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On the risk of extinction of a wild plant species through spillover of a biological control agent: analysis of an ecosystem compartment model

Morteza Chalak-Haghighi, Lia Hemerik, Wopke van der Werf, and Ekko C. van Ierland

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Mansholt Graduate School of Social Sciences

Hollandseweg 1, 6706 KN Wageningen,
The Netherlands
Phone: +31 317 48 41 26
Fax: +31 317 48 47 63
Internet: http://www.mansholt.wur.nl/
e-mail: office.mansholt@wur.nl

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Morteza Chalak-Haghighi	Environmental Economics and Natural Resources Group Wageningen University, Hollandseweg 1, 6706 KN Wageningen, The Netherlands
Lia Hemerik	Biometris, Department of Mathematical and Statistical Methods Wageningen University, P.O. Box 100, 6700 AC Wageningen, The Netherlands
Wopke van der Werf	Crop and Weed Ecology Group Wageningen University, Haarweg 333, 6709 RZ Wageningen, The Netherlands
Ekko C. van Ierland	Environmental Economics and Natural Resources Group Wageningen University, Hollandseweg 1, 6706 KN Wageningen, The Netherlands

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On the risk of extinction of a wild plant species through spillover of a biological control agent: analysis of an ecosystem compartment model

Authors:

Morteza Chalak-Haghighi[1], Lia Hemerik[2], Wopke van der Werf[3], and Ekko C. van Ierland[1]

[1]Wageningen University, Environmental Economics and Natural Resources Group, Hollandseweg 1, 6706 KN Wageningen, The Netherlands

[2]Wageningen University, Biometris, Department of Mathematical and Statistical Methods, P.O. Box 100, 6700 AC Wageningen, The Netherlands

[3]Wageningen University, Crop and Weed Ecology Group, Haarweg 333, 6709 RZ Wageningen, The Netherlands

Corresponding author: Morteza Chalak-Haghighi, Wageningen University, Hollandseweg 1, 6706 KN Wageningen, E-mail: Morteza.Chalak@wur.nl, telephone: +31317484255

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ABSTRACT

Invasive plant species can be controlled by introducing one or more of their natural enemies (herbivores) from their native range; however such introduction entails the risk that the introduced natural enemy will attack indigenous plant species in the area of introduction.

Here we study the effect of spillover of a natural enemy from a managed ecosystem compartment (agriculture) in the area of introduction to a natural compartment (non-managed) in which an indigenous plant species is attacked by the introduced natural enemy, whereas another indigenous plant species, which competes with the first, is not attacked. The combination of competition and herbivory may result in extinction of the attacked wild plant species. Using a modelling approach, we determine model parameters that characterize the risk of extinction.

Risk factors include: (1) a high attack rate of the introduced enemy on the wild non-target species; (2) factors favouring large spillover from the managed ecosystem compartment to the natural compartment; these include a moderately *low* attack rate of the introduced enemy on the target species, enabling large resident populations of the herbivore in the managed compartment and high dispersal; (3) niche overlap expressed as stronger competition between the attacked non-target species and its competitor(s).

These findings point to the importance of spillover and the relative attack rates (specificity) of introduced natural enemies with respect to target and non-target plant species.

INTRODUCTION

Invasive plant species pose a great problem to global agriculture and ecosystems, threatening valuable indigenous species and productivity in agricultural and natural systems (Callaway and Aschehour 2000; Pimentel 2002; Sheppard *et al.* 2003;). Classical biological control, i.e. the introduction of natural enemies from the native range of the invasive species, is widely regarded as a safe and suitable form to manage invasive species (Ehler 1998; Thomas and Willis 1998; Pemberton 2000;). Classical biological control can be highly costs effective, and it avoids the use of herbicides (Charudattan 2001). Chalak-Haghighi et al. (in press) has recently shown that an insect herbivore (*Apion onopordi*) can increase the net present value obtained from the pasture by reducing the growth rate of Californian thistle (*Cirsium arvense*).

An important issue in biological control is the safety of the agents and whether these may attack non-target species. Many authors have discussed the environmental risks of the introduction of natural enemies for classical biological control (e.g. Thomas and Willis 1998; Follett and Duan 1999; Wajnberg et al. 2001). In order to assess this risk we need to understand the ecological dynamics of biological control agent in the ecosystems where they are introduced, and their interactions with other species. These interactions include both local population interactions as well as spatial processes, e.g. spillover of enemies from one ecosystem compartment to another.

Mobility of biological control agents allows them to penetrate to remote native habitats (Henneman & Memmott 2001). Many of the biological control agents introduced for pest control in agricultural areas can feed on alternative host plants in natural habitats and are likely to disperse between agricultural and natural systems (Symondson et al. 2002; Rand et al. 2006; Wirth et al. 2007). These natural enemies can produce large negative effects in the natural habitats by their spillover or cross-edge invasion effects (Suarez at al. 1998; Cronin and Reeve 2005; Rand et al. 2006). For instance, adult beetles of the corn rootworm (*Diabrotica* ssp), which feed in agricultural land as larvae, largely spill over into tall-grass prairie causing damage to native plants (McKone et al. 2001).

Before introducing a natural enemy to a managed system it therefore is important to consider potential spillover effects to the natural environment, resulting in attack on endangered or protected species in the natural environment. For instance, a herbivore (*Rhinocyllus conicus)* was introduced to biologically control Platte thistle (*Cirsium canescens*) in the United States. After dispersal it attacked a protected and rare relative, the Pitcher's thistle (*Cirsium pitcheri*) (Louda et al. 1997; Louda 1999; Louda et al. 2003; Louda et al. 2005).

Because ecological conditions of the managed and natural systems can differ, many different plant species interactions (e.g. competition) can prevail in the managed and natural systems. Herbivores can disperse fast or slow between the systems, which affects the dynamics of species in both systems due to spillover. Currently, the conditions under which dispersal of a biological control agent from a managed to a natural system results in a spillover effect threatening biodiversity are not systematically analyzed and more work is needed to enable comprehensive assessments of risk (Rand et al. 2006).

In this paper, we use a modelling approach to elucidate risks of introduction of a herbivore species for biological control of a weed in agriculture. The model includes key processes such as the interaction between a herbivore and its target and non-target plant species, dispersal of the enemy from one ecosystem compartment to another, and the competitive relationships between a non-target species with other species in a natural compartment. The objective of the modelling is to identify those system characteristics that enhance or mitigate the risk of extinction of the non-target plant species in the natural compartment, and provide greater insight in the interrelationships between the different dynamic processes involved.

DESCRIPTION OF THE MODEL SYSTEM

We distinguish two parts in our model system: 1) a managed compartment where locally a herbivore (z_m) is introduced to control a pest weed (w), and 2) a natural compartment where the same herbivore species (here denoted as z_n) can attack a wild plant species (Figure 1). The two herbivore populations are linked by dispersal, enabling the natural enemy to spill over from one compartment to the other. In the natural compartment herbivores attack a non-target host plant species (x) which competes with another plant species or group of species (y). The main processes in the model are herbivory, competition and dispersal.

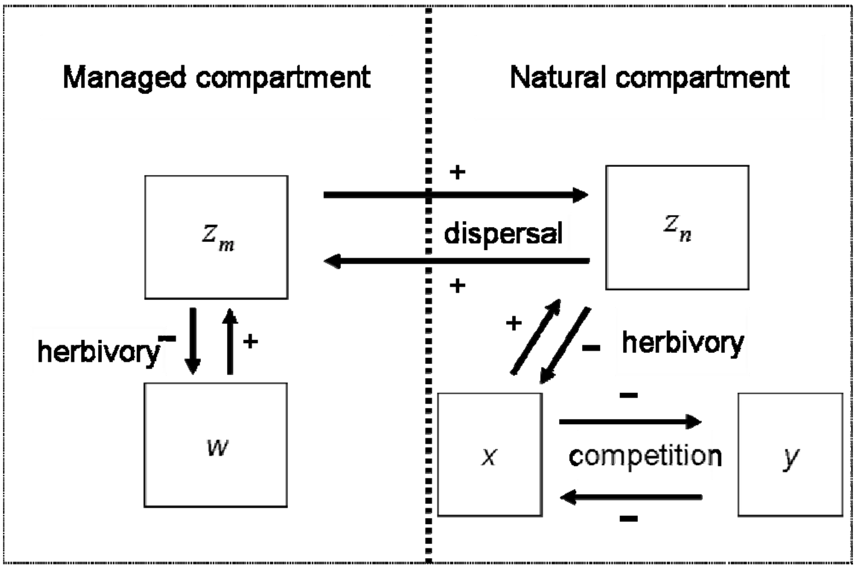

Figure 1: Schematic representation of the modelled system. Introduction of a herbivore to the managed compartment (e.g. pasture) suppresses the weed population (w). Herbivores disperse between the compartments. They feed on a wild plant species (x), which is in competition with one ore more other plant species (y). The subpopulations of the herbivore in the managed compartment and in the natural compartment are denoted as z_m and z_n respectively.

Without the insect herbivore, the two compartments (see fig. 1) would be strictly separated: the weed in the managed compartment does not influence the coexisting competing plant species in the natural compartment. However, when the herbivore is introduced, the systems are linked through dispersal of the herbivore. The link between species *w* (the weed) and *x* (the non-target wild species) can be characterized as apparent competition; they share a common herbivore (Holt, 1977). It is assumed that the initial situation in the natural compartment is characterized by stable equilibrium, i.e. the two competing species have less competitive effect on the other one than they do amongst themselves; they have sufficient niche differentiation to enable coexistence (Begon et al. 1996).

The arrival of a herbivore in the natural compartment, where it is assumed to attack one of the competing plant species, *viz x*, can offset the initially stable equilibrium between *x* and *y*. The competing species *y* can profit and increase in density. The non-target host plant, *x*, might go extinct due to the combination of herbivory and competition. The suppressive effect of herbivores on the wild non-target plant species could be further aggravated by sustained spillover of the herbivore from the managed compartment.

The dispersal of the herbivore influences both its own local densities and that of its host plant species (*x* and *w*) in both compartments. Net dispersal of herbivores is always to the compartment with a lower density, and a compartment with higher host plant density produces more herbivores. The weed can produce a large population and substantial spillover of herbivores to the natural compartment.

In the full system complex interactions between species exist. A mathematical analysis and numerical exploration and sensitivity analysis of our model are used to elucidate these interactions.

The dynamics of the weed, *w*, is modelled with a logistic growth equation:

$$\frac{dw}{dt} = wr_w\left(1 - \frac{w}{k_w}\right) \qquad (1)$$

where r_w is the growth rate of the weed, and k_w represents the carrying capacity of the weed. All model parameters are listed in Table 1.

The dynamics of the weed after introduction of the herbivore is modelled as:

$$\frac{dw}{dt} = wr_w\left(1 - \frac{w}{k_w}\right) - b_w z_m w \tag{2}$$

where b_w represents the attack rate or the probability per unit of time (yr^{-1}) that one individual of species z_m successfully encounters one shoot of weed.

The competitive interaction between plant species *x* and *y* in the natural compartment is modelled as a standard Lotka-Volterra competition system (e.g. Begon *et al.* 1996):

$$\begin{cases} \dfrac{dx}{dt} = r_x x\left(1 - \left(\dfrac{x + ya_{xy}}{k_x}\right)\right) \\ \dfrac{dy}{dt} = r_y y\left(1 - \left(\dfrac{y + xa_{yx}}{k_y}\right)\right) \end{cases} \qquad \text{(3a and b)}$$

where *x* and *y* are the two competing species. Their carrying capacities are denoted as k_x, k_y, and their intrinsic growth rates as r_x and r_y. The per capita effect of species *y* on species *x* is a_{xy}, and a_{yx} denotes the reciprocal effect.

The following Lotka-Volterra competition model represents the dynamics of species *x* and *y* after the herbivore has reached the natural compartment

$$\begin{cases} \dfrac{dx}{dt} = r_x x\left(1-\left(\dfrac{x+ya_{xy}}{k_x}\right)\right) - b_x z_n x \\ \dfrac{dy}{dt} = r_y y\left(1-\left(\dfrac{y+xa_{yx}}{k_y}\right)\right) \end{cases} \qquad \text{(4a and b)}$$

where b_x represents the attack rate or probability per unit of time (yr^{-1}) that one individual of species z_n successfully encounters one shoot of species x.

The dynamics of the herbivore in both the managed and the natural compartment is modelled as a Lotka-Volterra equation for predators, including metapopulation dynamics:

$$\begin{cases} \dfrac{dz_n}{dt} = fb_x x z_n - qz_n + d\left(z_m - z_n\right) \\ \dfrac{dz_m}{dt} = fb_w w z_m - qz_m + d\left(z_n - z_m\right) \end{cases} \qquad \text{(5a and b)}$$

where z_m respectively z_n represent the densities of herbivores in the managed and natural compartment, d is the dispersal rate of herbivores between the two compartments, f (fecundity coefficient) measures the number of herbivores that can be produced by removing one shoot of their host plant. The term $fb_x x z_n$ represents the herbivore's birth rate and q represents the mortality rate of the herbivore.

The system dynamics are thus completely described with five equations (2, 4a, 4b, 5a and 5b), containing 13 parameters: $b_w, b_x, k_w, k_x, k_y, r_w, r_x, r_y, a_{xy}, a_{yx}, f, q$ and d (Table 1).

MATHEMATICAL ANALYSIS

We analysed the 5-dimensional system comprising of the 2 equations from (4), the two herbivore equations (5) and the weed equation (2), because we would like to have all its equilibrium solutions explicitly with their stability. Its non-dimensionalization (see appendix) reduces the number of parameters from 13 (Table 1) to nine. Moreover, the combinations of original parameters into the new parameters help us to see which changes in original parameter values have the same effect on equilibrium values and/or stability.

We found at least 14 biologically relevant equilibria for the non-dimensionalized system, and these are listed in Table 2. In the second part of the appendix we derived the conditions to get equilibria, and the combinations of these conditions are also given in Table 2. Equilibrium **i**, where all state variables are zero, is trivial. There are three equilibria with a single non-zero state variable (**ii**, **iii** and **iv**), three equilibria with two non-zero state variables (equilibria **v**, **vi** and **vii**), three equilibria with three non-zero state variables (**viii**, **ix**, and **xi**), and three equilibria with four non-zero state variables (**x**, **xii**, and **xiii**). There is a single equilibrium **(xiv)** in which all five species can coexist. It should be noted, however, that the combination leading to **xiv** also can give not biologically relevant (i.e. negative) equilibrium solutions.

We are interested in stable equilibrium solutions of the system. For a locally stable equilibrium (attractor) all eigenvalues of the Jacobian matrix in that equilibrium should be negative. When an equilibrium is unstable, a small movement away from the equilibrium increases in the course of time. This can eventually lead to the extinction of one or more species. Note that the stability in a lower dimensional system (e.g. only 2 species) does not imply stability of the 5-dimensional system with only the two aforementioned species present. For instance Begon et al. (1995) suggest that interaction of only two competing plant species (e.g. x and y), can result in a stable equilibrium if β and $\delta<1$. But equilibria **vii** and **viii** are unstable for a large set of parameter values for our system (system 6) even when β and $\delta<1$. Because a small introduction of herbivores (z_m and/or z_n) or weed can attract the existing equilibrium to a new equilibrium where z_m, z_n or the weed get a positive value. For all equilibria except (**i-vi**) the derivation of the sign of all eigenvalues is not possible, even though we simplified the model by non-dimensionalization. Thus, we were not able to get explicit expressions for all equilibria and their stability. In the remainder of this paper, we therefore, use a numerical analysis to explore the characteristics of the equilibria.

NUMERICAL ANALYSIS

The numerical analysis shows that most equilibria are unstable for a wide range of parameter values. From the application point of view, the first 6 equilibria (equilibria **i-vi** in Table 2) with no herbivores are irrelevant, because we have introduced herbivores and assumed that they have established. Only two equilibria are of particular interest: 1) an equilibrium in which all species coexist (a positive solution for **xiv**), and 2) an equilibrium in which species x goes extinct because of the herbivores attack (equilibrium **x**). A trajectory that starts close to the positive equilibrium **xiv** and connects to equilibrium **x** is of special interest because it allows us to investigate which parameters are forcing plant species x to extinction. In the model, species x can reach a stable steady state where it gets a zero or negative growth after introduction of herbivores, because x is suppressed by two forces : 1) competition with y, and 2) herbivory by z_n.

Below we explore the parameter space and determine which of these two equilibria can occur, and give figures in which the dependency of equilibrium solution on parameter values are shown. In these figures only stable equilibria are represented. The results of the sensitivity analysis are only given for a selection of parameters that we consider most relevant. We exclude presentation of other results from our sensitivity analysis because they can be easily understood from the presented results and the relationship between parameters driven from non-dimensionalized system (see appendix). Note that cases where no stable coexistence of species x and y is possible before introduction of the herbivore are not included.

Parameter values for numerical illustration of the behaviour of the system are based on expert estimation by the authors and literature data; they represent loosely a system of thistle species with a weevil species as herbivore (Table 1). All three species (x, y, and w) have in our specification a relative growth rate of 0.3 yr^{-1} and a carrying capacity of 80 shoots m^{-2} (Chalak-Haghighi in press; Schwinning and Parsons 1999). The attack coefficients of the herbivore species on the weed and the wild species are 0.01 $(shoot/m^2)^{-1}$ yr^{-1}. Competitive coefficients of both species are taken to be 0.8, representing a situation in which the species have rather similar resource requirements and niche overlap. The fecundity coefficient of the herbivore is 10 herbivores per shoot, and its death rate is 4 yr^{-1}. Finally, the dispersal coefficient is 0.5 yr^{-1}.

To illustrate the response of the system to parameter changes, and to identify factors that are related to extinction risk of the desired wild plant species, x, we first look at single parameter changes, notably in the coefficients for inter-plant competition, the attack coefficients, and the dispersal coefficient. Next, some of the combined effects of changes in parameters are illustrated.

The effect of the competition coefficient of y on wild plant species x, a_{xy}, is illustrated first. As a_{xy} increases, the equilibrium density of x goes down, while that of y goes up (Fig. 2A). When the competition coefficient becomes larger than 1, x is outcompeted by y, which conforms to results from the Lotka-Volterra competition model. These changes in the densities also affect the density of the herbivore in both system compartment.

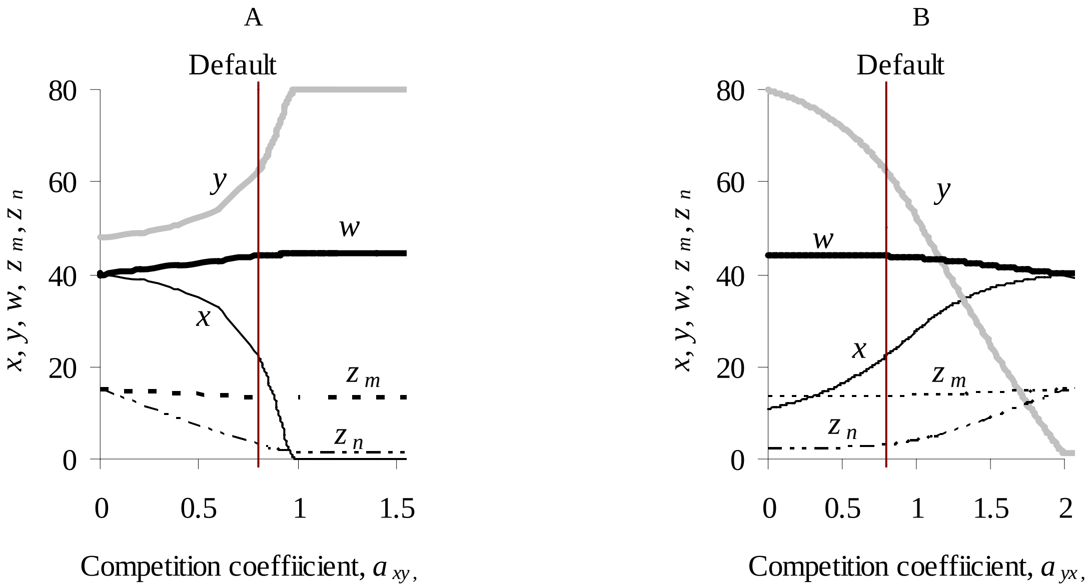

Figure 2: The relationship between the equilibrium densities of wild host plant (*x*), its competitor (*y*), herbivores in the managed and natural compartment (z_m and z_n), weed (*w*) and (A) the plant competition coefficient a_{xy} that expresses the influence of species *y* on species *x* and (B) the plant competition coefficient a_{yx} that expresses the influence of species *x* on species *y*. The vertical lines shows the default value for a_{xy} and a_{yx}, all other parameter are at their default values.

When a_{xy} increases, the density of the enemy goes down in the natural compartment, due to the decrease in host plant density, *x*, but it is hardly affected in the managed compartment, because here, the density of the natural enemy is maintained by its feeding on the weed. Due to spillover of enemies from the managed compartment to the natural compartment, however, an increase in a_{xy} causes a slight decrease in the density of the enemy in the managed compartment. This slight decrease in z_m then causes a small increase in weed density. Mutatis mutandis, an increase in a_{yx} has very similar effects (Fig. 2B). The example clearly demonstrates spillover and apparent competition effects (between *x* and *w*), and it shows that the risk of extinction, expectedly, increases when the desired wild species has a strong competitor, i.e. a_{xy} is large. All the densities represented in the figures represent long term steady states that reflect stable equilibria for the pertinent parameter values. For instance, the transition from a system with x to a system without x for $a_{xy}>1$ in Fig. 2A corresponds to a change from equilibrium (**xiv**) to equilibrium (**x**) (Table 2).

The effects of k_x and k_y can be deduced from the illustrated effects of a_{yx} and a_{xy}. As shown in the appendix (non dimensionalization), the ratio k_y/k_x has the same fundamental influence on system dynamics as a_{xy}, while the ratio k_x/k_y has the same fundamental influence on system dynamics as a_{yx}.

The effect of the attack coefficient b_x is straightforward. As this coefficient increases, x goes down and y, released from competition by x, goes up (Fig. 3A). Enemy density shows an optimum response to the attack coefficient, a behaviour well-known from Lotka-Volterra predator-prey models (Fig. 3A). At low b_x, the enemy is not finding many host plants, and thus has little effect on the host population, and maintains only a very small population itself. As the attack coefficient goes up, the enemy population increases, while the host plant population decreases, up to a point where the decrease in the host population backfires and the enemy population decreases again. In the chosen two-compartment system, the slight peak in the enemy population at intermediate b_x results in a *reduction* of the spillover from the managed to the natural compartment, thus increasing herbivory pressure on the weed in the managed compartment and reducing, slightly, its density.

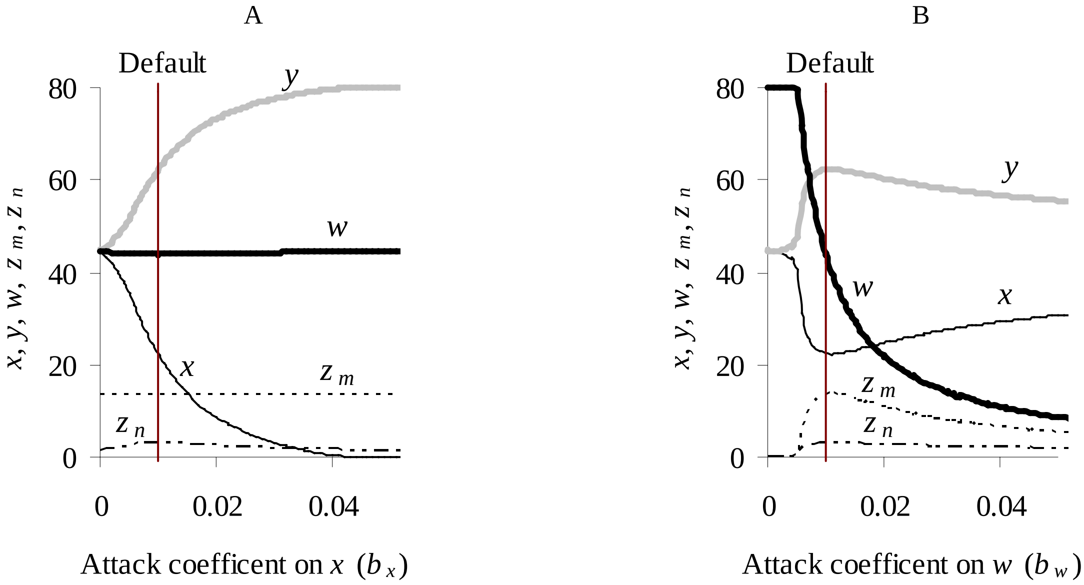

Figure 3: The relationship between herbivore attack coefficients of herbivores on plant species (b_x and b_w) and the equilibrium. Densities of wild host plant (*x*), its competitor (*y*), herbivores in the managed compartment (z_m), herbivores in the natural compartment (z_n), weed (*w*) and (A) herbivore attack coefficient b_x on species *x* and (B) herbivore attack coefficient b_w on species *w*. Vertical lines present the default values for b_x and b_w, other parameter are set at their default values.

Changes in the attack coefficient b_w on the weed in the managed compartment have somewhat more complicated consequences. For low values of b_w, there is no discernible effect on the weed. Equilibrium densities of z_m and z_n are low when b_w is low at the chosen parameter values, due to insufficient encounter with host plant. When b_w increases, natural enemy densities increase, similarly as seen with an increase in b_x, up to a point where the host is overexploited, and natural enemy densities go down again. As b_w is becoming large enough to enable significant population of z_m, the density of the weed decreases, and due to spillover of the enemy from the managed to the natural compartment, the desired wild species, *x*, is also reduced in density, which then releases *y* from competition by *x*, and increases its density.

The interplay between b_x and b_w is further illustrated in Fig. 4, showing relationships between the equilibrium density of *x* and the attack rate of the enemy on *x* for different values of the attack rate of the enemy on the weedy species in the other compartment. When the attack rate on the weed is 0.01, the spillover effect is maximal, resulting in the minimum amount of x. For greater and for smaller values of b_w the equilibrium values of x are higher.

(A)

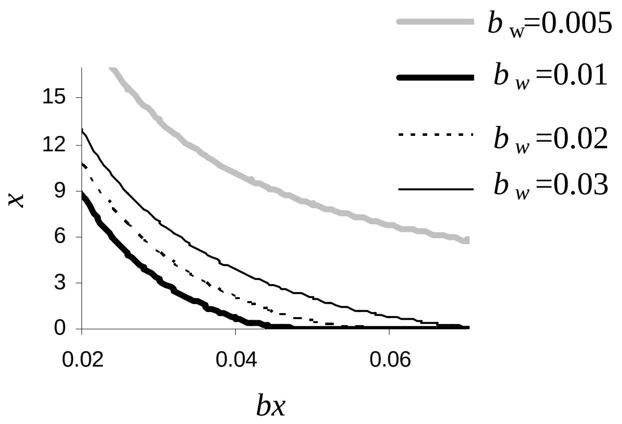

Figure 4: The relationship between attack coefficient of herbivores in the natural environment (b_x) and the equilibrium density of wild host plant (x) for different herbivores attack coefficients in the managed compartment.

Figure 5 summarizes the combined effect of b_w and b_x on the desired species by indicating which parameter combinations enable survival and which ones lead to extinction of x. The lowest values of b_x at which extinction occurs, are for b_w = 0.01, where the spillover effect is maximal. For lower b_w, the spillover effect rapidly dissipates, and hence much greater attack rates b_x are needed to drive x to extinction. If b_w is set to 0 (i.e. no spillover) extinction occurs only at a b_x of 3.83 ((shoot/m^2) $^{-1}$ yr^{-1}). Likewise, the spillover effect is reduced when b_w increases beyond 0.01, and accordingly, higher attack rates b_x are required to exterminate x at increasing b_w.

The dispersal coefficient mediates the spillover effect that is responsible for the effect of the enemy-weed interaction in the managed compartment on the extinction of x in the natural compartment. For high dispersal rate (Fig. 5B), the area of extinction of x is much larger than for a low dispersal rate (Fig. 5A). The threshold between the area of extinction and survival shows transition from equilibrium **xiv** to **x** (Table 2).

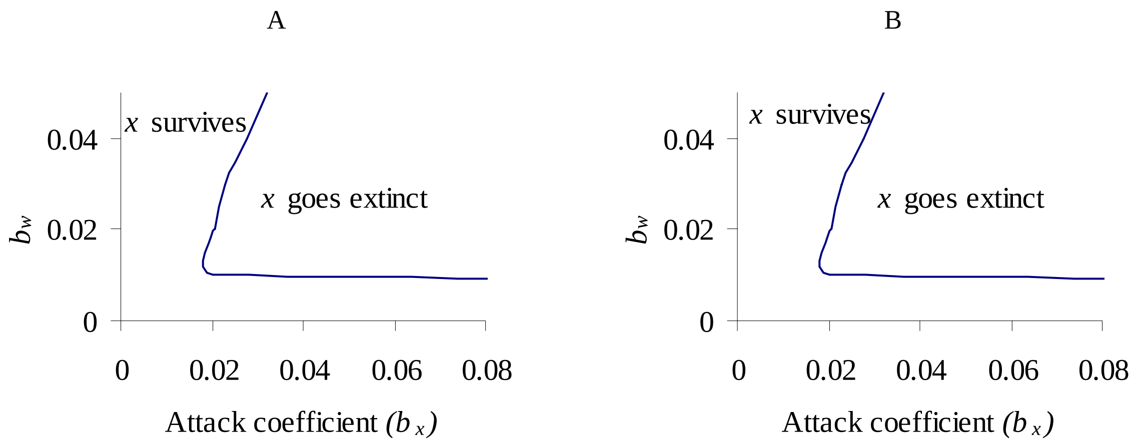

Figure 5: Extinction threshold of wild host plant (*x*) for herbivores attack coefficient in the managed compartment (b_w) and in the natural ecosystem (b_x) when (A): dispersal coefficient is 0.5; (B): Dispersal coefficient is 2.5. Other parameter values are set at their default values. Note when the density of wild host plant is lower than 0.1 shoot/m^2 it is regarded as extinct.

The fundamental effect of the dispersal parameter, *d*, is to equilibrate the densities of the natural enemy in the managed and natural compartments. If *d* is large, any differences are equilibrated very quickly, while, if *d* is small, some difference may be maintained between the enemy densities in the two compartments, due to differences in production and loss rates of enemies in the two compartments. There is more herbivore production in the managed compartment because the resident population of the weed is bigger than that of the species *x* in the natural compartment, so an increase in *d*, *decreases* enemy density in the managed compartment and *increases* density in the natural compartment due to increased spillover. As a result of the resulting decrease in *x* at greater spillover, *y* is released and its density increased (Fig. 6).

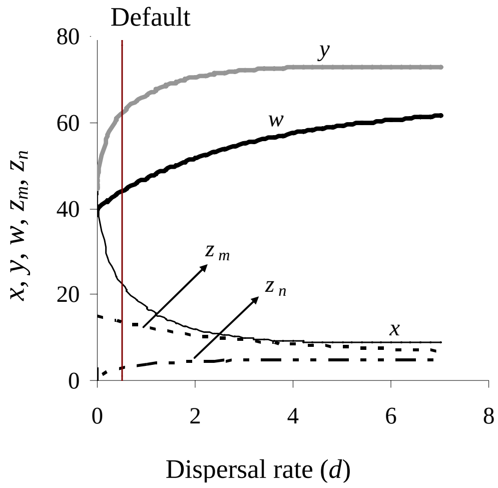

Figure 6: The relationship between dispersal rate d of the herbivore and the equilibrium densities of wild host plant (x), its competitor (y), herbivores in the managed compartment (z_m), herbivores in the natural compartment (z_n), weed (w). Vertical line present the default values for d, other parameter values are set at their default.

As shown in Figure 7, the results of combined parameter changes are predictable from the above reported effects of changes in single parameters. For instance, when the competitiveness of the competing species in the natural compartment is enhanced by increasing a_{xy} from 0.8 to 0.95, then over a wide range of attack coefficients, b_x and b_w, the density of the desired species x is diminished (Fig. 7A). Likewise, enhancing the spillover effect by increasing the dispersal coefficient d, diminishes the density of the desired species over a wide range of attack rates, b_x and b_w (Fig. 7B). Increasing the death rate of the enemy enhances densities of species x (Fig. 7C). Herbivores with a low death rate can drive the wild host plant to extinction, even if their attack rates (b_x, b_w) are low.

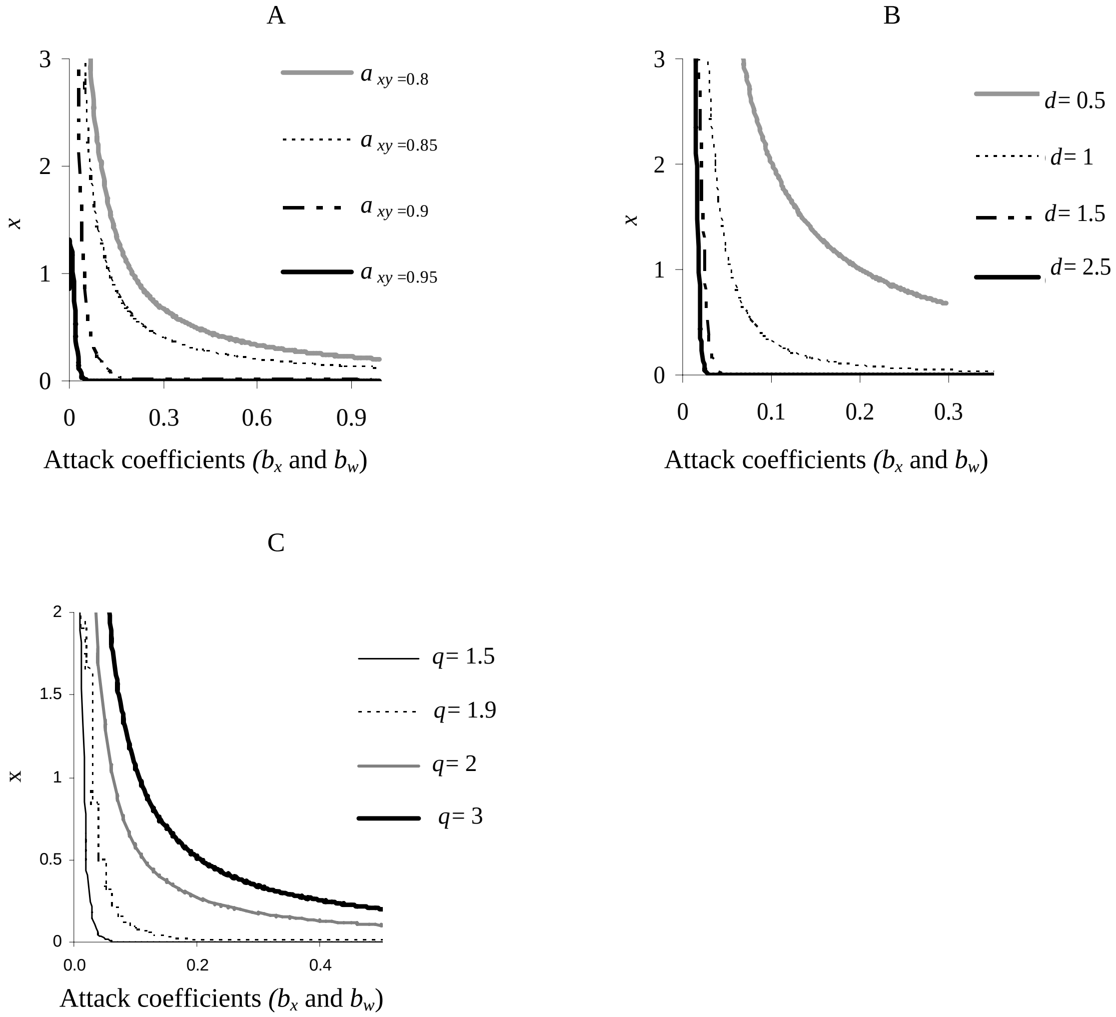

Figure 7: The relationship between attack coefficients b_w and b_x of the herbivore and the equilibrium density of species x for different levels of (A) a_{xy} (B) dispersal coefficient (C) herbivore's death rate q. Vertical line present the default values for b_x and b_w, and other parameter values are set at their default.

DISCUSSION

This paper puts forward a theoretical model framework for analysing which factors contribute to extinction risk of a wild non-target plant species due to spillover of a natural enemy introduced for biological control in agriculture. Extinction is enhanced by: (1) a large resident population of the natural enemy in the agriculture compartment, which is the case at intermediate values of the attack rate on the target weed; (2) a high attack rate of the enemy on the non-target wild species; (3) a high dispersal rate of the herbivore between the managed (target) compartment and the natural (non-target) compartment; and (4) presence in the natural compartment of a competitor species with high degree of niche overlap with the non-target host.

We highlight the importance of competition between plant species for the extinction of the wild host plant. Wild plant species which have a strong competitor are highly vulnerable to a mild attack from herbivores whereas wild plant species that do not have a strong competitor are better able to survive under attack from an introduced herbivore. Therefore, before introducing a herbivore, land managers have to study competition pressure on potential non-target host plants of the natural enemy considered for introduction. If a potential non-target host plant species is under high competitive pressure form other plants, the introduction of the herbivore to the managed compartment should be considered risky.

We showed that the dispersal quantity of the herbivore species plays an important role in the extinction of the favourable wild host plant species. Rand et al. (2006) suggested that spillover may negatively affect the natural habitat, but recommends further studies to clarify to what extent spillover of a natural enemy can influence the natural habitat. We show that spillover cannot only reduce the density of plant species in the natural habitat but also can cause extinction of a wild species. We demonstrated that the risk of extinction can be higher when the herbivores have a low attack rate on the targeted plant species due to high abundance of their host plants. This is in contrast with conclusions so far in the literature. Because a higher herbivore attack rate results in a lower density of their host plant species (Begon et al. 1996), herbivores with a lower attack rate have been regarded as safer for wild plant species. This also means that herbivores with lower attack rate on the target plants are not only doing a poor job in reducing the density of targeted plants (e.g. weeds) but also can pose a larger risk to wild species in the natural habitat.

CONCLUSIONS

We have analyzed how the introduction of a herbivore as a biological control agent in a managed compartment such as an agricultural system can cause biodiversity loss in the natural system by its spillover effects. It is possible that the herbivore establishes itself and affects wild plant species in the natural compartment. The risk of reducing biodiversity is highest if the dispersal rate of the herbivores between natural and managed compartment is high, and if the host plant in the natural compartment is under strong competition with other plant species. Therefore, the introduction of the herbivores when the conditions of the site allow for a high dispersal of herbivores from the managed compartment can result in biodiversity loss in the natural area. It is crucial that before introducing a biological control agent, the managers monitor the natural area for wild or protected plant species that can be on the menu of the proposed agent. Because if a wild plant species in the natural habitat is attacked by herbivores and is already under high competition pressure from other plants, even with a low herbivores dispersal, wild plant species can go extinct. We also conclude that the spillover of herbivores from a managed to a natural environment can cause extinction of a wild plant species, even if some parameter values suggest a low risk. Herbivores with a lower attack rate can reach high population densities in the managed compartment. In this case herbivores can highly disperse to the natural habitat and put a wild plant species at the risk of extinction. Therefore, our recommendation to land managers is to be very cautious with the introduction of herbivores with a low attack rate for the target plant species.

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Table 1. An overview of default parameter values

Parameter	Unit	Default Value	Explanation
r_x	yr^{-1}	0.3	Intrinsic growth rate of plant species *x*
k_x	shoot/m^2	80	Carrying capacity of plant species *x*
a_{xy}	None	0.8	Competition coefficient of species *y* with respect to species *x*
b_x	$(shoot/m^2)^{-1}\ yr^{-1}$	0.01	Attack rate of the herbivore *z* on plant species *x*
r_y	yr^{-1}	0.3	Intrinsic growth rate of plant species *y*
k_y	shoot/m^2	80	Carrying capacity of plant species *y*
a_{yx}	None	0.8	Competition coefficient of species *x* with respect to species *y*
r_w	yr^{-1}	0.3	Intrinsic growth rate of plant species *w*
k_w	shoot/m^2	80	Carrying capacity of plant species *w*
b_w	$(shoot/m^2)^{-1}\ yr^{-1}$	0.01	Attack rate of the herbivore *z* on plant species *w*
f	z $shoot^{-1}$	10	Fecundity coefficient of the herbivore
q	yr^{-1}	4	Relative death rate of the herbivore
d	yr^{-1}	0.5	Dispersal coefficient of the herbivore

Table 2: The steady states $\left(\overline{X},\overline{Y},\overline{Z}_n,\overline{Z}_m,\overline{W}\right)$ of the non-dimensionalized system

Name	$\left(\overline{X},\overline{Y},\overline{Z}_n,\overline{Z}_m,\overline{W}\right)$	Stability	Description/comment
(**i**) Trivial equilibrium (Combine conditions **Ia**, **IIa**, **Va** and no insects present)	$(0,0,0,0,0)$	Unstable	All species extinct
(**ii**) Single species equilibrium 1 Combine conditions **Ib**, **IIa**, **Va** and no insects present)	$(1,0,0,0,0)$	Unstable	*x* is at its carrying capacity
(**iii**) Single species equilibrium 2 (Combine conditions **Ia**, **IIb**, **Va** and no insects present)	$(0,1,0,0,0)$	Unstable	*y* is at its carrying capacity
(**iv**) Single species equilibrium 3 (Combine conditions **Ia**, **IIa**, **Vb** and no insects present)	$(0,0,0,0,1)$	Unstable	*w* is at its carrying capacity
(**v**) Two species equilibrium 1 (Combine conditions **Ib**, **IIa**, **Vb** and no insects present)	$(1,0,0,0,1)$	Unstable	both *x* and *w* are at their carrying capacity (no interaction)
(**vi**) Two species equilibrium 2 Combine conditions **Ia**, **IIb**, **Vb** and no insects present)	$(0,1,0,0,1)$	Unstable	both *y* and *w* are at their carrying capacity (no interaction)
(**vii**) Equilibrium 1 with only competition (Combine conditions **Ib**, **IIb**, **Va** and no insects present)	$(\frac{1-\beta}{(1-\beta\delta)},\frac{1-\delta}{(1-\beta\delta)},0,0,0)$	Unstable for a large range of parameter values	no herbivores; *x* and *y* in their stable competition equilibrium; *w* extinct
(**viii**) Equilibrium 2 with only competition (Combine conditions **Ib**, **IIb**,	$(\frac{1-\beta}{(1-\beta\delta)},\frac{1-\delta}{(1-\beta\delta)},0,0,1)$	Unstable for a large range of parameter values	no herbivores; *x* and *y* in their stable competition equilibrium; *w* at its carrying capacity

Vb and no insects present)			
(**ix**) Managed compartment only (Combine conditions **Ia**, **IIa**, **Vb** and insects present)	$(0,0,\frac{\mu(1-\overline{W})}{\eta(1+\zeta)},\mu(1-\overline{W}),\overline{W})$	Unstable for a large range of parameter values	With $\overline{W}=\frac{\zeta+\zeta(1+\zeta)}{\varepsilon(1+\zeta)}$; species x and y extinct
(**x**) Managed compartment and species y (Combine conditions **Ia**, **IIb**, **Vb** and insects present)	$(0,1,\frac{\mu\left(1-\overline{W}\right)}{\eta(1+\zeta)},\mu\left(1-\overline{W}\right),\overline{W})$	Depending on the parameter values	With $\overline{W}=\frac{\zeta+\zeta(1+\zeta)}{\varepsilon(1+\zeta)}$; species x extinct and y at its carrying capacity (no interaction between compartments)
(**xi**) Natural compartment only (species y extinct) (Combine conditions **Ib**, **IIa**, **Va** and insects present)	$(\overline{X},0,\alpha(1-\overline{X}),\frac{\eta\alpha}{(1+\zeta)}(1-\overline{X}),0)$	Unstable for a large range of parameter values	With $\overline{X}=\frac{\zeta+\zeta(1+\zeta)}{\vartheta(1+\zeta)}$ species w and y extinct (no interaction between compartments)
(**xii**) Natural compartment only (Combine conditions **Ib**, **IIb**, **Va** and insects present)	$(\overline{X},1-\delta\overline{X},\alpha\left(\frac{1-\beta-(1-\beta\delta))}{\overline{X}}\right),\frac{\eta\alpha\left(1-\beta-(1-\beta\delta))\overline{X}\right)}{(1+\zeta)},0)$	Unstable for a large range of parameter values	With $\overline{X}=\frac{\zeta+\zeta(1+\zeta)}{\vartheta(1+\zeta)}$ species w extinct (no interaction between compartments)
(**xiii**) Implicit equation (Combine conditions **Ib**, **IIa**, **Vb** and insects present)	$(\overline{X}_1,0,\overline{Z}_{n1},\overline{Z}_{m1},\overline{W}_1)$	Unstable for a large range of parameter values	Extinction of species y
(**xiv**) Implicit equation (Combine conditions **Ib**, **IIb**, **Vb** and insects present)	$(\overline{X}_2,\overline{Y}_2,\overline{Z}_{n2},\overline{Z}_{m2},\overline{W}_2)$	Depending on the parameter values	Possibly positive for all 5 species

Figure Legends

Figure 1: Schematic representation of the modelled system. Introduction of a herbivore to the managed compartment (e.g. pasture) suppresses the weed population (*w*). Herbivores disperse between the compartments. They feed on a wild plant species (*x*), which is in competition with one or more other plant species (*y*). The subpopulations of the herbivore in the managed compartment and in the natural compartment are denoted as z_m and z_n respectively.

Figure 2: The relationship between the equilibrium densities of wild host plant (*x*), its competitor (*y*), herbivores in the managed and natural compartment (z_m and z_n), weed (*w*) and (A) the plant competition coefficient a_{xy} that expresses the influence of species *y* on species *x* and (b) the plant competition coefficient a_{yx} that expresses the influence of species *x* on species *y*. The vertical lines shows the default value for a_{xy} and a_{yx}, all other parameter are at their default values.

Figure 3: The relationship between herbivore attack coefficients of herbivores on plant species (b_x and b_w) and the equilibrium. Densities of wild host plant (*x*), its competitor (*y*), herbivores in the managed compartment (z_m), herbivores in the natural compartment (z_n), weed (*w*) and (A) herbivore attack coefficient b_x on species *x* and (B) herbivore attack coefficient b_w on species *w*. Vertical lines present the default values for b_x and b_w, other parameter values are set at their default.

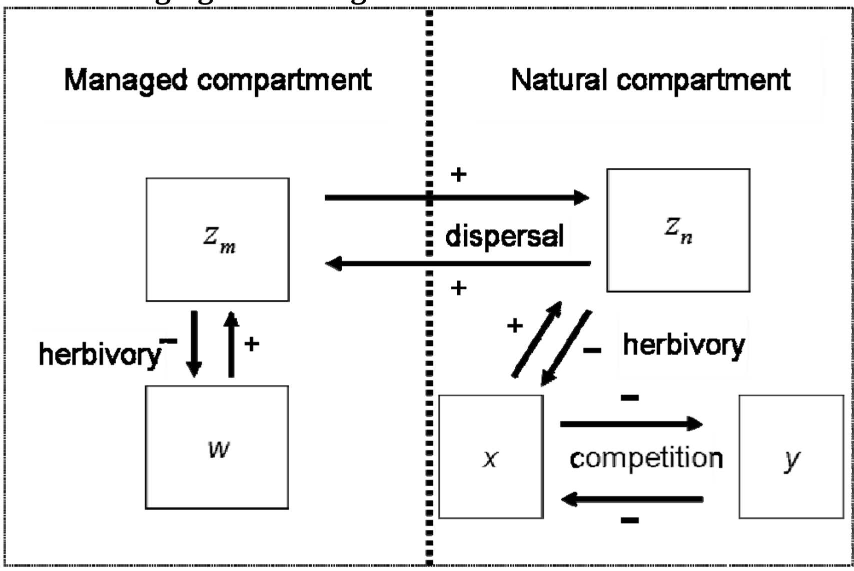
Figure 4: The relationship between dispersal rate *d* of the herbivore and the equilibrium densities of wild host plant (*x*), its competitor (*y*), herbivores in the managed compartment (z_m), herbivores in the natural compartment (z_n), weed (*w*). Vertical line present the default values for *d*, other parameter values are set at their default.

Figure 5: The relationship between attack coefficients b_w and b_x of the herbivore and the equilibrium density of species *x* for different levels of A) a_{xy} B) dispersal coefficient C) herbivore's death rate *q*. Vertical line present the default values for b_x and b_w, and other parameter values are set at their default.

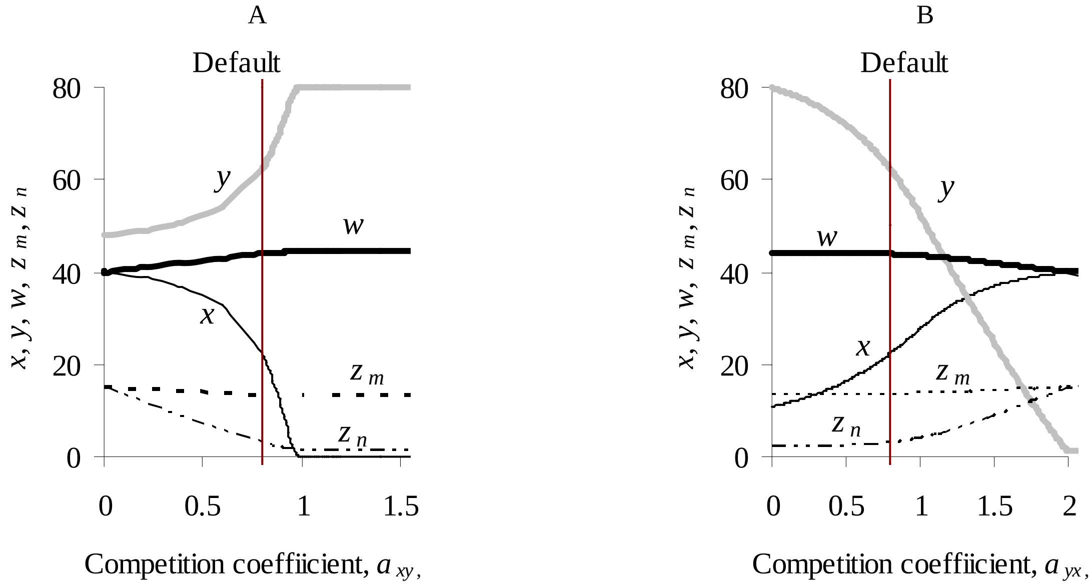
Figure 6: The relationship between attack coefficient of herbivores in the natural environment (b_x) and the equilibrium density of wild host plant (*x*) for: A) different competition effect of *y* on wild host plant, B) for different herbivores attack coefficients in the managed compartment.

Figure 7: Extinction threshold of wild host plant (*x*) for herbivores attack coefficient in the managed compartment (b_w) and in the natural ecosystem (b_x) when A: dispersal coefficient is 0.5 B: Dispersal coefficient is 2.5. Other parameter values are set at their default values. Note when the density of wild host plant is lower than 0.1 shoot/m^2 it is regarded as extinct.

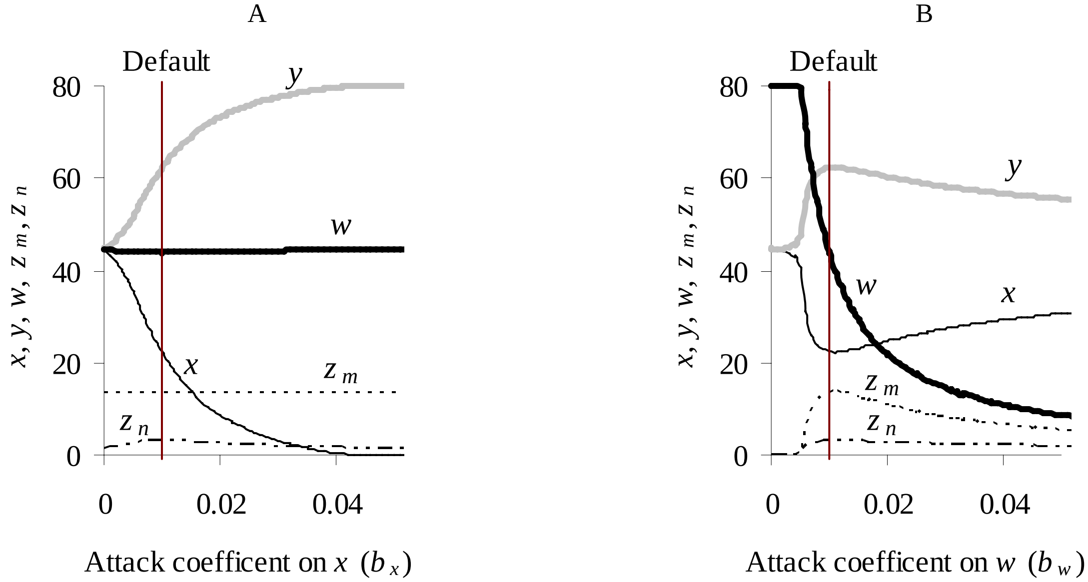
Chalak-Haghighi et al. Figure 1



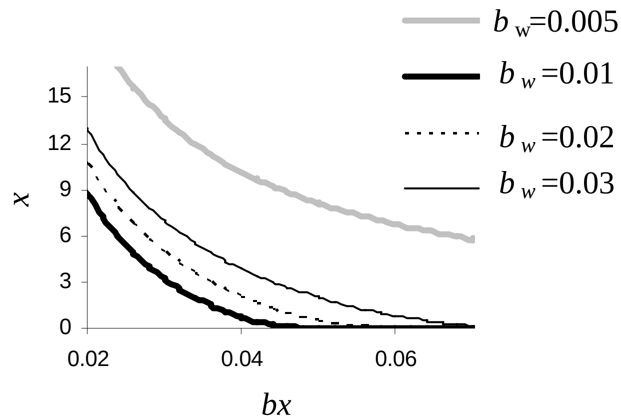
Chalak-Haghighi et al. Figure 2



Chalak-Haghighi et al. Figure 3



Chalak-Haghighi et al. Figure 4



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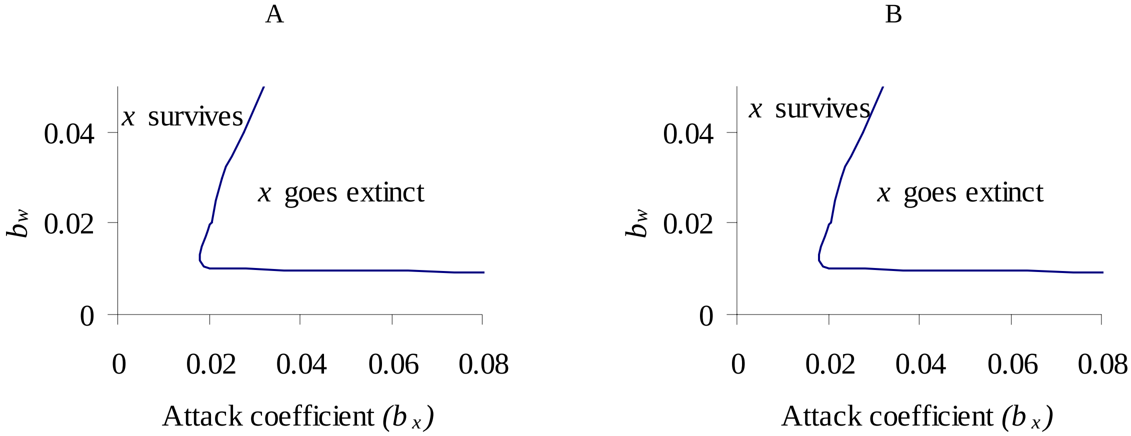

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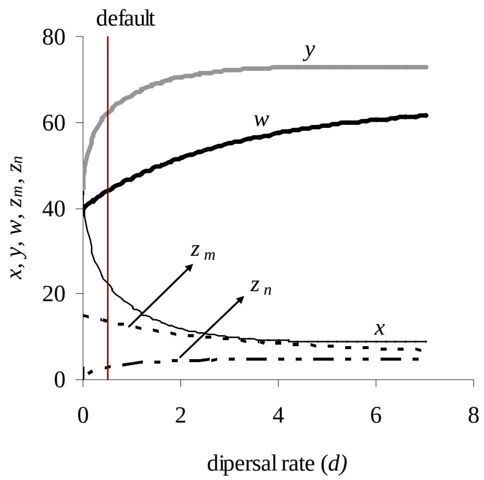
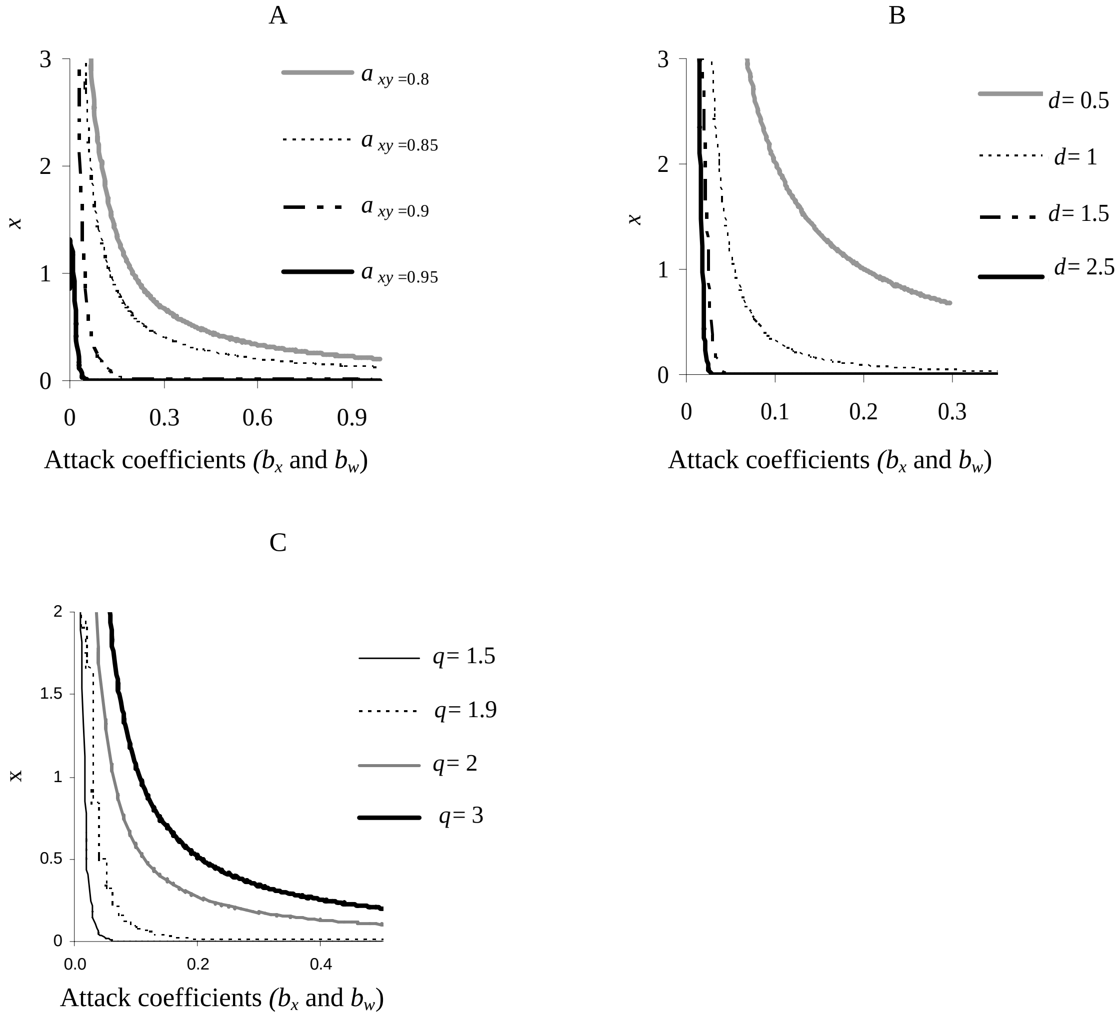


Chalak-Haghighi et al. Figure 7



Appendix

Non-dimensionalization

In order to facilitate mathematical analysis with respect to finding the equilibria and their stability by reducing the number of parameters, the system of five model equations is first non-dimensionalized by setting $t = \frac{T}{d}, x = k_x X, y = k_y Y, z_n = \frac{d}{b_x}, z_m = \frac{d}{b_w}, w = k_w W$. We get:

$$\left.\begin{aligned}
\frac{dX}{dT} &= \alpha X(1 - X - \beta Y) - Z_n X \\
\frac{dY}{dT} &= \gamma Y(1 - Y - \delta X) \\
\frac{dZ_n}{dT} &= \vartheta X Z_n - \zeta Z_n + (\frac{1}{\eta} Z_m - Z_n) \\
\frac{dZ_m}{dT} &= \varepsilon W Z_m - \zeta Z_m + (\eta Z_n - Z_m) \\
\frac{dW}{dT} &= \mu W(1 - W) - W Z_m
\end{aligned}\right\} \tag{6}$$

Where X is the non-dimensionalized density of the non-target species, Y is the non-dimensionalized density of its wild competitor, W is the non-dimensionalized density of weeds in the agriculture compartment, Z_m is the non-dimensionalized density of herbivores in the managed compartment, and Z_n is the non-dimensionalized density of herbivores in the natural compartment. The non-dimensional parameters are defined as:

$$\alpha = \frac{r_x}{d}, \beta = \frac{a_{xy} k_y}{k_x}, \gamma = \frac{r_y}{d}, \delta = \frac{a_{yx} k_x}{k_y}, \varepsilon = \frac{f}{d} b_w k_w, \zeta = \frac{q}{d}, \eta = \frac{b_w}{b_x}, \vartheta = \frac{f}{d} b_x k_x, \mu = \frac{r_w}{d}.$$

Derivation of the equilibria

From system (7) we get the following conditions that have to be combined for getting the equilibria

(**Ia**) $X = 0 \vee$ (**Ib**) $Z_n = \alpha(1 - X - \beta Y)$

$(\mathbf{IIa})\ Y = 0 \vee (\mathbf{IIb})\ Y = 1 - \delta X$

$(\mathbf{III})\ Z_n - \vartheta X Z_n + \zeta Z_n = \frac{1}{\eta} Z_m$

$(\mathbf{IV})\ Z_m - \varepsilon W Z_m + \zeta Z_m = \eta Z_n$

$(\mathbf{Va})\ W = 0 \vee (\mathbf{Vb})\ \mu(1-W) = Z_m$

The combination of conditions (**III**) and (**IV**) give either no insects present or the insects present in both compartments. No extra equilibria are found for the combinations (**Ia**, **IIa**, **Va** and insects present) and (**Ia**, **IIb**, **Va** and insects present) because of internal inconsistency. A summary of the results is given in Table 2.

Stability analysis of steady states

The general Jacobian Matrix in equilibrium point $(\overline{X}, \overline{Y}, \overline{Z}_n, \overline{Z}_m, \overline{W})$ is:

$$Jac(general) = \begin{pmatrix} \alpha(1-2\overline{X}-\beta\overline{Y})-\overline{Z}_n & -\alpha\beta\overline{X} & -\overline{X} & 0 & 0 \\ -\gamma\delta\overline{Y} & \gamma(1-2\overline{Y}-\delta\overline{X}) & 0 & 0 & 0 \\ \vartheta\overline{Z}_n & 0 & \vartheta\overline{X}-\zeta-1 & \frac{1}{\eta} & 0 \\ 0 & 0 & \eta & \varepsilon\overline{W}-\zeta-1 & \varepsilon\overline{Z}_m \\ 0 & 0 & 0 & -\overline{W} & \mu(1-2\overline{W})-\overline{Z}_m \end{pmatrix}$$

To test the stability of each equilibrium we substitute the equilibrium densities of all 5 interaction state variables and parameter values in the Jacobian matrix. If all 5 generated eigenvalues have negative real parts the equilibrium is (locally) stable. Otherwise the equilibrium is unstable. Analytical analysis show that equilibria (I-VI) are unstable (saddle points). For the other steady states a numerical analysis has been performed.