Role of inducible defenses in the stability of a tritrophic system

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ABSTRACT

Inducible defenses are a form of phenotypic plasticity that potentially modify direct interactions between various members of an ecological community, generating trait-mediated indirect effects. In this work, the hypothesis that inducible defenses increase the stability of tritrophic chains is tested, through the numerical analysis of a continuous-time model that discriminate between defenses affecting attack rate of predators, and defenses affecting predator handling time. In addition, discrimination between feeding costs of defenses affecting attack rate, and metabolic costs affecting feeding requirement for zero growth are considered. System stability was examined by computing dominant Lyapunov exponents, and through continuation routines of bifurcation points. Background parameter values were taken from two published studies. Our results show that a tritrophic system will generally be stabilized by the incorporation of inducible defenses and by their associated costs, but a number of new outcomes were obtained. Different long-term behavior is predicted if either one or two prey populations exhibit defenses. In the latter case, the defense of the basal prey dominates the dynamics. Handling time based inducible defenses exert a stronger stabilizing effect than attack rate based ones, but also impose a higher extinction risk for top predators. Inducible defenses in particular and trait-mediated indirect effects in general can be important sources of stability in natural systems.

1. Introduction

Inducible defenses constitute a widespread form of phenotypic plasticity whose impact at the population and community level is still poorly understood, except for very simple model structures (Ramos-Jiliberto et al., 2007). In biological terms, inducible defenses are phenotypic traits that provide some form of protection against predators, but are expressed only after the perception of an environmental cue informing about high predation risk (Harvell, 1990; Harvell and Tollrian, 1999). The traits in question can be morphological, physiological, behavioral or life-historical, and they are known to occur across a

wide range of taxa, from protists to higher plants and animals (Lass and Spaak, 2003). The evolutionary development of these kinds of defenses is favored when predation risk is variable or unpredictable, because the survival benefit of an inducible defense commonly trades-off with other fitness components such as feeding rate, metabolic expenditure, or increased vulnerability to other natural enemies. Therefore, in variable environments inducible defenses permit saving costs when predation risk is low enough.

A number of theoretical studies have shown that the effects of both constitutive and inducible defenses in ecological systems are mainly stabilizing (Ramos-Jiliberto, 2003; Vos et al., 2004a; Kopp and Gabriel, 2006; Ramos-Jiliberto et al., 2007), in the sense that increasing some measure of the level of defense in a population also increases the region of the parameter space where critical points are locally stable. This effect is intuitive, since inducible defenses generate a negative feedback in predators, arising from decreasing consumption of prey (and therefore a decrease of predator fitness) after increasing predator abundance. Nevertheless, inducible defenses can also destabilize systems under certain sets of plausible assumptions (Kopp and Gabriel, 2006; Ramos-Jiliberto and Garay-Narváez, 2007). On the other hand, the costs associated with an induced defense impose a decrease of prey fitness as predator abundance increases. However, the dynamic consequences of this process have been somewhat elusive from previous research (Ramos-Jiliberto, 2003).

Present knowledge of this field is predominantly based on studies of continuous-time (but see Kopp and Gabriel, 2006) bidimensional systems of one-prey–one-predator. Therefore stability studies have been largely confined to the mapping of stable and periodic solutions of largely idealized models with minimal complexity. In contrast, multidimensional systems have the potential for exhibiting complex (e.g. chaotic) dynamics and allow for considering both direct and indirect effects between members of an ecological community. For these reasons, higher-dimensional systems are able to reveal the propagation of effects of inducible defenses across the food web. For example, a prey can exhibit feeding costs when displaying a defense mechanism, meaning that food consumption by prey decreases with predator density. This translates to a fitness reduction of the prey and a fitness increase of the prey's resource, and therefore constitutes a trait-mediated indirect effect of the predator on the basal resource (Peacor and Werner, 2001; Bolker et al., 2003). Furthermore, a tritrophic system includes two prey populations, and allows that either one of them or both exhibit an inducible defense (Verschoor et al., 2004).

In this work, the hypothesis that inducible defenses (ID hereafter) increase the stability of tritrophic chains is tested. In order to accomplish this, appropriate functions representing both the ability of prey to change its vulnerability to predators as a response to higher predator densities, as well as the associated fitness costs were incorporated. We found necessary to discriminate between defenses affecting attack rate of predators, and defenses affecting predator's handling time per unit prey (Jeschke and Tollrian, 2000). In addition, discrimination between feeding costs of defenses affecting attack rate of prey on their resource, and metabolic costs affecting feeding requirement for zero growth are considered

Table 1 – Background parameter values used in the analyzed systems		
	Mathematical data	Biological data
r	7.44	1.42
ε_2	1	0.32
ε_3	1	0.5
a_1	4	0.77
a_2	2.25	2.73
λ_1	2.7	0.142
λ_2	0	0
λ_3	0.045	0
m	0.01	0.145
μ_2	1	1.17
μ_3	0.3	0.25
h_1	0.25	0.5
h_2	0.5	0.83
u	0.1	0.1
v	5	5

Mathematical and biological data were taken from Peet et al. (2005) and Vos et al. (2004b) respectively. See main text for definition of parameters.

(Ramos-Jiliberto et al., 2007). The set of combinations given by the type of defense and the type of costs are presented where the basal prey and middle prey populations display defenses induced by their respective predator. Because of the large number of free parameters associated with the set of models, we used published values of all parameter not associated directly with defenses.

2. The model

In order to maintain homogeneity of assumptions, we begin with a basic model (Ramos-Jiliberto, 2005) for the
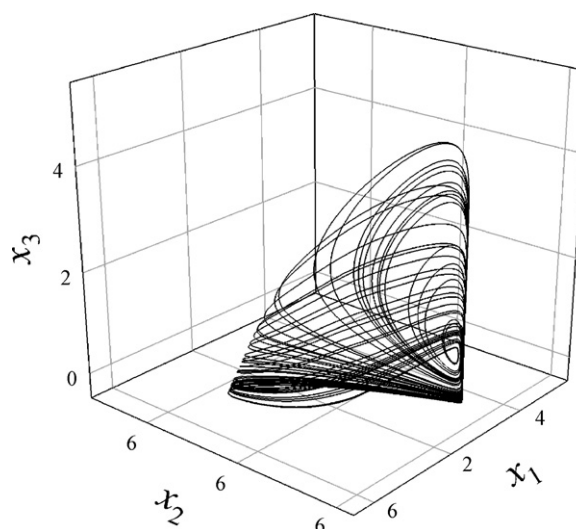

Fig. 1 – Chaotic attractor exhibited by the system without including inducible defenses, parameterized with the mathematical data. The trajectory is a run of 1000 time steps.

dynamics of any species of trophic level i and population size x_i:

$$\frac{dx_i}{dt} = x_i(\varepsilon_i(\phi_i - \gamma_i) - \lambda_i x_i) - x_{i+1}\phi_{i+1} \qquad (1)$$

where ε is conversion efficiency of assimilated food to per capita population growth, λ is a self-limitation (i.e. logistic) coefficient, and γ is the food consumption needed for zero population growth. Consumption rate of species i on its prey is denoted by ϕ_i, and consequently, predation rate on species i is ϕ_{i+1}. It is assumed that consumption (predation) rate is a monotonically saturating function of prey abundance (Holling type II):

$$\phi_i = \frac{A_{i-1}x_{i-1}}{1 + A_{i-1}H_{i-1}x_{i-1}}$$

If prey i exhibits attack rate based ID, then the predator's attack rate A_i will decrease with defense level D_i. For simplicity, we assume a linear relation:

$$A_i = a_i(1 - B_i D_i)$$

where a_i is the basal attack rate and B_i is the effectiveness of the defense against predation. On the other hand, if the defense is handling time based then:

$$H_i = h_i(1 + E_i D_i)$$

Likewise, E_i is the effectiveness of this type of defense for preventing prey mortality. If the defense carries out feeding costs, then the prey will show a lowered attack rate on its resource:
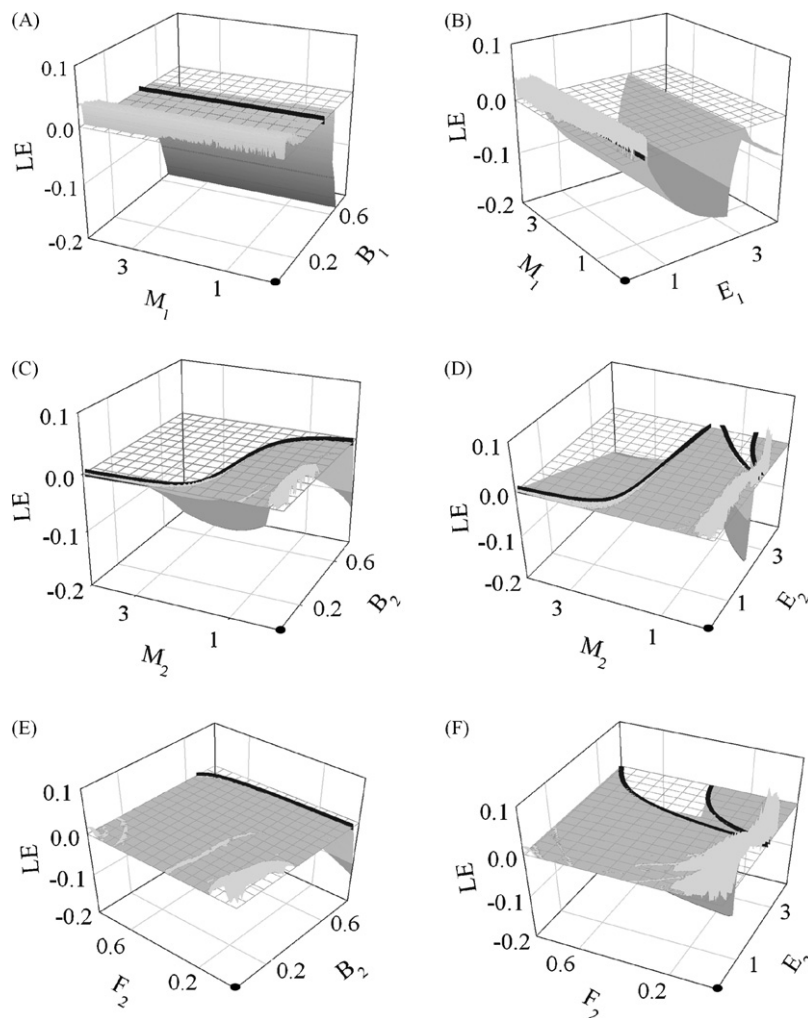
$$A_{i-1} = a_{i-1}(1 - F_i D_i)$$

Fig. 2 – Stability of the system parameterized with the mathematical data, as a function of defense effectiveness and costs. Only one prey species exhibits inducible defenses (ID). B_1: attack rate based ID of the basal species; B_2: attack rate based ID of the middle species; E_1: handling time based ID of the basal species; E_2: handling time based ID of the middle species; M_1: metabolic cost of the basal species ID; M_2: metabolic costs of the middle species ID; F_2: feeding costs of the middle species ID. The z-axis shows values of the dominant Lyapunov exponent (LE). Superimposed to the plane LE = 0 (grid), continuous lines indicate Hopf bifurcations as a function of the parameter values. Darker shading indicates more negative LE. The closed circle on the frontal lower corner shows the parameter coordinates were both ID and costs are absent.

and if there are metabolic costs, then

$$\gamma_i = \mu_i(1 + M_i D_i)$$

where D_i is the mean defense level of the prey, given by

$$D_i = \frac{(x_{i+1})^\upsilon}{(x_{i+1})^\upsilon + (u_i)^\upsilon} \tag{2}$$

which is an S-shaped curve with values between zero and one, with abruptness υ. Parameter u is the predator level for $D = 1/2$. This curve is typical for dose–response relationships and it has been used in Ramos-Jiliberto (2003) and in Vos et al. (2004a,b) for modeling defense level and induction of defense respectively. Arranging the above functions into (1) we obtain the tritrophic model

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1(r - m[1 + M_1 D_1] - \lambda_1 x_1) \\
&\quad - \frac{a_1[1 - B_1 D_1][1 - F_2 D_2]x_1}{1 + a_1[1 - B_1 D_1][1 - F_2 D_2]h_1[1 + E_1 D_1]x_1} y \\
\frac{dx_2}{dt} &= x_2 \varepsilon_2 \left(\frac{a_1[1 - B_1 D_1][1 - F_2 D_2]x_1}{1 + a_1[1 - B_1 D_1][1 - F_2 D_2]h_1[1 + E_1 D_1]x_1} \right) x_2 \varepsilon_2 \mu_2[1 \\
&\quad + M_2 D_2] - \lambda_2 (x_2)^2 \\
&\quad - \frac{a_2[1 - B_2 D_2]x_2}{1 + h_2[1 + E_2 D_2]a_2[1 - B_2 D_2]x_2} x_3 \\
\frac{dx_3}{dt} &= x_3 \left(\varepsilon_3 \left(\frac{a_2[1 - B_2 D_2]x_2}{1 + h_2[1 + E_2 D_2]a_2[1 - B_2 D_2]x_2} - \mu_3 \right) - \lambda_3 x_3 \right)
\end{aligned} \tag{3}$$

where D_1 and D_2 are given by Eq. (2). Feeding costs in species x_1 were not considered since its resource is not explicitly modeled. Thus, we define the constants $r = \varepsilon_1 \phi_1$ and $m = \varepsilon_1 \mu_1$. This system has been analyzed for simpler cases where defense does not take place, i.e. $D_1 = D_2 = 0$ (Hastings and Powell, 1991; Peet et al., 2005). The model of Hastings and Powell (1991) only included self-regulation in the basal species (i.e. $\lambda_2 = \lambda_3 = 0$) and showed the existence of chaotic dynamics under a given set of parameter values. Peet et al. (2005) found that strong self-regulation in the upper trophic levels increases the stability of the system.

In this work we study the effects of increasing levels of defense effectiveness and costs on model (3). Initially, we set parameter values according to the ones used by Peet et al. (2005) under chaotic regime, in order to see how ID affect chaotic behavior of a tritrophic system. This first data set will be referred to as mathematical data (Table 1). Next we analyze system (3) using parameter values obtained by Vos et al. (2004b) from a real ecological tritrophic system composed by green algae, herbivore rotifers, and carnivore rotifers. This last data set will be termed biological data (Table 1).

3. Analyses

As a measure of system stability, we computed the maximal Lyapunov exponents as a function of two parameters representing ID effectiveness or costs. Lyapunov exponents measure system sensitivity to initial conditions, such that negative values imply long-term convergence of neighboring trajectories toward a stable point or periodic attractor, while positive values are indication of chaos (Strogatz, 1994). The algorithm employed for determining Lyapunov exponents was proposed in Pokorny (2006), based on Wolf et al. (1985). It integrates the variational equations along with the original system of ordinary differential equations. Additionally, we performed bifurcation analyses using the software XPP-Auto Version 5.3 (Ermentrout, 2002). This allowed us to separate stable from oscillatory dynamics within the negative Lyapunov exponents region. Of particular interest are Hopf bifurcations, which indicate changes in stability of a critical point accompanied by the creation of a limit cycle (Kuznetsov, 2004). With the embedded package Auto (Doedel, 1984) two-parameter bifurcations diagrams were constructed for obtaining stability domains and extinction boundaries.

4. Results

4.1. One species exhibiting ID

4.1.1. Mathematical data
The basal state of the system, where defenses are absent, is depicted in Fig. 1, exhibiting deterministic chaos (Peet et al., 2005). This point in the parameter space corresponds to coordinates (0,0) in the parameter planes of Fig. 2. Next we will incorporate different levels of defense effectiveness and costs in order to see whether or not the systems gain stability.

For the studied cases where only the basal prey exhibits ID, stability is mostly increased with defense effectiveness, but defense costs have a marginal effect on the system stability. This is observed in Fig. 2A and B as a decrease of the dominant Lyapunov exponent with increasing effectiveness of both attack rate and handling time based ID (i.e. as parameters B_1 and E_1 increase from 0). Furthermore, stabilization is corroborated through bifurcation analysis and the limit between stable and unstable regions of the parameter space is shown as continuation of Hopf bifurcations, also shown in Fig. 2.
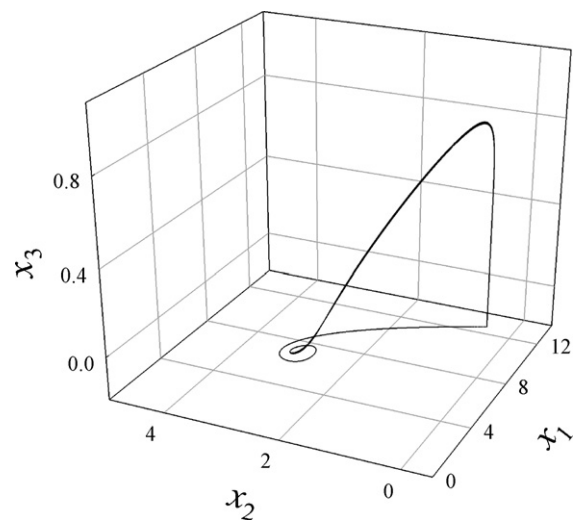

Fig. 3 – Attractor exhibited by the system without including inducible defenses, parameterized with the biological data. The trajectory is a run of 3000 time steps.

On the other hand, when the middle level species exhibits ID, both defense effectiveness and costs increase the system stability (Fig. 2C–F). Different types of costs (e.g. M_2 and F_2) lead to different stability domains. Metabolic costs exert a stronger stabilizing effect than feeding costs. On the other hand, a more complex behavior is observed if ID act through increasing handling times, since at low costs, increasing E_2 first stabilizes but then destabilizes the community (Fig. 2D and F). In all the cases studied in this section, ID moves the system away from the chaotic regime.

4.1.2. Biological data

The basal state of system (3), parameterized with biological data and where defenses are absent, is shown in Fig. 3. The trajectories are attracted to a periodic 2-cycle. This point in the parameter space corresponds to coordinates (0,0) in the parameter planes of Fig. 4.

The analyses made on the system of study, parameterized with the empirical data of Vos et al. (2004b) reveal some interesting differences from the previous parameterization. First, in this case both ID effectiveness and costs promote stability when the basal species is defended, although this is more pronounced for the attack rate based ID. Second, less ID effectiveness is required for stabilization to occur, as compared to the mathematical parameterization. Third, when the middle level species is defended, stabilization is less likely, since high ID effectiveness and low costs are required for obtaining negative Lyapunov exponents and for crossing the Hopf bifurcation (Fig. 4).

4.2. Two species exhibiting ID

4.2.1. Mathematical data

In this section we present results when two of the three species (x_1 and x_2) are simultaneously exhibiting ID against their corresponding predator (x_2 and x_3 respectively). Fig. 5 shows the stability domains in the parameter space spanned by the effectiveness of the ID exerted by both prey species, at
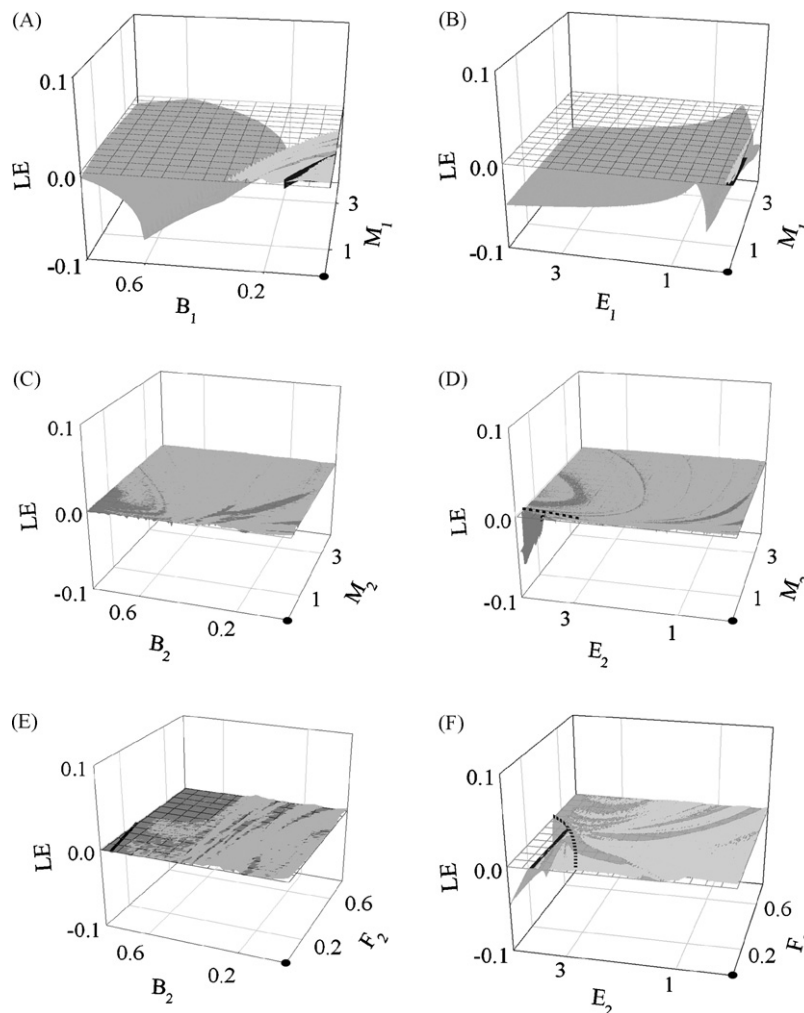

Fig. 4 – Stability of the system parameterized with the biological data, as a function of defense effectiveness and costs. Only one prey species exhibits inducible defenses (ID). The z-axis shows values of the dominant Lyapunov exponent (LE). Superimposed to the plane LE = 0 (grid), continuous lines indicate Hopf bifurcations, and dashed lines indicate extinction thresholds for top predators. Darker shading indicates more negative LE. The closed circle on the frontal lower corner shows the parameter coordinates were both ID and costs are absent. Note the different rotation of these plots as compared to Fig. 2. For parameter definitions, see legend of Fig. 2.
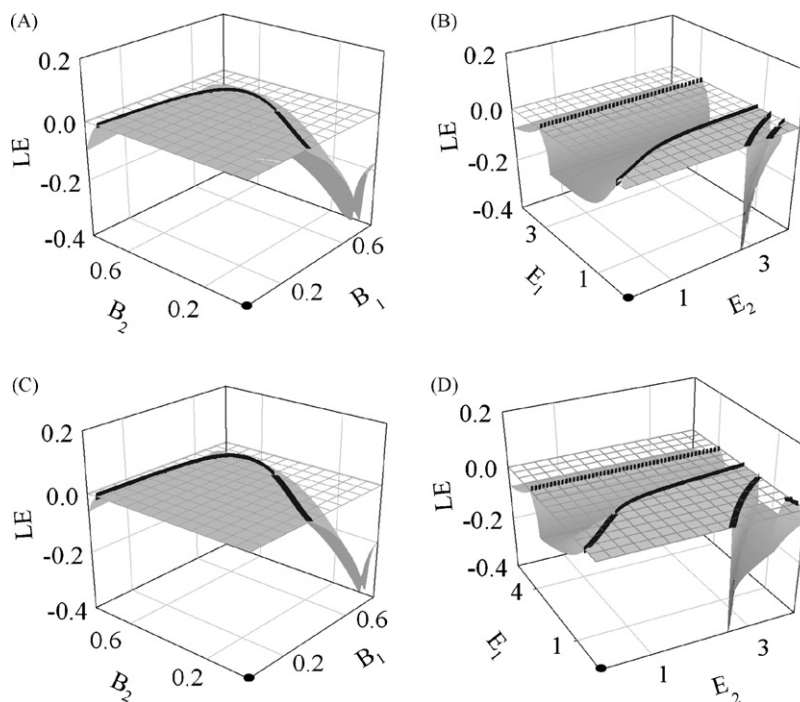
Fig. 5 – Stability of the system parameterized with the mathematical data, as a function of defense effectiveness of each prey species. Both basal and middle species exhibit inducible defenses (ID), and costs of ID are low. Upper graphs: both prey species exhibit metabolic costs ($M_1 = M_2 = 1.5$); lower graphs: basal and middle species exhibit metabolic and feeding costs respectively ($M_1 = 1.5$ and $F_2 = 0.6$). The z-axis shows values of the dominant Lyapunov exponent (LE). Superimposed to the plane LE = 0 (grid), continuous lines indicate Hopf bifurcations, and dashed lines indicate extinction threshold for top predators. Darker shading indicates more negative LE. The closed circle on the frontal lower corner shows the parameter coordinates were both ID and costs are absent. For parameter definitions, see legend of Fig. 2.

low costs. Fig. 5A show results when both species exhibit attack rate based ID, with effectiveness B_1 and B_2, and metabolic costs ($M_1 = M_2 = 0.5$). ID are able to stabilize the trophic chain but only after a large increase in defense effectiveness of one or both prey. The role of ID is asymmetric, and the system stabilizes more easily when the ID of the basal prey is increased.

With handling time based ID in both prey species (Fig. 5B), increasing moderately the effectiveness of the basal species (E_1) stabilizes the trophic chain. However, further increases in E_1 leads to extinction of the top predator. Conversely, increasing E_2 has comparatively little effect, and a narrow stable band occurs at high levels of E_2 and low E_1 values. Changing the costs of the second level prey into the attack rate based does not alter qualitatively the prior figure (Fig. 5C and D).

Fig. 6 shows the stability results of the same analyses shown above, but with higher level of ID costs. When ID is attack rate based for both prey and the costs are metabolic (Fig. 6A), the model predicts stable coexistence of the tritrophic chain over the whole parameter space explored. Values of maximal Lyapunov exponents decrease as ID effectiveness increases. If ID is handling time based (Fig. 6B), the model predicts stable coexistence of the three species at low and middle levels of ID effectiveness of the basal prey (E_1) but stable coexistence between basal and intermediate prey only, if E_1 is above ≈ 2.9. Minimal amounts of ID effectiveness in any

prey species stabilize the trophic chain when costs are metabolic and ID is attack rate based. If the cost of ID for the middle level species is attack rate based (Fig. 6C and D) the dynamics is quite similar to the one with low costs (Fig. 5).

4.2.2. Biological data

Here the type of costs exhibited by the upper level prey does not change noticeably the stability domains. Therefore, we only show results for metabolic costs in both prey species.

If the system is parameterized with the biological data at low costs, a small amount of ID effectiveness is enough to stabilize the dynamics (Fig. 7A and B). When ID is handling time based, an extinction threshold of the top predator is found at low levels of E_1 (Fig. 7B). A similar dynamics is found when costs are set to higher values (Fig. 7C and D) where the stable region covers the entire parameter space and extinction of x_3 occurs at low values of E_1. Moreover, an extinction boundary of x_3 is also found when ID are attack rate based (Fig. 7C), at a value of $B_1 \approx 0.4$. In all cases, dominant Lyapunov exponents decreased when ID effectiveness increases in the basal prey.

5. Discussion

Inducible defenses are a form of phenotypic plasticity that potentially modify direct interactions between various mem-
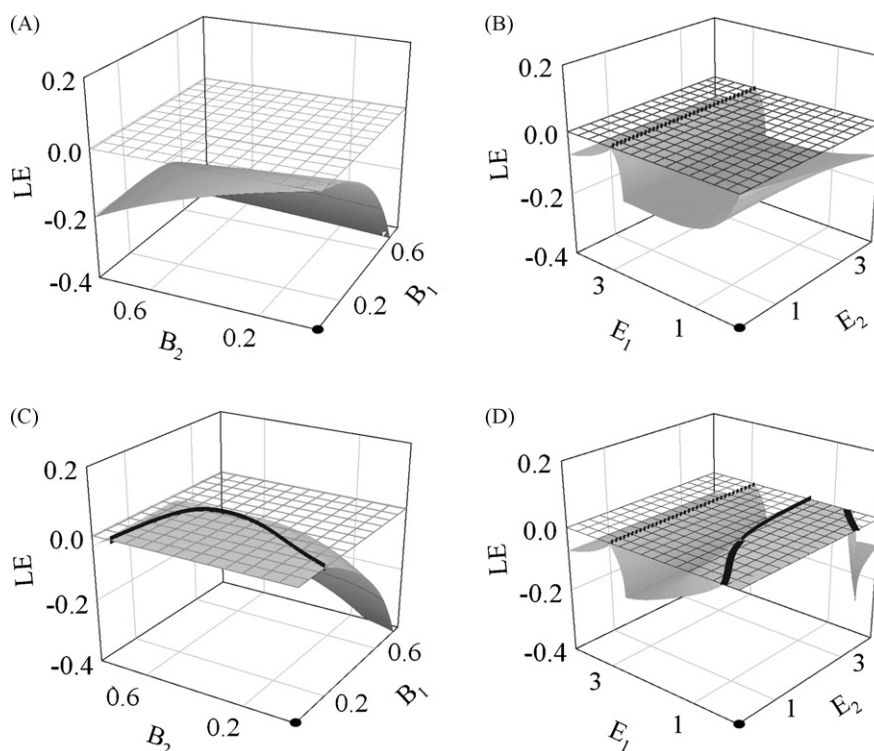
Fig. 6 – Stability of the system parameterized with the mathematical data, as a function of defense effectiveness of each prey species. Both basal and middle species exhibit inducible defenses (ID), and costs of ID are high. Upper graphs: both prey species exhibit metabolic costs ($M_1 = M_2 = 5$); lower graphs: basal and middle species exhibit metabolic and feeding costs respectively ($M_1 = 5$ and $F_2 = 0.3$). The z-axis shows values of the dominant Lyapunov exponent (LE). Superimposed to the plane LE = 0 (grid), continuous lines indicate Hopf bifurcations, and dashed lines indicate extinction threshold for top predators. Darker shading indicates more negative LE. The closed circle on the frontal lower corner shows the parameter coordinates were both ID and costs are absent. For parameter definitions, see legend of Fig. 2.

bers of an ecological community, generating trait-mediated indirect effects (Wootton, 2002; Bolker et al., 2003; Werner and Peacor, 2003). When a prey responds to predator density exhibiting a defensive behavioral, morphological or physiological trait, the direct interaction between prey and predator is suppressed. Furthermore, if the defense has costs, the growth rate of the prey is decreased (when costs are metabolic), or the interaction between the prey and its resource is suppressed (for feeding costs). In this way, ID are able to generate trait-mediated effects from the predator on itself, on its prey, and on the prey's resource, through interaction modifications (Wootton, 1993). Evolutionary ecological theory supports that inducible defenses are favored over constitutive counterparts if the defensive trait imposes costs to the prey (Harvell, 1990; Harvell and Tollrian, 1999). Therefore, the minimal system appropriate for studying the population-level effects of inducible defenses and their fundamental costs is a tritrophic chain.

Prior work on the effects of ID at the population and community levels has been done by analyzing one-prey–one-predator systems (Ives and Dobson, 1987; Abrams and Walters, 1996; Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto et al., 2002; Ramos-Jiliberto, 2003; Kopp and Gabriel, 2006). In these systems, defenses tend to stabilize the equilibria, except for some particular parameter combina-

tions. Tritrophic systems with prey exhibiting inducible defenses have also been analyzed in Vos et al. (2004a,b), where the authors focused on the effect of enrichment on the system stability and equilibrium densities. In the present work, our focus is to understand how different types and levels of defense and their associated costs affect the stability of a tritrophic chain.

Tritrophic systems without including ID have been studied by a number of authors and their dynamic properties are reasonably well understood. Hastings and Powell (1991) presented a tritrophic model with only the basal prey being self-regulated, and showed that for a given set of parameter values the system is chaotic. Subsequently, McCann and Yodzis (1994) showed that the parameter chosen in Hastings and Powell (1991) had rather extreme values from a biological point of view, and that more plausible parameter values makes the tritrophic system less likely to exhibit chaos. Recently, an extended version of the Hastings–Powell model was analyzed that included self-regulation in two and three trophic levels respectively (Xu and Li, 2002; Peet et al., 2005). The authors found that self-regulation is able to stabilize chaotic trajectories.

A strong theoretical school in population ecology has addressed the consequences of adaptive behavior in systems of two or more interacting populations (Abrams, 1984; Ives and
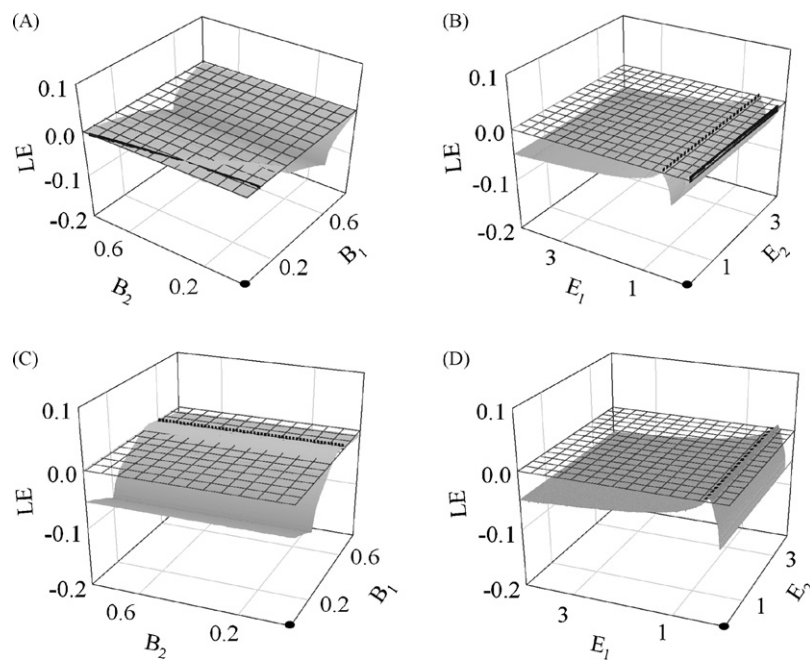
Fig. 7 – Stability of the system parameterized with the mathematical data, as a function of defense effectiveness of each prey species. Both basal and middle species exhibit inducible defenses (ID). Upper graphs: metabolic costs of ID are low ($M_1 = M_2 = 1.5$). Lower graphs: metabolic costs of ID are high ($M_1 = M_2 = 5$). The z-axis shows values of the dominant Lyapunov exponent (LE). Superimposed to the plane LE = 0 (grid), continuous lines indicate Hopf bifurcations, and dashed lines indicate extinction threshold for top predators. Darker shading indicates more negative LE. The closed circle on the frontal lower corner shows the parameter coordinates were both ID and costs are absent. For parameter definitions, see legend of Fig. 2.

Dobson, 1987; Abrams and Walters, 1996; Fryxell and Lundberg, 1998). Broadly speaking, these works have generally demonstrated stabilization. Our work did not incorporate any adaptive assumption but explore the parameter space without explicit constraints other than biological plausibility. In this way we showed that stabilization could result from the ID-generated feedback, independently of adaptive behavior. We consider that the use of adaptively adjusted parameter values is an insightful technique, but rests on strong assumptions that are difficult to meet in many real-world systems. Therefore, we decided to investigate what could be expected under different theoretical types and intensities of defenses, leaving the incorporation of adaptive assumption for further research.

In agreement with earlier works, our results show that a tritrophic system will generally be stabilized by the incorporation of ID and by the associated costs. Nevertheless, our analyses revealed that the trophic position of the defended prey, the type of ID, the type of costs, and the background parameter values define different shapes of the stability domains. On the other hand, the long-term persistence of the species is also affected by the same biological assumptions.

Our novel results can be summarized as follows: (a) when only one species exhibits ID, three-species coexistence is predicted in all analyzed cases (Figs. 2 and 4); (b) when both prey exhibit ID, the changes in the long-term dynamics of the system is dominated by the ID of the basal prey (Figs. 5–7); (c)

handling time based ID exert a stronger stabilizing effect than attack rate based ID; (d) extinction of top predators is more likely at high levels of handling time based ID of the basal prey (Figs. 5–7); (e) low levels of metabolic costs exert similar effects than higher levels of feeding costs, and as costs act mainly to stabilize the system, metabolic costs constitute a stronger stabilizing force than feeding costs (Fig. 2); (f) when only the basal prey exhibits ID, using the biological data (Fig. 4) predicts stable dynamics over a larger fraction of the parameter space, as compared to the mathematical data (Fig. 2), but the opposite is true when only the middle level prey exhibits ID; and (g) with two prey exhibiting ID, both system stability and predator extinction are more likely with the biological data (Fig. 7) than with the mathematical data (Figs. 5 and 6).

The increased effect of ID when they are exhibited at the basal versus upper trophic levels was also noted in previous work (see Van der Stap et al., 2007) and it constitutes an interesting topic for experimental research. Unfortunately we still lack of an intuitive explanation for this prediction. On the other hand, the relatively stronger effect exerted by handling time based ID is expectable, since the type II functional response is more sensitive to changes in handling time than to changes in attack rate. Likewise, metabolic costs exert stronger effects as compared to feeding costs since, for most parameter values, population growth is more sensitive to changes in the consumption rate required for zero growth than to changes in attack rate on the resource.

Oscillatory behavior is considered to be inherent to predator–prey systems lacking other stabilizing forces. Likewise, the seed for chaotic, aperiodic behavior is found in three and higher dimensional systems lacking other stabilizing forces. Therefore, if complex dynamics in natural communities are not so common (Ellner and Turchin, 1995), several stabilizing mechanisms should be operating in nature that prevent the general occurrence of unstable dynamics. The role of ID as a stabilizing mechanism in live communities has been supported for bitrophic (Van der Stap et al., 2006) as well as tritrophic chains (Verschoor et al., 2004). Interestingly, other types of indirect effects driven by interaction modifications also contribute to allow stable population coexistence in a simple community (van Veen et al., 2005). Therefore, ID in particular and trait-mediated indirect effects in general seem to be an important source of stability in natural systems, considering their wide occurrence across taxa and habitats (Tollrian and Harvell, 1999).

Two kinds of mechanisms may be responsible for the stabilizing effect of inducible defenses on the food chain. First, defensive traits decrease the functional response, and therefore weaken the focal predator–prey interaction. Additionally, the costs either reduce the prey growth rate (metabolic costs) or weaken the interaction between the prey and its resource (feeding costs). As shown by McCann et al. (1998), weakening trophic links is one of the stabilizing mechanisms in food webs. On the other hand, the signal for decreasing interaction strength comes from the abundance of predators, generating a negative feedback on itself (Abrams, 1984; Kopp and Gabriel, 2006). This negative feedback is a self-regulation process that is known to be a strong stabilizing force in populations systems (Puccia and Levins, 1985; Berryman, 1999; Dambacher and Ramos-Jiliberto, 2007) and in tritrophic chains in particular (Xu and Li, 2002; Peet et al., 2005). Therefore, ID in particular and trait-mediated indirect effects in general are able to reduce interaction strength, leading to dampening oscillations and promoting community stability.

There is a current interest in considering indirect effects caused by interaction modifications for understanding the behavior of communities (Werner peacor 03), (Dambacher and Ramos-Jiliberto, 2007). However, a great deal of novel knowledge can possibly be gained by studying the role of these complex interactions in the transmission, buffering or amplification of the negative impact of environmental stressors on the fate of populations immersed in real and model communities (Fleeger et al., 2003; Rohr et al., 2006). We are confident that basic and applied science will benefit from theoretical and experimental work addressing the consequences of interaction modifications on the structure and functioning of ecological networks.

Acknowledgements

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