



Adaptive prey behavior and the dynamics of intraguild predation systems

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ABSTRACT

Intraguild predation constitutes a widespread interaction occurring across different taxa, trophic positions and ecosystems, and its endogenous dynamical properties have been shown to affect the abundance and persistence of the involved populations as well as those connected with them within food webs. Although optimal foraging decisions displayed by predators are known to exert a stabilizing influence on the dynamics of intraguild predation systems, few is known about the corresponding influence of adaptive prey decisions in spite of its commonness in nature. In this study, we analyze the effect that adaptive antipredator behavior exerts on the stability and persistence of the populations involved in intraguild predation systems. Our results indicate that adaptive prey behavior in the form of inducible defenses act as a stabilizing mechanism and show that, in the same direction that adaptive foraging, enhances the parameter space in which species can coexist through promoting persistence of the IG-prey. At high levels of enrichment, the intraguild predation system exhibits unstable dynamics and zones of multiples attractors. In addition, we show that the equilibrium density of the IG-predator could be increased at intermediate values of defense effectiveness. Finally we conclude that adaptive prey behavior is an important mechanism leading to species coexistence in intraguild predation systems and consequently enhancing stability of food webs.

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1. Introduction

Intraguild predation (IGP) consists of a food web module of at least three-species, in which a predator and its prey, namely IG-predator and IG-prey respectively, are at the same time competitors for a shared resource population. This kind of species interaction has been demonstrated to be a widespread motif in real ecological communities (Polis et al., 1989; Polis and Strong, 1996; Arim and Marquet, 2004). It occurs across different taxa, trophic positions and ecosystems, and it has been recognized to potentially influence the abundance, distribution and evolution of the involved populations (Polis et al., 1989; Holt and Polis, 1997). Besides its empirical prevalence, a simple IGP interaction has the value of embracing a set of interspecific ecological interactions, namely, predation, omnivory, tri-trophic food chain, exploitative competition and polyphagy. Thus, the dynamics of an IGP module is governed by the interaction of several ecological forces, as occur in natural communities. In addition to affect the dynamics of the species directly involved in the IGP interaction, Kondoh (2008) and Stouffer and Bascompte (2010) showed that the stability properties of these modules have profound influences on the stability and persistence of the entire set of species belonging to the commu-

nity in which they are immersed. Therefore, the study of conditions ensuring or allowing stability of IGP modules is highly relevant for forecasting the stability of food webs and the maintenance of biodiversity.

The analysis of IGP dynamics by Holt and Polis (1997) showed that the persistence of the involved species is more likely at intermediate levels of basal resources, and that the IG-prey can only persist being a better competitor for the shared resource than the IG-predator. The requirement for a more efficient IG-prey than IG-predator for species coexistence, was later predicted in a wide range of modeling approaches, interaction patterns and species attributes (e.g. Diehl and Feiße, 2000, 2001; Krivan, 2000; Mylius et al., 2001; van de Wolfshaar et al., 2006). These authors were able to identify key conditions that allow species persistence and stability for IGP systems (see also Gismervik and Andersen, 1997; Hart, 2002). Nevertheless, those conditions are somewhat restrictive, in the sense that they leave a large portion of the parameter space where one or more species are predicted to go extinct. Recent studies have revealed that the addition of species or resources to the basal IGP system relax the above requirement for coexistence (Daugherty et al., 2007; Holt and Huxel, 2007; Namba et al., 2008). Nevertheless, these mechanisms of stabilization rely on a topological modification of the system and therefore do not point towards revealing causes of population coexistence inherent to the IGP module.

In the search of biological mechanisms accounting for why ecological systems are able to persist, in spite of stability constraints

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imposed by the destabilizing forces emerging in multidimensional dynamical systems (Ramos-Jiliberto et al., 2004), a line of research turned their eyes towards the adaptation capabilities of organisms shaped by natural selection (Kondoh, 2003, 2006, 2007; Guill and Drossel, 2008; Uchida et al., 2007). In doing so, a newer generation of theoretical works has included adaptive behavior as a realistic and empirically supported ingredient into population and community level model systems (Beckerman et al., 2006; Uchida et al., 2007). The incorporation of adaptive behavior into species interaction systems resulted to be stabilizing in food webs of small (Abrams, 1984; Krivan, 1996) to large (Kondoh, 2003, 2008; Drossel et al., 2001) complexity.

Among the optimizing behavioral decisions that have received considerable attention by theoreticians, adaptive foraging of predators (Stephens and Krebs, 1986; Krivan, 1996, 2007; Krivan and Sikder, 1999; Krivan and Eisner, 2003) and adaptive antipredator behavior of prey (Matsuda et al., 1996; Kondoh, 2007; Uchida et al., 2007) are the best known in their consequences for population and community dynamics. Both lie at the core of trophic interactions and there is a respectable amount of empirical knowledge supporting their widespread occurrence and functionality on organisms, as much as their physiological basis and evolutionary development (Engel and Tollrian, 2009; Kjellander and Nordström, 2003; Mougi and Nishimura, 2008; Pyke et al., 1977). In this vein, Krivan and Diehl (2005) studied the dynamical consequences of incorporating adaptive foraging of the top predator into the IGP interaction. Their results showed that adaptive behavior increased the likelihood of species coexistence, through allowing the persistence of the top predator within a parameter region where IG-predator would be excluded if no adaptive foraging were exhibited. Nevertheless, to our knowledge, no work has investigated the influence of adaptive prey behavior on the dynamics of IGP interactions, in spite of being widely documented across many taxa and ecosystems and considered to be a main component of predator-prey interactions (Tollrian and Harvel, 1999; Lass and Spaak, 2003; Relyea, 2003; Bernard, 2004; Schmitz et al., 1997, 2004; Cresswell, 2008; Boots et al., 2009). In this study we fill this gap through analyzing the effect that adaptive antipredator behavior displayed by the IG-prey exert on the stability and species persistence of the IGP system.

Our results show that, in the same direction that adaptive foraging, adaptive prey behavior favors IGP stability and facilitates species persistence. Particularly, the relation of competitive abilities found by Holt and Polis (1997) is relaxed under a subset of parameter conditions. The persistence of the IG-prey is favored by the adaptive prey behavior and, counter intuitively, the equilibrium density of the IG-predator could be increased at intermediate values of defense effectiveness.

2. The model

We begin formulating a tri-trophic system representing the population biomass per unit space of resources, prey and omnivorous predators, respectively. The dynamics is described by the following system of differential equations:

$$\begin{aligned} \frac{dx}{dt} &= x \left\{ r \left(1 - \frac{x}{K} \right) - \frac{a_{xy}y}{1 + h_{xy}a_{xy}x} - \frac{a_{xz}z}{1 + h_{xy}a_{xy}x + h_{yz}A_{yz}(B_{yz})y} \right\} \\ \frac{dy}{dt} &= y \left\{ \frac{\varepsilon_{xy}a_{xy}x}{1 + h_{xy}a_{xy}x} - \frac{A_{yz}(B_{yz})z}{1 + h_{xy}a_{xy}x + h_{yz}A_{yz}(B_{yz})y} - M_y(B_{yz}) \right\} \\ \frac{dz}{dt} &= z \left\{ \frac{\varepsilon_{xz}a_{xz}x + \varepsilon_{yz}A_{yz}(B_{yz})y}{1 + h_{xy}a_{xy}x + h_{yz}A_{yz}(B_{yz})y} - \mu_z \right\} \end{aligned} \quad (1)$$

where x , y , z are basal resource, IG-prey and IG-predator respectively. The resource population exhibits a density-dependent

growth, with intrinsic growth rate r and carrying capacity K . Parameter ε_{ij} is the conversion efficiency of species i to species j , a_{ij} is the attack rate of species j on species i , h_{ij} is the handling time spent by species j on a unit species i and μ_i is the density-independent mortality rate of species i . Function M_y represents per capita biomass loss rate attributed to factors other than predation. The value of M_y depends on the state of antipredator defense (B_{yz}) within the population. Function A_{yz} describes the attack rate of IG-predator on the IG-prey, as a function of the level of defense B_{yz} .

The IG-prey population is assumed to exhibit antipredator behavior or other kind of defenses in response to high predation risk. The level of induced defenses (ID) is represented by $B_{yz} \in (0, 1)$. Expressing the ID has an associated cost, which is assumed to increase the loss rate M_y :

$$M_y(B_{yz}) = \mu_y(1 + C_{yz}B_{yz}) \quad (2)$$

where $C_{yz} \in (0, \infty)$ is the cost of the expression of defenses on the growth rate of consumers.

On the other hand, ID decreases the vulnerability of the IG-prey to IG-predators. This gain is represented as a decrease in the attack rate A_{yz} of predators:

$$A_{yz}(B_{yz}) = a_{yz}(1 - E_{yz}B_{yz}) \quad (3)$$

where $E_{yz} \in (0, \infty)$ is the effectiveness of the IG-prey ID.

2.1. Adaptive prey behavior

In our model, we assume that IG-prey individuals are capable of adjusting its defensive behavior. An excessive increase in the ID at low levels of IG-predator abundance will cause the IG-prey to pay an unnecessary metabolic cost. To solve this tradeoff we assume that the IG-prey will adaptively tune up the levels of ID expression so that fitness is maximized. The dynamic equation governing the level of defense expression is:

$$\frac{dB_{yz}}{dt} = \eta_y B_{yz}(1 - B_{yz}) \left(\frac{\partial W_y}{\partial B_{yz}} \right) \quad (4)$$

where W_y is the fitness of consumers, represented by the per capita growth rate, η_y is the adaptation rate, and the factor $B_{yz}(1 - B_{yz})$ is included to bound the defense values between 0 and 1 (Kondoh, 2007). A summary of model parameters is provided in Table 1.

For analyzing the systems under study, we performed numerical bifurcation analyses using the package XPP-Auto version 5.3 (Ermentrout, 2002), using the adaptive Stiff integration algorithm.

3. Results

In Fig. 1 it is shown the stability regions for the asymptotic community dynamics. Fig. 1a and b shows the stability regions without ID for $\varepsilon_{yz} = 0.3$ and $\varepsilon_{yz} = 0.6$ respectively. A region of the parameter space allows the persistence of the three-species, while only either y or z can coexist with x in other regions. Note that the region of persistence of IG-prey is limited by the conversion efficiency of resource to IG-predator ε_{xz} . Fig. 1c and d shows the stability regions when IG-prey ID is included in the system. Here the asymptotic behavior changes, especially at high levels of enrichment K , where the region of persistence of the intermediate consumer gets larger, particularly at higher levels of conversion efficiency of prey to predator ε_{yz} . Furthermore, the incorporation of ID at higher levels of enrichment creates zones of complex dynamics (labeled “ma”) where multiple attractors can coexist, such as three-species stable coexistence, stable coexistence of resources and prey or of resources and predators, and three-species stable or unstable coexistence, stable or unstable coexistence of resources and prey.

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