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 Feißel, 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

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:

$$\frac{dx}{dt} = x\left\{ r\left(1 - \frac{x}{K}\right) - \frac{a_{xy}y}{1 + h_{xy}a_{xy}x} - \frac{a_{xz}z}{1 + h_{xy}a_{xy}x + h_{yz}A_{yz}(B_{yz})y} \right\}$$

$$\frac{dy}{dt} = y\left\{ \frac{\varepsilon_{xy}a_{xy}x}{1 + h_{xy}a_{xy}x} - \frac{A_{yz}(B_{yz})z}{1 + h_{xy}a_{xy}x + h_{yz}A_{yz}(B_{yz})y} - M_y(B_{yz}) \right\}$$

$$\frac{dz}{dt} = z\left\{ \frac{\varepsilon_{xz}a_{xz}x + \varepsilon_{yz}A_{yz}(B_{yz})y}{1 + h_{xy}a_{xy}x + h_{yz}A_{yz}(B_{yz})y} - \mu_z \right\}$$

$$(1)$$

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:

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

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:

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

where $C_{yz} \in (0, \infty)$ 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:

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

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.

Table 1
Description of model parameters. Parameter values were obtained from Krivan and Diehl (2005). Dimensionless parameters are indicated by d.l.

Symbol	Value	Unit	Short definition
r	0.3	h^{-1}	Maximum specific growth rate of the resource
K	Free	mg C/L	Carrying capacity of the resource
a_{xy}	0.037	L/(mg h)	Search rate of consumer for resources
a_{xz}	0.025	L/(mg h)	Search rate of predator for resources
a_{yz}	0.025	L/(mg h)	Search rate of predator for resources in absence of ID
h_{xy}	3	h	Time spent by consumer handling resources
h_{xz}	4	h	Time spent by predator handling resources
h_{yz}	4	h	Time spent by predator handling resources
ε_{xy}	0.6	d.l.	Conversion efficiency of resources into consumers
ε_{xz}	Free	d.l.	Conversion efficiency of resources into predators
ε_{yz}	0.3 or 0.6	d.l.	Conversion efficiency of consumers into predators
μ_y	0.03	h^{-1}	Mortality rate of consumers in absence of metabolic
μ_z	0.0275	h^{-1}	Mortality rate of predators
E_{yz}	Free	d.l.	Efficiency of defense
C_{yz}	Free	d.l.	Defense cost
η_y	1	d.l.	Adaptation rate of prey y

If we stand at the point ($K = 10$, $\varepsilon_{xz} = 0.3$, asterisk in Fig. 1) we can see how the asymptotic dynamics change as a function of efficiency and costs of ID (Fig. 2). Note that at low ε_{yz} (Fig. 2a) a lower level of defense effectiveness promote community coexistence, as compared to high values of ε_{yz} (Fig. 2b). Nevertheless, the region of complex dynamics (periodic oscillations and multiple attractors) is larger for low values of ε_{yz}.

Figs. 1 and 2 show conditions for species persistence, but in these scenarios ID do not seem to affect markedly the conditions for IG-predator persistence. Nonetheless, an analysis of the long-term population densities in relation to IG-prey ID reveals some appealing effects. In Fig. 3 it is shown the influence of the effectiveness of ID on the equilibrium abundances of the species. Graphs 1a–c

were obtained with $\varepsilon_{xz} = 0.1$, 0.2 and 0.3 respectively. Note in 3a and b that IG-predator equilibrium density z increases with E_{yz} at moderate levels of ID effectiveness, i.e. when the IG-prey persistence is ensured over a wide range of ID effectiveness (see Fig. 1), IG-predators could take advantage of some degree of increase in IG-prey defense effectiveness.

Among the model parameters, it could be of special interest those related to the adaptive induction of defenses. From Eq. (4) it can be seen that adaptation rate η_y is the only parameter governing the timing of induction. Our analyses indicated that variations in η_y do not change the long-term behavior of the system under study, but affect the rate of approaching the asymptotic dynamics (i.e. duration of the transient phase).
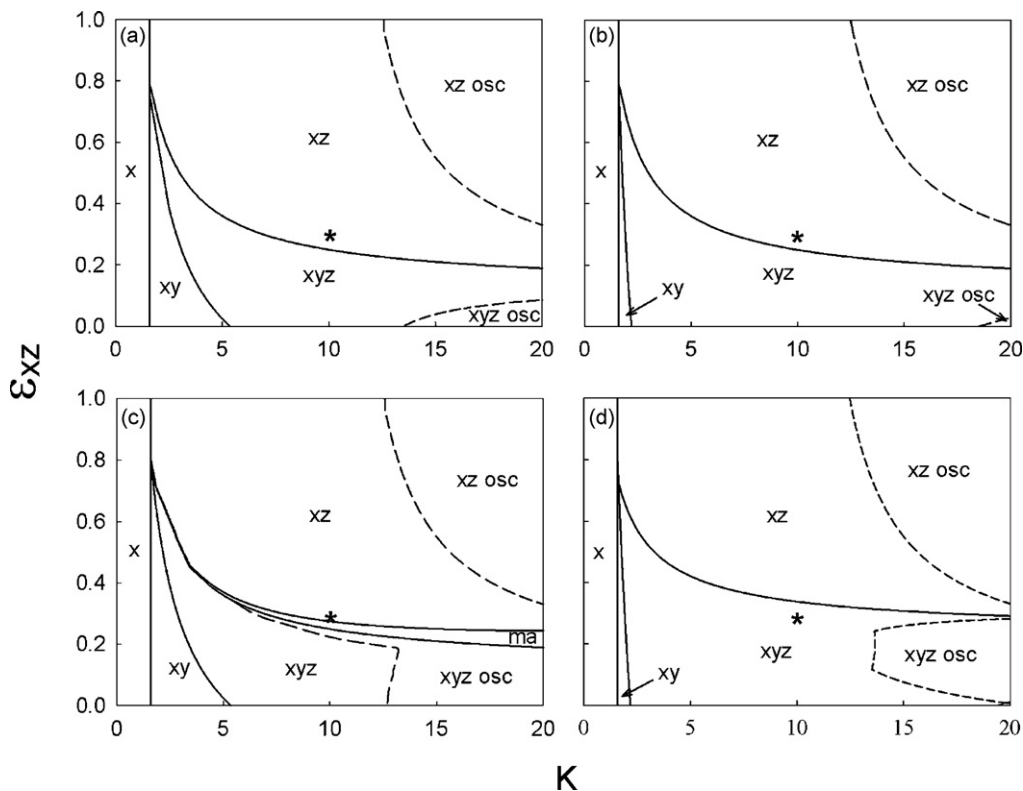

Fig. 1. Two-parameter bifurcation diagrams for the model system under study. The conversion efficiency of resource biomass to predator ε_{xz}, and the maximum carrying capacity of the resource are shown in the ordinate and abscissa, respectively. Different asymptotic states are labeled with their respective members; the label "osc" denotes an oscillatory asymptotic behavior. In the small region labeled "ma" multiple attractors can coexist (see text for details). Continuous lines denote extinction thresholds of one of the populations, and dashed lines denote changes in local stability (Hopf bifurcations). The asymptotic dynamics without ($E_{yz} = 0$ and $C_{yz} = 0$, graphs (a) and (b)) and with ($E_{yz} = 0.8$ and $C_{yz} = 0.3$, graphs (c) and (d)) induced defenses are shown. Conversion efficiency from prey to predator were $\varepsilon_{yz} = 0.3$ in (a) and (c), and $\varepsilon_{yz} = 0.6$ in (b) and (d). Other parameters values were set following Table 1.
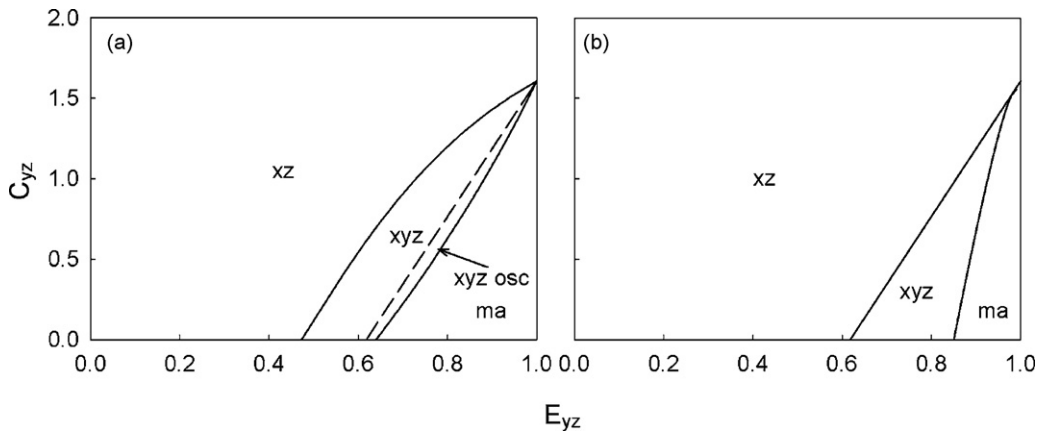
Fig. 2. Two-parameter bifurcation diagrams for the model system under study. Parameter values representing the cost and effectiveness of the induced defense are shown on the ordinate and abscissa respectively. These graphs show the point $K = 10$ and $\varepsilon_{xz} = 0.3$ of Fig. 1. Conversion efficiencies $\varepsilon_{yz} = 0.3$ and $\varepsilon_{yz} = 0.6$ were used for graphs (a) and (b) respectively. Labels show the regions of persistence of the indicated species (see Fig. 1). Continuous lines denote extinction thresholds of one species and dashed lines denote changes in local stability (Hopf bifurcations). Other parameters values were set following Table 1.
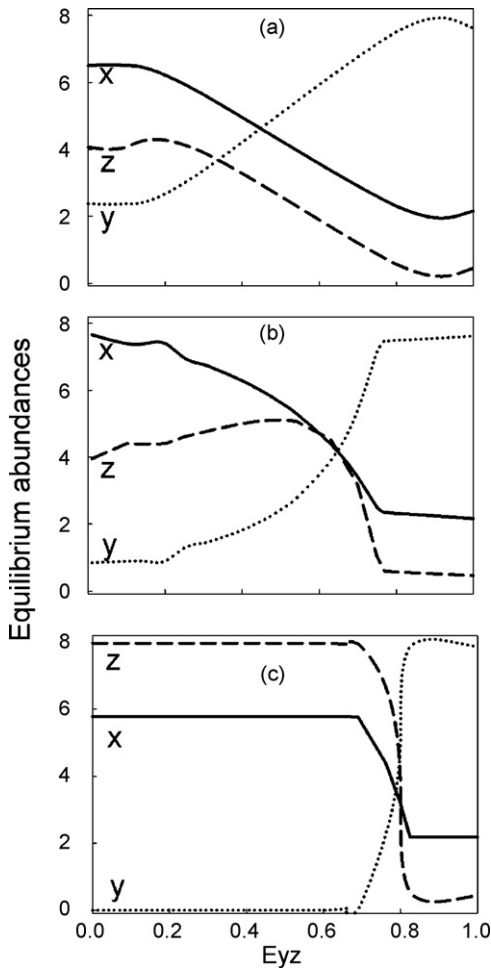

Fig. 3. Influence of effectiveness of defense on the equilibrium abundances of the species, as a function of carrying capacity K. Costs of defense C_{yz} were set to zero. Graphs (a)–(c) were obtained with $\varepsilon_{xz} = 0.1, 0.2$ and 0.3 respectively. Other parameters values were set following Table 1. Note in (a) and (b) that predator equilibrium density could increase with E_{yz} at moderate levels of effectiveness.

4. Discussion

The incorporation of adaptive prey behavior (APB) into an IGP system led to five main results. First, ID enlarges the 3-species coexistence region. Specifically, ID favors persistence of the IG-prey when the IG-predator posses a higher competitive ability than allowed in the absence of APB. This effect is possible at intermediate levels of enrichment and at high levels of ID effectiveness. Second, ID produces unstable dynamics at high levels of enrichment. Third, when the IG-prey constitutes a low-quality food source for the IG-predator, ID can drive extinction of the IG-predator. Fourth, when coexistence does not depend on effectiveness of ID, APB can increase the equilibrium abundance of IG-predator. Finally, an analysis of model results reveals that high levels of defense effectiveness weaken community stability, driving oscillatory dynamics and multiple attractors.

Adaptive behavior, and APB in particular, has been shown to increase species persistence in complex food webs (Kondoh, 2003, 2007). This is consistent with the fact that APB is able to stabilize the IGP module, which is a dominant constituent motif of food webs (Arim and Marquet, 2004). In particular, APB tends to reverse the complexity–stability relationship in food webs (Kondoh, 2007), from which follows that reducing the complexity via eliminating links, weakens the stabilizing effect of APB. Our results are in line with those of Kondoh (2007) in that weaker links, obtained from low values of ε_{yz}, produced that ID was less effective in favoring species persistence.

APB in the form of inducible defenses are known to be widespread in nature (Tollrian and Harvel, 1999), and there is both theoretical (Vos et al., 2004; Ramos-Jiliberto, 2003; Ramos-Jiliberto et al., 2008a,b) and empirical evidence (Verschor et al., 2004; Van der Stap et al., 2006, 2007) suggesting that ID stabilizes population dynamics of species conforming different food web modules. This stabilizing role of ID depends strongly on the level of defense effectiveness and its cost associated. Our results show that three-species persistence is particularly favored at intermediate levels of defense effectiveness and low costs. This occurs because high levels of ID effectiveness, together with positive fitness gradient that is ensured at low defense costs, suppress the trophic interaction between the IG-prey and the IG-predator. Under this scenario, the system tends to be purely competitive, where one of the consumers could be excluded. In addition, highly competitive states of the system also promoted oscillatory dynamics. Note that, unlike the model used by Krivan and Diehl (2005), ours do not allow switching on and off the defense. Instead, our model leads to a continuum between purely competitive systems and purely IGP systems. In a prior study, Abrams and Matsuda (1997) already noted that APB is able to generate cyclic behavior in predator–prey models with type-II functional responses, as opposed to systems with linear functional responses,

where stabilization is the rule (Abrams and Matsuda, 1997; Ives and Dobson, 1987). Those authors state that saturation of consumption rate caused by high prey densities can generate oscillations. This is in agreement with our results, where prey ID promotes the predator functional response saturating faster, through lowering the upper bound of consumption rate. The occurrence in our study system of a zone of complex dynamics, with multiple attractors at high levels of defense effectiveness and high K, agrees with the findings of Abrams and Matsuda (1997). Those authors found increasing levels of complexity in the predator–prey dynamics, associated to higher intensities of APB. Likewise, Verdy and Amarasekare (2010) also found multiple attractors in IGP systems with fixed interaction strength. In addition, our analyses showed that APB reinforces the paradox of enrichment (Rosenzweig, 1971), since destabilization in face of enrichment gets stronger with the incorporation of ID. The study of this effect deserves future analyses that lie beyond the scope of this work. Nevertheless, it has been reported that fast evolution of defensive or foraging traits weakens the ability of APB to stabilize the community exposed to increased enrichment (Mougi and Nishimura, 2008). Therefore, additional analyses of our system over a different parameter space would lead to a deeper understanding of the responses to enrichment of IGP systems with adaptive prey.

A perhaps surprising result is that at under certain set of parameter conditions, where persistence of IG-prey is assured at any level of defense effectiveness, permanence of top predators is enhanced by moderate levels of defense effectiveness of their prey. Although a rigorous explanation of mechanisms underlying this behavior requires further investigation, it can be hypothesized that moderate increases in defense effectiveness indirectly favors IG-predators through increasing IG-prey abundance. At higher levels of ID effectiveness, IG-predators do not gain enough resources due to reduced attack rate on the IG-prey and reduced abundance of basal resources derived from increased IG-prey abundance.

Previous theoretical results (Krivan and Diehl, 2005) propose optimal foraging as a stabilizing factor, through enlarging the coexistence regions in which IG-predator can persist, and only if IG-prey is more profitable than the basal resource. Our work extends the results of Krivan and Diehl (2005), through revealing that APB is an equivalent mechanism to optimal foraging, promoting species persistence in IGP systems. These adaptive behavioral traits eventually permits that stable IGP modules subsidize unstable modules and promote biodiversity in complex ecological networks (Kondoh, 2008).

While it becomes clear that optimal foraging promotes coexistence through enhancing persistence of IG-predators, and adaptive prey behavior promotes coexistence through enhancing persistence of the IG-prey, a challenge for future research is to understand the interactions between both forms of adaptive behavior in every species in the IGP module. Thus, APB can be present in the basal species both as a specific and generalized response to their predators, while IG-prey and IG-predators can exhibit APB and OF respectively. Of course, different details of prey defenses could eventually lead to different dynamic outcomes. Of particular relevance are the various forms of cost associated to prey responses. In this study we assumed that only mortality is affected as a by-product of exhibiting defensive responses. This was a choice in search of simplicity. Nevertheless, other costs affecting the strength of interactions between the defended prey and other species in the food web (e.g. feeding costs, Krivan and Sirot, 2004; Ramos-Jiliberto et al., 2008; or community trade-offs, Garay-Narváez and Ramos-Jiliberto, 2009) could drive unexpected population dynamics. These responses can generate several feedback structures whose understanding will improve our knowledge about the full potential of adaptive behavior as a determining force shaping community dynamics.

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