BIOLOGICAL INVASIONS, BIOLOGICAL DIVERSITY AND TRADE

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Abstract

The opening of new markets or trade routes has resulted in the deliberate or accidental introduction of new species, while the growth in the volume of trade has increased the frequency of species introductions. We model the connection between landscape heterogeneity, resource extraction, the level of biodiversity, and the level of trade. We show that the invasion risks of trade reduce the socially optimal level of imports and harvesting effort. We identify a "paradox of globalization": the higher the volume of trade, the greater the number of species introductions, the higher the "optimal tariff" on trade flows.

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1. Posing the problem

The widening and deepening of international trade has had a number of environmental consequences, of which the most significant may well be the redistribution of species. Ecologists and economists alike are paying increasing attention to the problems posed by the introduction of alien species that subsequently establish and spread in the host country. The problem is not new. While HIV/AIDS, SARS and avian flu, amongst other emergent zoonotic diseases, have recently been spread through the global air transport system (Hubalek, 2003; Daszak et al, 2000), the introduction of novel pathogens has often been an incidental effect of human migrations. For example, Diamond (1997) has compellingly explored the links between disease and the expansion of historic empires, paying special attention to the role of smallpox, influenza, measles and typhus in the conquest by Europeans of the New World. The link between the movement of goods and the introduction of new pest species is also a long-standing problem. The development of the 19th century wool trade between the UK and Australia, for example, introduced a set of passenger species to the UK – the so-called 'wool species' – many of which still survive (Williamson, 1996; Jenkins, 1996). What is new is the rate at which new introductions are occurring (McNeeley, 2001).

The recent growth and development of the world trade system has accordingly strengthened a long-standing trend in the redistribution of species (McNeely, 2001; Perrings et al, 2002; Perrings et al, 2005). The opening of new markets or trade routes has resulted in the introduction of new species either as the object of trade or as the unintended consequence of trade, while the growth in the volume of trade along existing routes has increased the frequency with which introductions are repeated, and hence the probability that an introduced species will establish and spread (e.g. Enserink, 1999, Cassey et al, 2004; Semmens et al, 2004). It has been shown that the more open economies are, the more vulnerable they are to biological invasions (Dalmazzone, 2000; Vilà and Pujadas, 2001). It has also been shown that trade patterns are a good empirical predictor of invasions (Levine and d'Antonio, 2003). Many of the most damaging species introductions, such as the Zebra Mussel (*Dreissena polymorpha*) and the Asian Clam (*Corbicula fluminea*), were an external effect of transport – they were introduced through ballast water exchange in ships (Margolis, Shogren and Fischer, 2005). Other introductions have been deliberate, such as the Nile perch (*Lates niloticus*) and Tanganyika sardine (*Limnothrissa miodon*) in the African lakes (Kasulo, 2000). Aid flows have been similarly implicated in the introduction and spread of both pests and pathogens. For example, grey leaf spot (*Circosporda zeae-maydis*) was first reported in South Africa in 1988, and was thought to have been introduced in US food aid shipments of maize in during the drought years of the 1980's (Ward et al., 1999). Similarly, parthenium weed from Mexico was first detected in Ethiopia in 1988 near food-aid distribution centres implying that it had accompanied wheat grain distributed as food aid during the drought (GISP, 2004).

Why is it a problem? The direct impact of pests and pathogens aside, invasive species are important for the effect they have on the functioning of ecosystems, frequently via their capacity to displace existing species through competition or predation in particular climatic conditions. Indeed, invasive species are commonly cited as the second most important cause of biodiversity loss after habitat conversion (Wilcove et al, 1998). Introduced pathogens, predators or competitors are all directly implicated in the loss of native species over a wide range of ecosystems (Daszak and Cunningham, 1999; Williamson, 1996). The loss of native species in turn affects the capacity of ecosystems to deliver the services that underpin much economic activity (Millennium Ecosystem Assessment, 2005), and to absorb anthropogenic and environmental stresses and shocks without losing resilience (Kinzig et al, 2006; Scheffer et al, 2000; Walker et al, 2004; Walker et al, 2006). Maintenance of functional diversity, in particular, supports the provision of ecosystem services over a range of environmental conditions (e.g. Kinzig et al, 2002; Loreau et al, 2003; Naeem and Wright, 2003; Reich et al, 2004; Hooper et al, 2005).

The biodiversity effects of invasive species are especially important for economies that are heavily dependent on natural resources. The first estimate of the costs of invasive species by the Office of Technology Assessment of the US Congress was concluded in 1993 (OTA, 1993). Since that time Pimentel and colleagues (Pimentel et al, 2000, 2001, 2005) have updated the OTA estimates and extended them beyond the US. For the agricultural sector, for example, they conclude that invasive species currently cause damage costs equal to 53% of agricultural GDP in the USA, 31% in the UK and 48% in Australia, but 96%, 78% and 112% of agricultural GDP in South Africa, India and Brazil were, respectively. Since these costs represent an externality of trade, and if they are the right order of magnitude, they indicate a significant economic problem. Invasive species have also had major impacts on both ecological and hydrological systems. The South African fynbos, for example, is affected by a number of invasive pinus, hakea and acacia species. By 2000 two thirds of the fynbos area in the Western Cape had been significantly impacted. Damage costs include a reduction in biodiversity and, in particular, of species important for the international flower trade. But they also include a change in ecosystem functioning and hydrology. For example, a number of studies have shown that fynbos mountain catchments are extremely valuable in terms of their water yield, and that the value of changes in water yields exceeded expected restoration costs (Higgins et al., 1997; van Wilgen et al, 1996; van Wilgen et al, 1997; Turpie and Heydenrych, 2000; le Maitre et al, 2002).

The general environmental implications of trade growth have been addressed in a substantial literature. One strand of this literature has focused on the potential for trade to have negative consequences where property rights in environmental resources are not well-defined (Chichilnisky, 1994; Brander and Taylor, 1997, 1998) or if the pollution externalities of trade are not addressed (Copeland and Taylor, 2003; Rauscher, 1997). Most recently Taylor and Copeland (2006) have shown that the degree to which renewable environmental resources may be damaged by opening an autarkic economy to trade depends on both resource prices and management capacity. They argue that at low resource prices open access always prevails, but at high resource prices either regulated common property or optimal management options exist.

The impact of trade on biodiversity as a specific environmental problem has been evaluated from two main perspectives. One focuses on the link between specialization under trade, habitat conversion, and species loss (Barbier and Schultz, 1997; Polasky et al, 2004). Using the species-area relationship (Macarthur and Wilson, 1967), these studies calculate the impact of trade on biodiversity from the proportion of the land area that is converted to the production of primary commodities. By assumption, this area is lost as natural habitat, and no longer available to support species. The number of species that can continue to be supported in the remaining area is therefore reduced. Polasky et al (2004) extend the analysis to the two country case. The same mechanism operates in each country. They argue that if there are high levels of endemism in each country, and if consumers are concerned to protect local biodiversity, trade can reduce the level of welfare. But where species are common to both trading partners and consumers are interested in global rather than local levels of biodiversity, trade is unambiguously welfare-enhancing.

The second perspective focuses on the problem of biological invasions as an externality of trade (Perrings et al, 2000; Perrings et al, 2002; Kohn and Capen, 2002; Costello and McAusland, 2003; McAusland and Costello, 2004). One issue in this literature has been to identify the optimal policy response to the risks posed by species introductions. Costello and McAusland (2003) explored the use of tariffs on imports to reduce the damage costs from accidental introductions. While they show that import tariffs will always reduce import volumes of potentially invasive species, they find that tariffs could have adverse effects if they alter the composition of imports, which might lead to land-use changes in such a way as to make ecosystems more vulnerable to invasive species. McAusland and Costello (2004) consider the efficiency of port inspections combined with tariffs on imported goods, and find that the optimal tariff covers inspection costs plus the potential damage costs from outbreaks of pests undetected during inspections. The optimal level of tariffs in each case depends on the risk of biological invasions and the expected level of damage they cause. A second issue has been to develop mechanisms to protect the global community against the risks posed by the fact that protection of society against invasive species is generally a 'weakest-link' public good (Perrings et al, 2002).

This paper considers the welfare implications of trade-induced biological invasions that affect local biodiversity, the provision of ecosystem services and the production of primary commodities. It explores the conditions under which the move from autarky to trade, or the growth of trade, is welfare-reducing or welfare-enhancing in small open economies. The range of conditions considered includes the properties of both the society and its environment. Socially, it includes the institutional conditions under which natural resources are exploited in both open and closed economies, especially the structure of property rights in natural resources. The polar cases are open access and complete property rights. The structure of property rights in turn reflects on the effectiveness with which environmental externalities and public goods are managed. Environmentally, the range of conditions includes the degree of heterogeneity, and hence species diversity, in open and closed economies with and without exploitation of natural resources. Since the level of exploitation of natural resources is assumed to affect the heterogeneity of the ecosystem, there are feedbacks between the volume of exports, the risk of biological invasions and the level of species diversity.

We wish to capture the impact of trade-induced biological invasions through its effects on the diversity of native species. That is, biological invasions impose costs or confer benefits by changing the diversity of species relative to the autarkic position, and hence the productivity of that system. Successful invasions imply success in interspecific competition with native species for limiting resources in the host system (Wilcove et al, 1998; Williamson, 1996, 1998, 1999). While interspecific competition has been included in some ecological-economic or bioeconomic models (e.g. Brock and Xepapadeas, 2004; Tschirhart, 2002; Tilman et al, 2005), it has not been evaluated as a mechanism for the displacement of native by invasive species in the economic literature. Changes in species diversity are then assessed through the effect they have on the value of the commodities produced in the system. The relation between biodiversity, ecosystem functioning and the production of ecosystem services is complex, and is not particularly well understood. What is clear, however, is that changes in species diversity affect the production of valued goods and services through their impact on the effectiveness of functional groups (Loreau et al, 2002; Hooper et al, 2005). Although it is possible that species diversity is valued for its own sake, we are interested in the effect it has on the capacity of functional groups to support production and consumption activities (*sensu* MA, 2005).

Of the ecological explanations for the existence of species diversity, we focus in this paper on the role of environmental heterogeneity. Since this is not independent of the level of human exploitation of that system, this enables us to investigate the economic causes and consequences of biodiversity change. Environmental heterogeneity is taken to mean that the landscape comprises patches in which environmental conditions may favor distinct species. While competitive exclusion may still operate to reduce diversity in each patch, a high degree of heterogeneity between patches leads to a high level of species diversity. Since an infinite number of species can in principle be packed into a system of given heterogeneity (Kinzig et al, 1999), we consider both discrete and continuous species formulations. Taking the case of autarky first, suppressing time arguments and assuming discrete species, the equation of motion for the i^{th} of m species takes the form:

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

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, ℓ_i, and a measure of the effectiveness of 'harvest' effort, a_i. $\sum_{i=1}^{m}\ell_i = L$, $0 \le L \le 1$ 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 $0 \le e(L) \le 1$ 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, with *m* depending on *e*. In the absence of trade there can never be more than this number of species (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 this can rise or fall as *e* rises or falls with *L*, but cannot exceed *m*. When we add trade we also add to the set of possible species that can be present in the system.

The function $\phi_i(e(L), m)$ determines the share of carrying capacity accessed by the i^{th} species. This depends on degree of heterogeneity of the landscape, the number of competing species in the system, and whether the i^{th} species is an '*r*' or '*K*' strategist (*r* strategists disperse widely and grow rapidly; *K* strategists are slower-growing competitive dominants with lower dispersal). At various points we will consider the special case where all *m* species in the system access an equal share of carrying capacity.

We report a number of findings. First, in an autarkic system subject to exploitation, the steady state socially optimal level of harvest effort of the i^{th} species (share of available labor committed to the production of the primary commodity deriving from the i^{th} species, $i \neq m$) is decreasing in the degree of environmental heterogeneity, while the degree of environmental heterogeneity is itself increasing in the degree of harvest effort. Second, in open access conditions where the user cost of the i^{th} species is ignored, the privately optimal level of harvest effort will be greater than the socially optimal level of effort. Third, in an open system where trade is associated with positive risks of biological invasions, the socially optimal level of imports and the socially optimal level of harvest are both lower than where there is no risk of biological invasions. Fourth, the degree of environmental heterogeneity, and hence biodiversity, may be either higher or lower with trade, depending on the impact of changes in the socially optimal level of effort on environmental heterogeneity.

2. Modeling the problem in a closed system

To begin with, we consider the problem in a natural closed system – that is in a system that neither open to the rest of the world nor is subject to exploitation. In this case [1] takes the form,

$$[2] \qquad \frac{ds_i}{dt} = s_i\left[r_i\left(1-\left(\frac{es_i}{K/\phi_i(e,m)}+\left(\frac{(1-e)S}{K}\right)\right)\right)-d_i\right].$$

i.e. there is no exploitation of the system, and the level of heterogeneity is the natural level. The number of species in the system, m_0, is defined by the set $\{s_i\}$for which the RHS of [2] is positive for some positive value of s_i given the initial level of environmental heterogeneity, e_0. In the steady state the net growth of all living species is zero.

Let [1,i] be the interval of indices between 1 and i. Let A^* be the set of species that are alive. Further, let $\phi(A)$ be a map from sets of indices to the positive reals. We take, as our leading example of this map, $\phi(A) = |A|$ where $|A|$ is the cardinality of set A. It then follows that for the set of live species in the steady state, A^*:

[3] $$\phi(A^*)es_i + (1-e)S(A^*) = K\left(\frac{r_i - d_i}{r_i}\right)$$

Defining

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

to be the maximum potential biomass of the i^{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.

We initially consider the case where species are discrete. Let the m potential species in the system be labeled such that $g_1 > g_2 > \cdots > g_{m-1} > g_m > 0$. Biologically, this tells us that species are competitively ranked by their equilibrium abundance if no other species is present, implying that they are *K*-selected (*K*-strategists outcompete *r*-strategists). A necessary though not generally sufficient condition for the existence of the i^{th} species is that $g_i > 0$: that it's net growth rate is positive. A sufficient condition is that:

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

where the sum is over the set of species whose equilibrium abundance is not less than than of the i^{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 living species that includes less abundant/productive species than i: i.e. it holds for any set of m species, where $m > i$. That is:

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

We now define the set of living species to be A^* (see Figure 1). In the present case A^* is an interval: $A^* = [1,m]$, but as the figure shows, this need not be the case. Note that, from [3],

[7] $$s_i = \frac{1}{\phi([1,m])e}\left(g_i - (1-e)S\right)$$

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

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

which yields:

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

Substitution into [6] implies that

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

For $s_i > 0$ it follows that:

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

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^{th} species is that:

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

and *m* is the maximum value of *i* for which this condition holds.

For the intuition behind this consider Figure 1, which graphs $g_i, (1-e)\overline{g}_i$ against *i* = 1,2,…, assuming continuous species, and shows the set of points, *i*, for which $g_i > (1-e)\overline{g}_i$. 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*] (the discrete species case is considered in [6]-[12]). 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* = 1), i.e. where the system is perfectly partitioned, [12] collapses to a condition that the net growth rate of the species that is the competitive dominant in each niche is positive. In the perfectly homogeneous case (*e* = 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 a natural autarkic system. In a physically closed system in which the dynamics of the i^{th} of *m* potential (discrete) species are described by [2], and species are competitively ranked by their equilibrium abundance, and ϕ 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 $g_i := K\left(\frac{r_i - d_i}{r_i}\right)$.

For the continuous species case, suppose that the set of potential species is [0,*m*] and that, as before *g*(*i*) is decreasing in *i*. We have:

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

with

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

being the integral of s(i) over all living species. It follows that if species *i* is alive in the steady state, then

[15] $g(i) = \phi([1,m])es(i) + (1-e)S$

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

[16] $g(m) = (1-e)S(m)$

where $\phi(\cdot)$ is evaluated at the set of living species [0,*m*], and where

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

In the special case where $\phi = m$ this implies that

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

and *m* is determined by [19]:

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

m^* , the lebesgue measure of the set A = [0,m^*], is then the solution to the equation:

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

and $\frac{d}{de}m^* > 0$ for all $e > 0$.

This may be restated as the following proposition:

Proposition 2: Species heterogeneity relationship. In a closed natural system, the number of species is increasing in the degree of environmental heterogeneity.

The economic problem

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 already described, $H = \int_0^m s(i)a(i)\ell(i)di$, 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 (autarkic) 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:

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

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 $U\left(H^{\beta}Q^{1-\beta}\right),\ U' > 0$. 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.

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

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

where *m* is the integral of all *i* that satisfy [24]. In the perfectly heterogeneous case, if $\frac{de}{d\ell_i} = 0$, implying that exploitation of the resource has no impact on environmental heterogeneity, then the first order conditions for the problem require that:

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

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 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:

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

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, 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] $$H^*(P) = \beta.\frac{1}{P} = \beta\frac{L_s + \pi(P)}{P}$$

and on the supply side:

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

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 under autarky to be:

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

we expect to be able to define a similar cut-off rule for any allocation of harvest effort. Ranking $\{g_i^A\}$, as before, such that $g_1^A > g_2^A > \cdots > g_m^A > 0$, we can obtain by similar reasoning a sufficient condition on g_i^A for the existence of the i^{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] $$g_i^A > (1-e)K\left(\frac{i-\sum_{j=1}^{i}\frac{d_i + a_i\ell}{r_i}}{\phi([1,m])e - i(1-e)}\right)$$

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 *g** 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 species corresponding to the autarkic system with maximum exploitation. This may be summarized in the following:

Proposition 3: Species existence in an autarkic economy. In a closed 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^{th} species in the steady state is that $g_i^A > (1-e)K\left(\frac{i-\sum_{j=1}^{i}\frac{d_i + a_i\ell}{r_i}}{\phi([1,m])e - i(1-e)}\right) > 0$, where

$$g_i^A := K\left(\frac{r_i - d_i - a_i\ell_i}{r_i}\right).$$

The effect of environmental heterogeneity

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. First consider the implications for biomass of the i^{th} species at different levels of environmental heterogeneity. Taking the case of extreme heterogeneity ($e = 1$) in the autarkic system with no exploitation ($L = 0$), we have that::

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

The steady state stock of the i^{th} species will converge to the maximum potential biomass of that species in extreme heterogeneity, i.e. when each of the *m* species is the competitive dominant species in some patch within the system. At the other extreme, when the unexploited ($L = 0$) autarkic system is characterized by extreme homogeneity ($e = 0$), we have:

[32] $$s_i = \begin{cases} K\left(\frac{r_i - d_i}{r_i}\right), g^A(s_i) = g_m^A \\ 0, g^A(s_i) \neq g_m^A \end{cases}$$

If the i^{th} species has the highest 'g' value, or net regeneration potential, it will converge to the maximum potential biomass of the competitive dominant, otherwise it will be driven to local extinction.

If an extremely heterogeneous autarkic system is exploited, ($e = 1$, $L > 0$), we have the following conditions on s_i and ℓ_i:

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

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

from which it is immediate that ℓ_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. In the extremely homogeneous case, ($e = 0$), [33] and [34] are of the form:

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

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

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 $0 < e < 1$. In the autarkic unexploited system:

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

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.

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:

$$[38] \qquad \ell_i = \frac{1}{a_i}\left(r_i \left(1 - \left(\frac{ems_i + (1-e)S}{K} \right) \right) - d_i \right)$$

As before, it is immediate that ℓ_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. ℓ_i is either decreasing or increasing in *e*, as $\frac{ems_i - S}{K}$ is positive or negative. This is summarized in proposition 4 below:

Proposition 4: The effect of heterogeneity in autarkic economy. 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.

The social decision problem in the autarkic economy

The social decision-problem in the autarkic system reflects the fact that while *e* depends on the effort committed to resource-based production, the representative firm may not take into account the effect of their decisions on heterogeneity in the general system. For a given value of *e* in [0,1] we define the harvest function:

[39] $$h(L;e) := Max\int_i v_i a_i s_i \ell_i \, di$$

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:

[40] $$Max_L \{Ph(L;e) - L\}.$$

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

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

subject to

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

and *L** is given by,

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

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

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

is the same as L^* in [43]. In general, a first order necessary condition for maximizing social welfare with respect to L is:

[45] $U_H(h_L + h_e e_L) - U_Q = 0$.

In the equilibrium defined by [41] – [43], the term $h_e e_L$ is absent: i.e. the representative firm ignores its effect on heterogeneity. Note that the equilibrium defined by [41] – [43] 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

[46] $Max_L \pi_S = \int_{i=0}^{m} (P s_i v_i a_i \ell_i - \ell_i) di$

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

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

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. This is measured 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 5. *e*-externalities in the autarkic system. If property rights to natural resources are defined, but exclude rights to the heterogeneity of the system, then the competitive equilibrium will generate costs defined by $U_H h_e e_{\ell_i} > 0$. For the social profit maximization problem, the heterogeneity externality of the allocation of $\ell^*(i)$ is defined by: $\int_{j \neq i}^{m} \lambda_j s_j r_j \left(\frac{\phi([1,m])s_j - S}{K} \right) \frac{de}{d\ell_i} dj$.

The 'simplification' of the autarkic system

To see the implications for the biodiversity in the autarkic economy 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 $j \in \{1,2,\ldots, m\}$and normalize its value. We then have $Pv(j)=1, Pv(i)=0, i \neq j$.

Consider again the problem defined by equations [46] and [1]. The first order conditions for the maximization of social profit for the unvalued species *i* require that:

$$[48] \qquad -1 = \lambda_i s_i \left[a_i + r_i \left(\frac{\phi([1,m])s_i - S}{K} \right) \frac{de}{d\ell_i} \right], i \neq j$$

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

$$[47] \qquad h_i{}^* = \ell_i \left[- s_i r_i \left(\frac{\phi([1,m])s_i - S}{K} \right) \frac{de}{d\ell_i} - \frac{1}{\lambda_i} \right], i \neq j \, .$$

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 [47]. 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 increased if that species has greater than average abundance, and will be reduced if it has less than average abundance. If, $de/d\ell_i > 0$ 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 5. Homogenization and the harvest of unvalued species in the autarkic system. If only some species are positively valued, 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 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.

3. Trade and invasive species

The opening of an autarkic economy to trade also opens it to a new set of species. We suppose that there are n species in the general system and that $n \geq m$: i.e. that the number of species in the global system is at least as great as the number of species in the autarkic system alone. The composition and volume of trade determines the rate at which species are dispersed within the global system. This includes both intentional and unintentional introductions. Intentional introductions include, for example, agricultural crops and livestock strains, biocontrol agents and patented genetic material. Unintentional introductions include the accidental dispersion of species as externalities of trade, transport and travel. We define the steady-state number of post-trade species in the home/host system as $m^* = m^*(m,M,e^*)$, where m is the number of pre-trade species in the system, M is the volume of trade and e^* is post-trade environmental heterogeneity. It follows that $m^* \leq n$, but we allow m^* to be either greater than, equal to or less than m: i.e. the number of species in the home system after trade increases may rise or fall relative to the pre-trade position depending on whether introduced species competitively exclude existing species.

In all cases, the intrinsic growth (*r*), death (*d*) and harvest susceptibility (*a*) rates of introduced species are those that apply in the host (rather than the source) system. Many invasive species succeed because their competitiveness in the host system is greater than in the system of origin, either because of differences in general environmental conditions (temperature, precipitation, soil type, latitude, altitude and so on) or more likely because of differences in the mix of predators and pathogens. More particularly, many introduced species become invasive because the absence of local pests and predators reduces their death rates relative to local competitor species.

For discrete species, the social objective in an open system takes the general form:

[48] $$Max_{L,M} \int_{t=0}^{\infty} \{U((H - X),(1 - L) + M)\} e^{-\rho t} dt$$

where $H = \sum_{i=1}^{n} v_i a_i s_i \ell_i$; X denotes aggregate exports of harvested stocks, S; and M denotes aggregate imports of manufactures. The level of exports being determined from the trade balance $M - P^*X = 0$, in which P^* denotes the world index price of harvested biomass implying that P^*v_i is the world 'price' of the i^{th} resource.

Without loss of generality we take the case where the price of manufactures under autarky coincides with the world price of manufactures, implying that the specialization induced by trade depends solely on the relative world and domestic price of natural resources. Once again we focus on the $\rho = 0$ case, and look for the solution to the static problem:

[49] $$Max_{L,M}\{U((H-X),(1-L)+M)\}$$

subject to:

[50] $$0 = s_i\left[r_i\left(1-\left(\frac{e*\phi([1,m*])s_i+(1-e(L)).S}{K}\right)\right)-d_i-a_i\ell_i\right] \quad i = 1,2,\ldots,m*$$

in which $m*$ includes trade-induced species introductions. If trade related species introductions occur in a biologically depauperate system, the likelihood that they will encounter predators or pathogens system is low, and hence the likelihood that they will establish and spread is high. Put another way, the likelihood that the 'g' value of introduced species is high relative to native species is a decreasing function of m. The increase or decrease of biomass of the i^{th} species as a direct effect of trade has immediate implications for the steady state biomass and harvest effort associated with that species, which we note in passing. As before, this is sensitive to the level of environmental heterogeneity in the system. In the case where $\phi([1,m*]) = m*$, and for different levels of environmental heterogeneity, the steady state biomass of the i^{th} species is a root of:

[51] $$0 = s_iK(r_i-d_i-a_i\ell_i)-r_im*s_i^2;\ e* = 1$$

[52] $$0 = s_i\left[K\left(r_i - d - a_i\ell_i\right) - r_i\left(1 - e^*\right)S\right] - r_i e^* m^* s_i^{\,2};\ \ 0 < e^* < 1$$

and for $e^* = 0$ is found from

[53] $$0 = \begin{matrix} s_i K\left(r_i - d_i - a_i\ell_i\right) - r_i s_i^{\,2}, g(s_i) = g_1 \\ 0, g(s_i) \neq g_1 \end{matrix};\ \ e^* = 0$$

while the steady state level of harvest effort satisfies:

[54] $$\ell_i = \frac{1}{a_i}\left(r_i\left(1 - \frac{m^* s_i}{K}\right) - d_i\right);\ \ e^* = 1$$

[55] $$\ell_i = \begin{cases} \frac{1}{a_i}\left(r_i\left(1 - \frac{S}{K}\right) - d_i\right), g(s_i) = g_1 \\ 0, g(s_i) \neq g_1 \end{cases};\ \ e^* = 0$$

[56] $$\ell_i = \frac{1}{a_i}\left(r_i\left(1 - \left(\frac{e^* m^* s_i + \left(1 - e^*\right)S}{K}\right)\right) - d_i\right);\ \ 0 < e^* < 1$$

So the direct impact of trade on steady state levels of biomass and harvest effort associated with the i^{th} species existing depends on whether trade increases or decreases biomass of that species through the effect it has on the share of carrying capacity – the impact of competition between species. If trade-related species introductions change the number of species in the home/host system from m to m^*, then the steady state values of the i^{th} species:

[57] $$s_i = \frac{1}{\phi([1,m])} g_i \gtrless s_i = \frac{1}{\phi([1,m^*])} g_i$$

as $m \gtrless m^*$ through the competition effect. Suppose that g_i is the dominant pre-trade species, and that trade at the level of M brings a draw of $g_1, \cdots, g_n$, then g_i is dominated if Max{g_k, k =1,…,n}>g_i. The impact on welfare then depends on the relative value of s_i and s_k. In the extreme case, if s_i is a monoculture and labor has been expended to 'weed out' other species in the pre-trade economy, and if s_k is an economically valueless competitor, then the loss associated with the draw $g_1, \cdots, g_n$ could be very large. This is summarized below:

Proposition 7. Impact of trade on species richness and abundance. The introduction of species through trade affects species richness (m^*) and abundance through the impact on interspecific competition (g_i^* $i \in \{1,\ldots,m^*\}$). If trade introduces species with 'g' values that dominate the 'g' values of the i^{th} existing species, it will reduce the likelihood that species will survive in the steady state.

As in Brander and Taylor (1997), the response to the opening of the economy to trade depends on (a) the world price of the primary commodity relative to the domestic price, and (b) the nature of property rights in the resource base. We take our two cases in turn.

First, if the property rights regime is such that firms ignore the shadow value (the user cost) of ecological resources, and if the i^{th} species is grown as a monoculture, then if P^* <1 implying that the world index price of natural resources is less than the domestic price, then labor will be reallocated from the harvest of natural resources to the production of manufactured goods. If $P^* > 1$, the world index price of natural resources is greater than the domestic price, then the economy will specialize in the harvest of natural resources. If $P^* = 1$ the opening of the economy will have indeterminate effects.

Second, if there are well-defined property rights to the resource base, so that decision-makers take the user cost of the resource base into account, then the response to the opening of the economy will be as follows: for a given marginal rate of substitution U_H/U_Q, if $P^* v_i a_i s_i < (Pv_i - \lambda_i) a_i s_i$, implying that the world price of the i^{th} species is less than the domestic price net of user costs, then labor will be reallocated to the manufacturing sector. If $P^* v_i a_i s_i > (Pv_i - \lambda_i) a_i s_i$, the world price is greater than the domestic price net of user costs, then labor will be reallocated to production of the i^{th} species. If $P^* v_i a_i s_i = (Pv_i - \lambda_i) a_i s_i$, the opening of the economy will have indeterminate effects.

The impact of changes in harvesting effort on biodiversity depends on the relation between the 'g' values of species and L. Denoting the maximum potential biomass of the i^{th} harvested resource under trade

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

and assuming that $g_1^* > g_2^* > \cdots > g_{m^*}^* 0$, if $e(L)$ is a monotonically decreasing function of L, any increase in the level of harvesting effort will raise the cut-off $g^*(e)$, and so reduce the number of species in the system at the steady state. If the shadow value of species is positive, but is ignored under prevailing property rights regimes, this would lead to higher levels of harvesting effort – other things being equal. So if the efficiency of harvesting effort is the same in both cases, well-defined property rights should be associated with more species diversity.

There are, however, two qualifications to this. First, if $e(L)$ is non-monotonic, the impact will depend on the value of L under autarky (the initial value). Second, if a_i is sensitive to the form of property rights (if the technologies developed under well-defined property rights regimes are technically more efficient than those in open access regimes), the steady state level of species diversity may fall to allow specialization in species with a high '*g*' value. So even without the invasive species risks of trade, the opening of an autarkic system can have a substantial impact on biodiversity and productivity through the effect it has on optimal harvest effort, given the degree of environmental heterogeneity in the natural system and given the level of harvesting effort under autarky. We summarize this in the following proposition:

Proposition 8. Impact of trade on harvesting rate and species richness. If the world price of the *i*^th^ species is greater than the domestic price net of user costs, $P^* v_i a_i s_i > (Pv_i - \lambda_i) a_i s_i$, the home country will commit additional resources to harvesting that species under all property rights regimes. This will raise the cut-off $g^*(e)$, and so potentially reduce the number of species in the system at the steady state. If the property rights regime is such that the harvester ignores the user cost of the i^{th} species, λ_i, the resources committed to harvest will be greater than if the user cost is taken into account, and will potentially reduce species richness in the steady state.

We now consider the effect of trade on the risk of invasive species, and the implications this has for biodiversity and the value of output. The introduction of alien species is taken to be an increasing function of the volume of trade, while the likelihood that an introduced species will competitively exclude native species depends on a range of factors comprising the invasiveness of the species (a property of species traits, including plasticity), the vulnerability of the host system to invasion just mentioned (a property of disturbance, including fragmentation and species loss), and the bioclimatic similarity between the source and host countries. We take the probability of a successful biological invasion to be increasing in the volume of imports.

Each unit of imports, *M*, from some country takes a sample from the community of potentially invasive species in that country. Although invasive species may, in principle, confer benefits as well as imposing costs, the definition of invasive species in the Convention on Biological Diversity includes only harmful species. Hence we take only species whose value is less than or equal to zero. Since the dominant mechanism by which an introduced species becomes invasive is competitive exclusion, the probability that trade will be lead to an invasive species is the probability that a species will be introduced whose '*g*' value dominates that of at least some living native species.

We consider the effect of trade-related invasive species risks on both the level of harvest effort. Consider the environmentally homogeneous, $e(L) = 0$, case first. This includes both the case of a naturally homogeneous ecosystem in which a single competitive dominant species survives and the case of a landscape molded by people to allow a monoculture of the most highly valued species. Denote the dominant species by $g_1^*(e)$. We measure the volume of trade, *M*, in units of "samples", where one unit of trade is one sample. In *M* samples we only need one sample to exceed $g_1^*(e)$to be successful. In order to compute the probability of this happening, letting $g := g_1^*(e=0)$ to lighten the notation, we need $\Pr\{X_i \le g; i = 1,2,...,M\}$, where *M* is treated as an integer. It is assumed that the X_i are independent. It might be helpful to think of each unit of trade being a container representing one sample of the species in the source country, X_i, i = 1,2,...,*M*. The probability that one invasion attempt succeeds in *M* containers is equal to one minus the probability that all *M* containers fail to bring an invasive: i.e.

[59] $$F(g := \Pr\{X_i \le g\})\Pr\{I / M\} = 1 - F(g)^M$$

It follows that as *M* goes to infinity the probability of a successful invasion goes to one.

We study a very stark case to get some understanding of the biodiversity tradeoff that an autarkic economy faces when being opened to trade: the autarkic system comprises a monoculture ($e = 0$). In this polar case, if a species successfully invades it displaces the currently dominant species. This helps to make the implications of opening the system to trade quite transparent. Let us take a problem where species 'relax' to their steady state abundances rapidly relative to the time scale of trade flows:

[60] $$Max_{L,X,M_I} \left(F^M\right)U\left(\left(H - X\right), 1 - L + M\right) + \left(1 - F^M\right)U\left(M_I, 1 - X_I\right)$$

where $H(L) = v_1 s_1 a_1 L$ defines aggregate harvest, and M_I is the volume of imports that yields an invasive species. This is subject to the condition for zero net growth of the pre-trade competitive dominant species in the case $e = 0$:

[61] $$s_1 = \frac{K}{r_1}\left[r_1 - d_1 - a_1 L\right]$$

and the trade balance requirements with and without a successful biological invasion:

[62] $P * X = M$ if an invasion does not occur

[63] $P* M_I = X_I$ if an invasion occurs

Substituting [61] into [60] and defining: $U_I := \max U\left(M_I, 1 - X_I\right)$ and $U := \max U\left(\left(H - X\right), 1 - L + M\right)$, where $U_I < U$, the problem now takes the form:

[64] $Max_{L,M_I} \left(F^M\right) U\left(\left(H - X\right), 1 - L + M\right) + \left(1 - F^M\right) U_I$

Note that $H = v_1 a_1 \frac{K}{r_1}\left[r_1 - d_1 - a_1 L\right] L$ is concave. We show that $L^*\left(F = 1\right) > L^*\left(F < 1\right)$: i.e. that the introduction of a positive invasive species risk reduces the socially optimal level of harvest, and that this is true for any concave harvest function, *H*(*L*). The first order necessary conditions for the optimization of [64] require, with respect to *L*:

[65] $U_H H'\left(L\right) = U_Q$

and with respect to *M*:

[66] $\ln F\left(U - U_I\right) - U_H \frac{1}{P^*} + U_Q = 0$

where *U* and U_I are evaluated at the optimum. Now insert [65] into [66] and rewrite [66] as:

[67] $\ln F\left(U - U_I\right) - U_H\left[\frac{1}{P^*} - H'\left(L\right)\right] = 0$

implying that

[68] $$H'(L) = \frac{1}{P^*} - \frac{\ln F(U - U_I)}{U_H}$$

i.e. that $H'(L)$ is a decreasing function of F, and since $H''(L) < 0$ due to the concavity of $H(L)$, we have that:

$$L^*(F = 1) > L^*(F < 1)$$

We summarize this in Proposition 9 below.

Proposition 9. Invasive species risks of trade and the rate of harvest effort. If there is a positive invasion risk associated with imports, $F^M < 1$, and if the system is perfectly homogeneous, then the socially optimal level of harvest effort is strictly less than the socially optimal level of harvest effort where there is zero invasion risk, $F^M = 1$, and tends to zero as the invasion risk tends to one.

Now consider the impact of invasive species risks on imports. We take the problem described by equations [49] and [50], and recall that the number of species in the open economy is a function of import volumes, i.e. that $m^* = m^*(m,M,e^*)$. We relax the assumption that the system is perfectly homogeneous so that $0 < e \leq 1$ and more than one species coexists. Substituting the trade balance requirements and the dependence of species numbers on import volumes into [49] and [50] yields the problem:

[69] $$Max_M \{U((H - M / P^*),(1 - L) + M)\}$$

subject to:

[70] $$0 = s_i\left[r_i\left(1-\left(\frac{e*\phi([1,m*(M)])s_i+(1-e(L)).S}{K}\right)\right)-d_i\ -a_i\ell_i\right]\ i = 1,2,\ldots,m*$$

The first order necessary conditions for the optimization of [69] with respect to imports require that :

[71] $$-\frac{U_H}{P*}+U_Q-\sum_{i=1}^{m*}\frac{\lambda_i s_i^2 r_i e*}{K}\frac{d\phi}{dM}=0$$

which we can write in the form

[72] $$\frac{U_H}{U_Q}=P*\left[1-\frac{D}{U_Q}\frac{d\phi}{dM}\right]$$

where $D=\sum_{i=1}^{m*}\frac{\lambda_i s_i^2 r_i e*}{K}$. The term $-P*\frac{D}{U_Q}\frac{d\phi}{dM}$ measures the indirect effect of trade on biodiversity in the open economy, and $P*\left[1-\frac{D}{U_Q}\frac{d\phi}{dM}\right]$ defines the ratio of resource to (world) manufactured goods prices taking the environmental impact of imports into account. Substituting for *P** from [62] yields the socially optimal volume of imports corresponding to this price ratio:

[73] $$M^* = \frac{U_H}{U_Q}\frac{X}{\left[1 - \frac{D}{U_Q}\frac{d\phi}{dM}\right]}$$

In the absence of price corrections, the volume of imports will be given by $M = \frac{U_H}{U_Q}X$.

This will be below the socially optimal level of imports, *M**, if $d\phi/dM > 0$ and above the socially optimal level of imports if $d\phi/dM < 0$. It follows that the socially optimal level of imports will be below the 'free trade' volume of imports wherever trade-induced species introductions reduce biodiversity. In this case, i.e. where $d\phi/dM < 0$, imposition of a tariff such that the post-tariff price ratio is

[74] $$P^T = P^*\left[1 - \frac{D}{U_Q}\frac{d\phi}{dM}\right]$$

will assure the socially optimal volume of imports.

Figure 2 about here

Figure 2 illustrates this case. The autarkic production possibilities frontier is denoted PPF^A. To simplify things the figure assumes that preferences are such that people choose to consume a constant quantity of the natural resource. At the autarkic price of the natural resource, *P*, and preferences $U(H,Q)$, this quantity is H_0, and the corresponding quantity of the manufactured good is Q_0. If the economy is opened up to trade at the international resource price P^*, consumption of domestic and imported manufactured goods rises to Q_1 (trade triangle a,b,c). Since the impact of trade-related species introductions negatively affects ecosystem productivity, the production possibilities frontier moves to PPF^T with maxH^T < maxH^A, and consumption of Q falls to Q_2 (trade triangle d,e,f). Introduction of an optimal tariff on imports, yielding a price ratio P^T further reduces imports, and consumption of manufactured goods falls to Q_3 (trade triangle g,h,j). In the case illustrated in Figure 2 $Q_3 < Q_{0,}$ implying that trade is 'immiserizing', but in fact all outcomes are possible. Hence we have what we may call the paradox of globalization, summarized in proposition 10.

Proposition 10. The paradox of globalization. Trade liberalization that increases import volumes, M^*, also increases the rate at which new species are introduced, establish and become invasive. If this affects ecosystem productivity through its impact on biodiversity, m^*, it imposes a social cost measured by the reduction in the value of harvest. In this case, the higher the volume of imports, the higher is the optimal tariff.

4. Discussion

Our primary focus in this paper has been the impact of economic activity on environmental heterogeneity, biodiversity and ecosystem productivity, and the effects of opening the economy to trade. In this final section, we discuss the general implications of our findings for invasive species policy. The most common instruments discussed in the economic literature on invasive species are tariffs and inspections. As one would expect, an increase in tariffs generally reduces the volume of imports and hence the rate of introductions. However, where this stimulates domestic activity, particularly in agriculture, (Costello and MacAusland, 2003) find that it may increase the cost of biological invasions invasions. That is, there are both direct and indirect effects. In our case there are also direct and indirect effects. Increasing tariffs reduce the volume of imports, and hence species introductions. However, the indirect effects are different, and work through the effect of trade on (a) ecological heterogeneity and (b) species richness. The effect of trade on both ecological heterogeneity, e^*, and species richness, m^*, can go in either direction. In general we would expect that increasing activity homogenizes the system and so reduces biodiversity. However, other outcomes are possible.

The choice between tariffs and inspections has also been evaluated in the literature. Where the expected damage of unintercepted introductions is high, inspections dominate tariffs. Where the infection rate is high, tariffs dominate inspections (McAusland and Costello 2004). We do not formally consider inspections and exclusions as a policy instrument, but it is intuitive that if the invasive species risk associated with a given volume of trade imports can be changed through expenditure on inspections, it will be optimal to increase inspection expenditures up to the point where the marginal cost of inspection is equal to the marginal damage avoided by exclusion of imports inspected and found to be infected.

In this paper we have two main sources of externality: the introduction of new species in trade/aid shipments and the effect of harvest on environmental heterogeneity and hence biodiversity. Tariffs and inspections/exclusions address the first of these by reducing, respectively, the volume of trade and the probability that trade will introduce new species. As in Costello and McAusland (2003), and McAusland and Costello (2004), trade growth increases species introductions and hence the risk of biological invasions. Moreover, consistent with McAusland and Costello (2004) tariffs equivalent to the shadow value of the change in trade-related invasion risks can reduce the level of imports to the socially optimal level. However, a second result from Costello and McAusland (2003) raises more interesting questions. They argue that contrary to the received view, freer trade may reduce the damage due to exotic species if it leads to changes in production that make a host country less vulnerable. For example, they claim that if freer trade leads to a reallocation of resources from agriculture to manufacturing, it will reduce the potential damage from agricultural pests and pathogens. This is because even if damage to other parts of the ecosystem grows as a result of the increase in invasion risks associated with freer trade, the value of that damage may be less than the value of damage to agriculture. The results in this paper support that finding in the following restricted sense. If changes in relative prices induce a reallocation of effort from production of the primary commodity to manufactures, the possible future displacement of existing species by exotics through competitive exclusion or predation will have no effect on social well-being and so no consequences for the allocation of resources.

However, wherever it is optimal to commit some share of available labor to the production of the primary commodity ($L > 0$), then an increase in trade – however it is induced – will increase invasion risks and reduce the optimal level of harvest effort. The implications of this for (a) biodiversity and (b) the likelihood of successful invasions will then depend on the effect of a change in the level of harvest effort on environmental heterogeneity, and hence on biodiversity. This in turn depends on the form of the function $e = e(L)$. While the mechanism involved is quite different, the result matches the ambiguity of the result reported by Costello and McAusland (2003). In this case it is not the product mix that drives the result, but the effect of harvest effort on the level of environmental heterogeneity and hence biodiversity. In cases where the level of harvest effort is low, an increase in effort may have a positive effect by increasing the patchiness or heterogeneity of the environment.

In general, we expect the net effect of the two sources of externality - the risk of the introduction of invasive species and the biodiversity-effects of changes in the level of exploitation of the environment – to be negative. However, both forces are at play. If exploitation of the environment is leading 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 is similar to the effect of 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.

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. Excluding the shadow value of the exploited species from calculation changes the level of harvest activity and imports generally leads private decision-makers to opt for higher levels of both than in the socially optimal case. The ambiguity of the effect of effort on environmental heterogeneity qualifies this remark, but since open access means that decision-makers ignore both sources of externality we would ordinarily expect open access to result in higher levels of effort than are socially optimal. The bottom line, though, is that the invasive species externalities of trade create what we have called the 'paradox of globalization': the higher the level of trade in natural resources, the greater the homogenization of the system, the more vulnerable is it to biological invasions, the higher the potential cost of those invasions and the higher is the optimal tariff.

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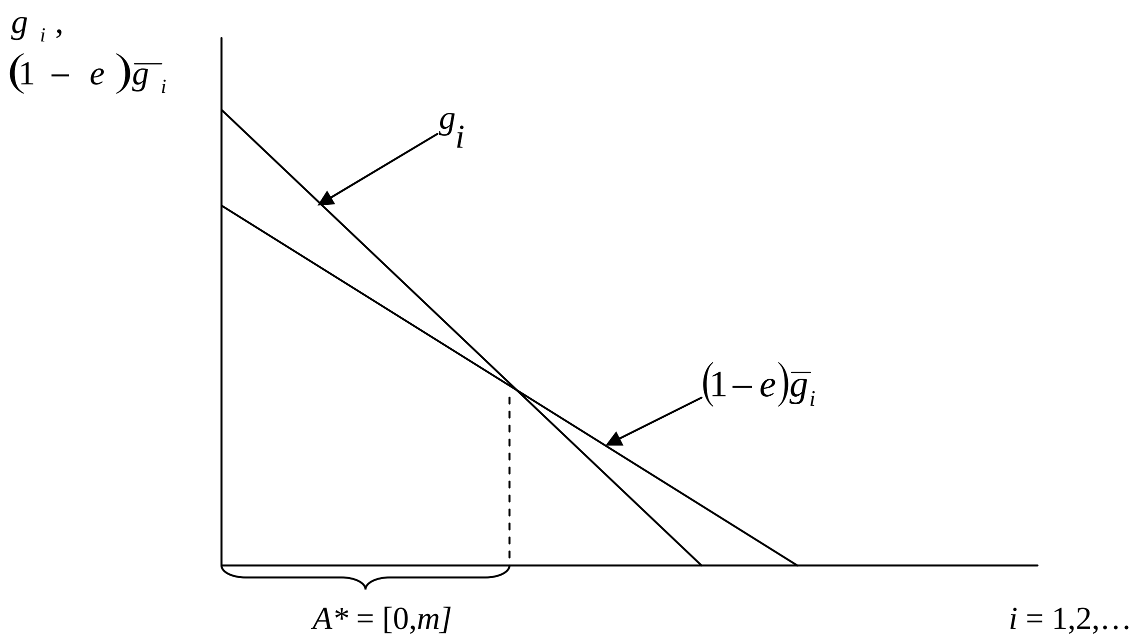
Figure 1 The set of existing species

(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*]**

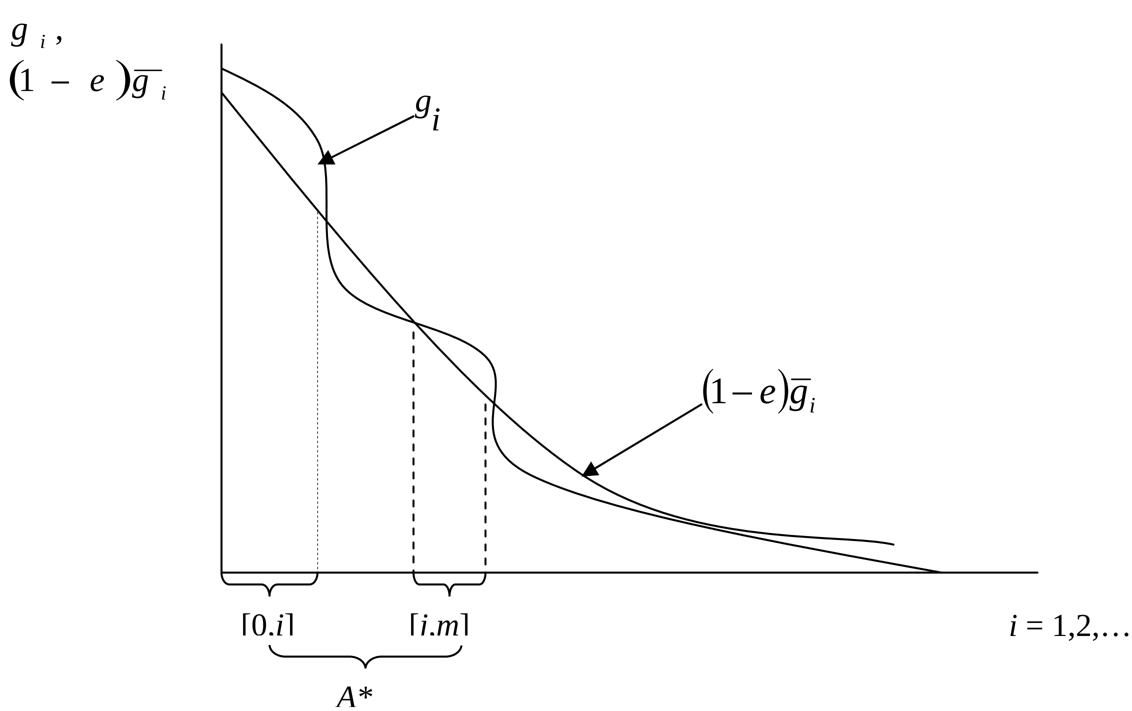


Figure 2 Impacts of trade-induced invasive species