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Induced defenses within food webs: The role of community trade-offs, delayed responses, and defense specificity

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In nature, prey and predator species are embedded in complex networks of ecological interactions. As a consequence, organism level reactions such as predator-induced prey defenses will not only influence the dynamics of both the prey exhibiting the response and its inducer predator, but also that of a wider set of populations that interact directly or indirectly with them.

In this work our aim is to determine the consequences of community-level side effects, defense specificity, and timing of inducible defenses for the stability of model ecological communities. We shall consider small webs of two and three trophic levels, containing one to three species per level. The model food webs include well-known community motifs that will be studied by means of qualitative analyses of the community matrix. Our results show that side effects that suppress non-focal interactions were able to decrease community stability, particularly when defensive responses were delayed. Conversely, side effects that increase the strength of non-focal interactions stabilized communities. This work also shows that as the defensive response became more specific, it is more likely to obtain a stable community. In general terms, our results revealed that delayed responses decrease the likelihood of system stability. Our results highlight the importance of the underlying biology of species interactions for the definition of the proper topology, and consequently dynamics, of complex ecological networks.

1. Introduction

When modeling complex communities, it has been traditionally assumed that the per capita interaction strength between species pairs is constant over time and space. Nevertheless, changes in density and/or functioning of any species within a community can either enhance or suppress the strength of interactions (Peacor and Werner, 2001; Vos et al., 2001, 2004b; Arditi et al., 2005; Dambacher and Ramos-Jiliberto, 2007; Kondoh, 2007; Kratina et al., 2007; van der Stap et al., 2007). Inducible defenses (IDs) exhibited by prey species embedded in food webs are a form of phenotypic plasticity that suppresses the strength of predator–prey interactions. These phenotypic changes are expressed in response to spatial and/or temporal variation in predation risk, and act diminishing the rate of successful attacks by predators (Tollrian and Harvell, 1999).

Empirical evidence shows that ID are ubiquitous in nature. Changes in morphological, behavioral, or life-historical traits (Bernard, 2004), in response to chemical, mechanical or visual signals from predators, can be developed by bacteria (Corno and Jürgens, 2006), protozoa (Kuhlmann and Heckmann, 1985), green algae (Hessen and van Donk, 1993), cladocerans (Krueger and Dodson, 1981; Lampert, 1989; Lass and Spaak, 2003), rotifers (Gilbert, 1966; Lass and Spaak, 2003), fish (Brönmark and Miner, 1992), amphibians (Skelly and Werner, 1990; Smith and Van Buskirk, 1995), mammals (Pusenius and Ostfeld, 2000), and higher plants (Karban and Baldwin, 1997).

Such phenotypic plasticity will influence the dynamics of both the prey exhibiting the defensive response and the inducer predator, but could also affects the entire set of populations that interacts directly or indirectly with them. In other words, the direct consequence of ID on the per capita interaction strength among the focal populations can lead to indirect effects through changes in the per capita interaction strength between these focal species and other non-focal species within the community (Dambacher and Ramos-Jiliberto, 2007; Peacor et al., 2007). We will refer to these non-focal interaction modifications as *community-level side effects of ID*. Non-focal interaction modifications reported in the literature include increases in predation risk by other (non-inducer) predator species, and decreases in feeding rate of the defended prey on its resource (Harvell, 1990; Losey and Denno, 1998; Sih et al., 1998; Agrawal and Karban, 1999; Dicke, 1999; Dicke and Grostal, 2001; Bolker et al., 2003; Werner and Peacor, 2003; Peacor and Werner, 2004). These effects represent costs of ID acting at the community level, and thus they have been named ecological costs by Strauss et al. (2002), community trade-

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offs (Berenbaum and Zangerl, 1999), and environmental costs (Harvell, 1990) of ID. These costs acquire crucial importance when trade-offs at the individual level cannot be detected (Dicke, 1999; Agrawal and Karban, 1999; Berenbaum and Zangerl, 1999; Gilbert, 1999). Furthermore, some systems exhibit changes in non-focal interactions driven by ID which do not represent costs; for example when defended prey increase their feeding rate (Pusenius and Ostfeld, 2000) or decrease their vulnerability to other predators (Sih et al., 1998; Bolker et al., 2003), or when predators decrease their relative preference for the defended prey (Bolker et al., 2003; Jeschke, 2006). The understanding of the population dynamics consequences of ID in real ecosystems requires the consideration of the propagation of effects through the interaction network, as illustrated above. This work is directed towards addressing this issue.

In real communities species are embedded in an intricate informational web (Tollrian and Dodson, 1999; Vos et al., 2006). In real multipredator environments the degree of specificity of the induction of prey defenses determines the complexity of feedback mechanisms leading to indirect effects. Defense specificity can be evaluated at two stages (Ramos-Jiliberto et al., 2008a): (i) prey that develops ID could perceive and react to one or more predator signals (Vos et al., 2006), and (ii) an ID could be effective against one or more predators (Boeing et al., 2006; Laforsch and Tollrian, 2004). On the other hand, different prey species could perceive signals from a common predator (Vos et al., 2006). We address the role of defense specificity in community stability as a second major point of the present work.

Our third goal is to evaluate the effect of delays in the prey's defensive response to predators. The time interval between the increase in predation risk and the development of a defensive trait by prey species is variable. Changes in behavioral traits such as escape reactions can be displayed within seconds after risk perception, so they can be considered to be instantaneous reactions. Other more complex defensive traits such as morphological, chemical, or life-historical ones are exhibited after a considerable time lag from the instant of risk perception (Fryxell and Lundberg, 1998; Tollrian and Harvell, 1999; Luttbeg and Schmitz, 2000).

Consequently, the aim of this work is to determine the role of community-level side effects, specificity, and timing of ID on the stability of model ecological communities. We shall consider small webs of two and three trophic levels, containing one to three species per level. The model food webs include well-known community motifs that will be studied by means of qualitative analyses of the community matrix (Levins, 1974, 1975; Puccia and Levins, 1985; Dambacher et al., 2002; Dambacher and Ramos-Jiliberto, 2007).

2. General models

In order to assess the role of delays in the development of ID on the community stability, we analyzed two versions of each food web motif, *D*-models and *I*-models. Both models have population sizes of the interacting species as state variables. *D*-models include a delay in the expression of ID through incorporating – as a state variable – the bioavailable amount of the cue in the environment, which triggers the development of defensive traits (Ramos-Jiliberto and Garay-Narváez, 2007). Equations for *D*-models are given by:

$$\begin{aligned} \frac{dx_i}{x_i dt} &= r_i + \sum_j \alpha_{ij} f_{ij}(k_j) x_j \\ \frac{dk_j}{k_j dt} &= \frac{u_j x_j}{k_j} - \nu_j \end{aligned} \qquad (1)$$

where r_i is the density-independent growth rate of population i of size x_i. Coefficients α_{ij} are per capita interaction effects of species j on species i, k_j is the bioavailable concentration of cues released by predator j at a rate u_j, with decay rate (e.g. by bacterial decomposition) ν_j. The term f_{ij} is an interaction modification function (Dambacher and Ramos-Jiliberto, 2007), that defines the sign and magnitude of the impact of predator cues on the interaction. On the other hand, equations for *I*-models are:

$$\frac{dx_i}{x_i dt} = r_i + \sum_j \alpha_{ij} f_{ij}(x_j) x_j \qquad (2)$$

where r_i, α_{ij}, and f_{ij} have the same meaning as for *D*-models. The interaction modification function is defined as

$$f_{ij}(\varsigma) = 1 + m\varsigma \qquad (3)$$

where $\varsigma = x_j$ for *I*-models and $\varsigma = k_j$ for *D*-models. Parameter m represents the modification strength, which will be <0 for suppressed interactions and >0 for enhanced interactions.

In both types of models the development of ID results in a modified (suppressed) predator–prey interaction, identified as the focal interaction. This focal interaction modification can lead to secondary modifications of other pairwise interactions within the community. These interaction modifications arisen as side effects of ID will be named non-focal interaction modifications.

The basic structures of the studied model communities are shown in Fig. 1. From them we derived specific models through incorporating ID in prey (i.e. focal interaction modification) and a set of biologically grounded community side effects of ID (i.e. non-focal interaction modifications) that alter the network topology.

In order to control for the effect of the number of state-variables on the system stability, k_j is always included in *D*-models as state variable, although its effect can be switched off by setting $m = 0$. For all models we assume: (a) there exists a positive community equilibrium point, (b) self-effects, α_{ii}, are null except for the basal trophic level. In particular, for *I*-models we assume that the effect of predator abundance on the per capita growth rate of the defended prey is always negative. For *D*-models we assume (a) the effect of predator cues on per capita growth rate of defended (focal) prey is always positive, and (b) the effect of predator cues on per capita growth rate of the inducer (focal) predator is always negative. Finally, we assume for both types of models that if

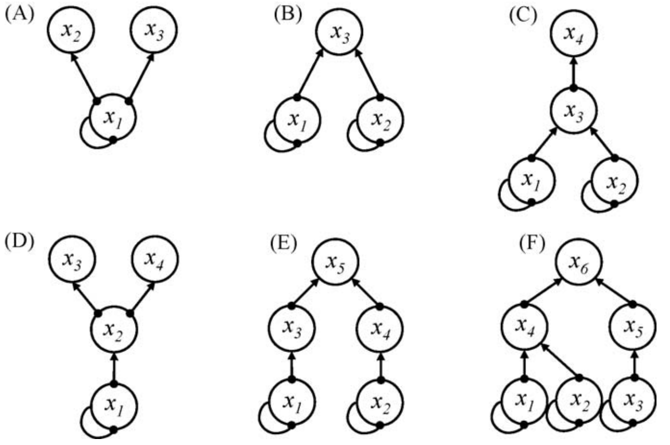

Fig. 1. Digraphs representing community matrices for the six food webs motifs analyzed. Nodes represent populations, and arcs represent predator–prey interactions where arrow and circle ends depict positive and negative effects, respectively. For all systems we assume that self-effects are null except for the basal species.

predation pressure is increased on a non-focal prey as a side effect of ID, only the loss rate of that prey is enhanced and not the numerical response of the predator.

Each of the six resulting food webs motifs (Fig. 1) was studied in the two forms represented by equations (1) and (2) for delayed (*D*-models) and instantaneous (*I*-models) responses, respectively. This brings a total of 94 specific models that were analyzed for the purposes of this work.

3. Methods

Each of the community motifs obtained from general models (1) and (2) under different ecological assumptions was studied through analyzing their community matrix **A**. Elements of **A** are the partials of the per capita growth equations at equilibrium, and for a qualitative analysis we only consider their sign. Therefore, qualitative community matrices and their equivalent digraphs contain the sign structure (1, −1 or 0) of direct interactions in the system (Dambacher et al., 2005).

Two necessary and sufficient conditions for Lyapunov stability are (i) characteristic polynomial coefficients must be of the same sign, and (ii) successive Hurwitz determinants ($\Delta_2 \ldots \Delta_{n-1}$) must be positive (Dambacher et al., 2003). The fulfillment of these two conditions ensures that the real parts of all eigenvalues are negative. In this work we used traditional sign convention (Levins, 1974, 1975; Puccia and Levins, 1985) in which all polynomial coefficients must be negative in stable systems.

Regarding that the strength of direct interactions varies between communities as well as within a community, we use a measure of uncertainty (the relative proportion of feedback cycles that have opposite sign) for the two Hurwitz criteria. Weighted feedback (wF_n) is the ratio of the net to the absolute number of cycles at each level in the system. The absolute number of cycles are the coefficients F_n^* of the polynomial obtained through solving

$$\text{permanent}\,(\mathbf{A}^* + \lambda \mathbf{I}) = 0 \tag{3}$$

where $\mathbf{A}^*$ is a matrix whose elements are the absolute values of the corresponding qualitative community matrix elements. We obtained the values of weighted feedback through

$$wF_n = \frac{F_n}{F_n^*} \tag{4}$$

Values range from −1 for a system with completely unambiguous conditions for stability, to +1 for a system with completely unambiguous conditions for instability. From results on Monte Carlo simulations, values equal or lower than −0.5 are considered to have a high probability of passing the first Hurwitz criterion for system stability (Dambacher et al., 2003).

Weighted determinants, $w\Delta_n$, are the ratio of the net to the absolute number of terms within each of successive Hurwitz determinants, and they are calculated by:

$$w\Delta_n = \frac{\Delta_n}{\Delta_n^*} \tag{5}$$

where Δ_n are the n Hurwitz determinants and Δ_n^* (absolute number of terms) is obtained using the permanent function and polynomial coefficients from equation (1) in:

$$\Delta_n^* = \text{permanent}\begin{bmatrix} -F_1^* & -F_3^* & \ldots & -F_{2n-1}^* \\ -F_0^* & -F_2^* & \ldots & -F_{2n-2}^* \\ 0 & -F_1^* & \ldots & -F_{2n-3}^* \\ 0 & -F_0 & \ddots & \vdots \\ \vdots & \vdots & \ldots & -F_n^* \end{bmatrix} \tag{6}$$

Reference models (linear food chains with the same number of variables than the tested model, and self-regulation in the basal species) whose weighted determinants ($w\Delta_n^r$) are near zero, were used to establish the threshold for the fulfillment of the second Hurwitz criteria. Thus, a model will have a high probability of being stable when its weighted determinants are equal or greater than those of the reference model (Dambacher et al., 2003). A system will be considered qualitatively stable if and only if it passes both criteria.

4. Results

Fig. 2 shows the interaction modifications included in the two predators–one prey motif, with their corresponding versions for

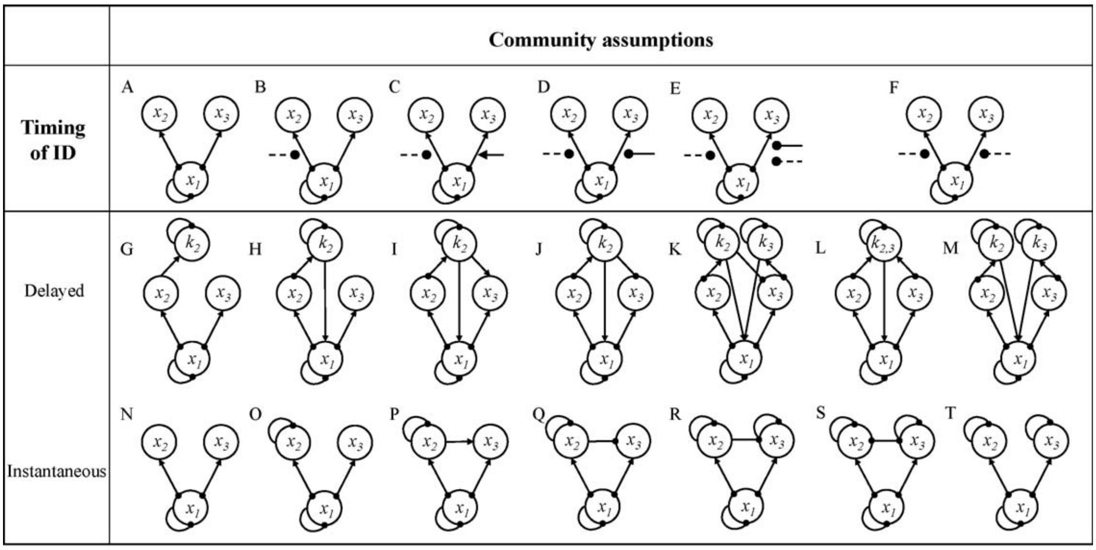

Fig. 2. Digraphs representing webs of two predators and one prey under different ecological assumptions. Basal systems (i.e. with no ID) are shown in A–F, where arcs going towards trophic interactions indicate interaction modifications. Arcs ending in a filled circle denote a suppressed interaction and those ending in an arrow denote an enhanced interaction. Dashed lined arcs indicate the suppressed focal interaction between predator(s) species and the defended prey, and solid lined arcs indicate altered non-focal interactions. Systems of second and third rows result from incorporating the community assumptions depicted in A–F into *D*- and *I*-models, respectively. Note that two versions of the community assumption F were derived. Delayed defense systems (i.e. *D*-models) include predator cues (k) as an additional state variable.

D- and *I*-models. In Fig. 2A, it is shown the "naked" motif, and the ID is incorporated in Fig. 2B without further interaction modifications. In Fig. 2C, the predation rate of the non-focal predator is enhanced. In Fig. 2D–F the interactions between the prey and the two predator species are suppressed by the ID of the prey, but differences are found respect to (a) the specificity of the induction, where either prey perceive differentially or not the cues released by each predator, and (b) the specificity of the response, where either prey develop specific defensive responses that are effective against each of the two predators, or develops a single response that is effective against both predators. From Fig. 2D, the resulting digraphs for *D*- and *I*-models are shown in Fig. 2J and Q, respectively. They represent the community matrix of a system where predator x_2 induces a specific ID in the prey x_1, and the ID is effective also against non-focal predator x_3. In Fig. 2E, it is shown the case where each predator induces a specific ID in the prey, but ID of x_1 against x_2 is also effective against predator x_3. Fig. 2F shows systems in which the prey develops ID against both predators (i.e. focal interaction between predators x_2 and x_3 and the prey x_1 is suppressed), in Fig. 2L and S are shown *D*- and *I*-models wherein the prey do not make distinction between predators, and a single ID is effective against both predator species. In contrast, in Fig. 2M and T each predator provides particular information to the prey, and the prey develops a specific ID against each predator.

In Fig. 3, it is shown the interaction modifications included in the one predator–two prey motif, and their corresponding versions for *D*- and *I*-models. In Fig. 3A, it is shown the naked motif, and the ID is incorporated in Fig. 3B. In Fig. 3C, the predation pressure on the non-focal prey is enhanced. In Fig. 3D, it is shown the case where both prey populations exhibit ID against the shared predator. With this motif we can obtain systems in which either one (i.e. single ID shown in Fig. 3B) or two prey species (i.e. double ID shown in Fig. 3D) perceive the predator cue. This motif is included in the communities represented by Fig. 1B, C, E and F. *I*-models are not shown for systems 3C and 3D because network topology is not modified under these assumptions.

Fig. 4 shows the interaction modifications included in the three species trophic chain motif and their corresponding versions for *D*- and *I*-models. In Fig. 4A, it is shown the naked motif, and the ID is incorporated in Fig. 4B. In Fig. 4C and D, the predation rate on the basal prey is suppressed and enhanced, respectively. This motif is included in the communities represented by Fig. 1C–F.

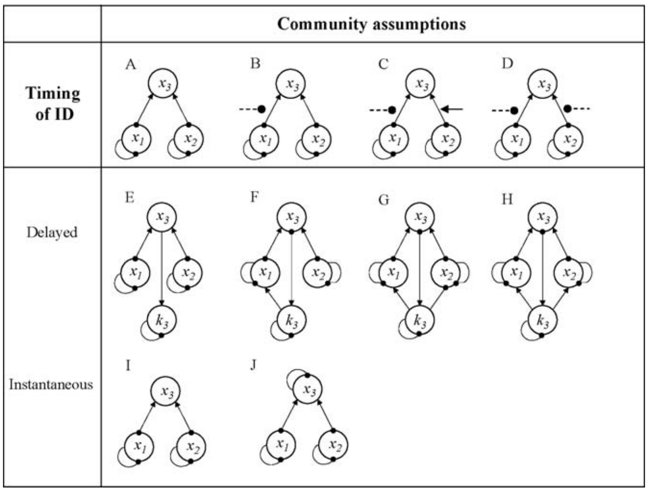

Fig. 3. Digraphs representing webs of one predator and two prey under different ecological assumptions. Basal systems (i.e. with no ID) are shown in A–D. Meaning of symbols and line patterns as in Fig. 2.

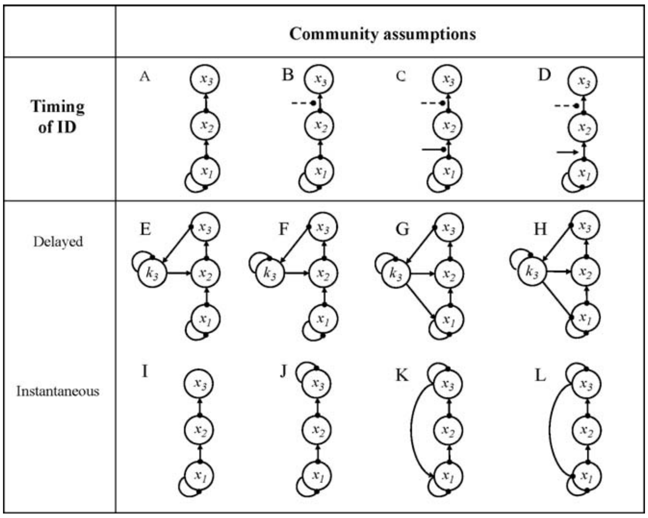

Fig. 4. Digraphs representing webs of three species in a trophic chain under different ecological assumptions. Basal systems (i.e. with no ID) are shown in A–D. Meaning of symbols and line patterns as in Fig. 2.

4.1. Three species systems

Stability results of systems with three interacting species, belonging to two motifs (Fig. 1A and B), are summarized in Table 1 for *D*- and *I*-models.

4.1.1. Two predators and one prey

Community assumptions for *D*- and *I*-models, and associated community matrices are shown in Fig. 2. Stability results are summarized in Table 1I. Basal systems, represented by the naked motif of Fig. 2A and digraphs of Fig. 2G and N, are prone to be unstable by failing Hurwitz criterion (hereafter HC) i and ii.

Systems with ID (Fig. 2B), whose community matrices are represented by digraphs of Fig. 2H and O for *D*- and *I*-models, respectively, have a high probability of being stable, indicating that ID stabilizes initially unstable systems with two predators and one shared prey.

When, in addition to the ID, the non-focal interaction is modified (Fig. 2C–F) *D*- and *I*-models differ in some results. The *I*-model with ID and enhanced non-focal interaction (Fig. 2P) has a high probability of being stable. Likewise, *I*-models represented by Fig. 2R and T have also a high probability of being stable. Under the same community assumptions *D*-models fail HCii (Fig. 2I) or HCi. Both, *D*- and *I*-models are prone to instability by failing HCi when the prey exhibits an ID against one predator that is also effective against the non-focal one (Fig. 2D); and when prey have ID, with unspecific effectiveness and unspecific perception, against both predators (Fig. 2L and S). Even though *D*-models where ID has specific effectiveness and specific perception (Fig. 2K and M) do not pass HCi, the incorporation of specific induction tends to stabilize the system, with values of weighted feedback that are $0 > wF_n > -0.5$, in contrast with systems where induction is non-specific and $wF_n = 0$.

Through performing a symbolic derivation of the stability conditions for these models (through HCi), we noted that the incorporation of ID leads to the formation of cycles that contribute conditionally to the system stability in *D*-models, and unconditionally in *I*-models (Fig. 2H and O, respectively). For *D*-models these cycles can be grouped as:

$$\Omega^D_{ij} = \alpha_{k_jx_j}\alpha_{x_ik_j}\alpha_{x_jx_i} - \alpha_{k_jx_j}\alpha_{x_jk_j}\alpha_{x_ix_i} \qquad (7)$$

Table 1

Stability results for three species systems, showing the list of enhanced (+) or suppressed (−) interaction(s) for delayed (*D*-models) and instantaneous (*I*-models) inducible defenses (ID). Focal predator–prey interaction modifications are indicated in bold. Letter U represents qualitatively unstable systems, with the Hurwitz criteria that the system fails (i, ii or both). Letter S represents qualitatively stable systems. In section I, in parentheses are indicated those cases of exploitative competition in which interaction modifications are driven by two different cues, one from each predator.

Timing of ID	Interaction modification						
	Basal system	$\mathbf{x_1 - x_2}$	$\mathbf{x_1 - x_2}, x_1 + x_3$	$\mathbf{x_1 - x_2}, x_1 - x_3$	$(\mathbf{x_1 - x_2}, x_1 - x_3), (\mathbf{x_1 - x_3})$	$\mathbf{x_1 - x_2, x_1 - x_3}$	$(\mathbf{x_1 - x_2, x_1 - x_3})$
I. Two predators–one prey							
Delayed	$U_{i,ii}$	S	U_{ii}	U_i	U_i	U_i	U_i
Instantaneous	$U_{i,ii}$	S	S	U_i	S	U_i	S

Timing of ID	Basal system	Interaction modification		
		$\mathbf{x_1 - x_3}$	$\mathbf{x_1 - x_3}, x_2 + x_3$	$\mathbf{x_1 - x_3, x_2 - x_3}$
II. One predator–two prey				
Delayed	S	S	S	U_i
Instantaneous	S	S	–	–

In a stable system, it should be satisfied that

$$\Omega_{ij} < 0 \tag{8}$$

This means that the product of the negative cycle $\alpha_{k_j x_j}\alpha_{x_j k_j}$ between the predator and its cue and the self-loop $\alpha_{x_i x_i}$ of a defended prey must be larger than the positive length-3 cycle involved in the release of the cue by species *j*, induction of defenses in species *i*, and food flux from species *i* to species *j* (Ramos-Jiliberto and Garay-Narváez, 2007). In *I*-models, on the other hand, the ID generates a negative self-effect on the focal predator that contributes to system stability.

In *D*- and *I*-models, the community assumption of an increase in predation pressure from the non-focal predator (Fig. 2C), is translated into a positive effect on the per capita growth rate of the non-focal predator that comes from either the cue (*D*-models) or from the focal predator itself (*I*-models). This modification in the graph structure increases stability through the formation of one negative (stabilizing) cycle at the highest feedback level. In *D*-models this cycle corresponds to a length-4 cycle sketched from the cue to the non-focal predator, focal prey, and focal predator (Fig. 2I). In *I*-models, the corresponding length-3 cycle is sketched from the focal predator to the non-focal predator, and the focal prey (Fig. 2P). This cycle has a net stabilizing effect in *I*-models but not in *D*-models (which fails HCii). This occur since in *I*-models the increase in the number of feedback cycles in the highest feedback level is countervailed by the addition of one negative feedback cycle in the lower feedback level (Puccia and Levins, 1985) constituted by the negative self-loop of focal predator, generated by the addition of ID. This cycle prevent failing HCii.

The decrease in predation pressure on the prey by the two predator species can occur because: (i) the prey exhibits ID against one predator, and the non-focal interaction is suppressed (i.e., ID with unspecific effectiveness; Fig. 2J and Q), (ii) both predator species induce ID in the prey which has specific perception, but one of the defensive traits has unspecific effectiveness (Fig. 2K and R), or (iii) both predator species induce ID in prey that has both unspecific perception and unspecific effectiveness (Fig. 2L and S). All these systems presented increased instability, which is explained by the addition of a feedback cycle at the highest feedback level, equivalent to that described for enhanced non-focal interaction but with opposite sign (i.e. a positive, destabilizing cycle).

4.1.2. One predator and two prey

Community assumptions of this section and associated community matrices are shown in Fig. 3. Stability results are summarized in Table 1II.

Basal systems (i.e. with no ID; Fig. 3A) are prone to being locally stable. This high probability of being stable is maintained almost in all cases, irrespective of the timing of ID or community assumptions (Table 1II). Only the *D*-model with defense in both prey species is prone to instability by failing HCi.

Although apparently a single ID has no effect on stability; the symbolic analysis shows that ID has a different effect on community stability than that described for two predators and one prey systems. For *D*-models basal systems present a high probability of being stable, with values of $wF_{1\ldots n} = -1.0$ and $w\Delta_{1\ldots n} > w\Delta^{r}_{1\ldots n}$. When ID is introduced, these values are reduced because the term Ω_{ij} appears within wF_{n-1} and wF_n. On the other hand, within *I*-models ID is always stabilizing.

Enhanced non-focal interactions, tested only in *D*-models, are stabilizing due to the addition of a negative cycle of length four at the highest feedback level. This cycle is generated, as in two predators and one prey systems, by the negative effect of the predator cue on the non-focal species (Fig. 3G). In the same way, when the non-focal interaction is suppressed, i.e. both prey species have perception to the one single predator species, a length-3 cycle is added (Fig. 3H), but with opposite sign (i.e. a positive destabilizing cycle).

4.2. Four species systems

Stability results of systems with four interacting species, belonging to two web motifs (Fig. 1C and D), are summarized in Table 2.

For food web motifs with three trophic levels (with four and more species) we analyzed *D*- and *I*-models with ID exhibited by species belonging to either the intermediate or the basal trophic level.

4.2.1. One predator–one consumer–two prey

In this food web motif we incorporate the modules shown in Figs. 3 and 4. The only systems that are prone to be locally unstable are *D*-models whose community assumptions are illustrated by Fig. 4G and fail HCi and ii; and *D*-models including the community assumptions of Fig. 4G and H. This new community assumption consists of enhancing consumption of the intermediate defended species on one of the basal species and suppressing consumption on the other (Fig. 4C *plus* 4D), and has the effect of adding stabilizing as well as destabilizing feedback cycles to the system (Fig. 4G–H and K–L, for *D*- and *I*-models, respectively). One derived stability condition for *D*-models under this assumption is:

$$\eta^{D}_{ij} = \alpha_{k_l x_l}\alpha_{x_l x_k}(\alpha_{x_j k_l}\alpha_{x_k x_j} - \alpha_{x_i k_l}\alpha_{x_k x_i}) \tag{9}$$

$$\eta^{D}_{ij} < 0 \tag{10}$$

Table 2

Stability results for four species systems, showing the list of enhanced (+) or suppressed (−) interaction(s) for delayed (*D*-models) and instantaneous (*I*-models) inducible defenses (ID). Focal predator–prey interaction modifications are indicated in bold. Letter U represents qualitatively unstable systems, with the Hurwitz criteria that the system fails (i, ii or both). Letter S represents qualitatively stable systems. In section II, in parentheses are indicated those cases of exploitative competition in which interaction modifications are driven by two different cues, one from each predator.

Timing of ID	Interaction modification							
	Basal system	$\mathbf{x_1}-\mathbf{x_3}$	$\mathbf{x_1}-\mathbf{x_3}$, x_2+x_3	$\mathbf{x_1}-\mathbf{x_3}$, $\mathbf{x_2}-\mathbf{x_3}$	$\mathbf{x_3}-\mathbf{x_4}$	$\mathbf{x_3}-\mathbf{x_4}$, x_1-x_3	$\mathbf{x_3}-\mathbf{x_4}$, x_1+x_3	$\mathbf{x_3}-\mathbf{x_4}$, x_2-x_3, x_1+x_3
I. One predator–one consumer–two prey								
Delayed	S	S	S	S	S	$U_{i,ii}$	S	U_i
Instantaneous	S	S	–	–	S	S	S	S

Timing of ID	Interaction modification								
	Basal system	$\mathbf{x_1}-\mathbf{x_2}$	$\mathbf{x_2}-\mathbf{x_3}$	$\mathbf{x_2}-\mathbf{x_3}$, x_2+x_4	$\mathbf{x_2}-\mathbf{x_3}$, x_2-x_4	$(\mathbf{x_2}-\mathbf{x_3}$, $x_2-x_4)$, $(\mathbf{x_2}-\mathbf{x_4})$	$\mathbf{x_2}-\mathbf{x_3}$, $\mathbf{x_2}-\mathbf{x_4}$	$(\mathbf{x_2}-\mathbf{x_3}$, $\mathbf{x_2}-\mathbf{x_4})$	$\mathbf{x_2}-\mathbf{x_3}$, x_2-x_1	$\mathbf{x_2}-\mathbf{x_3}$, x_2+x_1
II. Two predators–one consumer–one prey									
Delayed	$U_{i,ii}$	$U_{i,ii}$	S	S	U_i	U_i	U_i	U_i	U_i	S
Instantaneous	$U_{i,ii}$	$U_{i,ii}$	S	S	$U_{i,}$	S	U_i	S	S	S

Table 3

Stability results for five (I) and six (II) species systems, showing the list of enhanced (+) or suppressed (−) interaction(s) for delayed (*D*-models) and instantaneous (*I*-models) inducible defenses (ID). Focal predator–prey interaction modifications are indicated in bold. Letter U represents qualitatively unstable systems, with the Hurwitz criteria that the system fails (i, ii or both). Letter S represents qualitatively stable systems.

Timing of ID	Interaction modification					
	Basal system	$\mathbf{x_1}-\mathbf{x_3}$	$\mathbf{x_3}-\mathbf{x_5}$	$\mathbf{x_3}-\mathbf{x_5}$, x_4+x_5	$\mathbf{x_3}-\mathbf{x_5}$, $\mathbf{x_4}-\mathbf{x_5}$	$\mathbf{x_3}-\mathbf{x_5}$, x_1-x_3	$\mathbf{x_3}-\mathbf{x_5}$, x_1+x_3
I. One predator–two consumers–two prey species							
Delayed	S	S	S	S	U_i	U_i	S
Instantaneous	S	S	S	–	–	S	S

Timing of ID	Interaction modification				
	Basal system	$\mathbf{x_3}-\mathbf{x_5}$	$\mathbf{x_1}-\mathbf{x_4}$	$\mathbf{x_1}-\mathbf{x_4}$, x_2+x_4	$\mathbf{x_1}-\mathbf{x_4}$, $\mathbf{x_2}-\mathbf{x_4}$
II. One predator–one specialist consumer–one generalist consumer–three prey					
a. ID in the prey species					
Delayed	S	S	S	S	U_i
Instantaneous	S	S	S	–	–

Timing of ID	Interaction modification											
	Basal system	$\mathbf{x_5}-\mathbf{x_6}$	$\mathbf{x_5}-\mathbf{x_6}$, x_4+x_6	$\mathbf{x_5}-\mathbf{x_6}$, $\mathbf{x_4}-\mathbf{x_6}$	$\mathbf{x_5}-\mathbf{x_6}$, x_5-x_3	$\mathbf{x_5}-\mathbf{x_6}$, x_5+x_3	$\mathbf{x_4}-\mathbf{x_6}$	$\mathbf{x_4}-\mathbf{x_6}$, x_5+x_6	$\mathbf{x_4}-\mathbf{x_6}$, $\mathbf{x_5}-\mathbf{x_6}$	$\mathbf{x_4}-\mathbf{x_6}$, x_4-x_1	$\mathbf{x_4}-\mathbf{x_6}$, x_4+x_1	$\mathbf{x_4}-\mathbf{x_6}$, x_4-x_1, x_4+x_2
b. ID in the consumer species												
Delayed	S	U_i	S	U_i	U_i	S	S	S	U_i	U_i	S	S
Instantaneous	S	S	–	–	U_i	S	S	–	–	S	S	S

This means that in a stable system the negative path between the kairomone (released by top predators) and the defended species illustrated in Fig. 4H must be larger than the positive path between the kairomone and the species that develops the ID, which is illustrated in Fig. 4G.

It can be noted that this motif is almost equivalent to the one shown in Fig. 1B and explained in Section 4.1.2 but with one additional trophic level. The only stability output in which they differ is that obtained from the *D*-model where both prey species perceive a single predator cue (Fig. 3D).

4.2.2. Two predators–one consumer–one prey

In this food web motif we incorporate either the module of Fig. 2 or the one shown in Fig. 4. Additionally, we introduce ID in the basal species.

Basal systems (i.e. with no ID) tend to instability by failing HCi and HCii (Table 2II). *D*- and *I*-models tend to stability only if ID is displayed by the intermediate species. The same result is obtained whenever, in addition to the ID in the intermediate species, any non-focal interaction is enhanced (Figs. 2C and 4D).

On the other hand, *D*- and *I*-models are prone to instability by failing HCi when the prey exhibits an ID against one predator being also effective against the non-focal one (Fig. 2D); and when prey has ID, with unspecific effectiveness and unspecific perception, against both predators (Fig. 2L and S). Both *D*- and *I*-models differ in stability results when the intermediate species has specific perception against predators, and also when the non-focal interaction between the intermediate species and the non-focal prey is suppressed. Under these community assumptions, *I*-models (Figs. 2R, 2T, and 4K) are prone to stability and *D*-models (Figs. 2K, 2M, and 4G) are prone to instability by failing HCi.

It is important to point out that this motif is equivalent to the one shown in Fig. 1A for three species systems. The results show a general agreement, particularly on the effect that specificity in the induction exerts on the local stability.

4.3. Five species system

For the system of five interacting species shown in Fig. 1E, the stability results are summarized in Table 3I. Community assumptions for *D*- and *I*-models with ID in the intermediate species are those described by modules shown in Figs. 3 and 4. When ID is incorporated in the basal trophic level no further interaction modifications were considered.

We found that almost all *D*- and *I*-models have a high probability of being locally stable. Only *D*-models that include community assumptions illustrated either in Fig. 3D or Fig. 4C fail HCi.

4.4. Six species systems

Stability results for the system shown in Fig. 1F are summarized in Table 3II. The section IIa of Table 3 shows the stability results for *D*- and *I*-models with ID in the prey of either the specialist or the generalist predator. The module of Fig. 3 describes community assumptions of *D*- and *I*-models with ID in the prey of the generalist predator. Section IIb of Table 3 shows the stability results for *D*- and *I*-models with ID in the generalist and in the specialist consumer species. Fig. 3 describes community assumptions of *D*- and *I*-models with ID in the generalist consumer. In Fig. 4, there are shown the community assumptions for *D*- and *I*-models with ID in the specialist consumer.

Basal systems represented in Fig. 1F are prone to be locally stable. This high probability of being stable is maintained in systems with ID in the prey of either the generalist or the specialist species, irrespective of the timing of ID or community assumptions (Table 3IIa). Only the *D*-model with defense in both preys of the generalist species is prone to instability by failing HCi.

Some results differ between *D*- and *I*-models when ID is exhibited by the consumer species. *D*-models fail HCi either when the specialist consumer exhibits ID, or when the generalist consumer exhibits ID and one of its non-focal interactions with prey is suppressed (Fig. 4C). This feeding cost also impedes to pass HCi in *D*- and *I*-models with ID in the specialist consumer.

4.5. Effect of intraguild predation in four species motifs

In every four species system studied here we also evaluated the changes in stability due to the incorporation of intraguild predation (IGP). IGP was included among preys as well as among predators. We found that IGP has a destabilizing effect (almost all systems fail HCi and ii). Stability is maintained after the introduction of IGP only in the food web motif conformed by one predator–one consumer–two prey, under the following community assumptions (i) no interaction modification, (ii) ID in one of the prey species, (iii) ID in one of the prey and enhanced predation on the non-focal shared prey, (iv) ID in consumer species, only in *I*-models, and (v) ID in the consumer and enhanced predation on the shared non-focal prey, only for *I*-models.

5. Discussion

An increasing number of theoretical and empirical studies have analyzed the effects of ID in bitrophic and tritrophic systems. Most studies reveal that the incorporation of ID stabilizes the dynamics, dampening population oscillations and enhancing species persistence (Vos et al., 2004a; Miner et al., 2005; Ramos-Jiliberto et al., 2008b). Nevertheless, the effect of ID on the system stability has proven to be strongly dependent of model assumptions, such as the amount of delay taking place between the increase in predation risk and the antipredator response (Fryxell and Lundberg, 1998), the self-dampening structure of populations (Ramos-Jiliberto, 2003; Ramos-Jiliberto and Garay-Narváez, 2007), the incorporation of indirect effects (Bolker et al., 2003) and nutrient enrichment (Rinaldi et al., 2004; Vos et al., 2004a). The specificity of ID in a multipredator environment also exerts a considerable effect on the dynamic outcome. Particularly, when ID is predator-specific the systems have shown to increase their likelihood of stability and persistence (Kondoh, 2007; Ramos-Jiliberto et al., 2008a).

In the present work, we advance our understanding about the role of phenotypic plasticity in ecological communities and show that the effects of ID on the network stability are dependent on the three factors analyzed here: *side effects of ID at the community-level*, *defense specificity* and *response delay*.

We evaluated the stability consequences of assuming various plausible side effects of ID at the community level. For example, prey that exhibit defenses against a predator species *A* could suffers from increased predation by a second species *B* (Gilbert, 1999; Matsuda et al., 1996; Sih et al., 1998; Amo et al., 2004), increase predation rate of predator *A* on an alternative prey *C* (Abrams and Matsuda, 1993), decrease the consumption rate on its resources (Grabowski and Kimbro, 2005; Mortensen and Richardson, 2008), or indeed increase consumption of resources (Pusenius and Ostfeld, 2000; Beckerman et al., 1997). In more general terms, community-level side effects of ID can be split into two broad classes: those that suppress the strength of non-focal interactions, and those that increase them. Our results showed that side effects that suppress non-focal interactions are able to decrease community stability, particularly when defensive responses are delayed. Conversely, side effects that increase the strength of non-focal interactions stabilized communities. On the other hand, in models where we incorporated both classes of side effects simultaneously, stability was not altered (except for one case) relative to the one exhibited by basal systems without side effects.

Previous works dealing with stability changes driven by these kinds of side effects of ID are scarce. A kind of side effect that suppresses interaction strength is feeding cost. Earlier studies revealed that the effect of feeding costs do not present a clear pattern of effects on community stability (Ramos-Jiliberto, 2003; Ramos-Jiliberto and Garay-Narváez, 2007). On the other hand, predator switching could result from antipredator behavior when prey exhibit ID (Abrams and Matsuda, 1993; Yamauchi and Yamamura, 2005). This response falls within the side effects of ID that enhance strength of non-focal interactions, which we found to be stabilizing, in agreement with the general results of Kondoh (2003).

In nature, prey species can recognize and respond specifically to various simultaneous predator signals (Taraborelli et al., 2008; Epp and Gabor, 2008). The specificity of responses in some species can be influenced by characteristics and identity of both predator and prey (Smith et al., 2008). Our results show that as the defensive response became more specific, it is more likely to obtain a stable community. This result agrees with earlier works on food webs (Matsuda et al., 1996; Ramos-Jiliberto et al., 2008a) as well as in host–parasite interactions (Freeland and Boulton, 1992).

Although the delay between the increase in predation risk and the exhibition of ID by the prey could be considered negligible in some biological systems, it is also true that the effects of ID on system dynamics could depend strongly on the timing of that response (DeWitt et al., 1998; Underwood, 1998, 1999; Verschoor et al., 2004; Miner et al., 2005). In this regard, we considered here two confronting scenarios: an instantaneous response to the increase in predation risk where defenses are induced directly by predators, and a delayed defense where ID is developed in response to a predator-released cue that is treated as a dynamic variable. Thus, a time delay in the prey response is included into the path connecting the predator, the cue, and the prey.

In general terms, our results revealed that delayed responses decrease the likelihood of system stability. In systems with single ID and without exhibiting side effects, the timing of ID could appear to exert little or none effect on net stability outcomes. Nevertheless, a closer look at the measures of stability uncertainties reveals a net stabilizing effect of incorporating ID when defense is instantaneous, but a conditional stabilizing effect in systems with delayed defense. On the other hand, in systems with more complex topology – as those in which community side effects or multiple defenses occur – *D*-models present a higher propensity to fail stability criteria by the incorporation of destabilizing factors such as decrease in defense specificity or feeding costs.

As shown through this article, the effect of ID on qualitative stability of model food web showed to be largely sensitive to the ecological context, particularly the architecture of the food web matrix, the occurrence of indirect trait-mediated effects, the specificity of the prey defense, and time delays of the prey response to predators. Our results highlight the importance of the underlying biology of species interactions for the definition of the proper topology, and consequently dynamics, of complex ecological networks.

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