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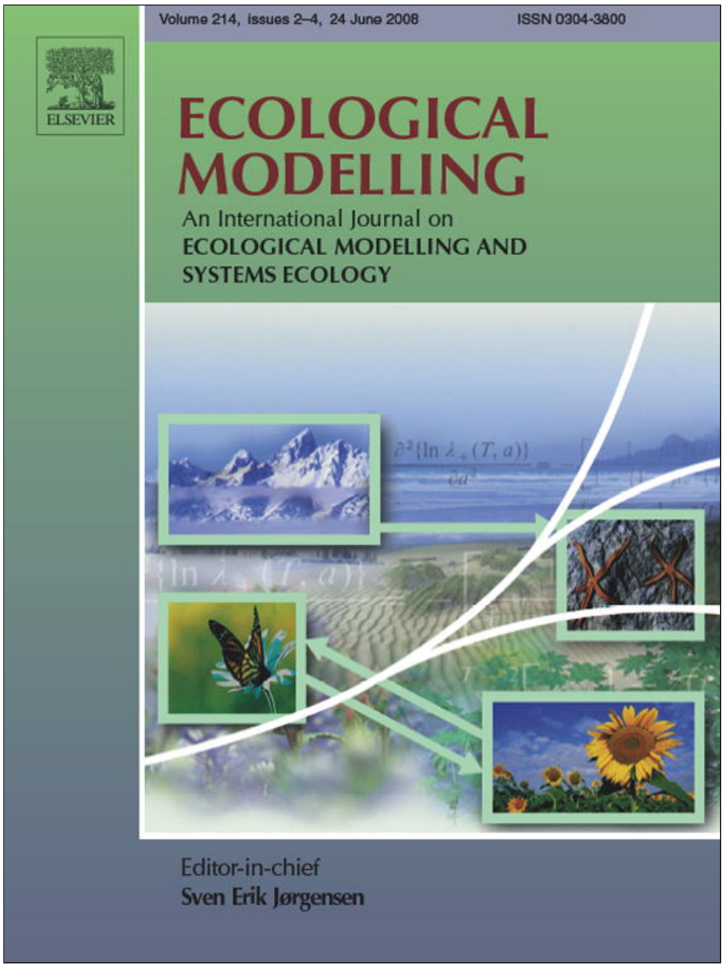

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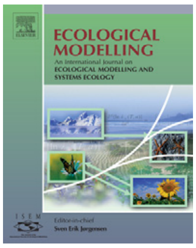

Dynamic effects of inducible defenses in a one-prey two-predators system

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ABSTRACT

Inducible defenses influence the dynamics of both the prey exhibiting the response and its predator, but it could affect indirectly other populations in the community. Earlier studies concerned with population dynamics of species exhibiting inducible defenses mostly considered simple one-prey-one-predator systems. In this work we analyze the dynamics of a system with a single prey exhibiting inducible defenses, and two predators. Particularly, we show the long-term stability of the systems as a function of effectiveness and costs of inducible defenses. Eight specific model systems are numerically studied, representing a set of biologically plausible interactions. The models are parameterized from published experimental information. Our results indicate that inducible defenses and costs favor system stability. The specificity of the defensive response increases coexistence probability. Complex dynamics, including coexistence of two and three attractors, emerge when two induced defensive traits operate simultaneously.

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1. Introduction

Much of the complexity of ecological systems relies on the multiple ways and paths of interactions among populations. Predator–prey relationships constitute core components of ecological interaction networks and food webs in particular, and their understanding is fundamental for representing, analyzing, and interpreting complex model communities.

Predators can exert both lethal and nonlethal effects on their prey (Lima, 1998). Nonlethal effects constitute a set of phenotypic responses of prey to predator's abundance or activity. One such responses are prey defenses, which can be divided into two broad classes. Constitutive defenses are based on traits expressed by the prey independent on the environment. Conversely, inducible defenses (ID) are behavioral, morphological, physiological, or life-historical plastic responses triggered by environmental cues associated to the density or harmfulness of natural enemies. (Harvell and Tollrian, 1999). Predation theory states that inducible defenses should be evolutionarily favored if three conditions are met: (i) predation risk is variable or unpredictable, (ii) there are reliable cues informing about predation risk, and (iii) the defended prey pay some cost for being less vulnerable to predation (Harvell, 1990; Harvell and Tollrian, 1999). Such phenotypic plasticity will influence the dynamics of the population that exhibits the defensive response, but potentially can also affect the entire set of populations that interact directly or indirectly with the former. Previous work dealing with population consequences of ID has shown that systems tend to stabilize when ID is added (Ives and Dobson, 1987; Sih, 1987; Ruxton, 1995; Abrams and Walters, 1996; Kopp and Gabriel, 2006; Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto

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and González-Olivares, 2000; Ramos-Jiliberto et al., 2002, 2007; Ramos-Jiliberto, 2003). Nevertheless, most of the earlier studies concerned with population dynamics of species exhibiting ID only consider a simple one-prey-one-predator system or trophic chains with one species per level (Vos et al., 2004a,b; Ramos-Jiliberto and Garay-Narváez, 2007; Ramos-Jiliberto et al., 2008). Although such studies are largely instructive in order to reveal the fundamentals of how ID alters the long-term properties of simple trophic chains, in order to understand the full role of ID in natural communities we need to move a step further and include ID into more realistic food web topologies (Kondoh, 2007). In this work we analyze the dynamics of a system consisting of a single prey exhibiting ID and two predators. Particularly, we will show the long-term stability of the system as a function of increasing effectiveness and costs of ID.

In real communities, ID are triggered when prey perceive environmental cues (e.g. visual or chemical signals) correlated with predation risk. In multipredator environments, prey living in an *olfactory sea* (Tollrian and Dodson, 1999; Vos et al., 2006) can be induced to develop a given defensive trait by the cues released by one or more predators. On the other hand, the defense can be effective in protecting the prey against one or more predators, irrespective of the origin of the cue. In other words, the induction and effectiveness of ID is not always specific to a particular predator and can be considered the result of a diffuse coevolution (Laforsch and Tollrian, 2004; Wohlfahrt et al., 2006). Moreover, prey could be able to exhibit more than one type of ID (e.g. a behavioral defense together with a life-historical defense), in response to a guild of potential predators. Therefore, the number of possible ways in which ID can act in even the simplest food web is considerably larger than considered previously. We investigate here a set of biologically plausible configurations in which a prey ID can function in a two-predator setting. Particularly, changes in system stability and population persistence are analyzed, as a function of the effectiveness and costs of prey defenses. Defenses can act via decreasing attack rate of predators, or via increasing handling time; and we will distinguish between both types of ID. Nevertheless, it has been shown that the balance of bottom-up and top-down control is dependent on when attack rate defenses act in the predation cycle (van der Stap et al., 2007). Our results show that the long-term population consequences of this form of phenotypic plasticity include changes in local stability, number of attractors, and species coexistence as a function of the ID related parameters.

2. The model

We used the following system as our base model:

$$\begin{aligned}\frac{dx}{dt} &= x[\varepsilon_x(r_x - M(y,z)) - \lambda_x x] - P_y(x,y,z)y - P_z(x,y,z)z\\ \frac{dy}{dt} &= y[\varepsilon_y(P_y(x,y,z) - m_y) - \lambda_y y]\\ \frac{dz}{dt} &= z[\varepsilon_z(P_z(x,y,z) - m_z) - \lambda_z z]\end{aligned} \qquad (1)$$

where x is population density of prey, and y, z are population densities of the two predators. Function M is the consumption requirement for zero prey growth in absence of predators, and P_y, P_z are the functional responses (Holling type-II) of predators y and z, respectively. The function describing consumption requirement for zero prey growth is

$$M(y,z) = m_x[1 + (C-1)(qD_1 + \bar{q}D_2)] \qquad (2)$$

with $\bar{q} = 1 - q$, such that M (y, z) increases linearly with prey defenses. Given that the prey could exhibit two types of defenses (D_1 and D_2), their effects are weighted by $q \in [0,1]$. Parameter C represents metabolic costs of defenses, measured as the relative increase in $M \in [m, mC]$ when defenses are fully expressed. Parameter m represents the value of M when no defenses are exhibited by prey.

Type-II functional responses are given by

$$P_j(x,y,z) = \frac{1}{[xA_j(y,z)]^{-1} + H_j(y,z)} \qquad (3)$$

being A and H the functions representing attack rate and handling time, respectively. These functions are described by

$$A_j(y,z) = a_j[1 + (E_A^j - 1)(w_jD_1 + \bar{w}_jD_2)] \qquad (4)$$

$$H_j(y,z) = h_j[1 + (E_H^j - 1)(k_jD_1 + \bar{k}_jD_2)] \qquad (5)$$

with $j = y, z$; $\bar{w} = 1 - w$, and $\bar{k} = 1 - k$. These functions increase (H) or decrease (A) linearly with prey defenses, in the same way that (2). The effectiveness of an attack rate based ID is given by $E_A \in [0,1]$. In this way, attack rate decreases with lower values of E_A. Likewise, effectiveness of a handling time based ID is represented by $E_H \in [1,\infty]$, and therefore handling time increases with higher values of E_H.

A defensive trait is considered to be an instantaneous response of the prey to the density of predators:

$$D_i(y,z) = \frac{(s_i^y y + s_i^z z)^{v_i}}{(s_i^y y + s_i^z z)^{v_i} + u_i^{v_i}} \qquad (6)$$

with $i = 1, 2$. This function describes a sigmoid increase in defense level as predator populations y or z get larger. Parameters s^y and s^z take values of zero or one, and define whether or not a given predator triggers the defensive trait. Parameter u defines the predator abundances for middle level of defenses, and v is the abruptness of the curve. The model presented here is an extension of the one presented in (Ramos-Jiliberto et al., 2007) to two predators.

Both predators are considered to be identical, except for the defense-related parameters. The basic parameter values (Table 1) were obtained from the experimental work reported in (Vos et al., 2004b). Parameter values that are specific to each sub-model are listed in Table 2.

For analyzing the systems under study, we performed bifurcation analyses using the package XPP-Auto version 5.3 (Ermentrout, 2002). Particularly, we performed two-parameter continuation of Hopf bifurcations and other special points in order to get stability domains on bidimensional parameter spaces. We also performed sensitivity analyses for the non-target parameters (varying 50% up and down the starting value) in order to check for the robustness of the results.

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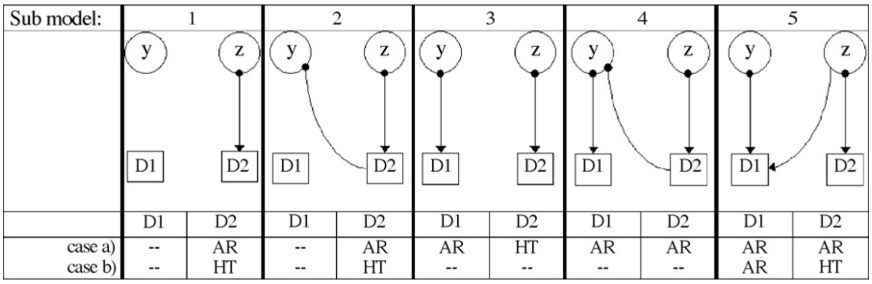

Fig. 1 – The eight study cases (five sub-models). D1 and D2 are alternative prey defensive traits either of the type attack rate based (AR) or handling time based (HT). Predators y and z are identical except for their ability to induce prey defenses, and their feeding susceptibility to them. Arrow-ended edges indicate induction of defenses by a given predator. Circle-ended edges indicate feeding inhibition of a predator, caused by the occurrence of a prey defensive trait.

Table 1 – Description of constant parameters used in all models. dl = dimensionless

	i = x	i = y, z	Unit	Short definition
ε_I	0.36	0.50	dl	Conversion efficiency
a_i	0.77	2.71	$(\text{mg C day})^{-1}\,\text{dm}^3$	Basal attack-rate
λ_I	0.10	0.10	$(\text{mg C day})^{-1}\,\text{dm}^3$	Self-limitation coefficient
m_i	0.47	0.25	day^{-1}	Feeding requirement for zero growth
h_i	0.50	0.83	day	Basal handling time
$u_{1,2}$	0.10		mg C dm^{-3}	Predators level for half defense level
$v_{1,2}$	5		dl	Abruptness of defense response
r	1.32		day^{-1}	Prey intrinsic growth rate

3. Results

From (1) we selected five plausible topologies (i.e. sub-models) of induction/effect of ID. Attack rate based ID as well as handling time based ID were considered. This renders a total of eight specific systems for study, which are diagrammatically shown in Fig. 1.

The first sub-model explores the dynamics of a system in which the prey exhibits ID induced by and against predator z. The predator y is a less efficient consumer and this can be interpreted as the prey having a constitutive defense against y. For case (a) both constitutive and inducible defenses are attack rate based (Fig. 2a) and for case (b) the defenses are handling time based (Fig. 2b). Here constitutive defenses (CD) are represented as a reduction in the functional response, through changing parameters A_y and H_y as $\text{CD}_A = a_y/n_A$ and $\text{CD}_H = h_y n_H$ for attack rate based and handling time based constitutive defenses, respectively.

If the prey exhibits a defensive trait, either inducible or constitutive, against only one predator population the dynamics does not vary noticeably and maintains the basal oscillatory regime. Conversely, if both defenses act simultaneously, the system stabilizes. Note that attack rate based defenses are more effective in stabilizing the system than their handling time based counterparts. Considering that this finding does not conform previous work (Vos et al., 2004a), more effort is needed in order to clarify whether this divergence is explained by the comunity structure at hand or by model peculiarities.

Table 2 – Description of parameters used for each sub-model (see Fig. 1). All parameters are dimensionless, except noted

	Sub-model								Short definition
	1a	1b	2a	2b	3	4	5a	5b	
s_1^y	–	–	–	–	1	1	1	1	Sensitivity of D_1 to predator y
s_2^y	0	0	0	0	0	0	0	0	Sensitivity of D_2 to predator y
s_1^z	–	–	–	–	0	0	1	1	Sensitivity of D_1 to predator z
s_2^z	1	1	1	1	1	1	1	1	Sensitivity of D_2 to predator z
q	1	1	0	0	0.5	0.5	0.5	0.5	Fraction of cost paid for D_1
w_y	0	0	0	0	1	0.5	1	1	Weight of D_1 for reduction of A_y
w_z	0	–	0	0	–	0	0	–	Weight of D_1 for reduction of A_z
k_y	0	0	0	0	–	–	–	–	Weight of D_1 for increase of H_y
k_z	–	0	0	0	0	–	–	0	Weight of D_1 for increase of H_z
E_A^y	0	0	Free	1	Free	Free	Free	Free	Effectiveness of attack rate based ID against y
E_A^z	Free	1	Free	1	1	Free	Free	1	Effectiveness of attack rate based ID against z
E_H^y	1	1	1	Free	1	1	1	1	Effectiveness of handling time based ID against y
E_H^z	1	Free	1	Free	Free	1	1	Free	Effectiveness of handling time based ID against z
a_y	Free	Free	$2.71\,\text{mg C day})^{-1}\,\text{dm}^3$						Basal attack rate of y
h_y	Free	Free	0.83 day						Basal handling time of y
C			Free						Cost of ID

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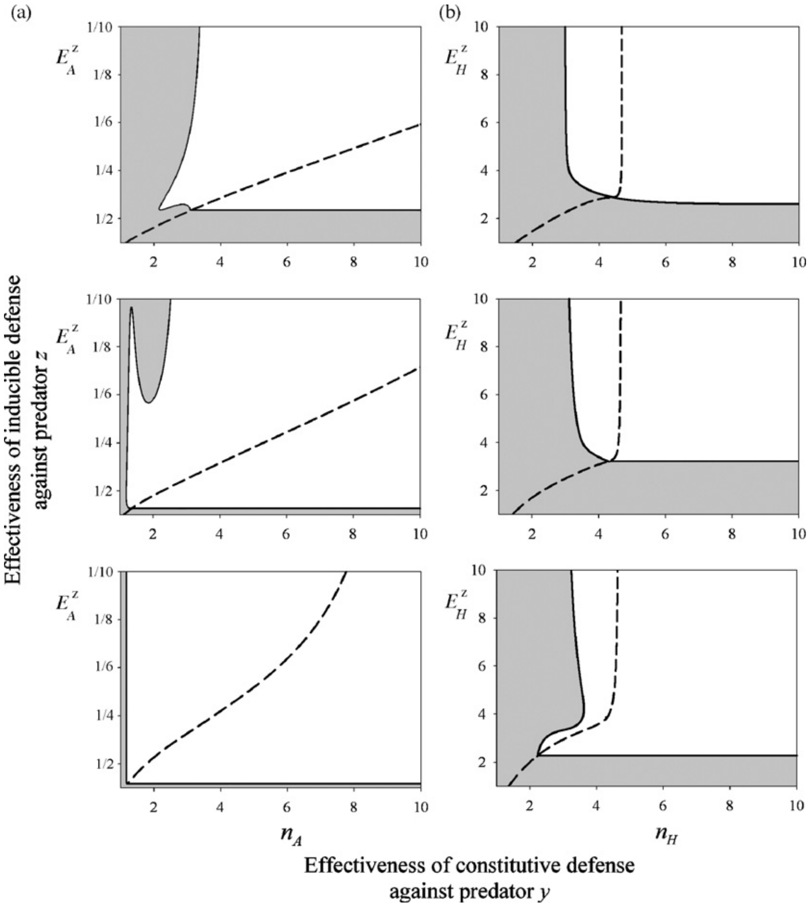

Fig. 2 – Two-parameter bifurcation diagrams for sub-model 1. The prey exhibits an inducible defense (ID) induced by and against z, and a constitutive defense (CD) against y (see text for details). The effectiveness of the ID and the CD is shown on the ordinate and abscissa, respectively. Continuous lines separate stable from unstable dynamics, and dashed lines indicate extinction thresholds for predator y. Below the dashed line population y is extinct. Light grey areas indicate periodic oscillations, and white areas indicate stable equilibrium points. (a) Attack rate based ID, (b) handling time based ID. Cost of ID are C = 1, C = 1.5, and C = 2 from the first to the third row of graphs.

On the other hand, at low or moderate level of attack rate based ID, the addition of constitutive defense against predator y leads to extinction of the latter (Fig. 2a). For handling time based defenses (Fig. 2b) the extinction of y driven by CD occurs at all levels of ID, although it is more likely at low ID. The effects of costs of ID (i.e. increasing parameter C) are more significant for attack rate based defenses. Here the stability zone is increased at higher cost and the parameter region allowing for coexistence of both predators is reduced. For handling time based defenses, increasing costs has a weak effect on the shape of stability domains, and has a negligible effect on the extinction thresholds.

Sub-model 2 considers the prey exhibiting an ID that is induced by predator z but affects the consumption rate of both predators (see Fig. 1). When the ID is attack rate based and no costs are involved (Fig. 3a, upper) the dynamics is similar to the first sub-model (Fig. 2a, upper). Nevertheless, a curved band appears (dark grey zone of Fig. 3a) where three equilibrium points coexist, two of them being attractors (bistability). As attack rate based ID become more costly, (a) local stability is less likely at larger values of E_A^y, (b) local stability is more likely at high values of E_A^z, (c) the slope of the y-extinction curve (dashed line) increases, and (d) the bistability band moves downwards. For handling time based ID, higher defense effectiveness against z (E_H^z) ensures the existence of a periodic attractor unless E_H^y is also high (Fig. 3b). Here a diagonal extinction threshold for y as well as a diagonal bistability band are also found. As costs are more severe, the instability region increases. With the highest cost (Fig. 3b, lower), there also appears a small zone (black) where three attractors coexist: two stable points and one periodic orbit.

Sub-model 3 considers the prey exhibiting two induced defensive traits, the one is an attack rate based ID induced by and affecting predator y, and the other is a handling time based ID induced by and affecting predator z. Without costs (Fig. 4a, upper) there appears the characteristic L-shaped instability region (light grey), inside which there exists a zone where two attractors coexist (a stable point and a stable orbit, dark grey), and a smaller region where two stable points and one stable orbit coexist (black). As costs increase, (a) the stability region is larger with high E_H^Z values, (b) the three-attractor zone disappears, and (c) the two-attractor zone

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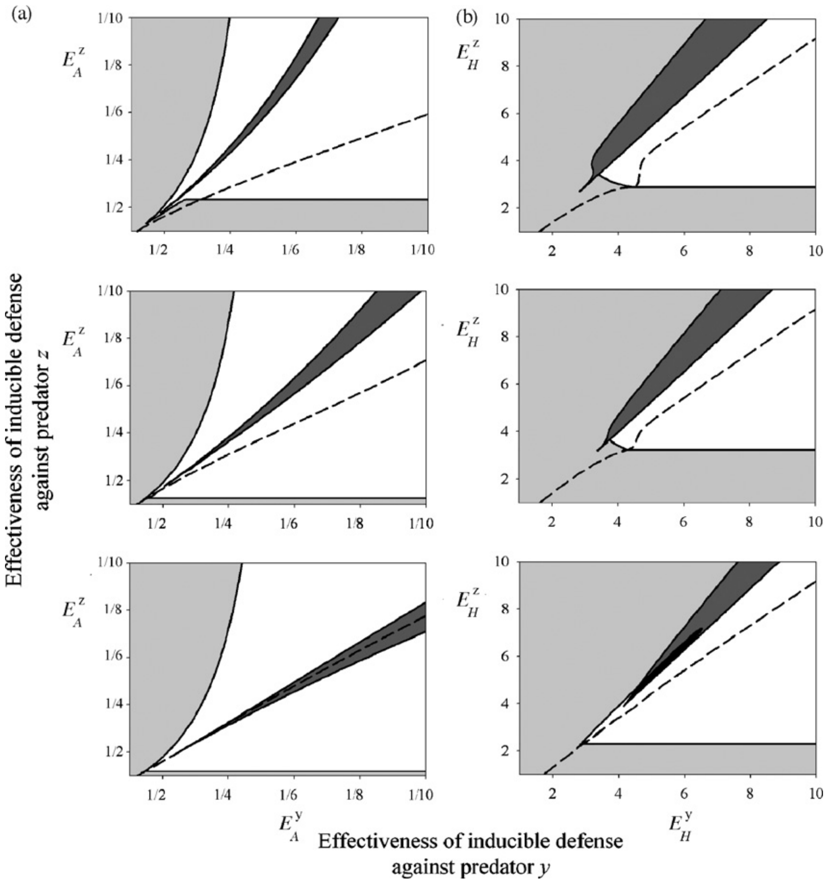

Fig. 3 – Two-parameter bifurcation diagrams for sub-model 2. The prey exhibits ID induced by z but affecting consumption by y and z. Symbols as in Fig. 2, plus a dark grey zone representing two stable-point attractors, and a black zone where three attractors coexist: two stable-point and one stable orbit. x-axis and y-axis are effectiveness of ID against predator y and z, respectively. (a) Attack rate based ID, (b) handling time based ID. Cost values are as in Fig. 2.

moves upwards. Unlike the previous cases, here does not appear an extinction curve and all three populations exist throughout the explored parameter space.

Sub-model 4 considers the prey exhibiting two attack rate based ID; one of them induced by and affecting y, and the other one induced by z but affecting both y and z. This sub-model presents an L-shaped instability region that changes little at increased costs (Fig. 4b). With uncostly ID there appears a zone containing two attractors (two stable points, dark grey on Fig. 4b) and a zone with three attractors (two stable points and one stable orbit, black). With a moderate addition of costs, the three-attractor zone disappears and the bistability zone enlarges considerably (Fig. 4b, middle). With even larger cost the dynamics simplify and only one attractor is possible. Here, deterministic coexistence is ensured over the explored parameter space.

Sub-model 5 considers the prey displaying two distinct ID. One ID is induced by both y and z but affects only y, while the other is induced by and affects z. In case 5a (Fig. 5a) both ID are attack rate based, and in case 5b (Fig. 5b) the ID affecting y is attack rate based and the other one is handling time based. Dynamics of this system (specially case (a)) is remarkably similar to that of sub-model 1, where the prey has a constitutive defense against y. In sub-model 5, the prey exhibits an ID induced by both predators, and thus it is likely for the prey to be permanently in a defended state, as happen with a constitutive defense. Case (b) presents an important difference respect to sub-model 1b, which is the shape of the extinction curve. Here, extinction of y occurs only at low values of E_H^z. Unlike case (a), case (b) is not conceptually equivalent to sub-model 1b since here the defense against y is attack rate based.

Sensitivity analyses indicated that moderate changes in the non-target parameters did not alter qualitatively the results reported here.

4. Discussion

Modelling aproaches have contributed in an important way to the understanding of the origin and maintenance of biodiversity in general, and the coexistence of competing populations in particular (see Jensen, 1987; Ekschmitt and Breckling, 1994; Ebenhöh, 1994). The competitive exclusion principle arisen at the beginning of the past century states that two or more consumers limited by a single resource could not coexist (Volterra, 1928; Hardin, 1960; Armstrong and McGehee, 1980; den Boer, 1986). More contemporary research revealed, nev-

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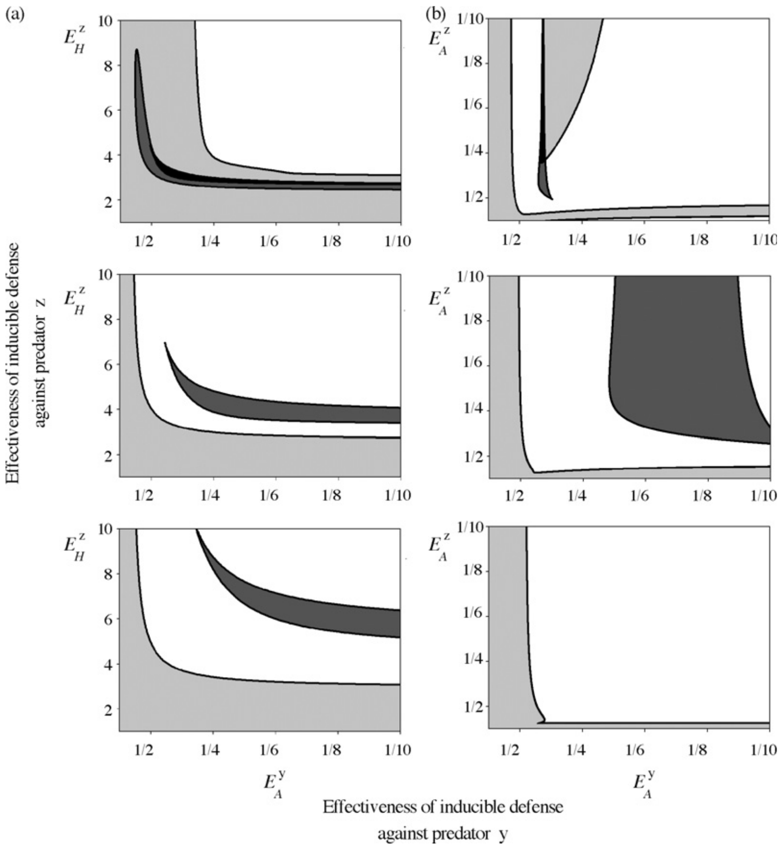

Fig. 4 – Two-parameter bifurcation diagrams for sub-models 3 and 4. (a) Sub-model 3, the prey exhibits one attack rate based ID induced by and affecting y, and one handling time based ID induced by and affecting z. (b) Sub-model 4, the prey exhibits two attack rate based ID; one of the induced by and affecting y, and the other one induced by z but affecting both predators. On the dark grey zone two attractors coexist: one stable-point and one stable orbit. On the black zone three attractors coexist: two stable-point and one stable orbit. *x*-axis and y-axis are effectiveness of ID against predator y and z, respectively. Cost values are as in Fig. 2.

ertheless, that coexistence of several consumers and one resource is possible under sustained population oscillations driven by either endogenous or exogenous forces (Koch, 1974; Armstrong and McGehee, 1980; Abrams and Holt, 2002). Sufficient conditions for coexistence of two consumers on a single resource is that at least one consumer population should exhibit a saturating functional response, or that one of the functional responses should be lower than the other at high prey densities (Armstrong and McGehee, 1976; Abrams and Holt, 2002). Therefore, currently it is usually assumed that the competitive exclusion principle only applies for stable dynamics. In this regard, the present work contributes from two corners to the competition-coexistence debate. First, we present inducible defenses as a coexistence-promoting mechanism by which two functional responses can reach different heights, due to a decrease in prey vulnerability induced by high predator abundances. Second, our study reveals that coexistence of two consumers and a single resource is possible under stable states in a constant external environment. Furthermore, we develop the theory of inducible defenses through presenting novel insights about coexistence and stability of prey confronted to a multipredator environment.

In this work, we focused on the role of inducible defenses in shaping the long-term population dynamics of a model system comprising a prey and two predators. We emphasized the asymmetry of prey defense capabilities against otherwise identical predators. Our analyses showed that a simple system with a prey exhibiting defenses against two predators can show a wide range of dynamics, from stable coexistence of the three species, three dimensional limit cycles, up to two and three attractors coexisting in a region of the parameter space. We argue that the projected dynamics is likely to be found in real systems since: (a) the structure of the model relies on plausible biological assumptions (Tollrian and Dodson, 1999; Strauss et al., 2002), (b) our parameterization comes from real data (Vos et al., 2004b), and (c) our results showed to be robust to moderate changes in parameter values.

When each of the two predators activates a specific defensive trait in the prey (i.e. sub-models 3 and 4), deterministic three-species coexistence is predicted over all the tested parameter space. Conversely, whenever a defense is either permanently induced (sub-model 1), not induced (sub-model 2), or induced by both predators (sub-model 5), a region of extinction appears for one of the predators, and the dynamics is reduced to two-dimensional.

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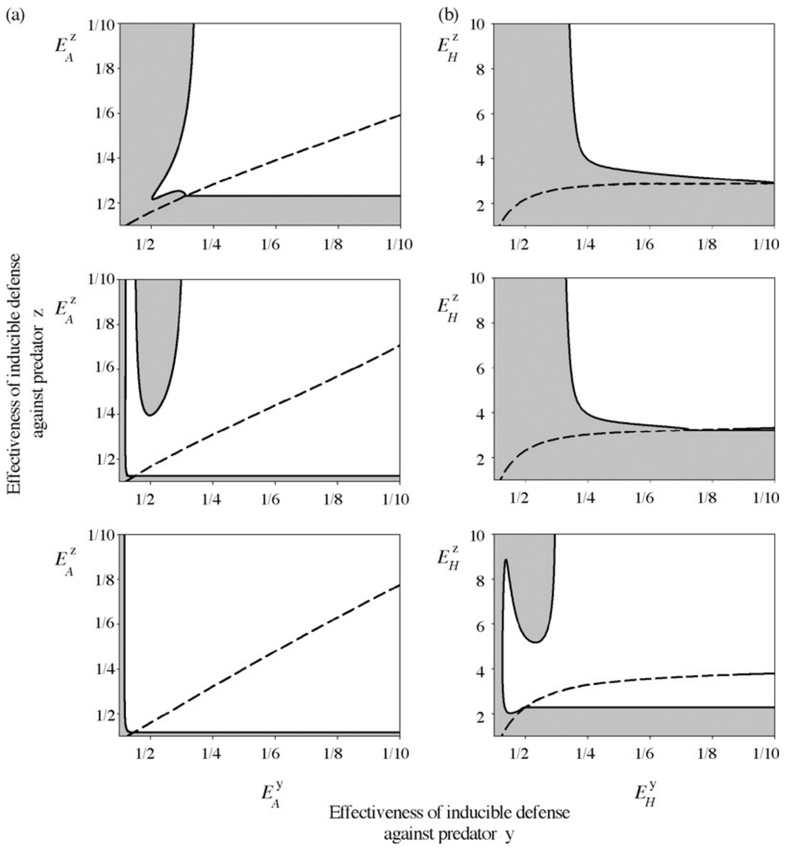

Fig. 5 – Two-parameter bifurcation diagrams for sub-model 5, where the prey exhibits one ID induced by both y and z but affecting only y, and one ID induced by and affecting z. (a) Both ID are attack rate based, (b) the ID against y is attack rate based, and the other one is handling time based, x-axis and y-axis are effectiveness of ID against predator y and z, respectively. Cost values are as in Fig. 2.

Results from sub-model 1 reveal that induced defenses favor system persistence over constitutive ones. Also, it is noticeable the effects of increased costs of ID: the likelihood of local stability increased while the likelihood of coexistence decreased.

When a defense is induced by one specific predator, but protects the prey against both enemies (sub-model 2), coexistence probability increases with ID effectiveness against the inducer predator and decreases with ID effectiveness against the not-inducer predator. However, when effectiveness against the not-inducer is negligible, the interior equilibrium is unstable and the populations fall in an oscillatory regime. In this sub-model, balanced defense effectiveness against both predators may lead to the occurrence of multiple attractors.

Sub-models 3–5 explore cases where the prey develops two distinct ID (e.g. a behavioral and a morphological defense). When one of the ID is unspecific for its induction (sub-model 5) it may act as a constitutive defense, since predator cues are abundant. In these cases, costs are relevant for shaping the stability domains, like in sub-model 1a.

For the set of models studied here, coexistence is ensured where there are two distinct ID, each of them triggered by different predators. In these systems, complex structures such as two and three simultaneous attractors appear when cost is low and ID effectiveness is moderate.

In general terms, this work support early knowledge in that ID favor system stability. Our findings also indicate that costs of ID also promote stability, and that unspecific defensive responses increases extinction probability. Furthermore, complex dynamics emerge when two induced defensive traits operates simultaneously.

Our results unavoidably rest on model assumptions, i.e. continuous growth, unstructured populations, type-II prey-dependent functional responses, among many others. However, an important assumption is that defenses develop and reverse instantaneously. This can be true for many behavioral defenses, or indeed morphological defenses in fast-growing clonal organisms such as zooplankton. Nonetheless, instantaneous ID cannot be considered as the general rule. Time lags spanning from hours to generations operate for the development as well as for reversing the defense, and this can play an important role for the dynamics (Miner et al., 2005). We find that an interesting research avenue in this field is to understand the control mechanisms of the timing of defenses, and incorporate this knowledge into more realistic models. Another limitation of this study is that we did not consider cases of enhanced risk to one predator or natural enemy as a side-effect of defending from another predator (Sih et al., 1998; Decaestecker et al., 2002; Strauss et al., 2002). Future extensions of this study should also include the effects of multiple prey on defense development. A recent work of

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Kratina et al. (2007) showed that the presence of non-prey species suppresses predation rate on the focal prey, probably due to the wasted-time effect. Since ID induced by one o more predators could make a prey inedible for a set of predators, ID could reduce predation strength of many non-focal interactions within complex communities.

This work demonstrates how phenotypic plasticity in the prey, in the form of ID, modifies interaction strength and alters population dynamics as well as community persistence. Predator-induced defenses generate or increase self-limitation in the inducer predator (Dambacher and Ramos-Jiliberto, 2007; Ramos-Jiliberto and Garay-Narváez, 2007). On the other hand, costs of ID constitute nonlethal predation effects that increase the negative outcome of predators on their prey. We noted also that much complexity is generated in multipredator environments when defenses are unspecific, since a trait-mediated indirect effect is incorporated between competing predators. In this way, a simple exploitative competition interaction is modified by the incorporation of ID through altering the strength of interactions as well as adding new effects between species. Therefore, the structure of the system is modified in both quantitative (interactions strength) and qualitative (network topology) terms. Furthermore, strong nonlinearities inherent to ecological systems create particular outputs that are unpredictable from pure conceptual arguments.

Nonlethal effects of predation in particular (Lima, 1998), and phenotypic plasticity in general (Miner et al., 2005) lead to important modifications in both direct and indirect interactions within food webs, which defines core dynamic properties such as population stability and community persistence (Peacor and Werner, 2001; Wootton, 2002; Werner and Peacor, 2003). A more complete understanding of the biology behind the density-dependence of interactions is of great theoretical value. Nevertheless, applied issues such as predicting the effects of contaminants on real communities rest on our ability to explain how lethal and nonlethal effects of environmental stressors propagates, amplifies or buffer in a population network (Fleeger et al., 2003; Rohr et al., 2006). Theoretical studies of ecological networks fed by empirical research on the biology of interactions among biotic and abiotic ecosystem components represent a promising field for future work.

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