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# Using economic instruments to develop effective management of invasive species: insights from a bioeconomic model

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**Abstract.** Economic growth is recognized as an important factor associated with species invasions. Consequently, there is increasing need to develop solutions that combine economics and ecology to inform invasive species management. We developed a model combining economic, ecological, and sociological factors to assess the degree to which economic policies can be used to control invasive plants. Because invasive plants often spread across numerous properties, we explored whether property owners should manage invaders cooperatively as a group by incorporating the negative effects of invader spread in management decisions (collective management) or independently, whereby the negative effects of invasive plant spread are ignored (independent management). Our modeling approach used a dynamic optimization framework, and we applied the model to invader spread using *Linaria vulgaris*. Model simulations allowed us to determine the optimal management strategy based on net benefits for a range of invader densities. We found that optimal management strategies varied as a function of initial plant densities. At low densities, net benefits were high for both collective and independent management to eradicate the invader, suggesting the importance of early detection and eradication. At moderate densities, collective management led to faster and more frequent invader eradication compared to independent management. When we used a financial penalty to ensure that independent properties were managed collectively, we found that the penalty would be most feasible when levied on a property's perimeter boundary to control spread among properties. At the highest densities, the optimal management strategy was "do nothing" because the economic costs of removal were too high relative to the benefits of removal. Spatial variation in *L. vulgaris* densities resulted in different optimal management strategies for neighboring properties, making a formal economic policy to encourage invasive species removal critical. To accomplish the management and enforcement of these economic policies, we discuss modification of existing agencies and infrastructure. Finally, a sensitivity analysis revealed that lowering the economic cost of invader removal would strongly increase the probability of invader eradication. Taken together, our results provide quantitative insight into management decisions and economic policy instruments that can encourage invasive species removal across a social landscape.

**Key words:** bioeconomic model; dispersal; dynamic optimization; independent vs. collective management; invasive species management; *Linaria vulgaris*; yellow tadflax.

## INTRODUCTION

Invasive species are a leading component of environmental change (Mack et al. 2000) and cost billions of dollars annually in ecological damages and economic losses (Pimentel et al. 2005). Two critical issues in the study of invasive species are understanding the causal factors of species invasions and developing approaches to reduce their spread. Studies have linked human activities to invasive species spread (Vitousek 1997, McKinney 2001, Leprieur et al. 2008). For example, land use change associated with urban and suburban development have been associated with an increase in

exotic species, especially plants (Taylor and Irwin 2004, Gavier-Pizarro et al. 2010), due to landscape disturbance and the importation and dispersal of exotic propagules (Rouget and Richardson 2003, Lockwood et al. 2005). Given that human activities are linked to the distribution and abundance of invasive species, we propose that human economic instruments, policies used to achieve the control or regulation of environmental problems, could be powerful tools to reduce the spread of invasive species. Examples of economic instruments range from public expenditure policies (i.e., subsidies, grants, tax allowances) to revenue-generating policies (i.e., taxes, penalties, and fees) to revenue-neutral policies (i.e., deposit–refund systems). The goal of this study was to combine economic, ecological, and sociological factors to assess the degree to which penalties and subsidies could be used to manage invasive plants.

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There are many approaches to managing invasive plants. The removal of invaders can occur through chemical application or mechanical/hand-pulling, as well as biological control, grazing, and fire (DiTomaso 2000, Paynter and Flanagan 2004, Simberloff et al. 2005). The removal of invaders can also be encouraged through the planting of native species that can compete with or outcompete invasive species (Sheley and Petroff 1999), assuming native species with such high competitive abilities can be identified. These and other approaches have achieved success for the control of some invasive plants (reviewed in Simberloff et al. [2005]). However, the rate of spread of invasive species, especially on private lands (Epanchin-Niell et al. 2010), suggests that these approaches may not be implemented effectively by many stakeholders given the many constraints they face (Aslan et al. 2009). The degree to which economic policies, such as penalties and subsidies, could be implemented to affect the net benefits of implementation of these approaches for successful invasive species management warrants further investigation.

Human social factors are also important to consider in the management of invasive species. For example, how one property owner (hereafter referred to as owner) manages invasive plants may affect the ability of adjacent owners to control invaders (akin to a classic collective action problem; Olson 1965) due to potential spread of invaders among properties. Developing approaches to reduce the spread of invaders must account for this spatial complexity in property ownership and management and the dispersal ability of invaders (Gutrich et al. 2005, Epanchin-Niell et al. 2010). Owners could each choose to manage invaders independently, thus ignoring how the damages or costs of invader spread (i.e., negative externalities) among adjacent properties affect management (hereafter referred to as independent management). Or owners could work cooperatively to control invaders, recognizing that they both receive and donate propagules, and that their ability to control invaders is affected by the actions of neighbors (hereafter referred to as collective management; Shogren and Crocker 1991). Theoretical and empirical studies suggest that collective management generally increases the net benefits of invasive species control relative to independent management (Shogren and Crocker 1991, Rich et al. 2005, Yu and Leung 2006, Bhat and Huffaker 2007), but there are exceptions (Shogren and Crocker 1991, McKee 2006). Owners working independently can choose instead to work with others by either voluntarily choosing to work collectively with their neighbors, or policy incentives can be implemented so that invaders spreading onto adjacent land are considered in management strategies. Previous research has emphasized the potential for voluntary invasive species control across independently managed properties, including unilaterally removing invaders (Jones et al. 2000), voluntary collaboration by sharing

control costs (Grimsrud et al. 2008), and coordinating management through transfer payments (Bhat and Huffaker 2007). However, little is known about the use of formal economic instruments, such as penalties for noncompliance or subsidies for compliance, to encourage the removal of invaders across independently managed properties. Formal economic instruments have been implemented on economic activities contributing to invasive species spread (Barbier and Shogren 2004, Knowler and Barbier 2004, Richards et al. 2010) and may provide a powerful approach to change human behaviors and encourage collective management of invasive species.

Here, we explored how ecological, economic, and social conditions affect optimal invasive plant management, and introduce two economic instruments (a penalty and a subsidy) to encourage the control and eradication of invaders under collective vs. independent management. The economic instruments we propose are based on the spread of invasive species among properties, their life history, and the resulting economic costs of removal and damages of invaders spreading among adjacent properties. In addition, we allowed for adjustments in the economic instruments over time as the economic and ecological conditions change. We addressed three objectives. First, we developed a general theoretical bioeconomic model that illustrates the difference between managing invasive species collectively vs. independently. We used a dynamic optimization framework (Leonard and Van Long 1992, Chiang 1999) that includes natural resource benefits, costs of management strategies, damages from invasive species, and biological responses of the invasive species and co-occurring native species. Second, we applied the model to a case study of an invasive plant, *Linaria vulgaris* (yellow toadflax, Plantaginaceae), in the Rocky Mountains of western USA. Although this work is focused on *L. vulgaris*, it shares life history characteristics with other common invaders (Sheley and Petroff 1999), and so the results may be broadly applicable to other invasions. Third, we used a sensitivity analysis to explore more generally when economic instruments may be effective for invasive species control. Finally, in the *Conclusions*, we discuss the monitoring and enforcement infrastructure needed to implement these economic policy instruments. We focus on invasive plant management on private land, but the model and results are germane to adjacent public lands managed by different agencies, and the methods can be applied to other taxa.

#### BIOECONOMIC MODEL FOR THE MANAGEMENT OF INVASIVE PLANTS

Our bioeconomic model includes two competing species (one native and one invasive) established on two adjacent, independently owned properties (property 1 and property 2). Our model only includes two properties and does not include a more complicated

spatially explicit landscape with varying sizes or shapes of properties; the importance of spatial scale and spread dynamics in bioeconomic assessments of invasive species management has been reviewed recently (Epanchin-Niell and Hastings 2010) and can be incorporated in future research. The spatial simplicity of our approach allowed us to solve for optimal control strategies that may not have been possible in more spatially complex models. We assumed owners had four general management strategies: prevention, eradication (removal of the invader from their own land), control (removing some invaders but not enough for eradication), and no action (do nothing) (Wittenberg and Cock 2001, Pysek and Richardson 2010). Landscape-scale prevention of invasive species introductions was not considered in our model because we assumed invasive plants already exist on the landscape at a given density. In the model, owners choose among the three management strategies to maximize their net benefits over a period of time.

We modeled the number of individuals of the native plant  $x_i$  (hereafter referred to as number of native plants or natives) on property  $i$  as

$$\frac{dx_i}{dt} = G^{x_i}(x_i, x_j, y_i, y_j) + P_i \tag{1}$$

where  $i, j =$  properties 1, 2 ( $i \neq j$ ), and the number of individuals of the invasive plant (hereafter referred to as number of invasive plants or invasives) is given by  $y_i$ . Population growth rate of natives,  $G^{x_i}$ , is positively correlated with the number of native plants,

$$\frac{\partial G^{x_i}}{\partial x_i} = G^{x_i} > 0 \quad \frac{\partial G^{x_i}}{\partial x_j} = G^{x_i} > 0$$

and negatively correlated with the number of invasive plants,

$$\frac{\partial G^{x_i}}{\partial y_i} = G^{x_i} < 0 \quad \frac{\partial G^{x_i}}{\partial y_j} = G^{x_i} < 0$$

where subscripts denote partial derivatives. We assumed that increasing the number of native plants via the planting of natives,  $P_i$ , is a management strategy based on the biotic resistance hypothesis (Elton 1958).

The number of individuals of the invader,  $y_i$ , on property  $i$  is modeled as

$$\frac{dy_i}{dt} = G^{y_i}(x_i, x_j, y_i, y_j) - H_i \tag{2}$$

where invasive plant population growth rate,  $G^{y_i}$ , is negatively correlated with the number of native plants,

$$\frac{\partial G^{y_i}}{\partial x_i} = G^{y_i} < 0 \quad \frac{\partial G^{y_i}}{\partial x_j} = G^{y_i} < 0$$

and positively correlated with the number of invasive plants,

$$\frac{\partial G^{y_i}}{\partial y_i} = G^{y_i} > 0 \quad \frac{\partial G^{y_i}}{\partial y_j} = G^{y_i} > 0.$$

Removal of invasive plants,  $H_i$ , decreases the number of invaders.

We assumed that owners receive benefits from native plants, which generally include those that are aesthetic (i.e., the beauty of wildflowers; Sabre et al. 1997), environmental (i.e., stabilizing soil, encouraging the residence of beneficial insects; Van Dersal 1938, Vitousek 1990, Brown et al. 2002), and financial (i.e., increased property values, reduced maintenance cost along roads as natives tend to be drought resistant; Stigarll and Elam 2009). We assumed that the economic benefits of native plants,  $B_i(x_i)$ , increase as a function of the number of native plants, but at a decelerating rate at higher numbers of individuals, as indicated by the first- and second-order partial derivatives (see Varian 1992):

$$\frac{\partial B_i(x_i)}{\partial x_i} = B'_i(x_i) > 0 \quad \frac{\partial^2 B_i(x_i)}{\partial x_i^2} = B''_i(x_i) < 0.$$

Owners also experience economic damages from invasive plants. Here, economic damages measure the extent of harm in financial terms caused by the invader and can include reduced property value from smaller native plant populations (Stigarll and Elam 2009) and increased soil erosion (Lacey et al. 1989, but see Wang et al. 2006). We modeled the damages,  $D_i(y_i)$ , as an increasing function of the number of invasive plants and at an increasing rate (see Varian 1992):

$$\frac{\partial D_i(y_i)}{\partial y_i} = D'_i(y_i) > 0 \quad \frac{\partial^2 D_i(y_i)}{\partial y_i^2} = D''_i(y_i) > 0.$$

In the model, owners incur economic costs (i.e., financial expenses) from removing invasives and planting natives. Removal costs for invaders can include garbage disposal fees if they pull the invader, the price of herbicide, special equipment (i.e., herbicide sprayer, gloves, trash bags), and the time or labor to remove or spray the invaders. Direct planting costs of natives can include the price of native seeds or plants, accessories needed for planting (i.e., shovels, fertilizer), and the time or labor spent planting. The costs of removal,  $C_{H_i}(H_i)$ , and planting,  $C_{P_i}(P_i)$ , are modeled as increasing functions of the number of invaders removed,  $H_i$ , and natives planted,  $P_i$ , where

$$\frac{\partial C_{H_i}(H_i)}{\partial H_i} = C'_{H_i}(H_i) > 0 \quad \frac{\partial^2 C_{H_i}(H_i)}{\partial H_i^2} = C''_{H_i}(H_i) > 0$$

and

$$\frac{\partial C_{P_i}(P_i)}{\partial P_i} = C'_{P_i}(P_i) > 0 \quad \frac{\partial^2 C_{P_i}(P_i)}{\partial P_i^2} = C''_{P_i}(P_i) > 0$$

(Varian 1992), such that the costs of removal and planting increase at an increasing rate over time.

We used dynamic optimization to solve for the optimal number of invasives removed and natives planted that generated the largest net benefits to owners over time for both collective and independent manage-

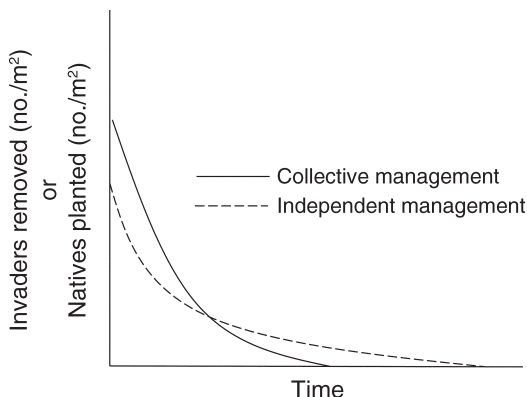


FIG. 1. Theoretical bioeconomic model showing the number of invaders removed or natives planted over time for collective (solid line) and independent (dashed line) management. Under collective management, owners work cooperatively as a group by incorporating the negative effects of invasive plant spread in management decisions, whereas under independent management, owners ignore the negative effects of invasive plant spread. Properties working collectively remove more invaders and plant more natives in early time periods compared to properties working independently. Thus, independent management results in removal and planting that must occur over longer time periods for the control or eradication of invaders. Removal or planting rates decline as saturating functions until the control or eradication of the invader is achieved.

ment (Appendix A). The maximized net benefits were calculated as the benefits from natives less economic damages from invaders and the economic costs incurred from applying control methods. Net benefits can take on values that range from positive to negative. When net benefits are positive, benefits exceed damages plus costs, and conversely, when net benefits are negative, damages plus costs exceed benefits. Under collective management, owners simultaneously maximized their benefits from native plants and minimized costs and damages from

invasive plants on both properties while recognizing the movement of natives and invaders between properties 1 and 2, whereas under independent management, owners only maximized benefits on their own property and ignored any benefits of the movement of native plants and any disadvantages of movement of invasive plants.

*Theoretical comparison of collective vs. independent management*

In the theoretical model, removing invaders and planting natives had similar outcomes (Fig. 1). Therefore, we only describe the outcome for removing invaders (see Appendix B for a description of the outcome for planting natives). The benefits from the removal of invaders are direct and indirect (Table 1). The direct benefits of invader removal are the reduction in the number of invasive plants on property  $i$ ,  $G_{y_i}^{y_i}$  and their associated damages  $D'_i(y_i)$ , and both are recognized by collective and independent management. In addition, both collective and independent management include the indirect benefit of reductions in the number of invaders due to increased competition with natives,  $C'_{P_i}(P_i)G_{y_i}^{x_i}$ . Under collective management, however, there are additional indirect benefits not included in independent management (Table 1). The additional benefits recognize the importance of reducing the spread of invasive plants from an adjacent property, which reduces the need to plant natives and the associated costs of planting,  $C'_{P_i}(P_j)G_{y_i}^{y_j}$ , and reduces costs associated with removing invaders,  $C'_{H_j}(H_j)G_{y_i}^{y_j}$ .

Differences in benefits for collective vs. independent management impact the initial decision of owners to remove invaders, and their management decisions over time. Relative to collective management, owners managing independently will remove fewer invaders per area initially, and removal must occur over a longer time period to eradicate an invader (Fig. 1). There are differences in removal rates because owners working

TABLE 1. Dynamic optimization solutions for the initial number of invaders removed and removal rates over time under collective and independent management.

| Management scenario | Initial removal   | Removal over time  |
|---------------------|---|--|
| Collective          | $C'_{H_i}(H_i) = \frac{\omega_h - C'_{P_j}(P_j)G_{y_i}^{y_j} + C'_{H_j}(H_j)G_{y_i}^{y_j}}{(\rho - G_{y_i}^{y_i})}$ | $\frac{dH_i}{dt} = \theta_h + \frac{C'_{P_j}(P_j)G_{y_i}^{y_j} - C'_{H_j}(H_j)G_{y_i}^{y_j}}{C'_{H_i}(H_i)}$ |
| Independent         | $C'_{H_i}(H_i) = \frac{\omega_h}{(\rho - G_{y_i}^{y_i})}$   | $dH_i/dt = \theta_h$   |

Notes: The number of invaders removed was determined where the marginal costs from removal equaled the marginal benefits. Dynamic optimization solutions for planting natives are provided in Appendix B. Under collective management, owners work cooperatively as a group by incorporating the negative effects of invasive plant spread in management decisions, whereas under independent management, owners ignore the negative effects of invasive plant spread. Variable definitions are:  $C_H$  and  $C_P$ , cost functions;  $H_i$ , number of invaders removed each period in property  $i$ ;  $P_i$ , number of natives planted each period in property  $i$ ;  $G$ , native and invasive growth function;  $\rho$ , discount rate;  $\omega_h$ , variable used to simplify the optimal removal equations where  $\omega_h = D'_i(y_i) - C'_{P_i}(P_i)G_{y_i}^{x_i}$ ; and  $\theta_h$ , variable used to simplify the optimal removal equations where  $\theta_h = \{[C'_{H_i}(H_i)]/[C'_{H_i}(H_i)]\}(\rho - G_{y_i}^{y_i}) - [\omega_h/C'_{H_i}(H_i)]$ . Definitions of the subscripts are:  $i, j$ , properties 1 and 2;  $h$ , represents that we are indicating  $\omega$  and  $\theta$  in the optimal removal conditions;  $x$ , number of individuals of native; and  $y$ , number of individuals of invader.

independently fail to recognize that invaders are spreading among properties, and thus, their removal rate does not take into account this invasive plant spread.

Differences in removal rates between collective and independent management will affect net benefits. Collective management experiences higher removal costs initially compared to independent management because of higher invader removal rates. However, higher initial removal costs under collective management are offset by an increase in net benefits over time. The increase in net benefits is associated with reduced damages from invaders and a greater abundance of natives over a shorter time period. The trade-off between the ecological benefits of removal and the economic costs of doing so will determine whether collective or independent management has larger net benefits.

*Economic policy instruments*

Based on the theoretical bioeconomic model, independent management should result in more invaders and fewer natives relative to collective management averaged over time. To resolve this issue of insufficient management by owners working independently (Fig. 1), we introduced a penalty and subsidy into the model that influence removal and planting rates, respectively. In the independent-management scenario, we introduced (1) a per capita penalty on the invader ( $t_i$ ) to account for the negative externality of invader spread onto adjacent properties. The penalty behaves like a Pigouvian tax by charging owners for the damages associated with invasive plant spread onto adjacent property, and charging for those damages may encourage invasive plant removal. Pigouvian taxes are levied to correct for negative externalities, and in this case, the negative externality is invasive plant spread. We also introduced (2) a per capita subsidy ( $s_i$ ) on planting natives to account for the positive externality of native spread onto adjacent properties. The model could be modified for penalties or subsidies to be applied per unit biomass or area rather than per individual.

The penalty and subsidy necessary to encourage independently managed properties to work collectively are given by the following (for derivations, see Appendix A):

$$t_{it} = C'_{P_j}(P_{jt})G^{y_{jt}}_{y_{it}} - C'_{H_j}(H_{jt})G^{y_{jt}}_{y_{it}} \quad (3)$$

$$s_{it} = C'_{P_j}(P_{jt})G^{x_{jt}}_{x_{it}} - C'_{H_j}(H_{jt})G^{x_{jt}}_{x_{it}}. \quad (4)$$

The penalty and subsidy are derived from the damages and benefits accruing to neighboring properties and should, in theory, lead to lower numbers of invaders and higher numbers of natives over time. It is important to note that, as the population sizes of invaders and natives change over time, the marginal damages and benefits from plant spread will also change. Therefore, the penalty/subsidy will decline over time as the optimal

control strategy is achieved. Adding these per capita penalties and subsidies to the independent-management scenario ensures that the independent outcome is equal to the collective outcome. Subsidizing the cost of planting has fiscal implications, but could come in the form of coupons or reduced fees for purchasing native plants. Moreover, because we propose a program with both penalties and subsidies, some of the funds derived from levying penalties could be used to pay for subsidies.

APPLICATION OF THE BIOECONOMIC MODEL:  
CASE STUDY USING *LINARIA VULGARIS*

We applied the bioeconomic model and economic policy instruments to invasive plant management using *L. vulgaris* in Colorado, USA. *L. vulgaris* originated in Eurasia and was introduced into North America at least 300 years ago (Saner et al. 1995). It is considered a noxious weed in natural areas and rangelands in the Rocky Mountain west (Lajeunesse 1999), although it is not considered highly invasive in eastern North America.

*Study system*

*Linaria vulgaris* is a rhizomatous perennial and reproduces sexually as an obligate outcrosser (Arnold 1982). Ramets vary in the number of seeds they produce, ranging from 0 to 6000 seeds per year (reviewed in Saner et al. [1995]). Over 80% of seeds fall within 0.5 m of the parent plant with seed viability <40% (Nadeau and King 1991). Seeds can remain dormant in the soil for a number of years prior to germination (Carder 1963). *L. vulgaris* also reproduces vegetatively through the production of adventitious shoots from the main and lateral roots. In the model below, we focused on *L. vulgaris* ramets (hereafter referred to as *L. vulgaris* plants for simplicity) because ramets are extensively connected underground and it is not possible to identify genets in the field. Genet dynamics have been successfully described by ramet dynamics in other systems (Caswell 1986, but see Munzbergova et al. 2005), and there is strong competition for resources among ramets even in the same genet, suggesting low clonal integration (Hellström et al. 2006).

Although *L. vulgaris* was likely originally introduced as an ornamental and may have some folk medicinal properties (reviewed in Mitich [1993], Saner et al. [1995], and Sing and Peterson [2011]), there are negative ecological and economic impacts following *L. vulgaris* invasion. Ecological impacts include reducing native plant richness and evenness as well as native floral abundance (Wilke and Irwin 2010). Changes in native plant communities associated with *L. vulgaris* can increase soil erosion, surface runoff, and sediment yield (Lajeunesse 1999). Moreover, *L. vulgaris* is mildly poisonous to some wildlife and to cattle (Mitich 1993), and may serve as a reservoir of pathogens for some crop and ornamental species (Rist and Lorbeer 1989). These

TABLE 2. Definitions, units, and values of parameters used in the empirical bioeconomic model for the case study of *Linaria vulgaris* (case study) and the range of values used in the sensitivity analysis (range of values).

| Symbol     | Definition   | Units  | Case study | Range of values |
|------------|--|--|------------|-----------------|
| $r_{x_i}$  | native intrinsic growth rate                           | plants·plant <sup>-1</sup> ·yr <sup>-1</sup> | 0.06       | 0.01005–0.157   |
| $r_{y_i}$  | invasive intrinsic growth rate                         | plants·plant <sup>-1</sup> ·yr <sup>-1</sup> | 0.622      | 0.09–0.77       |
| $K_{x_i}$  | native plant carrying capacity                         | plants/m <sup>2</sup>                        | 90         | 36–372          |
| $K_{y_i}$  | invasive plant carrying capacity                       | plants/m <sup>2</sup>                        | 120        | 46–486          |
| $a_{xy}^i$ | competition coefficient of invasive on native          | ...  | 2.5        | 0–3.6           |
| $a_{yx}^i$ | competition coefficient of native on invasive          | ...  | 0.001      | 0–2.5           |
| $m_{x_j}$  | per capita native dispersal from plot $j$ to plot $i$  | plants·plant <sup>-1</sup> ·m <sup>-2</sup>  | 0.54       | 0.12–1.52       |
| $m_{y_j}$  | per capita invader dispersal from plot $j$ to plot $i$ | plants·plant <sup>-1</sup> ·m <sup>-2</sup>  | 0.05       | 0.0077–0.151    |
| $b_i$      | benefit per native plant                               | \$/plant                                     | 1          | 0.40–3.4        |
| $d_i$      | damage per invasive plant                              | \$/plant                                     | 0.00472    | 0.0023–0.0218   |
| $C_{P_i}$  | cost of planting per native                            | \$/plant                                     | 0.40       | ...             |
| $C_{H_i}$  | cost of removal per invader                            | \$/plant                                     | 0.19       | 0.0095–0.330    |
| $\rho$     | discount rate  | \$/plant                                     | 0.075      | ...             |

Notes: Benefits, costs, and damages per plant (in U.S. dollars) were considered on a per-plant-density basis to control for area when included in the model. Descriptions of how the values were calculated and the data used are in Appendix C. Ellipses indicate no units or no range of values.

ecological impacts have the potential to translate into economic consequences for property value and local farming and ranching (Lacey and Olsen 1991, Sing and Peterson 2011). Moreover, many regions in the Rocky Mountains rely on their natural landscapes with diverse native flowering displays for the tourism industry.

In Colorado, where much of the fieldwork to parameterize the model was conducted, *L. vulgaris* is currently managed under the Colorado Noxious Weed Act (List B), which encourages management to stop further spread. To ensure the act is adhered to, weed coordinators and management plans have been established to assist landowners with invasive plant identification and removal strategies and promote invasive plant education (Hershendorfer et al. 2007). However, the change in the number of acres with *L. vulgaris* from 2002 to 2005 increased in counties with >50% privately owned land compared to counties dominated by public land ( $t_{20,15} = 2.92$ ,  $P < 0.008$ ; data from Colorado Department of Agriculture, Lakewood, Colorado, USA; data available online),<sup>2</sup> suggesting that additional policies, such as the penalty and subsidy described here, may be needed for more effective control of *L. vulgaris* on private property.

*Parameterizing the bioeconomic model*

*Ecological component.*—To take into account intra- and interspecific competition, we used a modified Lotka-Volterra competition model to describe the competitive relationship between *L. vulgaris* and a representative native species. We realize that this competition model represents a simplification of how intra- and interspecific competition regulate changes in population size; nonetheless, it provides a starting point for understanding how ecology and economics can be integrated to

understand invasive plant management, and more complex models can be incorporated in future work. On property  $i$ , the population sizes of the native,  $x_i$ , and *L. vulgaris*,  $y_i$ , grow according to the following two equations:

$$\frac{dx_i}{dt} = r_{x_i}x_i \left( 1 - \frac{x_i + a_{xy}^i(y_i + m_{y_j}y_j)}{K_{x_i}} \right) + m_{x_j}x_j + P_i$$

$$\frac{dy_i}{dt} = r_{y_i}y_i \left( 1 - \frac{y_i + a_{yx}^i(x_i + m_{x_j}x_j)}{K_{y_i}} \right) + m_{y_j}y_j - H_i$$

The intrinsic growth rate of the native and *L. vulgaris* is represented by  $r_{x_i}$  and  $r_{y_i}$ , respectively. Carrying capacity enters the model for the native as  $K_{x_i}$ , and *L. vulgaris* as  $K_{y_i}$ . The competition coefficients of *L. vulgaris* on the native and the native on *L. vulgaris* are represented as  $a_{xy}^i$  and  $a_{yx}^i$ , respectively. We include the movement of native and invasive plants between properties as  $m_{x_j}$  and  $m_{y_j}$ , respectively. Movement between the two properties occurs via dispersal of seeds and is represented as the expected per capita dispersal and establishment of seeds onto the adjacent property. For simplicity, we ignored the movement of the invader among properties via vegetative growth, but such life history could be incorporated in future modeling efforts.

To parameterize the ecological components of the model, we used values from field or greenhouse studies specific to *L. vulgaris* in Colorado and average values from natives that commonly occur in areas where *L. vulgaris* grows (Table 2; Appendix C). If parameter estimates were not available, we used average values from the literature for *L. vulgaris* growing in other regions or for invaders with similar life history characteristics as *L. vulgaris*.

*Economic component.*—We used functions for the economic components of the model based on theory and empiricism in economics. For the economic benefits, we

<sup>2</sup> [http://www.colorado.gov/cs/Satellite?c=Page&childpagename=ag\\_Conservation%2FCBONLayout&cid=1251629559735&pagename=CBONWrapper](http://www.colorado.gov/cs/Satellite?c=Page&childpagename=ag_Conservation%2FCBONLayout&cid=1251629559735&pagename=CBONWrapper)

assumed a saturating function,  $B_i(x_i) = 2b_ix_i^{1/2}$ , where  $b_i$  is the benefit per native plant (Weitzman 1978, Rollins and Lyke 1998). Damages from *L. vulgaris* and the economic costs of removing *L. vulgaris* and planting natives were represented by accelerating functions with

$$D_i(y_i) = \frac{d_i y_i^2}{2}$$

where  $d_i$  is the damage per unit of invader (Olson and Roy 2002)

$$C_{H_i}(H_i) = \frac{C_{H_i} H_i^2}{2}$$

where  $C_{H_i}$  is the cost of removing an individual invader, and

$$C_{P_i}(P_i) = \frac{C_{P_i} P_i^2}{2}$$

where  $C_{P_i}$  is the cost per native planted (Hueth and Regev 1974, Weitzman 1978). To parameterize the economic components of the model, we calculated values from data specific to Colorado and/or from the other areas when region-specific data were not available from valuation studies in the published literature and personal interviews (Table 2; Appendix C). We recognize that estimating the economic benefits of natives and damages and removal costs of invaders is difficult (Olson 2006, McIntosh et al. 2009) and had to make some simplifying assumptions. For example, we assumed that owners did not receive any aesthetic value from the presence of *L. vulgaris* and *L. vulgaris* removal was successful and did not result in nontarget effects such as invasion of other nonnative species. Benefits were calculated from factors such as the aesthetic value of native plants (using a replacement-cost approach) and an increase in property value associated with natives (Appendix C). A number of approaches have been used to estimate the economic damages from invaders, but no single approach has been widely accepted (Olson 2006). We calculated damages as direct, measurable economic effects caused by *L. vulgaris* or other invaders (Appendix C).

#### Bioeconomic model simulation

Simulations were generated using the mathematical programming system GAMS (General Algebraic Modeling System; *available online*)<sup>3</sup> based on the ecological and economic data in Table 2. One limitation of our simulations is that we did not incorporate error in our parameter value estimates; however, the sensitivity analysis (see *Sensitivity analysis* below) allowed us to assess how sensitive our model results were to variation in model parameters. We ran the simulations over a 12-year period, the national average time period of household property ownership (Emrath 2009), and over

longer time periods in some cases to capture longer returns on land investment. All values involving invader and native abundance were calculated on a per-area basis (per square meter) to control for property size, and we assumed that a property had a homogeneous density of *L. vulgaris*. Including more complicated spatial structure of properties and spatially varying *L. vulgaris* densities within properties was beyond the scope of this model, but could be assessed in future work. Using the model specified for owners  $i$  and  $j$ , we ran simulations to explore the optimal removal and planting strategies across a range of initial *L. vulgaris* densities, from 2 to 120 *L. vulgaris*/m<sup>2</sup> and assuming an initial 15 natives/m<sup>2</sup>. These densities of *L. vulgaris* and natives are representative of what is found in nature (Nadeau et al. 1991, Pauchard et al. 2003, Egan and Irwin 2008, Wilke and Irwin 2010). We present simulation results from representative low, moderate, and high densities of *L. vulgaris* invasion (5, 30, and 60 plants/m<sup>2</sup>, respectively). Penalties were applied based on *L. vulgaris* densities (*L. vulgaris*/m<sup>2</sup>), which is a measure of abundance that is more robust than area infested and simpler to estimate than biomass.

In the model, owners chose between eradication, control, and no action based on the net benefits. Eradication occurred when its net benefits were greater than the net benefits of control. Likewise, owners chose to control when its net benefits were greater than the net benefits of no action. The simulations assumed that each property had identical numbers of *L. vulgaris* and ecological and economic conditions (homogenous properties), or different numbers of *L. vulgaris* on each property (heterogeneous properties). For simulations involving homogeneous properties, the ecological and economic impacts to the properties were the same, and so we only present results from one of the properties. Using the simulations, we examined the conditions under which collective vs. independent management provided similar or better control or eradication of *L. vulgaris*, and we explored the economic policies (e.g., penalties or subsidies) needed to ensure owners managed or contained the invader.

#### Results and discussion of the case study

Our empirical data show that the competition coefficient of the native on *L. vulgaris* was near zero (Table 2; Appendix C), indicating that the competitive effect of natives on *L. vulgaris* was negligible. Thus, planting natives as a form of control was not optimal in the model. This result is not surprising, given that invasive plants are often competitively dominant in their new range (Vilà and Weiner 2004, Ridenour et al. 2008), and the rare instances where natives are used to competitively exclude invaders often involve native grasses (Prather et al. 1991, Bakker and Wilson 2004). Thus, the results we describe only focus on controlling *L. vulgaris* via removal, and not planting natives nor subsidizing the cost of planting natives.

<sup>3</sup> <http://www.gams.com/>



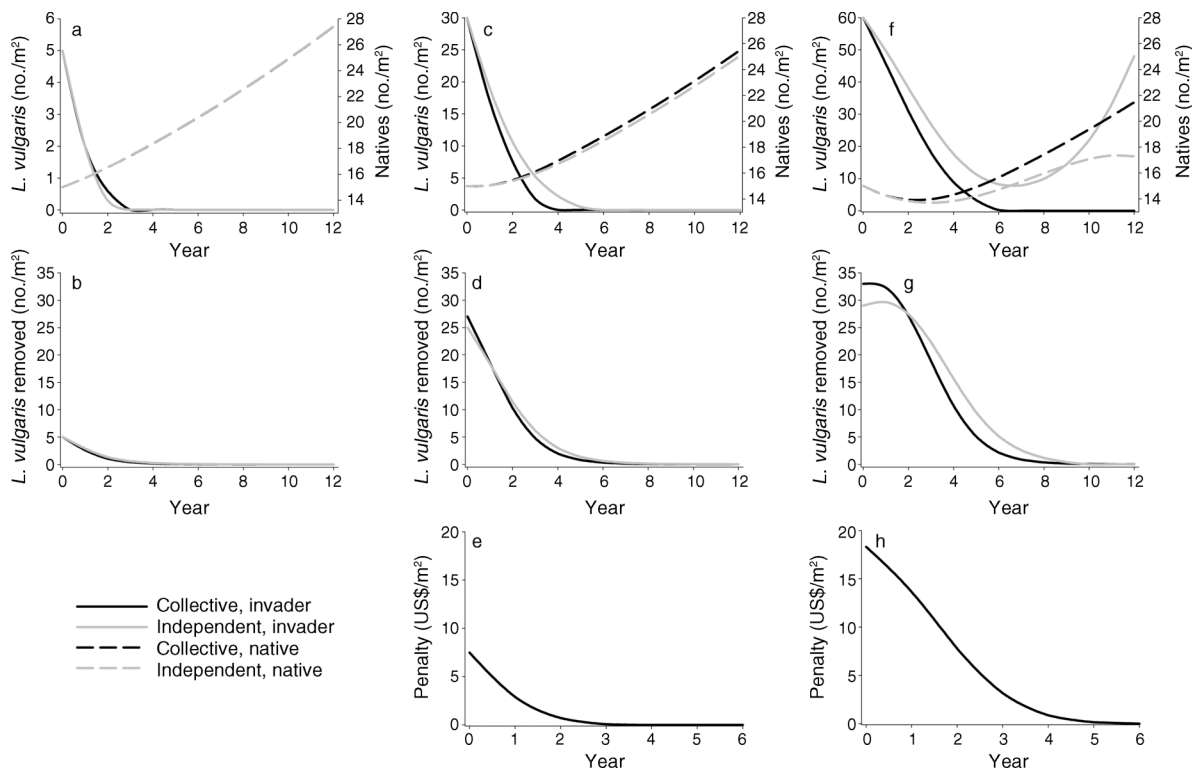


FIG. 2. Homogeneous properties: optimal management strategies varied as a function of initial *Linaria vulgaris* density. At low *L. vulgaris* density (5 invaders/m<sup>2</sup>), (a) the density of *L. vulgaris* (left-hand axis) and natives (right-hand axis) over time and (b) the *L. vulgaris* removal rate were nearly identical for collective and independent management. At moderate *L. vulgaris* density (30 invaders/m<sup>2</sup>), (c, d) owners managing collectively removed more *L. vulgaris* initially and eradicated the invader faster than owners managing independently, but (e) a penalty can be implemented to ensure that independent properties remove *L. vulgaris* at the same rate as collective management. At a high density (60 *L. vulgaris*/m<sup>2</sup>), (f, g) owners managing collectively eradicated *L. vulgaris*, but those managing independently changed their management decision from control to no action, requiring (h) a penalty that would encourage collective management. Note the different y-axis scales in panels (a), (c), and (f).

*Homogenous properties*

*Low invader density.*—Owners managing collectively or independently responded similarly to low densities of *L. vulgaris* (<7 plants/m<sup>2</sup>; Fig. 2a, b). Under both management strategies, it was optimal to eradicate *L. vulgaris* within the first two years because the benefits of removal outweighed the costs. In addition, the net benefits of the two management strategies measured in dollars per square meter were almost identical (Fig. 3a); in part, because movement of *L. vulgaris* was low between properties at low invader densities. Thus, ignoring movement between properties (i.e., independent management) had little effect on *L. vulgaris* eradication. For both collective and independent management, native plants experienced minimal competition with *L. vulgaris*, and native population sizes were nearly identical under both management strategies (Fig. 2a). These results highlight the importance of detecting and removing invaders early in the invasion process before they reach high densities (Simberloff et al. 2005). Management that focuses on invasive plant identification and early removal may have the strongest economic and ecological benefits (Olson and Roy 2002, Pluess et

al. 2012), and also does not depend on invoking collective- or independent-management strategies. Because collective and independent management resulted in eradication over a similar time period, no penalty to encourage removal was necessary.

*Moderate invader density.*—At moderate densities (7–59 *L. vulgaris*/m<sup>2</sup>), we found small differences between collective and independent management in both the rate of *L. vulgaris* removal and the time period over which removal occurred (Fig. 2c, d). However, both management strategies chose eradication over control or no action based on net benefits (Fig. 3b).

The simulations for moderate *L. vulgaris* density matched the theoretical predictions, with independent management removing *L. vulgaris* at a lower initial rate than collective management; and thus, independent management had to remove the invader over a longer time period (Fig. 2c, d). The additional time required for *L. vulgaris* removal under independent management occurred because the removal rate did not take into account movement of the invader between properties. Averaged over the 12-year period, properties managed independently had 19% more invaders and 1.3% fewer

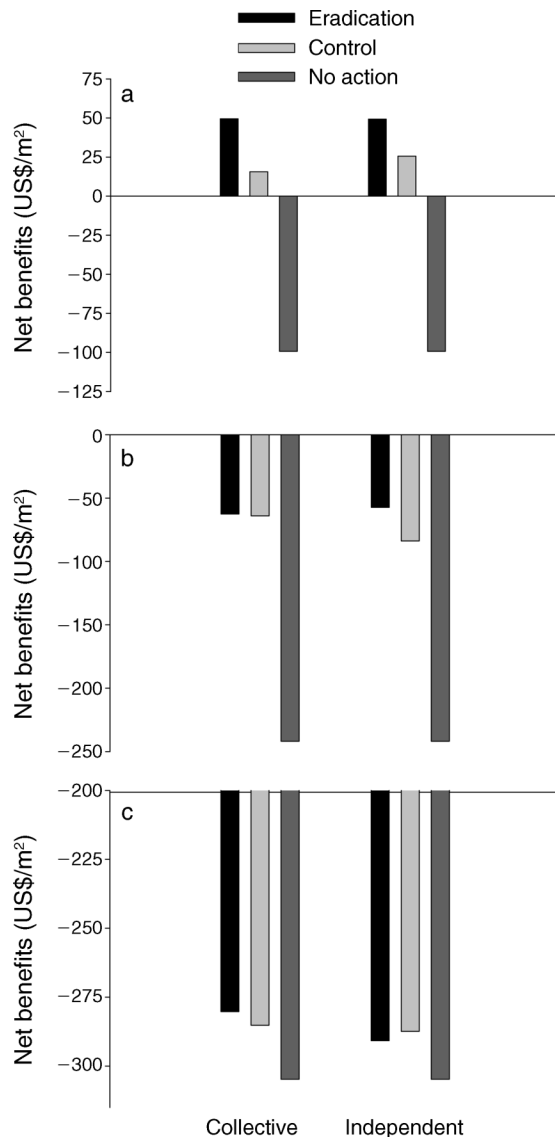


FIG. 3. Average net benefits per square meter over a 12-year period for homogeneous properties with (a) low, (b) moderate, and (c) high initial densities of *L. vulgaris*, assuming collective vs. independent management. Average net benefits were calculated assuming eradication (removal of the invader from property), control (removing some invaders but not enough for eradication), and no action (do nothing) scenarios. Low, moderate, and high *L. vulgaris* densities were 5, 30, and 60 plants/m<sup>2</sup>, respectively.

natives compared to those managed collectively. Thus, even the small differences in the time period required for collective vs. independent management to eradicate *L. vulgaris* (1 year; see Fig. 2c) can result in *L. vulgaris* being present on the landscape longer and in sufficient quantities to have ecological and economic consequences. One caveat to consider in the interpretation of these results is that, over the 12-year simulation period, the net benefits of eradication in both collective and

independent management were negative, although they were less negative if owners chose eradication over no action (Fig. 3b). Positive net benefits of eradication would only be accrued over longer time periods. In this simulation, it took ~23 years to see positive net benefits from eradication. Thus, invasive species management may be better thought of as a long-term investment, similar to capital improvements that have high initial costs, with positive net benefits accrued over long time periods (Andersson and Jacobsson 2000).

At moderate *L. vulgaris* densities, the longer time period required for eradication and the higher average *L. vulgaris* density over time (Fig. 2c, d) suggest that properties managed independently should be encouraged to work collectively, which can be achieved via a penalty. The penalty per *L. vulgaris* is dependent upon the density of *L. vulgaris* and its rate of removal in both properties (Eq. 3). The penalty decreases over time as the number of *L. vulgaris* decrease due to removal. Assuming an initial density of 30 *L. vulgaris*/m<sup>2</sup>, the penalty in the first year would be \$7.49/m<sup>2</sup> (in U.S. dollars), declining as a decelerating function until all *L. vulgaris* are removed (Fig. 2e). One caveat is that the penalty necessary to ensure collective management is extremely high when calculated per acre, in part because of the high densities of the invader, and because we assumed that the entire parcel has a homogeneous density of the invader. Thus, a penalty may be more financially and ecologically reasonable when applied on a linear scale to property borders (i.e., perimeter) rather than an areal scale, also in part because property borders are more likely to donate seeds to neighboring properties. Moreover, focusing on property borders is important because two properties with identical area can differ substantially in property border length depending on their shape. When applied on property borders, the penalty may create barrier zones to contain the invasion or reduce the spread to new areas along the growing invasion front (Sharov and Liebhold 1998). Future research would need to generate the optimal framework to identify efficient cycles of investment in barrier zones that are nested within a larger management area.

*High invader density.*—Collective and independent scenarios resulted in different management outcomes at high invader densities. For example, at densities of 60–61 *L. vulgaris*/m<sup>2</sup>, collective management was optimal for eradicating *L. vulgaris*, whereas independent management was only optimal for controlling the invasion (Fig. 3c). Owners managing collectively eradicated *L. vulgaris* by year 7, allowing for the population size of natives to grow without continued competition with *L. vulgaris* (Fig. 2f, g). However, under independent management, the number of *L. vulgaris* initially declined, but eventually increased toward its carrying capacity because (1) the removal rate did not keep up with the movement of *L. vulgaris* from the neighboring property and (2) the owners changed their management decision from control to no action because the costs of

removal became too high relative to its benefits (Fig. 3c). As a result, natives experienced strong competition from *L. vulgaris*, and any initial benefits of *L. vulgaris* removal for native population size were overwhelmed by strong competition with the invader at later time periods (Fig. 2f). Averaged over the 12-year period, collective management resulted in 51% fewer *L. vulgaris* and 7.6% more natives than independent management. To encourage properties managed independently to work collectively, a penalty could be implemented for an initial invasion of 60 *L. vulgaris*/m<sup>2</sup> and decline at a decelerating rate over time until all *L. vulgaris* are removed (Fig. 2h). Here, the penalty is important to ensure that independently managed properties do not continue to act as propagule sources within the landscape (Epanchin-Niell et al. 2010).

The ability of collective- and independent-management strategies to control or eradicate *L. vulgaris* at very high densities was limited. We found that for densities >63 *L. vulgaris*/m<sup>2</sup>, it was optimal for properties managed either collectively or independently to do nothing. No action occurred because the costs of removal strongly outweighed any benefits. This finding was consistent over a range of densities of natives. The inability of collective or independent management to control *L. vulgaris* at very high densities is relevant because many areas with established *L. vulgaris* report densities this high (reviewed in Saner et al. [1995]). For these high densities of invaders where it was optimal to do nothing, a fine could be implemented on the negative externality of *L. vulgaris* movement to neighboring properties. Because the goal is to reduce *L. vulgaris* spread, a fine applied to the property edge would be most appropriate (Sharov and Liebhold 1998). We can base the fine on the number of *L. vulgaris*/m<sup>2</sup> multiplied by the per capita *L. vulgaris* dispersal among properties ( $m_{yij}$ ) and the per capita cost of invader removal ( $c_{H_2}$ ). Because most *L. vulgaris* seeds do not disperse further than 0.5 m, a 1-m<sup>2</sup> border around a parcel could provide some containment of the invader. Doing so for a density of 120 *L. vulgaris*/m<sup>2</sup> around a 0.4-ha (1-acre) square parcel totals ~\$278. It is important to note that this fine simply discourages invasive species spread among properties by fining owners based on the number of *L. vulgaris* that would spread to neighboring properties, and the cost of removing those spreading plants when the optimal management strategy is no action.

#### *Heterogeneous properties*

When we examined properties with different initial densities of *L. vulgaris*, we found two important outcomes. First, variation in invader densities across the landscape can result in different management strategies. For example, an unequal number of *L. vulgaris* on adjacent properties can lead to unilateral eradication when one owner chooses control or no action and the other chooses eradication. An example of unilateral eradication occurs when adjacent properties

have low and high densities of *L. vulgaris* (e.g., 5 vs. 60 *L. vulgaris*/m<sup>2</sup>). Based on the net benefits, the owner with low invader density eradicates *L. vulgaris* under both collective and independent management (Fig. 4a, b). However, the owner with high invader density will only eradicate under collective management (Fig. 4c, d). Owners managing independently initially remove *L. vulgaris*, but the removal rate does not keep pace with population growth, so the owner eventually chooses no action given the high costs of removal. Thus, *L. vulgaris* would continue to spread to neighboring properties, making a formal economic policy important. Our penalty to encourage collective management (Eq. 3) is applicable in these heterogeneous environments and can be applied under unilateral eradication to force owners managing independently to eradicate *L. vulgaris* as if they were behaving collectively (Fig. 4e).

Second, different densities of *L. vulgaris* on adjacent properties also altered the removal rate of *L. vulgaris* compared to homogeneous densities. For example, under collective management, initial removal on the property with 60 *L. vulgaris*/m<sup>2</sup> was 9% lower when densities were heterogeneous (60 and 5 *L. vulgaris*/m<sup>2</sup> on each property) compared to homogenous (60 *L. vulgaris*/m<sup>2</sup> on both properties). The lower initial removal rate occurs in the heterogeneous scenario for owners working collectively because they recognize that fewer *L. vulgaris* are spreading to their property from the neighboring property. However, this lower initial removal rate results in a longer removal period for eradication. Consequently, the total number of *L. vulgaris* removed over the 12-year period in a heterogeneous landscape is 8.5% higher than the homogenous setting. Because heterogeneous densities of invaders are common across landscapes subdivided into individually owned properties (Epanchin-Niell et al. 2010), economic policies that can encourage increased coordination among owners may provide the best management success.

#### SENSITIVITY ANALYSIS

To gain additional intuition from the model, we conducted a sensitivity analysis in which we varied the ecological and economic parameters in the model using realistic ranges of values (Table 2; Appendix C). We varied one parameter at a time to explore its effects on the model output. We focused on results from homogeneous properties and determined the range of initial *L. vulgaris* densities for which owners chose eradication, control, or no action based on the maximum net benefits.

In most of the sensitivity analyses, collective management outperformed independent management in terms of the maximum number of invaders that could be eradicated under different model parameters (Appendix D), as well as the net benefits accrued when comparing eradication vs. control vs. no action. Thus, we primarily highlight how modifying model parameters affected removal costs, net benefits, and the possibility for eradication.

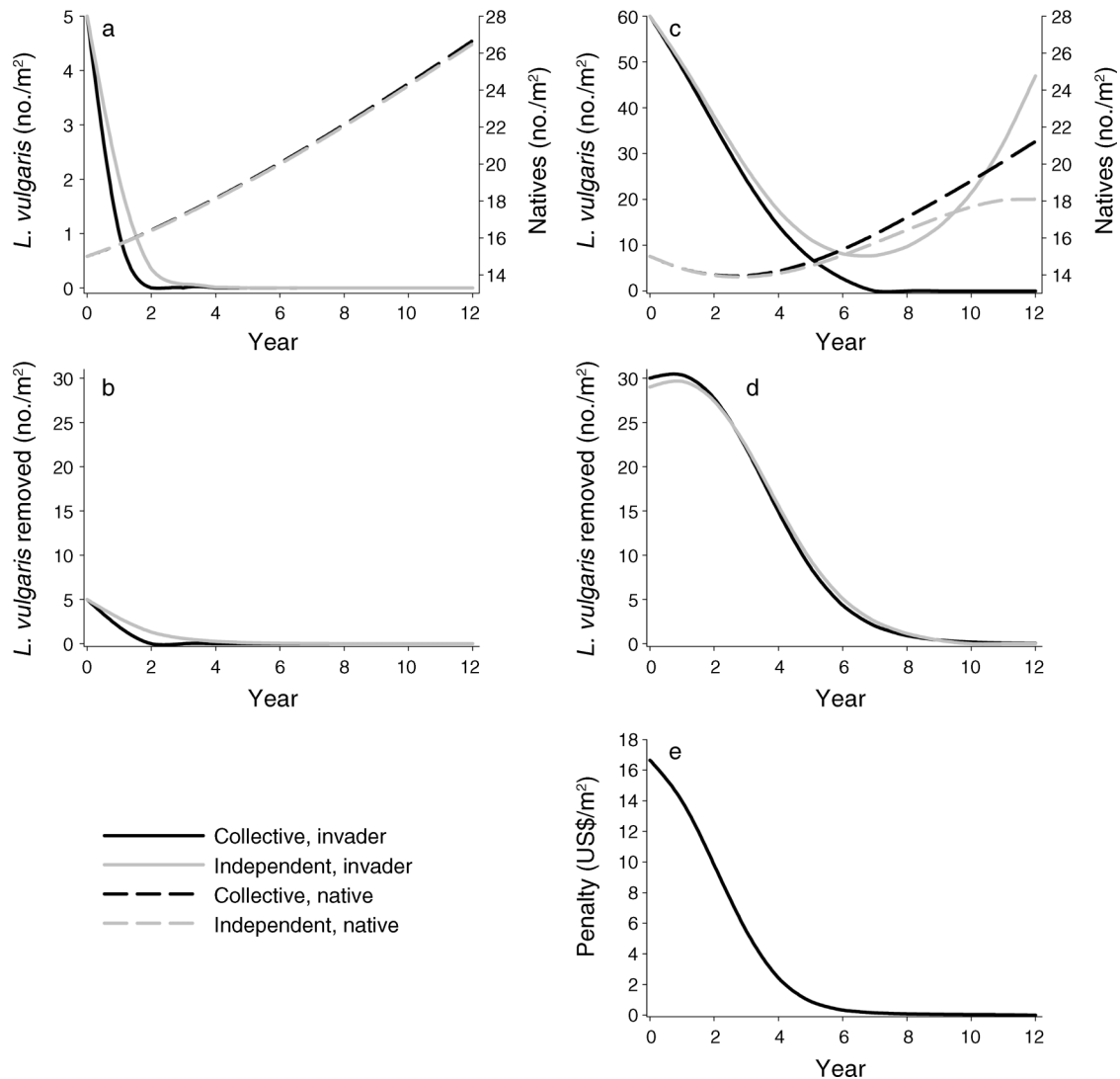


FIG. 4. Heterogeneous properties: optimal removal strategies for properties with (a, b) low (5 plants/m<sup>2</sup>) and (c, d) high (60 plants/m<sup>2</sup>) *L. vulgaris* densities, illustrating unilateral removal and (e) a property-specific economic policy to hold the high-invasion property to a collective standard. Note the different *y*-axis in panels (a) and (c).

#### Ecological parameters

Varying the ecological parameters of the model had some intuitive and some surprising results. Altering native plant parameters, including the intrinsic growth rate  $r_{x_i}$ , carrying capacity  $K_{x_i}$ , and movement  $m_{x_{ij}}$ , had little impact on the optimal removal rates of *L. vulgaris* and the net benefits from eradication, in part because *L. vulgaris* has a strong competitive effect on native plants and natives have a weak effect on *L. vulgaris*. These results suggest that the population biology of native plants may not rescue them from the harmful effects of invaders if their competitive abilities are low.

The one native plant parameter that influenced management outcomes was the competitive effect of natives on *L. vulgaris*,  $a_{yx}^i$ . Increasing this competition coefficient decreased the probability of eradication while

increasing the probability of control. Highly competitive natives were able to decrease the population growth of the invader, resulting in reduced damages and removal costs, thus making the net benefits of control higher than eradication. When  $a_{yx}^i = 1.50$ , both collective and independent management controlled up to 120 *L. vulgaris*/m<sup>2</sup>; double the amount when compared to  $a_{yx}^i = 0$ . This result highlights the value of competitively strong natives for assisting in control and lowering the cost of invasive species management. However, one challenge will be identifying native plants with strong competitive abilities against invaders. The majority of native plants in invaded communities are likely weak competitors with invaders on a pairwise basis (Vilà and Weiner 2004); however, screening programs that take a landscape-scale approach to identify the composition of

native plant communities with low invasion rates may be a good starting point (Bakker and Wilson 2004).

Not surprisingly, increasing the intrinsic growth rate  $r_{yi}$ , carrying capacity  $K_{yi}$ , and competitive ability of the invader  $a'_{xy}$ , resulted in higher removal rates of the invader and lower probability of eradication. However, modifying the movement of *L. vulgaris* ( $m_{yji}$ ) affected the decision to eradicate the invader depending on invader density for collective, but not independent management. At low-to-moderate densities of the invader, increasing  $m_{yji}$  resulted in a decrease in *L. vulgaris* and an increase in natives over time for owners working collectively. The driver behind this counterintuitive result is that higher movement of the invader implies larger benefits from removing the invader to prevent its spread onto adjacent properties. This result suggests that working collectively may have the greatest benefits for invasive species that spread easily. However, this is only the case at low-to-moderate invader densities. For high densities of the invader with high values of  $m_{yji}$ , the economic costs from invader removal become so high that they outweigh any benefits under collective management, and as a result, owners managing collectively will choose to do nothing. Properties managed independently, however, do not recognize the additional benefits of reducing the spread of the invader, and thus, do not adjust their decisions based on changes in movement of the invader at any plant density.

#### *Economic parameters*

Varying the economic parameters provided insight into the role of government assistance for controlling and eradicating invaders. As we increased the benefit per native relative to the costs of invader removal, it became optimal to eradicate *L. vulgaris* over larger initial densities. Larger benefits from natives are able to offset the costs of greater invader removal rates. For example, under collective management, the likelihood of eradication increases by 10% when the per capita economic benefits of natives triple. Moreover, lower costs of *L. vulgaris* removal increase eradication possibilities. If we reduced removal costs by 73%, then it always became optimal to eradicate the invader. These results are similar to Grimsrud et al. (2008), who found that, if 75% of the costs of removal of the invader are shared between owners, then eradication at higher invader densities can occur. These results highlight that penalties are not the only economic policy useful for invasive species control. Accurate valuation of native species can be equally important. Also, government assistance to subsidize the cost of removal may be an important alternative (Dehnen-Schmutz et al. 2004).

We also examined the effect of damages by the invader on the model output. We found that reducing damages lead to lower likelihood of invader eradication due to the costs of removal, and conversely, increasing economic damages primarily lead to higher likelihood of eradication. Thus, educating owners about the damages

they incur from invaders on their property may encourage management when the damages associated with invaders are high relative to the costs of removal (Wittenberg and Cock 2001). Moreover, research is needed that links ecological impacts of an invader to their economic damages to identify invaders with the greatest ecological and economic impacts to target for management with economic policies.

#### CONCLUSIONS

Here we used a bioeconomic model to illustrate that economics can be used to guide invasive species management. By developing a model with ecological, economic, and human social parameters, we were able to identify the conditions under which eradication of invasive species resulted in the highest net benefits, how managing adjacent properties collectively or independently can affect native and invader population sizes, and explored whether economic policy instruments (penalties and subsidies) can be used to encourage invasive species management. Our results have four policy implications for invasive plant management.

First, our results indicate that owners will experience the highest net benefits if they eradicate the invader at low plant densities, highlighting the importance of detecting and removing invaders early in the invasion process. Thus, policies that develop programs in invasive plant identification, removal, and their ecological and economic damages may have the greatest management impacts. This result mirrors a recent analysis suggesting that eradication campaigns against invaders are most successful at low invader densities early in the invasion process (Pluess et al. 2012). In a similar vein, invasive plant education programs targeted at the expanding edge of plant invasions or in small satellite populations may have the greatest management impacts (Moody and Mack 1988, Sharov and Liebhold 1998).

Second, our numerical simulations suggest that economic policy instruments, such as penalties or fines on property boundaries, could be useful for changing human behaviors about invasive plant management on private property. Our work is novel in that it introduces a formal penalty, which to our knowledge has been rarely done for invasive species management around property boundaries, and it may be useful for agencies overseeing large amounts of land with multiple users that also differ in shape and hence, the length of property borders. Although the model requires measurements of plant density, management agencies could focus on specific categories of invasive plant density (i.e., low, medium, and high) that could be assessed quickly and visually, yet would be more quantitative than using area infested. It is likely that any campaign for invasive plant management through penalties will only be successful at a local scale (similar to Pluess et al. 2012), given that economic costs and benefits, weeds to target, and heterogeneity in invader density will be locally or regionally specific. Moreover, qualitative

assessment suggests that local and regional coordination of stakeholders may be the most effective management scheme (Epanchin-Niell et al. 2010). Further research is needed, however, to assess appropriate appraisal and enforcement approaches of any potential economic policies. For example, as one approach, the monitoring and enforcement costs to operationalize economic policy instruments, such as penalties, could come from changing the goals of existing local weed coordinators from removal to monitoring and enforcement, as well as the penalties or fines generated from the economic policy instruments themselves. Implementing these changes would require input from policy- and lawmakers at the local and national levels.

Third, our general theoretical model and simulations demonstrate that collective management generally leads to fewer invaders and more natives than independent management at moderate invasive plant densities. Collective management accounts for the spatial relationships of biological and economic interactions in invasive plant management decisions. In addition, collective management allows for a wider range of eradication possibilities. The results highlight that invasive plant management requires social, economic, and ecological solutions. Recent qualitative studies highlight the need for coordinated control efforts across management mosaics (Epanchin-Niell et al. 2010). Our results provide quantitative insight into the economic policy instruments that could be used to encourage coordination of weed management.

Fourth, the sensitivity analysis may assist managers deciding when, where, and how much time and effort to devote to invader management. For example, some invaders may not be worthwhile to manage if the economic damages incurred are too low or the costs of removal are too high. Moreover, the sensitivity analysis suggests that penalties are not the only economic policy instrument to encourage invasive plant management on private property. A reduction in the costs of *L. vulgaris* removal would encourage eradication under both collective and independent management and across high densities of the invader. One way that costs could be reduced is by providing subsidies for removal (Dehnen-Schmutz et al. 2004). Subsidizing the cost of removal (or a government cost-sharing program) may be more politically appealing than penalties, in part due to the unpopularity of charging for compliance, but also because a subsidy or cost-sharing program does not require the economic and ecological property information required to calculate, implement, and enforce a penalty-based program (Baumol and Oates 1971, Xepapadeas 1992).

By combining economic, ecological, and social factors, we were able to develop a theoretical model and numerical simulation of how economics can guide invasive plant management. Our results provide insight into management decisions and the economic policy instruments that could encourage invasive plant removal.

Our findings suggest that economic policy instruments could be powerful tools in invasive species eradication programs. Future work will benefit from examining invasive species management policies over more than two properties and across multiple invaders simultaneously, allowing for spread and establishment uncertainty, and implementing the idea of barrier or containment zones and penalties/subsidies. The next step is to evaluate cost-effective monitoring and enforcement policies and to encourage dialog (Dietz et al. 2003) between scientists, managers, and government agencies to determine how to successfully implement economic policies to encourage invasive species removal.

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#### LITERATURE CITED

- Andersson, B. A., and S. Jacobsson. 2000. Monitoring and assessing technology choice: the case of solar cells. *Energy Policy* 28:1037–1049.
- Arnold, R. M. 1982. Pollination, predation and seed set in *Linaria vulgaris* (Scrophulariaceae). *American Midland Naturalist* 107:360–369.
- Aslan, C. E., m. B. Hufford, R. S. Epanchin-Niell, J. D. Port, J. P. Sexton, and T. M. Waring. 2009. Practical challenges in private stewardship of rangeland ecosystems: Yellow star-thistle control in Sierra Nevada foothills. *Rangeland Ecology and Management* 62:28–37.
- Bakker, J. D., and S. D. Wilson. 2004. Using ecological restoration to constrain biological invasion. *Journal of Applied Ecology* 41:1058–1064.
- Barbier, E. B., and J. F. Shogren. 2004. Growth with endogenous risk of biological invasion. *Economic Inquiry* 42:587–601.
- Baumol, W. J., and W. E. Oates. 1971. The use of standards and prices for protection of the environment. *Swedish Journal of Economics* 73:42–54.
- Bhat, M., and R. Huffaker. 2007. Management of a transboundary wildlife population: a self-enforcing cooperative agreement with renegotiation and variable transfer payments. *Journal of Environmental Economics and Management* 53:54–67.
- Brown, B. J., R. J. Mitchell, and S. A. Graham. 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* 83:2328–2336.
- Carder, A. C. 1963. Control of yellow toadflax (*Linaria vulgaris*) by grass competition plus 2, 4-D. *Weeds* 11:13–14.
- Caswell, H. 1986. The evolutionary demography of clonal reproduction. Pages 187–224 in J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. *Population biology and evolution of clonal organisms*. Yale University Press, New Haven, Connecticut, USA.
- Chiang, A. C. 1999. *Elements of dynamic optimization*. Waveland Press, Prospect Heights, Illinois, USA.
- Dehnen-Schmutz, K., C. Perrings, and M. Williamson. 2004. Controlling *Rhododendron ponticum* in the British Isles: an

- economic analysis. *Journal of Environmental Management* 70:323–332.
- Dietz, T., E. Ostrom, and P. C. Stern. 2003. The struggle to govern the commons. *Science* 302:1907–1912.
- DiTomaso, J. M. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48:255–265.
- Egan, J. F., and R. E. Irwin. 2008. Evaluation of the field impact of an adventitious herbivore on an invasive plant, yellow toadflax, in Colorado, USA. *Plant Ecology* 199:99–114.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago, Illinois, USA.
- Emrath, P. 2009. How long buyers remain in their homes. *Housing Economics*. <http://www.nahb.org/generic.aspx?sectionID=734&genericContentID=110770&channelID=311>
- Epanchin-Niell, R. S., and A. Hastings. 2010. Controlling established invaders: integrating economics and spread dynamics to determine optimal management. *Ecology Letters* 13:528–541.
- Epanchin-Niell, R. S., M. B. Hufford, C. E. Aslan, J. P. Sexton, J. D. Port, and T. M. Waring. 2010. Controlling invasive species in complex social landscapes. *Frontiers in Ecology and the Environment* 8:210–216.
- Gavier-Pizarro, G. I., V. C. Radeloff, S. I. Stewart, C. D. Huebner, and N. S. Keuler. 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications* 20:1913–1925.
- Grimsrud, K. M., J. M. Chermak, J. Hansen, J. A. Thacher, and K. Krause. 2008. A two-agent dynamic model with an invasive weed diffusion externality: an application to Yellow Starthistle (*Centaurea solstitialis* L.) in New Mexico. *Journal of Environmental Management* 89:322–335.
- Gutrich, J., et al. 2005. Science in the public process of ecosystem management: lessons from Hawaii, Southeast Asia, Africa and the US Mainland. *Journal of Environmental Management* 76:197–209.
- Hellström, K., M. M. Kytöviita, J. Tuomi, and P. Rautio. 2006. Plasticity of clonal integration in the perennial herb *Linaria vulgaris* after damage. *Functional Ecology* 20:413–420.
- Hershendorfer, M. E., M. E. Fernandez-Gimenez, and L. D. Howery. 2007. Key attributes influence the performance of local weed management programs in the southwest United States. *Rangeland Ecology and Management* 60:225–234.
- Hueth, D., and U. Regev. 1974. Optimal agricultural pest management with increasing pest resistance. *American Journal of Agricultural Economics* 56:543–552.
- Jones, R. E., D. T. Vere, and M. H. Campbell. 2000. The external costs of pasture weed spread: an economic assessment of serrated tussock control. *Agricultural Economics* 22:91–103.
- Knowler, D., and E. Barbier. 2004. Importing exotic plants and the risk of invasion: are market-based instruments adequate? *Ecological Economics* 52:341–354.
- Lacey, J. R., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3:627–631.
- Lacey, J., and B. Olsen. 1991. Environmental and economic impacts of noxious range weeds. Pages 5–16 in L. F. James, J. O. Evans, M. H. Ralphs, and R. D. Child, editors. *Noxious range weeds*. Westview Press, Boulder, Colorado, USA.
- Lajeunesse, S. 1999. Dalmatian and yellow toadflax. Pages 202–216 in R. L. Sholey and J. K. Petroff, editors. *Biology and management of noxious rangeland weeds*. Oregon State University Press, Corvallis, Oregon, USA.
- Leonard, D., and N. Van Long. 1992. *Optimal control theory and static optimization in economics*. Cambridge University Press, Cambridge, Massachusetts, USA.
- Leprieur, F., O. Beauchard, S. Blanchet, T. Oberdorff, and S. Brosse. 2008. Fish invasions in the world's river systems: When natural processes are blurred by human activities. *PLoS Biology* 6:404–410.
- Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20:223–228.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- McIntosh, C. R., D. C. Finnoff, C. Settle, and J. F. Shogren. 2009. Economic valuation and invasive species. Pages 151–179 in R. P. Keller, D. M. Lodge, M. A. Lewis, and J. F. Shogren, editors. *Bioeconomics of invasive species: integrating ecology, economics, policy, and management*. Oxford University Press, New York, New York, USA.
- McKee, G. J. 2006. Modeling the effect of spatial externalities on invasive species management. *Agribusiness and Applied Economics Report Number 583*. Agricultural Experiment Station, North Dakota State University, Fargo, North Dakota, USA.
- McKinney, M. L. 2001. Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biological Conservation* 100:243–252.
- Mitich, L. W. 1993. Intriguing world of weeds-yellow toadflax. *Weed Technology* 7:791–793.
- Moody, M. E., and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* 25:1009–1021.
- Munzbergova, Z., M. Krivanek, A. Bucharova, V. Juklickova, and T. Herben. 2005. Ramet performance in two tussock plants: do the tussock-level parameters matter? *Flora* 200:275–284.
- Nadeau, L. B., M. R. T. Dale, and J. R. King. 1991. The development of spatial pattern in shoots of *Linaria vulgaris* (Scrophulariaceae) growing on fallow land or in a barley crop. *Canadian Journal of Botany* 69:2539–2544.
- Nadeau, L. B., and J. R. King. 1991. Seed dispersal and seedling establishment of *Linaria vulgaris* Mill. *Canadian Journal of Plant Science* 71:771–782.
- Olson, L. 2006. The economics of terrestrial invasive species: a review of the literature. *Agricultural and Resource Economics Review* 35:178–194.
- Olson, L. J., and S. Roy. 2002. The economics of controlling a stochastic biological invasion. *American Journal of Agricultural Economics* 84:1311–1316.
- Olson, M. 1965. *The logic of collective action: public goods and the theory of groups*. Harvard University Press, Cambridge, Massachusetts, USA.
- Pauchard, A., P. B. Alaback, and E. G. Edlund. 2003. Plant invasions in protected areas at multiple scales: *Linaria vulgaris* (Scrophulariaceae) in the West Yellowstone area. *Western North American Naturalist* 63:416–428.
- Paynter, Q., and G. J. Flanagan. 2004. Integrating herbicide and mechanical control treatments with fire and biological control to manage an invasive wetland shrub, *Mimosa pigra*. *Journal of Applied Ecology* 41:615–629.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.
- Pluess, T., R. Cannon, V. Jarosik, J. Pergl, P. Pysek, and S. Bacher. 2012. When are eradication campaigns successful? A test of common assumptions. *Biological Invasions* 14:1365–1378.
- Prather, T. S., R. H. Callihan, and D. C. Thill. 1991. *Common crupina: biology, management and eradication*. Report CIS 880. University of Idaho, Moscow, Idaho, USA.
- Pysek, P., and D. Richardson. 2010. Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* 35:25–55.
- Rich, K. M., A. Winter-Nelson, and N. Brozovic. 2005. Modeling regional externalities with heterogeneous incentives and fixed boundaries: applications to Foot and Mouth

- Disease control in South America. *Review of Agricultural Economics* 27:456–464.
- Richards, T. J., P. Ellsworth, R. Tronstad, and S. Naranjo. 2010. Market-based instruments for the optimal control of invasive insect species. *Journal of Agricultural and Resource Economics* 35:349–367.
- Ridenour, W. M., J. M. Vivanco, Y. Feng, J. Horiuchi, and R. M. Callaway. 2008. No evidence for trade-offs: *Centaurea* plants from America are better competitors and defenders. *Ecological Monographs* 78:369–386.
- Rist, D. L., and J. W. Lorbeer. 1989. Occurrence and overwintering of cucumber mosaic virus and broad bean wilt virus in weeds growing near commercial lettuce fields in New York. *Phytopathology* 79:65–69.
- Rollins, K., and A. Lyke. 1998. The case for diminishing marginal existence values. *Journal of Environmental Economics and Management* 36:324–344.
- Rouget, M., and D. M. Richardson. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist* 162:713–724.
- Sabre, M., K. D. Holl, R. E. Lyons, and J. Cairns, Jr. 1997. Potential use of wildflower species for landfill restoration in southwestern Virginia. *HortTechnology* 7:383–387.
- Saner, M. A., D. R. Clements, M. R. Hall, D. J. Doohan, and C. W. Crompton. 1995. The biology of Canadian weeds. 105. *Linaria vulgaris* Mill. *Canadian Journal of Plant Science* 75:525–537.
- Sharov, A. A., and A. M. Liebhold. 1998. Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecological Applications* 8:833–845.
- Sheley, R. L., and J. K. Petroff. 1999. *Biology and Management of Noxious Rangeland Weeds*. Oregon State University Press, Corvallis, Oregon, USA.
- Shogren, J. F., and T. D. Crocker. 1991. Cooperative and noncooperative protection against transferable and filterable externalities. *Environmental and Resource Economics* 1:195–214.
- Simberloff, D., I. M. Parker, and P. B. Windle. 2005. Introduced species policy, management, and future research needs. *Frontiers of Ecology and the Environment* 3:12–20.
- Sing, S. E., and R. K. D. Peterson. 2011. Assessing environmental risks for established invasive weeds: Dalmatian (*Linaria dalmatica*) and yellow (*L. vulgaris*) toadflax in North America. *International Journal of Environmental Research and Public Health* 8:2828–2853.
- Stigarll, A., and E. Elam. 2009. Impact of improved landscape quality and tree cover on the price of single-family homes. *Journal of Environmental Horticulture* 27:24–30.
- Taylor, B. W., and R. E. Irwin. 2004. Linking economic activities to the distribution of exotic plants. *Proceedings of the National Academy of Sciences USA* 101:17725–17730.
- Van Dersal, W. R. 1938. *Native woody plants of the United States: their erosion-control and wildlife values*. Government Printing Office, Washington, D.C., USA.
- Varian, H. R. 1992. *Microeconomic analysis*. W. W. Norton, New York, New York, USA.
- Vilà, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species? Evidence from pairwise experiments. *Oikos* 105:229–238.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.
- Vitousek, P. M. 1997. Human domination of Earth's ecosystems. *Science* 277:494–499.
- Wang, Q., S.-Q. An, Z.-J. Ma, B. Zhao, J.-K. Chen, and B. Li. 2006. Invasive *Spartina alterniflora*: biology, ecology and management. *Acta Phytotaxonomica Sinica* 44:559–588.
- Weitzman, M. L. 1978. Optimal rewards for economic regulation. *American Economic Review* 68:683–691.
- Wilke, B. J., and R. E. Irwin. 2010. Variation in the phenology and abundance of flowering by native and exotic plants in subalpine meadows. *Biological Invasions* 12:2363–2372.
- Wittenberg, R., and M. J. W. Cock. 2001. *Invasive alien species: a toolkit of best prevention and management practices*. CAB International, Wallingford, Oxon, UK.
- Xepapadeas, A. P. 1992. Environmental policy design and dynamic nonpoint-source pollution. *Journal of Environmental Economics and Management* 23:22–39.
- Yu, R., and P. Leung. 2006. Optimal pest management: a reproductive pollutant perspective. *International Journal of Pest Management* 52:155–166.

## SUPPLEMENTAL MATERIAL

### Appendix A

Mathematical derivations of the theoretical equations for the removal of invasive plants and planting of natives for collective and independent management, and for the penalty/subsidy policy instruments ([Ecological Archives A023-057-A1](#)).

### Appendix B

Theoretical comparison of collective vs. independent management for the planting of natives ([Ecological Archives A023-057-A2](#)).

### Appendix C

Ecological and economic parameter estimates for the bioeconomic model and sensitivity analysis ([Ecological Archives A023-057-A3](#)).

### Appendix D

Results from the sensitivity analysis ([Ecological Archives A023-057-A4](#)).