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Slow treatment promotes control of harmful species by multiple agents

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Abstract

The management of harmful species, including invasive species, pests, parasites, and diseases, is a major, global challenge. Harmful species cause severe damage to ecosystems, biodiversity, agriculture, and human health. The control of harmful species is challenging and often requires cooperation among multiple agents, such as landowners, agencies, and countries. Agents may have incentives to contribute less, leaving more work for other agents, which can result in inefficient treatment. Here we present a dynamic game theory model and we show that slow treatment may promote a stable solution (Markovian Nash equilibrium) where all agents cooperate to remove the harmful species. The efficiency of this solution depends critically on the life history of the harmful species that determines the speed of optimal treatment. Furthermore, this cooperative equilibrium may coexist with other Nash equilibria, including one dictating no treatment of the harmful species, which implies that coordination among agents is critical for successful control.

KEYWORDS
dynamic games, ecosystem management, harmful species, multiple agents, optimal control

1 | INTRODUCTION

Harmful species, among which are invasive species, pathogens and various pests, threaten ecosystems worldwide and are a major cause of biodiversity loss. Specifically, invasive species may displace key native species, alter ecosystem function, and cause significant biodiversity loss (Chapin III et al., 2000; Liebhold & Tobin, 2008; Pimentel, Zuniga, & Morrison, 2005; Sala et al., 2000); pathogens may damage trees and destroy forests (Rohr et al., 2011; Sturrock et al., 2011) and threaten other key species such as bees (Potts et al., 2010); other pests may damage agriculture (Brewer & Goodell, 2012; Lefebvre, Langrell, & Gomez-y Paloma, 2015; Luck et al., 2011); and diseases may threaten human well-being (Barrett & Hoel, 2007). Cost-effective manage-

ment of harmful species may lead to their eradication or to the control of their population at some low density (Barrett, 2004; Bomford & O'Brien, 1995; Clark, 2010; Liebhold & Tobin, 2008). Several studies used bioeconomic models, assuming a single manager (social planner) whose objective is to minimize the net cost over time (Barrett & Hoel, 2007; Born, Rauschmayer, & Bräuer, 2005; Clark, 2010; Epanchin-Niell & Hastings, 2010). Incorporated in this cost are the expenses incurred by the treatment of the harmful species as well as the damage done by the harmful species to both market and nonmarket goods. Some of these studies consider implicit spatial models and focus on how to allocate a budget over time (Clark, 2010; Lampert & Hastings, 2014), while others utilize spatially explicit models and search for strategic loci to prioritize restoration or eradication (Crossman, Bryan,

Ostendorf, & Collins, 2007; Moody & Mack, 1988; Thomson, Moilanen, Vesk, Bennett, & Mac Nally, 2011; Wilson et al., 2011).

In practice, however, harmful species management often entails investments by multiple agents, such as land-owners, corporations, public agencies, and even countries (Coutts, Yokomizo, & Buckley, 2013; Dockner, Jørgensen, Long, & Sorger, 2000; Epanchin-Niell & Wilen, 2015; Lampert, Hastings, Grosholz, Jardine, & Sanchirico, 2014; Sims, Finnoff, & Shogren, 2016). Specifically, because harmful species can migrate across borders between lands that have distinct owners, a treatment implemented by one agent may have a marked effect on the efficiency of his/her neighbor's treatment. Therefore, cooperation between stakeholders is often critical to the outcome of efforts implemented to control harmful species. For example, the control of agricultural pests and invasive species, which may migrate readily or disperse over long distances, often entails the coordinated effort of multiple farmers and land-owners (Brewer & Goodell, 2012; Epanchin-Niell & Wilen, 2015; Lefebvre et al., 2015). Likewise, thwarting the spread of forest diseases necessitates the cooperation of the different managers that own the different areas of the forest (Macpherson, Kleczkowski, Healey, Quine, & Hanley, 2017). On a larger scale, harmful species can also migrate on international scales, meaning that countries can be affected by how their neighbors manage invasive species, pests, and diseases (Berlinguer, 1999; Genovesi & Shine, 2004) as well as by their neighbors' import/export regulations (Brewer & Goodell, 2012; Karesh, Cook, Bennett, & Newcomb, 2005; Lefebvre et al., 2015). For example, countries that invest less in biocontrol to prevent invasive species may become hot spots that spread these species globally (Drake & Lodge, 2004). In all these cases, each agent may aim to maximize his/her own net benefit while putting little or no weight on the benefits accrued or costs borne by other agents. That is, the contribution by a given agent has some beneficial consequences (positive externalities) for other agents, who may experience lower future damage from the harmful species. Therefore, agents may have an incentive to free ride, contributing less to the control effort while waiting for other agents to contribute. Consequently, treatment may be underprovided from a social planner's point of view. Namely, the aggregate contribution to harmful species eradication by a group of agents is likely to be less than that made by a single manager in the same system. In some cases, free-riding may result in a "tragedy of the commons (TOC)," where the harmful species proliferates.

One possible method to prevent the TOC in general is to impose enforcement mechanisms, such as punishment (e.g., taxation, penalties) for agents that do not control the harmful species or rewards (e.g., subsidies) for agents that control it (Barrett, 1994; Brewer & Goodell, 2012; Lefebvre et al., 2015; Ostrom, 1990). Enforcement, however, may also incur costs

and other negative consequences. Specifically, punishment mechanisms may necessitate the implementation of costly actions and institutions to monitor the actions of agents and to enforce the punishment (Benhabib & Radner, 1992; Kaitala & Pohjola, 1988; Nikiforakis, 2008). Moreover, laws that involve penalties often incur negative side effects (Lampert et al., 2014) and may encounter political and social restrictions (Dietz, Ostrom, & Stern, 2003). Subsidies, at the same time, may incentivize agents to care less about preventing degradation from occurring and also to exaggerate their true costs to obtain higher subsidies (Dockner et al., 2000). Also, subsidies that apply collectively may not suffice to prevent free-riding, while subsidies directed toward contributing agents may again entail costly monitoring.

In this article, we address the basic question of whether and under what conditions a group of agents will be more likely to voluntarily cooperate (i.e., without the need for enforcement) to eradicate and/or control a harmful species (or, more broadly, restore ecosystems). Specifically, we use a dynamic game theory model and focus on the following questions: (1) Are there stable solutions where sufficiently many agents contribute without enforcement or subsidy (Markovian Nash equilibria)? (2) How efficient are these solutions (compared with the socially optimal solution)? and (3) Are there cooperative solutions that coexist with a "TOC" solution, such that communication and coordination may lead agents to adopt more desirable solutions?

The problem of harmful species eradication and/or ecosystem restoration has received surprisingly little attention in the dynamic game theory literature. The majority of dynamic game theory literature on environmental management has focused on the harvesting of common resources by multiple agents (e.g., fisheries) (Dockner et al., 2000; Ostrom, 1990). Some previous studies used agent-based simulation to study harmful species eradication by multiple agents (Coutts et al., 2013; Epanchin-Niell & Wilen, 2015), but these approaches often take the behavior of the agents for granted and do not examine whether alternative equilibria could coexist. Other studies used a dynamic game approach to examine the general economic problems inherent in the establishment of a common project (or in the dynamic provision of a public good) (Admati & Perry, 1991; Fershtman & Nitzan, 1991; Itaya & Shimomura, 2001; Marx & Matthews, 2000; Wirl, 1996). These models, however, are neither motivated by environmental management nor do they incorporate biological constraints. Specifically, harmful species control is inherently dynamic and is constrained by the life cycles of the harmful species population and by other natural processes that may play out over years or decades. In the following, we focus on harmful species control as a case study, although the model is general and may apply broadly to investment in restoration of an ecosystem following its degradation.
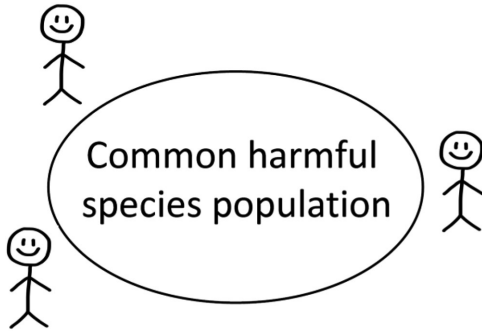
FIGURE 1 Illustrated is the model configuration where a common harmful species population threatens multiple agents.

2 | MODEL

We consider a harmful species population that causes damage to N agents (Figure 1). This harmful species may be characterized by a species that disperses rapidly between sites (e.g., locusts, scorpions, and diseases) or by a species that occupies a common habitat in which it affects all agents (e.g., pests in sewer systems, mosquitos in water ponds). Each agent, $1 \leq i \leq N$, uses a state-dependent (Markovian) strategy, $R_i(n) \geq 0$, which dictates how much he/she contributes to species removal over time as a function of species density, $n(t)$ (Dockner et al., 2000; Mehlmann, 1988). The underlying assumption is that agents know $n(t)$ at all times, but they do not observe the actions of the other agents. Consequently, the agents' strategies, $R_i(n)$, do not depend explicitly on the present and past investments by other agents.

We assume that the dynamics of the harmful species population density are given by

$$\frac{dn}{dt} = f(n) - g(n, R_{\text{tot}}), \quad (1)$$

where $f(n)$ is the natural growth rate of the harmful species, g is the rate at which the population of the harmful species declines due to the treatment, and R_{tot} is the instantaneous aggregate contribution by all agents at time t,

$$R_{\text{tot}}(n(t)) = \sum_{i=1}^{N} R_i(n(t)).$$

We assume that g is nondecreasing and concave with respect to R_{tot} ($\partial g / \partial R_{\text{tot}} \geq 0$ and $\partial^2 g / \partial R_{\text{tot}}^2 \leq 0$). The concavity means that treatment efficiency (marginal return on investment) at a given time t decreases as $R_{\text{tot}}(t)$ increases. These diminishing returns on instantaneous aggregate contributions are an expected consequence of the fact that treatment is often targeted at particular life stages of the harmful species. Therefore, treatment efficiency is constrained by the harmful specie's life cycle (Balaban, Merrin, Chait, Kowalik, & Leibler, 2004; Clark, 2010; Lampert et al., 2014).

We assume that each agent minimizes his/her net present cost, which comprises both private damage and treatment costs over time. Namely, the objective of agent i is to choose a strategy, $R_i(n)$, that maximizes his/her net present value, $\mathcal{V}_i$, given by minus the net present cost,

$$\mathcal{V}_i(R_i, R_{\text{tot}}, n_0) = - \int_0^\infty \left(C_i(n) + R_i(n) \right) e^{-\delta t} dt, \quad (2)$$

where $C_i(n)$ is the damage inflicted per-unit time by the harmful species on agent i (monotone increasing with n), δ is the discount rate (all agents have the same discount rate), and the initial conditions are $n(0) = n_0$.[1] Each agent considers the costs of his/her own damage while ignoring externalities that reduce the costs to other agents. As such, the model incorporates the idea that, when managing a common project, each agent has an incentive to contribute less and wait for the contribution by the other agents. Note that the model allows heterogeneous agents, each of which has his/her own cost function, C_i. The cost function may incorporate both the expected damage and the cost due to risk of unexpected damage. We assume that each agent knows the damage cost functions, $C_i(n)$, of all the agents ("complete information"). Also note that we do not distinguish between the cases in which agent i contributes a given amount and those in which he/she pays an equivalent amount to another agent or to a third party to do the job. Consequently, the treatment cost is the same for all agents (the coefficient of R_i in Equation (2) is 1, independent of i), and moreover, only the aggregate investment, R_{tot}, and not the cost per-agent, is assumed to incur diminishing returns (Equation (1)).

To solve the model, we find pure-strategy Markovian Nash equilibria, each of which defines a strategy for each agent such that, if used by all agents, no agent can increase his/her net present value by unilaterally changing his/her strategy. Namely, we find a set of strategies, $R_1^*, R_2^*, \ldots, R_N^*$, such that for all i ($i = 1, 2, \ldots, N$), $R_i(n) = R_i^*(n)$ is the strategy that maximizes $\mathcal{V}_i$ given that for all $j \neq i$, agent j uses the strategy $R_j^*(n)$. Note that the strategy of a given agent at time t may affect the state of the system, $n(t')$ at any time $t' > t$, and thereby affecting the future contributions of the other agents, $R_i(n(t'))$. Therefore, a reduced contribution by a given agent affects the state n and may be compensated for by a greater contribution from the other agents. Consequently, cooperation in a Markovian Nash equilibrium (where strategies depend on n), it is generally harder to achieve than in an open-loop Nash equilibrium where the agents do not know the state n (Fershtman & Nitzan, 1991).

Finally, to examine the efficiency of harmful species eradication by multiple agents, we examine how the Nash equilibria differ from the socially optimal solution, $\mathcal{V}_{\text{opt}}$, that maximizes the sum of the net present values of all agents. Equivalently, $\mathcal{V}_{\text{opt}}$ is given by the net
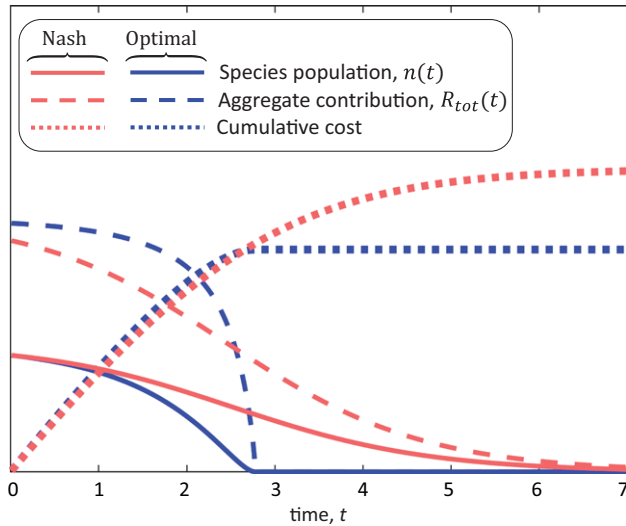
FIGURE 2 Demonstrated are the dynamics of the harmful species population in a common yard, subject to control by the agents. Specifically, we compare the dynamics subject to optimal treatment (blue lines) to the dynamics where treatment is given by a Nash equilibrium in which all agents contribute (orange lines). Solid lines show the harmful species density, $n(t)$, dashed lines show the aggregate contribution, R_{tot}, and dotted lines show the cumulative cost until time t. Control that follows Nash equilibrium may result in successful eradication of the harmful species. This solution is not as efficient as the socially optimal solution, but it is still more desirable for all agents than the absence of any treatment (which also comprise a Nash equilibrium in some parameter regions, as shown in Figure 3).

present value for the social planner (sole-owner) that uses $\mathcal{R}_{tot}$ that maximize

$$\mathcal{V}(R_{tot}, n_0) = -\int_0^\infty \left(\sum_i C_i(n) + R_{tot}(n) \right) e^{-\delta t} dt, \quad (3)$$

where dynamics of n are given by Equation (1). Accordingly, solution inefficiency is given by $\mathcal{V}_{opt} - \sum_i \mathcal{V}_i$.

3 | RESULTS

Our results show that, under certain conditions, there exist Markovian Nash equilibria where multiple (or all) agents simultaneously remove the harmful species (Figure 2 and Theorem 1). Cooperative eradication can be achieved via contributions by all agents simultaneously throughout the project, by a few agents simultaneously, or by different groups of agents in different stages (Figure 3). Removal rates in these equilibria are generally slower than the optimal rates. Specifically, the harmful species exhibits slow population decline, such that each agent benefits from maintaining his/her contribution to promote or accelerate removal. In Theorem 1

(Supporting Information), we specify sufficient conditions for the existence of these cooperative Nash equilibria. The first condition, Equation (S1), implies that the harmful species population either does not decline or is slow to decline naturally. (Otherwise, agents will not contribute since recovery proceeds rapidly enough without intervention (Lampert & Hastings, 2014).) The second condition, Equation (S2), implies that the cost to a given contributing agent due to the pest, C_i, is not much lower than that cost to the other agents. Finally, we assume that the discount rate is sufficiently low and that complete eradication can be achieved within a finite time via investment of a finite cost (see Supporting Information).

Furthermore, our results show that the efficiency of the cooperative Nash equilibria depends largely on how fast the returns on investment diminish with the aggregate contribution (Figure 3). If returns diminish slowly (g is approximately linear with respect to R_{tot}), then the difference between the Nash equilibrium under which agents eradicate the harmful species and the optimal solution is large (Figure 3A,B). But if returns diminish fast, Nash equilibria in which several agents contribute are much closer to the optimal solution (Figure 3B,D). The underlying mechanism is that, in Nash equilibrium, each agent has an incentive to eradicate more slowly to allow other agents to do the job, and therefore, eradication proceeds more slowly than in the optimal solution. In turn, if returns diminish fast, the optimal solution also dictates slow eradication because fast treatment (large R_{tot}) would result in a much lower marginal harmful species removal per unit of investment. Nevertheless, if returns diminish slowly with R_{tot}, the optimal solution is to eradicate faster as there is no reason to postpone the treatment, while fast treatment would minimize the net cost due to the harmful species.

Another result is that the cooperative solutions may coexist with the TOC solution, in which no agent contributes to eradication (Figure 3). Namely, in some parameter regions, the TOC solution as well as some solutions dictating contribution by several or all agents are all Markovian Nash equilibria. The stabilities of both the cooperative and the TOC solutions depend, to a large extent, on the discount rate and on the ratio between the cost of investment and the cost due to the pest, as given by the nondimensional discount rate, $\tilde{\delta} = \delta cn / \max\{C_i\}$, where c is the marginal cost of eradication, $c^{-1} = dg(n, 0)/dR_{tot}$. Specifically, as $\tilde{\delta}$ increases, fewer cooperative Nash equilibria remain. Moreover, if agents are identical, then the higher the number of agents that contribute, the further along the Nash solution exists as $\tilde{\delta}$ increases.

4 | DISCUSSION

We showed that selfish agents can cooperatively eradicate a common harmful species population. Each agent
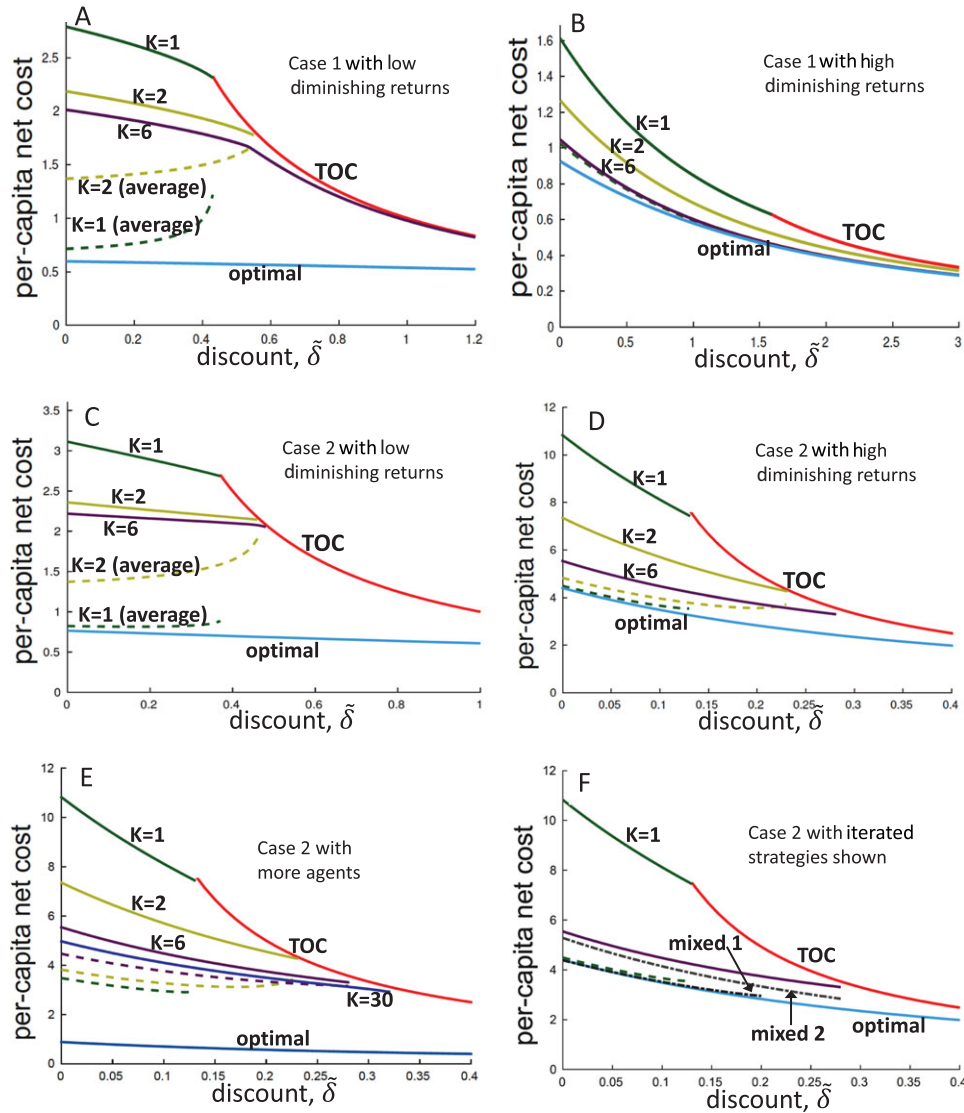
FIGURE 3 Demonstrated are the net present costs to the agents $(-\mathcal{V}_i)$ for several control strategies. Each curve demonstrates a certain solution by the agents, including (i) the tragedy of the commons (TOC) Nash equilibrium where no agent contributes (red), (ii) the socially optimal solution (lowest curve, light blue), and (iii) several Nash equilibria where k agents contribute to eradication, for various values of k (solid lines demonstrate the cost for the k agents that contribute, while dashed lines with respective colors demonstrate the average cost per-agent including the cost for the $N - k$ free riders. Each Nash equilibrium exists in a certain region of the nondimensional discount rate, $\tilde{\delta}$. Moreover, there may be multiple Nash equilibria for the same parameter value. In particular, at some parameter regions, the TOC solution coexists with solutions where some or all agents collectively contribute to eradication. This implies that an agent may benefit from joining a group of agents already engaged in eradication to accelerate the process, even where it is not profitable to eradicate alone. Moreover, note that if diminishing returns on investment in eradication are low (a,c), the differences between the cooperative Nash equilibria and the optimal solution are large; conversely, if diminishing returns are high (b,d), the cooperative Nash equilibria are much closer to the optimum. Here panels a and b show the results for "case 1," in which $g(R, n) = R^\alpha$ if $n > 0$ and $g(0, n) = 0$, with $\alpha = 0.8$ and $\alpha = 0.2$, respectively; c and d show the results for "case 2," in which $g(R, n) = R - \alpha R^2$ if $n > 0$ and $g(0, n) = 0$, with $\alpha = 0.1$ and $\alpha = 0.7$, respectively. Note that panels a–d show the results for $N = 6$ but the results for $N = 30$ are qualitatively similar (e). Also note that panels a–e show the results when k agents contribute simultaneously until eradication is complete. But there are additional solutions (f). For example, there exists a Nash equilibrium where one agent does the first half of the job and the another agent does the second half (iterated 1), and a solution where one agent is responsible for for the first third of the job, another agent performs the second third, and all agents contribute simultaneously to complete the final third of the job (iterated 2). Parameters: we considered $f(n) = n(1 - n)$, initial conditions $n_0 = 1$, and identical agents with, $C_i(n) = n$ for all i. (Therefore, the TOC solution dictates $n(t) = 1$ for all t, which implies $\mathcal{V}_i = -1/\delta$ for all i.)

eradicates slowly, which incentivizes the other agents to maintain their contributions. This results in a collective removal of the harmful species, but at a rate that is lower than the socially optimal one (Figures 2 and 3 and Theorem 1 (Supporting Information)). The magnitude of the inefficiency resulting from the slower removal depends largely on the biological factors that constrain the speed at which the harmful species can be removed. If the biological constraints are significant, then optimal eradication, which aligns with natural processes, is also slow. Therefore, the inefficiency is small and enforcement or subsidy may not be needed. Otherwise, optimal eradication is fast and the slow removal by the agents is highly inefficient, in which case some form of enforcement is essential for efficient treatment. In addition, we showed that although inefficiency increases with the number of agents N (Admati & Perry, 1991; Fershtman & Nitzan, 1991), agents can still cooperate when N is large (Figure 3E). This suggests that subsidy is more beneficial when the same harmful species population threatens many agents.

Our results also imply that agent coordination is critical for successful management. Specifically, cooperative Nash equilibria that promote eradication may coexist with a noncooperative Nash equilibrium that results in the TOC (Figure 3). Namely, if rational agents agree to contribute at the rates determined by a Nash equilibrium, even if the agreement is nonbinding, each agent will honor the agreement to maximize his/her profit. In contrast, if all agents believe that the other agents are not going to contribute, it will be in their best interest to avoid any contribution as well. Therefore, communication among the agents (cheap talk) may lead to a more efficient treatment and prevent the TOC, even without enforcement.

Furthermore, we showed that achieving eradication is feasible even if not all agents contribute. Specifically, harmful species eradication is successful if the number of agents that contribute is above some critical mass, which depends, in particular, on the relative costs of the damage and treatment, $\tilde{\delta}$ (Figure 3). The greater $\tilde{\delta}$ is, the greater the number of agents that need to contribute to enable effective treatment and thereby prevent the TOC (Figure 3). The fact that cooperation by some of the agents is sufficient is positive and makes successful management more plausible, but at the same time, it may lead to unfair solutions where some agents do the job for the others. To offset such unfairness, the government can use subsidies that are directed exclusively to the contributors (e.g., reimbursement), although these may entail monitoring and may be costly to implement.

The mechanism underlying the promotion of multiple Nash equilibria in our model is that the diminishing returns are on the aggregate contribution. Such diminishing returns characterize constraints on treatment efficiency that may result from biological factors, such as the life history of the harmful species, and how it is affected by the treatment. In contrast, most previous studies demonstrating cooperative Markovian

Nash equilibria in dynamic contribution of public goods games have focused on cases where only individual agent's investments (not aggregate investment) are subject to diminishing returns (Dockner et al., 2000). Diminishing returns on individual investment characterize limits on individual expenditures. For example, Fershtman and Nitzan (1991) assumed that the return on investment by a given agent diminishes when the agent invests more, but the individual costs do not depend on the investments by other agents. The authors also assumed that the marginal cost is zero when an agent's contribution is zero, and therefore, each agent contributes until it reaches the unique level where the agent's marginal benefit equals his/her marginal cost. This leads naturally to a unique Nash equilibrium where all agents contribute with no coexisting Nash equilibria. In our model, each agent can stably contribute more, but only slower contributions incentivize others to contribute, thereby stabilizing cooperation. Namely, slower contribution leads to alternative Nash equilibria where more agents contribute. The uniqueness of our results compared to previous studies indicates that there is a true need to use dynamic game theory to further explore across broader sets of problems in environmental management.

Although our study focuses on eradication of harmful species, it is also broadly applicable to restoration and conservation in general (the variable n may incorporate any kind of degradation in habitat quality). Invasive species, pests, and diseases spread over long distances that cross national boundaries, and therefore, inadequate control by some nations may promote the invasion of harmful species to other countries around the globe (Brown & Hovmøller, 2002; Drake & Lodge, 2004). Similarly, natural habitats of threatened species often expend spatially across multiple countries or reside in international waters (Hannah, 2010; Mittermeier et al., 2005). This necessitates transboundary management, in which multiple nations invest in harmful species control, habitat restoration, and other conservation activities. In particular, global climate change causes the natural habitat regimes of both invasive and native species to constantly shift, a scenario that will further necessitate transboundary conservation management in the future. Our results suggest that investment in transboundary conservation is underprovided, but at the same time, they show how coordination among nations could result in greater investment and better conservation outcomes.

ENDNOTE

[1] If the integral diverges for all R_i, then the objective of agent i is to choose $R_i = \lim_{T \to \infty} R_i^T$ where R_i^T maximizes $-\int_0^T (C_i(n) + R_i(n)) e^{-\delta t} dt$.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.