Optimal Control for a Dispersing Biological Agent

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A bioeconomic model is developed to analyze the optimal control management strategies for an introduced herbivore in a two-compartment ecosystem. This paper analyzes cost-effective control strategies that decrease the spillover effects of the herbivore on endangered plant species, thereby reducing extinction pressure and increasing benefits. The optimal level of control is presented in different circumstances. The level of optimal control is high if the herbivore has a relatively low attack rate on the target species, the nontarget host has a high biodiversity value, or the costs of controlling the herbivore are low.

Key words: biological control, economics, externality, optimization, spillover, weed

Introduction

Agricultural activities can lead to costly environmental problems across the world (Conway and Pretty, 1991; Stanners and Bourdeau, 1995; Bignal, 1998; Krebs et al., 1999; Pretty et al., 2000). One of these activities is the introduction of biological agents to control invasive species. Many studies show that the benefits of introducing a biological agent outweigh the costs (e.g., Julien and White, 1997; McConnachie et al., 2003; Jetter and Paine, 2004). Optimal timing of introducing biological agents depends on the ecological and economic conditions. Odom et al. (2003), for example, suggested that it is optimal to introduce biological control for a weed when the number of viable seeds of the weed per site exceeds 250. However, introducing biological agents can impose large ecological and economic costs to the environment. For example, in North America, an herbivore used for biological control of the invasive Pitcher's thistle (*Cirsium pitcher*) also attacked a valuable, protected plant species, Platte thistle (*Cirsium canescens*) (Louda et al., 2003, 2005). These attacks may occur despite regulatory tests. For example, *Larinus planus L.* (an herbivore) was introduced to control Canada thistle (*Cirsium arvense*) in North America, but it had a greater negative impact on a native thistle than on its target (Arnett and Louda, 2002; Louda and O'Brien, 2002).

   Introduced species can target endemic species in different parts of an ecosystem. Some authors have highlighted a problem in which biological control agents introduced into agricultural areas to control weeds have spilled over to other areas, where they have potential to cause the extinction of highly valued plant species (Suarez, Bolger, and Case, 1998; Symondson, Sunderland, and Greenstone, 2002; Cronin and Reeve, 2005; Rand, Tylianakis, and Tscharntke, 2006; Wirth et al., 2008; Chalak et al., 2010; Richards et al., 2010). This paper analyzes cost-effective control strategies to manage such biological agents that act as invasive species and spillover from a managed compartment to a natural compartment and target an endemic species.

Literature Review

Previous literature on the control of unwanted and invasive species falls into four main groups. The first group includes a considerable body of literature with a greater focus on temporal aspects of invasive species control and less focus on spatial aspects. Odom et al. (2003) studied the optimal strategies to control scotch broom (*Cytisus scoparius, L.*) in an Australian national park. Chalak, Ruijs, and Van Ierland (2011) studied the control of Californian thistle (*Cirsium arvense*) in New Zealand agriculture, and Burnett, Pongkijvorasin, and Roumasset (2012) studied optimal management options for brown tree snakes in Hawaii. Chalak and Pannell (2012) studied the control of blackberry in Australia. Most of these studies suggest that highly effective control strategies can be optimal, despite their higher costs, because they can minimize the infestation area and the future spread.

The second group of literature studies the spatial aspects of invasive species control. Brown, Lynch, and Zilberman (2002) analyzed spatial-temporal externality aspects in the management of invasive insect in wine grape farms. Epanchin-Niell and Wilen (2012) examined the spatial nature of optimal control of invasive weeds. Papers in this group mainly conclude that the size, location, control costs, and history of invasion are important factors affecting optimal control. They largely recommend putting control in the locations that impose lower control costs and/or stop the invasion spreading to a larger scale. For most cases, they recommend control if control costs are not large.

The third group analyzes the economics of multicompartment systems in which one species is potentially invasive to all compartments and can spread among them. In the multicompartment system literature, each compartment has different landowners. For example, Bhat, Huffaker, and Lenhart (1993) studied optimal strategies to minimize the invasion of beavers, which generate costs to individual landowners as they disperse across their properties. Bhat and Huffaker (2007) studied the optimal contracts of adjacent landowners to cooperate and control two dispersing nuisance-wildlife populations. Rich and Winter-Nelson (2007) studied regulatory interventions to control foot-and-mouth disease, which can disperse among countries; control in one country has important impacts on the neighboring countries. These studies show that if all involved parties do not agree to simultaneously control the population of undesirable species, the diffusion externality can decrease the incentive of individual parties to control it.

The fourth group analyzes cost-effective strategies for dealing with multi-use species (i.e., those species that have both positive and negative impacts). Zivin, Hueth, and Zilberman (2000) developed a bioeconomic model for feral pig populations that cause damage to agricultural systems but are also valued resources for hunting. Higgins et al. (1997) studied the conflict of interest in introducing a biological agent that has a positive impact on fynbos (a natural shrubland in the Western Cape of South Africa) systems, but negatively impacts the informal settlements that derive income from wood harvesting. Rondeau and Conrad (2003) studied a deer population that provides recreational benefits in addition to imposing damage to human properties. They showed that managing urban animal populations for a steady state can lead to inefficiencies and reduced community welfare. Horan and Bulte (2004) also studied multi-use species such as African elephant populations, which provide both harvesting and recreational benefits. They showed conservation versus harvesting elephants depends on the timing of the conservation policy and consequently the size of the elephant population. The main papers in this group generally conclude that the environmental values of multi-use species typically outweigh their detrimental effects on agricultural costs.

The existing literature, however, does not include a systematic analysis to account for a system consisting of multiple compartments, in which a biological agent disperses between compartments, generating benefits in one compartment by reducing weeds but also acting as an invasive species causing damages in another. This study contributes to the literature by analyzing such a system and assessing the optimal level to control the dispersing biological agent. It employs a novel bioeconomic optimization model that accounts for the interactions among four species: weeds in the managed agricultural system, a biological agent to control these weeds that may disperse to a natural system,
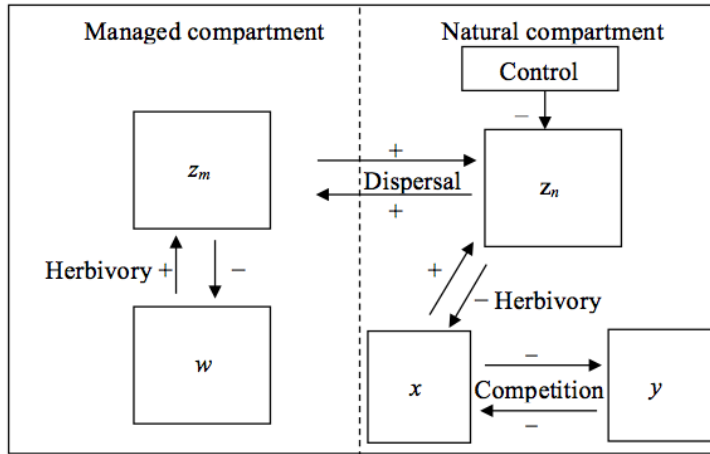
Figure 1. Schematic Representation of the Bioeconomic System

Notes: Introduction of an herbivore (z_m) in the managed compartment (e.g., pasture) suppresses the weed population (w). Herbivores disperse to the natural compartment and feed on an endemic plant species (x) that is in competition with another plant species (y). Species z_m represents the population of the herbivore in the managed compartment and z_n represents the population of the same herbivore species in the natural compartment. Chemical control reduces the density of herbivores in the natural compartment and reduces herbivory of the wild host plant (x).

and two plant species in the natural system, of which only one is affected by the biological control agent. The bioeconomic model accounts for the economic benefits of introducing the biological agent to the managed compartment and its costs to the natural compartment.

The paper first analyzes the stability of the system, then identifies the optimal effort to mitigate the adverse side effects of the introduced biological control agent at the steady state by factoring in the net benefits obtained from both the agricultural and natural compartments. This paper seeks to derive strategies for controlling the biological control agent in the natural area to maximize the overall net benefits. A sensitivity analysis is performed with the bioeconomic model in order to explore the relationship between optimal levels of control and the key parameters.

The Ecological System: Description of Species Interactions

This paper provides an analysis of an economic system built on a two-compartment ecological system developed by Chalak et al. (2010). The first ecosystem compartment is a managed compartment, such as a grassland used for grazing, that is infested by a weed (w). An insect herbivore (z_m) is introduced as a biological control agent into the managed compartment to control the weed population and thus increase agricultural benefits. The second compartment is a natural compartment (e.g., an unmanaged ecosystem) to which the same insect herbivore species (here denoted as z_n) can disperse and attack a nontarget wild plant species (x) (figure 1). In this compartment, plant species interaction is exemplified by considering competition between two species, x and y.

The two herbivore populations (z_m in the managed compartment and z_n in the natural compartment) are linked by dispersal because the introduced herbivore is able to spill over from one compartment to the other. The introduced herbivore spillover into the natural compartment results in damage to plant species x, causing environmental and economic losses. The bioeconomic model deals with these complex processes including herbivory, competition, dispersal, and control of the herbivore in the natural compartment.

The spillover of the herbivore is the only link between the two compartments; without dispersal the two compartments (figure 1) would be strictly separate. In that case, the herbivore would generate benefits by controlling the weed, but it would not have a negative effect on the natural compartment.

In the case of herbivore dispersal, however, the two compartments are intrinsically linked. The weed in the managed compartment can influence the coexisting competing plant species in the natural compartment by boosting the herbivore population in the managed compartment, resulting in its spillover to the natural compartment. The link between species w (the weed) and x (the nontarget wild species) can be characterized as apparent competition in that they share a common herbivore (Holt, 1977).

It is assumed that when the herbivore is absent or does not disperse between the two compartments, the natural compartment is characterized by a stable equilibrium. This means that individuals within each of the competing species (x and y) have sufficient niche differentiation to enable coexistence (Begon, Harper, and Townsend, 1990). This assumption is plausible if species x and y coexisted before the introduction of the herbivore.

Herbivores dispersing into the natural compartment attack species x, resulting in an increase of the density of its competitor, plant species y. The herbivory on x may destabilize the equilibrium between x and y, resulting in extinction of the nontarget host plant, x, due to the combined forces of herbivory and competition. Sustained spillover of the herbivore from the managed compartment can further aggravate the suppressive effect of herbivores on the wild nontarget species. In order to increase the density of x and reduce the negative externality, managers could decide to mitigate herbivore impacts by control in the natural compartment. Control in the managed compartment is not considered here because it would result in a greater interference with the desired effect of the biological control agent.

Controlling the herbivore in one compartment also affects plant interactions in the other compartment due to herbivore dispersal between the compartments. The net dispersal of herbivores is assumed to be proportional to the difference in density between the two compartments and is always toward the compartment with the lower density.[1] Therefore, if control affects the density of the herbivore in the natural compartment, the resulting change in net spillover will result in a lower density of the herbivore in the managed compartment as well. This results in some release of the weed from herbivory and increases its density. With control of z_n, the suppressive effect of the herbivore on the desired species x is diminished. Thus, species x rebounds in the direction of its original equilibrium density without the herbivore, and species y decreases. As the managed compartment can carry a high weed population, it can produce a large population of the herbivore and cause substantial herbivore spillover to the natural compartment.

In the full system, complex interactions exist between the control of the weed, the control of the herbivore, net spillover, and competitive relationships between species x and y in the natural system. A mathematical analysis and numerical exploration together with sensitivity analysis of a bioeconomic model are used to elucidate these interactions. Below, the set-up of the different elements of the bioeconomic model is described in more detail.

Two-Compartment Ecological Model

The dynamics of weed density (w) are modeled by combining a term for logistic growth with a term for herbivory:

$$(1) \qquad\qquad \dot{w} = r_w w \left(1 - \frac{w}{k_w} \right) - b_w z_m w,$$

where k_w represents the carrying capacity of the weed (m^{-2}) and r_w is its intrinsic growth rate (yr^{-1}). The introduced herbivore (z_m, m^{-2}) negatively affects the weed dynamics by herbivory. Parameter b_w represents the attack rate of the herbivore and expresses the relative death rate of weeds, caused at the herbivore density of one per unit area.

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[1] This paper assumes that insects move randomly and thus there would on average be a net movement toward the compartment with lower density (see Kareiva, 1983). This simple assumption facilitates the complex mathematical analysis of this paper.

The competitive interaction between plant species x and y in the natural compartment is built on the standard Lotka-Volterra competition model (Begon, Harper, and Townsend, 1990) in which the herbivory effect on species x is also incorporated. Using the Lotka-Volterra competition model including herbivory effects, the dynamics of species x are represented by the following formula:

$$(2) \qquad \dot{x} = r_x x \left(1 - \left(\frac{x + y a_{xy}}{k_x} \right) \right) - b_x z_n x,$$

where carrying capacity of species x is denoted as k_x and its intrinsic growth rate as r_x. The competitive effect of species y on species x is represented by parameter a_{xy}. Variable z_n represents the density of herbivores in the natural compartment and parameter b_x represents the attack rate of the herbivore and expresses the relative death rate of x caused at the herbivore density of one per unit area. The dynamics of species y according to Lotka-Volterra competition (Begon, Harper, and Townsend, 1990) are presented as

$$(3) \qquad \dot{y} = r_y y \left(1 - \left(\frac{y + x a_{yx}}{k_y} \right) \right),$$

where the carrying capacity of species y is denoted as k_y and its intrinsic growth rate as r_y. The competitive effect of species x on species y is represented by parameter a_{yx}.

The dynamics of the herbivore in both the managed and natural compartments are modeled as a Lotka-Volterra equation for predators. This paper also includes the metapopulation dynamics to represent the dispersal of the herbivore between the two compartments, with parameter d as the dispersal rate of herbivores between the two compartments. Thus, the dynamics of herbivores in the managed compartment are

$$(4) \qquad \dot{z}_m = f b_w w z_m - q z_m + d(z_n - z_m),$$

where variables z_m represent the density of herbivores in the managed compartment. The fecundity coefficient (f) equals the number of herbivores produced per consumed host plant,. The term $f b_w w z_m$ in equation 4 represents the herbivores' total birth rate and $q z_m$ represents their natural mortality in the managed compartment.

Using the Lotka-Volterra equation for predators, the dynamics of the herbivore in the natural compartment are modeled as

$$(5) \qquad \dot{z}_n = f b_x x z_n - q z_n - g z_n + d(z_m - z_n),$$

where g is a decision variable and represents the extra relative mortality rate arising as a result of the control measure to reduce the herbivore population in the natural compartment. The term $f b_x x z_n$ represents the herbivores' total birth rate and $q z_n$ represents their natural mortality rate in the natural compartment.

The Economic System

Social welfare is calculated by summing the financial benefits obtained from the managed compartment plus benefits from non-use values obtained from natural compartment. The financial benefits obtained from the managed compartment (BM) depend negatively on the density of the weed (w) and are calculated as follows:

$$(6) \qquad BM = F \left(1 - \frac{w}{k_w} \right),$$

where parameter F represents the benefits obtained from the managed compartment in the absence of the weed. This equation expresses the principle that the crop and the weed are in complete

competitive exclusion (Zimdahl, 2007). When the weed attains carrying capacity (i.e., a pure weed canopy), then crop value is reduced to 0. Although there may still be some residual crop biomass when weed density is at carrying capacity, its value is often zero due to lack of allocation of energy to grain production or harvesting difficulties. In the absence of weeds, the crops reach their carrying capacity and thus benefits are at their maximum level.

In the natural compartment, benefits are assumed to be intangible (non-use) and are a function of the densities of species x and y. These benefits are assumed to follow a Constant Elasticity of Substitution (CES) utility function. The benefits of the natural compartment (BN) are calculated with the following function:

$$(7) \qquad\qquad BN = \mu(x^\rho + y^\rho)^{1/\rho} - cg,$$

where $0 \neq \rho < 1$. Parameter μ converts the species density to a monetary value and parameter c represents the costs of herbivore control per unit of g (e.g., insecticides).

A manager chooses the level of herbivore control, g, that maximizes the net present value of benefit function subject to the ecological dynamics of the three plant species w, x, and y (equations 1–5). Therefore, the optimal control problem follows:

$$(8) \qquad\qquad \max_g \int_0^\infty \left(\mu(x^\rho + y^\rho)^{1/\rho} - cg + F\left(1 - \frac{w}{k_w}\right) \right) e^{-\sigma t} dt,$$

subject to equations 1–5, where σ represents the discount rate.

The Hamiltonian of the above optimization problem and the first-order conditions associated with this infinite-time control problem in continuous time (Seierstad and Sydsæter, 1987) are presented in Appendix A.

Numerical Analysis for Testing System Stability and Assessing Optimal Control Level

To test the stability of the full bioeconomic system, the Jacobian matrix of the system (equations A3–A12 in Appendix A) and its number of negative eigenvalues are determined in MATLAB using the parameter values shown in table 1. To find the optimal level of herbivore control, objective function (equation 8) is solved subject to the first-order conditions. Analysis showed that the global optimum was achieved because different initial conditions resulted in the same optimal control. Parameter values loosely represent the introduction of an herbivore (*Apion onopirdi*) as a biological agent to control Californian thistle in New Zealand, where it can potentially attack endemic species in nature (Bourdôt et al., 1995; Chalak-Haghighi et al., 2008; Chalak, Ruijs, and van Ierland, 2009; Hurrell, Bourdôt, and Saville, 2001; Chalak et al., 2010) (table 1). This paper helps policy makers to understand ecological-economic implications of possible attack of herbivore on alternative hosts in nature.

Most of the parameter values are obtained from Chalak et al. (2010), who performed an extensive literature review to find the most reliable data for parameter values. For parameters for which published data did not exist, they identified a list of experts on crop, insect, and plant competition. Parameter values obtained from each expert were discussed with other experts for review and improvements. In order to deal with uncertainty about parameter values, an extensive sensitivity analysis is performed in this paper to test the impacts of different parameter values on results.

Results

Stability of the Bioeconomic Model

Using the parameter values in table 1, computing the Jacobian matrix of the bioeconomic system (equations A3–A12 in Appendix A) at a fixed point admits five eigenvalues with negative real parts.

Table 1. Explanation of Parameters

Symbol	Default Value	Units	Meaning
r_x	0.3	yr^{-1}	Intrinsic growth rate of plant species x
k_x	80	shoots m^{-2}	Carrying capacity of plant species x
a_{xy}	0.8	-	Competition coefficient of species y with respect to species x
b_x	0.01	(shoot m^{-2})$^{-1}$ yr^{-1}	Attack rate of the herbivore z on plant species x
r_y	0.3	yr^{-1}	Intrinsic growth rate of plant species y
k_y	80	shoots m^{-2}	Carrying capacity of plant species y
a_{yx}	0.8	-	Competition coefficient of species x with respect to species y
r_w	0.3	yr^{-1}	Intrinsic growth rate of plant species w
k_w	80	shoots m^{-2}	Carrying capacity of plant species w
b_w	0.01	(shoot m^{-2})$^{-1}$ yr^{-1}	Attack rate of the herbivore z on plant species w
f	10	herbivores shoot^{-1}	Fecundity coefficient of the herbivore
q	4	yr^{-1}	Relative death rate of the herbivore
d	0.5	yr^{-1}	Dispersal coefficient of the herbivore
c	0.01	Euros m^{-2} yr^{-1}	Control costs
ρ	0.5	-	Exponent in Cobb Douglas function for species x
ϕ	0.5	-	Exponent in Cobb Douglas function for species y
F	0.04	Euros m^{-2} yr^{-1}	Benefit obtained from the managed compartment in the absence of weed
σ	0.05	yr^{-1}	Discount rate
μ	1	Euros	Monetary value of one plant

Sources: Schwinning and Parsons (1999); Chalak-Haghighi et al. (2008); Chalak, Ruijs, and van Ierland (2009); Chalak et al. (2010).

A fixed point can be achieved when the initial values for x, y, w, z_m, and z_n are set close to their values for an ecological system that involves the interactions of these species without economic components such as control (g). These values were obtained from Chalak et al. (2010). The initial values of shadow prices for species x, y, z_m, z_n, and w at first are determined close to zero, which is close to a fixed point such that the economic trajectory converges to the fixed point.

There are some unlikely scenarios in which species y, w, z_m and z_n can become extinct. For example, the weed can become extinct if the herbivore has an unrealistically high attack rate, and y can become extinct if it receives a very high competition effect from x (a_{yx}). The populations of z_m and z_n can become extinct if their food sources (x and w) become extinct. Excluding these unlikely scenarios, the important question is which circumstances render the equilibrium with all species unstable, followed by a system evolution toward an equilibrium in which species x is extinct. Analysis showed that the system can reach a stable steady state in which species x becomes extinct after the introduction of herbivores because plant species x is suppressed by two forces: 1) competition with plant species y and 2) herbivory. However, as explained above, controlling the herbivore can prevent the extinction of species x, as control reduces the negative impacts of herbivory upon species x. The control can increase the benefits in the natural compartment but decrease benefits in the managed compartment. The key parameter values that impact species interactions are varied, and the optimal levels of control are assessed for the range of parameter values. This allows for an observation of the relationship between the optimal control strategy of the herbivore in the natural compartment and species densities in different circumstances. The results of the sensitivity analysis are only given for the selection of parameters for which the results are not trivial.

Effects of Plant Competition on Species Densities and Optimal Levels of Control

Herbivory and competition with y are two factors suppressing the density of species x. The strength of the competition that x receives from species y can be crucial for its survival as x is also attacked by the herbivore z_n. Due to the CES functional form and the default parameter values adopted
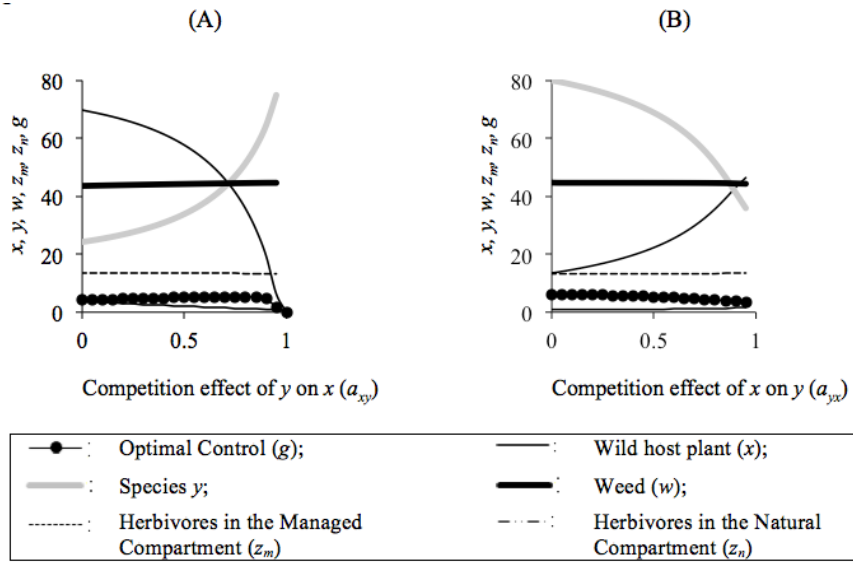
Figure 2. Effect of Competition Coefficients on Optimal Control Effort (g) and Species Density

(table 1), the highest benefit from the natural compartment will be obtained when species x and y have equal densities. Therefore, if parameter a_{xy}—representing competitive strength of y on x—increases, the optimal level of control is expected to increase since the scarcer that x is, the more beneficial it becomes to protect it from herbivory. Figure 2A shows that this indeed occurs. Control of the herbivore, however, increases until the point at which competition by y alone is sufficient to allow x to become extinct. At that point, optimal control drops to zero as there will be no species x left to protect. In this case, the system with five species becomes unstable, resulting in a system with four species.

Figure 2A shows that even when the density of species x is higher than that of species y, it is still optimal to control the herbivore and increase the density of x, although it is expected that more benefit is obtained when the density of species x and y is equal. The main reason for this is that the increase in the density of species x, due to control of the herbivore, is higher than the decrease in the density of species y. In other words, the negative effect of herbivory on x is larger than its positive impact on y due to reduced competition. Parameter a_{xy} is varied from 0 to 1 to present the full range of possible change.

Increasing competitive strength of species x on y (a_{yx}) is expected to have the opposite effect as the increase in a_{xy}, explained above. This is the case for most values of a_{yx} where it ranges from 0 to 1 (figure 2B). Only when a_{yx} is almost equal to one (the competitive strength of species x is high) does the the density of species x exceed that of species y; the optimal level of control drops accordingly as it does not pay to maintain high levels of control to protect species x from herbivore attack.

These results are similar to the results found in the multi-use species literature. The multi-use species literature suggests that it is optimal to favor environmental conservation above other users (e.g., Zivin, Hueth, and Zilberman, 2000; Rondeau and Conrad, 2003; Horan and Bulte, 2004). The current two-compartment model also suggests that it is optimal to control the herbivore in order to protect species x in the environment under a wide range of parameter values, even though control would reduce agricultural production. However, unlike current analysis, literature on multi-use species does not analyze the relationship between optimal control and environmental and agricultural

species. In addition, this paper gives new insight into how plant competition between desirable species can affect optimal control in a two-compartment system.

Effects of Herbivore Attack Rates on Species Densities and Optimal Levels of Control

The attack rates of the herbivore on species x are one of the most important herbivore characteristics affecting the density of species x. It also affects other species densities as well as the optimal levels of herbivore control. The relationship between the attack rate, optimal control, and species density is presented for a wide range of attack rates (0.01–0.02 (shoot m^{-2})$^{-1}$ yr^{-1}) to represent herbivores with different preferences for their host (figure 3A–B).

First a case is analyzed in which the attack rate on species x (b_x) varies for the same attack rate on weeds (b_w). Results show that the relationship between b_x and control is straightforward (see equation 5 and figure 3A). If coefficient b_x goes up while b_w stays the same, then the birth rate of the herbivore in the natural compartment increases and herbivore densities increase in the absence of control as a result. This would result in lower levels of x and consequently lower benefits. Therefore, to reach the economic optimum for a steady state, control of the herbivore increases as b_x increases to protect species x and increase its density. Figure 3A shows that even a very high level of herbivore control cannot permanently remove the herbivores from the natural compartment because of spillover from the managed compartment.

These results are comparable to those found in the literature on the spatial control of invasive species (e.g., Carlson and Wetzstein, 1993; Brown, Lynch, and Zilberman, 2002; Epanchin-Niell and Wilen, 2012). For example, much of this literature has shown that if initial infestation is in the middle of the landscape, the invasive species has an improved ability to attack neighbors and subsequently requires higher levels of control. This is consistent with the result of the current model, as more control is needed if the herbivore has an enhanced ability to attack its prey (i.e., higher b_x). Current analysis accounts for the negative impact of herbivores in the natural compartment as well as their positive impact in the managed compartment. However, many invasive species do not have benefits to society. Therefore a majority of the studies on the spatial control of invasive species (e.g., Brown, Lynch, and Zilberman, 2002; Epanchin-Niell and Wilen, 2012) do not account for their positive impacts. Consequently, these studies may suggest a higher control than the current analysis suggests

An increase in b_w (while b_x stays the same) at first slightly increases density of the herbivore in the managed compartment due to increase in its birth rate. This increases the spillover of herbivores to the natural compartment increasing control to protect x. At higher levels of b_w, the herbivore density in the managed compartment becomes lower due to reduced density of its food source (the weed). Owing to the lower herbivore density in the managed compartment, the spillover of herbivores to the natural compartment is also reduced. Therefore, a higher herbivore attack rate on the weed (b_w) reduces the extent of herbivore attack on species x, increasing its density. Consequently, optimal levels of control decrease, as less control is required to protect x. This is a counterintuitive result because herbivores with a low attack rate have been regarded as safer by other authors (e.g., Begon, Harper, and Townsend, 1990). In contrast to the literature, the results of the current model show that herbivores with intermediate attack rates on weeds (b_w) that maximize the herbivore population in the managed compartment can be a stronger threat to species x and biodiversity. The main reason for these differences is that Begon, Harper, and Townsend (1990) did not consider multicompartment systems.

Effects of the Fecundity Coefficient (F) on Species Densities and Optimal Levels of Control

An increase in the fecundity coefficient (f) of the herbivore increases the birth rate in both compartments (figure 4). As a consequence, high levels of control are required to reduce economic damage on x. Therefore, an increase in f is compensated by higher levels of control and densities
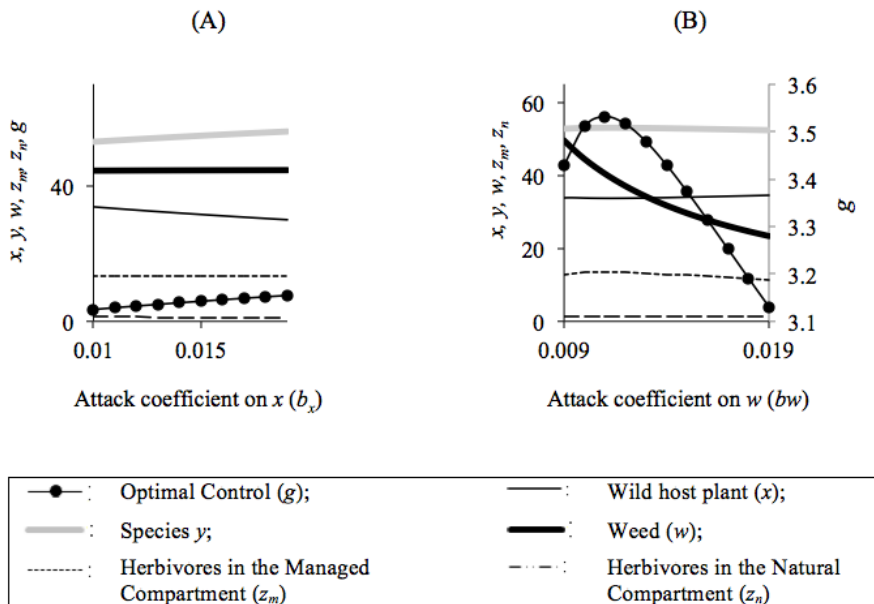
Figure 3. Effect of Herbivore Attack Coefficients (b_x and b_w) on Optimal Control Effort and the Equilibrium Density of Five Species
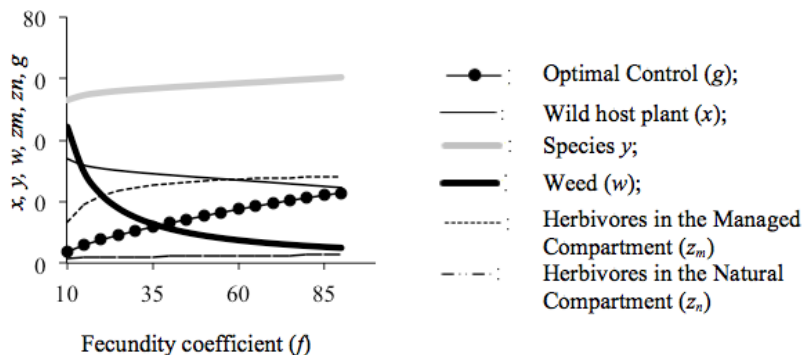

Figure 4. Relationship between Optimal Control, the Equilibrium Density of Five Species, and Fecundity Coefficient (f)

of x and y remain almost constant. To present a large range in the birth rate of the herbivore, the fecundity coefficient is varied from 10–85 (herbivores shoot^{-1}) with seventy-five intervals.

Effects of the Dispersal Rate (D) on Species Densities and Optimal Levels of Control

To present a large range of dispersal rates between compartments, d is varied between 0 and 8 (yr^{-1}) with twenty intervals. Optimal control and species densities are presented in figure 5. If $d = 0$, there is no dispersal of the herbivore between the two compartments; $d = 0.5$ means that the dispersal results in equal density of herbivores between the two compartments in two years (1/0.5 of the time unit). If $d = 1$, the two compartments will attain equal densities after one year.

There are two food sources for herbivores: species x in the natural compartment and the weed in the managed compartment. In principle, the herbivore's food source in the managed compartment

(weed) is larger than in the natural compartment (species x) because x has a smaller population due to competition with y. However, in the case of this paper (according to the growth rate and carrying capacity of weed presented in table 1), the weed does not have such a strong natural competitor in the managed compartment. Therefore, herbivore density in the managed compartment is larger than in the natural compartment. Thus, if the dispersal coefficient (d) increases, more herbivores spill over to the natural compartment, releasing the weed from herbivory, which increases the weed density. An increase in the number of herbivores in the natural compartment reduces x and increases economic damages. Therefore an increase in control is needed to reach the optimum (figure 5). These results are similar to the results identified in economic studies pertaining to multicompartment systems in which each compartment has a different manager. The literature in multicompartment systems also typically shows that economic damage increases if the rate of spread of invasive species between neighbors increases (e.g., Bhat, Huffaker, and Lenhart, 1993; Bhat and Huffaker, 2007). It also shows it is optimal if neighboring compartments cooperate to control invasive species (e.g., Bhat, Huffaker, and Lenhart, 1993; Bhat and Huffaker, 2007). Unlike a multicompartment analysis, the current analysis represents a social planner scenario that optimizes benefits for both compartments. In a multicompartment analysis with similar biophysical characteristics to the current system, the manager of the natural compartment may potentially use more control than the current social planner case. This is because in a multicompartment scenario, only the manager of the managed compartment bears the economic costs of control due to increased weed density. If the current analysis had two managers similar to a multicompartment system, the managed compartment could pay incentives to the natural compartment to reduce the control of herbivores.

Results of this model show if the dispersal rate of herbivore exceeds a certain threshold level (i.e., $d = 6$), the optimal level of control reduces again. The main reason for this is that in the case of high levels of dispersal, higher levels of control in the natural compartment would significantly reduce herbivore densities in the managed compartment. The resulting increase in weed densities in the managed compartment reduces benefits. As a result, it is optimal to decrease control levels again when the dispersal rates between the two compartments are high in order to avoid the economic damage caused by the weed (see figure 5). This is similar to the results of multicompartment systems with different managers. In multicompartment systems, it becomes less cost-effective to control an invasive species if the rate of spread from the neighbors increases due to an increase in the diffusion externality (Bhat, Huffaker, and Lenhart, 1993; Bhat and Huffaker, 2007; Rich and Winter-Nelson, 2007).

The reaction of species x and y to variation in the dispersal rate is interesting. If the dispersal rate increases up to 2.2 yr^{-1}, the increase in the density of herbivores in the natural compartment due the higher spillover is larger than the decrease in the density of herbivores due to control. Therefore, increase in dispersal rate increases z_n, decreasing its host plant density (species x) and releasing y from competition. However, for higher levels of dispersal rate (i.e., $d > 2.2$ yr^{-1}), the negative effect of control on herbivores in the natural compartment is higher than the positive effect of spillover from the managed compartment. This increases the density of species x, reducing its competitor (y).

Effects of the Economic Parameters on Species Densities and Optimal Levels of Control

A large range of values for the scale parameter, μ, ($0.2 < \mu$ with fifteen intervals) is chosen to represent a large range of values for species in the natural compartment. Results show a low level of control is optimal if the species in the natural compartment have little value, as characterized by a small value of the scale parameter μ (figure 6). Thus, the costs of control are saved and total benefits maximized. Low control results in relatively high herbivore density in the natural compartment and consequently in low levels of x and high levels of y. For higher levels of μ, marginal benefits of herbivore control will be higher, resulting in higher control levels. This decreases herbivory pressure on x, increasing the density of x and decreasing the density of y. In addition, a decrease in herbivore density in the natural compartment increases herbivore spillovers from the managed to
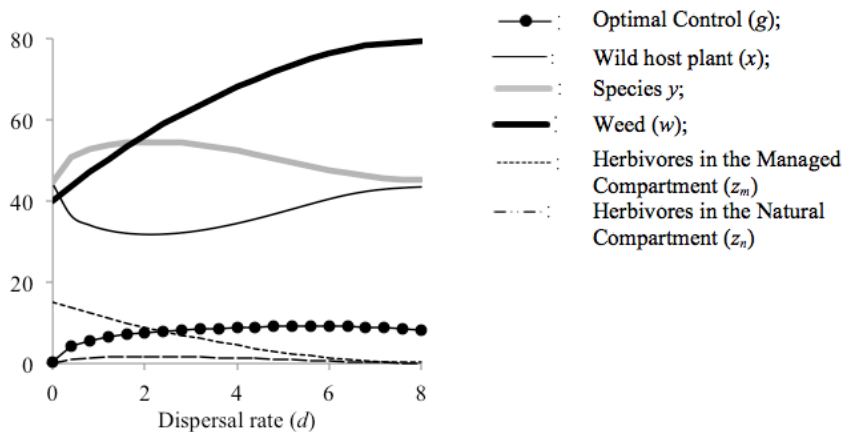
Figure 5. Relationship between Optimal Control, the Equilibrium Density of Five Species, and Dispersal Rate (d)
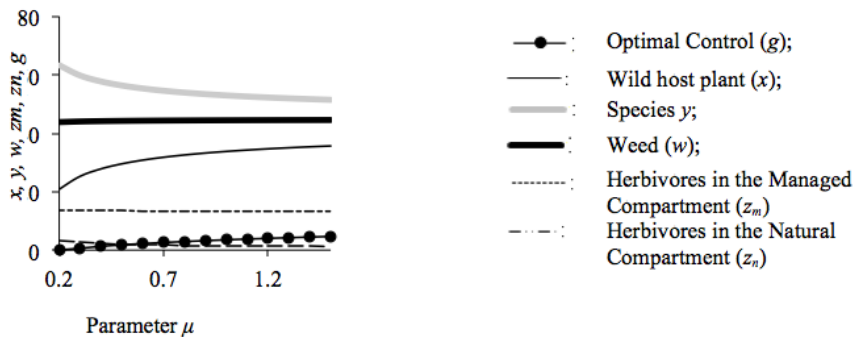

Figure 6. Relationship between Optimal Control, the Equilibrium Density of Five Species, and the Monetary Value of Wild Plant Species (μ)

the natural compartment. As a result, herbivore densities in the managed compartment decrease and weed density increases.

Control costs are varied over the range from 0 to 0.05 with ten intervals. If control costs increase, the optimal level of control decreases (figure 7). This leads to higher herbivore densities and therefore lower densities of weed and species x. The reduction in the weed density is much smaller, as the main reduction of herbivore density occurs in the natural compartment and the herbivore density in the managed compartment is only affected by the changing level of herbivore dispersal between the managed and the natural compartments.

The relationship between shadow prices and parameter values is presented in Appendix B.

Conclusions

This paper analyzes cost-effective strategies to deal with spillovers of an herbivore from a managed area to an area of natural habitat. A bioeconomic model is developed and a numerical analysis performed to analyze the relationship between control levels, competition, herbivory, dispersal, and variation in a number of key parameters at steady states.
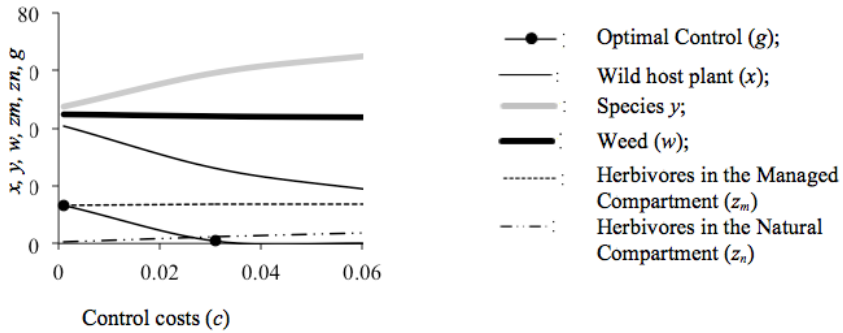
Figure 7. Relationship between Optimal Control, the Equilibrium Density of Five Species, and the Costs of Control (c)

The results of the analysis show that the optimal level of control for the herbivore in the natural compartment is high when the density of the wild, nontarget host species x is low. Even though other authors have concluded that herbivores with lower attack rates pose lower threats to their hosts (e.g., Holt and Hochberg, 2001), these results show that under certain circumstances an herbivore with a lower or intermediate attack rate can be a larger threat to nontarget host species than herbivores with a high attack rates. The main reason for this is that herbivores with a lower attack rate on weeds produce a higher population in the managed compartment, resulting in a higher spillover of herbivores to the natural compartment. The results of this paper are different because unlike previous studies, (e.g., Holt and Hochberg, 2001; Begon, Harper, and Townsend, 1990), this research accounts for possible dispersal of an herbivore to a natural compartment and its attack on endemic species. Furthermore, this paper reports an ambiguous relationship between the dispersal rate of herbivores and optimal levels of control, showing the importance of this factor on the spillover effect of herbivores and optimal levels of control. When the dispersal rate is low, an increase in the dispersal rate increases the optimal level of control, but when the dispersal rate is high, an increase in the dispersal rate decreases the level of control. The economic values of a nontarget host plant and its competitor(s) strongly influence the optimal level of control. When the nontarget host species has low value compared to its competing species, a low control would be optimal to suppress herbivores.

This paper highlights the importance of the externalities of introduced species, especially when there is any possibility that the introduced species will attack a nontarget endemic species that has strong competitors in the environment. Decision makers must be aware that the negative effect can be amplified when the environmental factors warrant a high dispersal of the introduced species to the habitat of the nontarget species. Although the benefits of the introduction of biological control agents depend on the specific local ecological and economic circumstances, they may have a negative impact on ecosystems. This calls for a very strict assessment and screening before biological control agents are newly introduced. In many cases, it will be very difficult to control the agents once they have become established in natural systems, and the required control costs could be well in excess of the expected biological control benefits.

For future research, this paper recommends an analysis of more complex production and benefit functions. Studying the interactions of different species in the natural system is recommended because nonlinear interactions may result in counterintuitive results, as shown in this paper.

[Received April 2013; final revision received July 2014.]

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Appendix A

The Hamiltonian of the optimization problem is

$$
(A1) \quad H = \begin{aligned} &\mu(x^\rho + y^\rho)^{1/\rho} - cg + F\left(1 - \frac{w}{k_w}\right) + \Gamma\left\{r_x x\left(1 - \left(\frac{x + a_{xy}y}{k_x}\right)\right) - b_x z_n x\right\} + \\ &\Theta\left\{r_y y\left(1 - \left(\frac{y + a_{yx}x}{k_y}\right)\right)\right\} + \Xi\{fb_w w z_m - q z_m + d(z_n - z_m)\} + \\ &\Psi\{fb_x x z_n - q z_n - g z_n + d(z_m - z_n)\} + \xi\left\{r_w w\left(1 - \frac{w}{k_w}\right) - b_w z_m w\right\}. \end{aligned}
$$

The first order optimality conditions are

$$
(A2) \qquad \frac{\partial H}{\partial g} = -\Psi z_n - c = 0;
$$

$$
(A3) \qquad \dot{x} = \frac{\partial H}{\partial \Gamma} = r_x x\left(1 - \left(\frac{x + a_{xy}y}{k_x}\right)\right) - b_x z_n x;
$$

$$
(A4) \qquad \dot{y} = \frac{\partial H}{\partial \Theta} = r_y y\left(1 - \left(\frac{y + a_{yx}x}{k_y}\right)\right);
$$

$$
(A5) \qquad \dot{z}_m = \frac{\partial H}{\partial \Xi} = fb_w w z_m - q z_m + d(z_n - z_m);
$$

$$
(A6) \qquad \dot{z}_n = \frac{\partial H}{\partial \Psi} = fb_x x z_n - q z_n - g z_n + d(z_m - z_n);
$$

$$
(A7) \qquad \dot{w} = \frac{\partial H}{\partial \xi} = r_w w\left(1 - \frac{w}{k_w}\right) - b_w z_m w;
$$

$$
(A8) \qquad \dot{\Gamma} = \begin{aligned} &\sigma\Gamma - \frac{\partial H}{\partial x} = \sigma\Gamma + \Gamma\left(\frac{r_x x}{k_x} - r_x\left(1 - \left(\frac{x + a_{xy}y}{k_x}\right)\right) + b_x z_n\right) + \\ &\frac{a_{yx} r_y \Theta y}{k_y} - \rho\mu x^{\rho-1}(x^\rho + y^\rho)^{-1/2} - b_x f\Psi z_n; \end{aligned}
$$

$$
(A9) \qquad \dot{\Theta} = \begin{aligned} &\sigma\Theta - \frac{\partial H}{\partial y} = \sigma\Theta - r_y\Theta\left(1 - \left(\frac{y + a_{yx}x}{k_y}\right)\right) + \\ &\frac{r_x \Theta y}{k_y} + \frac{a_{xy} r_x \Gamma x}{k_x} - \rho\mu y^{\rho-1}(x^\rho + y^\rho)^{-1/2}; \end{aligned}
$$

$$
(A10) \qquad \dot{\Xi} = \sigma\Xi - \frac{\partial H}{\partial z_m} = \sigma\Xi - \Xi(b_w fw - d - q) + b_w \xi w - d\Psi;
$$

$$
(A11) \qquad \dot{\Psi} = \sigma\Psi - \frac{\partial H}{\partial z_n} = \sigma\Psi - d\Xi + b_x\Gamma x - \Psi(b_x fx - d - q - g);
$$

$$
(A12) \qquad \dot{\xi} = \sigma\xi - \frac{\partial H}{\partial w} = \sigma\xi - \xi\left(r_w\left(1 - \frac{w}{k_w}\right) - b_w z_m - \frac{r_w w}{k_w}\right) + \frac{F}{k_w} - b_w f z_m\Xi;
$$

where Γ, Θ, Ξ, Ψ, and ξ are shadow prices for the respective constraints in equation (1).

Appendix B

The relationship between shadow prices under optimal herbivore control and change in parameter values at steady states are presented in figure A1. These shadow prices correspond to the species densities presented in figures 2–7. As shown in the manuscript, an increase in a_{xy}, b_x, f, and control costs (c) decreases the density of plant species x and increases y at optimal control (see figures 2–7). Thus, the benefit obtained from an additional individual of x increases, while it decreases for an additional unit of y. In other word, Γ (shadow price for x) is an increasing and Θ (shadow price for y) is a decreasing function of a_{xy}, b_x, f, d, control costs (c), and parameter ρ.

One exception is the reaction of Γ to a change in parameter μ. As μ increases, the density of x increases, while its shadow price (Γ) increases as well. This is because the positive effect of increasing μ on Γ is larger than the negative effect of increasing x. An increase in μ results in a decrease in y; thus the benefit obtained from an additional level of species y increases the benefit. Hence the shadow price of species y (Θ) increases. Another exception is the reaction of Γ to changes in the dispersal rate (d). For lower levels of dispersal rate, the density of x is a decreasing function of d. In these cases the shadow price of d is an increasing function of d. This is because the shadow price of x increases as it becomes less abundant. However, for higher levels of dispersal rate, increase in d results in increase in x, decreasing the shadow price of x.

An increase in a_{yx} increases the density of species x and decreases y (see figures 2 and 3). Thus, the benefit obtained from an additional unit of x decreases while it decreases for an additional unit of y. Consequently, the shadow price for x (Γ) decreases and the shadow price for y (Θ) increases. A similar relationship holds for b_w and its shadow price, but in the case of b_w change in the shadow price is marginal.

Due to the higher contribution of species x and y to the benefit function, the reactions of Ξ, Ψ, and ξ (i.e., shadow prices for z_m, z_n, and w) to the change in parameter values are smaller than the reactions of Γ and Θ (shadow prices for x and y); (see figure A1). Changes in the parameter values have a smaller effect on Ξ, Ψ, and ξ because—on the one hand—these species have a smaller effect on the benefit than species x and y do; on the other hand, a change in the parameter values has a smaller effect on z_m, z_n, and w than it has on x and y (see figures 2–7).
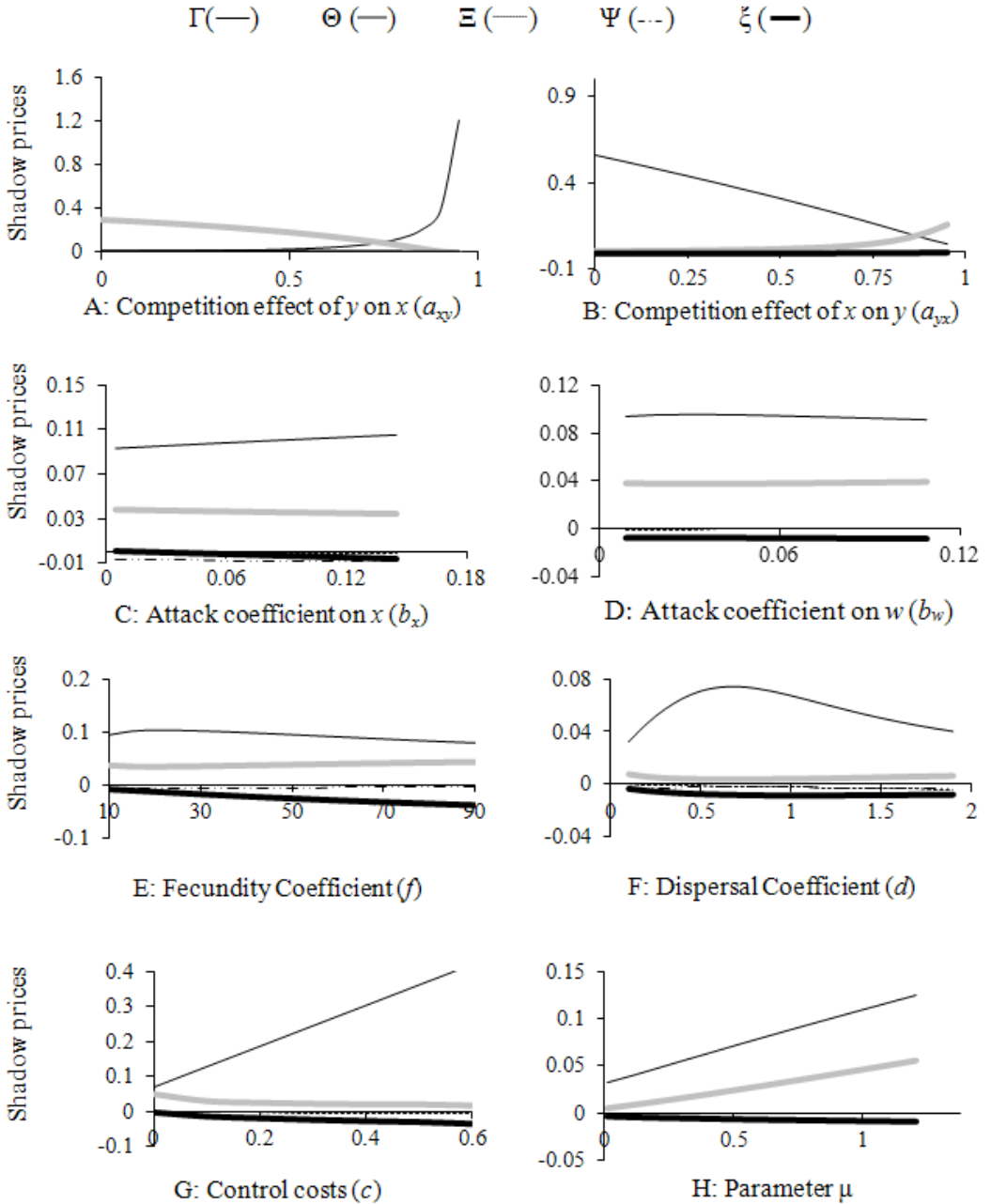
Figure A1. Relationship between Γ, Θ, Ξ, Ψ, and ξ (i.e., the Shadow Prices of Species *x*, *y*, z_m, z_n, and *w*) and Optimal Control (*g*) at Steady States

Notes: These relationships are demonstrated for different range of (A–B) competition effect of species *y* on *x* and *x* on *y* (a_{xy} and a_{yx}), (C–D) attack coefficient of the herbivore on *x* and *w* (b_x and b_w), (E–F) fecundity coefficient and dispersal rate of the herbivore (*f* and *d*), (G–H) control costs (*c*) and parameter μ,