



Multiple agents managing a harmful species population should either work together to control it or split their duties to eradicate it

Adam Lampert^{a,b,1}

^aSchool of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287; and ^bSimon A. Levin Mathematical, Computational and Modeling Science Center, Arizona State University, Tempe, AZ 85287

Edited by Arild Underdal, University of Oslo, Oslo, Norway, and approved March 13, 2020 (received for review October 10, 2019)

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. In particular, managing harmful species often requires cooperation among multiple agents, such as landowners, agencies, and countries. Each agent may have incentives to contribute less to the treatment, leaving more work for other agents, which may result in inefficient treatment. A central question is, therefore, how should a policymaker allocate treatment duties among the agents? Specifically, should the agents work together in the same area, or should each agent work only in a smaller area designated just for her/him? We consider a dynamic game-theoretic model, where a Nash equilibrium corresponds to a possible set of contributions that the agents could adopt over time. In turn, the allocation by the policymaker determines which of the Nash equilibria could be adopted, which allows us to compare the outcome of various allocations. Our results show that fewer agents can abate the harmful species population faster, but more agents can better control the population to keep its density lower. We prove this result in a general theorem and demonstrate it numerically for two case studies. Therefore, following an outbreak, the better policy would be to split and assign one or a few agents to treat the species in a given location, but if controlling the harmful species population at some low density is needed, the agents should work together in all of the locations.

dynamic games | environmental management | harmful species | international cooperation | multiple agents

The management of harmful species, such as invasive species, pests, parasites, and diseases, is a major challenge. In recent years, for example, the US government has spent over 100 billion dollars annually only to prevent and mitigate the damage caused by invasive species (1). In turn, managing harmful species often requires the cooperation and coordination of multiple agents. At regional scales, failing to manage pests and diseases by one or more landowners may lead to an outbreak that affects all their neighbors (weakest link effect) (2–7). Moreover, insufficient investment by landowners to treat the harmful species after its outbreak may allow the species to spread further. At the international scale, when countries do not properly manage invasive species and diseases within their national borders, the species may spread into other countries (8–10). Specifically, evidence has shown that a large portion of the invasive species and diseases invades from certain hot spots, which may be countries that do not properly manage the invasive species or diseases within their borders (11, 12), or regions with high international trade traffic (13). Each country or landowner can take several actions within her/his borders or land to prevent the species from spreading or to control it after infestation has occurred (10, 14–16). However, these actions might not be sufficient, and to overcome the weakest link effect, it is often necessary for countries or landowners to intervene and treat the species population in those locations where it is not properly managed (7, 13), even if those locations are outside their property. For example, the best strategy for some rich countries might be to combine their

efforts to treat or to subsidize the treatment of the harmful species in the hot spots where it is not properly managed, even if these hot spots are outside the countries' national borders (Fig. 1). An example where such a subsidy has occurred is the eradication of smallpox (11) and the attempt to eradicate several other diseases (12). Nevertheless, such an effort of multiple agents (countries or landowners) to manage a common harmful species population necessitates coordination and cooperation among the agents. In particular, each agent may have the incentive to free ride and let the other agents perform the treatment, which may lead to the eventual failure of the treatment (7, 17). Furthermore, international agreements are difficult to enforce, with each country seeing opportunity to opt out and not contribute to the treatment (18, 19); namely, the contribution has to be voluntary, which makes the free-riding a significant issue.

The goal of this paper is to examine how multiple agents can effectively cooperate to manage harmful species in those hot spots where it is not properly managed otherwise, and how the best solution depends on the biological properties of the harmful species and its response to the treatment. We consider this problem from the point of view of both 1) the agents and 2) the policymaker who needs to determine which allocation would be best for society as a whole (namely, minimize the net cost over time for all of the agents combined). In particular, the key question is how the policymaker should allocate the job among the various agents that could potentially participate, where the goal is to maximize social welfare under the constraint that each agent contributes voluntarily—only if it is beneficial for her/him

Significance

Harmful species are becoming increasingly prevalent due to trade globalization and climate change. A major question is how international cooperation and coordination can help to mitigate the spread of harmful species. In this study, we show that a single country may be able to abate the harmful species population effectively. However, when the countries need to control the harmful species at a low density for prolonged periods, a joint effort results in maintaining the harmful species at a lower density. In particular, controlling the harmful species in certain hot spot locations is often the key to preventing global spreads of harmful species, which implies that international cooperation is necessary for achieving effective treatment.

Author contributions: A.L. designed research, performed research, and wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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¹Email: adam.lampert@asu.edu.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1917028117/-DCSupplemental>.

First published April 24, 2020.

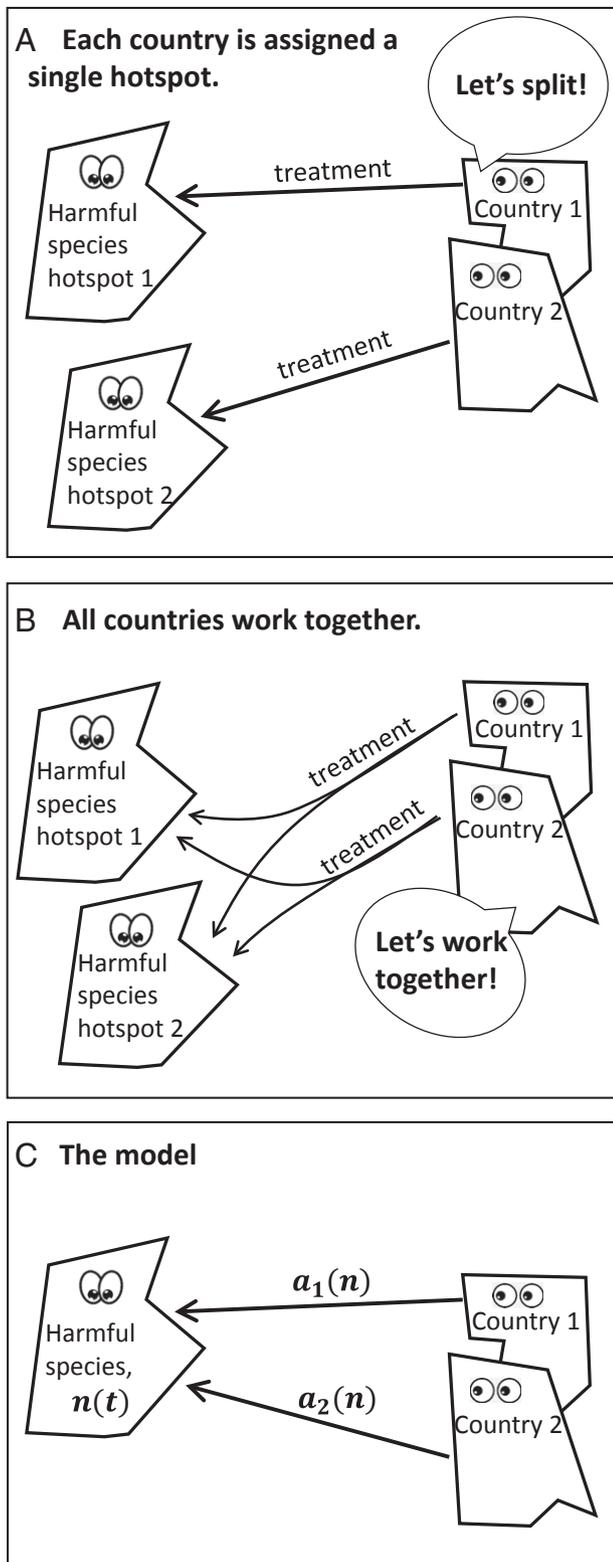


Fig. 1. Illustration of the research question and the model. Two countries/agents would like to treat a harmful species population that resides in two hot spots. (A) The countries may decide to split, such that each country treats the harmful species only in its designated hot spot. (B) Alternatively, the countries may work together in both hot spots. (C) To examine which allocation results in a more desirable outcome, we focus in our model on a single hot spot, and we compare between the Nash equilibria in which one country is assigned to the hot spot [e.g., $a_1^*(n) > 0$ and $a_2^*(n) = 0$] and the Nash equilibria in which multiple countries work together [e.g., $a_1^*(n) = a_2^*(n) > 0$].

(second-best solution). Specifically, one possible allocation is to assign each agent to treat the harmful species in a certain location (Fig. 1A). For example, following that allocation, 1) each hot spot is managed by a designated country that volunteers to contribute or 2) each landowner treats her/his own land. However, in that case, a country that is assigned to treat a given hot spot may consider only its own damages from the potential infestation of the harmful species from that hot spot, and therefore, it may underprovide treatment there (i.e., it might treat too slowly and/or allow for a higher level of the harmful species to persist and cause higher invasion risks). Alternatively, another possible allocation dictates that the contributing agents stick together and treat the harmful species jointly in all of the locations (Fig. 1B). However, in that case, the treatment might be slower because each agent would have an incentive to reduce her/his contribution and wait for the other agents to contribute. The question is, therefore, how can the policymaker determine which allocations would result in a more desirable outcome?

We use a dynamic game-theoretic model to examine the outcome of each allocation and to determine which allocation could maximize social welfare, under the assumption that each agent would adopt a strategy that minimizes her/his own net cost. We consider a single population of some harmful species (e.g., a single hot spot/location), and we consider multiple agents, each of which decides how much to contribute annually to the treatment and how her/his contribution would vary over time. In particular, the agents' strategies determine how fast they abate the harmful species and which density the species ultimately approaches. In turn, a Nash equilibrium corresponds to a possible set of contributions of the agents over time. For example, a Nash equilibrium in which a single agent contributes corresponds to a stable agreement in which a single agent is assigned to treat the harmful species in a given hot spot, whereas a Nash equilibrium in which multiple agents contribute simultaneously corresponds to an agreement or an allocation in which multiple agents treat the harmful species together in the focal location. Other Nash equilibria may correspond to cases in which different agents treat the species at different times. In turn, we compare the social welfare associated with each of these Nash equilibria to determine the optimal allocation. For simplicity, we assume that all of the agents have the same cost due to damages from the harmful species. Our results show that a simple rule applies. If the annual cost of investment needed for maintaining the species population at a given density, $C_m(n)$, decreases as the density, n , decreases, then the eradication by fewer agents is faster and more socially desirable. However, if $C_m(n)$ increases as n decreases, then the control of the population to maintain it at some low density is necessary, and a joint treatment in which many agents work together at the same location would result in controlling the population at a lower density and is more socially desirable. In turn, biological factors that determine the population growth as well as the population's response to the treatment determine the function $C_m(n)$. While the main result is proven in a theorem, we also analyze numerically two case studies, each of which is characterized by a different slope of $C_m(n)$. We discuss how the function $C_m(n)$ depends on the biological properties of the harmful species and how the solution extends to cases where the harmful species reside in multiple hot spots.

Model

We consider N agents (countries or landowners) that incur damages due to a common population of a harmful species residing in a given hot spot (Fig. 1C). Each agent decides what her/his annual contribution would be to the treatment of the harmful species and how her/his contribution would vary over time. Specifically, we assume that each agent adopts a state-feedback (Markovian) strategy in which her/his annual contribution, $a_i(n)$,

depends on the density of the harmful species, n . In turn, the dynamics of n follow

$$\frac{dn}{dt} = f(n) - g(n, A), \quad [1]$$

where f is the natural growth rate of the population (without treatment), g is the rate at which the harmful species is being removed due to the treatment, and A is the total annual contribution to the treatment (by all of the agents):

$$A(n) = \sum_i a_i(n). \quad [2]$$

Note that there is no distinction in this model between the case in which an agent contributes a given amount and the case in which she/he pays the equivalent of that amount to another agent or to a third party to do the job. In turn, the forms of f and g are determined by the particular biological system. In our theoretical analysis, which we use to prove the general theorem, we consider the general form given in Eq. 1. For our numerical analysis, we consider logistic natural growth with possibly some constant immigration of the harmful species into the hot spot:

$$f(n) = r_0 + r_1 n \left(1 - \frac{n}{K}\right), \quad [3]$$

where $r_0 \geq 0$ is the immigration rate, r_1 is the per-capita natural growth rate of the harmful species population that already resides within the hot spot when the population is near, and K is the population's carrying capacity. In turn, we consider two common case studies characterized by two different forms of g . In the first case, we consider an aerial treatment in which the effect on each individual does not depend on the population density. This may characterize the application of pesticides to treat insects. The response of the population to the treatment in this case is proportional to n [$g(n, A) = nh(A)$] (20, 21). In the second case, we consider a harmful species that is visible and easily detectable, such as large invasive plants, in which case the treatment can be targeted in locations with higher population densities. Consequently, the efficiency of the treatment is less sensitive to changes in n (e.g., g does not depend on n) (7, 22, 23).

In turn, the objective of each agent is to minimize her/his own cost due to both 1) the damages incurred to her/him due to the harmful species and 2) her/his own contribution to the treatment over time. We assume that the agents are symmetric; namely, agents are identical in the sense that they all have the same annual cost due to the harmful species, $C_n(n)$. This cost incorporates the direct damages from the harmful species, and if the hot spot is outside of the territories of the agents, this cost also incorporates the risk of invasion from the hot spot. It follows that the utility, or the net present value of agent i (given by minus her/his net cost), is given by

$$\mathcal{V}_i = -\int_0^\infty (C_n(n) + c_a a_i(n)) e^{-\delta t} dt, \quad [4]$$

where c_a is the cost per unit of investment and δ is the discount rate. In turn, we consider a Markovian Nash equilibrium as a possible set of strategies that could be adopted by the agents. Specifically, a Markovian Nash equilibrium is given by a set of strategies, $a_1^*(n), a_2^*(n), \dots, a_N^*(n)$, such that for each i , $a_i^*(n)$ is the optimal control strategy of agent i (maximizes \mathcal{V}_i) given that for each $j \neq i$, agent j 's strategy is $a_j^*(n)$. Namely, if the agents agree to adopt these strategies, no agent has an incentive to deviate and change her/his strategy.

Finally, to determine the best policy, we compare the outcome of the various Nash equilibria, and we seek to find the Nash

equilibria that result in higher social welfare, given by the sum of utilities of all of the agents:

$$W = \sum_i \mathcal{V}_i. \quad [5]$$

Specifically, to examine the efficiency of the allocation in which only one agent is assigned to treat the harmful species in the given hot spot, we consider the efficiency of the Nash equilibria in which $N - 1$ agents do not contribute at all. In turn, to examine the allocation in which multiple agents work together in the same hot spot, we consider the Nash equilibria in which several agents contribute at all times (if such an equilibrium exists). More generally, in what follows, we consider four types of Nash equilibria: 1) no contribution is made by any agent [$a_i(n) = 0$ for all i]; 2) the entire contribution is made by a single agent [$a_i(n) > 0$ for some i , and $a_j(n) = 0$ for all $j \neq i$]; 3) several agents contribute simultaneously at all times; and 4) several agents contribute, but each agent contributes during a different period.

Results

Treatment Could Be Done by a Single Agent or by Multiple Agents (Multiple Nash Equilibria Exist). Our first result, which is the baseline for the analysis in this paper, is that multiple Nash equilibria exist in our model (see also ref. 7). Specifically, a Nash equilibrium in which one agent contributes and the remaining $N - 1$ agents do not contribute exists if and only if the net cost to the agent that contributes is lower than the net cost of damages per agent when the species is left untreated (7, 11). In turn, if the treatment is abandoned, the cost of damages is inversely proportional to δ . [For example, if the harmful species has reached its carrying capacity, $n = K$, then abandoning the treatment would imply that $n(t) = K$ and the net cost to the agent is given by $C_n(K)/\delta$.] Consequently, a Nash equilibrium in which only one agent contributes exists if δ is sufficiently small, $\delta < \delta_1$, whereas if $\delta \geq \delta_1$, a Nash equilibrium in which no treatment is provided exists [$a_i^*(n) = 0$ for all i] (see also refs. 7 and 11).

At the same time, there also exist Nash equilibria in which multiple agents contribute. Specifically, for each $k = 2, \dots, N$, if δ is sufficiently small ($\delta < \delta_k$), there exist one or more Nash equilibria in which exactly k agents contribute simultaneously at all times (and the other $N - k$ agents free ride and do not contribute) (7), where in general, the threshold value δ_k is monotone increasing in k (7, 11).

In turn, in any Nash equilibrium, the treatment can result in either 1) complete eradication (n approaches zero) or 2) control of the harmful species to maintain it at some low density ($n \rightarrow n^* > 0$ as $t \rightarrow \infty$) (7, 21, 22). As a rule of thumb, if the marginal cost of abatement does not depend on the population density (i.e., g does not depend on n), the equilibrium treatment results in eradication (7, 22, 23). However, if the marginal cost of abatement is proportional to the population density (i.e., g is proportional to n), the equilibrium treatment results in the control of the population to maintain it at some low density (21). Also, note that if a Nash equilibrium in which k agents contribute simultaneously results in the control of the species at some $n^* > 0$, then multiple other Nash equilibria may exist, all of which include k agents that contribute simultaneously but each of which has a different level at which the harmful species is being controlled.

How Do We Determine Which Allocation Is More Desirable? To determine which allocation is more socially desirable, we compare between the various Nash equilibria. First, note that if a Nash equilibrium in which k agents contribute does not exist for a given k , then assigning k agents to the hot spot would result in no treatment, which in general implies that the policymaker should seek to find a better allocation. Therefore, the policymaker

should restrict attention to those values of k for which at least one Nash equilibrium exists [i.e., $k = 1, 2, \dots, N$ if δ is sufficiently small and $k \geq k_c$ if δ is larger (7)]. Second, if there exist multiple Nash equilibria in which the same k agents contribute simultaneously, the policymaker should restrict attention to the equilibrium that results in the highest social welfare: Our results show that such a Nash equilibrium is also the most desirable one for each of the k agents, and we assume that the policymaker could coordinate the k agents to adopt the more desirable Nash equilibrium. In what follows, we distinguish two factors that determine the efficiency of each solution: 1) the density at which the harmful species population is being controlled in the long-run, n^* (asymptotic value of n), and 2) the speed at which this density is being approached. In general, the more efficient solutions are those that result in a lower asymptotic level and approach this level faster. (The optimal solution may as well imply some strictly positive n^* and strictly positive time to approach n^* , but in a Nash equilibrium, both of these are larger than the optimum due to the underprovision of the treatment.)

Which Allocation Results in the Control of the Harmful Species at a Lower Density? Our main result shows that a simple criterion determines which Nash equilibrium results in controlling the harmful species population at a lower density (Figs. 2 and 3). Specifically, the solution depends on whether it is more costly to maintain the population at a higher density or at a lower density. If it is less costly to control the population at lower densities, then the treatment often results in complete eradication. However, if it is more costly to control the population at lower densities, then the Nash equilibria in which more agents work together result in maintaining the population at lower densities (Figs. 2 C–D and 3 A–C). To be more precise, denote $n^{(k)}$ as the density at which the population is being controlled when k agents contribute simultaneously ($n \rightarrow n^{(k)}$ as $t \rightarrow \infty$ in Nash equilibrium). In turn, denote $C_m(n)$ as the cost of treatment needed for maintaining the population density at a level n . Our result implies that for $l < m$, $n^{(l)} \geq n^{(m)}$ if $C_m(n)$ increases as n decreases, whereas $n^{(m)} \geq n^{(l)}$ if $C_m(n)$ decreases as n decreases. (In the latter case, since complete eradication is a common outcome, the equality $n^{(m)} = n^{(l)} = 0$ often holds.) This result is the content of the following theorem (the proof is given in *SI Appendix, section S2*).

Theorem. Consider the N -players game in which the utility of agent i is given by Eq. 4 and the dynamics of the state variable n are given by Eqs. 1 and 2, where $C_n(n)$ is monotone increasing in n and $f(n)$ and $C_n(n)$ are differentiable functions. Assume that the response of the population to the treatment is linear in A , i.e., $g(A, n) = Ah(n)$, where $h(n)$ is a nonnegative differentiable function. Also assume that the population density cannot become negative: $f(0) \geq 0$ and $h(0) = 0$. Denote as \mathcal{K} the set of all values of k for which there exists at least one Nash equilibrium where exactly k agents contribute simultaneously the same amount at all times, while the other $N - k$ agents do not contribute at all [e.g., if δ is sufficiently small, $\mathcal{K} = (1, 2, \dots, N)$ (7)]. In turn, for each $k \in \mathcal{K}$, denote $n^{(k)}$ as the lowest asymptotic value of n that could be approached in such a Nash equilibrium. Denote $C_m(n)$ as the aggregate annual cost of investment that is needed to maintain the system at state n , which is given by $C_m(n) = c_d f(n)/h(n)$. It follows that for all $k \in \mathcal{K}$, if $C_m(n)$ is monotone increasing in n , then $n^{(k)}$ is monotone increasing in k ($n^{(l)} \geq n^{(m)}$ if $l > m$), whereas if $C_m(n)$ is monotone decreasing in n , then $n^{(k)}$ is monotone decreasing in k .

Which Allocation Results in Faster Removal of the Harmful Species? Our second result shows that the eradication of the harmful species is faster in those Nash equilibria where fewer agents contribute (Figs. 2 A and B and 3). Also, if several Nash equilibria result in controlling the population at some positive density

but the density at a given time is still much higher than that asymptotic level, then the total contribution to the treatment, $A(n)$, is greater in those Nash equilibria where fewer agents contribute (Fig. 2 A and B). This result was obtained numerically for specific choices of f and g (Figs. 2 A and B and 3 D and E), but note that in the case where complete eradication is approached in all equilibria and δ is sufficiently small, this result is shown in *SI Appendix, section S3*. In turn, a simple rule of thumb can determine the number of agents, k_{opt} , that would result in the fastest abatement of the harmful species. On one hand, k_{opt} has to be sufficiently large to ensure that the net benefit for the agents that contribute is sufficiently large, such that these agents will not abandon the treatment. [Specifically, this implies that $k_{\text{opt}} \geq k_c$, namely, a Nash equilibrium in which k agents working together exists (7, 11).] On the other hand, our result shows that a Nash equilibrium in which fewer agents contribute results in faster eradication, and therefore, k_{opt} needs to be as small as possible under the above constraint, i.e., $k_{\text{opt}} = k_c$.

Tradeoff Between the Speed of Eradication and the Asymptotic Population Level (and How Assigning Different Agents to Contribute at Different Times May Be Beneficial). The results above imply that a tradeoff may exist between the speed of approaching n^* and the value of n^* . Specifically, if $C_m(n)$ decreases with n , then n^* is smaller if more agents contribute, but the time to approach n^* may still be shorter if fewer agents contribute. Therefore, it is still questionable which allocation is better in that case. In turn, our analysis shows that if δ is sufficiently small, then the effect of a lower n^* on social welfare is more significant than the effect of slower progress (Fig. 3 and *SI Appendix, section S3*). Specifically, in *SI Appendix, section S3*, we analyze a special case of the model and show that the difference between n^* in the various Nash equilibria approaches a strictly positive constant when $\delta \rightarrow 0$. Therefore, for a sufficiently small δ , the difference in the utility becomes unboundedly large, and at the same time, the speed at which n^* is approached remains a constant, even when $\delta \rightarrow 0$. This implies that for a sufficiently small δ , the asymptotic value of n^* is the dominant factor, and the Nash equilibria in which more agents contribute result in higher social welfare.

Furthermore, in those cases where $C_m(n)$ decreases with n , there exists a Nash equilibrium that is more efficient than any of the Nash equilibria described above and that leads to both lower n^* and faster eradication (Fig. 2 C and D). Specifically, in this Nash equilibrium, a single agent contributes until n equals $n_c > n^*$, and only then the other $k - 1$ agents join to remove the harmful species until $n = n^*$ and control it at that level thereafter. (Note that this Nash equilibrium exists only if n_c is above some critical threshold that is strictly greater than n^* , because if n_c is too close to n^* , it would not be beneficial for the other $k - 1$ agents to join.) In this Nash equilibrium, the harmful species is controlled at $n = n^{(k)}$, but the speed of approaching this density is higher.

Discussion

In this study, we showed that a general rule can be used to determine how a policymaker should allocate a job among agents participating in the treatment of a common harmful species population. Our main result shows that under certain assumptions, treatment by fewer agents in a given location results in a faster eradication of the harmful species; however, if the control of the harmful species at some low density is needed, then the simultaneous treatment by multiple agents working together results in maintaining the population at a lower density. Therefore, as a rule of thumb, following an outbreak in which the density of the harmful species becomes very high, the optimal

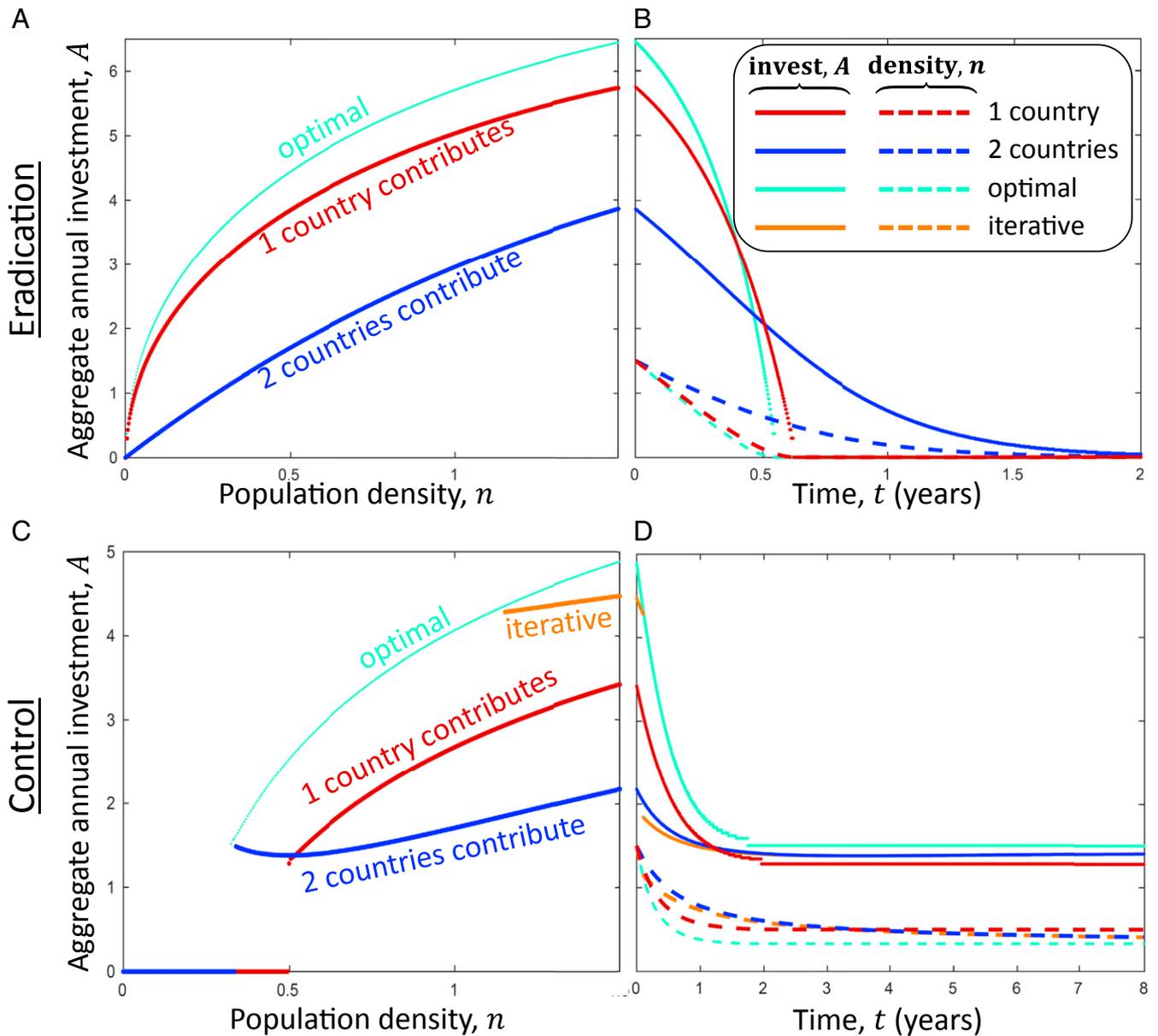


Fig. 2. A single country eradicates the harmful species population faster, but multiple countries working together may control it at a lower density. Demonstrated are the aggregate annual contributions, $A(n) = a_1(n) + a_2(n)$ as a function of the population density, n , for four different solutions: 1) a Nash equilibrium in which only one country contributes, $a_1^*(n) \geq 0$, $a_2^*(n) = 0$ (NE1, red line); 2) a Nash equilibrium in which two countries contribute, $a_1^*(n) = a_2^*(n)$ (NE2, blue line); 3) the optimal solution that maximizes $\mathcal{V}_1 + \mathcal{V}_2$ (light blue line); and 4) an iterative Nash equilibrium in which one country contributes if $n \geq n_c$ and both countries contribute if $n < n_c$ (orange line shows the solution for $n \geq n_c$, and the solution coincides with NE2 for $n < n_c$). (Left) $A(n)$ as a function of n and (Right) both A (solid lines) and $n(t)$ (dashed lines) as a function of time. (A and B) We consider a case in which complete eradication is approached ($n \rightarrow 0$). NE 1 results in a larger aggregate total contribution than NE 2: For each n , the contribution by the country that contributes alone in NE 1 is greater than the contribution of both countries combined in NE 2 (A). In turn, this results in a faster eradication in NE 1 compared to NE 2 (B). (C and D) We consider a case in which the harmful species is being controlled and maintained at some nonzero density ($n \rightarrow n^* > 0$). In NE 2, the population is controlled at a lower density: n^* in NE 2 (~ 0.4) is smaller than n^* in NE 1 (~ 0.5). In turn, the iterative Nash equilibrium results in the same n^* as that of NE 2, but if the initial population density is given by $n > n_c$, the density approaches n_c faster. Parameters are as follows: $r_0 = 0$, $r_1 = 1$, $K = 3$, $C_n = 0.7n$, $c_a = 1$, and $\delta = 0.01$; in A and B, $g = A - 0.05A^2$, and in C and D, $g = n(A - 0.05A^2)$.

policy would be to split and allocate a small number of agents to work in a given location (this small number, k_{opt} , is determined by the smallest number of agents that would ensure the agents will not abandon the system). However, if the species approaches a density at which it needs to be controlled for prolonged periods, then the optimal allocation is to assign many agents to work together in the entire region, which will allow the agents to maintain the harmful species at lower densities. We have made various simplifying assumptions, including the assumptions that

all countries have the same cost due to damages from the harmful species and that the dynamics are deterministic. These assumptions are similar to those made in some previous studies about the management of harmful species by multiple agents that considered either symmetric games or agent-based models with identical agents (5, 24), and future studies are needed for examining the consequences of relaxing these assumptions.

Some other key factors of the model include allowing multiple agents to treat the harmful species together in the same area and

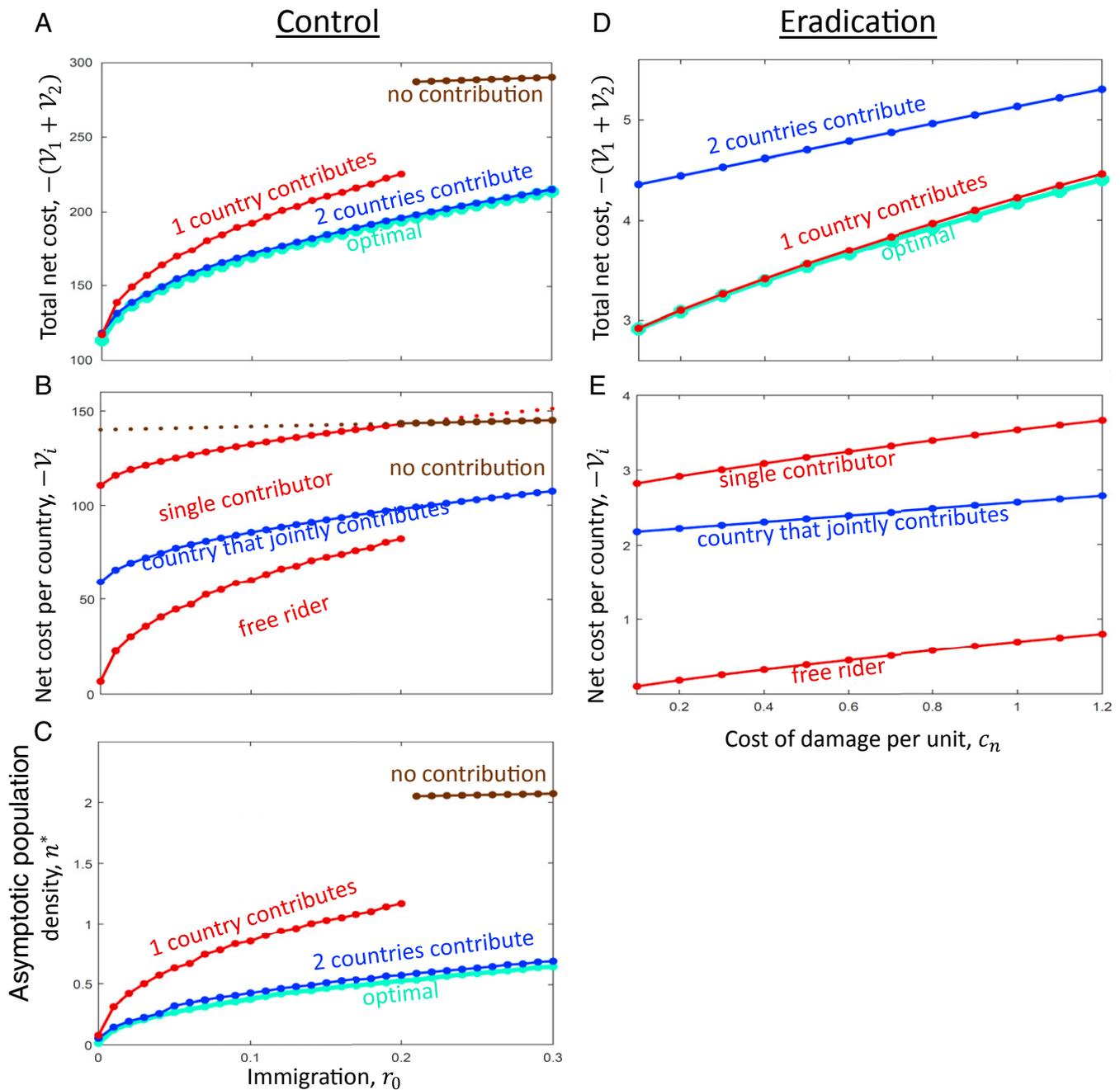


Fig. 3. If complete eradication of the harmful species is possible, then it is done more efficiently by a single country, but if the harmful species must be controlled to maintain it at some low density, then it is done more efficiently by multiple agents. We consider two countries that have damages from a common harmful species population, and we consider four possible solutions for the model: 1) a Nash equilibrium in which only one country contributes (NE 1, red), 2) a Nash equilibrium in which both countries contribute the same amount at all times (NE 2, dark blue), 3) a Nash equilibrium in which neither country contributes (NE 3, brown), and 4) the optimal solution that maximizes social welfare (light blue). For each solution, we plot the total net cost for the two countries (or minus the social welfare) for various parameter values, as well as the net cost for each country and the equilibrium density for the same parameter values. (Note that not all Nash equilibria exist for all parameter values.) We consider two cases: one in which the countries control the harmful species population at some strictly positive density, $n^* > 0$ (A–C), and one in which complete eradication is approached, namely, $n^* = 0$ (E and D). (A) In the first case (control), NE 2 results in lower net costs compared to NE 1 and NE 3. (B) In turn, NE1 exists if and only if it is beneficial for a single country to contribute alone, namely, if the net cost to the contributor in NE1 is lower than the cost per country in the case where no country contributes (upper red line is below the brown dots). Specifically, this occurs if the immigration rate is below a certain threshold, whereas above this threshold, the solution in which no country contributes becomes a Nash equilibrium. (C) In turn, n^* is lower in NE 2 compared to its value in NE 1 and NE 3. (D and E) In the second case (eradication), NE 1 results in a lower net cost and is closer to the optimal solution compared to NE 2. (NE 3 does not exist for the parameter values used in D and E.) Parameters are as follows: $r_1 = 1$, $K = 3$, $c_a = 1$, $\delta = 0.01$, and $C_n(n) = c_n n$; in A–C, $g = n(A - 0.05A^2)$ and $c_n = 0.7$, and in D and E, $g = A - 0.05A^2$ and $r_0 = 0$.

allowing a continuum of possible eradication and control strategies that differ in treatment intensity and how it varies over time. Consequently, multiple Nash equilibria exist, each of which is characterized by a different equilibrium population density and/or a different speed at which this density is approached. Some previous studies have also considered cases in which there are multiple Nash equilibria that differ in the speed at which eradication is approached: one study (7) concluded that the efficiency of the Nash equilibria is closer to the efficiency of the socially optimal solution if the diminishing returns on the investment in eradication are high; another study (17) showed that eradication speed might even be optimal if the costs of damages due to the harmful species are sufficiently high. In turn, while our goal was to find those Nash equilibria that are more desirable and that maximize social welfare, some other studies have considered the problem of how the agents can coordinate to adopt the more desirable Nash equilibrium if multiple Nash equilibria exist. In the context of harmful species, some authors have used agent-based simulation models (5, 24) and behavioral experiments (25) to examine how agents would coordinate to select the more desirable solution in cases where both eradication and no treatment are stable solutions. They also have examined how coordination could be approached via communication, agreements, and information sharing. Furthermore, note that we focused on cases where eradication or control in the hot spot is optimal, and we only asked how this can be done effectively by multiple agents. In turn, some previous studies have examined whether the harmful species in the hot spot should be treated at all, where the alternative is to take actions that prevent the species from entering the agent's property (5, 11, 13, 26).

Our results show that the key indicator that determines whether a control with multiple agents working together is optimal in a given system is whether the annual cost of maintaining the population at density n , $C_m(n)$, decreases or increases with n . If $C_m(n)$ decreases with n , the level at which the species is being controlled, n^* , is smaller and closer to the socially optimal level if many agents treat the harmful species simultaneously. Otherwise, if C_m increases with n , then n^* either approaches 0 (complete eradication) or approaches lower values if fewer agents are treating the harmful species. In turn, the function $C_m(n)$ depends on biological factors of the harmful species, such as its natural growth rate, $f(n)$, and its response to the treatment, $g(n)$ [e.g., if $g(n, A) = Ah(n)$, then $C_m(n) = c_af(n)/h(n)$]. In the common case of using pesticides to treat invasive insects, the pesticides are often applied over a given area and kill a certain fraction of the insect population (27, 28). The managers cannot target individual insects, and therefore, even when the insect population declines, the pesticides are still applied over a similar area, where the number of insects they kill is proportional to n [$g(n, A) = nh(A)$]. In this case, if the per-capita natural growth rate decreases with n (e.g., due to carrying capacity or immigration; Eq. 3), then $C_m(n)$ decreases with n . On the other hand, in the cases of the eradication of the invasive cordgrass *Spartina alterniflora* in Willapa Bay, WA (29), and invasive hybrid *Spartina* in San Francisco Bay, CA (23), the managers could target and treat areas covered with *Spartina* meadows and apply the treatment there (either by spraying or physical removal). In these cases, the efficiency of the treatment depended much less on n and could reasonably be modeled as $g(n, A) = g(A)$ (23). For logistic growth functions (Eq. 3), this results in a $C_m(n)$ that increases with n for sufficiently low values of n .

At the same time, note that the same considerations determine whether the species needs to be controlled or eradicated. Those cases in which $g(n)$ is proportional to n are typically those in which it is inefficient to fully eradicate, and consequently, controlling the population at some $n^* > 0$ is optimal (21). On the other hand, the cases in which $g(n)$ does not depend on n are those that could result in successful eradication (7, 22,

23), e.g., invasive *Spartina* in Willapa Bay has been fully eradicated (29) [in San Francisco Bay, the treatment was altered due to an endangered species (23)]. Alternatively, a strong Allee effect, in which $f(n)$ decreases with n when the population is rear, may result in eradication being feasible and in some cases optimal (and at the same time, it may lead to C_m that decrease with n for sufficiently small n). Namely, in general, those cases in which C_m increases are those cases in which complete eradication is feasible, whereas those in which C_m declines are those where the population needs to be controlled. Therefore, as a general rule of thumb, to achieve a complete eradication the policymaker should split the job and assign one or a few agents to treat each location, whereas for controlling the population at some low levels, the policymaker should assign a larger number of agents to work together in the entire region.

In the model, we considered the management of a single population, but some of the results can be generalized to the management of multiple harmful species or to cases where the population is subdivided into multiple sites, at least in the following special cases. First, consider countries that manage harmful species hot spots located outside of the countries' national borders [e.g., rich countries eradicating diseases in developing countries (11, 12) and invasive species management in high-traffic marine ports (13)]. The cost that a participating country incurs from the harmful species is due to the risk of their invasion from the hot spots into the country. The population at distinct hot spots could occupy the same species or occupy different species. Assume that the harmful species populations do not migrate between the hot spots and that the cost incurred to each country due to a given hot spot does not depend on the state of the other hot spots (namely, the cost to each country is given by the sum of the costs from all of the hot spots; e.g., with two hot spots, the cost of damages equals the cost incurred due to hot spot 1 plus the cost incurred due to hot spot 2). Then, the management in one hot spot does not affect the cost-effectiveness of the management in other hot spots, and our solution is valid in each and every hot spot. (Namely, if the cost is additive and there is no migration, then there is no coupling between the hot spots, and the problem of treating M hot spots is equivalent to solving M independent problems of treating a single hot spot.) Therefore, if eradication is needed, one or a few countries should participate in the management in each hot spot (Fig. 1A), whereas if control is needed, multiple countries should participate in managing all of the hot spots (Fig. 1B). In turn, our model also incorporates cases in which the sites are the agents' properties, assuming that the harmful species population migrates rapidly between the sites and spreads equally among the sites regardless of where it is treated. This situation is more common in local management by landowners, but it is also possible at the international scale if the harmful species migrates rapidly between countries. [Examples of harmful species that spread over entire continents include certain plant pathogens (9), insect pests (30), and mammals (31).] In turn, further research is needed to determine whether and how the results extend to more general cases, such as spatially extended systems with intermediate migration rates and systems where the cost from multiple invasive species hot spots is nonadditive.

Despite global efforts to prevent their spread, invasive species are only becoming more prevalent (32–34). The international spread of infectious diseases is also prevalent, and the threat might become even more severe due to globalization and climate change (35). At the same time, the treatment of agricultural pests via spraying is becoming inefficient due to pest adaptation, and integrated pest management methods that require cooperation among multiple farmers are becoming necessary (3, 6). Therefore, there is an increased need for cooperation and coordination among multiple agents for treating harmful species at both the domestic and international scales. We showed that

there are two cases in which cooperation among multiple agents in the same location is necessary: 1) one agent is not sufficiently incentivized to treat the harmful species, in which case more than one agent needs to work jointly, and 2) the control of the harmful species at some low density is necessary, in which case multiple agents working together could control it at a lower density. Therefore, determining how to allocate the job among multiple agents is critical for the success of harmful species management.

Methods

We consider a game with N identical players, each of which adopts a Markovian strategy, $a_i(n)$, and has a utility V_i given by Eq. 4, while the dynamics of n and how they depend on the strategies are given by Eqs. 1 and 2. Our study includes both analytical and numerical analyses of the model. The analytical methods that we used to prove the theorems are based on the Pontryagin's maximum principle in optimal control analysis and are given in *SI Appendix, sections S1 and S2*. We also find closed-form solutions to the

model in some simple cases in *SI Appendix, section S3*. In turn, to find the Markovian Nash equilibria numerically, we consider the more specific form of f given by Eq. 3 and g that either is proportional to n or does not depend on n . We implemented the algorithm for finding the Markovian Nash equilibria in C/C++. The algorithm uses backward induction and finds a Nash equilibrium at each stage of the treatment, and it either converges to the correct Nash equilibrium or indicates that the particular Nash equilibrium does not exist. The Nash equilibrium that the algorithm seeks to find in each stage is in accordance with the one that we are looking for in the particular simulation, i.e., to find several Nash equilibria the algorithm runs several times, each time with the specific configuration that would enable finding a particular Nash equilibrium if it exists.

Data Availability. No datasets were used in the study. All of the parameter values needed to reproduce the results and figures are given in the text.

ACKNOWLEDGMENTS. I sincerely thank Charles Perrings and the three anonymous reviewers for their helpful comments on the manuscript.

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Supporting Information for Multiple agents managing a harmful species population should either work together to control it or split their duties to eradicate it

Adam Lampert

S1 Optimal control of the harmful species by a single agent

We consider the model that is given in the main text and we derive here the optimal strategy in the case where a single agent manages the harmful species population. We assume that the response of the species to the treatment is linear,

$$g(n, A) = a_1(n)h(n), \quad (\text{S1})$$

where $a_1(n)$ is the annual contribution of the agent to the treatment, and $A = a_1(n)$ because there is only one agent. Since the response to the treatment and the cost of treatment are both linear in a_1 (Eqs. S1 and (4)), it follows from the Pontryagin's maximum principle (Refs. [S1, S2]) that the optimal strategy of the agent is a "bang-bang strategy": In every state n , the agent should either (i) abate the species as fast as possible ($a_1(n) \rightarrow \infty$ or $a_i(n) \rightarrow a_i^{max}$), (ii) do not contribute ($a_i(n) = 0$), or (iii) control the species to maintain it at density n ($a_1(n) = f(n)/h(n)$).

To find the optimal strategy, one needs to dictate which of these three options the agent adopts for each value of n . While the solution depends on the functions and parameters, some characteristics are more general. In particular, the asymptotic density at which the agent needs to control the species, n^* , satisfies the condition in which the marginal benefit from the contribution due to reducing n equals the marginal cost of the treatment [S2, S3]. In turn, the marginal cost due to the treatment for reducing n is given by c_a/h , and the marginal benefit is given by $(dC_n/dn + dC_m/dn)/\delta$, where C_m is the cost of maintenance ($C_m(n) = c_a f(n)/h(n)$), and the term $1/\delta$ appears because the reduction in n is permanent [S2]. Therefore, n^* satisfies

$$\delta \frac{c_a}{h(n^*)} = \frac{dC_n(n^*)}{dn} + \frac{dC_m(n^*)}{dn}. \quad (\text{S2})$$

Note that, if n is slightly smaller than n^* , the optimal strategy would be not to contribute. But if n is slightly greater than n^* , the optimal strategy may dictate either (i) instantaneous abatement of the harmful species to reduce its density to $n = n^*$ or (ii) no contribution, $a_1(n) = 0$, if the population declines naturally at a sufficiently fast rate ($f(n)$ is negative and $|f|$ is above some threshold) [S3]. We elaborate more on these issues below.

Three types of asymptotic states

Assume that the agent adopts her/his optimal strategy. We define n^* as an asymptotic value of n if there exists $n_0 \neq n^*$ such that $n(t) \rightarrow n^*$ when $n(0) = n_0$. (Note that there could be multiple asymptotic values, and which one is ultimately being approached depends on the initial conditions.) It follows from the analysis above that n^* has to satisfy at least one of the following three conditions:

I. n^* satisfies Eq. (S2). [n^* is exactly where the agent is indifference between maintaining the population at $n = n^*$ and maintaining it at a density n that is slightly lower or higher than n^* .]

II. n^* is a stable steady state of the natural dynamics, given by $dn/dt = f(n)$, and n^* also satisfies the inequality

$$\delta \frac{c_a}{h(n^*)} > \frac{dC_n(n^*)}{dn} + \frac{dC_m(n^*)}{dn}. \quad (\text{S3})$$

[It is not beneficial for the agent to contribute in the neighborhood of $n = n^*$, but $n(t)$ approaches n^* naturally.]

III. $n^* = 0$, and for $n > 0$ in the neighborhood of $n = 0$,

$$\delta \frac{c_a}{h(n)} < \frac{dC_n(n)}{dn} + \frac{dC_m(n)}{dn}. \quad (\text{S4})$$

[It is beneficial for the agent to abate the population for any $n > 0$, but s/he cannot reduce the population below zero ($h(0) = 0$).]

When does it worth to let the harmful species population decline naturally

For values of n in which $f(n) < 0$, the harmful species population declines naturally and it might not be beneficial for the agent to contribute. However, if $f(n)$ is negative but its absolute value is small, then the natural decline rate of the population might be too slow and it might still be beneficial for the agent to contribute (see also Ref. [S3]). This is shown in the following lemma.

Lemma 1

Consider a single agent whose strategy, $a_1(n)$, dictates how much s/he invests in the treatment of some population. The utility of the agent is given by \mathcal{V}_1 (Eq. (4) in the main text) where the cost function $C_n(n)$ is monotone increasing, and the dynamics of the state variable (population density), n , are given by

$$\frac{dn}{dt} = f(n) - a_1(n)h(n). \quad (\text{S5})$$

Denote $a_1^*(n)$ as the optimal strategy of the agent ($a_1^*(n)$ maximizes \mathcal{V}_1 subject to Eq. (S5)). Assume that if $a_1(n) = a_1^*(n)$ for all n and $n(0) = n_0 > n^*$, then $n(t) \rightarrow n^*$ as $t \rightarrow \infty$.

It follows that $a_1^*(n_0) > 0$ if and only if

$$f(n_0) > -f_c(n_0), \quad (\text{S6})$$

where $f_c(n_0)$ is a positive constant given by

$$f_c(n_0) = \frac{(C_n(n_0) + \delta\mathcal{V}^*(n_0))h(n_0)}{c_a}, \quad (\text{S7})$$

and $\mathcal{V}^*(n_0)$ is the utility of the agent given that s/he adopts the optimal strategy and $n(0) = n_0$.

Proof of Lemma 1

First, note that if $f(n_0) \geq 0$, then the fact that $a_1^*(n_0)$ is positive follows directly from the assumption that $n^* < n_0$ (because dn/dt has to be negative when $n = n_0$). Therefore, it remains to show that the lemma holds for values of n_0 in which $f(n_0) < 0$. From the Pontryagin's maximum principle, it follows that either $a_i^*(n_0) \rightarrow \infty$ or $a_i^*(n_0) = 0$. Assume that the agent reduces n instantaneously ($a_1(n_0) \rightarrow \infty$) until the population density becomes $n = n_0 - dn$ (where dn is infinitesimally small), and uses her/his optimal strategy for any $n \leq n_0 - dn$. In this case, the agent invests $c_a dn/h(n_0)$ for reducing n by dn , and therefore, it follows that the agent's utility is given by

$$\mathcal{V}_1^+ = -\frac{c_a}{h(n_0)}dn + \mathcal{V}^*(n_0 - dn). \quad (\text{S8})$$

Alternatively, assume that $f(n) < 0$, and the agent lets the population density decline naturally until $n = n_0 - dn$ ($a_1(n_0) = 0$), while still using her/his optimal strategy for any $n \leq n_0 - dn$. In that case, the utility is given by

$$\mathcal{V}_1^- = -C_n(n_0)dt + \mathcal{V}^*(n_0 - dn)(e^{-\delta dt}), \quad (\text{S9})$$

where $dt = -dn/f(n_0)$ is the time that it takes $n(t)$ to approach $n_0 - dn$ if $a_1(n_0) = 0$ (note that $f(n_0)$ is negative). In turn, note that in the limit where dt is infinitesimally small, $e^{-\delta dt} = 1 - \delta dt$.

It follows that

$$\mathcal{V}_1^- = \frac{C_n(n_0)}{f(n_0)}dn + \frac{\delta\mathcal{V}^*(n_0 - dn)}{f(n_0)}dn + \mathcal{V}^*(n_0 - dn). \quad (\text{S10})$$

(Note that $f(n_0)$ is negative, and therefore, the right-hand side is negative.) In turn, it is beneficial for the agent to invest if and only if $\mathcal{V}_1^+ > \mathcal{V}_1^-$. Therefore, it follows from Eqs. (S8) and (S10) that $a_1^*(n_0) > 0$ if and only if

$$-\frac{c_a}{h(n_0)} > \frac{C_n(n_0) + \delta\mathcal{V}^*(n_0)}{f(n_0)}, \quad (\text{S11})$$

or

$$f(n_0) > -\frac{(C_n(n_0) + \delta\mathcal{V}^*(n_0))h(n_0)}{c_a}. \quad (\text{S12})$$

It remains to show that f_c is positive. In turn, the fact that $C_n(n_0) + \delta\mathcal{V}^*(n_0)$ is positive follows from the fact that n decreases over time even if $a_1(n) = 0$ for all n (because $f(n_0) < 0$). Specifically,

it follows directly from Eq. (4) and the fact that $C_n(n)$ is monotone increasing that $C_n(n_0) > -\delta\mathcal{V}_1(n_0|a_i(n) = 0$ for all n). In turn, $\mathcal{V}^*(n_0) \geq \mathcal{V}_1(n_0|a_i(n) = 0$ for all n), which implies that $C_n(n_0) > -\delta\mathcal{V}^*(n_0)$. And since $h(n_0) > 0$ and $c_a > 0$, it follows that $f_c(n_0) > 0$. This completes the proof of Lemma 1.

S2 Proof of Theorem 1

In this section, we prove Theorem 1. The proof is based in part on the analysis in section S1, including Lemma 1. The proof comprises three steps. In step 1, we construct a solution (set of strategies, not necessarily a Nash equilibrium) that results in $n(t) \rightarrow n^{(k)}$ as $t \rightarrow \infty$. In step 2, we show that $n^{(k)}$ is monotone decreasing in k if $dC_m(n)/dn$ is monotone decreasing in n . In step 3, we show that it follows from the way that we construct the solution in step 1 that (i) there exists a Nash equilibrium in which k agents contribute simultaneously and $n(t) \rightarrow n^{(k)}$, and (ii) there is no Nash equilibrium in which exactly k agents contribute simultaneously and n approaches a value that is lower than $n^{(k)}$.

Step 1: construction of a solution in which $n(t) \rightarrow n^{(k)}$ as $t \rightarrow \infty$

Denote $A_0(n)$ as the contribution that is sufficient exactly for the control/maintenance of the population at density n if $f(n) \geq 0$:

$$f(n) - A_0(n)h(n) = 0, \quad (\text{S13})$$

namely,

$$A_0(n) = f(n)/h(n). \quad (\text{S14})$$

Consider a solution (set of strategies, not necessarily a Nash equilibrium) in which $k - 1$ agents, $i = 2, \dots, k$, each adopts the strategy

$$a_i(n) = \begin{cases} \frac{1}{k}A_0(n) & \text{if } f(n) \geq 0 \\ 0 & \text{otherwise} \end{cases} \quad (\text{S15})$$

for all n , while $N - k$ agents, $i = k + 1, k + 2, \dots, N$, each adopts the strategy $a_i(n) = 0$ for all n . It follows that the total contribution, excluding that of agent 1, is given by

$$A_{-1}(n) = \begin{cases} \frac{k-1}{k}A_0(n) & \text{if } f(n) \geq 0 \\ 0 & \text{otherwise.} \end{cases} \quad (\text{S16})$$

In turn, it follows that the optimal strategy of agent 1 under these circumstances is given by the solution to the optimal control problem analyzed in Section S1, only with the contribution of the

other agent taken as given. Specifically, the optimal strategy of agent 1 is given by the function $a_1(n)$ that maximizes \mathcal{V}_1 subject to the constraint given by Eq. (1) with $f(n) \rightarrow \tilde{f}_1(n)$, where

$$\tilde{f}_1(n) = \begin{cases} \frac{1}{k}f(n) & \text{if } f(n) \geq 0 \\ f(n) & \text{otherwise.} \end{cases} \quad (\text{S17})$$

Finally, assume that the agents adopt the strategies as described above, and denote M as the set of all values of n that are asymptotic values, i.e., $n \in M$ if and only if there exists $n_0 \neq n$ such that $n(t) \rightarrow n$ as $t \rightarrow \infty$ if $n(0) = n_0$. In turn, denote $n^{(k)}$ as the smallest asymptotic value, i.e., $n^{(k)} = \min\{n|n \in M\}$.

Step 2: Showing that $n^{(k)}$ is monotone increasing in k if $dC_m(n)/dn$ is monotone increasing in n

Next, we show that $n^{(k)}$ is monotone decreasing in k if $dC_m(n)/dn \leq 0$ for all n . Note that c_a and C_n do not depend on f , but C_m does depend on f . Specifically, if $f(n) \geq 0$, the contribution of agent 1 to maintaining the population at density n (where $k - 1$ other agents contribute equally (Eq. (S15))) is given by

$$C_m^1(n) = \frac{c_a f(n)}{k h(n)} = \frac{1}{k} C_m(n). \quad (\text{S18})$$

Also, note that $f(n^{(k)})$ has to be non-negative. Therefore, it follows from Section S1 that $n^{(k)}$ satisfies either one of the following three conditions:

I. $n^{(k)}$ satisfies

$$\delta \frac{c_a}{h(n^{(k)})} = \frac{dC_n(n^{(k)})}{dn} + \frac{1}{k} \frac{dC_m(n^{(k)})}{dn}. \quad (\text{S19})$$

II. $n^{(k)}$ is a stable steady state of the dynamics given by $dn/dt = f(n)/k$, and $n^{(k)}$ also satisfies the inequality

$$\delta \frac{c_a}{h(n^{(k)})} > \frac{dC_n(n^{(k)})}{dn} + \frac{1}{k} \frac{dC_m(n^{(k)})}{dn}. \quad (\text{S20})$$

III. $n^{(k)} = 0$, and for $n > 0$ in the neighborhood of $n = 0$,

$$\delta \frac{c_a}{h(n)} < \frac{dC_n(n)}{dn} + \frac{1}{k} \frac{dC_m(n)}{dn}. \quad (\text{S21})$$

Next, consider some integer number m that satisfies $k \leq m \leq N$. Note that if $dC_m/dn \leq 0$ for all n , then $(1/k)dC_m/dn$ does not decrease as k increases, and therefore,

$$\frac{1}{m} \frac{dC_m(n)}{dn} \geq \frac{1}{k} \frac{dC_m(n)}{dn} \quad (\text{S22})$$

holds for all n . We use this inequality to show that $n^{(k)}$ is monotone decreasing in k in each of the three cases.

Case I

If $n^{(k)}$ satisfies Eq. (S19), then it follows from Eq. (S22) that $n^{(k)}$ must also satisfy

$$\delta \frac{c_a}{h(n^{(k)})} \leq \frac{dC_n(n^{(k)})}{dn} + \frac{1}{m} \frac{dC_m(n^{(k)})}{dn}. \quad (\text{S23})$$

Therefore, if $m - 1$ other agents contribute, then it is worth for agent 1 to reduce the population to a value that is $\leq n^{(k)}$, and therefore, $n^{(m)} \leq n^{(k)}$ in Case I.

Case II

Assume that $n^{(k)}$ is a stable steady state of the dynamics when the agents do not contribute and Eq. (S20) holds. In turn, either (i) Eq. (S20) still holds at n^* if $1/k \rightarrow 1/m$, in which case agent 1 does not contribute even when $m - 1$ other agents contribute and $n^{(k)}$ is still an asymptotic value, or (ii) Eq. (S20) does not hold if $1/k \rightarrow 1/m$, in which case, if $m - 1$ other agents contribute, the asymptotic value must be lower than $n^{(k)}$. In summary, if $m \leq k$ agents contribute, there exists an asymptotic value that satisfies $n^* \leq n^{(k)}$, which implies that $n^{(m)} \leq n^{(k)}$.

Case III

If Eq. (S21) is satisfied for all $n > 0$ in the neighborhood of $n = 0$, then $n^{(k)} = 0$. But if Eq. (S21) is not satisfied, then

$$\delta \frac{c_a}{h} > \frac{dC_n}{dn} + \frac{1}{m} \frac{dC_m}{dn} \quad (\text{S24})$$

is also satisfied, and therefore, $n^{(m)} = 0$ as well. This shows that, in all three cases, if $C_m(n)/dn \leq 0$ for all n , then $n^{(m)} \leq n^{(k)}$.

Step 3: construction of a Nash equilibrium in which $n(t) \rightarrow n^{(k)}$

Until this point, we described a specific solution in which $n(t) \rightarrow n^{(k)}$ as $t \rightarrow \infty$, and we showed that $n^{(k)}$ is monotone decreasing with k if $dC_m/dn < 0$. However, the solution that we constructed is not necessarily a Nash equilibrium. Therefore, it remains to show that: (A) There exists a Nash equilibrium in which k agents contribute the same amount in the neighborhood of $n^{(k)}$, the other $N - k$ agents do not contribute, and n approaches $n^{(k)}$; and (B) there is no Nash equilibrium in which k agents contribute, $N - k$ agents do not contribute, and n approaches a value that is lower than $n^{(k)}$. We distinguish two cases: $k = 1$ and $k \geq 2$.

Case I: One agent contributes ($k = 1$)

If $k = 1$, the strategy of agent 1 described in step 1 is, by definition, its optimal strategy given that

the other agents do not contribute. In turn, $a_i(n) = 0$ is the best response of the other agents in the neighborhood of $n^{(1)}$. Specifically, if n is slightly greater than $n^{(1)}$, then agent 1 already contributes the maximal amount and the other agents cannot benefit from contributing. At the same time, if $n < n^{(1)}$, the fact that the optimal strategy of agent 1 is $a_1(n) = 0$ implies that $a_i(n) = 0$ is optimal for all the agents because the game is symmetric and no other agent contributes for any $n < n^{(1)}$.

Case II: Several agents contribute ($k \geq 2$)

In turn, for $k \geq 2$, the proof of part (A) follows from Lemma 1 and from the proof of the theorem in Ref. [S4] as described below. Denote $\tilde{f}_i(n)$ as the effective growth rate of the population from the perspective of agent i who conceives the contribution of the other agents as given:

$$\tilde{f}_i(n) \equiv f(n) - A_{-i}(n)h(n), \quad (\text{S25})$$

where $A_{-i}(n)$ is the total contribution of all the agents except agent i . Consider a density n_0 at which, if A_{-i} is given by Eq. (S16) and $n(0) = n_0$, the best response of agent 1 is to abate the population until $n \rightarrow n^{(k)}$. If agent i 's optimal response is to contribute and reduce n when $n = n_0$, then $n(t)$ approaches a value that is lower than n_0 , and then it follows from Lemma 1 that the agent's best response is to contribute as long as

$$\tilde{f}_i(n_0) < -f_c(n_0), \quad (\text{S26})$$

where $f_c(n_0) > 0$ is some positive constant (see also [S3, S4]). In turn, if $\tilde{f}_i(n_0) < -f_c(n_0)$, the agent's best response is $a_i(n_0) = 0$, and if $\tilde{f}_i(n_0) = -f_c(n_0)$, the agent has the same utility regardless of how much s/he contributes when the density is n . This is true for any $n_0 > n^{(k)}$ that is in the basin of attraction of $n^{(k)}$. Therefore, there exists a Nash equilibrium in which k agents contribute

$$a_i^*(n) = \begin{cases} \frac{1}{k-1}(f(n) + f_c(n)) & \text{if } n > n^{(k)} \text{ and } f(n) > -f_c(n) \\ \frac{1}{k} \frac{f(n)}{h(n)} & \text{if } n = n^{(k)} \\ 0 & \text{otherwise} \end{cases} \quad (\text{S27})$$

each, while the other $N - k$ agents do not contribute for any n ($a_i^*(n) = 0$). Then, for each of the k agents that contribute, $\tilde{f}_i(n) = -f_c(n)$ if $n > n^{(k)}$, and none of these agents can benefit from unilaterally changing her/his strategy. At the same time, for each of the other $N - k$ agents, $\tilde{f}_i(n) = -\frac{k+1}{k}f_c(n) < f_c(n)$, and therefore, not contributing is their best response, which completes the proof of part (A).

Finally, to prove part (B), assume that there exists a Nash equilibrium in which $n(t) \rightarrow \hat{n} < n^{(k)}$ as $t \rightarrow \infty$. But from step 1, we know that $a_i(\hat{n}) = 0$ is the best response of an agent if the contribution of the other agents is given by $A_{-i}(\hat{n}) \leq A_0(\hat{n})(k-1)/k$. In turn, if k agents control the population at $n = \hat{n}$, then $A_{-i}(\hat{n}) \leq A_0(\hat{n})(k-1)/k$ has to hold for at least one of them, which implies that the control by k agents at $n = \hat{n}$ cannot occur in a Nash equilibrium. This completes the proof of Theorem 1.

S3 Analytic solutions for some special cases

Finding the asymptotic population level, n^*

In this section, we find a closed-form expression for the asymptotic value n^* in a Nash equilibrium where k agents contribute, in a special case in which $f(n) = r_0 + r_1n$, $g = nA$, and $C_n(n) = c_n n$. Namely, the dynamics of n are given by

$$\frac{dn}{dt} = r_0 + r_1n - nA, \quad (\text{S28})$$

and it follows that

$$C_m(n) = c_a(r_1 + r_0/n). \quad (\text{S29})$$

From Eq. (S19), it follows that

$$\delta \frac{c_a}{n^*} = c_n - \frac{r_0 c_a}{k(n^*)^2}, \quad (\text{S30})$$

or

$$c_n(n^*)^2 - \delta c_a n^* - \frac{r_0 c_a}{k} = 0. \quad (\text{S31})$$

This implies that

$$n^* = \frac{1}{2}\delta c + \frac{1}{2}c\sqrt{\delta^2 + 4r_0/kc}, \quad (\text{S32})$$

where

$$c \equiv \frac{c_a}{c_n}. \quad (\text{S33})$$

Specifically, it follows that

$$n^* \rightarrow \frac{r_0}{kc} \quad \text{as } \delta \rightarrow 0. \quad (\text{S34})$$

Note that n^* is strictly positive, even in the non-discounted case. Also note that, in accordance with Theorem 1, n^* declines as k increases.

Finding the equilibrium contribution when $n > n^*$

Next, we derive a closed-form expression for the Nash equilibrium in which k agents contribute in the special case where $\delta = 0$ and $g(n, A) = Ah(n)$. Specifically, consider a Nash equilibrium in which the agents abate the harmful species until its density approaches $n = n^*$, where initially $n(0) > n^*$. Denote $C^+(n)$ as the additional annual cost that each of the k contributors has because the population is still at a state $n > n^*$ instead of being already controlled at $n = n^*$:

$$C^+(n) \equiv C_n(n) - \left(C_n(n^*) + \frac{1}{k}C_m(n^*) \right) \quad (\text{S35})$$

It follows from Ref. [S3] that, in the case where $\delta = 0$, for each $n > n^*$, $a_i(n)$ is given by the solution to

$$\max_a u = \frac{C^+(n) + a}{f(n) + (a + (k-1)b)h(n)} \quad (\text{S36})$$

under the constraint $b = a$. In the following, we find a as a function of n (for simplicity of the notations, we omit the variable n from all the functions). To find the value of a that maximizes u , note that

$$\frac{du}{da} = \frac{f + (a + (k - 1)b)h - (C^+ + a)h}{(f + (a + (k - 1)b)h)^2} = 0. \quad (\text{S37})$$

Next, substituting $a = b$ implies

$$f + (ka - C^+ - a)h = 0. \quad (\text{S38})$$

Namely, for $k \geq 2$

$$a_i = \frac{C^+h - f}{(k - 1)h} = \frac{C^+ - f/h}{k - 1}, \quad (\text{S39})$$

for each of the k agents that contribute, and the total contribution is given by

$$A = ka_i = \frac{k}{k - 1}(C^+ - f/h). \quad (\text{S40})$$

Note that, in accordance with Theorem 1, A decreases as k increases.

References for Supporting Information

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