

BIOLOGICAL INVASIONS IN AQUATIC SYSTEMS: THE ECONOMIC PROBLEM

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ABSTRACT

Biological invasions are recognised to be a problem of growing severity. Encompassing new human pathogens, weeds or pests in terrestrial systems, and dominant alien species in freshwater or marine aquatic systems, they are the second most important proximate cause of biodiversity loss worldwide. They also impose significant costs in terms of forgone output or costs of control in every major system except for pelagic marine systems. Coastal, coral reef, and estuarine systems are among the most vulnerable. This paper considers the economics of the problem in the context of a simple generic model of invasions and invasion control. It shows that the dynamical characteristics of the problem are driven not only by population dynamics but by the costs and benefits of ‘native’ and alien ‘invasive’ species.

Most ecosystem types—terrestrial, freshwater, and marine—have been affected to a greater or lesser extent by biological invasions (Parker et al., 1999; Williamson, 1998, 2000). One of the best-known examples of a marine invasive species is in the Black Sea, where the establishment of the comb jelly *Mnemiopsis leidyi* has transformed the ecology of the system. The zebra mussel, *Dreissena polymorpha*, has had similar effects in freshwater systems in both Europe and America. It is now thought to have invaded about one-third of all freshwater aquatic environments in the United States (Williamson, 1996). These are only the most familiar examples, however, of a phenomenon that is rapidly growing with the widening and deepening of international markets in goods and services. The most severe costs of invasions may be due to their impact on local and global biodiversity (Glowka et al., 1994; Czech and Krausman, 1997; Wilcove et al., 1998), but they also impose significant costs in forgone output or defensive expenditure in a wide range of activities. Knowler (1999) and Knowler and Barbier (2000) have examined the role of *Mnemiopsis* in changing the cost of fishing effort in the Black Sea. Attempts have also been made to estimate the costs imposed by the green crab, *Carcinus maenas*, on the North Pacific Ocean fisheries (Cohen et al., 1995) and by the zebra mussel on industrial plants in both Europe and the USA (Khalanski, 1997).

What makes the problem particularly interesting from an economic perspective is that it is usually an external effect of market transactions, and its control is a public good of a particularly intractable sort. The wider impacts of invasive species are ignored by those responsible for their introduction, establishment, or spread. These impacts may be localized and of relatively short duration, but they may also be widespread and have periodic, chronic, or potentially irreversible effects. Ecosystems vary in their natural susceptibility to invasion. Although pelagic marine systems appear to be least susceptible, mixed island systems and lake, river, and near-shore marine systems are especially vulnerable (Heywood, 1995). Of course, the probability of establishment of intentionally introduced species is higher than that of unintentionally introduced species simply because the former have been selected for their ability to survive in the environment where they are introduced (Smith et al., 1999) and may be introduced repeatedly (Enserink, 1999), but the probab-

ity of both establishment and spread also depends on ways in which the environment is altered by human behavior.

The best-understood source of marine invasions is the transfer of species in water ballast (Carlton and Geller, 1993), but marine invasions are frequently induced by changes in environmental conditions due to the effects of pollution. Among the most striking information reported by the Independent World Commission on the Oceans (1998) is that 77% of global marine pollution is now thought to derive from land-based sources either directly or through the atmosphere. Changing patterns of land use in watersheds have had major effects on flood regimes worldwide by changing in-stream flows. In some areas, increasing surface run-off due to deforestation has boosted the frequency and severity of floods. In others, increasing rates of water abstraction have had the opposite effect. Both pollution and changes in stream flows have altered estuarine and coastal ecosystems in ways that make them more susceptible to invasion.

Many marine systems are characterized by multiple locally stable states. The characteristics and the economic value of such states may be very different. For example, sewage and fertilizer run-off has caused coral reefs with high diversity of fishes and other aquatic organisms to be flipped into a low-value state dominated by algae and otherwise low levels of aquatic diversity (Roberts, 1995). It turns out that biological invasions are frequently induced by changes of this sort. Terrestrial pollution is, for example, implicated in the susceptibility of the Black Sea to invasion by *Mnemiopsis* (Knowler and Barbier, 2000).

Here, I consider biological invasions and their control as an economic problem. I identify the factors that determine whether a system affected by an invasion will experience a change of state. The control of biological invasions involves measures that increase or reduce the resilience of the system in either the 'exclusion' or the 'invaded' state. It is shown that the optimal level of the control is sensitive to the value of the system in either state, as well as to the costs of control.

A MODEL OF BIOLOGICAL INVASIONS

The generic problem of biological invasions involves four phases: the introduction, establishment, naturalization, and spread of a species outside its normal range (Williamson, 1996). In what follows these four phases are all subsumed under the spread of invasives. The process is held to be analogous to that of a virus entering and spreading within a host population (Delfino and Simmons, 2000). Indeed, the model is developed from the Kermack and McKendrick (1927) model behind epidemiological theory. Unlike those in epidemiological models, however, the state variables are measures of the space occupied by 'invasive' and 'native' species, rather than the population or biomass of those species. Because a biological invasion involves the occupation of habitat, it can be modeled as the growth of the space occupied by the invasive species. The problem will only be interesting if that space is otherwise occupied by species that yield a flow of goods or services. These will be referred to, for convenience, as 'native' species. The 'invaded' space is the space occupied or affected by alien invasive species, and the 'native' space is the space occupied by native species.

For simplicity, the total space is assumed to be constant over the time horizon of interest. The state variables are denominated in terms of that space. They are the proportion of

the total space occupied by native and invasive species, denoted $x(t)$ and $y(t)$ respectively. If a control program clears invasive species from some part of the total space, then $x(t) + y(t) < 1$. The rate of change in the space occupied by the invasive species is taken to be proportional to the product of the space occupied by the invasive and native species. This assumption implies that the spread of invasive species is proportional to the zone of contact between native and invasive species. As invasive species become established and begin to spread, the rate is low. It increases up to the point where the total space is split evenly between the native and invasive species and decreases again as the space occupied by the invasive species approaches the total space. The invasion rate, α , is taken to be a constant parameter in what follows, although I later consider the connection between the invasion rate and resource use.

In general, the control of invasive species includes a number of options: exclusion, eradication, containment (control), mitigation, and adaptation. Exclusion implies the uses of measures such as quarantine, blacklists, or inoculation to prevent the introduction of potentially invasive species. Eradication is typically, but not always, an option only in the early stages of the spread of an invasive species. Containment implies the restriction of the space occupied by an invasive species. Mitigation and adaptation imply measures to accommodate the invasive species. In what follows these measures are collapsed into a single index of control, $\beta(t)$, that is a measure of the effort committed to clearing the invasive species. The space occupied by invasive species is taken to be proportional to the product of the space occupied by natives and invasives. Similarly, the space cleared of invasives is taken to be proportional to the product of the space occupied by the invasive species and the space cleared of invasives. It is assumed that the space cleared of invasives can be returned to native species at some positive rate, the restoration rate, γ . The restoration rate is assumed here to be a constant parameter, but it might easily be analyzed as a choice variable.

The equations of motion for the state variables are as follows:

$$\dot{x} = -\alpha x(t)y(t) + (1 - x(t) - y(t))\gamma \quad \text{Eq. 1}$$

$$\dot{y} = \alpha x(t)y(t) - (1 - x(t) - y(t))\beta y(t) \quad \text{Eq. 2}$$

in which α (= the invasion rate, $-1 \leq \alpha \leq 1$) and γ (= the restoration rate, $0 \leq \gamma \leq 1$) are fixed parameters, and $\beta(t)$ (= the control rate, $0 \leq \beta(t) \leq 1$) is a choice variable.

$1 - x(t) - y(t)$ is the proportion of the total space cleared of invasive species. For most biological invasion problems, α will be strictly positive, implying that invasives spread at a positive rate, but α may also be negative. This is the case where introduced species are unable to establish themselves, naturalize, or spread.

With these we can identify some of the dynamics of the native and invasive species. Once a potentially invasive species has been introduced, $y(t) > 0$, the condition for it to spread is that it become established. A potentially invasive species may be said to be established when it has passed the threshold for growth. This threshold is defined by the values of $x(t)$ and $y(t)$ at which $\dot{y} > 0$. From Eq. 2 it follows that the invasive species will spread only if

$$y(t) > 1 - x(t) \left(1 + \frac{\alpha}{\beta(t)} \right)$$

We can denote the threshold value of $y(t)$ as

$$\underline{y}(t) = 1 - x(t) \left(1 + \frac{\alpha}{\beta(t)} \right) \quad \text{Eq. 3}$$

It follows that the threshold will increase with the control rate (the rate at which the invaded space is cleared of invasive species) and decrease with the invasion rate. Because the control rate is a function of the costs and benefits of control, the establishment threshold for invasive species is similarly a function of economic variables.

To see the relation between the threshold and the costs of control, consider the social decision problem. The social objective is taken to be to maximize some index of well-being through choice of the control rate, $\beta(t)$. I assume that the index of well-being is a measure of discounted net benefit. Hence the problem is to

$$\text{Max}_{\beta(t)} \int_0^{\infty} e^{-\delta t} [R(x(t)) - C(y(t), \beta(t))] dt \quad \text{Eq. 4}$$

subject to Eq. 1, Eq. 2, and

$$x(0) = x_0, y(0) = y_0 \quad \text{Eq. 5}$$

where δ = the discount rate; $R(x(t))$ = revenue, a function of native species; and $C(y(t), \beta(t))$ = costs, a function of invasive species and their control.

It is assumed that biological invasions and the control of biological invasions are both costly. Indeed, this assumption is built into the definition of invasive species in the Convention on Biological Diversity. The model does apply in cases where invasive species yield net benefits to society, but that is not the problem being discussed here.

The maximum condition for this problem is

$$C_{\beta} = -\mu(1 - x(t) - y(t))y(t) \quad \text{Eq. 6}$$

in which μ is the co-state variable/shadow price of $y(t)$. The maximum condition requires that the marginal cost of control, C_{β} , be equal to the marginal benefits from the direct reduction of $y(t)$ due to the act of clearing out the invasive species. Using Eqs. 6 and 2,

$$\underline{y}(t) = -\frac{C_{\beta}\beta}{\mu\alpha x(t)}, \quad \text{Eq. 7}$$

from which it follows immediately that the establishment threshold for an invasive species increases with decreasing marginal cost of control and increasing impact of that species on social welfare. Put another way, the establishment threshold for an invasive species is not independent of the actions taken against it. It is certainly not a scientific datum that is exogenous to the control problem.

The reason is that the optimal level of control is increasing in the social cost (damage) of the invasive species and is decreasing in the marginal cost of control. The first-order conditions for optimization of Eq. 4 include Eqs. 1, 2, 5, and 6 and the following conditions on the evolution of the co-state variables, the adjoint equations:

$$\dot{\lambda} - \delta\lambda = -R_x + \lambda(y(t)\alpha + \gamma) - \mu y(t)(\alpha + \beta(t)) \quad \text{Eq. 8}$$

$$\dot{\mu} - \delta\mu = C_\beta + \lambda(\alpha x(t) + \gamma) - \mu(x(t)(\alpha + \beta(t)) - \beta(t)(1 + 2y(t))) \quad \text{Eq. 9}$$

These imply that the optimal control rate is

$$\beta^* = \left(\frac{\delta - \alpha(x^* - y^*)}{1 - x^* - y^*} \right) \left(\frac{\lambda}{\mu} - 1 \right) + \left(\frac{R_x + C_y}{C_\beta} \right) \quad \text{Eq. 10}$$

From Eq. 10, it is apparent that the optimal level of control of invasive species is increasing in the marginal benefit of native species and the marginal cost of invasive species and is decreasing in the marginal cost of control. The control effort will be positive if the effective invasion rate is less than the rate of discount and if the shadow price of native species is greater than the shadow price of invasive species. The effective invasion rate is defined to be the product of the invasion rate and the difference between the space occupied by native and invasive species at equilibrium, $\alpha(y^* - x^*)$.

The important point here is that the control of invasive species, and therefore their establishment and spread, are sensitive to the relative costs and benefits of invasive and native species and to the cost of invasive control.

CONTROLLING THE RESILIENCE AND STABILITY OF THE INVADED STATE

To understand how the control of invasive species works, let us go back to the dynamics of the invasive and native species described by Eqs. 1 and 2. The system has up to two equilibria depending on the parameter values. For all admissible parameter values, one equilibrium exists at which the invasive species is completely excluded from the system. In xy space this equilibrium is defined by

$$(x_1^*, y_1^*) = (1, 0) \quad \text{Eq. 11}$$

This is the equilibrium of the exclusion state.

In the case where invasive species spread at a positive rate, i.e., for $0 \leq a \leq 1$, a second equilibrium exists, at which the invasive and native species coexist. It is

$$(x_2^*, y_2^*) = \left(\frac{\beta^* - \gamma}{\alpha + \beta^*}, \frac{\gamma}{\beta^*} \right) \quad \text{Eq. 12}$$

where β^* is the optimal control rate. This is referred to as the invaded state.

Both the location of the equilibrium corresponding to and the convergence path to this equilibrium depend on the level of control. Without characterizing the control trajectory, consider what its effect on the stability and resilience of an invaded system might be.

Two cases must be considered: $-1 \leq \alpha < 0$ and $0 \leq \alpha \leq 1$. In the first, an introduced species is not able to establish itself, naturalize, and spread. This may be thought of as the general case in the sense that it applies to the majority of introductions. Only one equilibrium exists under these conditions—that corresponding to the exclusion state, $(x_1^*, y_1^*) = (1, 0)$. In the second case, the species has at least the potential to establish itself, naturalize, and spread. If $-1 \leq \alpha < 0$, then the exclusion state is a stable equilibrium. If $0 \leq \alpha \leq 1$, any exclusion state is an unstable equilibrium.

Consider the stability of the exclusion state when the invasion rate is negative. The Jacobian of $F(x_1^*, y_1^*)$, $DF(x_1^*, y_1^*)$ is

$$DF(x_1^*, y_1^*) = \begin{bmatrix} -\gamma & -(\alpha + \gamma) \\ 0 & \alpha \end{bmatrix} \quad \text{Eq. 13}$$

If $-1 \leq \alpha < 0$, the trace of $DF(x_1^*, y_1^*)$ is positive, and the determinant is negative. The equilibrium (x_1^*, y_1^*) is stable. The dynamics in this case are illustrated in Figure 1.

The optimal level of the control in this case is zero. Because the introduced species are excluded from the system by competition or predation from native species, no control is needed to keep them in check.

Now take the case where an introduced species is able to establish itself and spread, i.e., where $0 \leq \alpha \leq 1$. In this case the system has two equilibria. The first corresponds to the exclusion state, the second to the invaded state. Because the trace of $DF(x_1^*, y_1^*)$ is negative and the determinant is positive, the equilibrium corresponding to the exclusion state is unstable. In contrast, the equilibrium corresponding to the invaded state, (x_1^*, y_1^*) , is stable. Both equilibria are illustrated in Fig. 2.

The Jacobian of $F(x_2^*, y_2^*)$ Eq. 12, $DF(x_2^*, y_2^*)$, is

$$DF(x_2^*, y_2^*) = \begin{bmatrix} -\gamma \left(\frac{\alpha}{\beta^*} + 1 \right) & -\left(\frac{\beta^* (\alpha + \gamma)}{(\alpha + \beta^*)} \right) \\ \gamma \left(\frac{\alpha}{\beta^*} + 1 \right) & \gamma \end{bmatrix} \quad \text{Eq. 14}$$

Because $0 \leq \alpha \leq 1$, $0 \leq \beta(t) \leq 1$, and $0 \leq \gamma \leq 1$, the trace of $F(x_2^*, y_2^*)$ is negative, whereas the determinant is strictly positive for all $y > 0$, implying that the interior equilibrium (x_2^*, y_2^*) is a stable spiral.

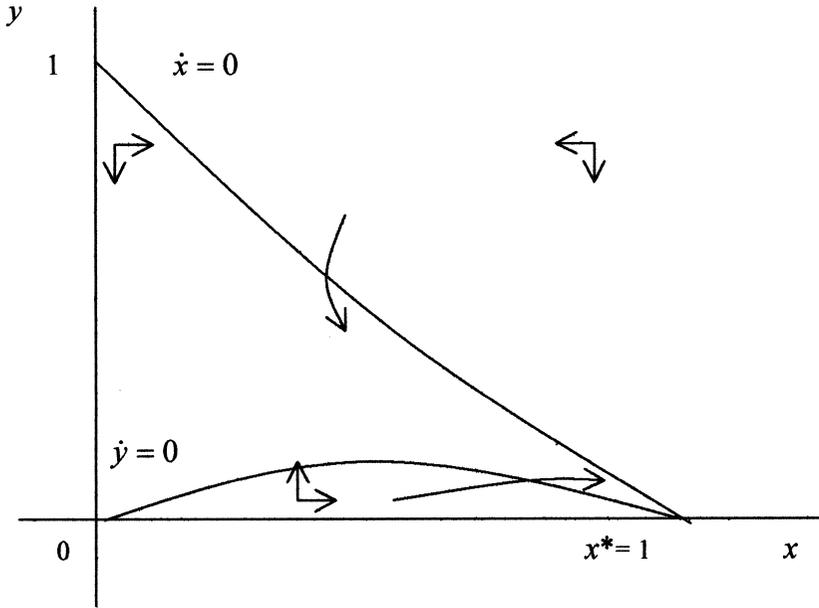


Figure 1. Stable exclusion state.

In the general case—if the exclusion equilibrium is stable—there is no control problem. Competition or predation will ensure that introduced species are automatically driven from the system. This is the case described in Figure 1. If the introduction of an alien species is interpreted as a shock to the system, the invasion rate is a measure of the system response to such a shock. A negative invasion rate implies that the response is to exclude the introduced species. No matter what proportion of the total space is occupied by an alien species at time $t = 0$, the proportion of the space occupied by natives will tend to

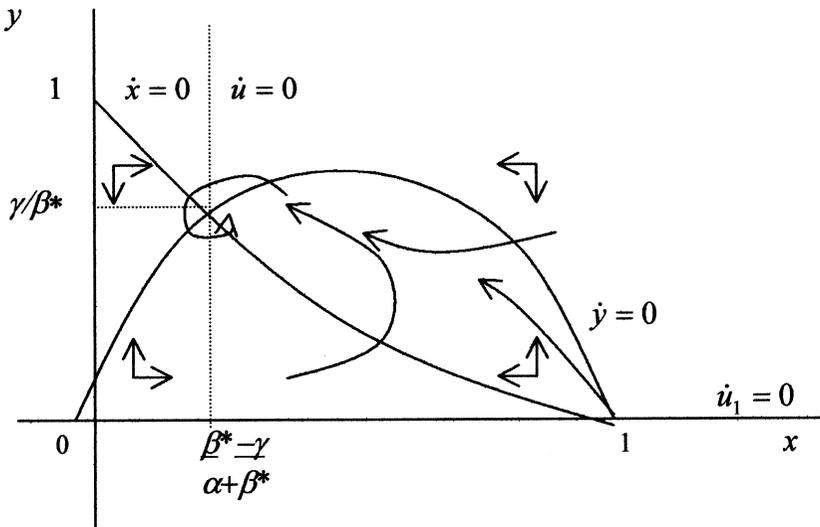


Figure 2. Unstable exclusion state, stable invaded state.

unity as t tends to infinity. We can interpret this value as a measure of the resilience, sensu Holling (1973), of the ecosystem indexed by $x(t)$ with respect to shocks imposed by the introduction of $y(t)$. Moreover, we have a natural measure of that resilience. It is the maximum share of the total space that the native species can lose to an introduced species and still recover. In this case, that measure is unity. It is a measure of the distance from the stable equilibrium to the boundary of the stability domain. Clearly, an analog of the measure of resilience sensu Pimm (1984) is the maximum time taken for $x(t)$ to converge on the stable equilibrium (Perrins, 1998).

Although both the invasion and restoration rates have been treated parametrically in this paper, they are in fact sensitive to the way that the host ecosystem is managed. Species are often able to invade precisely because of the pattern of resource use. A change in the pattern of resource use, perhaps associated with a change in institutional or market conditions, can change the invasion rate. Therefore, if the invasion rate is not a fixed parameter of the system but a choice variable, one strategy for dealing with the risk of invasive species may be to increase the resilience of the host system to invasion shocks (to drive the invasion rate below zero). This strategy has not been formally modeled here, but it is intuitive that where the costs of control are greater than the costs of increasing the resilience of the host system, the latter will be the more cost-effective solution.

Let us return to the special case—where the invasion rate is positive and the exclusion state is an unstable equilibrium. The introduction of an invasive species into even a small proportion of the total space will lead the system to converge along a heteroclinic orbit to a stable interior equilibrium, the invaded state. In a stochastic environment, this result makes the invaded state the default state, but notice that the location of the interior solution depends on the choice of the control rate, $\beta(t)$. The higher the control rate, the lower the proportion of the total space occupied by the invasive species at equilibrium. Like the invasion and restoration rates, $\beta(t)$ influences the resilience of the managed native system.

Once again we can begin with an extreme case: that in which the optimal control rate is zero or very small (Fig. 3). The control rate may reflect the relative social costs and benefits of control either because that invasive species is benign (does not impose costs on society) or because the cost of control is prohibitive. It may also reflect a market failure due to the public good nature of invasion control. Indeed, a general problem with invasive species is that their costs are not adequately observed through market prices—the effects of invasives are external to the market. In Fig. 3, our measure of the resilience of the ecosystem is clearly close to zero. Conversely, the resilience of the invaded state is close to unity.

It is useful to interpret the dynamics of the system under different control rates in terms of the resilience of the invaded state. If the optimal control rate is positive, then the default state will be an interior solution to the problem. The greater the control rate, relative to the other system parameters, the higher the proportion of the total space occupied by native species at equilibrium and the lower the resilience of the invaded state.

Figure 4 illustrates the case where the control rate is ‘high’ and hence where the invaded state is less resilient. More precisely, because the value of $x(t)$ at equilibrium is just $(\beta^* - \gamma)/(\alpha + \beta^*)$, we have the following measure of the resilience of the invaded state:

$$\rho(\beta^*) = \frac{\alpha + \gamma}{\alpha + \beta^*} \quad \text{Eq. 15}$$

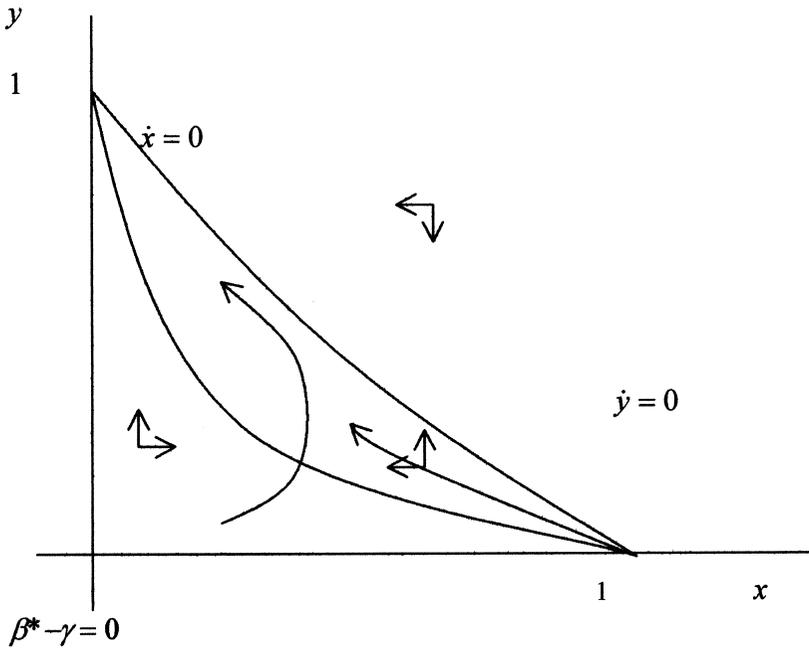


Figure 3. Stable invaded state.

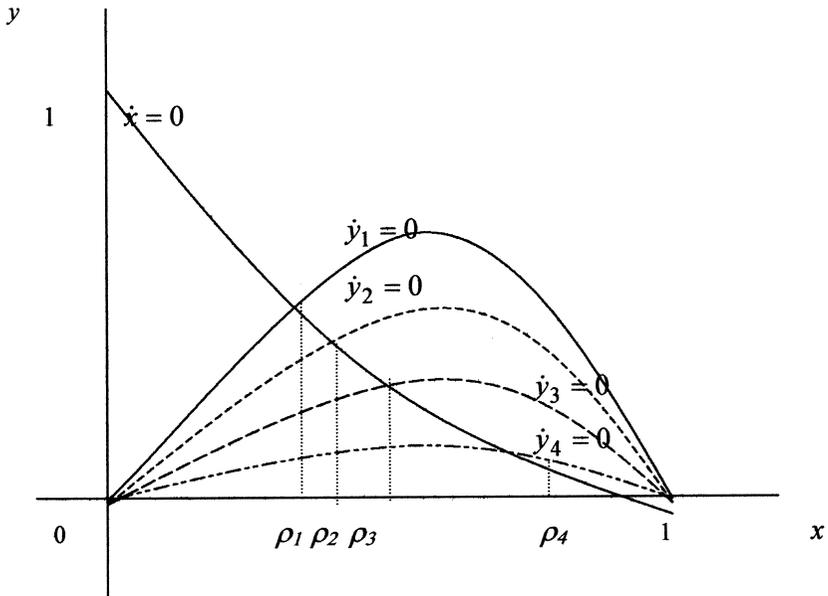


Figure 4. Reducing the resilience of the invaded state.

Moreover, this value is immediately decreasing in β^* . Although we conventionally think of resilience as a desirable property of the system, whether it is desirable or not in any particular case depends on whether the system delivers net benefits or costs. Because the invaded state is assumed to be less valuable than the exclusion state, the resilience of the invaded state is 'bad'. Hence the effect of the control is to reduce the resilience of the invaded state or, put another way, to reduce the maximum share of the total space that an invasive species can lose to the control process and still recover. Control strategies that seek to maintain the system as close to the exclusion state as possible can be interpreted as strategies to minimize the resilience of the invaded state.

CONCLUDING REMARKS

The point has already been made that if a system is unobservable it will not be possible to guide it to the desired state through the application of the controls. We know, however, that even if exploited ecological systems are neither observable nor controllable, as is the case with many marine systems, they may still be 'stabilizable'. This finding implies that exploitation of the system is restricted to levels at which the uncontrolled part (the ecological processes) can continue to function over the expected range of environmental conditions. Because the exclusion state in this case is unstable, it is not resilient with respect to environmental shocks. In the absence of accurate measures of the system, it could not be stabilized in this state. It could be stabilized only in the invaded state. If the system is neither observable nor controllable, the choice of $\beta(t)$ will still fix the stable level of the invasive species.

The choice of $\beta(t)$ in these circumstances may reflect a precautionary approach. Typically, this statement is taken to imply action in advance of proof. The Declaration of the Third Ministerial Conference on the North Sea identified a precautionary approach to marine pollution as involving "action to avoid potentially damaging impacts of substances that are persistent, toxic and liable to bioaccumulate even where there is no scientific evidence to prove a causal link between effects and emissions" (Haigh, 1993). The precautionary approach is also often associated with a shift in the burden of proof onto those whose decisions are the source of damage (Costanza et al., 1998). Perrings et al. (2000) have argued that in the case of invasive species this shift implies the adoption of control instruments, such as the environmental assurance bond. Such instruments have two functions: to provide coverage against risks of biological invasions that may not be commercially insurable and to shift the burden of proof onto those whose activities lead to the introduction of potential invaders.

Institutional and market conditions that encourage resource users to ignore the consequences of their actions increase the susceptibility of countries to invasive species. Markets generally fail to accommodate the risks posed by invasive species. Although many private benefits of species introductions are captured in market prices, many of their social costs are not. In the case of biological invasions, however, we have another reason to believe that insufficient control will be exercised by the society concerned. The control of invasive species generally, like the control of communicable human diseases, is a public good with several dimensions. Invasive species threaten biodiversity, and the gene pool is a global public good. Invasive species also disrupt ecosystem functions in terrestrial and aquatic systems alike. In terrestrial systems, the effect of invasive *Pinus* and

Acacia species on the hydrological services provided by the Fynbos in the Cape of Good Hope is one such example. In marine systems, the impact of pathogens spread from shrimp culture on the role of mangroves as fish nurseries is another. Although the main costs and benefits of actions to control biological invasions may be local, biological invasions almost always involve two or more countries; the actions of one affect the welfare of another. In the absence of bilateral or multilateral agreements, insufficient resources will be allocated to national control.

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