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Managing beyond the invader: manipulating disturbance of natives simplifies control efforts

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Summary

1. Invasive plants have negative impacts on ecosystems worldwide. Several ecological studies have identified disturbance as a causative mechanism of plant invasions. Changes to natural disturbances and/or newly imposed disturbances can favour an invader over native species especially those that are better adapted to prior conditions.

2. To link the disturbance ecology of invasives to their management, we investigated the benefit of incorporating actions that manipulate disturbance (natural or imposed) into control efforts. We developed a simple model that describes the dynamics of an invader whose establishment is preferentially favoured by disturbance.

3. The model includes the probability of disturbance differentially affecting sites occupied by natives and invaders. Invaded sites are disturbed by alternative control measures, which act to kill and/or remove above-ground biomass and reduce the seed bank. We couched the model in a decision theory tool, stochastic dynamic programming, and applied it to the management of *Mimosa pigra*, a pan-tropical invasive perennial shrub.

4. We found that targeting the above-ground biomass of the invader (current population) was optimal when the probability of disturbance of native sites and the invader seed bank size were low to moderate. When both the rate of disturbance of native sites and invader seed banks were high, the best measure was that with the highest probability of reducing the seed bank (future populations). This measure was optimal despite its trade-off of having the highest probability of reinvasion.

5. *Synthesis and applications.* Manipulation of disturbance regimes in both native and invaded sites can simplify control efforts. If there is a high probability that native vegetation will be disturbed, then management efforts should focus on future populations by attempting to reduce the size of the invader seed bank. This complicates control, as seed bank size is difficult to measure and reducing it requires intensive actions, which are likely to also negatively affect the seed bank of native species. If, however, the probability of disturbance of native sites can be reduced, practitioners can shift control from future populations to the current population, which is more straightforward to implement and monitor.

Key-words: integrated weed management, *Mimosa pigra*, stochastic dynamic programming, seed bank dynamics, weed control, population dynamics, decision-making, seed dispersal

Introduction

Across the world, invasive plants continue to spread into and dominate new areas, despite large investments of time and money into control efforts. Because of their high impact, ecological studies have focused on isolating the causal mechanisms behind invasion (Parker *et al.* 1999; Levine *et al.* 2003). Several studies have identified imposed exogenous disturbance and/or alterations to existing endogenous disturbance as facilitating the recruitment of invaders over natives better adapted to previous regimes (Hobbs & Atkins 1988; Seabloom *et al.* 2003; MacDougall & Turkington 2005).

Disturbance is a complex mechanism, as on one hand, it can facilitate co-existence and maintain biodiversity by increasing opportunities for adapted natives to establish (Connell 1978), while on the other hand, changes to or newly imposed disturbance can create conditions that favour the dominance of one species over others (Connell 1978). The

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effect disturbance has on species richness will vary depending on its inherent frequency, intensity, duration, timing, scale and distribution (Connell 1978; White & Pickett 1985; Lockwood *et al.* 2007). The species that assemble after disturbance will also depend on the characteristics of the individual ecosystem, including the composition of the seed bank, resource availability, and competitive hierarchies between species (Davis *et al.* 2001; Daehler 2003; Lockwood *et al.* 2007).

Disturbance can directly facilitate plant invasion by reducing the physical presence of native species, thereby reducing competition and increasing essential resources for germination, seedling survival and growth (Pickett *et al.* 1989). Disturbance can also indirectly facilitate invasion by changing resource availability so that conditions are no longer suitable for native species (i.e. increased soil nutrient levels or the availability of light). Disturbance, therefore, can modify both the abiotic and biotic conditions that promote the recruitment and subsequent persistence of invasives and directly or indirectly suppress natives (Hobbs & Huenneke 1992; Davis *et al.* 2005). In this case, the invader may only be a symptom of the effects of disturbance and not itself directly impacting on native species or as described by MacDougall & Turkington (2005), the 'passenger' not the 'driver'. It can, however, still be desirable to reduce invader densities in disturbed ecosystems where they are not the direct drivers of impacts to reduce propagule supply into more pristine areas or to slow down spread across the landscape (Buckley 2008; Jodoin *et al.* 2008).

If disturbance is found to preferentially favour the recruitment of an invader, then actions taken to either reduce or stop the causal disturbance could aid control efforts. Targeting disturbance is not, however, always straightforward from a management perspective. Some disturbances can be controlled, i.e. baiting or trapping feral animal populations, adding carbon to reduce nutrient levels in enriched soils or the prevention of unnecessary land clearing. However, it may be difficult or undesirable to control all causal disturbances, as some are essential to the integrity of an ecosystem including aiding the dispersal and survival of native species (e.g. intermittent flooding in seasonal wetland regions), while others are highly valued economically and socially (e.g. disturbances associated with agriculture).

Control measures available to practitioners can also create disturbances. Disturbances due to application of herbicides, bulldozing and burning resemble natural disturbances because they act to remove or kill plants. The difference is that the frequency and intensity of management disturbances are prescribed and ideally target the invader. The composition of the plant community that assembles after the disturbance depends on how the control measure alters the biotic and abiotic conditions (Horvitz *et al.* 1998; Rouget & Richardson 2003). Some management disturbances may, inadvertently, create the ideal conditions for a disturbance promoted invader to re-establish. Asymmetries between disturbance regimes in native and invaded sites, either natural or management imposed, can have profound effects on invasion dynamics and management options. Buckley *et al.* (2007) showed that when disturbance to native sites is high, management actions which disturb invaded sites can result in Allee effects where above a threshold, the management of invader density is no longer effective.

Here we develop a simple model to further explore how asymmetries in disturbance between native and invaded sites affect optimal management decisions. We then couch this model in a rigorous decision theory tool, stochastic dynamic programming (SDP), to solve for the optimal control measure. To illustrate the utility of this approach for invasive plant management, we apply it to a case study of one of the most serious threats to Australian tropical ecosystems – the invasion of *Mimosa pigra*, a perennial legume shrub. Finally, we put forward useful generalizations for practitioners managing land areas degraded by disturbance and invasive plant species.

Case study: the invasion of *Mimosa pigra*

Mimosa pigra (hereafter *Mimosa*) is a woody legume species native to Central and South America that has become a serious weed of tropical wetlands in Australia, Vietnam and Thailand (Cronk & Fuller 1995). In Australia, it is one of 20 weeds of national significance because of its potential for further spread and socioeconomic and environmental costs (Thorp & Lynch 2000).

Since its introduction into Australia in the early 1900s (Lonsdale 1992), *Mimosa* has spread long distances across the flood plain regions of the Northern Territory. It is believed that unusually heavy seasonal rain coupled with heavy grazing by feral animals in the 1970s facilitated long-distance dispersal (Lonsdale & Farrell 1998). *Mimosa* is now found in most major river systems and dominates areas previously covered by native grasses and sedges. It has an estimated range of more than 800 km^2 and is described as having the capacity to double this area every year (Cook & Setterfield 1996; Paynter & Flanagan 2004). Flooding during the wet season in this region is common and favours the spread of *Mimosa* because seed pods float and remain viable on the surface of rivers or flood waters. Mean dispersal distances of 14 to 195 m per year have been recorded (Lonsdale 1993).

Mimosa forms dense monocultures up to 6 m in height that greatly reduce the availability of key resources, such as light, for native species (Lonsdale & Farrell 1998). The invasion of *Mimosa* into the Northern Territory is exacerbated by disturbances associated with the foraging behaviour of water buffalo *Bubalus bubalis*. Buffalo graze heavily on natives and disturb the soil (Lonsdale 1992). These disturbances act to reduce competition and increase resources such as light (Lonsdale *et al.* 1988; Lonsdale & Farrell 1998), creating the ideal seed bed for germination and establishment by *Mimosa*.

Methods

SITE TRANSITIONS

In the model, we describe an area that is divided into Z sites. Each site can be in one of five states including two temporary states. Let

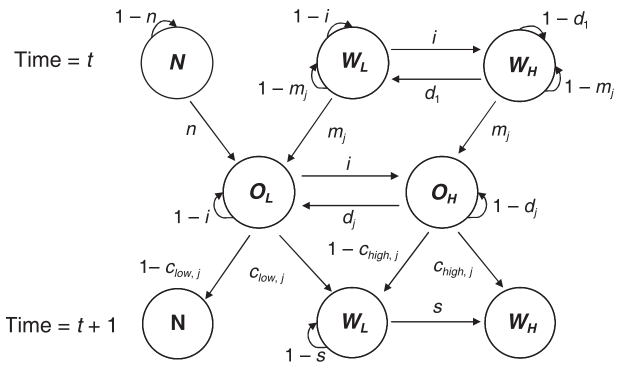

Fig. 1. Transitions between states for one site, the states are: N, sites occupied by native plant species; W_L, sites occupied by the invader with a low seed bank; W_H, sites occupied by the invader with a high seed bank; O_L, sites cleared of vegetation by disturbance so open with a low seed bank; and O_H, disturbed sites that are open with a high seed bank. The open sites are temporary, changing to one of the other three states before the end of the time-step; n is the probability that a site occupied by a native population is disturbed; m_j is the probability that a control measure (j) successfully removes or kills the invader from a site; probability of seed bank decrease (d_j) and increase (i); probability of invader establishment of an open site with a low seed bank ($c_{low,j}$) and the probability an open site with a high seed ($c_{high,j}$) remains an invader occupied site with a high seed bank. Probability of seed bank growth, s.

N be the number of sites occupied by native vegetation, W_L the number of sites that have been recently invaded so have a low seed bank, W_H the number of sites invaded with a high seed bank, O_L the number of sites that have been recently disturbed with a low seed bank (temporary) and O_H the number of sites disturbed with a high seed bank (temporary) (Fig. 1). O_L and O_H are temporary in that sites cannot remain open at the end of each time step.

We assume that disturbance affects each site independently and all invader-occupied sites are treated with the same control measure at each time step (native-occupied sites are not treated). In each time step, there are five processes that can change the state of a site: disturbance, seed bank decrease, seed bank increase due to dispersal, invader establishment, and invader reproduction (parameters defined in Fig. 1).

DISTURBANCE

Disturbance kills and/or removes vegetation from a site. Disturbances that negatively affect natives occur with probability n, and promote invasion by opening up micro-sites and changing resource conditions, i.e. land clearing, grazing, trampling etc. Disturbances to sites occupied by the invader are control measures indexed by the integer j (i.e. herbicides, bulldozing and prescribed burning), with their effectiveness given by the disturbance probability m_j (Fig. 1).

Given the probability m_j that an invader-occupied site with a low seed bank (W_L) becomes an open site with a low seed bank (O_L) under control measure j, the probability that l of the low seed bank invader sites become open sites with a low seed bank is (Fig. 1):

$$P_{m_j}(l, W_L) = \binom{W_L}{l} m_j^l (1 - m_j)^{W_L - l},$$

where $W_L \geq l \geq 0$ and $\binom{W_L}{l}$ is the binomial coefficient, representing the number of possible ways to choose l transitions in W_L tries with probability m_j.

Given the same probability of transition m_j, the probability that h of W_H invader-occupied sites with a high seed bank become open sites with a high seed bank is:

$$P_{m_j}(h, W_H) = \binom{W_H}{h} m_j^h (1 - m_j)^{W_H - h},$$

where $W_H \geq h \geq 0$.

Similarly, given the probability n that a native site becomes an open low seed bank site, let $P_n(u,v)$ be the probability that u of v native sites (where $v = Z - W_H - W_L$) become open sites:

$$P_n(u, v) = \binom{v}{u} n^u (1 - n)^{v-u},$$

where $v \geq u \geq 0$.

Changes in the seed bank of the invader

Invader-occupied sites and newly opened sites are described as having either a low or a high seed bank. We assume that in an existing invasion, every site has at least a low invader seed bank and that a decrease in seed bank size occurs first (Fig. 1).

Each control strategy j has a different probability d_j of reducing the size of the seed bank by accelerating the loss of viability (i.e. the use of soil-persistent herbicides or heat from fire); sites that are open with a high seed bank can become sites that are open with a low seed bank. The seed bank can also decrease in size due to variable natural seed decay, varying with site characteristics such as moisture and temperature; weed-occupied sites can change from having a high to a low seed bank (Fig. 1).

As a result of a seed dispersal event (i.e. intermittent flooding, high winds or the accidental introduction of seed due to large-scale landscape modification) seed bank increase can change O_L and W_L sites to O_H and W_H sites, respectively, with probability i. As before, we use a binomial distribution to find the probability of a number of sites transitioning between states (Fig. 1).

Establishment

Open sites (O) can be colonized or re-colonized by the invader, to become invader-occupied sites (W) (Fig. 1). The probability $c_{b,j}$ that an open site will be successfully colonized by the invader (while maintaining its seed bank level, i.e. O_L becomes W_L and O_H becomes W_H) depends on the type of control measure used j, and the size of the seed bank b (*high*, *low*). An open site with a high seed bank is certain to be colonized by the invader, but the seed bank size may be reduced. In other words, O_H sites can become either W_H sites with the probability $c_{high,j}$ or W_L sites with the probability $1 - c_{high,j}$. If open sites with a low seed bank are not colonized to become invader sites with a low seed bank, they are colonized by native vegetation; open sites no longer remain after the establishment transition. We use the binomial distribution to find the probability of a number of sites transitioning between states due to colonization.

Post-establishment seed bank growth

The final process is seed bank growth in invader-occupied sites due to production of seed by adult plants. A site occupied by the invader with a low seed bank W_L may increase its seed bank (to become W_H) with a probability s (Fig. 1). Sites occupied by the invader with a low seed bank at the beginning of the time step may have escaped control or were re-colonized by a fast-reproducing species and accumulated a high seed bank before the end of the growing season. We again use the binomial distribution to find the probability of a number of sites transitioning between states.

After calculating the probabilities of transition for each of these five sequential processes, we combine them in a Markov chain transition matrix $\mathbf{A}_j$. $\mathbf{A}_j$ contains the probabilities (for all possible values of W_L, W_H, x and y) that W_L low and W_H high seed bank invader sites at time t will become x low and y high seed bank invader sites at time $t + 1$. These probabilities differ depending on j, the control measure used. The Supplementary Material (Appendix S1) provides a detailed description of the transition probabilities.

Stochastic dynamic programming (SDP)

SDP is a rigorous tool that can be used to find the optimal state-dependent decisions for a stochastic system (Bellman 1957; Kennedy 1981; Mangel & Clark 1988). In our formulation, there are four possible control measures with the indices $j = 1, 2, 3$ and 4 that can be undertaken at each time step of the planning horizon ($t = 0, \ldots, T$). SDP finds the optimal control measure for each combination of low seed bank invader sites, W_L, and high seed bank invader sites, W_H, where each combination represents the extent of the invasion at each time step t in the planning horizon. The management objective we set is to maximize the number of sites occupied by native vegetation in the final time step T. This is expressed as

$$V(T, W_L, W_H) = Z - W_L - W_H,$$

where $V(T, W_L, W_H)$ is the value of having W_L low seed bank invader sites and W_H high seed bank invader sites at time T, and Z is the total number of sites. As we assume sites must either be occupied by the invader or by native vegetation at the end of each time step, we can calculate the number of native-occupied sites as the number not occupied by the invader.

At time T, the value function is calculated for every possible combination of W_L and W_H. The SDP then moves backwards through time, calculating the value of possible decisions for every scenario, assuming all subsequent decisions are optimal. The optimal decision for each scenario at each time step t is the action with the highest value, as given by the following dynamic programming equation:

$$V(t, W_L, W_H) = \max_{j=\{1,2,3,4\}} \sum_{x=0}^{Z} \sum_{y=0}^{Z-x} a^{j}_{W_L, W_H, x, y} V(t + 1, x, y)$$

$V(t, W_L, W_H)$ is the value of having W_L low seed bank invader sites and W_H high seed bank invader sites at time t, and $a^{j}_{W_L, W_H, x, y}$ is the element of the transition matrix $\mathbf{A}_j$ containing the probability that W_L low and W_H high seed bank invader sites at time t become x low and y high seed bank invader sites at time $t + 1$. $V(t + 1, x, y)$ is the value of having x low seed bank invader sites and y high seed bank invader sites at time $t + 1$.

Control of *Mimosa pigra*

Four potential management measures are included in the model: no control ($j = 1$), application of herbicides ($j = 2$), application of herbicides and mechanical removal of plants ($j = 3$), and application of herbicides and prescribed burning ($j = 4$). Each of these measures has a different probability of successfully killing and/or removing the invader from the site (m_j), reducing the size of the invader seed bank (d_j), and the invader re-establishing on a site ($c_{b,j}$) (Table 1).

The aerial application of herbicides ($j = 2$), has the lowest probability of killing *Mimosa* ($m_2 = 0{\cdot}65$). Achieving full coverage of all tissue using herbicides is difficult because of the broad-scale nature of an aerial application and the dense structure of *Mimosa* thickets. This measure will not accelerate natural seed decay within the seed bank ($d_2 = 0{\cdot}01$), but is, however, relatively simple to apply in terms of time and effort. If successful, this measure has the lowest probability that *Mimosa* will establish on open sites with a low seed bank because standing dead tissue is left behind ($c_{low,2} = 0{\cdot}29$). If a site is open with a high seed bank, this measure has the highest probability that the seed bank size will remain high ($c_{high,2} = 0{\cdot}71$).

Table 1. Trade-offs between alternative control measures including the probability of killing the invader, decreasing the seed bank size and the invader re-establishing

	Probability values			
Control measure	Kills invader m_j	Decrease in seed bank size d_j	Establishment (low seed bank) $c_{low,j}$	Establishment (high seed bank) $c_{high,j}$
1. No control	0·05	0·01	0·45*	0·55
2. Herbicide	0·65	0·01	0·29*	0·71
3. Herbicide + mechanical	0·75	0·15	0·45*	0·55
4. Herbicide + prescribed burn	0·70	0·29	0·80*	0·20

*Buckley *et al.* (2004).

Table 2. Baseline parameters used in the *Mimosa pigra* case study

Parameter	Description	Value
Probability a native species site is disturbed n		
n	Buffalo disturb a native species site	0·10*
Probability of an increase in seed bank size i		
i	Seed bank increase, flood event	0·10
Probability of a decrease in seed bank size d_j		
d_n	Feral buffalos disturb a site occupied by native species	0·01
Probability of establishment, $c_{b,j}$ where $b = low, high$		
$c_{low,n}$	Feral buffalos disturb a site occupied by native species (low seed bank)	0·45*
$c_{high,n}$	Feral buffalos disturb a site occupied by native species (high seed bank)	0·55
Probability of growth in the invader seed bank, s		
S	Site occupied by *Mimosa* with a low seed bank accumulate a high seed bank	0·80

*Buckley *et al.* (2004).

The combined treatment of herbicide and mechanical removal of plants ($j = 3$) has the highest probability of killing *Mimosa* ($m_3 = 0{\cdot}75$) because the application of herbicides prior to mechanical removal reduces regrowth. Mechanical removal has a higher probability of reducing the size of the seed bank than the use of herbicides alone because of the disruptive nature of using techniques such as bulldozers and raking ($d_3 = 0{\cdot}15$), with a moderate probability of the invader establishing if the seed bank is low ($c_{low,3} = 0{\cdot}45$). A site controlled with this measure and with a high seed bank has a moderate probability that the seed bank will remain high ($c_{high,3} = 0{\cdot}55$). This combined measure requires more effort and time than herbicide application alone.

The use of herbicides and then a prescribed burn ($j = 4$) has a higher probability of killing existing *Mimosa* populations ($m_4 = 0{\cdot}7$) than either using herbicides or fire alone, because *Mimosa* can be difficult to burn when it is green (Lonsdale, 1992). However, effectiveness is not as high as herbicides and mechanical removal ($j = 3$), because the extent of the coverage is not under as much control by the practitioner as mechanical methods. Herbicides plus burning is the measure with the highest probability of reducing the size of the seed bank, as intense fires have been found to reduce the viability of *Mimosa* seeds ($d_4 = 0{\cdot}29$) (Lonsdale & Miller 1993).

The trade-off of the herbicide and fire treatment is that this has the highest probability of *Mimosa* re-establishing if the seed bank is low ($c_{low,4} = 0{\cdot}80$), because fire has also been found to accelerate the breakdown of the outer coat of *Mimosa* seeds and increase the rate of germination (Lonsdale & Miller 1993). If an open site has a high seed bank, this measure has the lowest probability the seed bank will remain high when the invader re-establishes ($c_{high,4} = 0{\cdot}20$). This measure is the most challenging to apply as a prescribed burn requires expert knowledge of weather conditions and fuel loading to ensure the fire reaches the optimal temperature to destroy seeds and/or stimulate germination.

The precise value of the probabilities for each control measure is difficult to estimate accurately as it is likely to vary depending on the scenario; therefore, what is more important is the relative ranking. For example, the use of herbicides alone is likely to be less effective at killing an invasive plant like *Mimosa* than the combination control measure of herbicide plus mechanical and herbicide plus burning. Also, the herbicide and burn option is, in most situations, likely to stimulate the most germination from the *Mimosa* seed bank because of the known effects of smoke and heat.

Sites occupied by native species can be disturbed by feral animal grazing and trampling with the probability n, opening a site to invasion as competition from native grasses is reduced or removed and mineral soil is exposed (Table 2 shows baseline values for these parameters). The seed bank can also increase from low to high with the probability of a flood large enough to act as a seed dispersal agent i. In the SDP framework, we use a realistic management horizon of between 1 year and 10 years with a decision made about which control measure to use each year.

Results

The optimal decisions found using the baseline parameters (Tables 1 and 2) are shown in Figs 2 and 3a. For example in

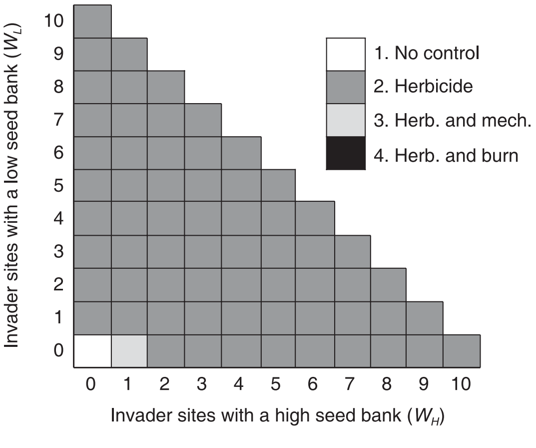

Fig. 2. The optimal set of control strategies at the start of the planning period depending on the management scenario (number of invader occupied sites with a low or high seed bank) using the baseline parameters presented in Tables 1 and 2 and with a planning time horizon of just 1 year. Each box represents the possible management scenario at the start of the planning period. The shade of the box indicates the optimal measure if the system is in that state at time **0**.

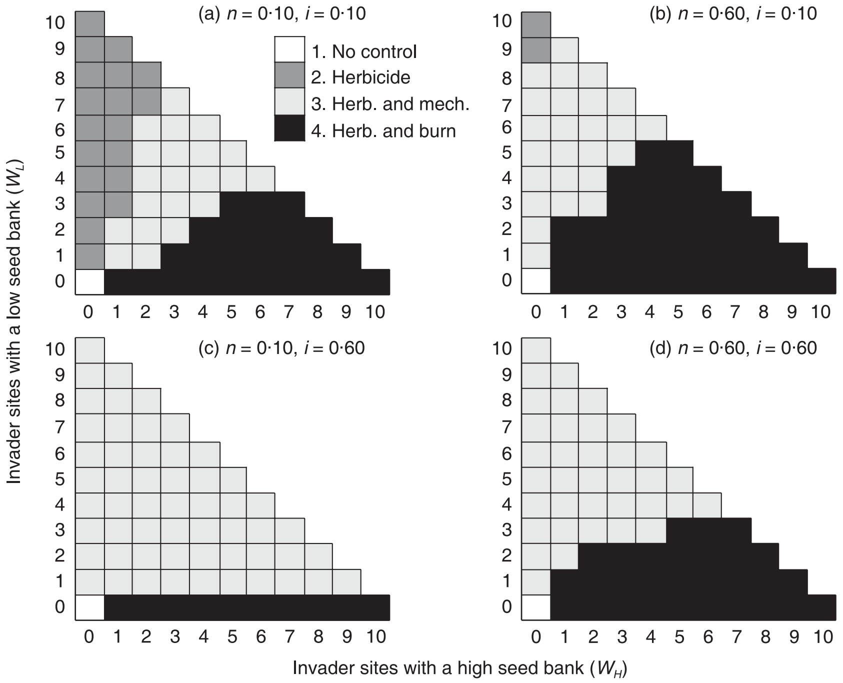

Fig. 3. Optimal control measures (at the start of the planning period) for all possible management scenarios and a planning time of **10** years when both the probability of disturbance, *n*, is increased (shown from left to right) and seed bank size due to dispersal (e.g. flooding), *i*, increases (shown from top to bottom).

Fig. 3a, if all 10 sites are occupied with *Mimosa* and have a high seed bank, then the optimal control measure is the combined application of herbicides and a prescribed burn. If all 10 sites are occupied by native species then the optimal measure is no control (Figs 2 and 3).

OPTIMAL CONTROL DEPENDS ON THE LENGTH OF THE PLANNING HORIZON AND EXTENT OF INVASION

For a planning horizon (T) of 1 year and > 1 sites occupied by *Mimosa* with a high seed bank, the optimal control measure is the application of herbicides. The merit of this result is not immediately obvious, as this measure has the lowest probability of successfully killing *Mimosa* ($m_2 = 0{\cdot}65$), but the key benefit is that it has the lowest probability of *Mimosa* re-establishing. Therefore, it is the optimal choice if planning on a year-to-year basis, but such a short-term outlook is not likely to be effective for such a highly prolific and resilient species as *Mimosa*.

If the planning horizon is between 3 years and 10 years, the optimal strategy set is constant from year to year during the planning period and does not change with T. The optimal management measure for extensive invasions is measure 4, applying herbicides and a prescribed burn (Fig. 3a). This control option only has a moderate probability of successfully controlling adult plants ($m_4 = 0{\cdot}7$), but the highest probability of reducing the size of the seed bank ($d_4 = 0{\cdot}29$, $c_{high,4} = 0{\cdot}20$). With a long-term planning horizon (3–10 years), management should shift focus from the current populations to the seed bank or future populations. This is despite the trade-off that measure 4 also has the highest probability that *Mimosa* will re-establish.

If the invasion of *Mimosa* is recent (i.e. where the majority of sites occupied by the invader have a low seed bank), then the most effective control measure is the herbicide-only measure (Fig. 3a). In the early stages of an invasion, seed bank size is not a primary concern, the focus is reducing the probability that *Mimosa* will re-colonize a site.

If the invasion is intermediate, with sites occupied by *Mimosa* with both high and low seed banks, the optimal control measure is herbicide and mechanical removal. Mechanical removal has the highest probability of successfully killing adult plants ($m_3 = 0{\cdot}75$), but a moderate probability that the seed bank size will remain high ($d_3 = 0{\cdot}15$; $c_{high,4} = 0{\cdot}55$) (Fig. 3a).

OPTIMAL CONTROL DEPENDS ON EXTENT OF INVASION AND NATIVE SITE DISTURBANCE

If the *Mimosa* invasion is at an early stage (only a few sites are occupied by the invader with a low seed bank), the optimal control measure depends on the probability of disturbance of native sites (Fig. 4a). If the probability of disturbance increases above 0·3, the optimal control measure shifts from the application of herbicides to the combined measure of herbicides and mechanical removal.

When there is at least one site with a high seed bank and the probability of disturbance increases above 0·1, the optimal measure changes from herbicides only to herbicides and mechanical (Fig. 4b), and if disturbance increases above 0·7, the optimal measure changes to the application of herbicides and a prescribed burn (Fig. 4b).

Where all sites are occupied by the invader but the majority have low seed banks, the application of herbicides alone is no longer optimal (Fig. 4c). When the probability of disturbance is less than 0·7, the herbicides and mechanical measure is optimal (Fig. 4c), which has the highest probability that the invaders will be successfully killed. However, if the probability of disturbance increases above 0·7, the optimal measure

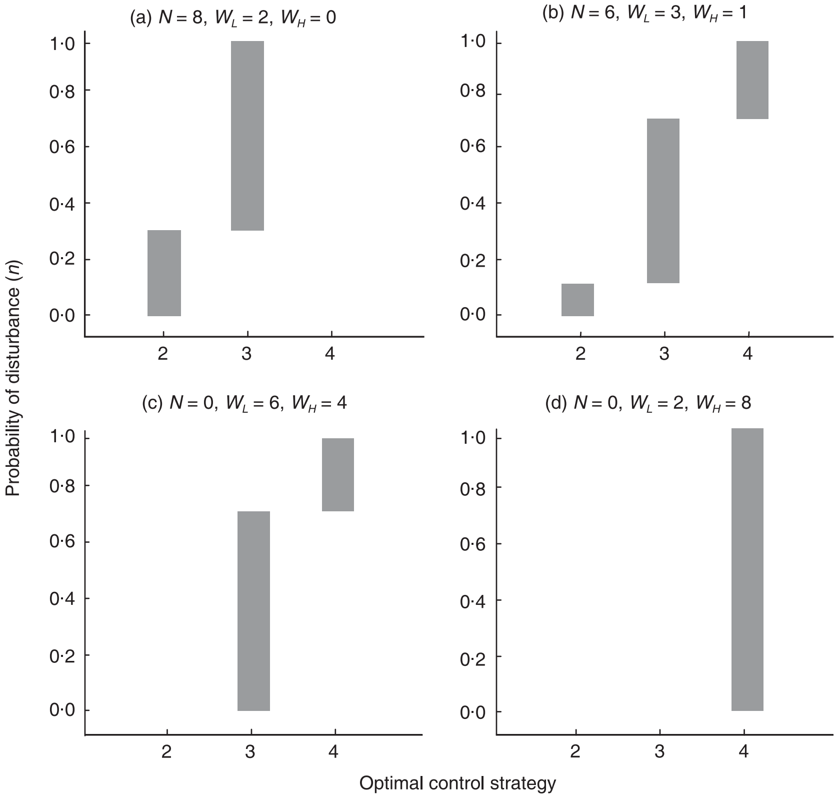

Fig. 4. Optimal control strategies (at the start of the planning period) as the probability of disturbance varies, the baseline parameters are in Tables 1 and 2. a) new invasion, d) well-established invasion, b) and c) represent scenarios between these two extremes. *N*, native species sites, W_L, invader sites with a low seed bank, W_H, invader sites with a high seed bank. Time horizon is 10 years.

becomes herbicides and a prescribed burn. If the invasion is extensive (all sites are occupied by the invader and the majority have a high seed bank; Fig. 4d), the optimal control measure does not change with the probability of disturbance, but instead remains the herbicide and prescribed burn measure.

OPTIMAL CONTROL DEPENDS ON SEED DISPERSAL

The probability of a seed dispersal event such as flooding also alters the optimal control measure (Fig. 3). If the probability of a flood increases from 0·1 to 0·6, the number of scenarios where herbicides and mechanical removal is optimal increases and the number where herbicide and burning is optimal decreases (compare Fig. 3a–c and Fig. 3b–d). When the probability of a site, whether open or occupied by the invader, moving from a low to a high seed bank due to a flood increases to 0·6, the herbicide only measure is no longer optimal for recent invasions.

If the probabilities of disturbance and flooding are both 0·6 (Fig. 3d) and the invasion is extensive, the optimal control measure is herbicide and burning. Again, an increase in the probability of disturbance shifts control efforts towards maximizing the probability the seed bank size is reduced.

Discussion

Several empirical studies have outlined the complex role disturbance plays in facilitating invasion (Hobbs & Atkins 1988; Seabloom *et al.* 2003; MacDougall & Turkington 2005) and modelling efforts have highlighted the importance of including the effects of disturbance in management efforts (Rees & Paynter 1997; Rees & Hill 2001; Buckley *et al.* 2004). More recently Buckley *et al.* (2007), using an analytical model, demonstrated the importance of considering the type and magnitude of disturbance to both native and invader populations. The aim of our study was to take these theoretical findings and link them to practical decision-making. We did this by using a tactical model set in a stochastic dynamic programming framework to explore the benefits of incorporating the effects of disturbance into management planning efforts. We found that the type of management targeted at invaded sites depends on disturbance rates in native sites. The implications of this finding for management is that control efforts can be simplified if disturbances that negatively affect native species and favour the recruitment of invaders can be reduced or mitigated.

Our approach has captured some of the complexity of incorporating disturbance effects into decision-making for invader management. We incorporate disturbances that have a detrimental effect on native species presence (i.e. feral animal disturbance). We also treat control measures as a type of disturbance that target the invader only and are detrimental to existing populations (above-ground invader presence) and future populations (size of the seed bank). We also consider disturbances that act as seed dispersal events (flooding), which cannot be controlled by practitioners.

The advantage of using an algorithm such as SDP is that it permits management alternatives to be evaluated systematically in a transparent framework. It also finds the exact optimal solution for the model and allows for the consideration of stochastic processes (Kennedy 1981). A disadvantage is that the model used in an SDP has to be of low dimension; otherwise, the solution may not be computationally tractable. For this reason, SDP cannot be used for evaluating alternatives for models with a large number of variables. This could, however, also be considered an advantage as SDP is a highly effective tool for addressing specific aspects of a management concern. For this reason, SDP has been used extensively within engineering, resource management and conservation (Kennedy 1981; Mangel & Clark 1988).

Previous studies that have used SDP for addressing pest management problems have provided useful guidelines for more effective decision-making. For example, Regan *et al.* (2006) used SDP to investigate when monitoring for an invasive plant should be stopped and eradication declared. Shea & Possingham (2000) used an SDP framework to investigate the optimal size and number of populations that should be released to maximize the success of a biological control programme. Pandey & Medd (1991) developed an SDP to recommend optimal rates of herbicides to be used in a cropping system invaded by *Avena fatua* L. (wild oats). Our study is the first to use SDP to investigate how incorporating current knowledge of the effects of disturbance to invaders and natives changes the optimal management decision.

A limitation of SDP is that the model used must have the Markov property, meaning that the current state of the system depends only on the state in the preceding time step, and not before. This is a limitation for the *Mimosa* case study, in that repeated flooding will act to disperse seed and increase the probabilities that *Mimosa* occupies disturbed sites. But repeated flooding could also act to increase the efficacy of control efforts by reducing the survival of *Mimosa* seedlings (and possibly native seedlings as well), as they require some leaves to be above the water level to continue to photosynthesize (Paynter & Flanagan 2004). The management implication of this cumulative effect of flooding has not been considered in the model.

Two other studies have recommended control strategies for *M. pigra*. Buckley *et al.* (2004) used a simulation model and Paynter & Flanagan (2004) used a large-scale field trial established in the Northern Territory of Australia. Both studies recommended combinations of control measures be carried out over multiple years (integrated weed management). Both approaches also provided valuable insights into the mechanisms behind invasion, but the control recommendations made can only be considered applicable to the site conditions present within each respective study. The benefit of our approach is that specific site conditions are not incorporated in the model. This has allowed us to identify broad-scale trends that are useful for guiding management actions.

A worthwhile extension of our approach would be to consider the spatial arrangement of sites, or a situation where different control strategies can be used in the same year, but carried out on different sites. For example, if a site is completely surrounded by invader-occupied sites, it is likely to be more susceptible to invasion. It is also likely that practitioners may decide on a different control measure for a site surrounded by *Mimosa* than if the site is surrounded by native vegetation. While we have included an estimation of effort of different control strategies here, it would be of value to include explicit costs of the different control measures and to explore how budgetary constraints change which is optimal.

Conclusions

Overall, we found that the extent of the invader and native populations, the effects of disturbances on both, and the length of the control programme are essential considerations when planning management actions. Intuitively, the best option for control would be the measure with the highest probability of successfully killing the invader. Our approach has shown that by considering the effects of disturbance when evaluating control alternatives, the obvious is no longer always optimal. For example, when disturbance to native sites was high, the optimal control measure shifted to that with the highest probability of reducing the invader seed bank. This is despite the short-term trade-off of this measure having the highest probability that the invader re-establishes. We also investigated how a disturbance (flooding) that acts as a seed disperser for the invader, affected the optimal control decision. This represents a type of disturbance that would be both difficult and undesirable to control in wetland areas, as it is essential for the persistence of native flora and fauna. Where there was a high probability of a wide-scale flood dispersing seed, we found that the optimal decision was, again, reducing the size of the seed bank.

There is a clear benefit in broadening the focus of a control programme from just targeting the invader population, to also protecting the integrity of sites occupied by native plants. If disturbance to native sites can be reduced, then control efforts can shift from attempting to reduce the size of the invader seed bank (a highly intensive task which will likely also damage seeds of natives) to focusing on killing the current population.

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References

Bellman, R.E. (1957) *Dynamic Programming* Princeton University Press, Princeton, NJ, USA.

Buckley, Y.M. (2008) The role of research for integrated management of invasive species, invaded landscapes and communities. *Journal of Applied Ecology*, **45**, 397–402.

Buckley, Y.M., Bolker, B.M. & Rees, M. (2007) Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters*, **10**, 809–817.

Buckley, Y.M., Rees, M., Paynter, Q. & Lonsdale, M. (2004) Modelling integrated weed management of an invasive shrub in tropical Australia. *Journal of Applied Ecology*, **41**, 541–560.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Cook, G.D. & Setterfield, S.A. (1996) Shrub invasion of a tropical wetland: Implications for weed management. *Ecological Applications*, **6**, 531–537.

Cronk, Q.B. & Fuller, J.L. (1995) *Plant Invaders. The Threat to Natural Ecosystems* Chapman & Hall, London, UK

Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology and Systematics*, **34**, 183–211.

Davis, M.A., Thompson, K. & Grime, J.P. (2001) Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions*, **7**, 97–102.

Davis, M.A., Thompson, K. & Grime, J.P. (2005) Invasibility: the local mechanisms driving community assembly and species diversity. *Ecography*, **28**, 696–704.

Hobbs, R.J. & Atkins, L. (1988) Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Australian Journal of Ecology*, **13**, 171–179.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity and invasion: implications for conservation. *Conservation Biology*, **6**, 324–337.

Horvitz, C.C., Pascarella, J.B., McMann, S., Freedman, A. & Hofstetter, R.H. (1998) Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Applications*, **8**, 947–974.

Jodoin, Y., Lavoie, C., Villeneuve, P., Theriault, M., Beaulieu, J. & Belzile, F. (2008) Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada. *Journal of Applied Ecology*.

Kennedy, J.O.S. (1981) Applications of dynamic programming to agriculture, forestry and fisheries: review and prognosis. *Review of Marketing and Agricultural Economics*, **49**, 141–173.

Levine, J., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond*, **270**, 775–781.

Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. (2007) Disturbance. *Invasion Ecology*, pp. 76–106. Blackwell Publishing, Oxford, UK

Lonsdale, M. & Farrell, G.S. (1998) Testing the effects on *Mimosa pigra* of a biological control agent *Neurostrota gunniella* (Lepidoptera: Gracillaridae), plant competition and fungi under field conditions. *Biocontrol Science and Technology*, **8**, 485–500.

Lonsdale, W.M. & Miller, I.L. (1993) Fire as a management tool for a tropical woody weed: *Mimosa pigra* in Northern Australia. *Journal of Environmental Management*, **39**, 77–87.

Lonsdale, W.M. (1992) The biology of *Mimosa pigra*. *A Guide to the Management of Mimosa Pigra* (ed. K.L.S. Harley). CSIRO, Canberra.

Lonsdale, W.M. (1993) Rates of spread of an invading species: *Mimosa pigra* in Northern Australia. *The Journal of Ecology*, **81**, 513–521.

Lonsdale, W.M., Harley, K.L.S. & Gillett, J.D. (1988) Seed bank dynamics in *Mimosa pigra*, an invasive tropical shrub. *Journal of Applied Ecology*, **25**, 963–976.

MacDougall, A.S. & Turkington, R. (2005) Are invasive species the divers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42–55.

Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioural Ecology* Princeton University Press, NJ, USA.

Pandey, S. & Medd, R.W. (1991) A stochastic dynamic programming framework for weed control decision making: an application to *Avena fatua* L. *Agricultural Economics*, **6**, 115–128.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.

Paynter, Q. & Flanagan, G.J. (2004) Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, *Mimosa pigra*. *Journal of Applied Ecology*, **41**, 615–629.

Pickett, S.T.A., Kolasa, J., Armesto, J.J. & Collins, S.L. (1989) The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos*, **54**, 129–136.

Rees, M. & Hill, R.L. (2001) Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology*, **38**, 364–377.

Rees, M. & Paynter, Q. (1997) Biological control of Scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *Journal of Applied Ecology*, **34**, 1203–1221.

Regan, T.J., McCarthy, M.A., Baxter, P.W.J., Panetta, F.D. & Possingham, H.P. (2006) Optimal eradication: when to stop looking for invasive plant. *Ecology Letters*, **9**, 759–766.

Rouget, M. & Richardson, D.M. (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *The American Naturalist*, **162**, 713–724.

Seabloom, E.W., Harpole, W.S., Reichman, O.J. & Tilman, D. (2003) Invasion, competitive dominance, and resource use by exotic and native California grassland species. *PNAS*, **100**, 13384–13389.

Shea, K. & Possingham, H. (2000) Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *The Journal of Applied Ecology*, **37**, 77–86.

Thorp, J.R. & Lynch, R. (2000) *The Determination of Weeds of National Significance*. National Weeds Strategy Executive Committee, Launceston, Australia.

White, P.S. & Pickett, S.T.A. (1985). Natural disturbance and patch dynamics. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White). Academic Press, New York.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. The nine transition probabilities that make-up the tactical model.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2664.2008.01510.x
(This link will take you to the article abstract).