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

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A B S T R A C T

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.

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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 Aschehoug, 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
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 (zm, 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 zn, 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).

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 herbivide densities in the natural compartment are subsidised by spillover from the managed compartment.

The dispersal of the herbivore influences both its own local densities (zm and zn) 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:

\[
\frac{dw}{dt} = rww \left( 1 - \frac{w}{kw} \right)
\]  \hspace{1cm} (1)

where \( rw \) is the growth rate of the weed, and \( kw \) 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

\[
\frac{dw}{dt} = rww \left( 1 - \frac{w}{kw} \right) - bwwzmw
\]  \hspace{1cm} (2)

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

$$\frac{dx}{dt} = r_x x \left(1 - \frac{x + y axy}{k_x}\right)$$

$$\frac{dy}{dt} = r_y y \left(1 - \frac{y + x axy}{k_y}\right) \quad (3)$$

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:

$$\frac{dx}{dt} = r_x x \left(1 - \frac{x + y axy}{k_x}\right) - b_x z x$$

$$\frac{dy}{dt} = r_y y \left(1 - \frac{y + x axy}{k_y}\right) \quad (4a\text{ and } b)$$

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:

$$\frac{dz_m}{dt} = b_x x z_n - q z_n + d (z_m - z_n) \quad (5a\text{ and } b)$$

$$\frac{dz_n}{dt} = b_w w z_m - q z_m + d (z_n - z_m)$$

where $z_n$ and $z_m$, 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 $b_x x z_n$ 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: $b_w$, $b_x$, $k_w$, $k_x$, $k_y$, $r_x$, $r_y$, $a_{xy}$, $a_{yx}$, $f$, $q$ 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 (i, ii 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 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Default Value</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x$</td>
<td>shoots m$^{-2}$</td>
<td>None</td>
<td>Density of species $x$</td>
</tr>
<tr>
<td>$y$</td>
<td>shoots m$^{-2}$</td>
<td>None</td>
<td>Density of species $y$</td>
</tr>
<tr>
<td>$w$</td>
<td>shoots m$^{-2}$</td>
<td>None</td>
<td>Density of species $w$</td>
</tr>
<tr>
<td>$z_n$</td>
<td>m$^{-2}$</td>
<td>None</td>
<td>Density of herbivores in the natural compartment</td>
</tr>
<tr>
<td>$z_m$</td>
<td>m$^{-2}$</td>
<td>None</td>
<td>Density of herbivores in the managed compartment</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Unit</th>
<th>Value</th>
<th>Explanation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_x$</td>
<td>yr$^{-1}$</td>
<td>0.3$^a$</td>
<td>Intrinsic growth rate of plant species $x$</td>
<td>From Chalak-Haghighi et al. (2008).</td>
</tr>
<tr>
<td>$k_x$</td>
<td>shoots m$^{-2}$</td>
<td>80$^b$</td>
<td>Carrying capacity of plant species $x$</td>
<td>Based on longevity of adult weevils provided by Theodoor Heijerman.</td>
</tr>
<tr>
<td>$a_{xy}$</td>
<td>None</td>
<td>0.3$^a$</td>
<td>Competition coefficient of species $y$ with respect to species $x$</td>
<td>Expert opinion of the authors.</td>
</tr>
<tr>
<td>$b_{xy}$</td>
<td>(shoots m$^{-2}$)$^{-1}$ yr$^{-1}$</td>
<td>0.01$^a$</td>
<td>Attack rate of the herbivore $z$ on plant species $x$</td>
<td>From Chalak-Haghighi et al. (2008).</td>
</tr>
<tr>
<td>$r_y$</td>
<td>yr$^{-1}$</td>
<td>0.3$^a$</td>
<td>Intrinsic growth rate of plant species $y$</td>
<td>Expert opinion of the authors.</td>
</tr>
<tr>
<td>$k_y$</td>
<td>shoots m$^{-2}$</td>
<td>80$^b$</td>
<td>Carrying capacity of plant species $y$</td>
<td>Based on longevity of adult weevils provided by Theodoor Heijerman.</td>
</tr>
<tr>
<td>$a_{yx}$</td>
<td>None</td>
<td>0.3$^a$</td>
<td>Competition coefficient of species $x$ with respect to species $y$</td>
<td>Expert opinion of the authors.</td>
</tr>
<tr>
<td>$b_{yx}$</td>
<td>(shoots m$^{-2}$)$^{-1}$ yr$^{-1}$</td>
<td>0.01$^a$</td>
<td>Attack rate of the herbivore $z$ on plant species $w$</td>
<td>From Chalak-Haghighi et al. (2008).</td>
</tr>
<tr>
<td>$f$</td>
<td>Offspring per shoot</td>
<td>10$^b$</td>
<td>Fecundity coefficient of the herbivore</td>
<td>Based on longevity of adult weevils provided by Theodoor Heijerman.</td>
</tr>
<tr>
<td>$q$</td>
<td>yr$^{-1}$</td>
<td>4$^a$</td>
<td>Relative death rate of the herbivore</td>
<td>Expert opinion of the authors.</td>
</tr>
<tr>
<td>$d$</td>
<td>yr$^{-1}$</td>
<td>0.5$^a$</td>
<td>Dispersal coefficient of the herbivore</td>
<td>Expert opinion of the authors.</td>
</tr>
</tbody>
</table>
Steady states \( \langle W, \tilde{Z}, \tilde{y}, \tilde{x} \rangle \) 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.

<table>
<thead>
<tr>
<th>Name</th>
<th>[ \langle W, \tilde{Z}, \tilde{y}, \tilde{x} \rangle ]</th>
<th>Stability</th>
<th>Description/comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i) Trivial equilibrium</td>
<td>((0, 0, 0, 0, 0))</td>
<td>Unstable</td>
<td>All species extinct</td>
</tr>
<tr>
<td>(ii) Single species equilibrium</td>
<td>((1, 0, 0, 0, 0))</td>
<td>Unstable</td>
<td>(w) is at its carrying capacity</td>
</tr>
<tr>
<td>(iii) Single species equilibrium</td>
<td>((0, 0, 0, 1, 0))</td>
<td>Unstable</td>
<td>(y) is at its carrying capacity</td>
</tr>
<tr>
<td>(iv) Single species equilibrium</td>
<td>((0, 0, 0, 1))</td>
<td>Unstable</td>
<td>(x) is at its carrying capacity</td>
</tr>
<tr>
<td>(v) Two species equilibrium</td>
<td>((1, 0, 0, 0, 0))</td>
<td>Unstable</td>
<td>Both (x) and (w) are at their carrying capacity</td>
</tr>
<tr>
<td>(vi) Two species equilibrium</td>
<td>((1, 0, 0, 1, 0))</td>
<td>Unstable</td>
<td>Both (y) and (w) are at their carrying capacity</td>
</tr>
<tr>
<td>(vii) Equilibrium 1 with only competition</td>
<td>((0, 0, \frac{1-\beta}{(1-\beta_1)}, \frac{1-\beta}{(1-\beta_2)})</td>
<td>Unstable</td>
<td>No herbivores; (x) and (y) in their stable competition equilibrium; (w) extinct</td>
</tr>
<tr>
<td>(viii) Equilibrium 2 with only competition</td>
<td>((1, 0, 0, \frac{1-\beta}{(1-\beta_1)}, \frac{1-\beta}{(1-\beta_2)})</td>
<td>Unstable</td>
<td>No herbivores; (x) and (y) in their stable competition equilibrium; (w) at its carrying capacity</td>
</tr>
<tr>
<td>(ix) Managed compartment only</td>
<td>((\bar{W}, \mu(1-\bar{W}), \frac{\mu(1-\bar{W})}{W_{\text{max}}}, 0, 0))</td>
<td>Unstable</td>
<td>With (W = \frac{\mu(1-W)}{W_{\text{max}}}); species (x) and (y) extinct</td>
</tr>
<tr>
<td>(x) Managed compartment and species (y)</td>
<td>((\bar{W}, \mu(1-\bar{W}), \frac{\mu(1-\bar{W})}{W_{\text{max}}}, 1, 0))</td>
<td>Depending on the parameter values</td>
<td>With (W = \frac{\mu(1-W)}{W_{\text{max}}}); species (x) extinct and (y) at its carrying capacity</td>
</tr>
<tr>
<td>(xi) Natural compartment only (species (y) extinct)</td>
<td>((0, \frac{\mu}{W_{\text{max}}}(1-\bar{X}), \alpha(1-\bar{X}), 0, \bar{X}))</td>
<td>Unstable</td>
<td>With (\bar{X} = \frac{\alpha(1+\bar{X})}{\mu}); species (w) and (y) extinct</td>
</tr>
<tr>
<td>(xii) Natural compartment only</td>
<td>((0, \frac{\mu}{W_{\text{max}}}(1-\bar{X}), \alpha(1-\bar{X}), 1-\bar{X}, \bar{X}))</td>
<td>Unstable</td>
<td>With (\bar{X} = \frac{\alpha(1+\bar{X})}{\mu}); species (w) extinct</td>
</tr>
<tr>
<td>(xiii) Implicit equation</td>
<td>((\bar{W}_1, \bar{Z}, \bar{z}, 0, \bar{X}))</td>
<td>Unstable</td>
<td>Extinction of species (y)</td>
</tr>
<tr>
<td>(xiv) Implicit equation</td>
<td>((\bar{W}_2, \bar{Z}, \bar{z}, 0, \bar{X}))</td>
<td>Depending on the parameter values</td>
<td>Possibly positive for all five state variables</td>
</tr>
</tbody>
</table>

\(^a\) For a large range of parameter values.
\(^b\) No interaction between compartments.

We are here particularly interested in the boundary equilibrium \(\mathbf{x}\) in which \(x\) is not present, i.e. \(x^* = 0\). In terms of stability of the equilibrium, we are particularly interested in knowing which parameter changes make the interior equilibrium \(\mathbf{x}_{\mathbf{IV}}\) unstable whereby stability is transferred to boundary equilibrium \(\mathbf{x}\), 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 \(\beta \) and \(\delta < 1\) (see Appendix A). But equilibria \(\mathbf{vii}\) and \(\mathbf{viii}\) are unstable for a large set of parameter values for our system (system A1, in Appendix A) even when \(\beta \) 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 \(\mathbf{i}–\mathbf{vi}\). For the other equilibrium a numerical analysis is performed.

4. Numerical analysis

For the numerical analysis, two equilibria are of particular interest: \(\mathbf{i}\) equilibrium \(\mathbf{x}_{

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 \(\mathbf{x}_{\mathbf{IV}}\) \((w^*\), \(z^*_n\), \(z^*_m\), \(y^*\), \(x^*\)) and parameter values are shown. Simulations showed that stable equilibrium 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 \(x, y, w\) have a default relative growth rate of 0.3 yr⁻¹ and a carrying
capacity of 80 shoots m\(^{-2}\) (Schwinning and Parsons, 1999; Chalak-Haghghi 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, 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 \(x_{iv}\) to equilibrium \(x_{iv}\). 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 compartments.

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 \(a_{xy}\) has a similar effect, but mirrored: if \(a_{xy}\) increases, \(y\) 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 \(a_{xx}\) 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 \(a_{xx}\).

The effect of 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 \(b_w\) at which extinction occurs are for \(b_{x} = 0.01\), where the spillover effect is maximal. For lower \(b_{x}\) (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 (given in shoots m\(^{-2}\) 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. 3.** Effect of competition coefficients \(a_{xy}\) and \(a_{xx}\) 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), \(z_m^*\) and \(z_n^*\) (herbivore densities in the natural and managed compartments). The vertical lines show the default value for \(a_{xy}\) and \(a_{xx}\), all other parameters are at their default values.
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 ($b_n$) 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 $\text{x XIV}$ to $\text{x}$ (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 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 ($b_n$) 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. 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.
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 \( y \) \( (a_{xy}) \), 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 \( k_y \). 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 \( x \) \( (a_{xy}) \) 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 \( z_w \) 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 \( (z_{wy}) \). The equilibrium density \( z_w \) 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.
ented in Fig. 9I and J. Parameters $k_x$ and $a_{px}$, which increase the herbivores’ food density ($x$), have a strictly positive effect on $z_n$. In contrast, $k_y$ and $a_{py}$ 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 $b_w$ 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 sword, 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 lower 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.

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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 $t = T/d$, $x = ksX$, $y = kyY$, $z_n = (d/bw)z_n$, $z_m = (d/bw)z_m$, $w = kwW$. We get:

$$
\begin{align*}
\frac{dW}{dT} &= \mu W(1 - W) - WZ_m, \\
\frac{dz_n}{dT} &= \varepsilon WZ_n - \xi Z_n + (\eta Z_n - Z_m), \\
\frac{dz_m}{dT} &= \delta XZ_n - \xi Z_m + (\frac{1}{\eta} Z_m - Z_n), \\
\frac{dY}{dT} &= \gamma Y(1 - Y - \delta X), \\
\frac{dX}{dT} &= \alpha X(1 - X - \beta Y) - Z_nX
\end{align*}
$$

(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

$$
\begin{align*}
\alpha &= \frac{r_s}{d}, \quad \beta = \frac{a_{py}k_y}{k_x}, \quad \gamma = \frac{r_y}{d}, \quad \delta = \frac{a_{px}k_x}{k_y}, \quad \varepsilon = \frac{f}{d}b_wk_w, \quad \xi = \frac{q}{d}W, \\
\theta &= \frac{b_w}{b_x}, \quad \eta = \frac{f}{d}b_xk_x, \quad \mu = \frac{r_w}{d}.
\end{align*}
$$

A.2. Derivation of the equilibria

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

$$
\begin{align*}
(Ia) & W = 0 \lor (Ib) \mu(1 - W) = Z_m, \\
(II) & Z_m - \varepsilon WZ_m + \xi Z_n = \eta Z_n, \\
(III) & Z_n - \delta XZ_n + \xi Z_m = \frac{1}{\eta} Z_m, \\
(IVa) & Y = 0 \lor (IVb) Y = 1 - \delta X, \\
(Va) & X = 0 \lor (Vb) Z_n = \alpha(1 - X - \beta Y)
\end{align*}
$$

(A2)-(A6)
A.3. Stability analysis of steady states

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

\[
\begin{pmatrix}
\frac{\eta}{\xi} & -W & 0 & 0 & 0 \\
\xi \bar{W} & -\xi & -\xi & \eta & 0 \\
0 & \frac{\eta}{\xi} & -\bar{X} & -1 & 0 \\
0 & 0 & \gamma (1 - 2 \bar{Y} - \delta X) & -\gamma \delta \bar{Y} & 0 \\
0 & 0 & -\bar{X} & -\alpha \delta \bar{X} & \alpha (1 - 2 \bar{X} - \beta \bar{Y}) - \bar{Z} \\
\end{pmatrix}
\]

(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


