



Mitigation and adaptation strategies for 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.

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1. Mitigation and adaptation

Most ecosystem types have already been impacted to a greater or lesser extent by 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. Research on invasive species worldwide has tended to focus either on human

pathogens such as HIV or SARS or on ‘pests’ whose economic costs in terms of morbidity, mortality, lost output in agriculture, forestry and fisheries, treatment and control are considerable (Perrings et al., 2000; Pimentel et al., 1999; *in press*). 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 invasions also have major implications for the evolution of biodiversity (Clout et al., 1996).

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Whether any sequence of actions will result in the introduction, naturalisation and spread of an invasive species is uncertain. Whether a successful invader will have economically significant effects is also uncertain. 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. Ecosystems vary in their natural susceptibility to invasion. While pelagic marine systems appear to be least susceptible, mixed island systems, lake, river and near-shore marine systems are especially vulnerable (Heywood, 1995). 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). 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).

There are two ways decision-makers can respond to uncertainty: by actions designed to affect the probability of an outcome (referred to as mitigation) and by actions designed to affect the value of an outcome (referred to as adaptation). Of course most decisions involve both elements, but it is useful to distinguish clearly between them. The two approaches have already been identified in the literature on biological invasions (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. Whether an action involves mitigation or adaptation depends on the decision point. If we take species introductions as the decision point, examples of mitigation include actions designed to reduce the likelihood of new introductions, such as

red/green lists, quarantine restrictions or trade measures permitted under the Sanitary and Phytosanitary Agreement of the General Agreement on Tariffs and Trade, or the International Plant Protection Convention. Examples of adaptation to the risks of species introductions 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. On the other hand, if the decision point is the establishment, naturalisation and spread of species that have already been introduced, then eradication and control are both examples of mitigation, while insurance or the accommodation of invasive species is an example of adaptation.

Which strategy is appropriate therefore depends partly on the decision point (where the decision-maker is able to intervene, what the boundaries of the problem are) and in part on the degree to which the system is either observable or controllable (whether it is predictable, and whether policy or management tools can reach their targets). Williamson (1999) argues that many if not most new impacts by invasive species are not predictable. Support for Williamson comes from a number of quarters. Lawton (1999) claims 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., 2000; Kareiva et al., 1996). Williamson (1999) found that the only acceptable predictor other than propagule (e.g. seed) 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. According to this view, it is possible to understand both the invasiveness of different species, and the invasibility of different habitats (Rejmanek, 1989). 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, is 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 et al. (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 stochastic processes

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 the transition probabilities are independent of time, the matrix of transition probabilities, \mathbf{P} , defines a homogeneous Markov chain.¹ 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 is not necessarily equal to m . The dynamical implica-

tions 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.² From the definition of the conditional probabilities $p_{ij}(s, t)$, it 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. These can be thought about as the long-run equilibria of the system. To see the significance of the limiting transition probabilities for the introduction of potentially invasive species, consider the properties of the Markov chain corresponding to \mathbf{P} . Note that a Markov chain is ‘proper’ if \mathbf{P} has no eigenvalues equal to -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:

$$\mathbf{P}^\infty = \left[\begin{array}{ccc|c} \mathbf{P}_{11}^\infty & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & \mathbf{P}_{mm}^\infty & 0 \\ \hline \mathbf{Q}_\infty & & & 0 \end{array} \right] \quad (2)$$

where \mathbf{Q}_∞ defines the limiting transition probabilities of the submatrices \mathbf{P}_{ij} ($i=m+1, \dots, n; j=1, 2, \dots, m$).

¹ For the general approach, see Karlin and Taylor (1981) and Dynkin and Yushkevich (1979).

² 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.

That is, the limiting transition probabilities $\mathbf{P}_{m+1m+1}^\infty, \dots, \mathbf{P}_{nn}^\infty$ are all equal to zero. If the introduction of an invasive species has any long-run effect this will be reflected in the limiting transition probabilities on the principle diagonal (the blocks $\mathbf{P}_{11}^\infty, \dots, \mathbf{P}_{mm}^\infty$).

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, and is independent of the control regime.
- (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.

2.1. 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 implies that the limiting transition probabilities associated with the set of potential states of nature $S_1(t), S_2(t), \dots, S_n(t)$ is the same as that associated with the set $S_1(0), S_2(0), \dots, S_m(0)$. In this case Eq. (2) implies that the introduced species would fail to establish, naturalise and spread. They would be excluded from the system in the limit.

2.2. The probability that an introduced species succeeds in establishing naturalising and spreading is positive, and is independent of the control regime

This case implies that the limiting transition probabilities associated with the set of potential states of nature $S_1(t), S_2(t), \dots, S_n(t)$ is not the same as that associated with the set $S_1(0), S_2(0), \dots, S_m(0)$.

We first consider the case where \mathbf{P} is both proper and regular.³ In this case, \mathbf{P} is irreducible. It cannot be decomposed into the normal form described in Eq. (1); i.e. there are no multiple limiting states (equilibria). It also follows that the limiting transition probabilities are positive and independent of the initial invaded state. No matter what resources are committed to eradicating or containing the invader, and no matter how the invasion takes place, the system will converge on the same limiting 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). Second, 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.

2.3. 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

³ 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.

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 Eq. (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 nonessential and essential states, between nonessential 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 Eq. (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.

2.4. 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 .⁴ 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. Specifi-

cally, 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 proba-

⁴ 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.

abilities define the probability that the system in one state will change to another state.

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 for a system to be 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 nonessential or transient states are not resilient. All limiting or recurrent states are resilient to some degree.⁵

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 provides guidance on the need for a response, as well as the nature of the response.

3. The control strategies

Now consider the two potential 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 (control-ability) 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. If we take the decision point to be the introduction of potentially invasive species, adaptation includes actions that directly change the abundance of introduced species through, for example, pest control. Such adaptation does not make introduction of invasive species 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. Indeed the harvest of wild species can be seen as an adaptive strategy given the intrinsic dynamics of those species.

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

$$\dot{\mathbf{x}} = \mathbf{P}\mathbf{x}(t) + \mathbf{u}(t) \cdot \quad (4)$$

Since the choice of $\mathbf{u}(t)$ has no implications for \mathbf{P} , it does not change the transition probabilities.

⁵ 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.

Mitigation. The second approach to the control of invasive species involves changes to the probability law itself through, for example, 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, $\mathbf{F}(t)$, that works on the set of state variables over which the decision-maker has control, defined by $\mathbf{C}\mathbf{x}(t)$. Hence, $\mathbf{u}(t)$ in Eq. (4) takes the form $\mathbf{F}(t)\mathbf{y}(t)$, where $\mathbf{y}(t)=\mathbf{C}\mathbf{x}(t)$, and the equations of motion can be written as:

$$\dot{\mathbf{x}} = \mathbf{P}\mathbf{x}(t) + \mathbf{F}(t)\mathbf{C}\mathbf{x}(t). \tag{5}$$

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

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:

$$V(\mathbf{x}(t), \mathbf{u}(t), t) = E\left(\int_{t=0}^{\infty} e^{-\delta t} W(\mathbf{x}(t), \mathbf{u}(t))dt\right) \tag{6}$$

$$V(\mathbf{x}(t), \mathbf{F}(t), t) = E\left(\int_{t=0}^{\infty} e^{-\delta t} W(\mathbf{x}(t), \mathbf{F}(t))dt\right) \tag{7}$$

in which $W(\cdot)$ is a strictly concave continuous function defining social preference orderings over the set of all feasible $\mathbf{x}(t)$ and $\mathbf{u}(t)$ or $\mathbf{F}(t)$. $\delta(t)$ is a discount rate. $W(\cdot)$ is the discounted flow of benefits deriving from the use of all resources.

The problem in both cases is to find the ‘control’ sequence that maximizes W , subject to the dynamics of the system given by Eq. (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:

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

$$\tilde{\mathbf{H}}(\mathbf{x}(t), \mathbf{F}(t), \mu(t), t) = E(W(\mathbf{x}(t), \mathbf{F}(t))) + \mu(t)(\mathbf{P}\mathbf{x}(t) + \mathbf{F}(t)\mathbf{x}(t)) \tag{8b}$$

implying (amongst others) the following first order necessary conditions for maximization of Eq. (6) (7) subject to Eqs. (4) and (5):

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

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

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

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

$$\dot{\mathbf{x}} = \mathbf{P}(t)\mathbf{x}(t) + \mathbf{u}(t) \tag{11a}$$

$$\dot{\mathbf{x}} = \mathbf{P}\mathbf{x}(t) + \mathbf{F}(t)\mathbf{C}\mathbf{x}(t) \tag{11b}$$

$$\mathbf{x}(0) = \mathbf{x}_0 \tag{12}$$

$$\lim_{t \rightarrow \infty} \mu(t) = 0 \tag{13}$$

where \mathbf{p}_i and \mathbf{f}_i are the i th columns of \mathbf{P} and \mathbf{F} , respectively. Eqs. (9a) and (9b) require that the control policy, $\mathbf{u}(t)$ and $\mathbf{F}(t)$, be selected so as to maximize 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. Eqs. (10a) and (10b) are conditions on the rate of change of the multipliers. In Eq. (10a) μ_i has the natural interpretation of the shadow value of the i th resource. In Eq. (10b), it defines the shadow value of the probability law governing that resource. Eqs. (11a), (11b) and (12) 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 Eq. (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, for example, the regulation of invasion pathways, as in Eq. (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 a matrix of full rank. That is, if the equations of motion takes the form of Eq. (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 Eq. (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 incen-

tives) the rank condition defines the limits of their effectiveness.

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 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 $(\mathbf{F}, \mathbf{PF}, \mathbf{P}^2\mathbf{F}, \dots, \mathbf{P}^{n-1}\mathbf{F})$ 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 the 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 maximization 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. This 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.

Now consider mitigation. In this case, the control is not over the value of the state variables, but over the transition probabilities themselves, p_{ij} . For example, if p_{ii} is the probability that a system will remain in that state, a policy aiming to change the propagule pressure through the use of red (black) lists 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 \mathbf{F} , or the number of processes that are influenced by the policy. If \mathbf{F} is less than full rank, the system will not be controllable. To illustrate, suppose that \mathbf{P} is reducible as follows:

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

implying that

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

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

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

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 $\mathbf{P}+\mathbf{F}$ is stochastic, it follows that the ‘controlled’ system has the transition probabilities:

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

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 to the stochastic equilibrium; but if $f_{12} \neq 0$ and the limiting absolute transition probabilities for both states are strictly positive, the control policy would have ensured that the probability that the system is in state 2 in the limit was greater than zero.

As has been observed in the case of climate change, many invasive species control strategies involve elements of both adaptation and mitigation, and whether a strategy involves mitigation or adaptation depends on the decision point. 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.

There are a number of other factors to take into account in the choice of strategy. These include the significance of irreversible effects where there are multiple stable states, the speed of convergence

(which regulates the timing of the costs and benefits of alternative control options), and the equity implications of strategies that require significantly different initial outlay. 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. A discussion of these issues is beyond the scope of this paper, but they are important nevertheless.

The central point at issue in all decisions involving uncertainty is whether it is possible to identify a path between present actions and future outcomes, and whether it is possible to attach probabilities to the outcomes of distinct actions. If it is possible to do so, then it is also possible to consider mitigation as an option. If it is not possible to do so, then adaptation after the fact is the default strategy. In many cases, it is not possible to trace the paths between actions and outcomes, or to attach probabilities to those outcomes, because of fundamental scientific uncertainty about the dynamics of the system; but wherever it is possible to do so then the optimal policy will consider both strategies. In an environment in which decision-making is increasingly dominated by non-probabilistic ‘scenarios’ which drive decision-makers to focus on adaptation, it is important to remind ourselves that this may be both inefficient and inequitable.

References

- Clout, M., Lowe, S., and the IUCN/SSC Invasive Species Specialist Group, 1996. Draft IUCN Guidelines for the Prevention of Biodiversity Loss due to Biological Invasion. URL: <http://www.weeds.merriweb.com.au/IUCN-inv.htm>.
- Dynkin, E., Yushkevich, A., 1979. *Controlled Markov Processes*. Springer-Verlag.
- Enserink, M., 1999. Biological invaders sweep in. *Science* 285, 1834–1836.
- Heywood, V. (Ed.), 1995. *Global Biodiversity Assessment*. Cambridge University Press, Cambridge.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annual Review of Ecological Systems* 4, 1–24.
- Kareiva, P., Parker, I., Pascual, M., 1996. How useful are experiments and models in predicting the invasiveness of genetically engineered organisms? *Ecology* 77, 1670–1675.
- Karlin, S., Taylor, H.M., 1981. *A Second Course in Stochastic Processes*. Academic Press.
- Law, R., Weatherby, A., Warren, P.H., 2000. On the invisibility of persistent protist communities. *Oikos* 88, 319–326.
- Lawton, J.H., 1999. *Biodiversity and Ecosystem Processes: Theory, Achievements and Future Directions, the Biology of Biodiversity*. Springer-Verlag, Tokyo, pp. 119–131.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10 (3), 689–710.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1, 3–19.
- Perrings, C., 1998. Resilience in the dynamics of economy–environment systems. *Environmental and Resource Economics* 11 (3–4), 503–520.
- Perrings, C., Williamson, M., Dalmazzone, S., 2000. *The Economics of Biological Invasions*. Elgar, Cheltenham.
- Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 1999. *Environmental and Economic Costs Associated with Non-indigenous Species in the United States*, College of Agriculture and Life Sciences. Cornell University, Ithaca, NY.
- Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien species in the United States. *Ecological Economics* 52, 273–288.
- Rejmanek, M., 1989. Invasibility of plant communities. In: Drakem, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmanek, M., Williamson, M. (Eds.), *Biological Invasions: a Global Perspective*, SCOPE 37. Wiley, New York, pp. 369–383.
- Shogren, J., 2000. Risk reduction strategies against the explosive invader. In: Perrings, C., Williamson, M., Dalmazzone, S. (Eds.), *The Economics of Biological Invasions*. Elgar, Cheltenham, pp. 56–69.
- Shogren, J., Crocker, T., 1999. Risk and its consequences. *Journal of Environmental Economics and Management* 37, 44–51.
- Smith, C.S., Lonsdale, W.M., Fortune, J., 1999. When to ignore advice: invasion predictions and decision theory. *Biological Invasions* 1, 89–96.
- Vila-Gispert, A., Moreno-Amich, R., 2002. Life-history patterns of 25 species from European freshwater fish communities. *Environmental Biology of Fishes* 65, 387–400.
- Watkinson, A., Freckleton, R.P., Dowling, P.M., 2000. Weed invasions of Australian farming systems: from ecology to economics. In: Perrings, C., Williamson, M., Dalmazzone, S. (Eds.), *The Economics of Biological Invasions*. Elgar, Cheltenham, pp. 94–116.
- Wilcove, D.S., et al., 1998. Quantifying threats to imperilled species in the United States. *Bioscience* 48, 607–615.
- Williamson, M., 1998. Measuring the impact of plant invaders in Britain. In: Starfinger, S., Edwards, K., Kovarik, I., Williamson,

- M. (Eds.), *Plant Invasions. Ecological Mechanisms and Human Responses*. Backhuys, Leiden, pp. 57–70.
- Williamson, M., 1999. Invasions. *Ecography* 22, 5–12.
- Williamson, M., 2000. Quantifying the ecological and economic risks of invaders and GMOs. *Proceedings of the Workshop on Plant Health in the New Global Trading Environment: Managing Exotic Insects, Weeds and Pathogens*, Canberra.
- Williamson, M., Fitter, A., 1996. The varying success of invaders. *Ecology* 77, 1661–1666.