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The interplay among Allee effects, omnivory and inundative releases in a pest biological control model

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HIGHLIGHTS

- We devised an omnivory dynamical model to describe biological pest control.
- Pest and agent have Allee effects and are consumed by an omnivorous predator.
- Pest extinction is related to inundative releases of agent.
- Allee effect in the agent and omnivorous predator density generate similar dynamics.

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ABSTRACT

Failures of biological control strategies are attributed, among varied explanations, to the action of Allee effects on the agent and the evidence that these released enemies not only interact with the target pest, but also with other native species of the local ecosystem. By means of a theoretical omnivory dynamical model we show that these explanations are qualitatively coherent with the results of the proposed theoretical omnivory dynamical model and that pest eradication or suppression is strongly related to inundative releases of the pest natural enemies.

1. Introduction

Allee effects have played a major role in the understanding of extinction of endangered, rare or declining populations (Courchamp et al., 2008), and their importance has also been acknowledged in the dynamics of invasive species (Taylor and Hastings, 2005; Tobin et al., 2011). A technical term for Allee effects is positive density dependence which can be seen, for instance, as a positive relationship between the overall individual fitness, usually quantified by the *per capita* population growth rate, and population size or density – the so called demographic Allee effect. Much of what is known about Allee effects comes from mathematical models (Courchamp et al., 2008), and on account of that they have been an important means to assess the potential importance of Allee effects for population and community dynamics (Peng and Zhang, 2016; Wang et al., 2014; Morozov et al., 2004; Lewis and Kareiva, 1993).

Biological control agents are natural enemies of invasive species (the pest) that are deliberately introduced to control (or eradicate) the pest (Blackwood et al., 2012; Suckling et al., 2012). Cases of success of this pest biocontrol tactic have been reported, but failures have been equally reported (see Hopper and Roush, 1993 and references therein). An Allee effect acting on the agent is frequently put forward as a possible cause of these failures (Boukal et al., 2007; Bompard et al., 2013). In addition, it has been put forward that released pest enemies not only interact with the target pest, but also with other native species of the local ecosystem (Wajnberg et al, 2001). For instance, these native species could interact with the agent as an intraguild (or omnivorous) predator or as a hyperpredator (as shown in Fig. 2.1 on page 17 in Wajnberg et al. (2001)). Based on experimental evidence, Boukal et al. (2007) also suggested the negative effects of interaction between native species and the introduced agent as factors of pest control failure. However, in their work they analyze a predator–prey model with Allee effect only in the prey and without this additional trophic level of the native species.

Given these two factors – Allee effect in the agent and interaction of the agent with native species – that may impair pest biolog-

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ical control, in this work we put forward an omnivory dynamical model where the basal species is the pest and the intermediate consumer is the deliberately introduced biological control agent. The omnivorous predator is assumed to be a native species of the ecosystem which, in the proposed model, portrays a natural enemy of both the pest and the agent. One feature of the model concerns the assumption that the omnivorous predator is generalist in the sense that it does not have a response from the consumption of its exotic prey (pest and agent). Therefore, its population is considered to be constant over time. This is in accordance with the modeled biological setup, once a native predator already possesses its original prey items (to which it certainly responds with variation in its density, but it is not explicitly considered in the proposed model). The introduced agent and the pest, both exotic species, are in this case additional items of the omnivorous predator's diet. Hence, an eventual extinction of the agent and the pest cannot cause the omnivorous predator extinction. Another characteristic of the proposed model is the assumption that the intermediate consumer (the agent) is subject to an Allee effect, which is mathematically translated by a hyperbolic function that modulates its conversion efficiency as a function of its density (Zhou et al., 2005; Verdy, 2010; see also Bompard et al., 2013 for a discrete time host – parasitoid model). With respect to the pest populations two biological setups will be assumed: (i) pest without an Allee effect; (ii) pest with a strong demographic Allee effect (Boukal et al., 2007).

In practical terms, confirming and identifying the pest invasion the manager proceeds to pinpoint a proper agent to control the invasion (for instance, managers introduce exotic agents such as the wasp parasitoid *Ooencyrtus kuvanae* (Elkinton and Liebhold, 1990), and the carabid predator *Calasoma sycophanta* (Alalouni et al., 2013) so as to deter the invasive species gypsy moth (*Lymantria dispar*) in North America). However, to undertake this procedure the manager can be faced at least with two problems: (i) the existence and intensity of an Allee effect in the agent, which will depend on its choice and (ii) the native generalist omnivorous predator population density, which is beyond the manager's control. Therefore, given these characteristics of this biological framework, we propose to assess the efficiency of the released enemy strategy to control pest outbursts (or preferably, to induce pest suppression) by means of the generalist omnivorous predator population size (assumed to be constant over time) and the intensity of the agent's Allee effect.

It is important to remark that the population dynamical models used in this work are of strategic type (May, 2001). Strategic models do not usually describe the dynamics of a specific real community. Instead, they provide a conceptual framework to understand some relevant aspects of the species dynamics of a relatively vast class of communities. Moreover, the proposed models involve a large number of parameters. Hence, this study intends to show some possible outcomes related to the hypothetical chosen sets of parameter values of these strategic models, rather than provide an exhaustive study of conditions required for all possible outcomes generated by these models (Abrams and Roth, 1994). It is almost certain that some parameter values in real systems are quite different from the ones used in the analyzed models and therefore they might not reproduce the dynamical results to be presented in this work. However, it is important to emphasize that the intention of this study is to demonstrate through numerical bifurcations of strategic models the potential of dynamical behaviors generated by these hypothetical parameter values and their possible qualitative interpretations in pest biological control. Nonetheless, we call attention to the fact that the choice of the parameter values was primarily guided by an intention to create, when possible, a high number of coexistence populations of pest and agent in the analyzed models. Such setup would probably describe a complex pest control scenario. On the other hand, future studies of the proposed models containing extended parameter spaces with regard to additional dynamical behaviors would surely be of great interest.

2. Methods

2.1. An omnivory food web model with Allee effect in the consumer population

The omnivorous food web to be analyzed is schematically displayed in Fig. 1.

Fig. 1 consists basically of an omnivory model where both prey (pest, R) and consumer (agent, C) suffer from an Allee effect. The omnivorous predator P is a natural and native enemy of both R and C.

A time continuous dynamical model for the trophic scheme of Fig. 1 with multispecies functional responses of P on R and C and functional response type 2 of C upon R can be given by:

$$\frac{dR}{dt} = rR\left(1-\frac{R}{K}\right) - \frac{a_{CR}R}{1+a_{CR}T_{hCR}R}C - \frac{a_{PR}R}{1+a_{PR}T_{hPR}R+a_{PC}T_{hPC}C}P \qquad (1)$$

$$\frac{dC}{dt} = e_{RC}\left(\frac{C}{\theta_C+C}\right)\left(\frac{a_{CR}R}{1+a_{CR}T_{hCR}R}\right)C - \frac{a_{PC}C}{1+a_{PR}T_{hPR}R+a_{PC}T_{hPC}C}P - m_C C$$

The densities of prey and consumer will be denoted by R and C, respectively (the terms density and size will be used interchangeably throughout this work), while P represents the constant density of an omnivorous predator; r is the maximum *per capita* rate of prey growth and K is its carrying capacity; a_{CR} represents the attack coefficient of the consumer C upon the prey R; T_{hCR} is the manipulation time of R by C, while e_{RC} is the predator food–to–offspring conversion coefficient; $\frac{C}{\theta_C+C}$ describes the Allee effect in the response of C where θ_C denotes its intensity (Zhou et al., 2005; Verdy, 2010); $\frac{a_{PC}C}{1+a_{PC}T_{hPC}C+a_{PR}T_{hPR}R}$ is a multispecies functional response (Case, 2000) of the omnivorous predator P upon the consumer C, where a_{PC} is the attack coefficient, T_{hPC} its manipulation time. Since P also preys upon R, a_{PR} is the attack coefficient of P on R and T_{hPR} is the manipulation time of R by P; m_C is the density independent *per capita* mortality rate of C.

Model (1) will be supposed to represent a pest biological control scenario. The predation of the agent C by a native omnivorous predator P is corroborated by the experimental evidence that natural native enemies of agents are very common in natural systems (Boukal et al., 2007 and references therein). Since C represents an agent, it is supposed to prey upon the pest with a functional response type 2 because this response exerts a strong predation pressure when pest population is low (that is, when the pest population is low, the risk of an individual pest being killed by the

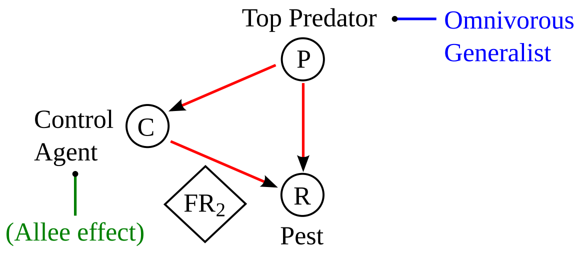

Fig. 1. A generalist omnivorous predator (P) acts upon the consumer (C) and the prey (R) with a multispecies functional response and the consumer (C) preys upon the prey (R) with a functional response type 2. Allee effects act on C. Arrows represent consumption.