

Integrated Pest Management in a Predator-Prey System with Allee Effects

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Keywords

Allee dynamics, biological control, ditrophic system, inoculative release, sustainable pest management

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Abstract

A commonly used biocontrol strategy to control invasive pests with Allee effects consists of the deliberate introduction of natural enemies. To enhance the effectiveness of this strategy, several tactics of control of invasive species (e.g., mass-trapping, manual removal of individuals, and pesticide spraying) are combined so as to impair pest outbreaks. This combination of strategies to control pest species dynamics are usually named integrated pest management (IPM). In this work, we devise a predator-prey dynamical model in order to assess the influence of the intensity of chemical killing on the success of an IPM. The biological and mathematical framework presented in this study can also be analyzed in the light of species conservation and food web dynamics theory.

Introduction

Invasive species increasingly threaten ecosystems worldwide, jeopardizing, among other instances, food production. To counteract the threat imposed by invasive and/or native species to agroecosystems, several tactics of control of pest species (e.g., mass-trapping, manual removal of individuals, and pesticide spraying) are combined so as to effectively impair pest outbursts. This combination of strategies to control pest species dynamics is usually named integrated pest management (IPM) (Tobin *et al* 2011).

A commonly used biocontrol strategy consists of the deliberate introduction of natural enemies of an invasive pest species (Blackwood *et al* 2012, Suckling *et al* 2012), taking advantage of the acknowledged fact that demographic and/or component Allee effects are commonly present in the dynamics of an invasive species. In this way, it is expected that natural enemies drive the pest population below a critical threshold from where Allee effects of the pest population take over and eliminate it. Cases of success and failures of this strategy have been reported (Hopper & Roush 1993, and references therein).

One of the alleged reasons of failure has been frequently related to Allee effects inherent to the biological control agent (Boukal *et al* 2007).

In this work, in order to assess the effectiveness of an IPM strategy consisting of biological and chemical procedures, we devised a predator-prey dynamical model where the prey species is the pest and the consumer is the deliberately introduced biological control agent. That is to say, in our proposed model, both pest and control agent are supposed to be exotic species. Based on the empirical evidences mentioned before, it is supposed that the consumer (the biological control agent) has an Allee effect in its numerical response (Zhou *et al* 2005, Verdy 2010).

It is also assumed that the pest (an invasive species) possesses a demographic Allee effect (Boukal *et al* 2007). As to the chemical pest control in the IPM, it is supposed that it affects both pest and biological control agent (Van Lenteren & Woets 1988, Lu *et al* 2003). With this proposed biological and chemical framework, we intend to tackle the following problem regarding pest control: how does the intensity of chemical killing in an IPM affect pest dynamics? The answers to this question will be provided by an analysis consisting of one-parameter bifurcation diagrams drawn by means of the

XPPAUT package (Ermentrout 2002) and their respective phase planes drawn by program MATLAB.

It is important to remark that the population dynamical models used in this work are of strategic type (May 2001), and as such, they do not correspond to a specific real community. Instead, they provide a conceptual framework to understand some aspects of the species dynamics of a relatively broad class of communities. Furthermore, although the proposed models involve only two dynamical variables (pest and its introduced natural enemy populations), they have a large number of parameters. Hence, this study is concerned with showing possible outcomes related to the hypothetical chosen sets of parameter values of these strategic models, rather than providing an exhaustive study of conditions required for all possible outcomes (Abrams & Roth 1994).

Material and Methods

Predator-prey model with functional response type 2 and Allee effect in prey and predator

The population framework to be analyzed is schematically displayed in Fig 1 (hereinafter FR_i , ($i=1,2$) will denote functional response type i , and the terms density and number of individuals will be used interchangeably).

It consists basically of a ditrophic food chain with prey (pest, x) and predator (an introduced natural enemy of pest, y). A continuous time dynamical model for the trophic scheme of Fig 1 with functional response type 2 (FR_2) of the predator (y) upon the prey (x) can be given by the following:

$$\begin{aligned} \frac{dx}{dt} &= rx \left(\frac{x-x_{cr}}{K} \right) \left(1 - \frac{x}{K} \right) - \left(\frac{a_{yx}x}{1 + a_{yx}T_{hyx}x} \right) y - F_x x \\ \frac{dy}{dt} &= ef_{xy} \left(\frac{y}{\theta_y + y} \right) e^{-\alpha_y y} \left(\frac{a_{yx}x}{1 + a_{yx}T_{hyx}x} \right) y - m_y y - \beta F_x y \end{aligned} \tag{1}$$

where x is the density of pest individuals and y is the density of biological control agent individuals. r is the maximum per capita rate of pest growth and K is its carrying capacity. x_{cr} is the critical threshold of a demographic Allee effect level of the pest. a_{xy} represents the attack coefficient of the introduced biological control agent y upon the pest x . T_{hyx} is the manipulation time of x by y , while ef_{xy} is the biological control agent's food-to-offspring (x to y) conversion efficiency coefficient. $y/(\theta_y+y)$ describes the Allee effect in y where θ_y denotes its intensity. $e^{-\alpha_y y}$ describes a negative density dependent effect impinged on y and α_y is its intensity. m_y is the density independent per capita mortality rate of y .

This work will focus upon IPM where y is supposed to have a functional response type 2 on the pest (x), since this response exerts a strongly predation pressure—a desirable feature of a biological control agent. The

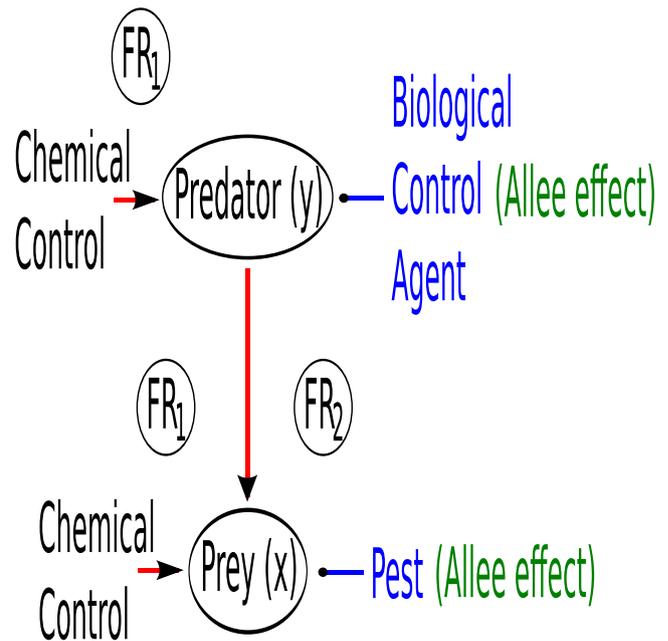


Fig 1 A predator (y) acts upon the prey (x) with functional response type 2. Allee effects and chemical control act simultaneously on x and y .

chemical part of the management, which in this case takes on the form of pesticide application, will be described by the terms F_x and βF_x . Note that the chemical procedure incurs losses to the pest (x) as well to the biological control agent (y) proportional to their respective densities, and these losses are modulated by the constant $\beta > 0$ (see Davidson *et al* 2002 for similarly reported cases in pest management). In this way, model (1) can be seen as describing an IPM: (i) pesticide application ($-F_x x$ and $-\beta F_x y$) and (ii) introduction of a pest natural enemy (y).

Predator-prey model with functional response type 2 and Allee effect only in predator

Another possible scenario is the absence of Allee effect in the pest population (Bompard *et al* 2013), which can be modeled in our setup by the elimination of the term $(x - x_{cr})/K$ in the pest equation (x). This can be considered as the worst-case scenario since there is no a priori demographic Allee effect in the pest population. Therefore, pest population cannot be lowered down to a level where the control procedures are discontinued and Allee effects set in leading the pest population to extinction.

Consider the following predator-prey model:

$$\begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K} \right) - \left(\frac{a_{yx}x}{1 + a_{yx}T_{hyx}x} \right) y - F_x x \\ \frac{dy}{dt} &= ef_{xy} \left(\frac{y}{\theta_y + y} \right) e^{-\alpha_y y} \left(\frac{a_{yx}x}{1 + a_{yx}T_{hyx}x} \right) y - m_y y - \beta F_x y \end{aligned} \tag{2}$$

Results

Predator-prey model with functional response type 2 and Allee effect in prey and predator

As mentioned before, in Fig 2, we resort to a bifurcation diagram of model (1) as a function of F_x —the intensity of

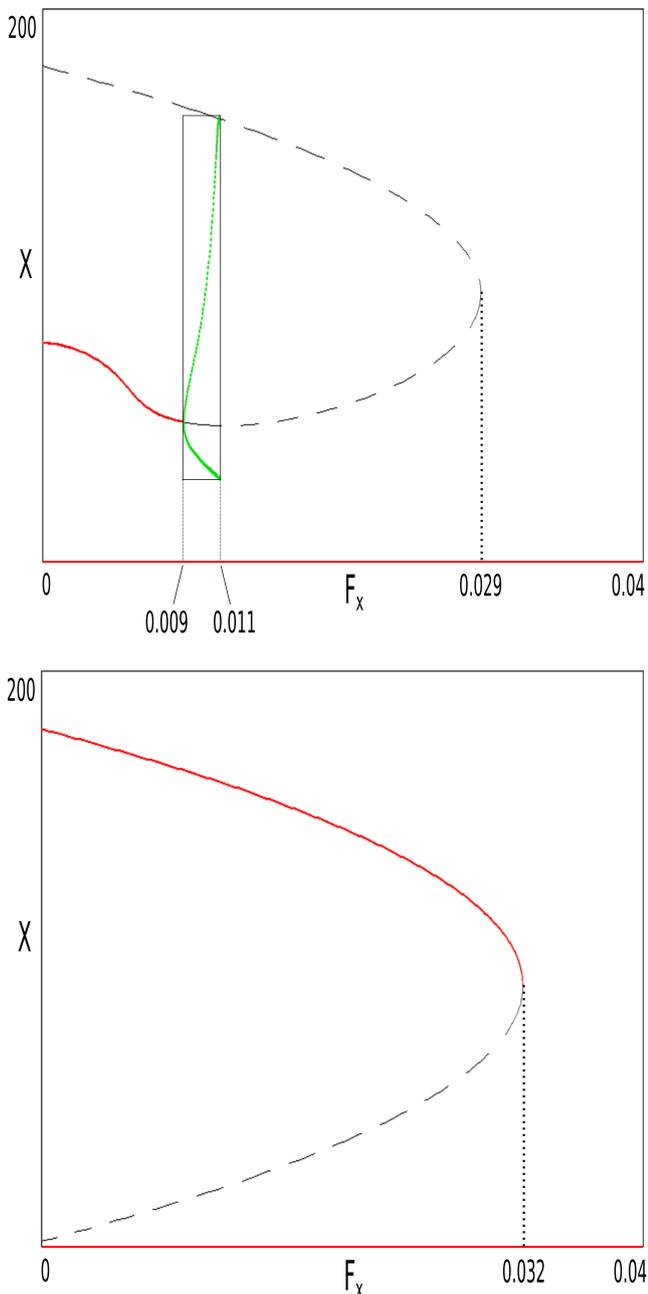


Fig 2 Bifurcation diagram of model (1) as a function of F_x —the intensity of pesticide application. *Solid lines*, stable equilibrium point; *dashed lines*, unstable equilibrium point. (a) nontrivial equilibrium points $(x,y > 0)$; (b) boundary equilibrium point $(x=K(1-F_x/r), y=0)$ and point $(0,0)$. Parameter values: $r=0.131$; $K=180$; $x_{cr}=2$; $a_{xy}=0.002$; $T_{hyx}=1$; $ef_{xy}=1$; $m_y=0.019$; $\alpha_y=0.1$; $\beta=1$; $\theta_y=3$.

pesticide application—in order to assess how the pest density varies with this combination of chemical and biological procedure. Fig 3 shows phase planes of model (1) corresponding to the bifurcation regions of Fig 2.

For $F_x=0.007$ ($0 < F_x < 0.009$; case (a) in Fig 3), initial conditions at point A give rise to a stable coexistence. In terms of IPM, pest economic threshold (i.e., pest densities below a pre-determined threshold which are not harmful from the economic point of view (Boukal & Berec 2009)) will dictate whether this stable coexistence is efficient or not. Maintaining the pest population and increasing the initial condition of the biological control agent (point B) brings about the extinction of the biological control agent and stabilization of the pest near its carrying capacity—an undesirable outcome for IPM. Maintaining the same pest population and raising further the initial condition of the biological control agent (point C) causes the extinction of pest and biological control agent—a desirable result for IPM.

For $F_x=0.01$ ($0.009 < F_x < 0.011$; case (b) in Fig 3), the results are qualitatively the same as in (a) except for the initial condition in point A, which gives rise to sustained oscillations. This may be an undesirable result for IPM due to possible pest outbursts on account of the oscillations.

For $F_x=0.02$ ($0.011 < F_x < 0.029$; case (c) in Fig 3), there is no coexistence of pest and biological control agent. Note that the initial condition in A generates extinction of pest and biological control agent, while the initial condition in B (an increase in the biological control agent population and the same population of pest) causes biological control agent extinction and pest stabilization near its carrying capacity.

For $F_x=0.03$ ($F_x > 0.029$; case (d) in Fig 3), the results are the same as in case (c), but now a significant increase from A to B generates exclusively pest and biological control agent extinction.

Finally, for $F_x=0.035$ ($F_x > 0.032$; case (e) in Fig 3), the chemical intensity is so high that the sole outcome is pest and biological control agent extinction for all initial conditions.

In pest biological control when mass rearing is efficient, large numbers of natural enemies of pest can be introduced in a given area (inundative releases). However, it is known that mass rearing is usually not so efficient or is not economically feasible, and in that case, the natural enemies of pest are released in small numbers (inoculative releases).

In this view, an interesting feature emerges from cases (a)–(d) of Fig 3: success of the proposed IPM strategy does not only depend on the traits of the natural enemies of pest but also on their released quantities. This dependence, though, as evidenced in Fig 3, is not straightforward, since success and failure of IPM can alternate according to the initial population of the introduced biological control agent.

One possible way to compensate for these alternations of failure and success in IPM would be the enhancement of chemical application by means of increasing the term F_x in the pest

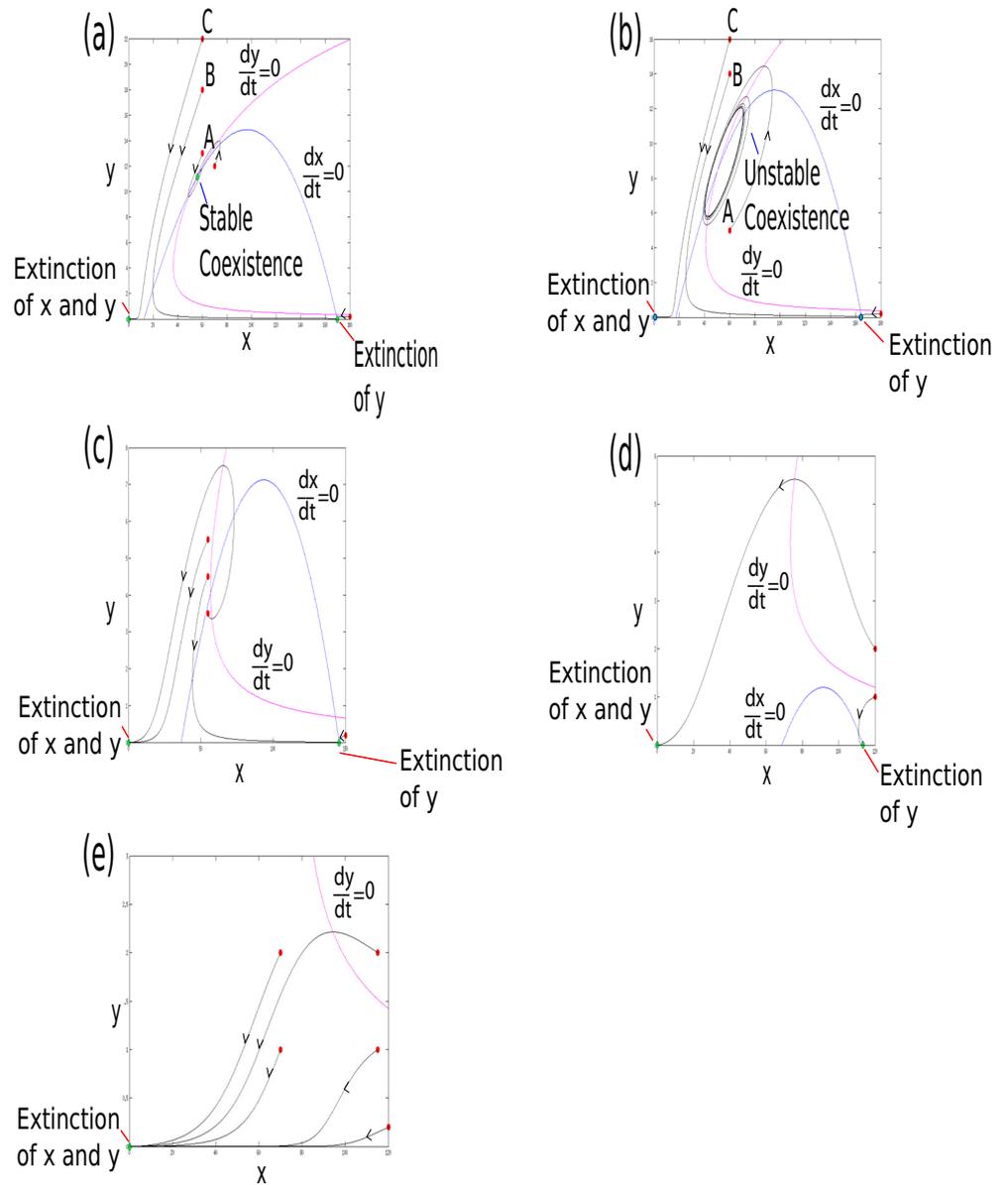


Fig 3 Phase plane of model (1). In case (a) ($F_x=0.007$) depending on initial conditions, there may occur stable coexistence, or pest and biological control agent extinction or only biological control agent extinction. In case (b), ($F_x=0.01$) it is possible to see an unstable coexistence sustained oscillations, or pest and biological control agent extinction or only biological control agent extinction, depending on initial conditions. In cases (c) ($F_x=0.02$) and (d) ($F_x=0.03$), also depending on initial conditions, there may occur pest and biological control agent extinction or only biological control agent extinction. Case (e) ($F_x=0.035$) depicts overall species extinction for all initial conditions. Parameter values: $r=0.131$; $K=180$; $x_{cr}=2$; $a_{xy}=0.002$; $T_{hyx}=1$; $ef_{xy}=1$; $m_y=0.019$; $\alpha_y=0.1$; $\beta=1$; $\theta_y=3$.

(x) dynamical equation. However, this would certainly concern environmental issues not contemplated in our models.

Predator-prey model with functional response type 2 and Allee effect only in predator

Fig 4 shows a bifurcation diagram of model (2) as a function of F_x —the intensity of pesticide application. Fig 5 shows a phase plane of model (2) corresponding to the bifurcation regions of Fig 4.

For $F_x=0.03$ ($0 < F_x < 0.047$; case (a) in Fig 5), initial conditions at point A lead to biological control agent extinction and pest stabilization near its carrying capacity—an undesirable result for IPM. Maintaining the density of the pest and increasing the number of introduced

biological control agent individuals (point B) leads to a stable coexistence of pest and biological control agent, the result of which will depend on pest tolerable economic thresholds. Case (b) in Fig 5 shows that increasing further the pest natural enemy initial condition up to C gives rise again to biological control agent extinction and pest stabilization near its carrying capacity—an undesirable result for IPM.

For $F_x=0.08$ ($F_x > 0.047$; case (c) in Fig 5), the chemical intensity is such that the sole outcome is biological control agent extinction and pest stabilization near its carrying capacity—again, an undesirable result for IPM.

For $F_x=0.15$ ($F_x > 0.131$; case (d) in Fig 5), the chemical intensity is so intense that the sole outcome is pest and biological control agent extinction for all initial conditions.

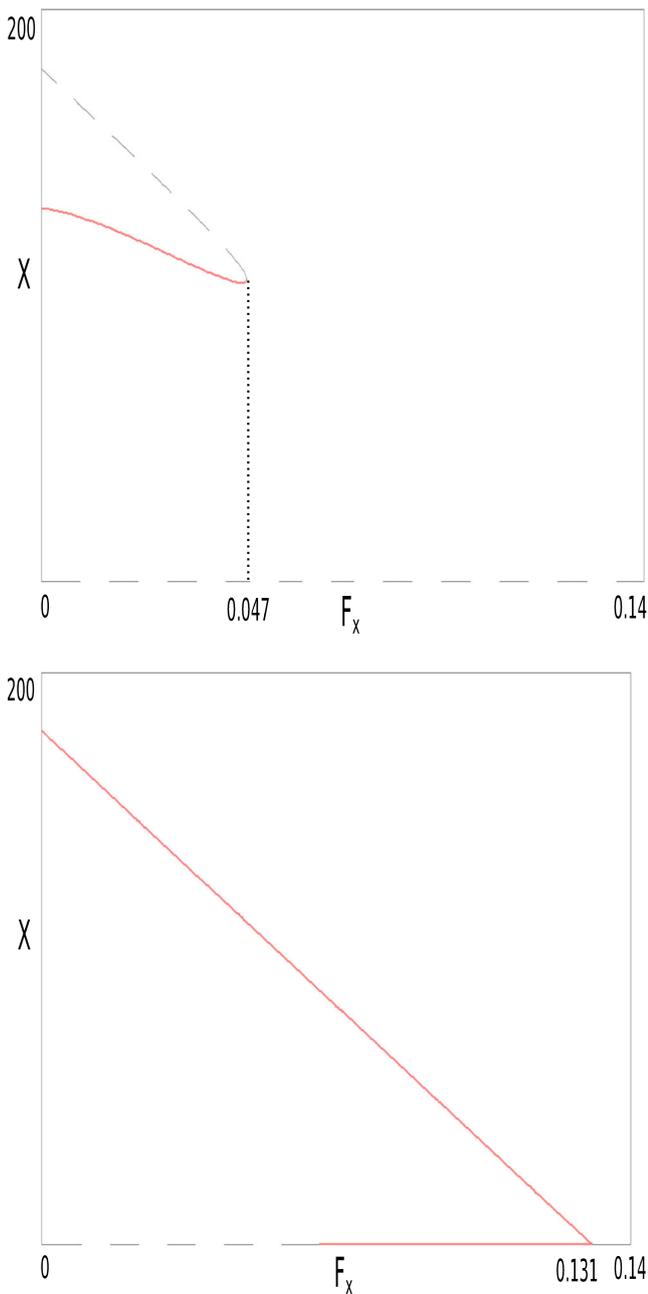


Fig 4 Bifurcation diagram of model (2) as a function of F_x —the intensity of pesticide application. *Solid lines*, stable equilibrium point; *dashed lines*, unstable equilibrium point. (a) nontrivial equilibrium points ($x, y > 0$); (b) boundary equilibrium point ($x = K(1 - F_x/r)$, $y = 0$) and point $(0, 0)$. Parameter values: $r = 0.131$; $K = 180$; $\alpha_{xy} = 0.002$; $T_{hyx} = 1$; $\epsilon f_{xy} = 1$; $m_y = 0.019$; $\alpha_y = 0.1$; $\beta = 1$; $\theta_y = 3$.

Unlike some of the results in section “Material and Methods”, only in Fig 5a, b the alternating nature of the outcomes happens. That is to say, an initial population at A leads to extinction of the biological control agent and stabilization of the pest near its carrying capacity. This outcome is clearly an undesirable result for IPM. In turn, an initial population at B leads to a stable coexistence of pest and its introduced natural enemy (the effectiveness of which will

depend on pest economic thresholds). Initial conditions at C lead to the same qualitative state as an initial population at A.

Fig 5c depicts a case where an increase of chemical intensity (compared with case (a)) causes the failure of IPM, since the extinction of the introduced pest natural enemy and stabilization of the pest near its carrying capacity under the chemical action is the only possible outcome (the sole stable equilibrium point of model (2) in this case). Absence of pest and biological control agent extinction in cases (a) and (c) of Fig 5 is due, in part, to the lack of a demographic Allee effect in the pest population. Fig 5d is an extreme instance where the chemical intensity is so strong that the sole outcome is overall species extinction, once the pest isocline ($dx/dt = 0$) lies completely below the x-axis.

Discussion

In order to investigate the influence of the intensity of chemical spraying on pest dynamics, an IPM was implemented to a ditrophic food chain model where the basal species portrayed the pest and the introduced biological control agent was cast as the predator. Concomitantly, chemicals were applied with negative effects both on the pest and its introduced natural enemy growth rates (Van Lenteren & Woets 1988, Lu et al 2003).

In the first analyzed framework, it was assumed that the pest possessed a strong demographic Allee effect and the results basically consisted of three dynamical outcomes: (i) unstable and stable coexistence of pest and its introduced natural enemy or overall species extinction depending on initial conditions; (ii) pest and its introduced natural enemy extinction for all initial conditions; and (iii) introduced pest natural enemy extinction and stabilization of the pest near its carrying capacity or overall species extinction depending on initial conditions. The possibility of overall species extinction in all cases is due to the strong demographic Allee effect in the pest and because the native predator of the introduced pest natural enemy was assumed to be a generalist predator (this generalist predator could be embedded, for instance, in the term m_y). Result (ii) is appropriate for IPM objectives, while (iii) is not appropriate. The usefulness of result (i) (stable case) to IPM purposes depends on pest economic thresholds (Boukal & Berec 2009). It is important to mention, though, that pest and its introduced natural enemy extinction for all initial conditions (result (ii) above) were obtained with relatively high dosages of chemicals. This, in fact, raises concerns as to environmental issues (Davidson et al 2002)

The second framework consisted of a pest without demographic Allee effect, which represents a rather worse situation with respect to the previous setup, since there is no critical pest threshold below which the pest population tends

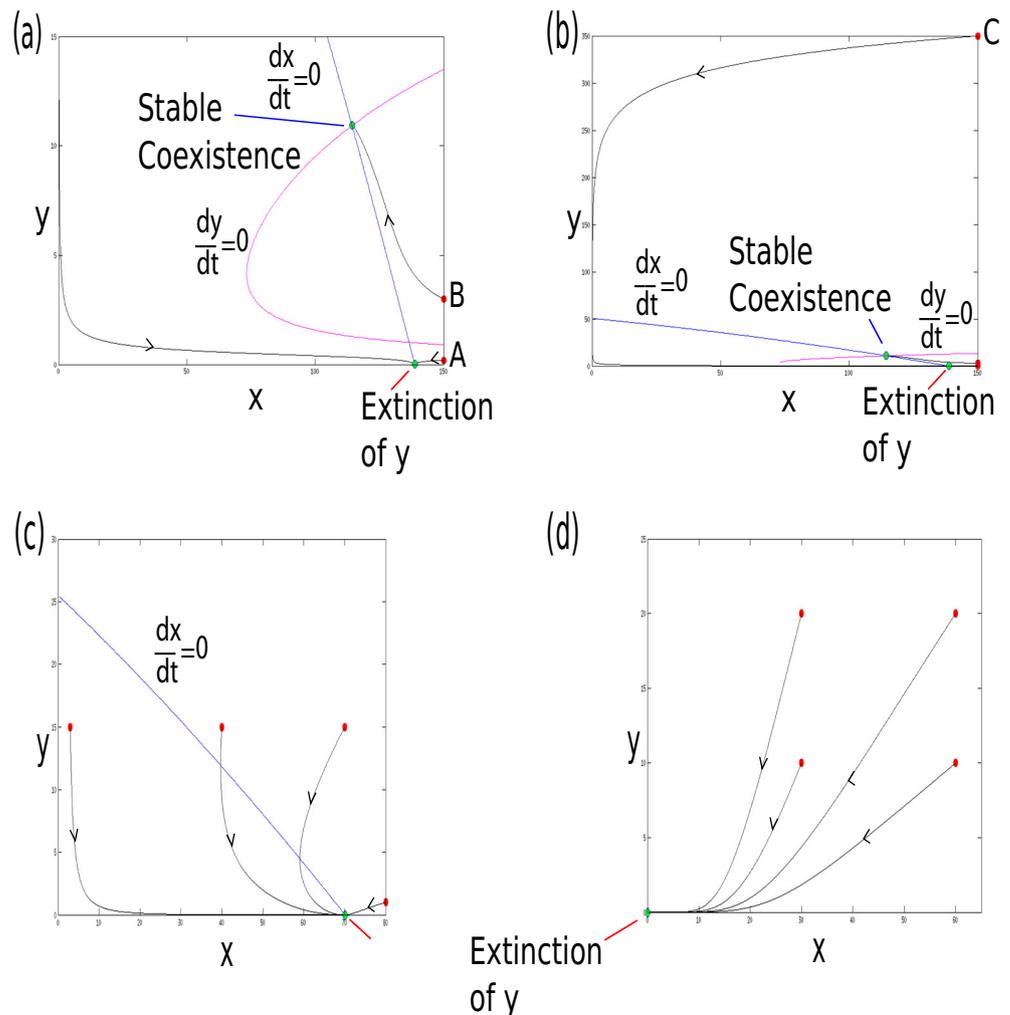


Fig 5 Phase plane of model (2). In case (a) ($F_x=0.03$) occurs stable coexistence or biological control agent extinction depending on initial conditions. Case (b) ($F_x=0.03$) is an expanded view of case (a) that includes an inundative release of pest natural enemy represented by an initial condition at C. In case (c) ($F_x=0.08$) only biological control agent extinction occurs with stabilization of the pest near its carrying capacity for all initial conditions. In case (d) ($F_x=0.15$) there occurs overall species extinction for all initial conditions. Parameter values: $r=0.131$; $K=180$; $a_{xy}=0.002$; $T_{hyx}=1$; $ef_{xy}=1$; $m_y=0.019$; $\alpha=0.1$; $\beta=1$; $\theta_y=3$.

inexorably to extinction. Due to the lack of a demographic Allee effect in the pest, pest extinction occurred only for elevated levels of chemical intensity for all initial conditions. Otherwise, depending on initial conditions, stable coexistence of pest and biological control agent or biological control agent extinction and stabilization of pest near its carrying capacity ensues. It is important to recall that stable coexistence of pest and biological control agent will be efficient in terms of IPM if pest levels are below an economic threshold, that is, pest densities that are not harmful from the economic point of view.

Regarding initial population densities, Boukal *et al* (2007) argued that inoculative releases (i.e., a small number of introduced natural enemies of pest) are not always successful, maybe due to Allee effects among the enemies released. Our proposed model confirms this argument. On the other hand, regarding inundative releases (i.e., a large number of introduced natural enemies of pest), an interesting feature emerges from the analyzed models: inundative releases of

natural enemies of a pest together with chemical spraying may cause failure of IPM. This result runs counter to a possible argument that a large number of introduced natural enemies of a pest could compensate for their inherent Allee effects (the alleged cause of biocontrol failure, Boukal *et al* 2007) in such a way that IPM would be successful.

In this study, we assumed an Allee effect acting on the introduced biological control agent as a possible reason of biological control failure when natural enemies of a pest are released. An additional explanation for this failure is based upon the mounting evidence that the released natural enemies of an exotic pest species not only interact with the target pest but also with other native species (Boukal *et al* 2007). Nonetheless, our proposed model can encompass this interaction if it is surmised that a generalist predator with functional response type 1 (a linear functional response without saturation) (Case 2000) preys upon the biological control agent. Such interaction could be described by an additional mortality rate term (due to predation) in the biological

control agent dynamical equation, e.g., P_y where P denotes the constant density of the native top predator (this procedure would be an alternative to the embedment of an additional mortality term in m_y , mentioned before). The assumption of constant density of P is reasonable according to the modeled biological setup because a native predator already possesses its original prey items. The introduced biological control agent (y), an exotic species, is in this case a mere additional item of the hyperpredator's (P) diet. This implies that the hyperpredator survival is not threatened by an eventual extinction of the biological control agent.

At this juncture, some comments on possible extensions of this work are in order. Since invasive species across taxa suffer the influence of different mechanisms that may generate different component and/or demographic Allee effects throughout food webs (Courchamp *et al* 2008, Tobin *et al* 2011), other forms of Allee effects both in the invasive and in the biological control agent species could be used. In this way, it would be possible to investigate whether these proposed terms describing additional types of Allee effects might qualitatively modify the dynamical outcomes contained in this analysis.

The trophic structure employed here can also be analyzed in the context of species conservation. The prey, x , can be seen as an endangered species that suffers from a strong demographic Allee effect (conveyed by the critical population threshold x_{cr}), and both prey and predator are under harvest process (F_x). One of the proposed measures to save an endangered species is to cull its predators (Boukal *et al* 2007). In this respect, in order to investigate the effect of this measure, culling of the predator y could be conveyed by the augmentation of per capita density independent mortality rate of the predator (m_y). These extensions clearly constitute examples in the broader context of food web dynamics theory, pointing therefore to some possible contributions of the present analysis to applied as well as to theoretical ecology issues.

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