Cooperation, Spatial-Dynamic Externalities, and Invasive Species Management

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Abstract

Most terrestrial biological invasions occur in landscapes comprising numerous, independently managed properties. Thus, control of invasion spread generally depends on the choices of many managers, each deciding the extent to control invasions on their property. Here we develop a spatially-explicit, integrated model of invasion spread and human behavior to examine how people's control choices under laissez-faire affect patterns of invasion spread and the total costs and damages imposed by an invader. We evaluate how characteristics of the bioeconomic and social system, including the extent of cooperation among managers, affect the divergence between socially optimal and private control efforts. We find that system-wide invasion externalities generally increase with the potential range size of an invader and with marginal damages from invasion and decrease with marginal control costs and with the size of the invasion when it is discovered. As expected, private control decisions tend to under-control the invasion relative to socially optimal control. However, we also find that less extensive cooperation is needed to control invasions whose costs and damages otherwise lead to the largest externalities. This novel finding suggests that even small amounts of cooperation can avoid some of the worst invasion outcomes and coordination of control can provide large social benefits. This research highlights the importance of human behavior for affecting invasion spread and economics outcomes.

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1. Introduction

Invasive species are one of the leading drivers of global environmental change, causing large ecological and economic impacts (Olson 2006). New invasions generally begin with the introduction of just one or a few individuals to a region. Then, through reproduction and dispersal, invasions spread and cause damages across large areas. Economists have begun examining how to optimally apply controls across time and space to minimize the total social costs and damages from invasion spread (Epanchin-Niell & Hastings 2010). However, most invasions occur in landscapes comprising numerous, independently managed properties. Thus, management of invasions generally depends on the control choices of many agents located across the landscape, each deciding the extent to control invasions on their property (Epanchin-Niell *et al.* 2009).

In this article we examine invasion management within the real-world context of placebased property rights, where managers can choose controls on their properties, but the invasive species can disperse across property boundaries. We examine how people's control choices affect the patterns and rates of invasion spread across the landscape and the total costs and damages imposed by an invader using an integrated model of invasion spread and human behavior. We also evaluate how characteristics of the bioeconomic and social system, including cooperation among agents, affect the divergence between socially optimal and private control efforts.

Although specification of property rights has long been recommended as a means for internalizing externalities associated with resource use, the existence of property rights is often not sufficient for efficient resource use (Holland 2004). Place-based property rights include

territorial use rights in fisheries in which managers are granted spatially-delineated rights to a fishery. This management approach generally fails to internalize fish stock externalities unless the territory is large enough to cover the full geographic range of the fishery or is applied to sedentary fish species, because managers have incentives to catch fish before they move into others' management areas (Holland 2004). Janmaat (2005) found that managers maintained lower than socially optimal stock levels of a harvestable marine resource when the resource could disperse between properties. In fact, greater dispersal of the species led to lower privately chosen stock levels. This occurs because resource dispersion leads to incomplete property rights for the resource. Similarly, Skonhoft (2005) compared unified versus private management of moose (*Alces alces*), which is both a pest and a resource. In situations where the species migrated between two locations, the divergence between unified and private management increased as the proportion of the population that migrated increased.

Some existing research has also considered management of dispersive pests or invasive species in landscapes with multiple managers or properties (e.g., Bhat *et al.* 1996; Jones *et al.* 2000; Rich *et al.* 2005a; Rich *et al.* 2005b; Burnett 2006; Yu & Leung 2006; Bhat & Huffaker 2007; Wilen 2007; Grimsrud *et al.* 2008; Epanchin-Niell *et al.* 2009). These studies show that individuals' private control choices are influenced by many factors, including the costs of control and the damages that managers face from the invasion. In addition, invasion levels on one parcel can affect control decisions on adjacent parcels (e.g., Bhat *et al.* 1996; Grimsrud *et al.* 2008), such that each agent's control decisions are affected by the control choices of other managers (Epanchin-Niell *et al.* 2009). Furthermore, this body of research again highlights that the ability for species to disperse across property boundaries can lead to externalities under private control (e.g., Bhat *et al.* 1996; Jones *et al.* 2000). Although managers generally can choose their control

levels, they lack full autonomy in choosing their level of invasion because property boundaries are porous to invasion spread. As with any resource that is shared or whose use by one agent affects its availability for other agents, private control choices for invasions are likely to diverge from socially optimal levels of control, so invasions are generally under-controlled. Several studies show, however, that cooperation among managers and coordination of invasion control can make agents better off than when they act independently or non-cooperatively (e.g., Bhat *et al.* 1996; Rich *et al.* 2005b; Yu & Leung 2006; Bhat & Huffaker 2007).¹

This existing research has provided insights about the presence of invasion externalities and the ability for cooperative control agreements to help internalize those externalities. These studies have focused on management of only two properties (e.g., Bhat *et al.* 1996; Jones *et al.* 2000; Grimsrud *et al.* 2008) or have treated the invasion either as a pure common pool resource (Yu & Leung 2006) or as prevalent across space (Rich *et al.* 2005a; Rich *et al.* 2005b).² With real invasions, however, managers at different locations are first affected by the invasion at different times dependent on the spread pattern of the invader and managers' control decisions, because an invasion initially occupies a small area and then spreads to affect more properties if

¹ Bhat et al. (1996) showed that a cooperative control agreement, in which agents chose Pareto-efficient control strategies, made agents better off than without cooperation in a two-agent model; long-term cooperation could be ensured by an appropriate payment structure between agents (Bhat & Huffaker 2007). Yu and Leung (2006) examined cooperative control of a common pool pest for which all agents experienced the same pest levels. Agents' control choices were modeled as a repeated game of infinite duration in which each agent chose how much to contribute to area-wide pest management based on current pest levels. As with Bhat et al. (1996), Yu and Leung found that all agents could be made better off if they participated in cooperative pest control, but incentives to cheat hindered cooperation. Cooperative agreements could be self-enforcing if the pest population was reduced to the socially optimal level prior to the start of the game. Finally, a set of studies by Rich et al. (Rich et al. 2005a; Rich et al. 2005b) considered how spatial interactions among agents affected disease prevalence using a spatial game in which the payoffs to an agent for controlling the disease depended on the control choices of neighbors. In this spatial adaptation of a Stag-Hunt coordination game, an individual's payoff was highest if he and most of his neighbors controlled; the payoff was lowest if he controlled and most of his neighbors did not. This game generally lead quickly to all agents opting not to control, resulting in high disease prevalence and smaller payoffs than if all agents chose high control levels. However, as found with the pest study by Yu and Leung (2006), coordination could be stable in the absence of idiosyncratic shocks if all agents initially synchronized on high control levels. ² Rich *et al.* (2005a; 2005b) assumed that disease outbreaks at any point in time and space depended only on local control actions at that time, without dependence on the location of outbreaks in previous time periods.

uncontrolled. Consequently, understanding invasion management in real landscapes requires considering both the spatial-dynamics of invasion spread and the control decisions of multiple managers in a common framework, our approach here.

For invasions in privately managed landscapes, the coordination of management actions across land parcels can range from uncoordinated, independent control decisions by many managers to implementation of optimal control efforts by a central planner. As highlighted by the research described above, independent uncoordinated management generally under-controls the invasion because managers only consider the damages that accrue to their property. In contrast, a social planner can account for the spatial-dynamics of invasion spread and the effect of control efforts on the propagation of damages to choose a control strategy that minimizes the total costs and damages of the invasion across the entire landscape (Epanchin-Niell & Hastings 2010).

In the absence of central planning, managers may internalize some of the externalities imposed by invasion spread by developing cooperative control agreements (Bhat & Huffaker 2007; Epanchin-Niell *et al.* 2009). Externalities, and thus cooperative control agreements, can arise among different groups of managers in the landscape. First, externalities can arise from dispersal among parcels that are currently invaded (e.g., Bhat *et al.* 1996; Jones *et al.* 2000; Yu & Leung 2006; Grimsrud *et al.* 2008). Secondly, externalities are imposed on agents further from the invasion front by under-control of the invasion by agents whose parcels are invaded (e.g., Jones *et al.* 2000; Wilen 2007). Agents further from the invasion cannot apply control to affect the invasion directly, but benefit from control efforts that delay or prevent invasion spread. Consequently, agents who are not yet affected by the invasion may have willingness to pay to increase control efforts by agents affected by the invasion. Various types of cooperative control

agreements may develop to internalize externalities imposed within the invaded area and between invaded and uninvaded regions of the landscape, dependent on agent interactions.

Figure 1 classifies some potential cooperative decision-making frameworks according to their extent of cooperation across the landscape. The x-axis represents the amount of coordination among agents, while the y-axis represents increasing involvement of agents further from the invasion front. If agents do not interact, but rather make control decisions independently ("unilateral management"; Fig. 1), none of the external costs of invasion spread are internalized and agents make control decisions based on local conditions to minimize the costs of control and damages accrued on their own properties. Alternatively, agents can develop cooperative control agreements that coordinate control efforts across space to reduce externalities from invasion dispersal across property boundaries. For example, agents currently affected by an invasion could form a management club or association that pools resources to control the invasion in a way that is Pareto-efficient from the perspective of the managers involved. This type of spatial coordination would allow agents to develop a long-term control plan in the group's best interest. We refer to this localized club formation as "cooperative management with local contributions" (Fig. 1). Without spatial coordination among managers, agents may instead internalize some of the invasion externality through local negotiations. For example, agents further from the invasion front may develop Coasian-type bargains with agents closer to the invasion in order to increase control efforts to delay or prevent the spread of the invasion. This "bilateral management" (Fig.1), perhaps among nearest neighbors, can internalize some externalities, but agents make control decisions relatively independently and based on local conditions. In this context of local negotiations, as with unilateral management, investments in long-term control (e.g., clearing invaded patches) can be stifled by uncertainty about reinvasion from elsewhere in the landscape,

since control is not coordinated across space. Alternatively, under "cooperative control with neighborhood contributions" (Fig. 1) agents may interact both to coordinate control efforts across space and to incorporate willingness to pay by agents further from the invasion front, such as through the formation of a more encompassing management club. This type of cooperative bargaining helps internalize externalities across both space and time (i.e., within the invaded area and between invaded and uninvaded regions of the landscape).



Figure 1. Classification of private decision-making frameworks under laissez-faire with respect to assumptions about cooperation among agents. In this paper we focus on unilateral management and cooperative management with local and neighborhood contributions.

In this article we develop an integrated model of invasion spatial-dynamics and human behavior to examine management under laissez-faire in a landscape comprising many independently managed land parcels. To evaluate the ability for private negotiations to internalize invasion externalities in landscapes with many managers and realistic spread dynamics, we compare invasion outcomes under unilateral management, cooperative management with local and neighborhood contributions, and management under a central planner (i.e., socially optimal control). We employ an approach that strips both the invasion process and the social landscape to its important features. We model invasion spread with a cellular automaton model in a grid landscape, where each cell of the landscape is invaded or uninvaded at each point in time. Spread occurs between adjacent cells at each time step in the absence of control efforts, and, without control, the invasion spreads to fill the entire landscape.³

We represent the social landscape of the invasion by assuming that each cell within the grid represents an independently managed parcel of land. Under laissez-faire, the manager of each parcel (grid cell) seeks to minimize his own costs and damages from the invasion by choosing how much to contribute to invasion control, where control options include preventing invasion spread and clearing parcels of the invasion.⁴ A manager can prevent invasion of his parcel by exerting control efforts along the boundaries that his parcel shares with invaded parcels, and a manager incurs damages while his parcel is invaded. We solve for patterns of invasion spread and total costs and damages under unilateral and cooperative management scenarios by simulating invasion spread under relevant assumptions about human behavior, and we solve for optimal control policies using integer programming. This model of spread and control provides an intuitive framework to examine how the micro-behavior of individuals and their interactions can affect the macro-pattern of invasion spread and associated damages.

Our approach, which accounts for invasion spatial-dynamics and human decision-making in a complex social landscape, allows us to explore a range of questions about invasion control under laissez-faire that have not previously been examined. For example, what components of the bioeconomic system make the system-wide invasion externality large or small, and how well

³ This invasion spread model approximates the basic pattern predicted with a reaction-diffusion process, which predicts a constant radial or linear rate of spread and provides a good description of observed spread patterns for a variety of species (Hastings *et al.* 2005; Wilen 2007).

⁴ Previous work on invasion control in multi-manager landscapes has not considered eradication as a management option, despite its importance.

does cooperation among agents internalize invasion externalities? We show that the magnitude of the externality imposed from invasion spread varies across space, even in homogeneous landscapes, because individuals nearest to the invasion receive the greatest benefit from invasion control. As expected, private control decisions tend to under-control the invasion relative to socially optimal control. We also find that the magnitude of the system-wide invasion externality increases with the size of the invasion's potential range, such that ecological and physiological barriers to invasion spread have important economic consequences. We find that cooperation among managers decreases the magnitude and occurrence of potential invasion externalities, Furthermore, less extensive cooperation is needed to control invasions whose costs and damages otherwise lead to the largest externalities. This novel finding suggests that even small amounts of cooperation have the possibility to avoid some of the worst invasion outcomes, and that coordination of control can provide large social benefits.

In the next section we describe the invasion spread model and economic framework in greater detail. In section 3 we describe the results of our model. We begin by considering a simple invasion example to examine how invasion control and system-wide externalities vary across decision-making frameworks and economic parameters. We then consider how landscape size (i.e., the potential range size of the invasive species) and initial invasion size affect control and resulting externalities. In sections 4 and 5 we discuss our results and conclude.

2. Methods

2.1 Invasion spread model

We employ a deterministic, discrete time, discrete space model to represent the spread of an invasive species. The landscape is represented as a grid of square cells (parcels). Each cell is labeled by its row i and column j in the landscape grid, and each cell can take on one of two

states: invaded $(x_{i,j} = 1)$ or uninvaded $(x_{i,j} = 0)$. In the absence of any human intervention, the species spreads from invaded cells to adjacent, uninvaded cells in each time period, based on rook contiguity. Thus, if cell (i,j) were invaded at time *t*, cells (i,j), (i,j+1), (i,j-1), (i+1,j), and (i-1,j) would be invaded in the next time period. In each subsequent time step, all cells sharing a contiguous border with an invaded cell also become invaded (Fig. 2).⁵



Figure 2. Parcels in a partially invaded landscape. If at time t only the black parcel is invaded, the solid grey (about to be invaded) parcels become invaded at time t+1 and the mottled grey (adjacent to about to be invaded) parcels become invaded at time t+2, in the absence of control. Under unilateral management managers of invaded and about to be invaded (solid grey and black) parcels choose independently whether to control the invasion on their properties. Under cooperative management with local contributions, these same managers develop cooperative control bargains. With neighborhood contributions, all non-white parcels (i.e., invaded, about to be invaded, and adjacent to about to be invaded) participate in cooperative control.

The size and shape of the landscape grid reflect the potential area that a species can invade, which is determined by biotic or abiotic constraints and can be predicted using ecological niche modeling (Peterson 2003; Elith *et al.* 2006). The choice of time step and cell size scale together, such that the invasion spreads at a rate of one grid cell per unit of time.

⁵ This model does not allow for long distance dispersal and implicitly assumes absorbing landscape boundaries by defining a finite landscape and a binary invasion status for each cell.

2.2 Economic model

We assume that each grid cell represents a parcel of land that is managed by an independent agent, and the manager of each parcel decides what control to apply to his land in order to minimize the expected net present value of total costs and damages on his parcel. Here we assume that all managers and parcels are homogenous; they differ only in their location in space.

Here we consider a situation where the damages imposed by an invader are incurred privately, such that a manager incurs damages *d* in all time periods that his parcel is invaded.⁶ A manager can prevent invasion of his parcel by exerting control efforts along each of his parcel boundaries that abuts an invaded parcel.⁷ Thus, the cost of excluding invasion from a parcel increases with the number of adjacent (rook contiguous) invaded parcels and equals *invaded_neighbors*b*, where *b* is the cost of preventing invasion along each boundary and *invaded_neighbors* is the number of invaded adjacent parcels ($0 \le invaded_neighbors \le 4$). Once a parcel has been invaded, it remains invaded unless the manager chooses to clear it at a cost *e*.⁸ Again, however, after clearing the parcel, a manager must apply control along adjacent invaded borders in following time periods to prevent reinvasion, at a cost *b* per invaded border per time period.

 ⁶ For example, damages may represent lost revenue due to the invasion, such as from forage loss from weed invasion. Here we do not consider public damages, such as the value of biodiversity loss from invasions.
 ⁷ For example, this control could include application of herbicide along a property boundary to eliminate any new

incursions of an invasive plant before it can establish.

⁸ By separately parameterizing removal costs e and spread prevention costs b, this model allows flexibility in specifying control costs based on species characteristics. For many species, such as for plants with long-lived seed banks, spread prevention is much less costly than removal, and this can be reflected in the choice of cost parameters. We assume the costs of clearing a parcel is greater than the costs of preventing invasion along four parcel boundaries (e > 4b).

2.3 Decision-making frameworks

We consider three private decision-making frameworks for invasion control under laissez-faire: unilateral management and cooperative management with local or neighborhood contributions (Fig. 1). Under unilateral management, agents do not communicate or coordinate control actions; agents make their decisions independently, based only on the direct costs and damages they face. In contrast, under cooperative management managers can form a management association or club that pools managers' resources to eradicate or contain the invasion. We compare invasion outcomes under these private decision-making frameworks to a social planner solution that implements optimal invasion control to minimize total costs and damages across the entire landscape. Our analysis assumes that property rights are defined, contracts are enforceable, and that agents are aware of each other's preferences and invasion status.

2.3.1 Unilateral management

Under unilateral management each agent decides his control actions independently and in his own best interest based on the control costs and damages he faces. Agents observe the invasion status of other cells and have expectations about other managers' incentives to prevent invasion, but they do not bargain with neighbors or otherwise coordinate to influence each other's control choices. Each agent assumes that other agents will prevent invasion of their respective properties only if it is in their best interest. In addition, agents assume that other agents do not clear properties unilaterally once they have become invaded.

Managers make control decisions in each time period to minimize their expected longterm costs and damages. The assumptions of constant marginal costs (b) and damages (d), binary invasion state, and agents' expectations that invaded parcels remain invaded, reduce the damage-

minimization problem faced by managers of uninvaded parcels from a dynamic optimization problem to a series of separable, myopic decisions that each minimize total costs and damages in that time period. Thus, in each time period managers whose parcels are about to be invaded (i.e. uninvaded parcels that are adjacent to at least one invaded parcel; Fig. 2) choose either to prevent invasion in the next time period at a cost b per invaded border or allow invasion and incur damages d, depending on which choice is less costly. In equation form:

if
$$x_{i,j,t-1} = 0$$
 and
$$\begin{cases} b*invaded_neighbors_{i,j,t-1} > d & \text{then } x_{i,j,t} = 1 \\ b*invaded_neighbors_{i,j,t-1} \le d & \text{then } x_{i,j,t} = 0 \end{cases}$$
 (1.)

where *invaded_neighbors*_{*i*,*j*,*t*} is the number of adjacent cells that are invaded at time *t*.

Managers of parcels that already are invaded decide whether or not to clear the invasion from their parcels in each time period based on the costs and damages they expect to incur under their alternative control choices. Each manager compares the long-term costs and damages from clearing his parcel, followed by managing unilaterally, to the total damages from allowing the invasion to persist. The damages incurred from continued invasion are straightforward to calculate $(\frac{d(1+r)}{r})$, but the long-term costs and damages that a manager expects to incur from clearing his land, $E(NPV_clear)_{i,j,r}$, depend on his expectations about his and others' future control choices. For example, if no other parcels are currently invaded and the manager expects his neighbors to unilaterally prevent invasion from his parcel, the manager's expected cost of eradication includes only the cost of clearing *e*. On the other hand, if the manager expects his neighbors to allow their parcels to become invaded, his expected cost of eradication includes the cost of clearing and either the costs of preventing reinvasion from his neighbors in perpetuity or the damages he would incur from being immediately reinvaded. Similarly, if more than one parcel in the landscape is invaded, a manager may predict that after clearing his parcel he subsequently would prevent reinvasion until or unless unilateral prevention ceased to be worthwhile because of neighboring invasions (as determined by eqn. 1).

We assume that each manager calculates the expected costs and damages from clearing his land $(E(NPV_clear)_{i,j,t})$ as the cost of clearing (*e*) plus the expected costs of long-term prevention and/or incurred damages when he and others manage unilaterally and no other managers clear their property. To calculate a manager's expected costs and damages from clearing, we "clear" the manager's parcel and then simulate invasion spread under unilateral prevention management (eqn. 1) by all managers for 150 time periods. The manager's total expected costs and damages from clearing ($E(NPV_clear)_{i,j,t}$) equal the total costs and damages incurred by the manager in this simulation plus a salvage value to convert to infinite time horizon costs.

In each time period a manager chooses to clear his parcel if his total expected costs and damages from clearing are less than the costs of continued invasion and remains invaded otherwise:

if
$$x_{i,j,t-1} = 1$$
 and
$$\begin{cases} E(NPV_clear)_{i,j,t} < \frac{d(1+r)}{r} & \text{then } x_{i,j,t} = 0\\ E(NPV_clear)_{i,j,t} \ge \frac{d(1+r)}{r} & \text{then } x_{i,j,t} = 1 \end{cases}$$
 (2.)

We predict landscape-wide invasion spread under unilateral management by simulating spread and control using equations 1 and 2, where $E(NPV_clear)_{i,j,t}$ in equation 2 is calculated using the sub-simulation described above. In each time period invaded parcels are cleared (i.e., converted to uninvaded) if their expected long-term costs of clearing are less then long-term damages from remaining invaded (eqn. 2), and each parcel that is about to be invaded is reclassified as invaded if its cost of prevention is greater than marginal damages *d* (eqn. 1).

2.3.2 Cooperative management

Under cooperative management, managers pool funds to implement long-term, coordinated control of the invasion.⁹ If managers' volunteered contributions are sufficient, the invasion is either contained in perpetuity or eradicated; otherwise agents revert to unilateral management. Containment or eradication of an invasion provides public benefits to managers by reducing private costs and damages from the invasion. Voluntary contributions generally underprovide public goods because individuals have incentives to free ride on others' contributions. Here, however, we consider a situation in which managers form associations or clubs that implement control and either facilitate cooperative bargaining or elicit control contributions through an assurance contract or provision point mechanism (Bagnoli & Lipman 1989)¹⁰, such that the public good of containing the invasion or eradication is provided if it is Pareto-efficient.

We consider two extents of cooperative bargaining: local cooperation in which only agents immediately affected by the invasion participate and neighborhood cooperation in which agents further from the invasion also participate (Fig. 1). Specifically, under cooperative control with local contributions, managers of invaded and about to be invaded parcels participate (i.e., solid black and grey parcels in Fig. 2).¹¹ This is the same group of managers that contribute to

⁹ By coordinating control efforts across space, cooperative management enables implementation of long-term, invasion-wide control efforts (e.g., eradication and containment) that cannot be guaranteed under unilateral management.

¹⁰ A provision point mechanism is a game theoretic mechanism that facilitates provisioning of a public good. Participants make binding pledges to fund a public good. If a certain, pre-specified threshold of contributions is achieved the public good is provided; otherwise the public good is not provided and any monetary contributions are refunded. This game provides an efficient mechanism for public good provision in the strong sense that every equilibrium outcome is efficient (Bagnoli & Lipman 1989). With this structure, each agent will offer up to his marginal benefit of the control action if total contributions would be insufficient without his contribution. Here the threshold for implementation of the public good is the cost of implementing control (i.e., eradication or long-term containment).

¹¹ We refer to uninvaded cells that are adjacent to invaded cells in time *t* as "about to be invaded" because they will be invaded in time t+1 if they do not control along their borders. We refer to parcels that are adjacent to at least one "about to be invaded" parcel in time *t* and are not either currently invaded or "about to be invaded" as "adjacent to about to be invaded" parcels. Managers of these parcels will incur invasion in time t+2 if neither they nor their neighbors prevent invasion spread.

control under unilateral management; however, here managers' control actions are coordinated across space and time. Under cooperative control with neighborhood contributions, agents adjacent to about to be invaded parcels also participate in cooperative management (i.e., mottled grey parcels in Fig. 2). Although these managers are not immediately threatened by invasion, they benefit from control by avoiding future control costs or damages and thus are willing to pay to prevent invasion spread.

Long-term containment of an invasion requires preventing spread from invaded to uninvaded parcels in perpetuity:

$$Cost_containment_{t} = \left(\sum_{\substack{(i,j)\in\\about_to_be_invaded}} b*invaded_neighbors_{i,j,t-1} \right) * \frac{(1+r)}{r}$$
(3.)

Each manager of an uninvaded parcel is willing to contribute to the long-term containment of the invasion an amount up to the long-term costs and damages he expects to incur without cooperation (i.e., under unilateral management):

 $WTP_contain_{i,j,t;(i,j)\in uninvaded} = NPV_unilateral_{i,j,t}$.¹² In contrast, managers of invaded parcels receive no benefit from containing the invasion, and thus are not willing to contribute to this control option ($WTP_contain_{i,j,t;(i,j)\in invaded} = 0$) and instead manage unilaterally.

Permanent eradication of an invasion requires application of clearing efforts to all invaded parcels and spread prevention along the invasion front (i.e., the boundary between invaded and uninvaded parcels) for one time period:

$$Cost_eradication_{t} = \sum_{\substack{(i,j) \in \\ about_to_be_invaded}} b*invaded_neighbors_{i,j,t-1} + \sum_{(i,j)} e*x_{i,j,t-1}$$
(4.)

¹² A manager's willingness to pay is the maximum contribution that he is willing to make. His actual contribution to cooperative management may be smaller. Here we do not specify how the gains from cooperation are distributed among participants.

Each manager of an invaded parcel is willing to contribute to eradication an amount up to the total costs and damages he expects to incur from managing unilaterally (i.e., the lesser of his damages incurred in perpetuity, $\frac{d(1+r)}{r}$, and his unilateral costs of clearing, $E(cost_clear)_{i,j,t}$):

$$WTP_eradicate_{i,j,t;(i,j)\in invaded} = \min\left(\frac{d(1+r)}{r}, \ E(cost_clear)_{i,j,t}\right)$$
(5.)

Managers of uninvaded parcels gain no additional benefits from eradication relative to long-term containment, so their total willingness to pay for eradication equals the total costs and damages under their next best alternative, which is the lesser of a) the cost of containing the invasion in perpetuity (i.e., their total expected contributions for containment) or 2) their total expected costs and damages under unilateral management:

$$\sum_{\substack{(i,j)\in\\participating_uninvaded_parcels}} WTP_eradicate_{i,j,t} = \min\left(Cost_containment_{t}, \sum_{\substack{(i,j)\in\\participating_uninvaded_parcels}} NPV_unilateral_{i,j,t}\right)$$
(6.)

Under cooperative management, if the total contributions from participating managers (i.e. local or neighborhood contributions) are sufficient to eradicate the invasion, each agent pays his contribution and eradication is achieved. Alternatively, the invasion is contained in perpetuity if the contributions from uninvaded parcels are sufficient to fund control. If neither of these control strategies can be achieved through cooperative bargaining, the invasion is controlled unilaterally for a time period and then agents attempt cooperative management again in the next time period:

if
$$\left(\sum_{\substack{(i,j)\in\\participating_uninvaded_parcels}} WTP_eradicate_{i,j,t} + \sum_{\substack{(i,j)\in\\invaded_parcels}} WTP_eradicate_{i,j,t}\right) \ge Cost_eradication_t$$

then invasion is eradicated (7.)
else if $\sum_{\substack{(i,j)\in\\participating_uninvaded_parcels}} WTP_contain_{i,j,t} \ge Cost_contain_t$
then invasion is contained in perpetuity
else
invasion is managed unilaterally for one time period

2.3.3 Central planner (optimal control)

In addition to unilateral and cooperative management, we considered a social planner's control decision that optimizes control across the entire landscape. We assume that private damages coincide with public damages, such that social costs and damages equal the sum of private costs and damages.

Optimal control of the invasion requires minimizing the present value of the sum of control costs and invasion damages across space and time. We formulate this optimization problem as an integer programming problem as follows:

Minimize:
$$\sum_{t \in T, t > 0} \beta_t * \left(\sum_{(i,j) \in C} x_{i,j,t} d + \sum_{(i,j) \in C} y_{i,j,t} e + \sum_{(i,j,k,l) \in N} z_{i,j,k,l,t} b \right)$$
 (8.)

subject to:

$$x_{i,j,0} = \underline{x}_{i,j} \qquad \forall (i,j) \in C \tag{9.}$$

$$y_{i,j,0} = 0 \qquad \forall (i,j) \in C \tag{10.}$$

$$z_{i,j,k,l,0} = 0 \qquad \forall (i,j,k,l) \in N$$
(11.)

$$x_{i,j,t} \ge x_{i,j,t-1} - y_{i,j,t}$$
 $\forall (i,j) \in C, t \in T, t \ge 1$ (12.)

$$x_{i,j,t} \ge x_{k,l,t-1} - z_{i,j,k,l,t} - y_{i,j,t} \qquad \forall (i,j,k,l) \in N, t \in T, t \ge 1$$
(13.)

$$x_{i,i,t} \in \{0,1\} \qquad \forall (i,j) \in C, t \in T$$
(14.)

where

- $(i, j) \in C$ indexes parcels by row *i* and column *j*, and *C* is the set of all parcels in the landscape
- $(i, j, k, l) \in N$ indexes pairs of neighboring parcels, where $(i, j) \in C$ is the reference parcel, $(k, l) \in C$ is one of its neighbors, and N is the set of all neighboring parcel pairs

 $t \in T$ indexes time, where $T = \{0, 1, 2, \dots, T_{\text{max}}\}$

 $x_{i,j,t} \in \{0,1\}$ is the state of parcel (i,j) at time *t*, where $x_{i,j,t} = 1$ if the parcel is invaded and $x_{i,j,t} = 0$ otherwise

 $y_{i,j,t} \in \{0,1\}$ is a binary choice variable indicating if invasion is removed from parcel (i,j)

at time t, where $y_{i,j,t} = 1$ if the parcel is cleared and $y_{i,j,t} = 0$ otherwise

 $z_{i,j,k,l,t} \in \{0,1\}$ is a binary choice variable indicating if control efforts are applied along the border between parcel (i,j) and parcel (k,l) at time *t* to prevent spread from parcel (k,l) to parcel (i,j), where $z_{i,j,k,l,t} = 1$ if the border is controlled and

 $z_{i,j,k,l,t} = 0$ otherwise

 $\underline{x}_{i,j} \in \{0,1\}$ is the initial state (*t*=0) of invasion for parcel (*i*,*j*)

 β_t is the discount factor at time t (t>0), where $\beta_t = (1 + r)^{1-t}$ and r is the discount rate d, b, e are marginal (average) damage, clearing, and spread prevention costs, respectively Equation (9) establishes the initial state of the landscape by defining which parcels are invaded at t=0. Equations (10) and (11) specify that control efforts do not begin until the first

time period. Condition (12) requires that a parcel that was invaded in the previous time period remains invaded in the current time period unless removal efforts are applied. Equation (13) requires that parcel (i,j) become invaded at time *t* if it had an invaded neighbor in the previous time period, unless invasion is removed from parcel (i,j) or control is applied along the invaded border; this condition must hold for parcel (i,j) with each of its neighbors. Individually, constraints (12) and (13) provide necessary conditions for a parcel to be uninvaded at time *t*; together, constraints (12) and (13) provide sufficient conditions for a parcel to be uninvaded at time *t*. Specifically, an uninvaded parcel (i,j) will become invaded at time *t*+1 unless all of the borders it shares with invaded parcels at time *t* are controlled at time *t*+1 or removal efforts are applied to parcel (i,j) at time *t*+1. An invaded parcel (i,j) at time *t* remains invaded at time *t*+1 unless removal efforts are applied to it at time *t*+1.

For infinite time horizon problems, this system achieves a steady state equilibrium in which the proportion of invaded landscape ranges from none to all and a positive level of control is applied to landscapes that are partially invaded. In fact, with an infinite time horizon, time consistency requires that the system has reached this equilibrium if the invasion landscape remains unchanged between two time periods. In contrast, for a finite time horizon, the system can reach and maintain a steady state equilibrium for many time periods, but can depart from the steady state towards the end of the time horizon. An infinite time horizon problem can be solved with a finite time horizon specification by choosing an appropriate terminal condition or salvage value. However, specifying an appropriate terminal value is difficult because it depends on the equilibrium state of the system. To deal with this difficulty, the equilibrium solution can be "locked in" using constraints after the equilibrium has been reached, and a salvage value terminal function can be added based on the resulting solution. Here we employ an infinite time horizon, so we add the following constraints to the model defined above:

$$y_{i,j,t} = y_{i,j,t_mid} \qquad \forall (i,j) \in C, t \in T, t > t_mid$$
(15.)

$$z_{i,j,k,l,t} = z_{i,j,k,l,t_mid} \qquad \forall (i,j,k,l) \in N, t \in T, t > t_mid$$

$$(16.)$$

$$x_{i,j,t} = x_{i,j,t_mid} \qquad \forall (i,j) \in C, t \in T, t > t_mid$$
(17.)

where $1 < t_mid < Tmax$. We choose t_mid and Tmax large enough for an equilibrium to reached at t < t mid and maintained.¹³ We calculate the terminal value as:

$$\sum_{t=T+1}^{\infty} \beta_t * \left(\sum_{(i,j) \in C} x_{i,j,T} d + \sum_{(i,j) \in C} y_{i,j,T} e + \sum_{(i,j,k,l) \in N} z_{i,j,k,l,T} b \right)$$
(18.)

and include this value in the objective function.

2.4 Implementation

Individual-based, decision-making frameworks (i.e., unilateral management and cooperative control) were implemented as simulations programmed in Matlab R2008a (MathWorks, 2008). The social planner solution to invasion management was solved as a binary integer programming problem that was programmed in Zimpl (Zuse Institute Mathematical Programming Language, version 2.08) and solved using SCIP (Solving Constraint Integer Programs, version 1.1.0). To reduce the number of parameters, we scaled damages d to 1, and measured costs b and e as units of damage; this rescaling (i.e., nondimensionalization) imposes no loss of generality. We employed a discount rate of r=0.05. We examined spread and control for a variety of landscape sizes and initial invasion sizes and shapes. For each setting we

¹³ We set *Tmax*=100 and t_{mid} =50 for all optimizations, because this achieved and maintained steady states for all invasions considered.

predicted the spread and control of the invasion and calculated the present value of costs and damages for each decision-making framework.

3. Results

3.1 A simple invasion example

We begin by examining management of an invasion that initially occupies only a single parcel in the center of a 15 by 15 parcel landscape. This landscape comprises 225 managers that differ only in the location of their land parcel. We examine how invasion spread differs dependent on the costs of control and the extent of cooperation among agents in the landscape. We also examine how the system wide costs and damages, externalities, and gains from coordination differ across these economic and social factors. We also use this simple invasion example to explore how the value from containing an invasion differs across managers in the landscape based on their spatial location. Finally we examine how the size of the neighborhood involved in cooperative management affects the likelihood for an invasion to be controlled and the externalities resulting from failed control.

3.1.1 Invasion consequences

In our simple invasion example under unilateral management, the manager of the invaded parcel must choose whether or not to clear the invasive species from his parcel, and his neighbors must decide whether to prevent its spread onto their properties. Figure 3a shows the consequences of all 225 managers controlling unilaterally. The invasion is unilaterally eradicated only if the central (invaded) manager's removal costs *e* are less than the long-term damages he'd incur from continued invasion and spread prevention costs are low enough that his neighbors prevent invasion spread. If removal costs *e* are high and spread prevention costs are less than the invasion in damages (b < d), the managers adjacent to the invasion unilaterally contain the invasion in

perpetuity. However, if spread prevention $\cos t b$ is higher than damages d, no managers control the invasion and the invasion spreads through the landscape.

If agents whose parcels already are invaded or about to be invaded pool funds to cooperatively manage the invasion (i.e. local cooperation), they can achieve control across a greater range of control costs than under unilateral management without involving any additional managers (Fig. 3b). Managers are willing to contribute more to clearing efforts when control efforts are coordinated across space and time, because complete eradication can be guaranteed, providing long-term benefits from avoided costs and damages.

If the neighborhood of agents contributing to coordinated control is extended to also include managers that are two time steps away from the invasion (i.e., neighborhood contributions) then the range of control costs for which eradication or containment is achieved increases markedly (Figs. 3c). However, even with neighborhood cooperation, the range of control costs for which an invasion is contained or eradicated is far smaller than if the invasion were managed optimally (Fig 3d; note different axis scales). Optimal policy mandates containment over a large range of control costs for which unilateral management and cooperative management fail to contain the invasion at all.



Figure 3. Control outcomes under different management scenarios for a single parcel initially invaded. The initial invasion is a single, central (8,8) parcel in a 15 by 15 parcel landscape. Outcomes are graphed as a function of marginal eradication and border control costs. Note: The scale of axes in subfigure d differ from those in the other subfigures.

3.1.2 System-wide costs and damages

How do the total costs and damages of the invasion depend on the extent of coordination? The landscape-wide present value of total costs and damages are presented in Figure 4 and equal the sum of discounted control costs and damages across all time periods and all agents in the landscape. The magnitude of the system-wide costs and damages for our focal invasion (one central parcel in a 15 by 15 parcel landscape) depends on the per unit border control costs *b* and removal costs *e* and on the extent of cooperation.

Across all management scenarios, the total costs and damages are highest when per unit control costs are high enough that control of the invasion is abandoned, as shown by the black regions in Figure 4. (Note that the value of abandonment does not depend on control costs, because no control is applied.) Under private decision-making (Figs. 4a-c) abandonment occurs across large ranges of control costs. However, the transition between control and abandonment occurs at larger per unit control costs for cooperative management and when greater numbers of managers participate in the cooperative control; this transition is marked by a shift from lighter color to black in each subfigure (Fig. 4). Thus, when cooperation is limited or absent the system-wide costs and damages are high across wider ranges of border control and removal costs. As the extent of cooperation increases, the range decreases, but remains much larger than with optimal control because the neighborhood contributing to control under cooperative management is small relative to the size of the total landscape.



Figure 4. Present values of total system-wide costs and damages under different management scenarios for a single, central (8,8) parcel initially invaded in a 15 by 15 parcel landscape (as in Fig. 3). The present value is graphed in parameter space and represented by shading, with dark colors representing high net present value of costs and damages.

3.1.3 System-wide externality

The difference in total system-wide costs and damages between an optimally controlled invasion and one that is controlled by individual agents is the externality resulting from undercontrol of the invasion. We call this the system-wide externality. The shading in Figure 5 shows the size of this externality, as a function of per unit control costs, for each of the private decisionmaking frameworks, with darker shading representing larger externalities. The white regions in each subfigure show combinations of control costs for which no invasion externality occurs. Above a certain threshold of per unit control costs, the magnitude of the system-wide externality becomes zero across all management scenarios because the optimal control strategy and private management coincide: abandon the invasion. A lower control cost threshold also exists, below which individuals' control actions coincide with optimal control because agents opt to prevent the spread of the invasion or to eradicate it; this region is represented by the narrow, white areas along the left and bottom edges of each subfigure in Figure 5. The extent of this region, in which externalities are avoided, increases with increasing cooperation among agents.

Between the two regions of parameter space for which private control actions coincide with optimal control, the magnitude of the system-wide invasion externality decreases with increasing control costs across all management scenarios (Fig. 5). This occurs because the difference in total costs and damages between control and abandonment decreases with increasing control costs.

Importantly, cooperative management tends to most successfully control invasions that have low control costs, which are invasions that lead to the largest externalities without control. In addition, increasing cooperation (e.g., local vs. neighborhood cooperation) decreases the range of conditions for which invasion externalities occur and the maximum magnitude of the potential externality. These results are shown by the increasing region of white (no externality) and decreasing dark area (high externality), along the left and bottom edges of each subfigure (Fig. 5), with increasing coordination. These results show that cooperative management tends to control invasions whose control costs would otherwise lead to the highest externalities, and successful control by small amounts of cooperation can avoid the largest externalities.



Figure 5. Magnitude of system-wide externality under three private management scenarios for a single parcel initially invaded in the center (8,8) of a 15 by 15 parcel landscape (as in Figs. 3, 4). The value of the externality is graphed in parameter space and represented by shading, with dark colors representing high externalities.

3.1.4 Gains from coordination

Although neither cooperative management scenario eliminates the invasion externality across all control costs for the invasion that we have been considering, there are gains from cooperation for some ranges of control costs. These gains, relative to unilateral (independent) management, are shown in Figure 6a,b. The dark areas represent the largest gains and white areas represent no gains from coordination. As discussed with respect to the system-wide externality, the range of control costs for which gains are achieved from cooperation increases with the extent of managers contributing to control. However, the range of control costs for which gains are possible from central management (i.e., optimal control; Fig. 6c).



Figure 6. Gains (i.e. reduction in system-wide costs and damages) from cooperative management (a,b) and optimal control (c) relative to unilateral management. The initial invasion is a single, central parcel in 15 by 15 landscape (i.e. 225 managers) as in Figs. 3 to 5. The magnitude of the gains is graphed in parameter space and represented by shading, with dark colors representing high gains from coordination.

3.1.5 Value of containment to agents in the landscape

The value of a control action extends beyond the parcel that is immediately protected by the control. Figure 7 illustrates the value to each agent in the landscape of containing a single-parcel invasion in a 15 by 15 parcel landscape for one time step, relative to uncontrolled spread. The central agent, whose parcel is the source of initial invasion, does not benefit from containment because his parcel remains invaded with or without control. For the rest of the agents, the benefits of control are highest for those located closest to the invasion, whose parcels would become invaded soonest without control. Benefits decay with distance from the source of the invasion because they are discounted according to when they are realized (i.e., by when the invasion would have reached that location in space without control). Consequently, the distribution of impacts and externalities across the landscape depend on the spatial-dynamic process governing the unfolding of the invasion and the control decisions of managers in the landscape. Heterogeneity among agents thus can arise simply due to their location in space.



Figure 7. Value to each agent (grid cell) of containing a central invasion for one time step, relative to uncontrolled spread. Each cell represents a different parcel, and darker color shows higher value of containment for that parcel. The initial invasion is a single, central (8,8) parcel in a 15 by 15 parcel landscape (as in Figs. 3 to 6). (d=1).

3.1.6 Necessary size of cooperative neighborhood for containment

The cooperative management scenarios that we considered (i.e. with local and neighborhood contributions) involve agents only within two time steps of the invasion, and therefore do not account for potential benefits of control to agents further away. Clearly, expanding the size of the cooperating neighborhood, and thus the number of agents contributing to control, increases the likelihood that the invasion will be controlled and that a system-wide externality will be avoided. As an extreme case, if all agents in the landscape were included in a cooperative management effort, the invasion would be controlled if it were socially optimal to do so.¹⁴ An important question, however, is how large a cooperative neighborhood is needed to achieve optimal control?

¹⁴ In this research we consider invasions whose damages are incurred privately by individuals' whose land is invaded. If, on the other hand, invasion damages affect managers outside of the invaded region (i.e., cause public damages), then agents outside the potential invasion range (i.e., outside of our defined landscape) also may have willingness to pay to control the invasion. In this case, contributions from agents within the potential invasion range may not be sufficient to fund socially optimal control.

The size of neighborhood that is needed to achieve containment, and thus avoid incurring negative invasion externalities, is illustrated in Figure 8 for our example of a single, central parcel initially invaded in a 15 by 15 landscape. We consider a situation for which eradication is not optimal (for example, removal cost e = 4000). Not surprisingly, the minimum number of agents in the landscape that must be involved in cooperative management to achieve containment increases with the costs of controlling the invasion (Fig. 8a). We can define the cooperative neighborhood size based on the distance of participating agents from the invasion front (i.e., the number of time steps from the invasion without control), as we did for local and neighborhood cooperation (one and two time steps, respectively). Figure 8b shows the size of the neighborhood, in terms of time steps from the invasion, that is needed to contain the invasion dependent on spread prevention costs b. This figure shows that increasing the neighborhood size dramatically increases the range of control costs for which containment can be achieved. Figure 8c shows the magnitude of the invasion externality without successful containment; as we described before, the potential externality generally decreases with increasing per unit control costs. Together Figure 8 re-illustrates the point we made previously: when border control costs are low successful management requires the involvement of the fewest agents and has the greatest potential gains.



Figure 8. The extent of cooperation needed to contain an invasion (a,b) and the potential externality from sub-optimal control (c). The initial invasion is a single, central parcel in a 15 by 15 landscape (as in Figs. 2 to 7). Neighborhood size (b) is defined as the number of time steps from the invasion front of agents participating in cooperative management. e = 4000.

3.1.7 Effect of invasion damages

In our analyses we normalized damages to one and measured border control costs b and eradication costs e in damage units, as a form of nondimensionalization. Thus, an increase in damages is parameterized as a decrease in both removal and border control costs, so the results we presented thus far with respect to differences in control costs also correspond to differences in damages. Specifically:

- When damages are high relative to control costs, individual incentives lead to
 containment of an invasion without the need for cooperative management. In this case,
 unilateral management and optimal management strategies coincide so individuals'
 actions do not lead to an invasion externality and the net present value of costs and
 damages is relatively low.
- Similarly, when damages are very low relative to control costs, unilateral management and optimal management strategies coincide because it is optimal to abandon control. In this case, there also is no invasion externality.

• If damages are high relative to control costs, but not high enough to entice control under unilateral management, then large externalities result if cooperative management does not induce control. The system-wide externality, when it exists, is largest when damages are highest, and decreases with decreasing damages, and smaller extents of cooperation are needed control invasions when damages are higher.

3.2 Landscape size

How does the size of the landscape (i.e. potential invasion range) affect the ability for cooperative management to achieve optimal control and reduce the system-wide externality of an invasion? We find in the social planner framework that larger landscapes demand higher levels of control because the potential damages from spread are larger. However, the amount of control achieved under unilateral or cooperative management is not affected by the size of the landscape. Thus, the control outcomes for a single-parcel invasion in a larger or smaller landscape, for example 25 by 25 parcel or a 9 by 9 parcel landscape, are identical to those for the 15 by 15 landscape illustrated in Figure 3a-c. This occurs because contributions to control do not consider the benefits to the broader landscape; they depend only on the degree of cooperation and the size of the neighborhood contributing to control. In this sense, unilateral and cooperative management are spatially myopic with respect to the broader landscape.

Because the outcomes of the independent and cooperative management are invariant to landscape size, whereas optimal control mandates greater control in larger landscapes, both the range of control costs for which an invasion externality occurs and the maximum magnitude of the externality increase with increasing landscape size. This is illustrated in Figure 9 which shows the system-wide externality under three different management scenarios for a single, central parcel initially invaded in a 15 by 15 parcel landscape and a 9 by 9 parcel landscape,

respectively. The gains from successful cooperation are greater in larger landscapes because the potential system-wide externality for any combination of control costs is larger.



Figure 9. Magnitude of system-wide externality for two differently sized landscapes: a) 15 by 15 parcel landscape and b) 9 by 9 parcel landscape. In each case a single, central parcel is initially invaded. The value of the externality is graphed in parameter space and represented by shading, with dark colors representing high externalities.

3.3 Invasion size

An invasion may not be discovered or become the focus of control until after it has spread beyond the parcel it initially invaded. How does the size of the invasion when it is discovered affect its management and impact from that time forward? The same basic patterns of control occur for different sized invasions, with respect to the effects cooperation and control costs. For example, containment is achieved across a larger range of control costs when control efforts are more coordinated. However, unilateral management generally cannot achieve eradication if multiple parcels are invaded, because agents' private benefits of clearing are reduced by the presence of other invaded parcels. In fact, larger invasions generally are less likely to be controlled under any private management scenario, because the number of agents within a given distance of an invasion (i.e. the number of agents contributing to control) tends to grow relatively more slowly than the number of the borders that need to be controlled for containment and number of parcels that need to be cleared for eradication. Similarly, the range of control costs for which it is optimal to contain or eradicate an invasion tends to decrease with current invasion size, because containment and eradication costs are higher. Consequently, although private management efforts generally control larger invasions across a smaller range of control costs, the range of control costs for which potential invasion externalities exist also is smaller because control is less likely to be optimal. This pattern of system-wide externalities is illustrated in Figure 10 for an invasion that occupies 1 versus 5 parcels when discovered and management begins. Although large potential gains from cooperative management can exist for invasions that occupy large areas, these gains occur across a narrower range of control costs, and the potential gains from increasing cooperation decreases more rapidly than for smaller similar invasions.



Figure 10. Magnitude of system-wide externality for two differently sized initial invasions, a) one invaded parcel and b) 5 invaded parcels, under three management scenarios in a 15 by 15 landscape. The value of the externality is graphed in parameter space and represented by shading, with dark colors representing high externalities.

4. Discussion

4.1 Key findings

In this research we examined invasion control in a landscape comprising many individually managed parcels of land, which is applicable to most invasions. Externalities emerge in these landscapes because individuals consider the costs and damages accruing on their own property, rather than across the entire landscape, when making control decisions. We found that the range of conditions under which invasion externalities arise and the magnitude of such externalities depend on the characteristics of the invasion and the landscape, as well as the extent of coordination among agents. Potential invasion externalities generally increase with potential invasion range size and marginal damages and decrease with marginal control costs and with the

size of the invasion when it is discovered.

A somewhat counterintuitive feature of bioinvasions is that externalities may not arise at very low or high marginal control costs (relative to marginal damages) because optimal control and realized control may coincide in these instances, with high levels of control or no control at low or high marginal costs, respectively. Between these two extremes, however, the externality tends to be smaller for invasions with higher marginal costs, because costs and damages are higher even under optimal management. Analogously, invasion externalities, when they occur, tend to be higher for invasions that cause high marginal damages because under-control causes higher total damages.

One of our most interesting and reassuring findings on externalities and cooperation shows that achieving even modest levels of cooperation can avoid some of the largest invasion externalities. Specifically, less extensive cooperation is needed to achieve control when damages are high relative to control costs, which are conditions when successful control can provide the greatest gains for otherwise similar invasions.

4.2 Policy implications

We showed that gains from private and cooperative control efforts can be very large, so increasing private incentives to control and removing barriers to cooperation may provide societal benefits. For example, increasing managers' perceived damages or decreasing effective control costs, such as through education about control strategies and damages or implementation of control subsidies, fines, or taxes on invaded land, can increase private control efforts. Furthermore, reducing transaction costs by facilitating communication, coordination, or negotiation among managers could increase control levels by encouraging development of cooperative control agreements. Incentives for private control and for coordination could be

combined by requiring that the distribution of incentives, such as control subsidies, be contingent upon coordination of control efforts among groups of managers. The efficiency of different strategies for altering managers' incentives to cooperatively manage or privately control an invasion is an important research direction that would benefit from explicit consideration of invasion spread across property boundaries.

Our findings highlight the conditions when gains from coordination may be highest and externalities from failed control are greatest. In particular, invasions that can spread across large areas and that cause high damages, especially relative to control costs, will provide the greatest gains to society from successful control. Invasions that have high damages relative to costs also are most likely to be successfully controlled by private control efforts. In contrast, invasions that have large potential ranges may require larger cooperative neighborhoods to internalize the externalities. Transaction costs tend to increase with both the number and heterogeneity of involved agents (Hackett 1992; Ostrom *et al.* 1999; Lubell *et al.* 2002), and thus the likelihood for development of cooperative control agreements also decreases with the size of neighborhood required for success. In situations where expected externalities are large after accounting for the ability of private negotiations to internalize them, government action may be warranted.

This article focused on management in a landscape inhabited by individual landowners or managers. However, our results also apply to the management of invasions at the state or national scale. Counties and states often make their own laws regarding invasion management. With respect to plant invasions, this often involves county and state specific laws that mandate control of certain high priority species, where the control priority is likely to be based on the species' potential damages in the relevant jurisdictional area. However, our results highlight that the level of control established by a county or state is likely to be too low if the jurisdictional

area does not include the entire potential range of the invasion. For example, within a state, counties that are already highly invaded may find an invasion too widespread to control, despite the benefits that control would provide to other counties in the state. Thus, cooperation across county, state, and even country jurisdictional boundaries can improve invasive species management.

4.3 Considering human behavior when predicting invasion spread

Although ecological literature has made great strides in modeling spread patterns of invading species (Hastings 1996; Hastings *et al.* 2005), current approaches generally do not account for the role of human behavior in affecting spread patterns. It is generally assumed that patterns of invasion spread are driven by reproduction and dispersal, and the interaction of the species with its biotic and abiotic environment, including existing biological communities, climate, soils, etc. The role of human-mediated dispersal, such as the spread of zebra mussels by boaters, has gained more recent prominence as a driver of invasive species spread (e.g., Bossenbroek *et al.* 2001; Potapov & Lewis 2008).

Our research focuses on the important fact that invasion success and observed spread rates also can be affected by managers' control incentives. Private control can lead to eradication, containment, slowing, or uncontrolled spread of an invasion, thus influencing both its spread rate and ultimate extent. Our findings suggest that human control actions also could cause some invasion boundaries to ultimately align with sociopolitical boundaries, as some managers apply control to prevent invasion of their properties. These findings are important for understanding invasion spread processes, predicting invasion spread patterns under laissez-faire policies, and for research that seeks to learn about invasive species from observed spread data.

Furthermore, recognizing the effect of private control efforts on invasion spread highlights the need to consider human behavior when choosing a baseline against which to compare policy options. In many situations, the relevant baseline should be unilateral management rather than uncontrolled spread.

5. Conclusion

This work combines the spatial-dynamics of invasion spread and micro-behavior of interacting individuals into a common framework. This approach provides entry to future research examining institutions or incentives that might strategically target actions over space and time to reduce invasion spread and damage efficiently at the landscape level. In addition to addressing one of the leading causes of global environmental change, the approach and findings of this research are applicable to a diversity of other resource management issues in which the resource can disperse across political boundaries. For example, management of wildfire, epidemics, and wildlife all depend on the management decisions of multiple entities. Our work shows how coordination among managers across jurisdictional boundaries can have profound effects on the outcomes of management. We also show how biological models that ignore human behavior can poorly predict observed patterns of resource movement. Although economists have made much progress with both spatial models and dynamic models, the melding of the two is only just beginning to receive attention; this work contributes importantly to this area of research.

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