



The importance of bioeconomic feedback in invasive species management

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Received 7 February 2004; received in revised form 3 June 2004; accepted 15 June 2004

Available online 19 January 2005

Abstract

Invasive species can pose significant risks to society. Managing invasive risks cost-effectively would likely benefit from an integrated bioeconomic framework that accounts for the feedback links between the biological and economic systems. Modeling these feedbacks can be challenging relative to the standard “damage function” approach in which the parameters from one system are added to a model of the other, without any feedback. Given time constraints, the open question is whether the effort to capture feedback links is worthwhile and provides more useful information than not integrating. Herein, we use as our foil the case of zebra mussels in a Midwestern Lake. We consider responses from the removal of two forms of feedback: the loop between the firm and the biological system, and a loop between the manager and a firm. Our results suggest accounting for feedbacks can matter—but not in every dimension.

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Keywords: Invasive species; Bioeconomic feedback; Endogenous risk

1. Introduction

Invasive species are a leading cause of biodiversity loss and related economic damages (see Mack et al., 2000; Lodge, 2001). Managing these risks cost-effectively would benefit from a consistent integrated framework for bioeconomic risk assessment. Such a

framework would reflect the ever-increasing appreciation on why accounting for economic and biological circumstances and the feedback loops between the two matter (Daly, 1968; Crocker and Tschirhart, 1992; Perrings, 1998; Finnoff and Tschirhart, 2003). A bioeconomic model for invasive species should reflect the notion that people respond to changes in their surroundings and vice versa. Invasive species can alter human productivity in the economic system. People that recognize the productivity change can adapt. If societal adaptation is effective, our actions change the

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environment, which in turn may require a new societal response. Feedback can exist between society and the environment. These feedbacks are predicated on recognition of environmental change. In reality, substantial ecological change may occur, before society is directly affected, and may therefore be overlooked or may become too costly or impossible to rectify. When recognition fails, feedbacks may not be perceived, and the trajectory of invasions and damage may differ.

Given the potential importance of interactions between the biological and human systems, it is necessary to isolate those interactions that appear to matter given limited research budgets. While capturing all complexities within a sociobiological system is beyond any modeling exercise, the goal is to identify the key feedbacks to include in a tractable model. If outputs of the model do not differ with and without feedbacks, integration of the feedbacks is perhaps only an interesting academic exercise. Two key outputs considered herein are whether predicted biological populations differ with and without feedbacks, and if so, whether it matters for human well-being. The traditional “damage function” approach, in which biological parameters are fed into an economic model such that the biological response is taken as parametric, has been argued to be a reasonable approximation of the problem (e.g., see Carlson et al., 1993).

Recent work, however, suggests the damage function approach may be insufficient, and the inclusion of feedbacks may yield unexpected policy conclusions. Settle et al. (2002) and Settle and Shogren (2003), for instance, consider the case of exotic lake trout and their impact on native cutthroat trout in Yellowstone Lake, Wyoming. They found that accounting for feedback loops between individual visitors to Yellowstone and the ecosystem does matter for predicted trout populations. Under a best-case scenario (free removal of lake trout) with and without feedbacks, the steady-state population of cutthroat trout was 2.7 million versus 3.4 million. For a worst-case scenario (no removal), the populations were 1 million without feedback versus zero cutthroat trout with feedback. These are substantially different predictions by most yardsticks. Interestingly, however, if one accounts for the preferences of the average visitor who comes to Yellowstone, incorporation of feedbacks made little difference. The average Yellow-

stone visitor neither fishes nor perceives the link between cutthroat trout and the 40 species that rely on them for part of their food supply. This result comes about because most visitors cared more about the quality of the traditional site sighting attractions (e.g., Old Faithful) than the native cutthroat. Most people simply do not know about the risks of lake trout to cutthroat populations within the Park.

This paper considers whether accounting for feedback at several different levels matters for a higher profile invasive zebra mussel (*Dreissena polymorpha*) in a Midwest lake. Zebra mussels are of interest for several reasons. Zebra mussels clog water pipes and reduce water flow and currently cost U.S. industries an estimated US\$100 million per year in control costs (Pimentel et al., 1999), with little if any resources spent on prevention. Little is known about food web effects of zebra mussel. Regional and federal governmental agencies and private producers faced with the impacts (primarily power plants and water treatment facilities) continue to experiment with new control measures in an effort to maximize the benefits of zebra mussel control, and prevention of new infestations remains timely because zebra mussels are still expanding their range within North America (Bossenbroek et al., 2001). Zebra mussels have also been shown to cause substantial environmental impacts (Ricciardi and Rasmussen, 1998; Lodge, 2001).

Two levels of feedbacks are considered—(1) *Biological–Firm*, which captures the links between the private economic agent (power plant) and the biological system, and (2) *Manager–Firm*, reflecting the links between the policy maker, private economic agent, and biological system. The importance of feedbacks is identified by “turning off” specific interactions in the model. In the absence of *Biological–Firm* feedbacks, private economic agents behave as if there is never a change in the biological system—that is, they possess incomplete knowledge (or beliefs) about the nature of the system. In contrast, removing *Manager–Firm* feedbacks causes the policy maker, who decides prevention investment to keep zebra mussels out of a lake, to act as if the private agent would not respond to changes in the biological state. This creates a case in which the policy maker holds incomplete knowledge (or beliefs) over private agent behavior.

An endogenous risk framework is used here to integrate and account for feedbacks. Endogenous risk captures the risk-benefit tradeoffs created by jointly determined ecosystem conditions, species characteristics, and economic circumstances (Crocker and Tschirhart, 1992). Using stochastic dynamic programming simulation, the biological and economic consequences of ignoring critical feedback loops are explored. Results suggest accounting for feedbacks can matter—but not in every dimension. Both biological and economic consequences of not addressing feedbacks are sensitive to the initial conditions on the environment, behavioral perceptions about the state of the environment, and the completeness of the manager’s beliefs. In biological terms, a range of consequences is found in the absence of feedback loops. The consequences range from modest increases in the probability of invasion and invader abundances to significant increases. In economic terms, a range of welfare losses are also found when feedback loops are removed—effects vary from modest to substantial. Interestingly, welfare losses are not solely a function of increasing damages in the absence of feedback loops. Losses also occur because costs increase from the inefficient allocation of resources and lost opportunities due to under-production of economic output.

2. Discrete dynamic endogenous risk framework

The theory of endogenous risk model is used to frame the risk reduction problem for invasive species (Shogren, 2000). The general circumstance of invasive species is framed as the management of an impure public “bad”. Highly mobile invasive species with numerous transportation pathways are considered, such that private citizens or firms cannot control the entry of the invasive into the overall system (e.g., zebra mussels entering into the Great Lakes in the ballast water of ships).¹ Once established, the invader can cause adverse impacts, and

people or firms can either adapt to the invader or privately control local populations. Assume an over-reaching governmental agency that acts as a benevolent manager to control entry and growth of such pests through its collective prevention and control. These government actions provide a public good to private individuals who can respond to the invasion. The framework casts the benevolent manager making optimal decisions given the risks of invasion and behavior of private individuals who react to the consequences of invasion.

Private individuals (firms) are viewed as relatively myopic—they are relatively less farsighted than the benevolent manager. This restriction reflects the notion that firms make private decisions based on market discount rates, whereas the manager employs a rate based on social preferences. In general, assume the market discount rate does not exceed the social rate (e.g., Weitzman, 1994). For tractability, assume the firm is completely myopic with a discount rate of zero. Lacking foresight, the firm takes as fixed the state of nature as defined by the invasive species, and it ignores any future repercussions of its behavior (the problem from the firm’s viewpoint is therefore static).

In any period t , a representative firm maximizes utility subject to its budget constraint taking the current state as given. Let states be defined by current period invader abundance θ_t (state variable). Invader abundances cause damages D_t , where monetized damages serve to diminish initial wealth M_t . In response, a firm has costly strategies at its disposal and can adapt Z_t^P to the invader and/or privately control X_t^P local populations. Adaptation (or self insurance) accepts the direct damages and compensates in response to reduce the consequences of the damage. This strategy refers to those options available to a firm that allows it to compensate for the realized damages. For example, if the firm is a power plant, zebra mussels clog coolant systems. The plant could compensate/adapt to the damage inflicted by the mussels by employing factors of production and operating longer hours or burning more fuel than otherwise necessary. In contrast, control reduces actual damages and can indirectly influence the transition to future states. Examples of control include flushing coolant systems with chlorine.

¹ Other authors have used bioeconomic models to characterize control of invasive weeds in deterministic dynamic settings (see Regev et al., 1976; Regev et al., 1983) and static stochastic settings (see Archer and Shogren, 1996).

Inserting the firm's budget constraint into its utility function yields the objective function

$$\max_{Z_t^P, X_t^P} U_t(M_t - D_t(X_t^P, Z_t^P; \theta_t) - C_t(X_t^P, Z_t^P)), \quad (1)$$

for given state θ_t , where states (e.g., current period invader abundance) range from a minimum of zero before invasion or after total eradication to any level of abundance within the systems carrying capacity. C_t is the firm's cost function, assumed to be monotonically increasing in each argument. The first-order conditions for private control and adaptation are

$$- U' (M_t - D_t(X_t^P, Z_t^P; \theta_t) - C_t(X_t^P, Z_t^P)) \times [D_{X_t^P} + C_{X_t^P}] = 0 \quad (2)$$

$$- U' (M_t - D_t(X_t^P, Z_t^P; \theta_t) - C_t(X_t^P, Z_t^P)) \times [D_{Z_t^P} + C_{Z_t^P}] = 0 \quad (3)$$

in which we assume an interior solution, state notation is suppressed, and primes and subscripts indicate partial derivatives. As usual, Eq. (2) requires a balance of the marginal benefits of control with its marginal costs such that the marginal damage reduction $D_{X_t^P}$ equals the marginal cost of private control $C_{X_t^P}$. Here, benefits arise from reduced damages *in the current period*. Eq. (3) says adaptation is set so the marginal benefits of adaptation equal the marginal costs. This occurs when the marginal reduction in the consequences of damages $D_{Z_t^P}$ is just equal to the marginal cost of private adaptation $C_{Z_t^P}$. Benefits arise from reduced consequences of damages given the adaptation response, and all benefits and costs (from the firm's view point) accrue in the current period. Together Eqs. (2) and (3) determine the firm's optimal levels of control $\hat{X}_{t,\theta}^P$, and adaptation $\hat{Z}_{t,\theta}^P$, in any given period and state.

Given the firm's optimal choices, the benevolent manager maximizes expected social welfare subject to the risk of invasion. Let social welfare be the discounted stream of intergenerational individual utility augmented by the costs of collective action. Unlike the firm, the manager considers the dynamics of the invasion process and can partially control entry and growth of the invader. The manager then directly influences the realized state θ_t . The

manager reduces the damages associated with invasion *in future periods* through either collective control or prevention. An invader causes damages if it successfully traverses several interrelated processes: introduction, establishment, and growth. Not all species that invade become established; and not all established invaders cause damages (see Williamson, 1996). Once a species establishes itself, we consider the system *invaded*. After establishment, the invader can increase in abundance. Abundance is directly related to damages. Unlike other forms of pollution, in which remedial efforts can have lasting effects, biological organisms reproduce such that control efforts may be necessary in perpetuity.

To combat the risks of invasion and reduce the probability of damages, the resource manager can employ collective prevention S^G to reduce the probability that invasion occurs at all. Once an invasion has occurred, they can collectively control X^G to reduce the abundance and damages in the next period.

Let the risk of invasion be a multiperiod compound lottery that reflects a separation in the probability of invasion in noninvaded states and transition probabilities in invaded states. Fig. 1 presents a simplified view of a discrete invasion process for the first four periods of an invasion, t through $(t+3)$. In any time interval, there is only a single realized state. When forecasting the consequences of actions into the future, however, it is necessary to consider the probabilities of being in each possible state. For example, if the state of nature is uninvaded (current invader abundance $\theta_t=0$) in the initial period, there is some probability of invasion, $p_{t+1}(S_t^G)$, during the transition to $t+1$. Let this probability be a diminishing function of collective prevention applied in t such that $p_{t+1}(S_t^G)$ and $p_{t+1,S} < 0$, $p_{t+1,SS} > 0$, where the second set of subscripts indicate partial derivatives. If the invasion is successful, the invaders become established ($\theta_{t+1}=N_1$) and cause damages in $(t+1)$. If the invasion is unsuccessful, the invader does not become established ($\theta_{t+1}=0$), and there is no damage.

In the transition to $(t+2)$, the manager faces the threat of invasion in the noninvaded state (with probability p_{t+2}). In the invaded state, however, they

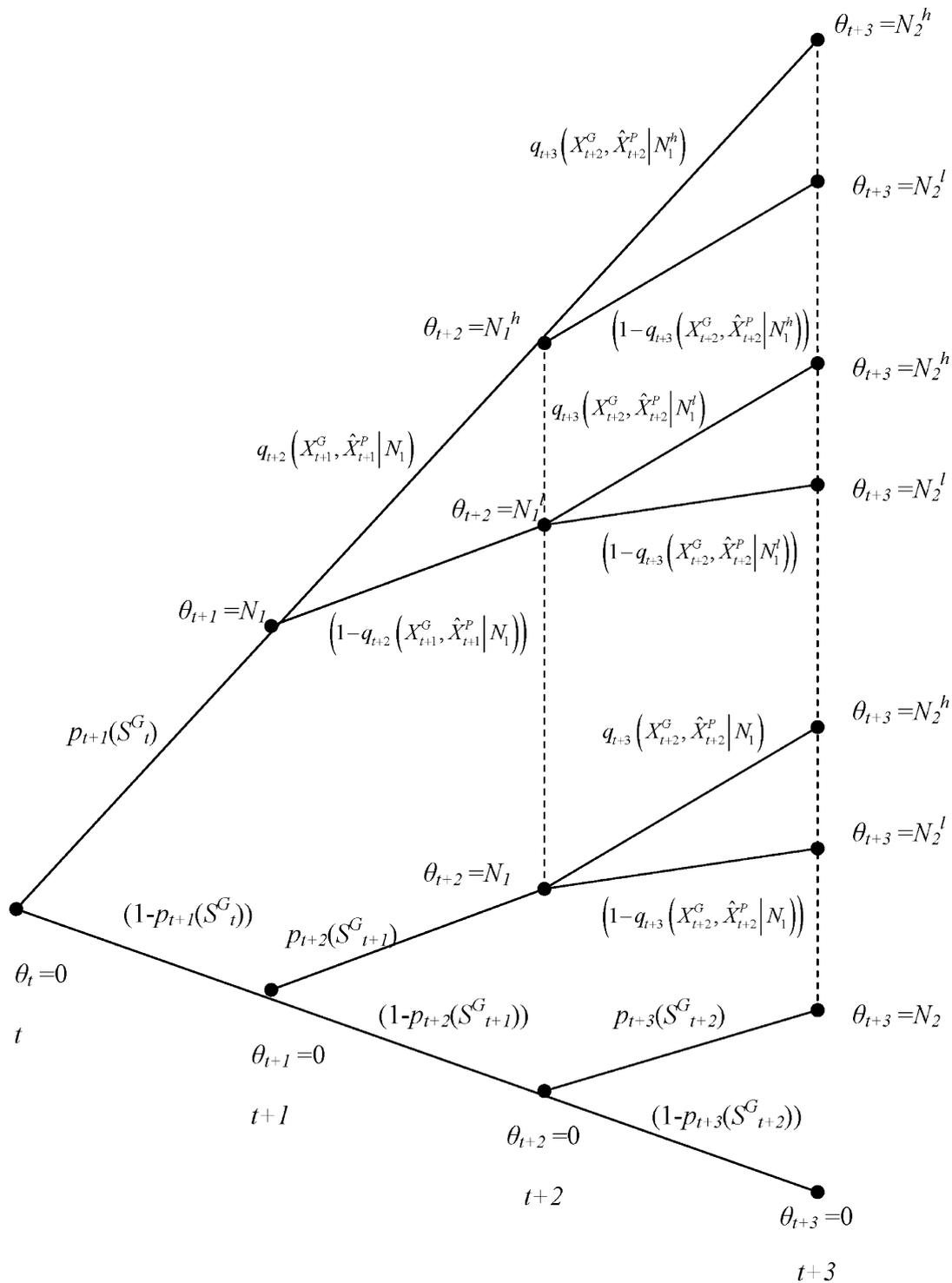


Fig. 1. Invasion process.

experience current period damages due to the abundance of the invader N_1 and face the threat of even larger damages the subsequent period through growth of invaders (with probability q_{t+2}). Projected future actions include application of prevention S_{t+1}^G and collective control measures X_{t+1}^G as the realized state is not known with certainty. The probability of growth (transition probability) is conditioned on the abundance and follows a population growth model. Collective control serves to reduce the reproducing invader population in $(t+1)$ so the magnitude of growth in the transition to $(t+2)$, $q_{t+2}(X_{t+1}^G, \hat{X}_{t+1}^P | N_1)$, depends on collective and private control,² and $q_{t+1, X} < 0$, $q_{t+1, XX} > 0$.³

If control measures are unsuccessful and the invader grows to a high level ($\theta_{t+2} = N_1^h$), there is damage, but if control is successful, the invader's growth is halted and there are low (or zero) damages ($\theta_{t+2} = N_1^l$). But even if control is successful, such that damage is low or zero in $(t+2)$, the biological population may grow and cause damages in future periods.

In our example, the manager takes current period damages as given, and their employment of collective prevention and control are costly in the current period yet influence the invasion process in the subsequent period. The manager's strategies add to total costs, represented by augmenting the cost function of Eq. (1) to be $C_t(X_t^G, S_t^G, \hat{X}_t^P, \hat{Z}_t^P)$, maintained as monotonically increasing in each argument.

The manager's objective is to maximize discounted social welfare over horizon T , where social welfare in t is initial social wealth M_t net of damages and the costs of invasion. In a discrete framework, write the stochastic dynamic programming equation (SDPE) as the summation of optimized discounted welfare in year t and all future years. Let W be the maximum discounted expected social welfare from the perspective of initial period. Periodic social welfare is U_t , an increasing ($U_t' > 0$) and strictly concave ($U_t'' < 0$) thrice-differentiable von

Neumann–Morgenstern utility function. The SDPE is,

$$W(\theta_t) = \max_{S_t^G, X_t^G} U_t(M_t - D_t(\hat{X}_t^P, \hat{Z}_t^P; N_t) - C_t(S_t^G, X_t^G, \hat{X}_t^P, \hat{Z}_t^P)) + \rho E_t W(\theta_{t+1}), \quad (4)$$

where current social welfare depends on damages due to current invader abundances, private optimal choices \hat{X}_t^P , \hat{Z}_t^P and their costs, while welfare in subsequent periods $t+1$ is discounted by factor ρ^4 and uncertain given random invasion, growth, and damage. E_t is the conditional expectation operator from the viewpoint of t . For expositional purposes in the analytics (although we do not adhere to these restrictions in the more general numerics) we employ a two-period, four state version of the SDP such that expected welfare in $(t+1)$ given by,

$$E_t W(\theta_{t+1}) = p_{t+1}(S_t^G)[q_{t+1}(X_t^G, \hat{X}_t^P | N_t)U_{t+1}(B_{t+1}) + (1 - q_{t+1}(X_t^G, \hat{X}_t^P | N_t))U_{t+1}(A_{t+1})] + (1 - p_{t+1}(S_t^G))U_{t+1}(A_{t+1}). \quad (5)$$

Net incomes in $(t+1)$ are described by the following conventions,

$$B_{t+1} = M_{t+1} - D_{t+1}(\hat{X}_{t+1}^P, \hat{Z}_{t+1}^P; N_{t+1}) - C_{t+1}(S_{t+1}^G, X_{t+1}^G, \hat{X}_{t+1}^P, \hat{Z}_{t+1}^P)$$

$$A_{t+1} = M_{t+1} - C_{t+1}(S_{t+1}^G, X_{t+1}^G, \hat{X}_{t+1}^P, \hat{Z}_{t+1}^P),$$

where $B_{t+1} < A_{t+1}$. As Eq. (5) demonstrates, odds exist q_{t+1} that the invader grows rapidly in the transition to $(t+1)$ and causes damages only in the invaded state. If control measures are successful ($1 - q_{t+1}$), such that control is 100% effective, the growth of the invader is halted with no damage. Note that the probability of growth and damage in the invaded state $q_{t+1}(X_t^G, \hat{X}_t^P | N_t)$ is conditioned on the abundance in t , while damages in $(t+1)$ depend on the abundance of invader in $(t+1)$, $D_{t+1}(\hat{X}_{t+1}^P, \hat{Z}_{t+1}^P; N_{t+1})$.

In period t , the first-order condition for optimal collective prevention is

$$W_{S^G} = -U_t'(B_t)C_{t, S^G} + \rho p_{t+1, S^G} q_{t+1}(U_{t+1}(B_{t+1}) - U_{t+1}(A_{t+1})) = 0 \quad (6)$$

² Private control works to reduce the probability of growth in the following period, although not directly through an intertemporal decision.

³ In this format, both prevention and control are also referred to as *self-protection* or *mitigation* strategies (see Ehrlich and Becker, 1972).

⁴ The discount factor ρ is related to the discount rate r by $\rho = 1/(1+r)$.

where primes and subscripted variables indicate partial derivatives. Eq. (6) requires the manager to employ prevention in t up to the level in which the marginal costs of its current employment (first term) equals the discounted expected marginal benefits in the following period. The welfare gains are the result of a reduced probability of invasion, and the increased chances of no damage in $(t+1)$.

The first-order condition for collective control is

$$W_{X^G} = -U_t'(B_t)C_{t,X_t^G} + \rho p_{t+1}q_{t+1,X_t^G}(U_{t+1}(B_{t+1}) - U_{t+1}(A_{t+1})) = 0 \quad (7)$$

that requires collective control to be employed in period t up to the level that equates the marginal cost of control in the current period to the discounted expected marginal benefits of control in the subsequent period. The marginal benefits result from a reduced chance of growth and damage in the invaded state in $(t+1)$.⁵

3. Including feedback loops

In this section, we implement the framework to determine what—if any—additional policy information is provided by including feedback loops in invasive species management. The question is addressed through numerical simulations based on a stochastic dynamic programming (SDP) version of the endogenous risk model. Let the representative individual be an electricity generator (firm). Given the regulated environment of the electric power industry such that firms must satisfy all the demand they face at regulated rates, output levels are exogenous.⁶ Also assume firms hire inputs of production in an optimal manner from perfectly competitive input markets. Adaptation, Z_t^P , is the additional factors firms hire to compensate for damages of the invader (given an exogenous output level). Damages in turn depend on the firm's private control effort, X_t^P . The Appendix lists all data sources (also see Leung et al., 2002; Finnoff et al., 2004).

In an SDP model, multiple levels of feedback exist within and across states and time, and between

economic and ecological behavior. We focus on two dimensions. First, the link between the biological system and firms, and the beliefs held by firms is examined. In the absence of this feedback dimension, the firm behaves *as if* there is no change in the biological system—that is, it has incomplete beliefs about the nature of the system.⁷ Here, the consequences depend on whether there is an invasion in the initial period such that $N_t=0$ or $N_t>0$, and whether the firm acknowledges the presence of the invader. For example, if there is no initial invasion (e.g., $N_t=0$), the firm neither controls nor adapts to an invasion. The consequences imply that as the biological system and states change, the firm either uses too few or too many inputs relative to our optimal baseline. In turn, output correspondingly either under- or overshoots its targeted level; either way, this results in opportunity cost losses from production shortages or surplus, determined ex post.

The second dimension is the feedback between the benevolent manager and firm, and the beliefs held by the manager. Removing the feedback causes the manager to act *as if* the firm does not respond to changes in state (in which only firm control matter). We define this situation to be when the manager holds incomplete beliefs over firm behavior. Also either $N_t=0$ or $N_t>0$ and the firm continues to behave as though circumstances remain constant. For example, following a successful invasion, the manager ignores the private control actions of the firm. This has direct welfare consequences as resources may not be allocated efficiently. When excluding feedbacks, the model necessarily determines the consequences of the invasion and behavior of firms, although the firm or social planner does not take them into account. The

⁵ Assume the second-order sufficiency conditions are maintained for both collective and private optimal choices, with the associated Hessian matrices negative definite.

⁶ See, for example, Christensen and Green (1976).

⁷ See Crocker et al. (1998) for a discussion on the nature of incomplete beliefs in accounting for environmental change. The foundation of the complete beliefs rests in the expression of values through repeated give and take with others in an active institution like the marketplace. The institution defines incentives and articulates knowledge and beliefs about relevant laws of nature and of humans. It relates a person's choice to the choices of others and to the resulting consequences. Absent such a comparative social reference, a person relies more on his personal resources. But since exchange institutions do not exist for many environmental assets, a person's incomplete beliefs go uncontested. He lacks incentive to act as implied by the rational maximization paradigm (see, e.g., Thaler, 1992).

current welfare is determined by all implemented strategies.

Table 1 illustrates 10 scenarios considered. The first six scenarios (1–6) remove the feedbacks between the biological system and the firm. Scenarios 1 and 2 remove feedback on firm adaptation (no impacts on firm control), such that adaptation decisions are made *as if* no initial invasion occurred ($N_t=0$) or *as if* the initial invasion conditions are a constant positive value ($N_t>0$). Scenarios 3 and 4 remove feedbacks for firm control for $N_t=0$ or $N_t>0$. Scenarios 5 and 6 examine the effect of no feedback for both adaptation and control for $N_t=0$ or $N_t>0$.

For the second dimension, feedbacks between the manager and the firm are removed, such that the manager's beliefs are incomplete. Scenarios 7 and 8 reflect the situations in which the manager acts *as if* the firm does not respond to changes in state in its control effort given either for $N_t=0$ or $N_t>0$. Finally, we consider two scenarios in which all feedbacks are removed and the firm does not respond to changes in the biological system, as the manager expects, for both noninvaded ($N_t=0$) and invaded initial conditions ($N_t>0$).

Tables 2–4 summarize the results from the simulations. The baseline scenario includes all feedbacks and serves as a natural reference point to compare all other scenarios. Table 2 presents the expected mean annual magnitudes of critical variables, Table 3 shows the percentage change in expected mean annual magnitudes from the baseline, and Table 4 illustrates

Table 1
Feedback scenarios

Scenario	Feedback dimension	Feedback removed	Initial invasion condition
1	Biology and firm	Adaptation	$N_t=0$
2			$N_t>0$
3		Control	$N_t=0$
4			$N_t>0$
5		Adaptation and control	$N_t=0$
6			$N_t>0$
7	Manager and firm	Control	$N_t=0$
8			$N_t>0$
9	Firm and biology and manager and firm	Biology–firm–manager	$N_t=0$
10			$N_t>0$

the changes in expected cumulative welfare (undiscounted) from the baseline. Four key results emerge from our numerical simulations. Consider each in turn.

Result 1. (*Biology–firm feedbacks and adaptation*): Removing the feedback for adaptation does not affect predictions for either the mean probability of invasion or invader abundance relative to the baseline case. Human consequences emerge, however, and these depend on whether the firm acts as if there was an initial invasion or not, i.e., $N_t=0$ versus $N_t>0$. The firm's adaptation efforts now undershoot the baseline without an initial invasion, and overshoot with invasion. In turn, production levels either undershoot and overshoot the required level, which results in opportunity costs and reduced welfare with or without initial invasions. Welfare losses are less with initial invasions given positive adaptation does exist.

The consistency in probability of invasion and invader abundance is expected given that adaptation has no biological impacts. If the firm perceives the state (defined ecologically by population abundance) as constant, adaptation does not adjust in response to changes. This lack of response causes the level of adaptation to undershoot the baseline when $N_t=0$, and to overshoot the baseline when $N_t>0$. The impacts on production result in opportunity cost losses and reduced welfare when these losses are taken into account (as demonstrated in Table 3). The magnitude of these losses is less for the case of constant initial conditions as the “additional” adaptation during periods of realized invasion dampens the opportunity cost losses in other periods.

Result 2. (*Biology–firm feedbacks and control*): Consequences now emerge in both the biological and economic systems. With initial invasions ($N_t>0$), the firm controls at a relatively high level—but the probability of invasion and invader abundance both nearly double. This result occurs because the manager free rides on the firm's control efforts and never chooses to use its own control or prevention efforts. Economic welfare also decreases relative to the baseline due to the firm's inefficient control. Without initial invasions ($N_t=0$), the firm never controls. The social planner now overcontrols relative to the baseline, which lowers welfare. In addition, overcontrol

Table 2
Annual expected magnitudes

Scenario	Expected mean annual magnitudes								
	Prob. of invasion	Invader abundance	Welfare ^a	Welfare net of opp. costs ^a	Firm			Collective	
					Adaptation	Control	Control	Prevention	
				Labor ^b	Capital ^c				
Baseline	0.134	5.787	47.934	47.934	4.353	13.511	0.003	0.060	0.723
<i>Biology–firm</i>									
Adaptation									
$N_i=0$	0.134	5.787	47.940	47.839	4.346	13.490	0.003	0.060	0.723
$N_i>0$	0.134	5.787	47.940	47.771	4.351	13.505	0.003	0.060	0.723
Control									
$N_i=0$	0.148	6.199	47.925	47.925	4.353	13.511	0	0.071	0.708
$N_i>0$	0.276	11.724	47.895	47.895	4.346	13.490	0.125	0	0
Adaptation and control									
$N_i=0$	0.148	6.199	47.931	47.831	4.346	13.490	0	0.071	0.708
$N_i>0$	0.276	11.724	47.895	47.822	4.351	13.505	0.125	0	0
<i>Manager–firm</i>									
Control									
$N_i=0$	0.133	5.634	47.934	47.934	4.353	13.511	0.003	0.061	0.723
$N_i>0$	1.000	125.600	46.765	46.765	4.429	13.748	0.061	0	0
<i>Biology–firm–manager</i>									
$N_i=0$	0.148	6.199	47.931	47.830	4.346	13.490	0	0.071	0.708
$N_i>0$	0.276	11.724	47.895	47.822	4.351	13.505	0.125	0	0

^a In millions of dollars.

^b In hundreds of employees.

^c In million BTU's.

Table 3
Percent changes from baseline

Feedback removed	Expected mean annual percentage change from baseline								
	Prob. of invasion	Invader abundance	Welfare	Welfare net of opp. costs	Firm Adaptation	Control	Collective Control	Prevention	
<i>Biology–firm</i>									
Adaptation									
$N_i=0$	0	0	0.013	–0.199	–0.159	0	0	0	0
$N_i>0$	0	0	0.013	–0.340	–0.049	0	0	0	0
Control									
$N_i=0$	10.827	7.117	–0.019	–0.019	–0.001	–100	18.818	–2.062	
$N_i>0$	106	103	–0.081	–0.081	–0.156	4671	–100	–100	
Adaptation and control									
$N_i=0$	10.827	7.117	–0.006	–0.216	–0.159	–100	18.818	–2.062	
$N_i>0$	106	103	–0.081	–0.233	–0.049	4671	–100	–100	
<i>Manager–firm control</i>									
$N_i=0$	–0.456	–2.647	0	0	–0.001	–2.259	1.269	0.016	
$N_i>0$	648	2070	–2.440	–2.440	1.751	2244	–100	–100	
<i>Biology–firm–manager</i>									
$N_i=0$	10.827	7.117	–0.006	–0.216	–0.159	–100	18.818	–2.062	
$N_i>0$	106	103	–0.081	–0.233	–0.049	4671	–100	–100	

Table 4
Expected cumulative welfare changes from baseline^a

Feedback removed	Expected welfare change	Expected welfare change net of opportunity costs
<i>Biology–firm</i>		
Adaptation		
$N_t=0$	\$307,730	–\$4,762,505
$N_t>0$	\$303,410	–\$8,158,251
Control		
$N_t=0$	–\$450,830	–\$450,830
$N_t>0$	–\$1,944,340	\$1,949,846
Adaptation and control		
$N_t=0$	–\$143,460	–\$5,172,622
$N_t>0$	–\$1,945,710	–\$5,580,819
<i>Manager–firm control</i>		
$N_t=0$	–\$7,200	–\$7,200
$N_t>0$	–\$58,467,700	–\$58,471,689
<i>Biology–firm–manager</i>		
$N_t=0$	–\$143,460	–\$5,173,762
$N_t>0$	–\$1,945,710	–\$5,580,819

^a All values are calculated without discounting for comparison purposes.

causes underprevention, which increases both the probability of invasion and populations.

When the firm ignores changes in state and $N_t>0$, the firm overcontrols in all periods to such an extent it is never optimal for the manager to employ control or prevention effort.⁸ The reductions in welfare are not due to damages because the firm's control is at an artificially high level which negates damages from increased probabilities of invasion and abundances. Rather, welfare falls due to the inefficient employment of control by the firm.

The reverse occurs if the firm acts as if $N_t=0$ —they never control. The social planner is then forced to overcompensate the reallocation of resources lowering welfare. Also, with greater collective resources channeled to control than would otherwise be optimal, prevention effort declines. With less prevention, the probability of invasion rises in turn resulting in slightly increased populations.

⁸ The percentage changes in Table 3 are high because while the baseline exhibits initial periods of control, these are followed by extended periods with no firm control. The firm does not control following initial periods as populations are maintained at low levels, making the mean level of firm control very low in the baseline.

Simultaneously removing biology–firm adaptation and control feedbacks finds that under both initial condition assumptions, the effects are additive across the above scenarios. If the firm perceives $N_t=0$, there is no firm level control and the manager controls far more than they need to while preventing a little less. The probability of invasion and invader abundance rise, and welfare without and including opportunity cost losses falls. On the flip-side, when the firm reacts to $N_t>0$ and does not alter their behavior with changes in state, the firm controls too much and collective control and prevention are completely neglected. The probability of invasion and invader abundance dramatically rise, and welfare falls with the over employment of firm control.

Result 3. (Manager–firm control): Now the biological and economic consequences depend notably on the initial conditions, $N_t=0$ versus $N_t>0$. If the manager believes the firm behaves as if $N_t=0$, he overemploys both collective prevention and control. This reduces the probability of invasion and reduces invader abundances. The firm now reacts by reducing its control and adaptation to (almost) perfectly offset the manager's overemployment. Consequently, we see no change in mean annual welfare and a modest reduction in cumulative welfare relative to the baseline. In contrast, if the belief is $N_t>0$, the results are reversed. Now the manager neglects prevention and control, which causes a rapid increase in invasion probabilities and invader abundance. Firms react by upping their control and adaptation—but not to the level the manager believes the firm is using (i.e., an initial invasion). The firm is left with persistent invader abundances, which reduces annual welfare and cumulative welfare.

With incomplete beliefs, if the manager believes the firm behaves as if $N_t=0$, their over-use of prevention and control causes the firm to reduce its actual control and adaptation (almost) perfectly. The situation reverses itself if the manager believes the firm behaves as if $N_t>0$. With the manager's neglect of prevention and control, the firm is faced with mounting damages and rapidly increases their control and adaptation effort to the optimal level (myopic) for the current population. As firm control keeps the population always below what it is initially, they never employ control up to the level the manager

believes they are using. When coupled with the lack of collective action, the firm is left with persistent invader abundances. This results in reduced annual welfare levels and dramatic cumulative welfare losses.

Result 4. (*All feedbacks removed*): If the firm behaves as if $N_i=0$, it neither controls nor adapts to invader damages. The manager must increase collective control and forgo some prevention, which increases the probability of invasion and invader abundances. Production is then constrained by underadaptation such that the firm does not meet its targeted output. Combining the opportunity costs due to underproduction and the suboptimal reallocation of resources, we see a relatively significant decline in both annual and cumulative welfare. If the belief is $N_i>0$, the manager believes the firm maintains nonoptimal levels of too much control. The manager now abstains from all prevention or control knowing the firm will maintain these inefficient levels. We now see a greater chance of invasion and increased populations, but the damages are negated by the high level of firm control. In addition, the firm overadapts (given control), which generates too much production and opportunity cost losses. Again, annual and cumulative welfare decline.

In the absence of Biology–Firm–Manager feedbacks, the firm neither changes its adaptation nor control strategies as the biological system changes, and the manager believes that they are non-responsive. Following a similar reasoning as above, when the firm behaves as if $N_i=0$, it does not respond. With under prevention by the manager, the probability of invasion and invader abundances rise, resulting in turn in increased damage. Production undershoots its required level resulting in opportunity cost losses, and the increased abundances in turn require more collective control.

If the firm behaves as if $N_i>0$, the firm confirms the managers beliefs that they maintain nonoptimal levels of adaptation and control prompting the manager to decline any collective prevention or control. Again, there is too much adaptation given the level of control. In result there is a surplus of production and opportunity cost losses. Taken together, these result in declines of mean annual and cumulative welfare.

4. Conclusions

Does the effort required to capture feedback links between ecology and economics provide sufficient additional information? Our results suggest that feedback can matter for the case of zebra mussel invasion in a Midwest lake—but not in every dimension. Both biological and economic consequences of not addressing feedbacks are sensitive to the initial conditions on the environment, behavioral perceptions about the state of the environment, and the completeness of the manager’s beliefs. Four main results emerge.

First, only relatively minor ecological consequences were found by not addressing the link between the biological system and the firm for adaptation; but substantial economic consequences were predicted. Second, a different outcome is suggested for control. Here, neglecting the feedback resulted in a deterioration of biological and economic outcomes, with the firm switching between over- and under-control. The manager either free rides off private investment or has sole responsibility for control, which crowds out preventative measures. The overall impacts are efficiency losses, increased probabilities of invasion, and increased invader abundances. Third, the biological and economic consequences of ignoring the feedback between manager and firm are more variable. Given a manager’s incomplete beliefs over firm behavior, the manager both overprevents and overcontrols with relatively minor impacts on the systems, or he completely neglects both strategies which induce severe biological and economic consequences. Finally, neglecting all feedbacks (e.g., biology and firm, and manager and firm) reduces the incompleteness of the manager’s beliefs. While detrimental economic and ecological consequences arise, they are tempered relative to the single manager–firm feedback case, as now the manager’s uncertainty over firm behavior is reduced.

A useful lesson from our results is two-part. First, even if firm beliefs over the biological system are incomplete, if the resource manager has a relatively good understanding of both the biological system and firm behavior, the consequences of not addressing the feedback may not be disastrous from a predictability standard. Second, whatever the firm’s beliefs over the

biological system, if a manager's beliefs over firm behavior are incomplete, the consequences of ignoring feedback may be severe. Future research exploring the robustness of our predicted consequences for either different invasive species or different environmental contexts seems worthwhile.

Acknowledgments

The Authors thank an anonymous referee, the participants at the University of Wyoming Bioinvasions Conference, and ISIS group members for the useful discussions. This research is supported by a grant from the National Science Foundation (DEB 02-13698).

Appendix A. SDP specification

In an SDP model, the invasive species manager maximizes the discounted expected welfare over a finite set of states $i \{i=0, 1, \dots, n\}$ and time $t \{t=0, 1, \dots, T\}$. States are discrete levels of population abundance N_{it} for each period t . Assume the state variable N_t is known before the manager makes decisions over controls S_t^G, X_t^G and private firms make decisions over adaptation Z_t^P and private control X_t^P (state subscripts are suppressed). These choices define the social welfare as $W(D(Z_t^P, X_t^P; N_t), C(S_t^G, X_t^G, Z_t^P, X_t^P))$ for that period and state, a function of the damages D caused by the abundance of the invader, and the costs of S_t^j and X_t^j for $j=\{G, P\}$. Future social welfare is uncertain because of the underlying stochastic ecological process governing transitions between states. Transitions between states over time through population growth are Markov and governed by $N_{t+1}=f(\epsilon_t, N_t(X_t^P)X_t^G)$, where ϵ_t represents stochastic population growth. Private control in period t reduces current populations; collective control reduces the reproducing population in t . Prevention effort is distinct in that its application in period t reduces the probability of invasion.

A.1. Biological processes

Following Leung et al. (2002), the invasion process is represented as a multistate compound

lottery. A continuum of states N_{it} is allowed between 0 (unsuccessful establishment) and the carrying capacity K (completely successful establishment). Assume a clear differentiation in the points of contact between prevention, control, and adaptation and the ecological system. In uninvaded states the probability of invasion is specified as,

$$p_{i,t+1}^a = p^b e^{-AS_{i,t}}, \quad (\text{A1})$$

where $p_{i,t+1}^a$ is the realized probability of invasion in the following period. $p_{i,t+1}^a$ depends on the baseline probability of invasion p^b , and the manager's prevention effort $S_{i,t}$ in the current period. Parameter A reflects the efficacy of mitigation efforts, and e is the exponential function.

Given an invasion and the initial establishment of the population, let $q_{i,t+1}$ be the probability of growth and greater damages in the following period. The realized degree of severity depends on initial population $N_{i,t+1}^b$, which in turn depends on collective control efforts in the preceding period $X_{i,t}^C$, stochastic population growth (from random variable $\epsilon_{i,t}$), and current period control $X_{i,t}^P$. The process is specified in three stages. First, in period t , private control reduces the abundance of invaders (private kill function),

$$N_{i,t}^b = \frac{N_{i,t}^o}{1 + v^P X_{i,t}^P} \quad (\text{A2})$$

where $N_{i,t}^b$ are residual initial invaders $N_{i,t}^o$ that survive private control measures and become established, and v^P is a parameter describing the effectiveness of private control. Second, collective control reduces the abundance of invaders that could reproduce during the transition to $(t+1)$; collective kill function),

$$N_{i,t}^a = \frac{N_{i,t}^b}{1 + v^G X_{i,t}^G}, \quad (\text{A3})$$

where $N_{i,t}^a$ are residual invaders that survive private and collective control measures and become estab-

lished, and v^G is a parameter describing the effectiveness of collective control. The accompanying stock growth uncertainty from random variable ϵ_t occurs through the logistic expression,

$$N_{i,t+1}^b = N_{i,t}^a + rN_{i,t}^a \left(1 - \frac{N_{i,t}^a}{K}\right) + \epsilon_{i,t}. \quad (A4)$$

K is the invader’s carrying capacity, and r the invader’s intrinsic growth rate. Together, Eqs. (A2), (A3), and (A4) dictate transition probabilities $q_{i,t+1}$. Combining Eqs. (A1), (A2), (A3), and (A4) defines the transition process.

For any given state and period, assume social welfare is a function of social net wealth SW . SW consists of the net income of a representative producer adversely impacted by an invasion, inclusive of both private and collective expenditures on prevention and control. The resource manager takes the producer’s optimal choices as given in the determination of optimal collective prevention and control. The producer optimally hires factors of production labor L and capital K in the production of their output Q . It is through excessive employment of these factors that firms are able to adapt to the consequences of an invasion [such that $Z(L,K)$]. Suppressing state and period subscripts, social welfare is

$$SW = [P_Q \hat{Q} - C_L \hat{L} - C_K \hat{K} - C_X \hat{X}^P] - C_S S^G - C_X X^G, \quad (A5)$$

where *hats* indicate variables endogenous to the firm. P_Q is the (constant) price of the producer’s output, C_L is the wage rate, C_K the rental rate of capital, C_S the per unit cost of preventative measures, and C_X per unit control costs. Following Lichtenberg and Zilberman (1986), the productivity of damage adaptation strategies are captured through a Cobb–Douglas production function,

$$Q = \alpha L^a K^{b1} D(N^b(X^P))^c, \quad (A6)$$

where α , a , $b1$, and c are parameters and $D(N^b(X^P))$ a damage function relating the impacts of the invader population net of private control to monetary damages. The exponential specification of D is modified to depend on the initial invader abundance N^b , itself a function of private control X^P , and parameter λ ,

$$D(N(X^P)) = 1 - e^{-\frac{\lambda}{N^b(X^P)}} = 1 - e^{-\frac{\lambda(1+v^P X_t^P)}{N_{i,t}^a}}. \quad (A7)$$

Eq. (A7) says that private control reduces the damages of greater abundances of invaders, increasing D towards its uninvaded magnitude of unity.

In the application the representative producer is an electricity generator. Given the regulated environment of the electric power industry such that firms must satisfy all the demand they face at regulated rates (Christensen and Green, 1976), output levels are exogenous.⁹ Also, assume firms hire inputs of production in an optimal fashion from perfectly competitive input markets. Exogenous output and input prices and endogenous factor employment make the dual formulation appropriate in the determination of optimal factor employment. As noted above, a firm’s adaptation efforts Z_t^P depend on the damages caused by the invader, which, in turn, depend on private control effort X_t^P . Adaptation is the additional factors that firms hire to compensate for the damages of the invader (given an exogenous output level). Given Eq. (A7), in any given state, the

⁹ An accompanying characteristic of the industry is that it possesses several inputs that are less variable than others, or quasi-fixed inputs. Additions and removals of generation assets typically require long periods of time, while the amount of electricity generated can vary substantially within the short run. While power generators may be able to hire variable inputs optimally, they may be in a temporary disequilibrium with respect to quasi-fixed inputs. While it would be preferable to incorporate these inputs into the analysis as demonstrated in Brown and Christensen (1981), Caves et al. (1981), Berndt and Hesse (1986), and Sickles and Streitwieser (1998), given the additional complexity their inclusion would force and data unavailability we are forced to investigate only short-run production.

conditions for factor and private control employment can be found as

$$\hat{L} = \left[\frac{Q}{\alpha}\right]^{\frac{1}{a+b1}} \left[\frac{b1C_L}{aC_K}\right]^{\frac{-b1}{a+b1}} \left[1 - e^{-\frac{\lambda(1+v^P X_{i,t}^P)}{N_{i,t}^o}}\right]^{\frac{-c}{a+b1}} \quad (A8)$$

$$\hat{K} = \left[\frac{Q}{\alpha}\right]^{\frac{1}{a+b1}} \left[\frac{aC_K}{b1C_L}\right]^{\frac{-a}{a+b1}} \left[1 - e^{-\frac{\lambda(1+v^P X_{i,t}^P)}{N_{i,t}^o}}\right]^{\frac{-c}{a+b1}} \quad (A9)$$

$$\hat{X} = \frac{N_{i,t}^o}{\lambda v^P} \ln\left[\frac{\lambda c v^P P_Q Q}{N_{i,t}^o C_X} + 1\right] - \frac{1}{v^P}. \quad (A10)$$

Appendix B. Key Parameters

Parameters employed in the simulations follow from the specifications detail in Appendix A. Ecological parameters were selected to represent a generic invasion process. Following the hypothetical example of Leung et al. (2002), consider a generic zebra mussel invasion of a lake and its impact on a representative electricity generation facility. Given the focus in this work on the importance of critical feedbacks in between the systems, real world data are employed in the parameterization of the economic components to make the magnitudes of change in the results are reasonable. Tables 1 and 2 present the data (see Finnoff et al., 2004).

Given observed data, the remaining economic variables and baseline parameters were determined through a calibration procedure (see Table 4). While no direct data exists for per unit prevention costs, the cost of zebra mussel control was set at \$1.6 million per control event (consistent with data from large power plants, Leung et al., 2002), which includes costs of molluscicide and reduced production during treatment. In the baseline simulation, our maintained assumption was the social planner employing a mix of control and prevention efforts, in which we used a sensitivity test to develop reasonable values. All production function parameters were found based on the assumption that all firms in the sample maximize profits subject to their specified production function. Employing the necessary conditions, the definition of the production function, imposing constant returns to scale on the production function and data from Table 2, parameters α , a , $b1$, and c were determined. A discount rate of 3% was employed in all scenarios.

For ecological parameters, the baseline probability of invasion p^b extrapolates the monthly value used in Leung et al. (2002) into an annual value of 0.0828. Efficacy of prevention efforts, A , was found from manipulation of Eq. (A1) and the assumption that a unit of prevention reduces the probability of invasion by 90%. An identical procedure was followed for v^G and v^P . λ followed from Eq. (A7), the (assumed representative, along with r) invader carry capacity K , and the assumption that if the invader population were to achieve its carrying capacity, production would be reduced to 50% of its nondamaged levels with all other variables held constant.

Table A1. Variables in the sample

Variable	Definition	Source	Mean
Q_t	Total output (MWH ^a)	Sales to ultimate customers	2,440,937
L_t	Labor inputs (number of employees)	Number of employees	434
K_t	Capital inputs (BTUs)	Inferred as the summation of utility fuel BTUs: calculated as the product of the quantity of fuel [coal (1000 tons), oil (1000 barrels), and natural gas (1000 MMBtu)] and the fuel specific BTU content for each firm.	13,496,686
TR_t	Total revenues (\$)	Total sales of electricity	185,261,805
$TC_{L,t}$	Total labor costs (\$)	Total salaries and wages	29,775,675
$TC_{K,t}$	Total capital costs (\$)	Capital expenses ^b	78,847,876

^a Megawatt hours.

^b Capital expenses are found as a residual of total electric operations and maintenance expenses net of total salaries and wages.

Table A2. Prices

Variable	Definition	Calculated value
P_Q	Price of output	47.48
C_L	Wage rate	4.29
C_K	Rental rate of capital	3.64
C_X	Per unit cost of control effort	1.6

Table A3. Parameters

Parameter	Definition	Baseline value
C_S	Per unit cost of mitigation effort	0.1
α	Production function parameter	0.641
A	Production function parameter	0.161
b_1	Production function parameter	0.423
C	Production function parameter	0.416
A	Efficiency of mitigation effort	2.303
V	Efficiency of adaptation effort	2.303
λ	Damage function parameter	660
K	Invading species carrying capacity	1000
R	Invading species intrinsic growth rate	1

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