Ecological Modelling 221 (2010) 1934–1943

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

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[a,*], Lia Hemerik[b], Wopke van der Werf[c], Arjan Ruijs[d,1], Ekko C. van Ierland[d]

[a] School of Agricultural and Resource Economics, Centre for Environmental Economics & Policy, University of Western Australia, 35 Stirling Highway, Crawley WA, Perth 6009, Australia
[b] Wageningen University, Biometris, Department of Mathematical and Statistical Methods, P.O. Box 100, 6700 AC Wageningen, The Netherlands
[c] Wageningen University, Plant Sciences, Centre for Crop Systems Analysis, Crop and Weed Ecology Group, P.O. Box 430, 6700 AK Wageningen, The Netherlands
[d] Environmental Economics and Natural Resources Group, Wageningen University, Hollandseweg 1, 6706 KN Wageningen, The Netherlands

ARTICLE INFO

Article history:
Received 18 September 2009
Received in revised form 10 March 2010
Accepted 7 May 2010
Available online 14 June 2010

Keywords:
Biological control
Invasive species
Dispersal
Spillover
Extinction risk
Ecosystem compartment model
Herbivory
Competition

ABSTRACT

Invasive plant species can be controlled by introducing natural enemies (insect herbivores) from their native range. However, such introduction entails the risk that the introduced herbivores attack indigenous plant species in the area of introduction. Here, we study the effect of spillover of a herbivore from a managed ecosystem compartment (agriculture) to a natural compartment (non-managed) and vice versa. In the natural compartment, an indigenous plant species is attacked by the introduced herbivores, 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 for a wild plant species. Risk factors include: (1) a high attack rate of the herbivores on the wild non-target species, (2) niche overlap expressed as strong competition between the attacked non-target species and its competitor(s), and (3) factors favouring large spillover from the managed ecosystem compartment to the natural compartment; these include (3a) a high dispersal ability, and (3b) a moderate attack rate of the introduced herbivore on the target species, enabling large resident populations of the insect herbivore in the managed compartment. The analysis thus indicates that a high attack rate on the target species, which is a selection criterion for biocontrol agents with respect to their effectiveness, also mitigates risks resulting from spillover and non-target effects. While total eradication of an invasive plant species is not possible in the one-compartment-one-plant-one-herbivore system, natural enemy spillover from a natural to a managed compartment can make the invasive weed go extinct.

1. 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 Aschehout, 2000; Pimentel, 2002; Sheppard et al., 2003). Classical biological control, by introducing natural enemies from the native range, is widely regarded as a valuable method for managing invasive species (Ehler, 1998; Thomas and Willis, 1998; Pemberton, 2000). Classical biological control avoids the use of herbicides and can be highly cost-effective (Charudattan, 2001). Chalak-Haghighi et al. (2008) have recently shown that an insect herbivore (*Apion onopordi*) can increase the net present value obtained from pastures in New Zealand by reducing the growth rate of Californian thistle (*Cirsium arvense*).

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

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 spill over from agricultural into natural systems (Henneman and Memmott, 2001; Symondson et al., 2002; Rand et al., 2006; Wirth et al., 2007). This spillover can result in important adverse consequences (Suarez et al., 1998; Cronin and Reeve, 2005; Rand et al., 2006). For instance, the weevil *Rhinocyllus*

* Corresponding author. Tel.: +61 8 64885508; fax: +61 8 6488 1098.
E-mail addresses: morteza.chalak@gmail.com, Morteza.Chalak@uwa.edu.au (M. Chalak).
[1] Current address: Water Economics and Institutions Group, Royal Haskoning, P.O. Box 151, 6500 AD Nijmegen, The Netherlands.

0304-3800/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecolmodel.2010.05.003

conicus, introduced for the biological control of Platte thistle (*Cirsium canescens*) in the United States, attacked a protected and rare relative, the Pitcher's thistle (*Cirsium pitcheri*) (Louda et al., 2003; Louda et al., 2005). Adult beetles of the corn rootworm (*Diabrotica* ssp.), which feed in agricultural land as larvae, spillover into tall-grass prairie causing damage to native plants (McKone et al., 2001). Thus, before introducing a herbivore to a managed system, it is important to consider potential spillover effects to the natural environment, resulting in attack on endangered or protected species in the natural environment.

Because ecological conditions of the managed and natural systems differ, a variety of plant species interactions can prevail in managed and natural systems. Thus, a herbivore may be able to build large populations in one compartment, spill over to another compartment, and affect species interactions and survival in this other compartment. There is a need for analysis of the conditions under which dispersal of a biological control agent from a managed to a natural system produces a spillover effect that is large enough to threaten biodiversity (Rand et al., 2006).

Here, we use a two compartment modelling approach to elucidate risks when releasing a biological control agent to a managed compartment that can spill over to another ecosystem compartment and attack a valuable indigenous species in this other compartment. We focus on the wild plant species' risk of extinction. There have been some studies on two compartment model systems (Vellend et al., 2003). While compartmentalised ecosystem models appear a very suitable tool to study spillover and its effect on ecosystems, such models have, to the best of our knowledge, to date not been used to study extinction risks resulting from spillover.

We develop here a model consisting of two compartments, that represents key processes such as the interaction between a herbivore and its target and non-target plant species, dispersal of the herbivore between ecosystem compartments, and the competitive relationships between a non-target species and other species in a natural compartment. The objectives are to identify those system characteristics that enhance or mitigate the risk of extinction of the non-target plant species in the natural compartment, and to gain insight in the interrelationships between the different dynamic processes involved. In the next section the model system is described, followed by a mathematical analysis. Next, a numerical analysis is presented and finally, conclusions are drawn.

2. Description of the model system

For our analysis we model our system as two compartments: (1) a managed compartment where a herbivore (z_m, numbers m^{-2}) is introduced to control a pest weed (w, shoots m^{-2}), and (2) a natural compartment where the same herbivore species (here denoted as z_n, numbers m^{-2}) can attack a valuable wild plant species (species x, shoots m^{-2}) (Fig. 1). The two herbivore populations are linked by dispersal, enabling the introduced species to spill over from one compartment to the other if the densities in the two compartments are different. In the natural compartment, the non-target host plant species (x) competes with (an)other plant species (y). The main processes in the model are herbivory, competition and dispersal.

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 the weedy species, w, and the non-target wild species, x, can be characterized as apparent competition; they share a common herbivore (Holt, 1977). It is assumed that the competing species in the natural compartment are in stable equilibrium if this compartment is considered in isolation and the herbivore is absent. Thus, the individuals of each of the competing species have less competitive effect on the other species than on their own; they have sufficient niche differentiation to enable coexistence (Begon et al., 2006).

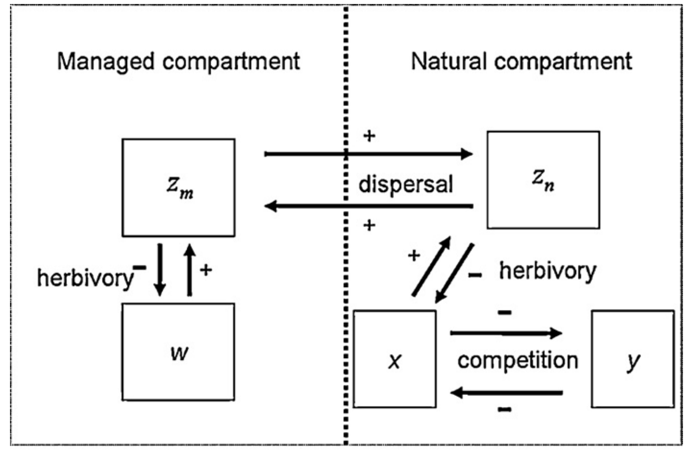

Fig. 1. Schematic representation of the modelled system. Introduction of a herbivore to the managed compartment (e.g. pasture) suppresses the weed population (w). Herbivores disperse between the compartments. They feed on a wild plant species (x), which is in competition with one or more other plant 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.

The arrival of a herbivore in the natural compartment, where it attacks only one of the competing plant species, namely x, can offset the initially stable equilibrium between x and y. As herbivory reduces the density of x, competing species y benefits and increases 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 can be especially severe if herbivore densities in the natural compartment are subsidised by spillover from the managed compartment.

The dispersal of the herbivore influences both its own local densities (z_m and z_n) and that of its host plant species (x and w) in both compartments. Indirectly, y is also affected. If motility of the herbivore is the same in both systems, the net dispersal of herbivores is towards the compartment with the lower density, and proportional to the density difference. The effect of spillover on viability of the valuable species x in the natural compartment depends on a combination of factors, and in particular on dispersal rate, size of the resident population of the herbivore in both compartments, and competitive relations in 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. A list of state variables is given in Table 1.

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

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

where r_w is the growth rate of the weed, and k_w represents the carrying capacity of the weed. All model parameters are also listed in Table 1. The dynamics of the weed in the presence of the herbivore is modelled as

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

where parameter b_w represents the attack rate of the herbivore and expresses the relative death rate of weeds, caused at a herbivore density of one.

Table 1
An overview of default parameter values and state variables.

Variable	Unit	Default Value	Explanation
x	shoots m^{-2}	None	Density of species x
y	shoots m^{-2}	None	Density of species y
w	shoots m^{-2}	None	Density of species w
z_n	m^{-2}	None	Density of herbivores in the natural compartment
z_m	m^{-2}	None	Density of herbivores in the managed compartment
Parameter			
r_x	yr^{-1}	0.3[a]	Intrinsic growth rate of plant species x
k_x	shoots m^{-2}	80[b]	Carrying capacity of plant species x
a_{xy}	None	0.8[b]	Competition coefficient of species y with respect to species x
b_x	$(\text{shoots } m^{-2})^{-1}\, yr^{-1}$	0.01[a]	Attack rate of the herbivore z on plant species x
r_y	yr^{-1}	0.3[a]	Intrinsic growth rate of plant species y
k_y	shoots m^{-2}	80[b]	Carrying capacity of plant species y
a_{yx}	None	0.8[a]	Competition coefficient of species x with respect to species y
r_w	yr^{-1}	0.3[a]	Intrinsic growth rate of plant species w
k_w	shoots m^{-2}	80[b]	Carrying capacity of plant species w
b_w	$(\text{shoots } m^{-2})^{-1}\, yr^{-1}$	0.01[a]	Attack rate of the herbivore z on plant species w
f	Offspring per shoot	10[a]	Fecundity coefficient of the herbivore
q	yr^{-1}	4[c]	Relative death rate of the herbivore
d	yr^{-1}	0.5[a]	Dispersal coefficient of the herbivore

[a] Expert opinion of the authors.
[b] From Chalak-Haghighi et al. (2008).
[c] Based on longevity of adult weevils provided by Theodoor Heijerman.

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., 2006):

$$\begin{cases} \dfrac{dx}{dt} = r_x x \left(1 - \left(\dfrac{x + y a_{xy}}{k_x}\right)\right) \\ \dfrac{dy}{dt} = r_y y \left(1 - \left(\dfrac{y + x a_{yx}}{k_y}\right)\right) \end{cases} \tag{3}$$

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 comparative 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:

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

where b_x represents the instantaneous attack rate of host plants (yr^{-1}) at a herbivore density of one.

The dynamics of the herbivore in both the managed and the natural compartment is modelled as a Lotka–Volterra equation for predators, extended with a term for dispersal between the two ecosystem compartments:

$$\begin{cases} \dfrac{dz_n}{dt} = f b_x x z_n - q z_n + d(z_m - z_n) \\ \dfrac{dz_m}{dt} = f b_w w z_m - q z_m + d(z_n - z_m) \end{cases} \tag{5a and b}$$

where z_m and z_n, respectively represent the densities of herbivores in the managed and natural compartment, and d is the dispersal rate of herbivores between the two compartments. The fecundity coefficient f is the number of herbivores produced per host plant consumed. The total production of herbivores depends further on the rate of encounter between herbivores and host plants ($b_x x z_n$). The term $f b_x x z_n$ thus represents the herbivore's birth rate in the natural compartment, while $q z_n$ represents the death rate.

The system dynamics are completely described with Eq. (2), (4a), (4b), (5a) and (5b). The entire system has 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).

3. Mathematical analysis

Before conducting numerical analyses, the 5-dimensional system was analysed mathematically to obtain all of its equilibria and determine their stability. To facilitate mathematical analysis, the model was first non-dimensionalized, i.e. units were removed from the state variables as well as from the parameters by substitution of variables (Appendix A). This non-dimensionalization reduces the number of parameters from 13 (Table 1) to nine (system (A1)). Moreover, the combinations of original parameters into the new parameters elucidate which changes in original parameter values have similar effects on the equilibrium values and the stability of the equilibria.

There is a single unique interior equilibrium where all state variables are non-zero (equilibrium **xiv** in Table 2). This equilibrium represents a situation where all three plant species are at a non-zero equilibrium, while the herbivore exists in a steady state density in both ecosystem compartments. All other equilibria are boundary equilibria, i.e. one or more of the state variables are zero. There are 13 biologically relevant boundary equilibria for the non-dimensionalized system listed in Table 2. In the second part of the Appendix A we derive the conditions for all equilibria, and the result of combining these conditions are given in Table 2. Equilibrium **i**, where all state variables are zero (all species extinct), is trivial. There are three equilibria with a single non-zero state variable, either one of the competing plant species in the natural compartment or the weed species in the managed compartment (**ii**, **iii** and **iv**), three equilibria with two non-zero state variables where two of the three plant species can exist (equilibria **v**, **vi** and **vii**), three equilibria with three non-zero state variables, either all three plant species or one of the host plant species with the herbivore in both compartments (**viii**, **ix**, and **xi**), and three equilibria with four non-zero state variables, where one of the plant species is extinct (**x**, **xii**, and **xiii**). There is a single equilibrium (**xiv**) in which all five populations coexist. However, it should be noted that equilibrium **xiv** can give negative, and therefore biologically not relevant solutions.

Table 2
Steady states $\left(\bar{W}, \bar{Z}_m, \bar{Z}_n, \bar{Y}, \bar{X}\right)$ of the non-dimensionalized system; the Greek symbols are non-dimensionalized parameters. Their description in terms of the original parameters can be found in Appendix A.

Name	$\left(\bar{W}, \bar{Z}_m, \bar{Z}_n, \bar{Y}, \bar{X}\right)$	Stability	Description/comment
(**i**) Trivial equilibrium	(0, 0, 0, 0, 0)	Unstable	All species extinct
(**ii**) Single species equilibrium	(1, 0, 0, 0, 0)	Unstable	*w* is at its carrying capacity
(**iii**) Single species equilibrium	(0, 0, 0, 1, 0)	Unstable	*y* is at its carrying capacity
(**iv**) Single species equilibrium	(0, 0, 0, 0, 1)	Unstable	*x* is at its carrying capacity
(**v**) Two species equilibrium[b]	(1, 0, 0, 0, 1)	Unstable	Both *x* and *w* are at their carrying capacity
(**vi**) Two species equilibrium	(1, 0, 0, 1, 0)	Unstable	Both *y* and *w* are at their carrying capacity
(**vii**) Equilibrium 1 with only competition	$\left(0, 0, 0, \frac{1-\delta}{(1-\beta\delta)}, \frac{1-\beta}{(1-\beta\delta)}\right)$	Unstable[a]	No herbivores; *x* and *y* in their stable competition equilibrium; *w* extinct
(**viii**) Equilibrium 2 with only competition	$\left(1, 0, 0, \frac{1-\delta}{(1-\beta\delta)}, \frac{1-\beta}{(1-\beta\delta)}\right)$	Unstable[a]	No herbivores; *x* and *y* in their stable competition equilibrium; *w* at its carrying capacity
(**ix**) Managed compartment only	$(\bar{W},\ \mu(1-\bar{W}),\ \frac{\mu(1-\bar{W})}{\eta(1+\zeta)},\ 0,\ 0)$	Unstable[a]	With $\bar{W} = \frac{\zeta+\zeta(1+\zeta)}{\varepsilon(1+\zeta)}$; species *x* and *y* extinct
(**x**) Managed compartment and species *y*	$(\bar{W}, \mu(1-\bar{W}), \frac{\mu(1-\bar{W})}{\eta(1+\zeta)}, 1, 0)$	Depending on the parameter values	With $\bar{W} = \frac{\zeta+\zeta(1+\zeta)}{\varepsilon(1+\zeta)}$; species *x* extinct and *y* at its carrying capacity[b]
(**xi**) Natural compartment only (species *y* extinct)	$(0, \frac{\eta\alpha}{1+\zeta}(1-\bar{X}), \alpha(1-\bar{X}), 0, \bar{X})$	Unstable[a]	With $\bar{X} = \frac{\zeta+\zeta(1+\zeta)}{\vartheta(1+\zeta)}$ species *w* and *y* extinct[b]
(**xii**) Natural compartment only	$(0, \frac{\eta\alpha(1-\beta-(1-\beta\delta)\bar{X})}{1+\zeta}, \alpha(1-\beta-(1-\beta\delta)\bar{X}), 1-\delta\bar{X}, \bar{X})$	Unstable[a]	With $\bar{X} = \frac{\zeta+\zeta(1+\zeta)}{\vartheta(1+\zeta)}$ species *w* extinct[b]
(**xiii**) Implicit equation	$(\bar{W}_1, \bar{Z}_{m1}, \bar{Z}_{n1}, 0, \bar{X}_1)$	Unstable[a]	Extinction of species *y*
(**xiv**) Implicit equation	$(\bar{W}_2, \bar{Z}_{m2}, \bar{Z}_{n2}, \bar{Y}_2, \bar{X}_2)$	Depending on the parameter values	Possibly positive for all five state variables

[a] For a large range of parameter values.
[b] No interaction between compartments.

We are here particularly interested in the boundary equilibrium **x** in which x is not present, i.e. $x^* = 0$. In terms of stability of the equilibria, we are particularly interested in knowing which parameter changes make the interior equilibrium **xiv** unstable whereby stability is transferred to boundary equilibrium **x**, as this represents the extinction of x. Moreover, we want to know which equilibrium solutions of the system are stable (see also Table 2).

For a locally stable equilibrium (attractor) all eigenvalues of the Jacobian matrix in that equilibrium should have negative real parts (Edelstein-Keshet, 1988). When an equilibrium is unstable, a small disturbance away from the equilibrium leads to a permanent departure from the equilibrium. This can eventually lead to the extinction of one or more species. Note that the stability in a lower dimensional system (e.g. only two species) does not imply stability of the 5-dimensional system with only the two aforementioned species present. In other words, adding a species or state variable can destabilise a stable equilibrium of the lower dimensional systems. This means that the system is vulnerable to invasion. For instance, Begon et al. (2006) suggest that interaction of only two competing plant species (e.g. x and y), can result in a stable equilibrium if β and $\delta < 1$ (see Appendix A). But equilibria **vii** and **viii** are unstable for a large set of parameter values for our system (system A1, in Appendix A) even when β and $\delta < 1$ because introduction of the herbivore destabilises equilibrium. The derivation of the sign of real parts of all eigenvalues is possible for equilibria (**i**–**vi**), for the other equilibria a numerical analysis is performed.

4. Numerical analysis

For the numerical analysis, two equilibria are of particular interest: (1) equilibrium **xiv** in which all species coexist and (2) equilibrium **x** in which species x is extinct due to the combination of herbivore attack by z_n and competition with y. A dynamic trajectory that starts from disturbance from the positive equilibrium **xiv** ending in equilibrium **x** is of special interest because it represents extinction of x, allowing us to investigate which parameter values would lead plant species x to extinction.

Below we explore the parameter space and determine which of these two equilibria can occur, and present figures in which the relationship between equilibrium solution **xiv** (w^*, z_m^*, z_n^*, y^*, x^*) and parameter values are shown. Simulations showed that stable equilibria were reached within 100 days (see for the default parameter values, Fig. 2). The model was run for 1000 days and once the stable equilibrium was achieved the species density did not change. We only study cases in which there is stable coexistence of species x and y if the herbivore is absent.

Nominal parameter values for numerical illustration of the behaviour of the system are based on expert estimation by the authors and literature data; they broadly represent the interaction between thistles (*Cirsium* spp.) and herbivorous beetles of the family Curculionidae (weevils) (Table 1). All three species (x, y, and w) have a default relative growth rate of $0.3\,\text{yr}^{-1}$ and a carrying

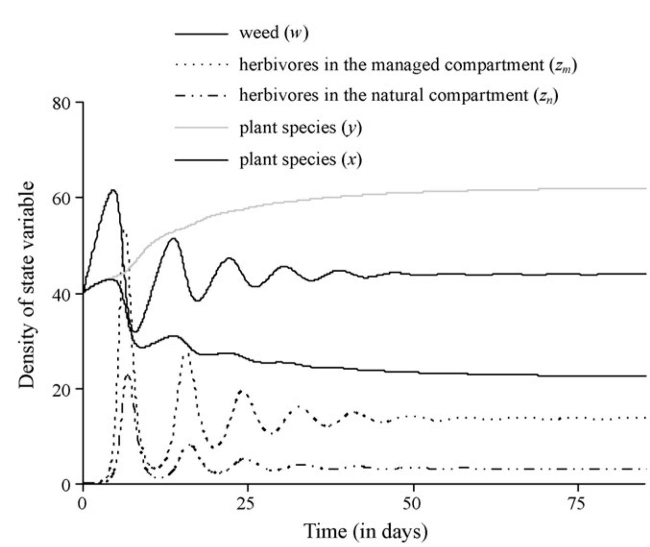

Fig. 2. The time evolution of the 5-dimensional system starting at $(w, z_m, z_n y, x) = (40, 0.1, 0, 40, 40)$. The internal equilibrium is reached in approximately 75 days.

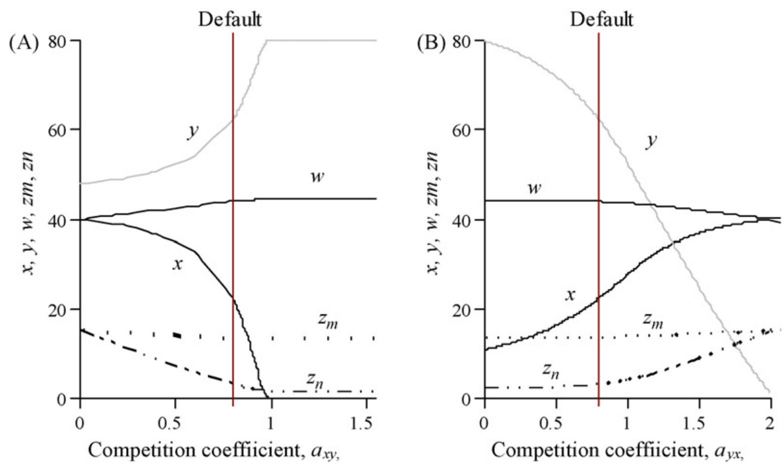

Fig. 3. Effect of competition coefficients a_{xy} and a_{yx} on equilibria of the modelled system. Equilibria are given for the five state variables in the system: x^* (wild plant species, susceptible to introduced herbivore), y^* (wild plant species, not susceptible to introduced herbivore), w^* (target weed for biocontrol in the managed ecosystem), z_n^* and z_m^* (herbivore densities in the natural and managed compartments). The vertical lines show the default value for a_{xy} and a_{yx}, all other parameters are at their default values.

capacity of 80 shoots m^{-2} (Schwinning and Parsons, 1999; Chalak-Haghighi et al., 2008; Chalak et al., 2009). The attack coefficients of the herbivore species on the weed and the wild species are 0.01 (shoots 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 considerable niche overlap. The fecundity coefficient of the herbivore is 10 herbivores per shoot, and its death rate is 4 yr^{-1}, representing an average life span of 3 months. Finally, the dispersal coefficient is 0.5 yr^{-1}, allowing substantial spillover at a time scale of 1 year.

To illustrate the response of the system to parameter changes, and to identify factors that are associated with extinction risk of the desired wild plant species, x, we study 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 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. 3A). The transition from a system with $x^* > 0$ to a system with $x^* = 0$ for $a_{xy} > 1$, as shown in Fig. 3A, corresponds to a change from equilibrium **xiv** to equilibrium **x**. When a_{xy} 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.

The herbivore population in the managed compartment is slightly affected by a change in a_{xy}, because here, the density of the herbivore is also maintained by its feeding on the weed. Due to enhanced 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 herbivore in the managed compartment. This slight decrease in z_m causes a small increase in weed density. An increase in a_{yx} has a similar effect, but mirrored: if a_{yx} increases, x increases somewhat allowing larger spillover of herbivores from the natural to the managed compartment, resulting in suppression of w (Fig. 3B). The example clearly demonstrates spillover and apparent competition effects between x and w, and it illustrates that the risk of extinction increases when the desired wild species has a strong competitor, i.e. a_{xy} is large.

The effects of k_x and k_y can be deduced from the illustrated effects of a_{yx} and a_{xy}. As shown by the non-dimensionalization (Appendix A), 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^* decreases and y^*, released from competition by x, increases (Fig. 4A). Herbivore density shows an optimum response to the attack coefficient, a behaviour inherited from Lotka–Volterra predator–prey models (Fig. 4A). At low b_x, the herbivore finds only few 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 herbivores' population increases, while the host plant population decreases, up to a point where the decrease in the host population backfires and the herbivore population decreases again.

Changes in the attack coefficient b_w on the weed in the managed compartment have somewhat more complicated consequences (Fig. 4B). For low values of b_w, there is no discernible effect on the weed. Equilibrium densities 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, the density of herbivores increases in the two compartments, as seen earlier upon an increase in b_x, up to the point where the host is overexploited, and z_m^* and z_n^* decrease again. As b_w becomes large enough to enable a significant population of z_m, the density of the weed decreases, and due to spillover of the herbivore from the managed to the natural compartment, the desired wild species, x, is also reduced in density. As a result y is released from competition by x, and increases its density.

The interplay between b_x and b_w is further illustrated in Fig. 5, showing relationships between the equilibrium density of x and the attack rate of the herbivore on x for different values of the attack rate of the herbivore 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.

Fig. 6 summarizes the combined effect of b_w and b_x on the species x by indicating which parameter combinations enable its survival and which ones lead to its extinction. 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 (e.g. 0.005), the spillover effect is much smaller, 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 ((shoots 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 again required to exterminate x at increasing b_w.

The dispersal coefficient mediates the spillover effect that is responsible for the effect of the herbivore-weed interaction in the

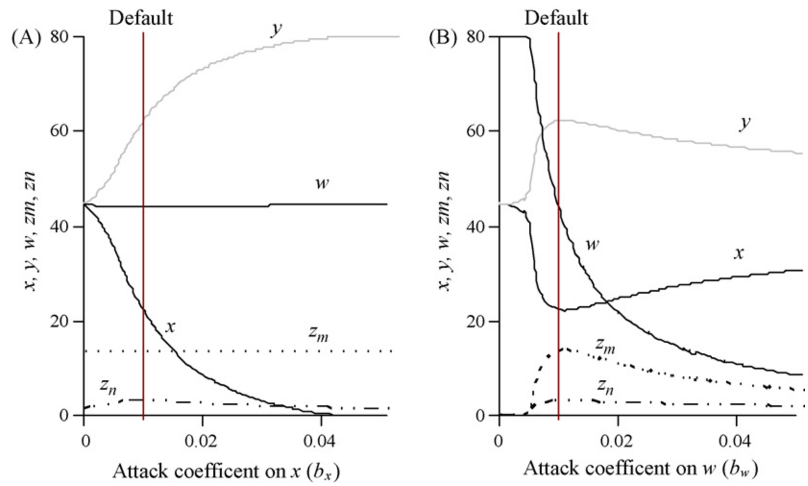

Fig. 4. Effect of herbivore attack coefficients b_x and b_w on equilibria of the modelled system. Equilibria are given for the five state variables in the system: x^* (wild plant species, susceptible to introduced herbivore), y^* (wild plant species, not susceptible to introduced herbivore), w^* (target weed for biocontrol in the managed ecosystem), z_n^* and z_m^* (herbivore densities in the natural and managed compartments). (A) Effect of attack coefficient b_x; on species x; (B) Effect of 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.

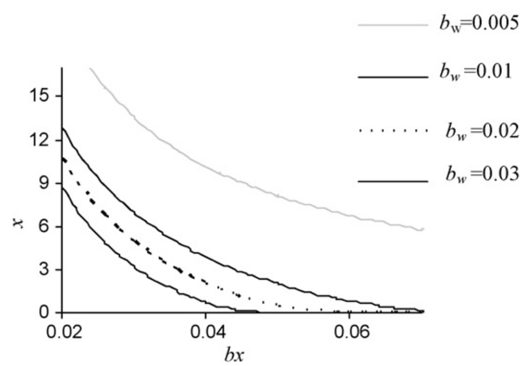

Fig. 5. Effect of the attack coefficient of herbivores in the natural compartment (b_x) on the equilibrium density of wild host plant (x^*) for different herbivores attack coefficients in the managed compartment.

managed compartment on the extinction of x in the natural compartment. With a high dispersal rate (Fig. 6B), the set of parameter values $\{b_x, b_w\}$ leading to extinction of x is much larger than with a low dispersal rate (Fig. 6A). The threshold between the area of extinction and survival shows transition from equilibrium **xiv** to **x** (Table 2).

The fundamental effect of the dispersal parameter, d, is to equilibrate the densities of the herbivore 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 herbivore densities in the two compartments, due to differences in production and loss rates of enemies in the two

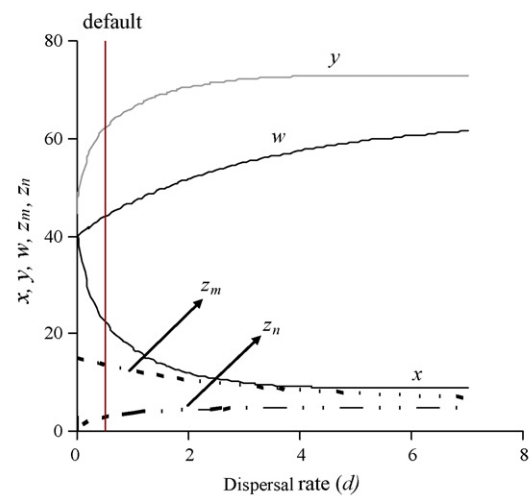

Fig. 7. Effect of dispersal rate d of the herbivore on the equilibrium densities of wild host plant (x^*), its competitor (y^*), herbivores in the managed compartment (z_m^*), herbivores in the natural compartment (z_n^*), and the weed (w^*). The vertical line represents the default value of d, other parameter values are set at their default.

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* herbivore 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

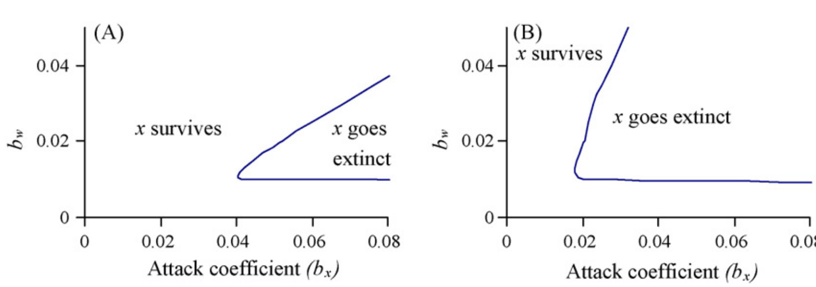

Fig. 6. Extinction threshold of the wild species (x^*) with respect to the attack coefficients in the managed compartment (b_w) and in the natural ecosystem (b_x) for two values of the dispersal coefficient d. (A) d = 0.5; (B) d = 2.5. Other parameter values are set at their default values. When the density of wild host plant is lower than 0.1 shoots m^{-2} it was regarded as extinct.

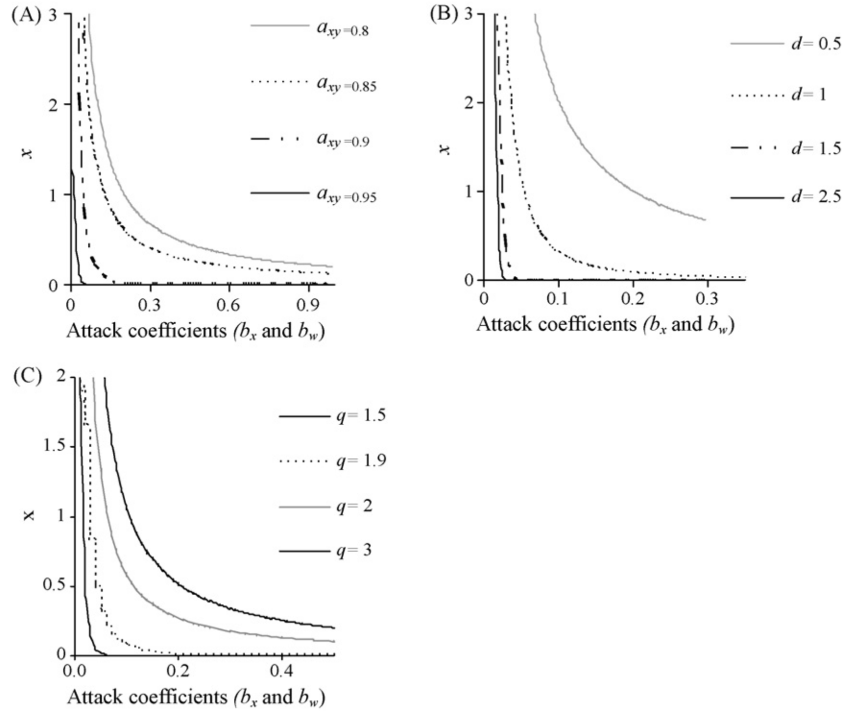

Fig. 8. Effect of the attack coefficients b_w and b_x of the herbivore on the equilibrium density of species x^* for different levels of (A) a_{xy}; (B) dispersal coefficient d; (C) herbivore's death rate q. The vertical line represents the default values for b_x and b_w, other parameter values are set at their default.

at greater spillover, y is released from competition with x and its density is increased (Fig. 7).

As shown in Fig. 8, the results of combined parameter changes are predictable from the above reported effects of changes in single parameters. For instance, when the competition between the 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. 8A). Likewise, enhancing the spillover effect by increasing the dispersal coefficient d, diminishes the density of the species x over a wide range of attack rates, b_x and b_w (Fig. 8B). Increasing the death rate of the herbivore enhances the density of species x (Fig. 8C). 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.

5. Comprehensive sensitivity analysis

A comprehensive local sensitivity analysis demonstrates the effect of all parameter values on the equilibrium densities of all state variables (Fig. 9). First, the relationship between percentage change from the default parameter values and the equilibrium density of plant species x is presented (Fig. 9A and B). The density of species x at equilibrium increases as x becomes a stronger competitor and herbivory on x decreases. Thus, on the one hand x is a strictly increasing function of competition effect of x on y (a_{yx}), death rate of herbivores (q), carrying capacity (k_x) and growth rate of species x (r_x). On the other hand x strictly decreases with herbivore attack coefficient b_x, fecundity coefficient (f), competition effect from species y (a_{xy}) and carrying capacity of y (k_y). Increase in the equilibrium density of the pest weed w results in more herbivores in the managed compartment and higher spillover of the herbivore to the natural compartment. Thus, increase in w due to increase in k_w and r_w decreases the density of plant species x.

Second, in Fig. 9C and D the sensitivity analysis for the equilibrium density of competing plant species y is presented. The equilibrium density of species y increases as y becomes a stronger competitor for x. Thus, on the one hand y is a strictly increasing function of the competition effect of y on x (a_{xy}) and its carrying capacity (k_y). The growth rate of species y (r_y) has no effect on y^*, similarly as in simple Lotka–Volterra competition systems. On the other hand y strictly decreases when the equilibrium density of its competitor (x) increases by increasing the competition effect from x (a_{yx}) or the carrying capacity of x (k_x). The equilibrium density of y is a strictly increasing function of the parameters that decrease the competition pressure of x on y by increasing herbivory on its competitor (x) expressed in the herbivores attack coefficient (b_x) or fecundity coefficient (f). As the dispersal coefficient of the herbivore (d) increases spillover of herbivores to the natural compartment, therewith increasing herbivory on x, this releases y from competition.

Third, the effect of changes from default parameter values on the equilibrium density of species w is presented in Fig. 9E and F. Weed density is mostly affected by its herbivore in the managed compartment. Thus, changes in the parameter values related to the species in the natural compartment essentially leave the weed density in the managed compartment little or not affected. However, parameters related to the birth and death rates of herbivores in the managed compartment (b_w, f and q) have a significant effect on w. The equilibrium density of w strictly decreases with increasing herbivore attack coefficient (b_w) and fecundity coefficient (f). Moreover, w^* is a strictly increasing function of herbivore death rate (q). This is consistent with Lotka–Volterra prey–predator models (Begon et al., 2006).

Fourth, the relationship between percentage change from the default parameter value and the equilibrium density of species z_m is presented (Fig. 9G and H). As r_w and k_w increase the density of weed in the managed compartment increases, resulting in increase in the density of its herbivores (z_m). The equilibrium density z_m strictly increases with the fecundity coefficient (f) and strictly decreases with the death rate of herbivores (q), respectively.

Fifth, the relationship between percentage change from default parameter value and the equilibrium density of species z_n is pre-

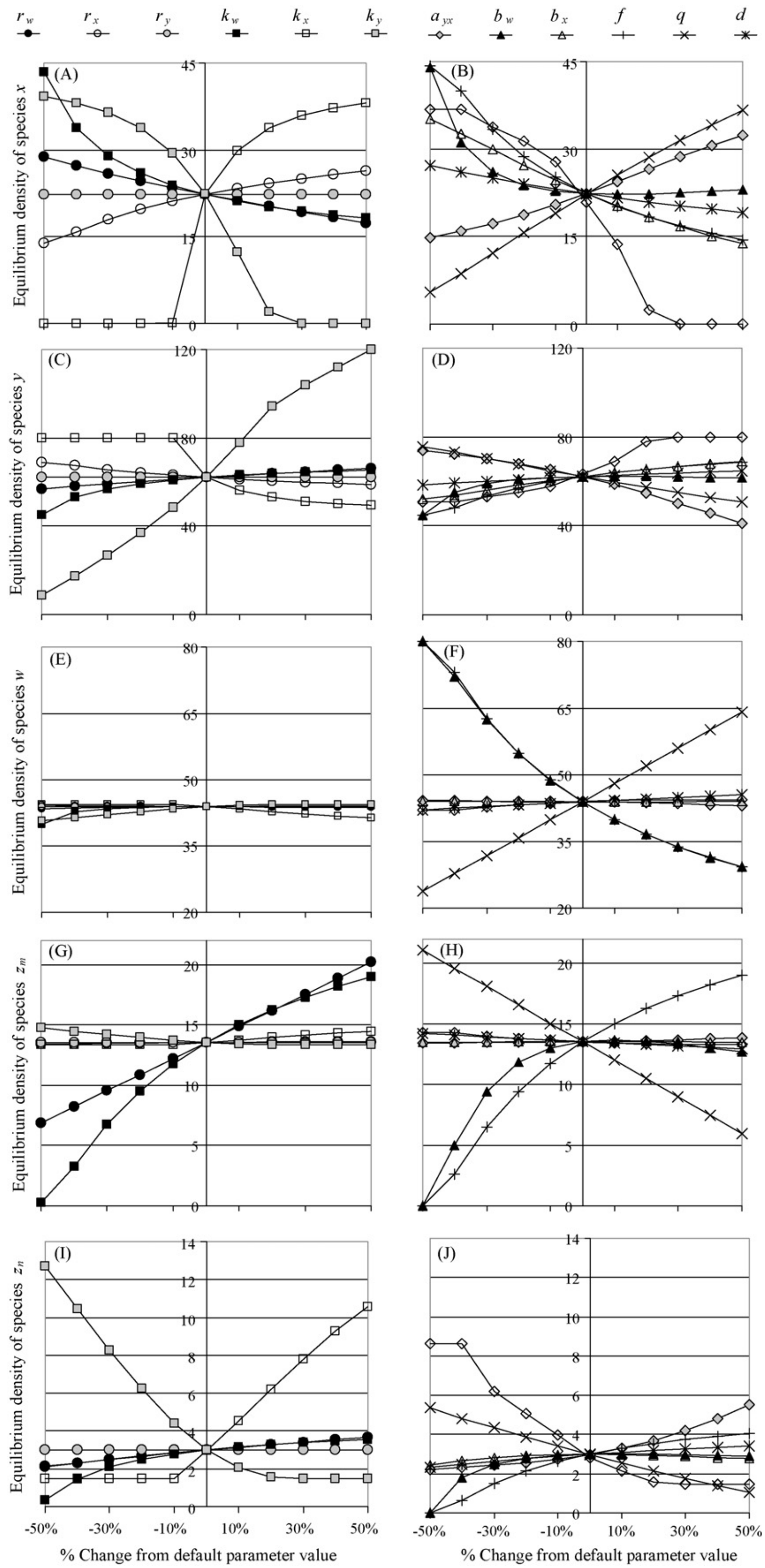

Fig. 9. Sensitivity analysis of the model for all parameters. We show the relationship between percentage change from the default parameter value and the respective equilibrium density of the 5 state variables of the model: the effect of changing parameter values on the (A and B) equilibrium density of plant species x that can be attacked by the insect herbivore in the natural compartment (C and D) equilibrium density of the competitor plant species y in the natural compartment (E and F) equilibrium density of the pest weed w in the managed compartment (G and H) equilibrium density of the insect herbivore z_m in the managed compartment (I and J) equilibrium density of the insect herbivore z_n in the natural compartment.

sented in Fig. 9I and J. Parameters k_x and a_{yx}, which increase the herbivores' food density (x), have a strictly positive effect on z_n. In contrast, k_y and a_{xy} have a decreasing effect on x, an therefore a strictly decreasing effect on z_n. The equilibrium density z_n is an increasing function of b_x and f and a decreasing function of herbivore death rate (q). Increases in k_w and r_w increase herbivore density in the managed compartment, increasing z_n due to a higher spillover of herbivore to the natural compartment.

6. 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 herbivore introduced for biological control in agriculture. Extinction is enhanced by: (1) a large resident population of the herbivore 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 herbivore 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 that 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 would benefit from knowledge of the competition pressure on potential non-target host plants of the herbivore 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 a potential threat to the persistence of the non-target host species.

We showed that dispersal of the herbivore species can play 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 recommend further studies to clarify to what extent spillover of a herbivore can influence the natural habitat. We show not only that spillover can reduce the density of plant species in the natural habitat but also that it can cause extinction of a wild species.

While spillover of the natural enemy from the managed to the natural compartment would generally be considered a negative externality, spillover of the natural enemy from the natural to the managed compartment could be advantageous. Natural enemy subsidy from a natural compartment lowers the equilibrium density of the weed in the managed compartment and it can make the invasive go extinct altogether (equilibrium **xii** in Table 2), something which is not possible in the standard one-compartment Lotka–Volterra host–herbivore system. However, this benefit comes at a price: introduction of a novel herbivore in the natural compartment. In the case of natural enemy spillover from a natural to a managed compartment, the natural compartment is providing the ecosystems service of biological control to the managed compartment (e.g. Bianchi and van der Werf, 2004; Tscharntke et al., 2005; Bianchi et al., 2006). Thus, spillover is a double-edged swoard, and the pros and cons of any spillover need to be considered on a case by case basis.

We further demonstrated that the risk of extinction can be higher when the herbivores have a low attack rate on the target plant species as a low attack rate can facilitate high densities of the target weed and attendant high herbivore populations and spillover to other ecosystem compartments. This finding is in contrast with reports in the literature that suggest that herbivores with a low attack rate may be safer for the host plant (e.g. Begon et al., 2006, p. 299). Thus, 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 they can also pose a larger risk to wild species in the natural habitat due to greater spillover. Thus, the requirements of a high attack rate on the target species and host specificity, also mitigate the chance of side effects because they reduce the consequences of possible spillover.

Acknowledgments

We thank Dr. A.J.V. Rotteveel and T. Heijerman for helpful discussions on the parameter values. We acknowledge E. Hendrix and D. Pannell for their useful comments. We thank two anonymous reviewers for insightful comments.

Appendix A. Appendix

A.1. Non-dimensionalization of the model system

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 $t = T/d$, $x = k_xX$, $y = k_yY$, $z_n = (d/b_x)Z_n$, $z_m = (d/b_w)Z_m$, $w = k_wW$. We get:

$$\left.\begin{aligned} \frac{dW}{dT} &= \mu W(1-W) - WZ_m \\ \frac{dZ_m}{dT} &= \varepsilon WZ_m - \zeta Z_m + (\eta Z_n - Z_m) \\ \frac{dZ_n}{dT} &= \vartheta XZ_n - \zeta Z_n + (\frac{1}{\eta}Z_m - Z_n) \\ \frac{dY}{dT} &= \gamma Y(1 - Y - \delta X) \\ \frac{dX}{dT} &= \alpha X(1 - X - \beta Y) - Z_nX \end{aligned}\right\} \tag{A1}$$

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

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

A.2. Derivation of the equilibria

From system (A1) we get the following conditions that have to be combined for getting the equilibria:

$$(\mathbf{Ia})\ W = 0 \vee (\mathbf{Ib})\ \mu(1 - W) = Z_m \tag{A2}$$

$$(\mathbf{II})\ Z_m - \varepsilon W\ Z_m + \zeta Z_m = \eta\ Z_n \tag{A3}$$

$$(\mathbf{III})\ Z_n - \vartheta X\ Z_n + \zeta Z_n = \frac{1}{\eta}\ Z_m \tag{A4}$$

$$(\mathbf{IVa})\ Y = 0 \vee (\mathbf{IVb})\ Y = 1 - \delta X \tag{A5}$$

$$(\mathbf{Va}) X = 0 \vee (\mathbf{Vb}) Z_n = \alpha(1 - X - \beta Y) \tag{A6}$$

The combination of conditions (**II**) and (**III**) give either no insects present (steady states **i**–**viii**, Table 2) or insects present in both compartments (steady states **ix**–**xiv**, Table 2). A summary of the results of combining insects absent or present with a combination of conditions (**Ia** or **Ib**) with (**IVa** or **IVb**) and (**Va** or **Vb**) is given in Table 2. For certain combinations no extra equilibria are found because of internal inconsistency (**Ia**, **IVa**, **Va** and insects present and **Ia**, **IVb**, **Va** and insects present).

A.3. Stability analysis of steady states

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

$$Jacobian(general) = \begin{pmatrix} \mu(1-2\bar{W})-\bar{Z}_m & -\bar{W} & 0 & 0 & 0 \\ \varepsilon\bar{Z}_m & \varepsilon\bar{W}-\zeta-1 & \eta & 0 & 0 \\ 0 & \dfrac{1}{\eta} & \vartheta\bar{X}-\zeta-1 & 0 & \vartheta\bar{Z}_n \\ 0 & 0 & 0 & \gamma(1-2\bar{Y}-\delta\bar{X}) & -\gamma\delta\bar{Y} \\ 0 & 0 & -\bar{X} & -\alpha\beta\bar{X} & \alpha(1-2\bar{X}-\beta\bar{Y})-\bar{Z}_n \end{pmatrix} \quad (A7)$$

To test the stability of each equilibrium we substitute the equilibrium densities of all 5 interacting 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. Analysis shows that equilibria (**i**–**vi**) are unstable (saddle points). For the other steady states a numerical analysis has been performed.

References

Begon, M., Townsend, C.R., Harper, J.L., 2006. Ecology: From Individuals to Ecosystems. Blackwell Publishing, Oxford.

Bianchi, F.J.J.A., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proceedings of the Royal Society, Series B 273, 1715–1727.

Bianchi, F.J.J.A., van der Werf, W., 2004. Model evaluation of the function of prey in non-crop habitats for biological control by ladybeetles in agricultural landscapes. Ecological Modelling 171, 177–193.

Callaway, R.M., Aschehout, E.T., 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290, 521–523.

Chalak, M., Ruijs, A., van Ierland, E.C., 2009. On the economics of controlling an invasive plant: a stochastic analysis of a biological control agent. International Journal of Environmental Technology and Management 11, 187–206.

Chalak-Haghighi, M., Ruijs, A., van Ierland, E.C., 2008. Management strategies for an invasive weed: a dynamic programming approach for Californian thistle in New Zealand. New Zealand Journal of Agricultural Research 51, 409–424.

Charudattan, R., 2001. Biological control of weeds by means of plant pathogens: significance for integrated weed management in modern agro-ecology. BioControl 46, 229–260.

Cronin, J.T., Reeve, J.D., 2005. Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. Proceeding of the Royal Society B 272, 225–2235.

Edelstein-Keshet, L., 1988. Mathematical Models in Biology. Random House, New York.

Ehler, L.E., 1998. Invasion biology and biological control. Biological Control 13, 127–133.

Follett, P., Duan, J., 1999. Nontarget Effects of Biological Control. Kluwer, Dortrecht/Boston/London, p. 316.

Henneman, M.L., Memmott, J., 2001. Infiltration of a Hawaiian community by introduced biological control agent. Science 293, 1314–1316.

Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12, 197–229.

Louda, S.M., Pemberton, R.W., Johnson, M.T., Follett, P.A., 2003. Nontarget effects—the Achilles heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annual Review of Entomology 48, 365–396.

Louda, S.M., Rand, T.A., Arnett, A.E., McClay, A.S., Shea, K., McEachern, A.K., 2005. Evaluation of population risk to populations of a threatened plant from an invasive biocontrol insect. Ecological Applications 15 (1), 234–249.

McKone, M., McLauchlan, K.K., Lebrun, E.G., McCall, A.C., 2001. An edge effect caused by adult corn-rootworm beetles on sunflowers in tallgrass prairie remnants. Conservation Biology 15, 1315–1324.

Pemberton, R.W., 2000. Predictable risk to native plants in weed biological control. Oecologia 125, 489–494.

Pimentel, D. (Ed.), 2002. Biological Invasion Economics and Environmental Costs of Alien Plant, Animal, and Microbe Species. CRC Press, Boca Raton, FL, USA.

Rand, T.A., Tylianakis, J.M., Tscharntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecology Letters 9, 603–614.

Schwinning, S., Parsons, A.J., 1999. The stability of grazing systems revisited: spatial models and the role of heterogeneity. Functional Ecology 13, 737–747.

Sheppard, A.W., Hill, R., DeClerck-Floate, R.A., McClay, A., Olckers, T., Quimby Jr.P.C., Zimmermann, H.G., 2003. A global review of risk–benefit–cost analysis for the introduction of classical biological control agents against weeds: a crisis in the market? Biocontrol News and Information 24, 91N–108N.

Suarez, A.W., Bolger, D.T., Case, T.J., 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79, 2014–2056.

Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47, 561–594.

Thomas, M.B., Willis, A.J., 1998. Biocontrol—risky but necessary? Trends in Ecology and Evolution 13, 325–329.

Tscharntke, T., Rand, T.A., Bianchi, F.J.J.A., 2005. The landscape context of trophic interactions: insect spillover across the crop–noncrop interface. Annales Zoologici Fennici 42, 421–432.

Vellend, M., Myers, J.A., Gardescu, S., Marks, P.L., 2003. Dispersal of *Trillium* seeds by deer: implications for long distance migration of forest herbs. Ecology 84, 1067–1072.

Wajnberg, E., Scott, J.K., Quimby, P.C., 2001. Evaluating Indirect Ecological Effects of Biological Control. CABI, Wallingford, Oxon, UK, p. 261.

Wirth, R., Meyer, S.T., Leal, I.R., Tabarelli, M., 2007. Plant–herbivore interactions at the forest edge. In: Lüttge, U., Beyschlag, W., Murata, J. (Eds.), Progress in Botany, vol. 69, pp. 423–448.