Short Note

Coexistence of multiple attractors in the coupling of an exploitative and an omnivorous food web

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ABSTRACT

This work shows that the coupling of an exploitative with an omnivorous food web can generate unstable dynamics as well as multiple basins of attraction as a result of slight parameter and initial population variation. In terms of pest biological control, the results point to the need of extreme care with regard to stock assessment of the involved populations when designing strategies in biocontrol. If these requirements are not met, pest management may become quite precarious.

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1. Introduction

Failures of pest management can be ascribed, among several factors, to interactions between introduced agent control and their native predators of the ecosystem. In this work we show that the existence of multiple control agents that are either naturally or artificially established may be deleterious to pest suppression. To this end, we propose a model of two coupled food webs: an exploitative and an omnivorous one. Slight variations of the involved population may bring about unstable dynamics as well as multiple basins of attraction. In terms of pest biological control, this means that stock assessment of these populations is crucial when designing strategies in biocontrol. If these requirements of precise stock assessments are not met, pest management may become quite precarious.

It is worthwhile to emphasize that the population dynamical models used in this work are of strategic type (May, 2001), and as such they do not necessarily correspond to a specific real community. Instead, they provide a conceptual framework to understand some aspects of the species dynamics of a class of communities. Moreover, the proposed model involves a large number of parameters. Hence, this study is also concerned with showing possible outcomes related to the hypothetical chosen sets of parameter values of this proposed strategic model, rather than providing an exhaustive study of conditions required for all possible outcomes generated by the analyzed model (Abrams and Roth, 1994).

2. An omnivorous and exploitative food web model

The framework to be studied is a food web where a native generalist omnivorous top predator (P) feeds upon the introduced control agent (Z) and upon the pest species (A), and the agent preys upon the pest species (A). The pest species is supposed to be under the control agent predation (Z – the artificially introduced enemy) and under predation of another native generalist predator (F_A – the naturally established enemy) with constant density over time. The trophic scheme of this biological setup is displayed in Fig. 1. Note that Fig. 1 depicts the coupling of one exploitative and one omnivorous food web (hereinafter FR_i denotes functional response type i (i = 2, 3) throughout this work, and the terms density and number of individuals will be used interchangeably).

A native generalist omnivorous predator (P) with constant density over time preys upon the agent (Z) and the pest (A) with functional response type 3, and the agent (Z) preys upon the pest (A) with functional response type 2. Concomitantly, another native predator with functional response type 3 and constant density over time (F_A) preys upon the pest (A).

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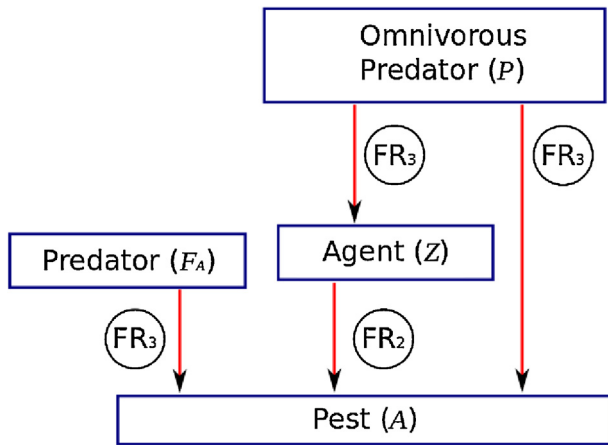
Fig. 1. A native generalist omnivorous predator (P) with constant density over time preys on the agent (Z) and the pest (A) with functional response type 3, and the agent (Z) preys on the pest (A) with functional response type 2. Concomitantly, another native generalist omnivorous predator with functional response 3 preys on the pest (A). This figure was one of the trophic schemes proposed by Yodzis (2001) in order to investigate the influence of predator culling on commercial fisheries.

A continuous time dynamical model for the trophic scheme of Fig. 1 can be given by:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) - \left(\frac{a_{ZA}A}{1 + a_{ZA}T_{hZA}A}\right)Z - \left(\frac{a_{PA}A^2}{1 + a_{PA}T_{hPA}A^2}\right)P$$
$$- \left(\frac{a_{FA}A^2}{1 + a_{FA}T_{hFA}A^2}\right)F_A \qquad (1)$$
$$\frac{dZ}{dt} = ef_{AZ}\left(\frac{a_{ZA}A}{1 + a_{ZA}T_{hZA}A}\right)Z - \left(\frac{a_{PZ}Z^2}{1 + a_{PZ}T_{hPZ}Z^2}\right)P - m_Z Z$$

A and Z are the densities of pest and agent, respectively, while P represents the constant density over time of a native omnivorous predator. This assumption means that P does not have a numerical response from the consumption of its exotic prey (pest (A) and control agent (Z)). This is in accordance with the modeled biological setup, once a native predator already possesses its original prey items. Hence, the introduced biological control agent and the pest, both exotic species, are in this case additional items of the omnivorous predator's diet, which is supposed to have a relatively broad diet as most predators do (Begon et al., 2006, p. 279). This proposed framework fits then a generalist predator where the omnivorous predator P in model (1) is in a dynamic association with several prey (i.e., the predator responds numerically to those prey), and consumes others as secondary resources. Hence, given such a similar assortment of prey items in our context (i.e., both A and Z are supposed to be secondary prey and therefore P does not respond numerically to them; moreover, the primary prey with which P is dynamically associated, are not considered explicitly in the model), an eventual extinction of the control agent (Z) and the pest (A) does not jeopardize the omnivorous predator (P) survival.

r is the maximum *per capita* rate of pest growth and K is its carrying capacity. a_{ZA} represents the attack coefficient of the control agent Z upon the pest A. T_{hZA} is the manipulation time of A by Z, while ef_{AZ} is the predator food-to-offspring conversion coefficient. $\frac{a_{PZ}Z^2}{1 + a_{PZ}T_{hPZ}Z^2}$ is a type 3 functional response of the omnivorous predator (P) upon the agent Z, where a_{PZ} is the attack coefficient, T_{hPZ} its manipulation time. P also preys upon A by means of a functional response type 3 (the interpretation of the predation terms is the same as those between P and Z, exchanging

only Z by A). $\frac{a_{FA}A^2}{1 + a_{FA}T_{hFA}A^2}$ is also a type 3 functional response of the other native predator (F_A) upon the pest A, where a_{FA} is the attack coefficient and T_{hFA} its manipulation time. The lack of a numerical response of F_A with respect to the pest and the consequent constant density over time follows the same reasoning applied to the omnivorous predator P. m_Z is the density independent *per capita* mortality rate of Z. Model (1) may well represent the case where a beetle (*Harmonia axyridis* – the omnivorous predator) consumes mummified aphids (*Macrosiphum euphorbiae* – the pest) that contain parasitoid (*Aphelinus asychis* – the agent) pupae (Hunter, 2009). Since the predation of the pest and the agent by the omnivorous predator (i.e., the omnivory/intraguild predation) is concomitant (hence, a concomitant omnivory/intraguild predation ensues), the manipulation time will be mainly due to digestion processes of pest and agent rather than search and capture of both pest and agent. Hence, we can resort to a simple functional response of P (e.g., type 3) instead of a multispecies functional response (Case, 2000). The choice of the functional response type 2 for the agent (Z) rests upon the fact that this functional response exerts an extremely strong predation pressure on the pest, which is a fairly suitable characteristic of a pest biological control agent.

Conservation biological control involves manipulations that augment the density of populations of generalist natural enemies that are native to the pest's new area (Barbosa, 1998). Within this context of pest control, the analysis of this work will consist of a bifurcation analysis of A and Z as a function of P (recall that P is a native enemy of the exotic species A and Z). Accordingly, we intend to investigate how the augmentation of the density of the native omnivorous predator (P) influences the dynamics of model (1). The resulting bifurcation diagram generated by the software XPPAUT (Ermentrout, 2002) is displayed in Fig. 2.
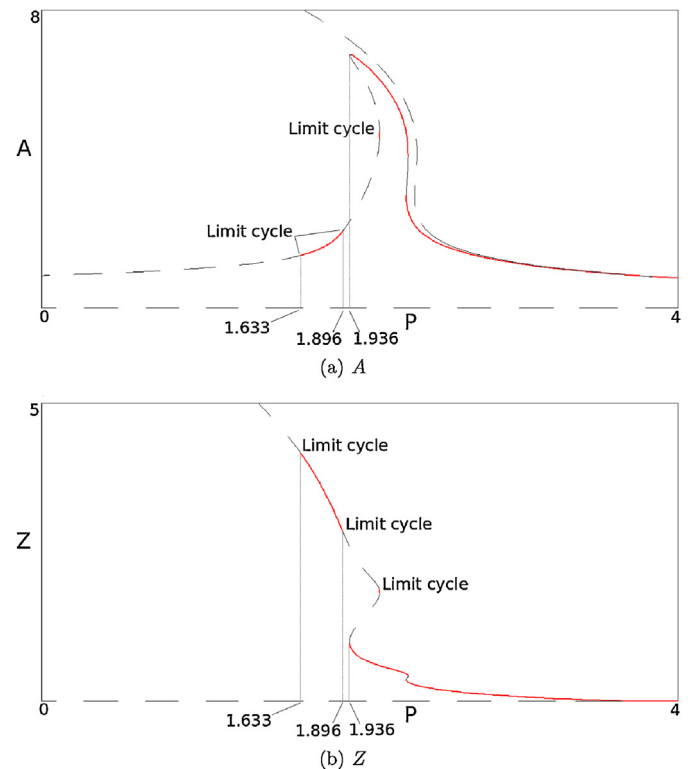
Fig. 2. Bifurcation diagrams of model (1) as a function of $0 < P < 4$; (a) A (pest species); (b) Z (control agent). Solid lines: stable equilibrium points; dashed lines: unstable equilibrium points. Parameter values: $r = 1.5$; $K = 10.8$; $a_{ZA} = 0.7$; $ef_{AZ} = 1$; $T_{hZA} = 4.5$; $a_{PZ} = 0.0519$; $m_Z = 0.163$; $a_{FA} = 0.05$; $T_{hFA} = 1$; $F_A = 0.0005$; $a_{PA} = 0.5$; $T_{hPA} = 0.5$; $T_{hPZ} = 20$.