

## **MODELING THE ECONOMICS OF BIODIVERSITY AND ENVIRONMENTAL HETEROGENEITY**

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## **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. While habitat conversion explains a large part of the decline in native species occurring in wild refugia, however, it ignores the impact of land use in the rest of the landscape. We address the problem of anthropogenic biodiversity loss across the whole landscape by modelling the connection between landscape heterogeneity, harvest intensity and the level of biodiversity. If the system is extremely homogeneous, it is assumed that forces of competitive exclusion will lead to a single surviving species. If the system is extremely heterogeneous, it is assumed that multiple species can coexist, with each species exclusively dominating the patch type to which it is best suited. Alongside the effects of harvest/pest control, we consider the effect of land use on environmental heterogeneity, and through that on species richness. We identify the externalities associated with each activity and the potential for applying corrective measures.

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## **1. Posing the problem**

The impact of economic activity on biodiversity has been evaluated from a number of perspectives. The most compelling arguments address the link between economic activity and the loss of natural habitats (e.g. Barbier and Schultz, 1997; Wilcove et al, 1998; Polasky et al, 2004). Using the species-area relationship (Macarthur and Wilson, 1967), such studies calculate the impact of economic activity on biodiversity from the proportion

of the land area that is converted to other uses, usually to agriculture or forestry. By assumption, the converted area is lost as natural habitat, and is no longer available to support species. The number of species that can continue to be supported is therefore reduced.

While this approach has much to say about species loss in diminishing wildlife refugia, however, it has little to say about species loss or persistence in the rest of the landscape. Species can persist in human managed or dominated landscapes, though the species-area approach described above assumes they cannot. Given the increasing human domination of the biosphere, understanding how human activities alter biodiversity in worked and altered landscapes is of growing importance (Perrings and Gadgil, 2003; Daily et al, 2000) and the consequences this has not just for the existence of species, but for the effects on ecosystem functioning (Hooper et al, 2005; Naeem and Wright, 2003) and the production of a range of ecosystem services and disservices (Millennium Ecosystem Assessment, 2005; Barbier, 2007; Barbier et al, forthcoming; Perrings et al, forthcoming). This poses a different modeling challenge. In this paper, we focus on one particular ecological explanation of species richness – the heterogeneity of the landscape. This is also related to land use, but unlike the conversion of habitats it addresses the causes and consequences of biodiversity change not only in refugia, but across the whole landscape.

We are interested in the relationship between environmental heterogeneity, the intensity with which species are harvested (or culled), and species diversity. Environmental heterogeneity in this case refers to the ‘patchiness’ of the landscape, and is taken to be a

function of land use or the way that species are exploited. A heterogeneous landscape is one in which distinct patches favor the existence of distinct species. While competitive exclusion will reduce diversity in each patch, a high degree of heterogeneity between patches leads to a high level of species diversity (Kinzig et al, 1999). Biodiversity – in this case measured by both environmental heterogeneity and species richness – is a function of the level of economic activity. Species richness may be reduced in two ways: through ‘harvest’ and through reduced environmental heterogeneity. We show that where the user cost of individual species is ignored, the privately optimal level of effort and hence the privately optimal level of environmental heterogeneity will diverge from the socially optimal level of effort and the socially optimal level of environmental heterogeneity. We note that harvest effort comprises both the extraction of desirable species and the control or removal of undesirable species. This is, to our knowledge, the first attempt to understand the interactions between environmental heterogeneity and species loss in the context of an economic model.

## 2. Modeling the relationship between species richness and environmental heterogeneity

Consider the growth of the  $i^{th}$  of  $m$  species. Suppressing time arguments, the equation of motion for this species takes the form:

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

where  $s_i$  denotes biomass of the  $i^{th}$  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  $i^{th}$  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,  $\ell_i$ , 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. This equation of motion takes as its departure the familiar logistic growth equation, augmented by death and harvesting as in Norberg et al (2001), and with terms describing the  $i^{th}$  species access to system-level carrying capacity as a function of heterogeneity in the system.

There are  $m$  species in the autarkic system and, in the absence of trade, there can never be more than this number of species (i.e. speciation is assumed to occur on longer time scales). So at any one moment the number of species in the natural autarkic system has an upper bound. If the natural system is exploited, the actual number of species can rise or fall as  $e$  rises or falls with  $L$ , but cannot exceed the potential number of species  $m$  (When species numbers rise, it is assumed that seedbanks or incoming propagules produced the ‘new’ species.) The expression  $\varphi_i(m)e(L)$  determines the share of carrying capacity

accessed by the  $i^{\text{th}}$  species. This depends on degree of heterogeneity of the landscape and the number of competing species in the system.

To begin with, we consider the system without human exploitation. In this case [1] takes the form,

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

i.e. there is no exploitation of the system, 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 RHS of [2] is positive given the initial level of environmental heterogeneity,  $e_0$ . In the steady state the net growth of all living species is zero.

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,  $A^*$ :

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

Defining

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

to be the maximum potential biomass of the  $i^{\text{th}}$  species in the ‘natural’ state, we can readily see the implications of environmental heterogeneity for the existence and abundance of species in the system.

Let the  $m_0$  potential species in the system be labeled such that

$g_1 > g_2 > \dots > g_{m_0-1} > g_{m_0} > 0$ . Biologically, this tells us that species are competitively ranked by their equilibrium abundance, implying that they are  $K$ -selected ( $K$ -strategists outcompete  $r$ -strategists). A necessary though not generally sufficient condition for the existence of the  $i^{\text{th}}$  species is that  $g_i > 0$ : that it’s net growth rate is positive. A sufficient condition is that:

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

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

$$[6] \quad g_i > (1-e_0)\bar{g}_i, \bar{g}_i = \sum_{k=1}^i \frac{g_k}{\varphi([1,m])e_0 + i(1-e_0)}$$

In the case just considered,  $A^*$  is an interval  $A^* = [1,m]$ . Note that, from [3],

$$[7] \quad s_i = \frac{1}{\varphi([1,m])e_0} (g_i - (1-e_0)S)$$

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  $A^* = [1,m]$ :

$$[8] \quad \sum_{i=1}^m s_i = \frac{1}{\varphi([1,m])e_0} \left( K \left( m - \sum_{i=1}^m d_i/r_i \right) - m(1-e_0) \sum_{i=1}^m s_i \right)$$

which yields:

$$[9] \quad \sum_{i=1}^m s_i = \frac{K \left( m - \sum_{i=1}^m d_i/r_i \right)}{\varphi([1,m])e_0 + m(1-e_0)}$$

Substitution into [6] implies that

$$[10] \quad s_i = \frac{1}{\varphi([1,m])e_0} \left( g_i - (1-e_0) \left( \frac{K \left( m - \sum_{i=1}^m d_i/r_i \right)}{\varphi([1,m])e_0 + m(1-e_0)} \right) \right), i = 1, 2, \dots, m$$

For  $s_i > 0$  it follows that:

$$[11] \quad g_i > (1 - e_0) \left( \frac{K \left( m - \sum_{i=1}^m d_i / r_i \right)}{\varphi([1, m]) e_0 + m(1 - e_0)} \right), i = 1, 2, \dots, m$$

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  $i^{\text{th}}$  species is that:

$$[12] \quad g_i > (1 - e_0) K \left( \frac{i - \sum_{j=1}^i d_j / r_j}{\varphi([1, i]) e_0 + i(1 - e_0)} \right)$$

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

For the intuition behind this consider Figure 1, which graphs  $g_i, (1 - e) \bar{g}_i$  against  $i = 1, 2, \dots$ , 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,  $\{[0, i], [j, m]\}$ .

(Figure 1 about here)

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  $i^{\text{th}}$  of  $m_0$  potential species are described by [2], where species are competitively ranked by their equilibrium abundance, and where  $\phi$  is evaluated at  $\phi([1, m])$ , a necessary and sufficient condition for the existence of that species in the

steady state is that:  $g_i > (1 - e)K \left( \frac{i - \sum_{j=1}^i d_j / r_j}{\phi([1, m])e + i(1 - e)} \right) > 0$ , where  $g_i := K \left( \frac{r_i - d_i}{r_i} \right)$ .

It is straightforward to show that the number of species that exist is increasing in the degree of environmental heterogeneity. To see this, 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:

$$[13] \quad \frac{ds(i)}{dt} = s(i) \frac{r(i)}{K} \left( g(i) - \phi([1, m])e_0 s(i) - (1 - e_0)S \right), i \in [0, m_0]$$

with

$$[14] \quad S = \int s(i) di$$

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

$$[15] \quad g(i) = \varphi([1, m]) e_0 s(i) + (1 - e_0) S$$

and the least productive of the surviving species – the species with the lowest ‘ $g$ ’ value – will solve:

$$[16] \quad g(m) = (1 - e_0) S(m)$$

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

$$[17] \quad S(m) = \left( \frac{1}{\varphi([0, i]) e_0 + (1 - e_0) m} \right) \int_0^m g(i) di$$

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

$$[18] \quad S(m) = \frac{1}{m} \int_0^m g(i) di$$

and  $m$  is determined by [19]:

$$[19] \quad g(m) = \frac{(1-e_0)^m}{m} \int_0^m g(i) di$$

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

$$[20] \quad \left( g(m)m - (1-e) \int_0^m g(i) di \right) = 0$$

implying that  $\frac{d}{de} m > 0$  for all  $e > 0$ . In other words, the number of surviving species is

increasing in the degree of natural environmental heterogeneity.

### 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,

$h=H/k$ .  $H$  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. The social problem accordingly takes the following general form:

$$[22] \quad Max_L \int_{t=0}^{\infty} \{U(H, Q)\} e^{-\rho t} dt$$

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 utility function takes the specific form  $U(H^\beta Q^{1-\beta})$ ,  $U' > 0$ . 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.

To begin with, we consider the decision problem in decentralized competitive equilibrium, assuming that firms internalize all spillovers except for those associated with the impact of effort on environmental heterogeneity. Each firm exploits a particular patch and selects the level of harvest effort to maximize steady-state profits from that patch. To make the biodiversity 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:

$$[23] \quad \text{Max}_{\ell(i)} \pi = P s(i) v(i) a(i) \ell(i) - \ell(i)$$

subject to [1], 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  $i^{\text{th}}$  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  $s(i) = g(i, \ell(i)) / \phi([1, m])$  to show that a sufficient condition for  $i$  to be in the set of harvested, living species is that:

$$[24] \quad Pv(i)a(i)K(r(i) - d(i)) > r(i)\phi([1, m])$$

where  $m$  is the integral of all  $i$  that satisfy [24]. In the perfectly heterogeneous case, if

$$\frac{de}{d\ell_i} = 0, \text{ implying that exploitation of the resource has no impact on environmental}$$

heterogeneity, then the first order conditions for the problem require that:

$$[25] \quad Pv(i)s(i)a(i) - 1 = \lambda(i)s(i)a(i)$$

That is, employment in the exploitation of the  $i^{th}$  resource will increase up to the point at which the marginal net private benefit of allocation  $\ell_i$  (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:

$$[26] \quad Pv(i)s(i)a(i) - 1 = \lambda(i)s(i) \left[ a(i) + r \left( \frac{s(i)(\phi([1, m]) - 1)}{K} \right) \frac{de}{d\ell_i} \right]$$

In other words the decision-maker does take into account the impact of their behavior on environmental heterogeneity in the  $i^{th}$  patch itself,  $\left( \frac{s(i)(\phi([1, m]) - 1)}{K} \right) \frac{de}{d\ell_i}$ , but neglects the wider effects of their decision on heterogeneity at the level of system,

$\int_{j \neq i}^m \lambda(j)s(j)r(j) \left( \frac{\phi([1, m])s(j) - S}{K} \right) \frac{de}{d\ell_i} dj$ . Note that whether the impact on employment

in the resource sector is positive or negative depends on the sign of  $\frac{de}{d\ell_i}$ . Although it is

generally the case that increasing exploitation of ecosystems reduces heterogeneity

through the development of monocultures, this is not always the case.

To obtain the supply curve for aggregate harvest, we evaluate  $H^*(P) = \int_i v(i)a(i)\ell(i)s(i)di$

at  $\ell^*(i)$ . The market clearing conditions for autarky (assuming that property rights are

well-defined) are, on the demand side:

$$[27] \quad H^*(P) = \beta \cdot \frac{1}{P} = \beta \frac{L_s + \pi(P)}{P}$$

and on the supply side:

$$[28] \quad L_s - L^* = (1 - \beta)(L_s + \pi^*(P))$$

For any  $e$  in  $[0,1]$  competitive equilibrium will determine  $L^*$  and hence  $e^*$ , the latter

being the solution to  $e = f(L^*(e))$ . It follows immediately that there may be many

competitive equilibria, but that they may also be welfare-ranked.

To see the effect of exploitation on biodiversity, we define the maximum potential

biomass of the  $i^{th}$  of  $m$  harvested (discrete) species to be:

$$[29] \quad g_i := K \left( \frac{r_i - d_i - a_i \ell_i}{r_i} \right)$$

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  $g_1 > g_2 > \dots > g_m > 0$ , we can obtain by similar reasoning a sufficient condition on  $g_i$  for the existence of the  $i^{\text{th}}$  species as a function of both the biological parameters,  $r_i$  and  $d_i$  and the level and effectiveness of harvest effort,  $a_i \ell_i$ :

$$[30] \quad g_i > (1-e)K \left( \frac{i - \sum_{j=1}^i \frac{d_j + a_j \ell_j}{r_j}}{\varphi([1, m])e - i(1-e)} \right)$$

In this case, as before, we take the case where  $A$  is an interval, i.e. the case shown Figure 1(a). 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 [18]. 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 may be summarized in the following:

**Proposition 2:** 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  $i^{\text{th}}$  species in the steady state is that

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

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  $\ell_i$ :

$$[31] \quad s_i = \frac{K}{m} \left( \frac{r_i - d_i - a_i \ell_i}{r_i} \right)$$

$$[32] \quad \ell_i = \frac{1}{a_i} \left( r_i \left( 1 - \frac{ms_i}{K} \right) - d_i \right)$$

from which it is immediate that  $\ell_i$  is increasing in  $r_i$ , the natural regeneration rate of the  $i^{\text{th}}$  species and decreasing in  $a_i$ , the technical efficiency of harvest. In the extremely homogeneous case, ( $e = 0$ ), [31] and [32] are of the form:

$$[33] \quad s_i = \begin{cases} K \left( \frac{r_i - d_i - a_i \ell_i}{r_i} \right), & g(s_i) = g_m \\ 0, & g(s_i) \neq g_m \end{cases}$$

$$[36] \quad \ell_i = \begin{cases} \frac{1}{a_i} \left( r_i \left( 1 - \frac{S}{K} \right) - d_i \right), & g(s_i) = g_m \\ 0, & g(s_i) \neq g_m \end{cases}$$

If the  $i^{th}$  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  $i^{th}$  species will be equal to  $L$  if that species has the highest ‘ $g$ ’ value, and will be zero otherwise.

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

$$[35] \quad s_i = \frac{K}{m} \left( \frac{r_i - d_i}{r_i} - \frac{(1-e)S}{K} \right)$$

As the degree of environmental heterogeneity rises from the point at which the  $i^{th}$  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  $i^{th}$  species is:

$$[36] \quad \ell_i = \frac{1}{a_i} \left( r_i \left( 1 - \left( \frac{ems_i + (1-e)S}{K} \right) \right) - d_i \right)$$

As before, it is immediate that  $\ell_i$  is increasing in  $r_i$ , the natural regeneration rate of the  $i^{th}$  species and decreasing in  $a_i$ , the technical efficiency of harvest.  $\ell_i$  is either decreasing or increasing in  $e$ , as  $\frac{ems_i - S}{K}$  is positive or negative. This is summarized in proposition 3 below:

**Proposition 3:** The effect of environmental heterogeneity in an economically exploited system. 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  $i^{th}$  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  $i^{th}$  species will be increasing in the natural regeneration rate rate of the  $i^{th}$  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.

## 5. 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:

$$[37] \quad h(L; e) := \text{Max} \int_i v_i a_i s_i \ell_i di$$

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:

$$[38] \quad \text{Max}_L \{Ph(L; e) - L\}.$$

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

$$[39] \quad (H^*, Q^*) = \arg \max \{U(H, Q)\}$$

subject to

$$[40] \quad P^* H + Q = 1 + \pi(H^*)$$

and  $L^*$  is given by,

$$[41] \quad L^* = \arg \max \{P^* h(L; e^*) - L\}.$$

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

$$[42] \quad L^* = \arg \max U(h(L;0), 1-L)$$

is the same as  $L^*$  in [41]. In general, a first order necessary condition for maximizing social welfare with respect to  $L$  is:

$$[43] \quad U_H(h_L + h_e e_L) - U_Q = 0.$$

In the equilibrium defined by [39] – [41], the term  $h_e e_L$  is absent: i.e. the representative firm ignores its effect on heterogeneity. Note that the equilibrium defined by [39] – [41] 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 [23] is

$$[44] \quad \text{Max}_L \pi_S = \int_{i=0}^m (P_{S_i} v_i a_i \ell_i - \ell_i) di$$

subject to the steady state value of [1]. The first order necessary conditions for the maximization of social profit include the requirement that:

$$[45] \quad Pv_i s_i a_i - 1 = \lambda_i s_i \left[ a_i + r_i \left( \frac{\phi([1, m]) s_i - S}{K} \right) \frac{de}{d\ell_i} \right], i = 1, 2, \dots, m.$$

Note that by comparison with [26] this requires the  $i^{th}$  firm to take account of the impact that its effect on environmental heterogeneity has on all others in the industry, measured

$$\text{by: } \int_{j \neq i}^m \lambda_j s_j r_j \left( \frac{\phi([1, m]) s_j - S}{K} \right) \frac{de}{d\ell_i} dj.$$

**Proposition 4.** If property rights to natural resources are defined, but exclude rights to the heterogeneity of the system, then the competitive equilibrium will generate external costs associated suboptimal levels of heterogeneity, defined by  $U_H h_e e_{\ell_i} > 0$ . For the social profit maximization problem, the heterogeneity externality of the allocation of

$$\ell^*(i) \text{ is defined by: } \int_{j \neq i}^m \lambda_j s_j r_j \left( \frac{\phi([1, m]) s_j - S}{K} \right) \frac{de}{d\ell_i} dj.$$

To see the implications for biodiversity we suppose, without loss of generality, that there are multiple species, i.e.  $e > 0$ , but that only one is economically valuable. We denote the single valuable species  $j \in \{1, 2, \dots, m\}$  and normalize its value. We then have

$$Pv(j) = 1, Pv(i) = 0, i \neq j.$$

Consider again the problem defined by equations [44] and [1]. The first order conditions for the maximization of social profit for the unvalued species  $i$  require that:

$$[46] \quad -1 = \lambda_i s_i \left[ a_i + r_i \left( \frac{\phi([1, m]s_i - S)}{K} \right) \frac{de}{d\ell_i} \right], i \neq j$$

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

$$[45] \quad h_i^* = \ell_i \left[ -s_i r_i \left( \frac{\phi([1, m]s_i - S)}{K} \right) \frac{de}{d\ell_i} - \frac{1}{\lambda_i} \right], i \neq j.$$

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  $i \neq j$ , 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 [45]. If  $de/d\ell_i = 0$ , 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  $de/d\ell_i \neq 0$  then whether the  $i^{th}$  unvalued species is ‘harvested’ depends on the sign of  $de/d\ell_i$  and its relative abundance. If  $de/d\ell_i < 0$ , implying that

harvest effort homogenizes the system, then the optimal level of ‘harvest’ of the  $i^{th}$  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,  $de/d\ell_i > 0$  implying that harvest effort heterogenizes the system, then the optimal level of ‘harvest’ of the  $i^{th}$  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  $i^{th}$  unvalued species will fall to zero if  $s_i r_i \left( \frac{\phi([1, m]s_i - S)}{K} \right) \frac{de}{d\ell_i} \leq \frac{1}{\lambda_i}$ .

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 4.** 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  $de/d\ell_i < 0$ , optimal level of ‘harvest’ of the  $i^{th}$  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  $de/d\ell_i > 0$ , then the optimal level of ‘harvest’ of the  $i^{th}$  unvalued

species will be decreased if that species has greater than average abundance, and will be increased if it has less than average abundance.

#### **4. Discussion**

The problem addressed in this paper is the economic causes and consequences of biodiversity change across the whole landscape. While we accept that the loss of refugia through, for example, the conversion of forests for agriculture is an important driver of biodiversity loss, it is not the whole story. In this paper we attempt to model a more general process. This is a process with two main strands. One is the adoption of land uses that affect the niche structure of the ecosystem. The other is the direct ‘harvest’ of species, either to exploit the properties of desirable species or to control undesirable competitor species (‘weeds’). Both strands of the process involve market failure.

While we specify the general form of the growth functions for all potential species in the system to accommodate the role of competitive exclusion in determining species richness in environmentally heterogeneous landscapes, we do not specify the form of the function  $e(L)$ . How anthropogenic exploitation affects environmental heterogeneity is an empirical question. Although we expect intensive high-input agriculture to lead to homogeneous species-poor landscapes, the relationship between effort and environmental heterogeneity is not necessarily monotonic. At relatively low levels of both heterogeneity and effort it is possible that environmental heterogeneity is increasing in effort. We show that if exploitation of the environment leads to its homogenization, and so to a loss of

biodiversity, the socially optimal level of effort committed to the harvest of the  $i^{th}$  species will be lower than if exploitation increases environmental heterogeneity. Moreover, different species may be treated in different ways in the same system. The species populating home gardens, for example, are exploited in fundamentally different ways from the species exploited in large scale commercial agriculture, and the environmental consequences of both activities are quite different.

The impact of declining environmental heterogeneity discussed in this paper includes the effect of declining habitat noted in a number of studies (e.g. Polasky, Costello and McAusland, 2004; Barbier and Shultze, 1997). In cases where increasing effort clearly decreases environmental heterogeneity, the results in this paper are similar to those identified in such studies. However, whereas these studies associate increasing levels of effort with declining habitat, and therefore identify a monotonic negative relation between effort and biodiversity, we allow the effect of effort on biodiversity to be either positive or negative. Activities that make the environment more patchy increase the level of species diversity, activities that make the environment more homogeneous have the opposite effect. We have not considered a second important impact of the loss of biodiversity associated with homogenization: the effect on the 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 loss itself, this is beyond the scope of the paper, but it is an important dimension of the value of biodiversity externalities.

Once again, the distinction between the case in which decision-makers are free to ignore the social cost of their access to natural resources and the socially optimal case are transparent. 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.

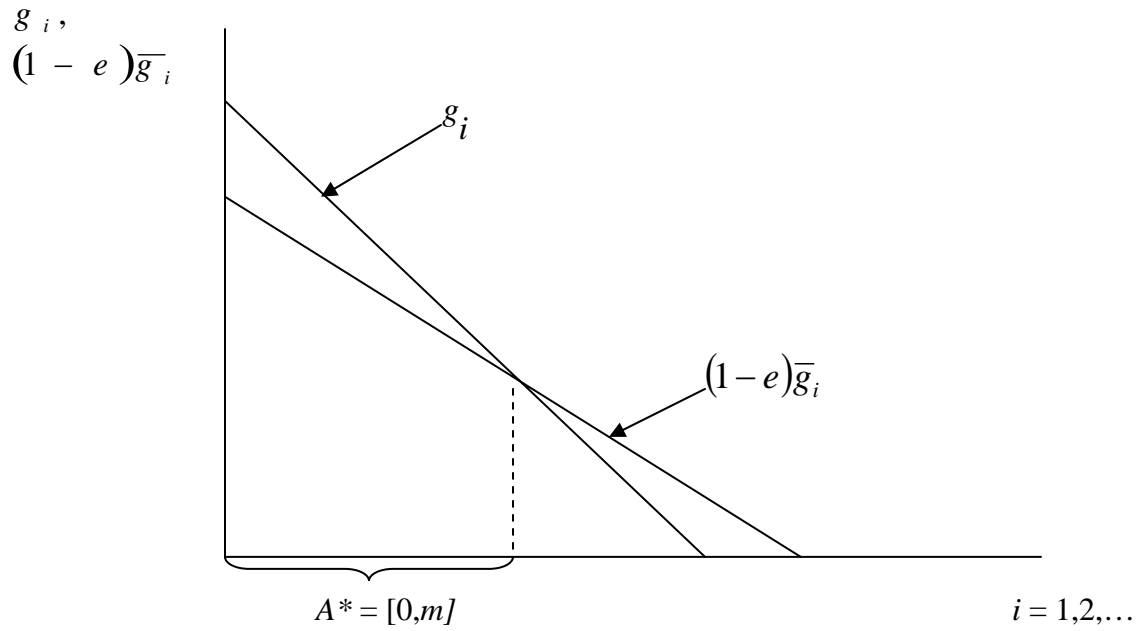
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**Figure 1** The set of existing species

(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  $[j,m]$

