

Mitigation and Adaptation Strategies in the Control of Biological Invasions

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Abstract

Biological invasions are recognised to be a problem of growing severity. Human pathogens, weeds or pests in terrestrial systems and dominant alien species in freshwater or marine aquatic systems all impose significant costs in terms of forgone output or costs of control in every major system. Like many of the other environmental consequences of globalisation biological invasions require that decisions be taken under uncertainty. Decision-makers in such circumstances have to choose between two main strategies: mitigation and adaptation. This paper characterises invasive species problems in terms of the properties of the stochastic processes they induce. It considers how mitigation and adaptation strategies may be modelled, and identifies the conditions in which each approach may be efficient and effective.

1. Introduction

The biodiversity problem is generally interpreted as the problem of biodiversity loss due to habitat conversion, and the consequences biodiversity loss has for ecosystem functioning. Increasing attention is, however, now being paid to another aspect of the biodiversity problem: biological 'invasions' – the introduction, establishment and spread of species outside their home range (Parker et al., 1999; Williamson, 1998, 2000). The majority of introductions are due to human activities, particularly trade, transport and travel. Human pathogens and other 'pest' species impose considerable economic costs in terms of morbidity, mortality, lost output in agriculture, forestry and fisheries, treatment and control (Perrings et al, 2000; Pimentel et al, 1999; 2002). The ecological impacts are often more difficult to evaluate in economic terms, but may be equally significant.

Invasive species are, for example, argued to be the second only to habitat destruction as a threat to biodiversity (Wilcove et al., 1998). By progressively breaking down the genetic isolation of communities of co-evolving species of plants and animals, invasive alien species also have major implications for the evolution of biodiversity (Clout, Lowe et al., 1996).

The impacts of invasive species may be localised and of relatively short duration, but they may also be widespread and have periodic, chronic or potentially irreversible effects. This depends in part on the characteristics of the invasive species themselves – their invasiveness – and in part on the vulnerability of the invaded ecosystems – their invasibility. Ecosystems naturally vary quite widely in their vulnerability to invasion. While pelagic marine systems appear to be least vulnerable, mixed island systems, lake, river and near-shore marine systems are especially vulnerable (Heywood, 1995). But the probability of both establishment and spread also depends on way in which the environment is altered by human behaviour, and the way that potentially invasive species are introduced (Mack et al, 2000). For example, the probability of establishment of intentionally introduced species is higher than that of unintentionally introduced species simply because intentionally introduced species 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). Similarly, the probability that an ecosystem will be successfully invaded increases with the level of anthropogenic stress on that system. For example, the invasion of coral reefs by blue green algae often depends on levels of sewage and fertiliser run-off (Roberts, 1995). Terrestrial pollution is also implicated in the invasion of the Black Sea by *Mnemiopsis leydii* (Knowler and Barbier, 2000). The invasibility of terrestrial systems is typically an increasing function of the degree to which they are disturbed by human activity (Williamson, 1996).

There are two ways decision-makers can respond to the prospect of biological invasions: through mitigation and adaptation (Shogren, 2000; Shogren and Crocker, 1999). Mitigation involves actions that reduce the likelihood of invasions by reducing the invasiveness of species or the invasibility of ecosystems. Adaptation involves actions that reduce the impact of introduction, establishment or spread without changing the likelihood that it will occur. Mitigation accordingly implies action before the event or process. Adaptation may involve actions taken before, during or after the process. It usually implies actions that reduce the expected damage of the process, but it also includes actions that pool or transfer the risks. Examples of mitigation include actions designed to reduce the likelihood of new introductions (the dispersal of species), such as red, green and amber lists, quarantine restrictions or trade measures permitted under the Sanitary and Phytosanitary Agreement. They also include actions to strengthen the resilience of existing systems to invasion through, for instance, conservation of biodiversity. Examples of adaptation include the dominant control options of eradication, the use of pesticides or biocontrol agents, but they also include actions to accommodate invasive species where control is either impossible or very costly.

Which strategy is appropriate depends in part on the degree to which the system is either observable or controllable. Williamson (1999) argues that many if not most new impacts by invasives are not predictable. Support for Williamson comes from a number of quarters. Lawton (1999) argues that to predict the population dynamics of particular species in particular habitats requires study of that species and that habitat (see also Law

et al., 1999; Kareiva et al., 1996). Williamson (1999) found that the only acceptable predictor other than propagule pressure was whether a species had invaded before.

Others take the view that invasions and the effects of invasions can be predicted from the general properties of species or habitats. This view holds that it is possible to understand both the invasiveness of different species, and the invasibility of different habitats (Rejmanek, 1989; Ross, 1991). The first depends on specific biological traits of introduced species. Specific traits such as high plasticity are considered to confer invasiveness. Invasiveness in aquatic species, for example, has been argued to be determined by biological traits such as dispersal ability, competitive ability, tolerance to temperature, salinity, oxygen concentration (Vila-Gispert and Moreno-Amich, 2002). The second depends on ecosystem integrity and the diversity of native species. Habitat fragmentation and pollinator loss are both thought to increase invasion risk through, for example, the increase of generalist mutualists (pollinators and dispersers) in local biotas. Watkinson, Freckleton and Dowling (2000), for example, argue that classical ecological models can be used i) to predict the numbers of weeds and the yield losses that result from their presence; ii) to test the sensitivity of population models in order to target key areas of the life-cycle at which control will be most effective; and iii) to explore the general determinants of invasions.

This paper attempts to characterise the problem of invasive species in a way that enables us to analyse the efficiency and effectiveness of the two control strategies. This involves a generic problem of anticipatory or precautionary action under uncertainty. It is therefore far wider in its relevance than the focus on invasive species suggests. Indeed, this characterisation carries over to a range of other environmental problems. However, it may be particularly helpful in developing responses to biological invasions where the choice of strategy is frequently the default strategy of adaptation after the event.

2 Biological invasions as a stochastic process

Biological invasions involve four stages: introduction, establishment, naturalisation and spread. Naturalisation is frequently combined with either establishment or spread. The importance of invasive species introductions is that they involve the insertion of new species with their own dynamics into a pre-existing system. Suppose that the uninvaded system, $S(0)$, can exist in m possible states: $S_1(0), S_2(0), \dots, S_m(0)$. Suppose, too, that the conditional probability that the system is in state j at time t given that it was in state i at time s is given by $p_{ij}(s, t)$ with $\sum_{j=1}^m p_{ij} = 1$, ($i, j = 1, 2, \dots, m$). The $p_{ij}(s, t)$ are the set of transition probabilities. If they are independent of time, the matrix of transition probabilities, \mathbf{P} , defines a homogeneous Markov chain. Now suppose that the introduction of a potentially invasive species between time 0 and time t changes the set of potential states from $S_1(0), S_2(0), \dots, S_m(0)$ to $S_1(t), S_2(t), \dots, S_n(t)$ where $n > m$. That is, it increases the set of possible outcomes from m to n . The dynamical implications of species introductions are then summarised in the associated probabilities transition matrix.

The matrix of transition probabilities, \mathbf{P} , is a stochastic matrix with the usual properties of such matrices: the rows sum to 1, the dominant eigenvalue of the matrix is 1 and the components of the corresponding eigenvector are all equal to 1. From the definition of the conditional probabilities $p_{ij}(s, t)$ it follows that $p_{ij}(t, t+1) = \sum_{h=1}^n p_{ih}(t) p_{hj}$ and hence that $\mathbf{P}(t+1) = \mathbf{P}(t)\mathbf{P}$. It also follows that $\mathbf{P}(t) = \mathbf{P}^t$, and hence that in the limit $\lim_{t \rightarrow \infty} \mathbf{P}(t) = \mathbf{P}^\infty$ (the RHS denoting $\mathbf{P}^{t \rightarrow \infty}$). The elements of this define the limiting transition probabilities of the system.

To see the significance of the limiting transition probabilities for the introduction of potentially invasive species, we need to consider the properties of the Markov chain corresponding to \mathbf{P} . Note that a Markov chain is 'proper' if \mathbf{P} has no eigenvalues ($\neq 1$) of

absolute value 1. It is 'regular' if it is both proper and 1 is a simple root of the characteristic equation of \mathbf{P} . All proper Markov chains have limiting transition probabilities. For the first case we consider Markov chains that are proper (and so have limiting transition probabilities) but that are not necessarily regular.

If \mathbf{P} is proper but not regular, it can be written in the normal form:

$$\mathbf{P} = \begin{bmatrix} \mathbf{P}_{11}^{\infty} & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & \mathbf{P}_{mm}^{\infty} & 0 & \cdots & 0 \\ \mathbf{P}_{m+11}^{\infty} & \cdots & \mathbf{P}_{m+1m}^{\infty} & \mathbf{P}_{m+1m+1}^{\infty} & \cdots & 0 \\ \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \mathbf{P}_{n1}^{\infty} & \cdots & \mathbf{P}_{nm}^{\infty} & \mathbf{P}_{nm+1}^{\infty} & \cdots & \mathbf{P}_{nn}^{\infty} \end{bmatrix} \quad (1)$$

in which $\mathbf{P}_{11}^{\infty}, \dots, \mathbf{P}_{mm}^{\infty}$ are irreducible stochastic matrices, with eigenvalues equal to 1, and $\mathbf{P}_{m+1m+1}^{\infty}, \dots, \mathbf{P}_{nn}^{\infty}$ are irreducible matrices whose dominant eigenvalues are strictly less than 1. This implies that in the limit:

$$\mathbf{P}^{\infty} = \left[\begin{array}{ccc|c} \mathbf{P}_{mm}^{\infty} & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & \mathbf{P}_{mm}^{\infty} & 0 \\ \hline & \mathbf{Q}_{\infty} & & 0 \end{array} \right] \quad (2)$$

where \mathbf{Q}_{∞} defines the limiting transition probabilities of the submatrices \mathbf{P}_{ij} , ($i = m+1, \dots, n; j = 1, 2, \dots, m$). That is, the limiting transition probabilities $\mathbf{P}_{m+1m+1}^{\infty}, \dots, \mathbf{P}_{nn}^{\infty}$ are all equal to zero. The implications this has for invasive species depends on how an introduced species features in the states of nature corresponding to the limiting transition probabilities on the principle diagonal.

Consider the following cases:

- a) *An introduced species fails to establish, naturalise and spread*
- b) *The probability that an introduced species succeeds in establishing naturalising and spreading is positive.*
- c) *The probability that an introduced species succeeds in establishing naturalising and spreading is positive, but has different effects in different states of nature.*
- d) *The probability that an introduced species succeeds in establishing naturalising and spreading is positive, but it does not converge to a stable population size.*

- a) *An introduced species fails to establish, naturalise and spread*

The first case is the most common. The probability that any one introduced species will establish and become a pest or pathogen is very low. Smith et al. (1999) suggest 2% for the probability of plant introductions into Australia becoming pests, somewhat higher than the 1% indicated by the tens rule of Williamson and Fitter (1996). The failure to establish turns out to have a very direct implication for the structure of the underlying Markov process. If the set of potential states of nature $S_1(t), S_2(t), \dots, S_n(t)$ differs from the set $S_1(0), S_2(0), \dots, S_m(0)$ by the fact that the last $n-m$ states include the introduced species and the first m states exclude the introduced species, then (2) implies that the introduced species would fail to establish, naturalise and spread. They would be excluded from the system in the limit.

- b) *The probability that an introduced species succeeds in establishing naturalising and spreading is positive.*

We first consider the special case where \mathbf{P} is both proper and regular. Regularity implies that the dominant eigenvalue of \mathbf{P} is equal to 1, and that all other eigenvalues have an absolute value less than 1. This has a number of implications. The first is that \mathbf{P} is irreducible. It cannot be decomposed into the normal form described in (1). There are not multiple limiting states (equilibria). The second is that the limiting transition probabilities are positive and independent of the initial state. This property is often referred to as 'the Markov property', although it is a property only of regular Markov chains. Furthermore, the limiting absolute probabilities, $\lim_{t \rightarrow \infty} p^{(t)} = (p_1^\infty, \dots, p_n^\infty)$, in which p_i^∞ is the

probability that the system will be in state S_i as time tends to infinity, are both strictly positive and independent of the initial probability. Initial conditions do not determine the final state of the system. In fact the vector of limiting absolute probabilities is an eigenvector corresponding to the dominant eigenvalue of \mathbf{P} (equal to 1). Third, the system is acyclic, implying that it will converge on $\lim_{t \rightarrow \infty} p^{(t)} = (p_1^\infty, \dots, p_n^\infty)$ and remain there. There are no limit cycles.

If the states of nature, $S_1(t), S_2(t), \dots, S_n(t)$, associated with the introduction of a potentially invasive species include at least one state in which the species is invasive, and if the transition probability matrix corresponding to $S_1(t), S_2(t), \dots, S_n(t)$ is regular, then there is a positive probability that the species will establish and spread. A necessary and sufficient condition that the limiting absolute probability that an introduced species will be invasive independent of the scale of the initial introduction is that the associated Markov chain is regular.

c) The probability that an introduced species succeeds in establishing naturalising and spreading is positive, but has different effects in different states of nature.

The third case of interest is where the probability that an introduced species becomes invasive is positive, but where the impact differs according to which of a number of possible attractors dominates. That is, the probability transition matrix and hence the Markov process is reducible, and may be represented as in (1). Each of the stochastic matrices $\mathbf{P}_{11}^\infty, \dots, \mathbf{P}_{mm}^\infty$ represents a separate attractor – what is referred to as either an essential or limiting state of the system. Transitions are only possible between non-essential and essential states, between non-essential states within the same group, and between essential states within the same group. The limiting absolute probabilities of essential states are positive. The limiting absolute probabilities of all other states are zero.

If an introduced species appears only in states S_{m+1}, \dots, S_n , and \mathbf{P} reduces to (1), the species will disappear from the system. On the other hand, if the probability transition matrix is proper but irregular, and if the states of nature, S_1, S_2, \dots, S_m , include the

introduced species as an invasive, then there is a positive probability that it will establish and spread in up to m different ways corresponding to the m different limiting states. This is perhaps the most general case.

d) The probability that an introduced species succeeds in establishing, naturalising and spreading is positive, but it does not converge to a stable population size.

The last case is a particular example of cyclic behaviour. Many pests and pathogens cycle through phases during which they are more or less abundant, more or less dominant, more or less virulent. This case corresponds to a Markov chain that is proper but not regular, in which there are h eigenvalues with an absolute value of r . If $h = 1$ then the chain is regular. If $h > 1$ then it is said to be 'imprimitive', and h is the index of imprimitivity. The matrix \mathbf{P}^h may be permuted to block diagonal form, in which the number of blocks is h and each block has the same dominant eigenvalue. The chain is said to have a period of h , implying that it repeats itself at intervals of h periods. The limit cycles generated in predator-prey systems are examples of this. Specifically, if the probability transition matrix is proper but cyclic, such that:

$$\mathbf{P}^h = \begin{bmatrix} \mathbf{P}_{11}^h & 0 & \cdots & 0 \\ 0 & \mathbf{P}_{22}^h & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \cdots & \mathbf{P}_{hh}^h \end{bmatrix} \quad (3)$$

then the introduced species will converge on a cycle with period h . In this case a number of states may be occupied in equilibrium. Such states are said to be recurrent. More particularly, a state, i , is said to be recurrent if $p_i^\infty = 1$ and is said to be transient if $p_i^\infty = 0$. That is, a state is recurrent if the system converges on that state and remains in it for infinitely many periods. Recurrent states are either occupied permanently or revisited periodically. Transient states are left after some finite time and never revisited thereafter. Recurrent states are the long-term equilibria of a system, and transient states are far-from-equilibrium positions.

Two observations follow directly from these four cases. First, both the stochastic long run equilibria of the system and the convergence paths are summarised by the matrix \mathbf{P} . It is the properties of \mathbf{P} that determine both the appropriate and feasible responses to species introductions. If the Markov chain is regular it is appropriate to base a response on the long-run equilibrium of the system. Since that is independent of initial conditions, changes to the current state of the system cannot affect the long run equilibrium. If the Markov chain is proper but irregular, the limiting absolute probabilities are path-dependent and initial conditions matter. The response should therefore address the path (in order to affect the long-run equilibrium of the system).

Second, an understanding of the transition probabilities in \mathbf{P} helps identify the need for a response. Since they measure the resilience of the system in each of a number of possible states, they identify the capacity of the system to recover to those states without intervention. The point has been made elsewhere (Perrings, 1998) that the transition probabilities in a Markov chain are natural measures of resilience (sensu Holling, 1973). Resilience in this sense is defined as a measure of the capacity of the system to remain in some state in the face of external shocks. For a given disturbance regime, the transition probabilities define the probability that the system in one state will change to another state. Hence the 'own' transition probabilities, $p_{ii}(s,t)$ define the probability that the system in some state at time s will still be in that state at time t .

The probability that the system will be in state i at time t is given by the absolute probability, $p_i(t)$, and the probability that it is in any one of n possible states by the vector $\mathbf{p}(t)$. Since the transition probabilities conditional on the state of the system at time t are given by \mathbf{P}^t , $\mathbf{p}(t)$ evolves according to the recursive relation, $\mathbf{p}(t) = \mathbf{P}^t \mathbf{p}(0)$, and the absolute limiting probabilities are defined by $\lim_{t \rightarrow \infty} \mathbf{p}(t) = \mathbf{P}^t \mathbf{p}(0)$. These limiting transition probabilities of the system are accordingly indirect measures of the Holling-resilience of the limiting states.

It follows that a necessary and sufficient condition that a system is Holling-resilient with respect to any perturbation is that the limiting absolute probabilities do not depend on the

initial absolute probabilities. This will be true if \mathbf{P} is regular. If \mathbf{P} is not regular, and is therefore reducible, then (a) the system may, in the limit, occupy any one of a finite number of closed classes (the limiting states); (b) it is sensitive to initial conditions, and (c) it is path dependent (the key properties of complex systems generally). In all cases the transition probabilities of the system at some time and state define the resilience of the system at that time and state. That is, $p_{ij}(s,t)$ is an indirect measure of the resilience of the system in state j at time t with respect to its 'perturbation' to state i . The limiting transition probabilities are accordingly general measures of resilience, since they capture the probability that a system will (re)converge on some state at any point in time if it has been perturbed to some other state. If \mathbf{P} is irregular, it follows immediately that all non-essential or transient states are not resilient. All limiting or recurrent states are resilient to some degree. It also follows that the minimum time to (re)convergence on some state, the 'hitting time', provides a measure of the resilience of that state in the sense of Pimm (1984) – the speed of return to (some) equilibrium.

In terms of the concerns of this paper, if a system in some limiting state has been perturbed by the introduction of a potentially invasive species, the limiting transition probabilities to that state are measures of its capacity to recover, and the associated hitting times are measures of the potential speed of recovery. The transition probabilities to other limiting states are measures of the propensity of the perturbed system to flip to some other equilibrium as a result of the introduction of the invasive species. The set of transition probabilities, if known, accordingly provide guidance on the need for a response, as well as the nature of the response.

3 The control strategies

Now consider the two potential control strategies: mitigation and adaptation. Suppose that the state of the system is described in terms of a set of produced and natural resources, denoted $\mathbf{x}(t) = (x_1(t), \dots, x_n(t))$. Natural resources in this context include the set of all species. Let S be the state space, $i \in S$ defining a state within S . Further, let the probability transition matrix for the system be denoted $\mathbf{P}(t)$. $\mathbf{P}(t) = \mathbf{P}$ for all t if the

transition probability matrix is time independent, as is assumed to be the case here. We suppose that the time path for the system is influenced by a policy described by either of the sequences $\{\mathbf{u}(t)\}$ or $\{\mathbf{F}(t)\}$. The efficiency and effectiveness (controllability) conditions for these two cases are simply stated here. Discussion is deferred to section 4.

Adaptation is defined as actions that change the value of uncertain outcomes without changing the likelihood that they will occur, defensive expenditures being good examples. That is, adaptive behaviour changes the payoffs associated with a set of outcomes, but not the probability density function associated of those outcomes. In the case of invasive species problems, we take a particular form of adaptation, namely action that directly changes the abundance of the invasive species through a process of, for example, pest control. Such adaptation does not make invasions less likely, but it does change the cost of invasions. In this case $u_i(t)$ measures the change in $x_i(t)$ brought about by the control at time t . It is directly analogous to the harvest of a natural resource, and indeed the harvest of wild species can be seen as an adaptive strategy.

The dynamics of the physical system can then be written as a linear function of $\mathbf{u}(t)$:

$$\dot{\mathbf{x}} = \mathbf{P}\mathbf{x}(t) + \mathbf{u}(t) \quad (t = 1, 2, \dots, T) \quad (4)$$

Since the choice of $\mathbf{u}(t)$ has no implications for \mathbf{P} it does not change the transition probabilities. The implications for the limiting absolute probabilities are, however, not quite so clear. If \mathbf{P} is regular then the limiting absolute probabilities are independent of the initial probabilities. In this case the control has no implications for the eventual state of the system. On the other hand, if \mathbf{P} is proper but not regular, then the limiting absolute probabilities do depend on the initial probabilities, and the current control may have implications for the eventual state of the system.

Mitigation. The second approach to the control of invasive species involves changes to the probability law itself through, for example, management of the 'invasibility' of systems or the regulation of invasion pathways associated with trade, transport and travel.

In this case the structure of the control problem is rather different. The control implies actions that change the transition probabilities through selection of a feedback matrix, $F(t)$, that works on the set of state variables over which the decision-maker has control, defined by $Cx(t)$. Hence $u(t)$ in (4) takes the form $F(t)y(t)$, where $y(t) = Cx(t)$, and the equations of motion can be written as:

$$\dot{x} = Px(t) + F(t)Cx(t) \quad (t = 1, 2, \dots, T) \quad (5)$$

If the decision-maker can reach all state variables in the system, then $Cx(t) = x(t)$, and the probability law for the system is given by $P + F(t)$.

In both cases, the policy is selected to optimise some value function, which we take to be a measure of the (weighted) utility gained from exploiting the n resources of the system. This has two forms depending on the control strategy:

$$V(x(t), u(t), t) = E \left(e^{-dt} W(x(T)) + \int_{t=0}^T e^{-dt} Y(x(t), u(t)) dt \right) \quad (6a)$$

$$V(x(t), F(t), t) = E \left(e^{-dt} W(x(T)) + \int_{t=0}^T e^{-dt} Y(x(t), F(t)) dt \right) \quad (6b)$$

in which $W(\cdot)$ and $Y(\cdot)$ are strictly concave continuous functions defining social preference orderings over the set of all feasible $x(t)$ and $u(t)$ or $F(t)$. $d(t)$ is a discount rate. Welfare is an algebraic function of the terminal value of the state variables, and an integral function of the state and the control variables over the whole period. More particularly, $W(\cdot)$ is the discounted value of both produced and natural resources at the terminal time, T , and $Y(\cdot)$ is the discounted flow of benefits deriving from the use of all resources over the interval $[0, T]$.

The problem in both cases is to find the 'control' history that maximizes V over the interval $[0, T]$, subject to the dynamics of the system given by (4) or (5). We are interested in two aspects of this problem. The first is the conditions for the efficiency of the control policy applied to the system. The second is the conditions for the effectiveness of the

control policy. It concerns the controllability of the system, and deals with the relation between the form of control and the structure probability transition matrix.

The necessary conditions for the efficiency of the control policy can be described briefly. The current value Hamiltonian for our two forms of the problem is:

$$\tilde{H}(\mathbf{x}(t), \mathbf{u}(t), \boldsymbol{\mu}(t), t) = E(W(\mathbf{x}(T)) + Y(\mathbf{x}(t), \mathbf{u}(t))) + \boldsymbol{\mu}(t)(\mathbf{P}\mathbf{x}(t) + \mathbf{u}(t)) \quad (8a)$$

$$\tilde{H}(\mathbf{x}(t), \mathbf{F}(t), \boldsymbol{\mu}(t), t) = E(W(\mathbf{x}(T)) + Y(\mathbf{x}(t), \mathbf{F}(t))) + \boldsymbol{\mu}(t)(\mathbf{P}\mathbf{x}(t) + \mathbf{F}(t)\mathbf{x}(t)) \quad (8a)$$

implying the following first order necessary conditions for maximisation of (6) subject to (4) and (5):

$$E(Y_{u_i(t)}) + \mu_i(t) = 0 \quad i = 1, \dots, n \quad (9a)$$

$$E(Y_{f_{ij}(t)}) + \mu_i(t)x_j(t) = 0 \quad i, j = 1, \dots, n \quad (9b)$$

$$\dot{\mu}_i - \mathbf{d}\mu_i(t) = E(Y_{x_i(t)}) + \boldsymbol{\mu}(t)\mathbf{p}_i \quad i = 1, \dots, n \quad (10a)$$

$$\dot{\mu}_i - \mathbf{d}\mu_i(t) = E(Y_{x_i(t)}) + \boldsymbol{\mu}(t)(\mathbf{p}_i + \mathbf{f}_i(t)) \quad i = 1, \dots, n \quad (10b)$$

$$E(W_{x_i(T)}) = -\mu_i(T) \quad i = 1, \dots, n \quad (11)$$

$$\dot{\mathbf{x}} = \mathbf{P}(t)\mathbf{x}(t) + \mathbf{u}(t) \quad (12a)$$

$$\dot{\mathbf{x}} = \mathbf{P}\mathbf{x}(t) + \mathbf{F}(t)\mathbf{C}\mathbf{x}(t) \quad (12b)$$

$$\mathbf{x}(0) = \mathbf{x}_0 \quad (13)$$

where \mathbf{p}_i and \mathbf{f}_i are the i th columns of \mathbf{P} and \mathbf{F} respectively. Equations (9a) and (9b) require that the control policy, $\mathbf{u}(t)$ and $\mathbf{F}(t)$, be selected so as to maximise the measure of expected utility. In both cases it implies that the vector of controls or the feedback matrix that make up the 'policy' should be selected so as to equate the expected marginal benefits and marginal user cost of the policy. Equations (10a) and (10b) are conditions on the rate of change of the multipliers. In (10a) $\boldsymbol{\mu}$ has the natural interpretation of the shadow value of the i th resource. In (10b) it defines the shadow value of the probability law governing that resource. Equation (11) requires that the expected marginal benefit of the set of resources at the terminal time is equal to the shadow price of those resources at that time. Equations (12a), (12b) and (13) restate the equations of motion, and the initial conditions.

For the invasive species problem, we can interpret the first order necessary conditions as follows. The first order necessary conditions on the vector of control variables, $\mathbf{u}(t)$,

require that the controls be increased up to the point where the expected marginal benefits of control just offset the marginal social cost of control. If the controls take the form of direct changes in the abundance of invasive species through, for example, a pest eradication or pest control programme, as in (4), then the marginal social cost of control is simply the shadow price of the resource given the transition probability matrix \mathbf{P} . If the controls take the form of modifications to the probability law of the system through the regulation of its invasibility, as in (5), then marginal social cost of control is the shadow value of the change in probabilities induced by the feedback matrix. As always the first order necessary conditions define the conditions that must hold along an optimum trajectory, but they do not ensure that such an optimum will exist, or that if it does exist it will be unique.

For the effectiveness of the control policy we need a measure of the controllability of the system. Controllability requires that the controls are able to reach the targeted state variables. The system just described is controllable if there exists a sequence $\{\mathbf{u}(t)\}$ or $\{\mathbf{F}(t)\}$ such that $\mathbf{x}(T) = \mathbf{x}_T$ given $\mathbf{x}(0) = \mathbf{x}_0$ - if there exists a control sequence that will guide the system from \mathbf{x}_0 to \mathbf{x}_T . This requires that the controllability matrix is of full rank. That is, if the equations of motion takes the form of (4) it requires that the rank of the controllability matrix $\mathbf{U}=(\mathbf{I},\mathbf{P},\mathbf{P}^2,\dots,\mathbf{P}^{n-1})$ is n . Similarly, if the equations of motion take the form of (5) and we assume that the feedback matrix is constant, it requires that the rank of the controllability matrix $\mathbf{Y}=(\mathbf{F},\mathbf{PF},\mathbf{P}^2\mathbf{F},\dots,\mathbf{P}^{n-1}\mathbf{F})$ is n . Controllability in both cases ensures that there exists a path between each state variable and a potential control. However, since the rank of the product of two matrices cannot exceed the rank of either factor, it follows that if only a subset of processes may be regulated, the controllability matrix will be of less than full rank, and it will not be possible to guide the system to any desired state. Whether the controls represent management actions (directly transforming the state variables or the transition probabilities) or economic actions (influencing resource use decisions through incentives) the rank condition defines the limits of their effectiveness.

For example, if p_{ii} is the probability that a system subject to a particular level of propagule pressure will remain in that state, a policy aiming to make particular states more resilient might seek to increase that probability. This potentially affects both the short and long run potential of the system in that it changes both the initial and limiting absolute probabilities.

The degree to which the system can be controlled in this way depends on the rank of F , or the number of processes that are influenced by the policy. If F is less than full rank the system will not be controllable. To illustrate, suppose that P is reducible as follows:

$$P = \begin{bmatrix} p_{11} & 0 \\ p_{21} & p_{22} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ p_{21} & p_{22} \end{bmatrix}$$

implying that

$$P^\infty = \begin{bmatrix} 1 & 0 \\ 1 & 0 \end{bmatrix}$$

with limiting absolute transition probabilities $\mathbf{p}^{(\infty)} = (1,0)$. The system would, in the limit, converge on state 1. Suppose that the objective of control was to maintain the system in state 2, using the feedback control

$$F = \begin{bmatrix} 0 & 0 \\ g(f_{22}) & f_{22} \end{bmatrix}$$

where $f_{22} < 1$. In other words, suppose that the control policy enhances the probability that the system in state 2 at time t will still be in state 2 at time $t + 1$, and allows the probability that it will be in state 1 at $t+1$ to be determined residually. Since the matrix $P + F$ is stochastic, it follows that the 'controlled' system has the transition probabilities:

$$P + F = \begin{bmatrix} 1 & 0 \\ p_{21} - f_{22} & p_{22} + f_{22} \end{bmatrix}$$

and the matrix of limiting transition probabilities is unchanged. The limiting absolute transition probabilities are still $\mathbf{p}^{(\infty)} = (1,0)$. In other words because the system is not controllable, application of the control has no impact on the limiting absolute probabilities. The system will still converge on the only essential state.

On the other hand, if F takes the form:

$$\mathbf{F} = \begin{bmatrix} -f_{11} & f_{12} \\ -f_{21} & f_{22} \end{bmatrix}$$

implying that

$$\mathbf{P} + \mathbf{F} = \begin{bmatrix} 1 - f_{11} & f_{12} \\ p_{21} - f_{21} & p_{22} + f_{22} \end{bmatrix}$$

then the limiting absolute transition probabilities for both states would be strictly positive. That is, the control policy would have ensured that the probability that the system is in state 2 in the limit was greater than zero.

Sections 2 and 3 may be summarised in the following propositions:

- i) Adaptation strategies will have no impact on the limiting state of the system if and only if the probabilities transition matrix/Markov chain is both proper and regular.
- ii) Adaptation strategies may affect the limiting absolute transition probabilities of the system only if the probabilities transition matrix/Markov chain is proper but not regular.
- iii) Adaptation strategies will be efficient only if the expected marginal net benefit of a control, $u_i(t)$, is equal to the user cost of the resource regulated by that control.
- iv) Adaptation strategies will be effective only if the controllability matrix, $(\mathbf{I}, \mathbf{P}, \mathbf{P}^2, \dots, \mathbf{P}^{n-1})$, is of full rank.
- v) Mitigation strategies will affect the long run equilibrium properties of the system if the probabilities transition matrix/Markov chain is proper.
- vi) Mitigation strategies will increase the resilience of the system in state i over some interval (s, t) only if $f_{ii}(s, t) > 0$ (noting that if $f_{ii}(s, t) > 0$, then $f_{ij}(s, t) < 0$ for at least one j).
- vii) Mitigation strategies will be efficient only if the the expected marginal net benefit of a control, $f_i(t)$, is equal to the user cost of all the processes affected by that control.
- viii) Mitigation strategies will be effective only if the controllability matrix, $(\mathbf{F}, \mathbf{P}\mathbf{F}, \mathbf{P}^2\mathbf{F}, \dots, \mathbf{P}^{n-1}\mathbf{F})$ is of full rank.

4. Discussion

To get a sense of the different implications of adaptation and mitigation as strategies for dealing with invasive species, recall that adaptation does not change the transition probabilities of the system. The control regime corresponding to this strategy directly or indirectly regulates the size of the state variables in the system, but otherwise has no impact on their dynamics. For an invasive species problem this form of control can be thought about as a regime of pest controls – actions that work on the biomass of the invasive species. Controls of this sort are efficient if they satisfy the first order necessary conditions for maximisation of the relevant measure of social well-being, and effective if they can reach and control the target species.

There are two cases to consider. If the transition probabilities matrix is regular such that the limiting absolute transition probabilities are independent of initial conditions, then a system of control that acts only on the biomass of invasive species has no effect on the long run outcome. Controls may have a short run effect on the time path of the species concerned, but will not affect the tendency of the system to move in a certain direction. The vector of limiting absolute transition probabilities is simply an eigenvector of \mathbf{P} corresponding to the dominant eigenvalue (equal to 1). Hence, if the control is relaxed the system will converge on the stochastic equilibrium.

If the transition probabilities matrix is not-regular, and specifically if there exist multiple equilibria, then controls over the biomass of invasive species may affect which of a number of limiting or essential states it converges on. This is not because the control has any impact on the transition probabilities, but because the limiting absolute probabilities depend on the initial probabilities. If \mathbf{P} is reducible, the limiting absolute probabilities corresponding to transient states will always be zero, but the limiting absolute probabilities corresponding to different essential states will depend on the initial probabilities and these may be affected by the control.

The first case defines a pure adaptation strategy. The autonomous dynamics of the system are taken as given, and the policy merely exploits those dynamics without in any way changing them. In the second case, the autonomous dynamics of the system are also taken as given, but the policy may have an affect on the outcome in the sense that it may affect the limiting absolute transition probabilities. If the system can exist in several states, the current policy can affect the limiting probability that it will be in any of those states. The

efficiency of that policy will depend on the expected net benefits of being in particular states and the user cost of the resource in those states.

To help give intuition to the important distinction between these two forms of control consider a particular example. In 1986 the UK horticulture industry was invaded by the Western Flower Thrips, *Frankliniella occidentalis*. The stylised facts of the invasion are as follows. There were a number of separate introductions (including one by two Belgian plant health inspectors) most of which were thought to be due to the horticultural trade with the Netherlands. The species affected glasshouses only, and its introduction and subsequent spread between glasshouses was solely due to anthropogenic movements of plant material. It is unable to survive outside of glasshouses in UK conditions. Similarly, its spread within glasshouses was largely dependent on pest control regimes. In principle, therefore, the transition probabilities were controllable.

For two years the UK Plant Health Service sought to eradicate the species, before admitting failure and advising producers to treat the organism as if it were endemic. The control method adopted during those two years was largely directed at eradicating the organism wherever it was detected by destruction of all infected plant material, followed by application of pesticides. This was combined with recommended preventive pest control regimes.

The case is currently under analysis and it is too early to report any empirical results. Nevertheless, the following is a reasonable first pass. The focus of the control was the abundance of the organism itself, rather than the transition probabilities. It was believed that the system might converge on one of two states: with and without the organism. The controls were intended to increase the limiting absolute probability that the organism would be eradicated. However, because (a) the transition probabilities (the transmission mechanisms) were not addressed, and (b) the control was not efficient, the strategy failed.

The illustration helps identify the limitations of an approach that fails to consider the processes that drive the system dynamics. As has been observed in the case of climate change, many invasive species control strategies involve elements of both adaptation and mitigation. Indeed, the optimal strategy will be one that equates the expected marginal net benefits of the two approaches. Wherever eradication fails, the optimal strategy should ensure that the system equilibria are economically sustainable – that the autonomous behaviour of the actors will maintain controls over invasive species at an

economically sustainable level. This may well require intervention to change the transition probabilities of the system. In the illustration, the fact that the transmission mechanisms were wholly anthropogenic means that the system was in principle controllable.

5 Implications for invasive species policy in Europe

The management of invasive species is primarily a problem in the management of risk. There are several recognised sources of risk: biological sources of risk include species and system based factors in the invasiveness of species and the vulnerability of ecosystems; abiotic sources of risk include the impact of climate change on the distribution of species; and socio-economic sources of risk include changes in trade transport and travel as a result of changes in the global economic system and enlargement of the EU. None of these sources of risk are very well understood and hence little can currently be said about the effect of a change in any of them on the probability that a particular introduction will lead to a damaging invasion. Nevertheless, there are clearly incentives to both the private and public sectors to develop better information on the invasion implications of their own actions.

Private resource users already have an incentive to protect themselves against damage to their own interests due to invasive pests and pathogens. But they have little incentive to mitigate damage to others. Nor are such risks commercially insurable for the reason that they are fundamentally uncertain and potentially very large. It is impossible to compute such risks actuarially. However, the EC White Paper on Environmental Liability (COM(2000) 66 final) anticipates a Community framework directive on environmental liability that will provide resource users with a much stronger incentive to take account of their actions, and hence to seek to insure themselves against invasions losses. The proposed Environmental Liability directive is expected to cover liability both for damage due to the use, transport and release into the environment of genetically modified organisms, micro-organisms, plant protection and biocidal products; and for damage to habitats or areas that subject to legal conservation/protection.

Collectively, environmental authorities also have a number of legal contractual commitments to address the problem of invasive species under the Convention on

Biological Diversity (CBD)¹, the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), the FAO International Plant Protection Convention (IPPC)². These commitments require an understanding of how invasion pathways have evolved with the expansion of trade, transport, travel and the greater coordination of activities in different locations. There is, however, still considerable uncertainty about how bioinvasions are affected by changes in the structure, direction and scale of pathways due to renegotiation of the General Agreement on Tariffs and Trade or enlargement of the EU. As of now it is not clear how trade routes, trade volumes, trade values, the regulatory environment, monitoring and scrutiny are related to propagule pressure. Nor are we able to predict the consequences of change in a) the economic variables driving the direction and volume of trade, and b) the regulatory regime.

So the first implication for policy is that a precondition for the rational evaluation of mitigation as an option to adaptation is an improvement in our understanding of the invasion outcomes associated with alternative actions. It must be possible to attach probability density functions to invasion outcomes in order to evaluate the invasion risks of different actions. If it is not possible to calculate invasion probabilities, then adaptation options will tend to dominate by default unless the potential risks warrant precautionary action. This has implications for the way that science supports the decision process.

If it is not possible to compare the expected value of mitigation and adaptation actions but the set of outcomes are thought to include some involving very high and potentially irreversible costs, then a precautionary response may be indicated. A precautionary response should allow learning about invasion probabilities without risking the worst consequences of invasions. If it is not possible to predict a probability distribution of outcomes with confidence, the information on which decision-makers will act will involve something less than scientific proof. Examples include ‘scientifically based suspicion’, ‘reasonable grounds for concern’ and the ‘balance of evidence’ (Harremoës et al, 2001). All involve projections or conjectures about the future costs of current activities that fail standard tests of scientific proof. They are ‘early warning signs’ rather than conclusive proof.

¹ Article 8h of the CBD requires signatories to “Prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species”.

² This requires signatories to secure common and effective action to prevent the spread and introduction of pests of plants and plant products, and to promote appropriate measures for their control.

There is a close connection between such early warning signs and bioinvasion models. For many environmental effects, the only credible sources of information about the potential future effects of different actions are models. Modelling offers a transparent basis for projecting if not predicting the future consequences of current actions. Where projections are based on model simulations rather than laboratory experiments, the test of admissibility is whether the model assumptions (or axioms) accord with reality, rather than the replication of experiments designed to test model predictions.

Non-probabilistic projections (scenarios) are not, however, well suited to the identification of the consequences of mitigation relative to adaptation. The evaluation of the consequences of bioinvasions policy options requires a probabilistic approach that includes feedbacks between the social and the natural system. Nevertheless, if model projections include outcomes that are particularly severe, they may trigger precautionary action. This is action to avoid the outcomes identified, whilst learning about their probability distribution. If, for example, the invasion of a dangerous pathogen is generated as an outcome of the propagule pressure models for reasonable sets of parameter values, and if the costs of adaptation to the invasion are high, then the outcome should trigger precautionary action. This may include standard quarantine restrictions, or the application of trade restrictions allowable under the SPS agreement, combined with research into the consequences of mitigation alternatives.

The potential environmental threats to human, animal and plant life authorise countries to impose trade restrictions under Article XX of the General Agreement on Tariffs and Trade and the SPS Agreement. Indeed, both Article XX and the SPS Agreement have been successfully invoked in many circumstances, but almost never by low income countries. In 1995-7, for example, there were 724 measures notified under the SPS Agreement. Of these 55 per cent were notified by high-income countries, 42 per cent by middle-income countries, and only 2 per cent by low-income countries (UNEP, 1999). In part this may be because trade restrictions under the SPS Agreement must be accompanied by research to prove or disprove the effects that motivate those restrictions. Low income countries are less able to undertake the necessary work.

In fact, the choice between adaptation and mitigation strategies is sensitive to the distribution of income and assets. In principle, adaptation strategies for the control of invasive species typically favour those with the resources to adapt after the fact. Mitigation strategies, on the other hand, typically favour those whose ability to adapt

after the fact is strictly limited, or who are unable to pool the risks of invasions. Exactly the same issues are raised by preventive versus curative medicine. But attitudes to risk depend on what decision-makers have to lose. The poor are generally willing to pay less to reduce risks than are the rich both because their ability to pay is less and because they have less to lose. Moreover, since control of invasive species is a public good of the weakest link variety, the risks to all depend on both the ability and willingness to pay to reduce risks of the weakest member of the community. Mitigation actions – including screening and quarantine – will accordingly be under-supplied by the market. Regardless of their perception of invasion risks, private resource users will invest less in mitigation actions the lower the scope for excluding others from the benefits of that investment and the less alarming are the potentially invasive species themselves. They will have a strong incentive to free-ride on public investment in the same things.

On top of this, even if the incentives are right, the weakest link problem remains. The protection provided to all will only be as good as the protection provided by the weakest link in the chain. This is a practical problem with no ready solution. A central source of information on invasive species may provide the data and technical advice to support mitigation actions. Indeed, the establishment of the National Institute of Invasive Species Science by the US Geological Survey is a first step towards this in this US. But such a Centre will not have the resources to mount campaigns against particular invaders. At a European scale there is a case for establishing an equivalent centre under the 6th Framework Programme, supported by resources to protect the community against the introduction of potentially invasive and harmful species. Internationally, in the absence of a World Environment Organisation commanding sufficient resources to fill this role, there seems to be little alternative to the GEF sponsors, UNEP, UNDP and the World Bank. They should be urged to consider the establishment of a resource capable of protecting both global and regional interests from the threat of Biological Invasions by strengthening the weakest links in the chain.

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