$. It then follows that $PH = \beta W$ and $Q = (1 - \beta)W$, where P is the domestic price of aggregate harvest, H, and W comprises both income from labor, L_s, and profits from firms producing H. Note that profits from firms producing Q are zero by the assumption of constant returns, and wages are set equal to unity.

We wish to understand the impact on biodiversity of the decisions of individual firms. We accordingly assume that firms internalize all externalities except for those associated with the impact of effort on biodiversity. Each firm is assumed to exploit a particular patch, and to select the level of harvest effort to maximize steady-state profits from that patch. To make the consequences of economic activity quite transparent, we consider the special case where future consumption is not discounted, i.e. $\rho = 0$, and confine our attention to steady states. In this case the representative firm solves a problem of the form:

$$Max_{\ell(i)}\pi = Ps(i)v(i)a(i)\ell(i) - \ell(i) \qquad (7)$$

subject to (1), and noting that $v(i)$ defines the species-specific weight on the domestic price of aggregate output, P. Hence $Pv(i)$ can be thought of as the domestic price of the ith harvested species.

The set of species that are actively harvested comprises all those i for which the value of the marginal physical product of labor is positive at $\ell(i) = 0$, i.e. for which $\frac{d\pi}{d\ell(i)} > 0$ at $\ell(i) = 0$. In the case where the system is perfectly heterogeneous, that is where $e = 1$, we can use the steady state formula for $s(i) = g(i, \ell(i))/\varphi([1, m])$ to show that a sufficient condition for i to be in the set of harvested, living species is that:

$$Pv(i)a(i)K(r(i) - d(i)) > r(i)\varphi([1, m]) \tag{8}$$

where m is the integral of all i that satisfy (8). In the perfectly heterogeneous case, if $\frac{de}{d\ell_i} = 0$, implying that exploitation of the resource has no impact on environmental heterogeneity, then the first order conditions for the problem require that:

$$Pv(i)s(i)a(i) - 1 = \lambda(i)s(i)a(i) \tag{9}$$

That is, exploitation of the ith species will increase up to the point at which the marginal net private benefit of allocation ℓ_i (the difference between the value of the marginal physical product and marginal cost of labor) is equal to its marginal user cost (the shadow value of the marginal impact of harvest effort on stock growth). In the more general case, where $0 < e < 1$ and $\frac{de}{d\ell_i} \neq 0$, the first order conditions for the private problem amongst e-taking firms require that:

$$Pv(i)s(i)a(i) - 1 = \lambda(i)s(i)\left[a(i) + r\left(\frac{s(i)(\varphi([1, m]) - 1)}{K}\right)\frac{de}{d\ell_i}\right] \tag{10}$$

In other words the decision-maker exploiting the ith patch does take account of the impact of their behavior on heterogeneity in the ith patch, $\left(\frac{s(i)(\varphi([1,m])-1)}{K}\right)\frac{de}{d\ell_i}$, but neglects the wider effects of their decision on heterogeneity at the level of system, $\int_{j\neq i}^m \lambda(j)s(j)r(j)\left(\frac{\varphi([1,m])s(j)-S}{K}\right)\frac{de}{d\ell_i}\, dj$. The value of this externality depends in part on the sign and magnitude of the marginal impact of effort on heterogeneity: $\frac{de}{d\ell_i}$. Although it is frequently the case that increasing exploitation of ecosystems reduces heterogeneity through, for example, the development of monocultures, this is not always the case. That is, neglect of the wider effects of private decisions may lead to either excessive heterogeneity or insufficient heterogeneity. This is summarized in the following proposition.

Proposition 3 *Private land use decisions and environmental heterogeneity. If the private firm exploiting the ith patch maximizes profit through choice of exploitation effort, (7), subject to the dynamics of species on that patch, (1), if environmental heterogeneity is intermediate, $0 < e < 1$, and is affected by the level of exploitation effort, $\frac{de}{d\ell_i} \neq 0$, then the first order conditions for maximization of private profit will include the impact of effort on within-patch heterogeneity, $\left(\frac{s(i)(\varphi([1,m])-1)}{K}\right)\frac{de}{d\ell_i}$, but will ignore the impact of effort on environmental heterogeneity in the rest of the system, $\int_{j\neq i}^m \lambda(j)s(j)r(j)\left(\frac{\varphi([1,m])s(j)-S}{K}\right)\frac{de}{d\ell_i}\, dj$. Environmental heterogeneity will be excessive or insufficient as $\frac{de}{d\ell_i} \gtrless 0$.*

Recall that biodiversity is affected by harvest effort both directly, through the impact of harvest on species abundance, and indirectly through the impact of effort on environmental heterogeneity. To see the direct effect of effort, we define the maximum potential biomass of the ith of m harvested (discrete) species to be:

$$g_i := K \left(\frac{r_i - d_i - a_i \ell_i}{r_i} \right) \tag{11}$$

We expect to be able to define a similar cut-off rule for any allocation of harvest effort. Ranking $\{g_i\}$, as before, such that $g_1 > g_2 > \cdots > g_m > 0$, we can obtain by similar reasoning a sufficient condition on g_i for the existence of the ith species as a function of both the biological parameters, r_i and d_i and the level and effectiveness of harvest effort, $a_i \ell_i$:

$$g_i > (1 - e)K \left(\frac{i - \sum_{j=1}^{i} \frac{d_i + a_i \ell}{r_i}}{\varphi([1, m])e - i(1 - e)} \right) \tag{12}$$

We take the case where A is an interval, i.e. the case shown Fig. 1a. The algorithm used to identify the level of species richness is as follows: for a given set of environmental conditions, e, set $L = 0$ and find the set of m species that satisfy condition (A13). Then increase L until the value of L is found that reduces the number of species from m to $m - 1$. Continue in this manner until $L = 1$ at which point $g_i = g(e(1))$ is the cut-off (marginal surviving) species. This is summarized in the following propositions:

Proposition 4 *Species existence in an economically exploited system. In an economic system based on the exploitation of up to m discrete species, ranked according to the maximum potential biomass net of harvest, a necessary and sufficient condition for the existence of the ith species in the steady state is that*

$$g_i > (1 - e)K \left(\frac{i - \sum_{j=1}^{i} \frac{d_i + a_i \ell_i}{r_i}}{\varphi([1, m])e - i(1 - e)} \right) > 0, \ \text{where} \ g_i := K \left(\frac{r_i - d_i - a_i \ell_i}{r_i} \right).$$

The probability that the ith species will exist in the steady state is accordingly decreasing in the rate at which it is 'harvested'.

Proposition 5 *The effect of environmental heterogeneity in an economically exploited system. Since the probability that the ith species will exist in the steady state is decreasing in environmental heterogeneity, the indirect effect of harvest depends on the extent to which it homogenizes the landscape. If the system is extremely homogeneous ($e = 0$), the steady state stock of the sole surviving species will converge to the maximum potential biomass of that species net of harvest. All other species will be driven extinct. The share of the labor force committed to harvest that species will be equal to L. If the system is extremely heterogeneous ($e = 1$), the steady state stock of the ith species will converge to the maximum potential biomass of that species in the patch within which it is the competitive dominant species. The share of the labor force committed to harvest the ith species will be increasing in the natural regeneration rate of the ith species and decreasing in the technical efficiency of harvest. For intermediate levels of heterogeneity, ($0 < e < 1$), the steady stock of species that are competitive dominants in existing patches converge to their maximum potential biomass net of 'harvest', and otherwise will fall to zero. For proof, see Appendix.*

4 The Economic Problem: The Socially Optimal Solution

The social decision-problem reflects the fact that while e depends on harvest effort by each firm, it also affects environmental heterogeneity in the system as a whole, and therefore the

number of surviving species. Yet the firm may have no incentive to take this into account. For a given value of e in [0,1] we define the harvest function:

$$h(L; e) := Max \int_i v_i a_i s_i \ell_i \, di \qquad (13)$$

in which $h(0, e) = 0$ for $e \in [0, 1]$. If property rights are such that the representative firm takes e as given, they solve the problem:

$$Max_L \{Ph(L; e) - L\}. \qquad (14)$$

subject to $\sum_i \ell_i = L$ and (1). The equilibrium associated with this structure of property rights is defined as $\{L^*, H^*, P^*(H), e^*\}$ such that

$$(H^*, Q^*) = \arg\max \{U(H, Q)\} \qquad (15)$$

subject to

$$P^*H + Q = 1 + \pi(H^*) \qquad (16)$$

and L^* is given by,

$$L^* = \arg\max \{P^*h(L; e^*) - L\}. \qquad (17)$$

Furthermore, the "rational point expectations" condition $e^* = e(L^*)$ holds. If $e(L) = e(0)$ is a constant function, the social welfare optimum

$$L^* = \arg\max U(h(L; 0), 1 - L) \qquad (18)$$

is the same as L^* in (17). In general, a first order necessary condition for maximizing social welfare with respect to L is:

$$U_H (h_L + h_e e_L) - U_Q = 0. \qquad (19)$$

In the equilibrium defined by (15)–(17), the term $h_e e_L$ is absent: i.e. the representative firm ignores its effect on heterogeneity. Note that the equilibrium defined by (15)–(17) assumes full property rights to the set of natural resources, but not to the heterogeneity and hence species richness of the general system.

Now consider the social problem confronting the resource extraction industry. The social equivalent of the problem specified by (7) is

$$Max_L \pi_S = \int_{i=0}^m (Ps_i v_i a_i \ell_i - \ell_i) \, di \qquad (20)$$

subject to (1). The first order necessary conditions for the maximization of social profit include the requirement that:

$$Pv_i s_i a_i - 1 = \lambda_i s_i \left[a_i + r_i \left(\frac{\varphi([1, m])s_i - S}{K} \right) \frac{de}{d\ell_i} \right], i = 1, 2, \ldots, m. \qquad (21)$$

Note that by comparison with (10) this requires the ith firm to take account of the impact that its effect on environmental heterogeneity has on all others in the industry, measured by: $\int_{j \neq i}^m \lambda_j s_j r_j \left(\frac{\varphi([1,m])s_j - S}{K} \right) \frac{de}{d\ell_i} \, dj$.

Proposition 6 *Environmental heterogeneity in the social problem. If* (20) *is optimized subject to* (1), *and if property rights are well defined, decision-makers will take account of the system-wide impact of their behavior on environmental heterogeneity:* $\int_{j\neq i}^{m} \lambda_j s_j r_j \left(\frac{\varphi([1,m])s_j - S}{K} \right) \frac{\mathrm{d}e}{\mathrm{d}\ell_i} \, \mathrm{d}j$. *The degree of environmental heterogeneity at the social optimum will be greater than than the degree of environmental heterogeneity at the private optimum if* $\frac{\mathrm{d}e}{\mathrm{d}\ell_i} > 0$, *and will be less than the degree of environmental heterogeneity at the private optimum if* $\frac{\mathrm{d}e}{\mathrm{d}\ell_i} < 0$.

5 Valued and Unvalued Species

What effect does the value of species have on environmental heterogeneity and biodiversity? Suppose that the system is characterized by both some degree of environmental heterogeneity, $e > 0$, and some level of biodiversity, $m > 1$, but that only one species is economically valuable. We denote the single valuable species $j \in \{1, 2, \ldots, m\}$ and normalize its value. We then have $Pv(j) = 1$, $Pv(i) = 0, i \neq j$. Consider again the problem defined by Eqs. (20) and (1). The first order conditions for the maximization of social profit for the unvalued species i require that:

$$ -1 = \lambda_i s_i \left[a_i + r_i \left(\frac{\varphi([1,m])s_i - S}{K} \right) \frac{\mathrm{d}e}{\mathrm{d}\ell_i} \right], i \neq j \tag{22} $$

implying that the optimal 'harvest' of i, $h^*(i) \geq 0$, satisfies:

$$ h_i^* = \ell_i \left[-s_i r_i \left(\frac{\varphi([1,m])s_i - S}{K} \right) \frac{\mathrm{d}e}{\mathrm{d}\ell_i} - \frac{1}{\lambda_i} \right], i \neq j. \tag{23} $$

Consider the conditions in which this term will be positive. From (1) the abundance of the valued species is impacted by the existence of all other species, regardless of whether it is the competitive dominant. Hence $\lambda_i < 0$ for all, and there exists an incentive to 'harvest' unvalued species. The two polar cases are where $j = 1$ (the valued species is the most abundant) and $j = m$ (the valued species is the least abundant). In both cases, the abundance of the valued species is affected by the existence of competitor species, but this effect is more significant in the second case. That is, the incentive to simplify the system by reducing the abundance of unvalued species is stronger the less abundant (the less competitive) is the valued species relative to other species.

Whether unvalued species are in fact 'harvested' depends on the relative strength of the two terms on the RHS of (23). If $\mathrm{d}e/\mathrm{d}\ell_i = 0$, implying that harvest effort has no impact on environmental heterogeneity at the margin, then $\lambda_i < 0$ is a sufficient condition for $h_i^* > 0$. However, if $\mathrm{d}e/\mathrm{d}\ell_i \neq 0$ then whether the ith unvalued species is 'harvested' depends on the sign of $\mathrm{d}e/\mathrm{d}\ell_i$ and its relative abundance. If $\mathrm{d}e/\mathrm{d}\ell_i < 0$, implying that harvest effort homogenizes the system, then the optimal level of 'harvest' of the ith unvalued species will be higher if that species has greater than average abundance, and will be lower if it has less than average abundance. If, $\mathrm{d}e/\mathrm{d}\ell_i > 0$ implying that harvest effort heterogenizes the system, then the optimal level of 'harvest' of the ith unvalued species will be decreased if that species has greater than average abundance, and will be increased if it has less than average abundance. In both cases, 'harvest' of the ith unvalued species will fall to zero if $s_i r_i \left(\frac{\varphi([1,m])s_i - S}{K} \right) \frac{\mathrm{d}e}{\mathrm{d}\ell_i} \leq \frac{1}{\lambda_i}$.

The implications of this for environmental heterogeneity and biodiversity are direct. Since the presence of unvalued competitor species imposes a social cost in the form of the reduced

abundance of valuable species, there is a positive incentive to reduce the abundance of those competitors. Whether this leads to positive rates of harvest depends on the impact of effort on heterogeneity. We summarize this in the following proposition:

Proposition 7 *Homogenization and the harvest of unvalued species. If only some species are positively valued, then since the abundance of those species is reduced by the existence of unvalued competitors the shadow value of those species will be negative, $\lambda_i < 0$ for all $i \neq j$. This implies a positive incentive to reduce their abundance. If $d e / d \ell_i < 0$, optimal level of 'harvest' of the ith unvalued species will be increased if that species has greater than average abundance, and will be reduced if it has less than average abundance. If $d e / d \ell_i > 0$, then the optimal level of 'harvest' of the ith unvalued species will be decreased if that species has greater than average abundance, and will be increased if it has less than average abundance.*

6 Discussion

The problem addressed in this paper is the impact on biodiversity of economic activities that transform the landscape at the same time as they alter the relative abundance of species. Biodiversity is affected by activities of this kind in two ways: directly through 'harvest' and other methods of controlling species abundance; and indirectly through changes in the heterogeneity or niche structure of the environment within which species live. 'Harvest', in this context, includes all actions that directly alter species abundance. In other words it includes not just the extraction of beneficial plants and animals, but also the control or eradication of weeds, pests and pathogens. The indirect effect is modeled as a change in the level of 'environmental heterogeneity'.

We specify growth functions for species that include both density-dependent and density-independent terms. The density-dependent terms reflect the effect of environmental heterogeneity on carrying capacity. The density independent terms capture the effects of harvest and species imports (whether through natural dispersal or human agency). The feature of the model that distinguishes it from others, is that effort committed to the exploitation of species has an indirect effect on landscape structure in addition to a direct effect on the abundance of targeted species and their predators and competitors. We do not specify the form of the function, $e(L)$, that relates exploitation and structure. How anthropogenic exploitation of the environment affects its heterogeneity is an empirical question. We expect that intensive high-input agriculture will lead to homogeneous species-poor landscapes, but the relationship between effort and environmental heterogeneity may not be monotonic. It is quite possible that environmental heterogeneity will be increasing in effort, at least over some interval.

Take agricultural ecosystems as an example. The inter-specific and intra-specific genetic diversity that supports crop and livestock production (genetic resources available both for selection of species for domestication or cultivation, and for the genetic improvement of domesticated and cultivated species) includes the wild or traditional genetic stocks that have historically been used for breeding or engineering resistance to plant and animal pests and pathogens. Specialization in agriculture has narrowed the genetic base of the activity to the point where more than 90% of global food supply derives from little more than a handful of species: wheat, rice, corn, oats, tomato, potato, cattle, sheep, pigs, chickens and ducks. The adoption of high yielding varieties during the Green Revolution, for example, led to the abandonment of thousands of traditional varieties bred to meet local conditions. Many landraces simply disappeared. At the same time, application of pesticides and fertilizers caused the loss not just of pests and predators, but also of beneficial organisms including

wild relatives (Conway 1993). In addition to this, agriculture has generally led to the displacement of species that are seen as competitors, pests or predators to the cultivated species, and hence to a loss in the non-provisioning services supported by those species. Yet this is not a universal characteristic of agriculture, nor is it inevitable. Conservation of agro-biodiversity and the adoption of biodiversity-based practices are common in many forms of agricultural production (McNeely and Scherr 2003; Jackson et al. 2007; MA 2005).

The development of urban ecosystems offers another example of heterogeneity-enhancing land use change. Both agriculture in peri-urban areas and the structure of urban landscapes involves the creation of a mosaic of highly variable niches, frequently associated with much higher levels of biodiversity than had existed in the unconverted landscape (Crane and Kinzig 2005). It is this range of possible responses we have in mind in specifying $e(L)$. We allow the effect of effort on biodiversity to be either positive or negative. Activities that make the environment more heterogeneous increase species diversity, activities that make the environment more homogeneous have the opposite effect. We show that if exploitation of the environment leads to its homogenization, and so to a loss of species that are positively valued, the socially optimal level of effort committed to the harvest of the ith species will be lower than if exploitation increases environmental heterogeneity. On the other hand, if exploitation of the environment leads to its homogenization, and so to a loss of species, and if these species are deemed harmful (e.g. pests and pathogens), the socially optimal level of effort committed to the harvest of the ith species will be higher than if exploitation increases environmental heterogeneity.

Whether species are positively or negatively valued depends on the balance between the value of the genetic information they contain, the value of the function they perform, and the value of their aesthetic, spiritual or cultural significance among other things. We do not model these phenomena since, once again, the value of species is an empirical question. Declining environmental heterogeneity means declining habitat for specialist species, but it may also imply declining resilience of the general system and its capacity to maintain productivity over a range of environmental conditions (Loreau et al. 2003; Kinzig et al. 2006). Since our concern is to model biodiversity change itself, this is beyond the scope of the paper, but it is an important dimension of the value of biodiversity externalities.

What is novel about the approach is its treatment of changes in environmental heterogeneity. Each land user makes independent decisions that affect the heterogeneity of the land under their control. This in turn affects the heterogeneity of the whole system, and in so doing affects the survival and growth potential of all species in the system. The impact that individual land users have on system wide heterogeneity is an externality, and is typically ignored in private land use decisions. So, for example, a forester who replaces old growth natural forest with a monoculture changes heterogeneity and diversity both in the area under their control, and in the whole system. They will take account of the former, but not the latter.

The implications of an externality of this sort are intuitive. In the general case, where decision-makers ignore the shadow value of exploited species and the impact of private land use decisions on environmental heterogeneity they will both overexploit species and generate a landscape that is less environmentally heterogeneous than is socially optimal. Once the source and magnitude of the externality has been identified, standard corrective instruments may be applied. The aim of the modeling exercise reported here is to help understanding of biodiversity externalities that include not just the contraction of wild refugia and overharvesting, both of which have been addressed in the literature, but also the impacts of changes in environmental heterogeneity. Since being 'like one's neighbor' increases the risk of extinction of species other than the competitive dominants, it involves an externality that may be amongst the most important inadvertent drivers of biodiversity loss.

Appendix

Proof of Proposition 1 From Eq. 5 we have:

$$g_i > (1 - e_0)\bar{g}_i, \quad \bar{g}_i = \sum_{k=1}^{i} \frac{g_k}{\varphi([1, m])e_0 + i(1 - e_0)} \tag{A1}$$

Recall that A^* is an interval, $A^* = [1, m]$, and note that from (3)

$$s_i = \frac{1}{\varphi([1, m])e_0}(g_i - (1 - e_0)S) \tag{A2}$$

where S is the aggregate biomass of the set of all living species, and $\varphi([1, m])$ is evaluated on that set. For the special case where $A^* = [1, m]$:

$$\sum_{i=1}^{m} s_i = \frac{1}{\varphi([1, m])e_0}\left(K\left(m - \sum_{i=1}^{m} d_i/r_i\right) - m(1 - e_0)\sum_{i=1}^{m} s_i\right) \tag{A3}$$

which yields

$$\sum_{i=1}^{m} s_i = \frac{K\left(m - \sum_{i=1}^{m} d_i/r_i\right)}{\varphi([1, m])e_0 + m(1 - e_0)} \tag{A4}$$

Substitution into [A1] implies that

$$s_i = \frac{1}{\varphi([1, m])e_0}\left(g_i - (1 - e_0)\left(\frac{K\left(m - \sum_{i=1}^{m} d_i/r_i\right)}{\varphi([1, m])e_0 + m(1 - e_0)}\right)\right), i = 1, 2, \ldots, m \tag{A5}$$

For $s_i > 0$ it follows that:

$$g_i > (1 - e_0)\left(\frac{K\left(m - \sum_{i=1}^{m} d_i/r_i\right)}{\varphi([1, m])e_0 + m(1 - e_0)}\right), i = 1, 2, \ldots, m \tag{A6}$$

But the same condition applies to each species added to the system after the first species, hence a generally sufficient condition for the existence of the ith species is that:

$$g_i > (1 - e_0)K\left(\frac{i - \sum_{j=1}^{i} d_j/r_j}{\varphi([1, i])e_0 + i(1 - e_0)}\right) \tag{A7}$$

and $m \leq m_0$ is the maximum value of i for which this condition holds.

Proof of Proposition 2 To see that number of species that can coexist in the system is increasing in the degree of environmental heterogeneity, consider the case where species are continuous. Suppose that the set of potential species is $[0, m_0]$ and that, as before $g(i)$ is decreasing in i. We have:

$$\frac{ds(i)}{dt} = s(i)\frac{r(i)}{K}(g(i) - \varphi([1, m])e_0 s(i) - (1 - e_0)S), i \in [0, m_0] \tag{A8}$$

with

$$S = \int s(i)\, di \tag{A9}$$

being the integral of $s(i)$ over all existing species. It follows that if species i exists in the steady state, then

$$g(i) = \varphi([1, m])e_0 s(i) + (1 - e_0)S \tag{A10}$$

and the least productive of the surviving species—the species with the lowest 'g' value—will solve:

$$g(m) = (1 - e_0)S(m) \tag{A11}$$

where $\varphi(.)$ is evaluated at the set of existing species $[0, m]$, $m \leq m_0$, and where

$$S(m) = \left(\frac{1}{\varphi([0, i])e_0 + (1 - e_0)m}\right) \int_0^m g(i)\, di \tag{A12}$$

In the special case where $\varphi(m) = m$ this implies that

$$S(m) = \frac{1}{m} \int_0^m g(i)\, di \tag{A13}$$

and m is determined by (19):

$$g(m) = \frac{(1 - e_0)}{m} \int_0^m g(i)\, di \tag{A14}$$

i.e., it is the Lebesgue measure of the set $A = [0, m]$, and the solution to:

$$\left(g(m)m - (1 - e) \int_0^m g(i)\, di\right) = 0 \tag{A15}$$

implying that $\frac{d}{de}m > 0$ for all $e > 0$.

Proof of Proposition 5 From the first order necessary conditions for the solution of the private problem where firms are e-takers, we can identify the steady state implications for biodiversity of different levels of environmental heterogeneity in the autarkic system. If the system is extremely heterogeneous, $(e = 1, L > 0)$, we have the following conditions on s_i and ℓ_i:

$$s_i = \frac{K}{m}\left(\frac{r_i - d_i - a_i \ell_i}{r_i}\right) \tag{A16}$$

$$\ell_i = \frac{1}{a_i}\left(r_i\left(1 - \frac{ms_i}{K}\right) - d_i\right) \tag{A17}$$

from which it is immediate that ℓ_i is increasing in r_i, the natural regeneration rate of the ith species and decreasing in a_i, the technical efficiency of harvest. In the extremely homogeneous case, $(e = 0)$, (A16) and (A17) are of the form:

$$s_i = \begin{cases} K\left(\frac{r_i - d_i - a_i \ell_i}{r_i}\right), & g(s_i) = g_m \\ 0, & g(s_i) \neq g_m \end{cases} \tag{A18}$$

$$\ell_i = \begin{cases} \frac{1}{a_i}\left(r_i\left(1 - \frac{S}{K}\right) - d_i\right), & g(s_i) = g_m \\ 0, & g(s_i) \neq g_m \end{cases} \tag{A19}$$

If the ith species has the highest 'g' value, or net regeneration potential, it will be the competitive dominant species. If not it will be driven extinct. Similarly, the labor committed to harvest the ith species will be equal to L if that species has the highest 'g' value, and will be zero otherwise.

Now consider the intermediate case where there is some environmental heterogeneity, i.e. where $0 < e < 1$. We have that:

$$s_i = \frac{K}{m}\left(\frac{r_i - d_i}{r_i} - \frac{(1-e)S}{K}\right) \tag{A20}$$

As the degree of environmental heterogeneity rises from the point at which the ith species is able to coexist with other species, the steady state stock of that species first increases and then declines. Moreover, if the system is subject to exploitation, $L > 0$, then the steady state share of the labor force committed to harvest the ith species is:

$$\ell_i = \frac{1}{a_i}\left(r_i\left(1 - \left(\frac{ems_i + (1-e)S}{K}\right)\right) - d_i\right) \tag{A21}$$

As before, it is immediate that ℓ_i is increasing in r_i, the natural regeneration rate of the ith species and decreasing in a_i, the technical efficiency of harvest. ℓ_i is either decreasing or increasing in e, as $\frac{ems_i - S}{K}$ is positive or negative.

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