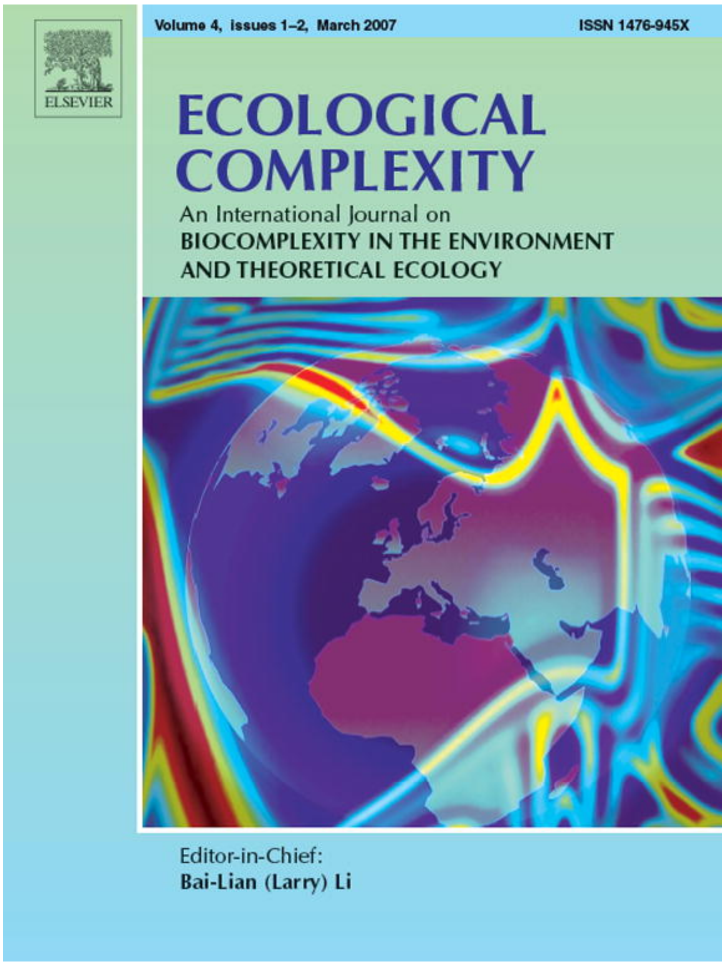
Volume 4, Issues 1–2, March 2007
ISSN 1476-945X
ECOLOGICAL COMPLEXITY
An International Journal on
BIOCOMPLEXITY IN THE ENVIRONMENT AND THEORETICAL ECOLOGY
Editor-in-Chief:
Bai-Lian (Larry) Li

ECOLOGICAL COMPLEXITY 4 (2007) 58–70

available at www.sciencedirect.com

journal homepage: http://www.elsevier.com/locate/ecocom

Qualitative effects of inducible defenses in trophic chains

Rodrigo Ramos-Jiliberto*, Leslie Garay-Narváez

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

ARTICLE INFO

Article history:
Received 21 November 2006
Received in revised form
2 March 2007
Accepted 2 March 2007
Published on line 6 April 2007

Keywords:
Trait-mediated indirect effects
Loop analysis
Community matrix
Stability
Press perturbation
Predator–prey
Tritrophic model
Antipredator behavior

ABSTRACT

By means of qualitative techniques we analyze the consequences of inducible defenses of species embedded in trophic chains on the community stability and responses of population equilibrium densities to press perturbations. Our results show that the inclusion of inducible defenses in trophic chains leads to profound changes in system dynamics. Inducible defenses increase the likelihood of instability, especially when exhibited by species of lower trophic levels. We obtained biologically reasonable feedback conditions that must be satisfied to ensure stability. Species responses to press perturbation are modified by inducible defenses and their associated costs in multiple ways. Many of the direct effects in the community are reinforced, while indirect effects are either weakened, if they propagate in a top–down direction, or are unaffected if they propagate from basal species. The dominant view of inducible defenses as a stabilizing force seems to be valid only within a biologically constrained parameter space.

1. Introduction

Since it is unfeasible for a species' phenotype to perform equally well on different sets of resources and habitat conditions, a convenient and widespread evolutionary strategy in variable environments is the ability of species to change the expression of phenotypic traits in response to perceived natural cues. Phenotypic plasticity of morphological, physiological, behavioral and life-historical traits induced by cues released by other member of the community has been extensively recognized in all major taxa (see Agrawal, 2001), but our understanding of how these individual-level responses propagate to higher ecological hierarchies, namely populations and communities, is still poor.

One of the best-known examples of phenotypically plastic responses to biotic cues are inducible defenses (ID) to predators (Tollrian and Harvell, 1999; Lass and Spaak, 2003; Bernard, 2004). For instance, protozoans change their cell shape in response to protozoan predators (Kuhlmann and Heckmann, 1985), green algae respond to herbivores by forming colonies (Hessen and Van Donk, 1993), rotifers (Gilbert, 1966) as well as cladocerans (Krueger and Dodson, 1981) develop body spines and other structures in the presence of carnivores, tadpoles (Smith and Van Buskirk, 1995) and fish (Brönmark and Miner, 1992) change their body shape, and behavioral responses are observed in zooplankton (Lampert, 1989) and anuran larvae (Skelly and Werner, 1990) when exposed to cues released from natural enemies.

Following Harvell (1990) and later work (e.g. Harvell and Tollrian, 1999), there is agreement in that ID should be evolutionary favored if three conditions are met: (1) predation risk is variable or unpredictable through time or space, (2) there exists reliable cues that are informative about predation risk, and (3) the defense is costly. An implicit assumption is, of

---

* *Corresponding author*. Tel.: +56 2 9787399; fax: +56 2 2727363.
E-mail address: roramos@uchile.cl (R. Ramos-Jiliberto).

1476-945X/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecocom.2007.03.001

course, that ID offers a survival benefit that overcomes any concurrent cost.

Much of the complexity observed or expected in ecological communities is rooted in the existence of multiple ways through which species affect others. Besides the simple direct effects that a population exerts on the growth rate of its resources and consumers, numerous indirect effects can be found in communities of only a few interacting species. Indirect effects are those exerted by one population on another not directly connected with the first, and they can be driven by changes in density and/or functioning of one or more intermediate species (Miller and Kerfoot, 1987; Wootton, 1993; Werner and Peacor, 2003; Arditi et al., 2005; Dambacher and Ramos-Jiliberto, 2007). Phenotypic plasticity, and ID in particular, is thought to be responsible for trait-mediated indirect effects in communities (Agrawal, 2001), and there is evidence that the magnitude of these effects can be as large as, or larger than, the magnitude of their density-mediated counterparts (Werner and Peacor, 2003). Considering both the ubiquity of ID in nature and their potential for triggering trait-mediated indirect effects in population systems, it becomes clear that analyzing the role of ID on system dynamics is highly relevant for a comprehensive understanding of the structure and functioning of ecological networks.

Earlier works on predator-induced defenses at the population level show in general that the defensive response tends to increase the equilibrium density of prey as well as system stability (Ives and Dobson, 1987; Sih, 1987; Ruxton, 1995; Abrams and Walters, 1996), but the effect attributed to the associated cost is less clear. More recent studies show that ID are able to generate intricate domains of attraction on the parameter space, and the effects of ID and their costs on the stability of the systems are functions of other parameters, e.g. density-dependence (Ramos-Jiliberto, 2003) and enrichment (Rinaldi et al., 2004; Vos et al., 2004a). Since models with a moderate degree of biological realism often includes too many parameters to drawn general conclusions, and the scarcity of experimental work dealing with ID at a population level prevents the accurate measurement of the parameter values needed, quantitative models usually present results with an unknown degree of generality.

Our aim in this work is to make use of qualitative modeling techniques to assess the effects of ID on the stability of trophic chains, and to understand how ID modify the interactions between the component populations via evaluating the qualitative responses of the species' equilibrium density to press perturbations (*sensu* Bender et al., 1984). By using qualitative analyses we gain in generality at a price of sacrificing precision (Levins, 1966).

2. Methods

Through taking the partial derivatives of the growth equations evaluated at equilibrium we obtained a qualitative Jacobian matrix (**A**) for each of the studied systems. Qualitative Jacobian matrices and their equivalent digraphs contain the sign structure (1, −1 or 0) of direct interactions in the system (Dambacher et al., 2003b).

Two necessary and sufficient conditions for Lyapunov stability are (i) characteristic polynomial coefficients must be of the same sign, and (ii) successive Hurwitz determinants, from level 2 to $n-1$, must be all positive (Dambacher et al., 2003b). The fulfillment of these two conditions ensures, respectively, that the real parts of all eigenvalues are negative (Dambacher et al., 2003b). 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, so that system dynamics that are self-damping can be understood in terms of negative feedback.

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 terms that are of 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 at each feedback level n is shown by the coefficients F_n^* of the polynomial obtained through solving

$$\mathrm{permanent}(\mathbf{A}^* + \lambda\mathbf{I}) = 0 \tag{1}$$

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

$$\mathrm{wF}_n = \frac{F_n}{F_n^*} \tag{2}$$

Values range from −1 for a system with completely unambiguous conditions for stability, to +1 for a system with completely unambiguous conditions for instability computation. 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., 2003b).

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

$$\mathrm{w}\Delta_n = \frac{\Delta_n}{\Delta_n^*} \tag{3}$$

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 Eq. (1) in:

$$\Delta_n^* = \mathrm{permanent}\begin{bmatrix} -F_1^* & -F_2^* & \cdots & -F_{2n-1}^* \\ -F_0^* & -F_1^* & \cdots & -F_{2n-2}^* \\ 0 & -F_0^* & \cdots & -F_{2n-3}^* \\ 0 & 0 & \ddots & \vdots \\ \vdots & \vdots & \cdots & -F_n^* \end{bmatrix} \tag{4}$$

Reference models (linear food chain with the same number of variables as tested model and self regulation in the basal species) whose weighted determinants 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 that of the reference model (Dambacher et al., 2003b). The system will be qualitatively stable if and only if satisfies both criteria.

The inverse of the negative Jacobian matrix predicts the equilibrium response of community members following a sustained (press) perturbation (Bender et al., 1984). For stable systems, the adjoint (adj) of the negative Jacobian matrix preserves the signs of the inverse, and can be used instead. Therefore, according to Dambacher et al. (2003a), we obtain net response matrices (usually called prediction matrices) $\mathbf{P}^m$ for each model m as

$$\mathbf{P}^m = \mathrm{adj}(-\mathbf{A}^m) \tag{5}$$

To obtain the net effects of induced defenses and/or associated costs in the species' responses to press perturbation, we calculated

$$\Delta\mathbf{P}^{m-r} = \mathbf{P}^m - \mathbf{P}^r \tag{6}$$

hereafter response modification matrix, which show the difference between the corresponding net response matrix $\mathbf{P}^m$ which includes the trait of interest, and a basal matrix $\mathbf{P}^r$ lacking that trait. This procedure accounts for feedback cycles that arise from the added trait.

Theoretical background and graphical algorithms for symbolic analyses were developed in Levins (1974, 1975) and Puccia and Levins (1985). Qualitative analyses and computing algorithms for stability conditions and qualitative predictions were developed in Dambacher et al. (2003a,b). For calculations, we wrote computer routines in Mupad-Pro Version 3.0 (SciFace Software GmbH and Co. KG, Germany).

3. The models

We defined three types of state variables for our food chain models. The first is population size of the interacting species; the second one is the bioavailable amount of the cue in the environment, which triggers the development of defensive traits. We account here for cues that act as dynamical variables, such as infochemicals released by organisms (in this case predators) as a function of the biological activity and temperature, and decaying through enzymatic decomposition (Dicke and Grostal, 2001; Burks and Lodge, 2002; Hay and Kubanek, 2002; Lass and Spaak, 2003). The third type of state variable considered here is energy (or food) storage, in order to allow for incorporating feeding costs of defenses in a more explicit way.

Two types of models were developed. B-models include population size and infochemical concentration as state variables. S-models include energy storage as an additional state variable. Equations for B-models are given by

$$\begin{aligned}\frac{dx_i}{dt} &= x_i(a_{i-1}x_{i-1} - b_ik_i - c_{i+1}k_{i+1} - \lambda_ix_i) - x_{i+1}(d_ix_i \\ &\quad - e_{i+1}k_{i+1} - f_{i+2}k_{i+2}),\\ \frac{dk_i}{dt} &= u_ix_i - v_ik_i\end{aligned} \tag{7}$$

where x_i ($i = 1, \ldots, 4$) is population size of a species belonging to trophic level i. Variable k_i represents the concentration of infochemical released by predators of trophic level i. This infochemical is perceived by a prey of trophic level $i-1$, inducing a defensive trait in direct proportion to k_i. In S-models, variable s_i denotes energy (or food) storage of species i. Equations of S-models are given by

$$\begin{aligned}\frac{dx_i}{dt} &= x_i(g_is_i - \lambda_ix_i) - x_{i+1}(d_ix_i - e_{i+1}k_{i+1} - f_{i+2}k_{i+2}),\\ \frac{ds_i}{dt} &= x_i(a_{i-1}x_{i-1} - b_ik_i - c_{i+1}k_{i+1} - j_is_i),\\ \frac{dk_i}{dt} &= u_ix_i - v_ik_i\end{aligned} \tag{8}$$

The ecological meaning of parameters is shown in Table 1. The sign structure of model (7) is reached from (8) through replacing s_i by its equilibrium value within the equation for x_i.

In order to control for the effect of the number of state-variables on the system stability, k_i is always included as state variable although its effect can be switched off by setting $b = c = e = f = 0$. For all models we assume: (a) there exists a positive community equilibrium point, (b) all parameters are non-negative, (c) the fitness gain due to the ID is larger than the cost, which translates to $e_{i+1}x_{i+1} > c_{i+1}x_i$ for B-models, and (d) predation rate can never be reduced to negative values, which translates to $d_ix_i > e_{i+1}k_{i+1} + f_{i+2}k_{i+2}$.

We analyzed a number of specific models derived from (7) and (8) following different ecological assumptions. In order to assess the role of ID and their costs in the stability of food chains, we analyzed all the combinations resulting from adding these traits to the different component species (see Table 2) in communities of 2–4 trophic levels. Since the lower-order negative feedback enhances the stability of model communities, we tested the combinations listed in Table 2 in communities where either none or all species exhibit direct density-dependence (i.e. with $\lambda_i = 0$ and $\lambda_i > 0$, respectively) with trophic length of 2–4. All models were constructed and analyzed in the two forms already presented: B (Eq. (7)) and S (Eq. (8)). This gives a total of 130 models for stability analyses.

For press-perturbation responses, we analyzed the subset of 47 models where all species showed direct density-dependence, and ID is displayed by either one species or two species of adjacent trophic levels.

Table 1 – Definition of parameters (all assumed to be non-negative) used in the models

Parameter	Short definition
a_i	Food conversion efficiency of species i
b_i	Decreasing of consumption rate caused by ID of prey $i-1$
c_i	Feeding cost of ID of species i
d_i	Predation rate on species i
e_i	Decreasing of consumption rate of predators $i+1$ caused by ID of species i
f_i	Decreasing of predation losses caused by feeding cost of predators' ID
λ_i	Direct density-dependence coefficient
g_i	Conversion efficiency from storage to growth
j_i	Mobilization of storage to growth
u_i	Release rate of infochemical by species i
v_i	Decay rate of infochemical released by species i

Table 2 – Combinations of species exhibiting inducible defenses and cost in the models analyzed for stability and press-perturbation responses (those indicated by * where not analyzed for press-perturbation responses)

Species exhibiting inducible defenses	Species exhibiting costs	
	B-models	S-models
Two-species chain		
None	nc	nc
x_1	nc	nc, x_1
Three-species chain		
None	nc	nc
x_1	nc	nc, x_1
x_2	nc, x_2	nc, x_2
$x_1 - x_2$	nc, x_2	nc, x_1, x_2, $x_1 - x_2$
Four-species chain		
None	nc	nc
x_1	nc	nc, x_1
x_2	nc, x_2	nc, x_2
x_3	nc, x_3	nc, x_3
$x_1 - x_2$	nc, x_2	nc, x_1, x_2, $x_1 - x_2$
$x_1 - x_3{}^*$	nc, x_3	nc, x_1, x_3, $x_1 - x_3$
$x_2 - x_3$	nc, x_2, x_3, $x_2 - x_3$	nc, x_2, x_3, $x_2 - x_3$
$x_1 - x_2 - x_3{}^*$	nc, x_2, x_3, $x_2 - x_3$	nc, x_1, x_2, x_3, $x_1 - x_2$, $x_2 - x_3$, $x_1 - x_3$, $x_1 - x_2 - x_3$

All models have a version without direct density-dependence ($\lambda_i = 0$), and a version with direct density-dependence ($\lambda_i > 0$). nc = without costs.

4. Results

4.1. *Two-species models*

Details of model building are provided in Appendix 1.

Stability results for two-species models are shown in Fig. 1A–D. The explanation of stability graphs is provided in Fig. 2. In the absence of direct density-dependence (Fig. 1A and B) basal systems (i.e. with no ID) fail Hurwitz criterion (hereafter HC) ii. On the other hand, basal systems present wF = −1.0 indicating that they pass HCi. In B-models weighted Hurwitz determinant wΔ_{n-1} is zero (indicating a tendency for neutral stability) and in S-models wΔ_{n-3}, …, wΔ_{n-1} are negative (indicating a tendency for instability). Systems with ID in the basal species fail HCi (in B and S-models). If the defended species displays costs (satellite in Fig. 1B), the system is prone to fail HCii (S-model). Therefore, our results indicate that two-species systems without direct density-dependence in which the prey exhibits ID will be locally unstable under most combinations of parameter values. Nevertheless, the system lacking ID tends towards instability due to the non-positive wΔ values, and we found that adding ID in bitrophic systems increases the values of wΔ and decreases wF resulting in a marginally increase in the conditions favoring stability. This means that ID increases the probability of stability, although that probability is still relatively low (Eqs. (2) and (3)).

When direct density-dependence exists for both species (Fig. 1C and D) the system gains a high probability of being stable regardless of the occurrence of ID and associated costs.

Through performing a symbolic analysis of the conditions for stability of these models (through HCi), we noted that the incorporation of ID leads to the formation of cycles that contribute to the stability of the system. Such cycles can be conveniently grouped as

$$\Omega_{ij}^{\mathrm{B}} = \alpha_{k_j x_j}\alpha_{x_i k_j}\alpha_{x_j x_i} - \alpha_{k_j x_j}\alpha_{x_j k_j}\alpha_{x_i x_i} \tag{9a}$$

$$\Omega_{ij}^{\mathrm{S}} = \alpha_{k_j x_j}\alpha_{x_i k_j}\alpha_{s_j x_i}\alpha_{x_j s_j} - \alpha_{k_j x_j}\alpha_{s_j k_j}\alpha_{x_j s_j}\alpha_{x_i x_i} \tag{9b}$$

for B and S-models, respectively (Fig. 3A and B), and in a stable system, it should be satisfied that

$$\Omega_{ij} < 0 \tag{10}$$

This means that the product of the negative cycle $a_{k_j x_j} a_{x_j k_j}$ between the predator and its infochemical 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 infochemical by species *j*, induction of defenses in species *i*, and food flux from species *i* to species *j* (Fig. 3A and B).

A related stability condition from HCi is

$$\phi_{ij} = \alpha_{x_i k_j}\alpha_{k_j x_j} - \alpha_{x_i x_j}\alpha_{k_j k_j} < 0 \tag{11}$$

for both B- and S-models (Fig. 3E).

The addition of direct density-dependence in both species is enough to stabilize the system, in spite of the occurrence of the counteracting cycles contained in (9a) and (9b).

4.2. *Three-species models*

Details of model building are provided in Appendix 1.

Our results for stability of tri-trophic chains are summarized in Fig. 1E–H. In the absence of direct density-dependence, basal systems (both B and S-models) show a high probability of being unstable by failing both HC. When ID is incorporated in the basal species, the systems either pass both HC (B-model) or fail HCii (S-model). Adding costs to the basal species (S-model) does not change the qualitative stability. When the second-level species presents ID, the systems have a high probability of being stable, but

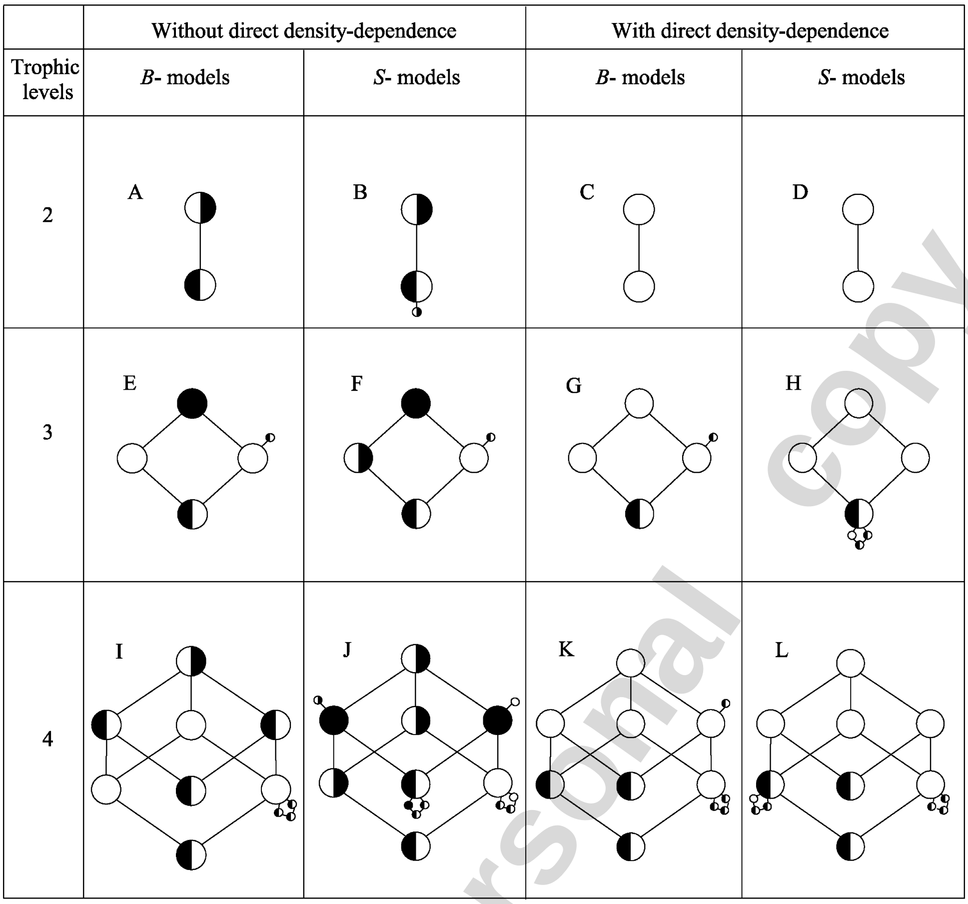

Fig. 1 – Stability results for food chains models, indicating number of trophic levels, inclusion of direct density-dependence, and type of model (B or S, see text or Figs. A1 and A2 for explanation). Both systems include population size and infochemical concentration as state variables, while S-models have energy storage as an additional state variable. When addition of costs results in changes of stability, these are shown as satellites. See Fig. 2 for explanation. The color of the left hemispheres indicates if the system pass (white) or not pass (black) Hurwitz criterion i. Right hemisphere corresponds to Hurwitz criterion ii.

the addition of costs increases the propensity to instability through failing HCi. The systems in which the two lower trophic levels display ID all fail HCi.

If all species have direct density-dependence (Fig. 1G and H) the system is prone to be locally stable when ID is either absent or it is exhibited by one of the species. If both prey species display ID, the system is prone to be unstable by failing HCi. The effect of costs is model-dependent, since costs act destabilizing the B-model when the middle species show ID, and stabilizing the S-model when both prey display ID but only the basal one exhibits a cost. In the remaining places, costs have no effect on the qualitative stability properties of tri-trophic systems.

Similar to the bitrophic cases, a term Ω_{ij} arises by the addition of a one-species ID, without exerting a qualitative change in the system stability. Nevertheless, if two species exhibit ID simultaneously, two terms Ω_{ij} appear, increasing considerably the total number of cycles within a given feedback level, which compose the denominator of the wF equation (Eq. (2)). This imposes a higher probability for instability by failing HCi.

Symbolic analyses reveal that, when one species other than the basal one exhibits ID and costs, a new combination of cycles appear that can be grouped as

$$\Psi^{S}_{ijh} = \alpha_{s_j x_i}\alpha_{x_i k_h} - \alpha_{x_i x_i}\alpha_{s_j k_h} \tag{12a}$$

$$\Psi^{B}_{ijh} = \alpha_{x_j x_i}\alpha_{x_h x_j}\alpha_{k_h x_k}\alpha_{x_i k_h} \tag{12b}$$

for S-models and B-models, respectively. Model stability requires

$$\Psi^{S}_{ijh} < 0 \tag{13}$$

implying that the cost of ID for food storage weighted by the resource self-effect must be greater than the indirect benefit obtained through the increase in resource growth associated with the reduction of the food consumption by the defended species (Eq. (12a)). In B-models the storage is implicit in the state variables, and the stability condition for (12b) is met if the positive link from k to the resource is enough small (Fig. 3C and D).

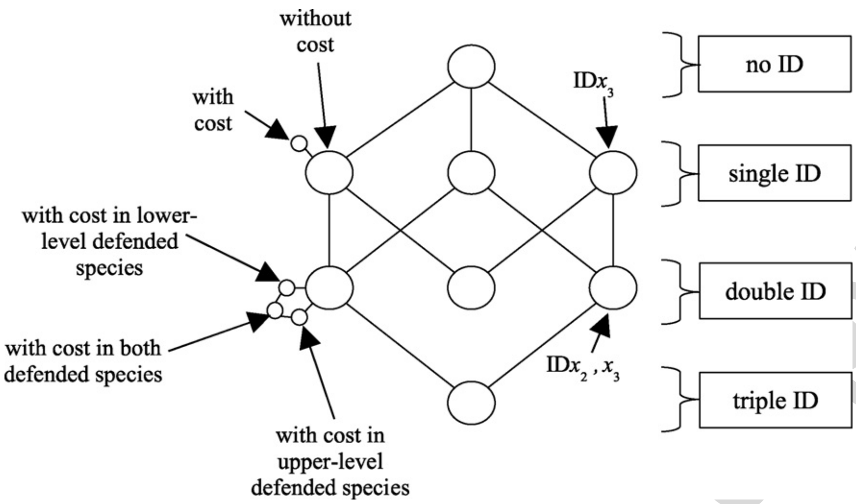

Fig. 2 – Meaning of stability graphs used in this work for a four-level trophic chain. Large circles represent stability results for models without inducible defenses (ID) (upper circle), and with ID in one, two or three trophic levels (lower circles). When costs of defense are included, stability results are shown into small circles (satellites). In single ID models, stability results for ID in x_1, x_2 and x_3 are represented by left, middle and right nodes, respectively. In this example costs are present in single ID models only for defense in x_1 (satellite). When more than one species exhibits ID and costs, multiple satellites are displayed. Lines born from single ID models indicate the resulting double ID models. Thus, left, middle and right nodes represent stability results for defense in x_1 and x_2, x_1 and x_3, and x_2 and x_3, respectively. The lowest node shows stability results for all three prey exhibiting ID.

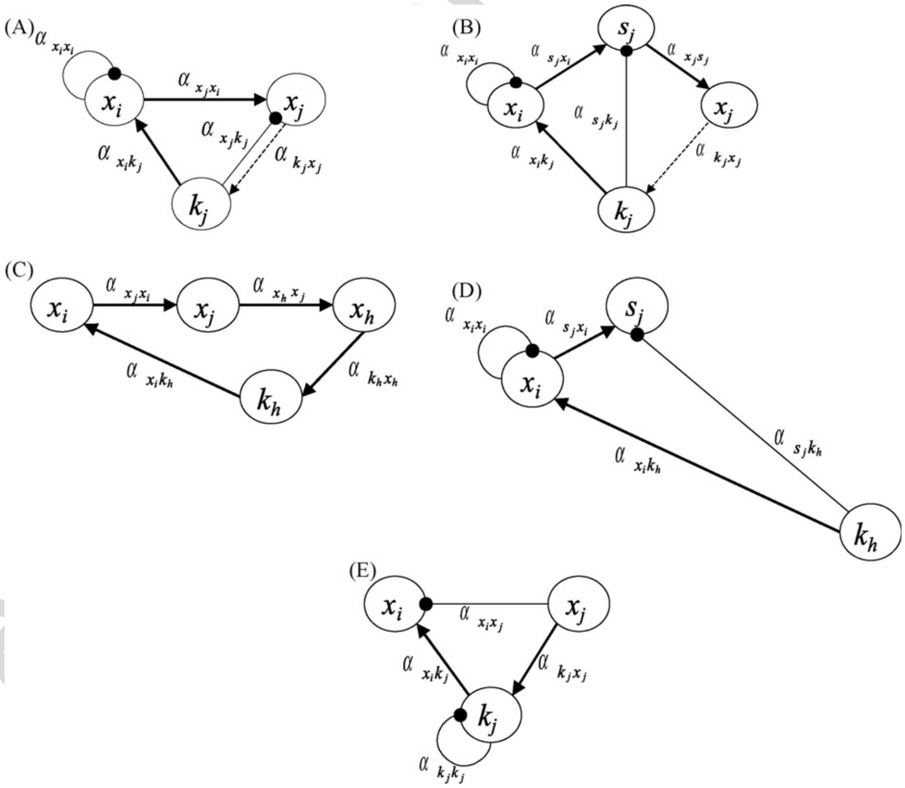

Fig. 3 – Cycles responsible for instability. A–E represents the terms Ω_{ij} (Eqs. (9)), Ψ_{ijk} (Eqs. (12)), and Φ_{ij} (Eq. (11)), for B- and S-models, respectively (see text or Figs. A1 and A2 for explanation). Bolded arrows form part of positive cycles, thin arrows form part of negative cycles, and discontinuous arrows form part of both positive and negative cycles, which have no effects on stability.

For S-models, when both species present costly defenses both terms Ω_{ij} and ψ_{ijh} are added together, that results in failing HCi. On the other hand, if all species exhibit direct density-dependence and only the basal species presents costs, the system gains stability since a negative cycle is incorporated by the feeding cost of the basal species, but not the full term ψ_{ijh}.

4.3. *Four-species models*

B and S-models with no direct density-dependence differ in some stability results (see Fig. 1I and J). Basal systems are prone to be locally unstable, and this trend hold when any one of the prey species exhibit ID, except for two cases where the system has a high probability of being stable: (a) for B-models when the ID is displayed by the second-level species; and (b) for S-models when the third-level species exhibits ID and costs. If the two lower-level species exhibit ID simultaneously, stability is predicted for B-models and instability for S-models, regardless of the presence of costs. If ID is displayed by the first and third-level species, the system is prone to instability by failing HCi. If the two upper-level prey species exhibit ID and no costs, the system is likely to be locally stable. Here, costs act destabilizing the equilibria except in S-models with only the upper prey exhibiting costs (Fig. 1J). When all prey species display ID the systems fail HCi.

In systems having direct density-dependence in all trophic levels, the results are generally consistent between B and S-models (Fig. 1K and L). Systems are stable if no ID is displayed, or if ID is displayed by any single species. The only exception (in B-models) is the case where the third-level species display costs. If the two lower-level species exhibit ID, instability is expected except for the case when costs are displayed by the first-level species in the S-model. If the first and third-level species exhibit ID, the systems are prone to instability through failing HCi. If the upper-level prey species possess ID the system is predicted to be locally stable, but here a cost in any species acts as a destabilizing force. Again, when the three prey species display ID, the systems are predicted to be unstable regardless of the existence of associated costs.

Symbolic analyses of four-species systems with single and double ID reveal that instability is due to the same cycles Ω_{ij} and ψ_{ijk} which confer sign ambiguity and whose effects on stability are additive. In loop-analysis terms, the incorporation of ID in the upper two trophic levels confers stability because the negative cycle between the basal prey and its predator is disjunct respect to the negative cycles between predators and infochemicals, and therefore there is an important contribution of negative (i.e. stabilizing) cycles.

4.4. *Net response matrices*

The response of the equilibrium state of one species to a sustained variation (i.e. a press perturbation, Bender et al., 1984) in the state of another species within a community is dependent on the sign and magnitude of the different paths stretched from the initiator to the receiver. Under a qualitative approach, these net responses are obtained through the adjoint of the negative Jacobian matrix (see methods section) and the resulting array is a net response (prediction) matrix **P**. We calculated matrices **ΔP** (see Eq. (6)) for finding how a net response is modified as a result of changing the model assumptions (i.e., by adding ID or costs in different species). Our results indicate that the net responses modifications are robust to variation in the number of trophic levels. On the other hand, press perturbation results are consistent for B and S-models, except for a few cases that will be noted. Since this approach considers local perturbations in the neighborhood of community equilibrium, the conditions for stability found previously are here used as conditions for symbolic evaluation of the elements of **ΔP**. For verbal simplicity, we define the length of an indirect effect from variable *j* to variable *i* as the length of the associated path of direct effects from *j* to *i*, which is equivalent to the number of intermediate variables along the path (those which connect *j* to *i*) plus 1.

Species' responses to press perturbation in basal (i.e. without ID) four-species trophic chains are shown in Fig. 4. As usual, direct top–down and bottom–up effects are negatives and positives, respectively. Indirect effects are all positive excepting the top–down effect of length-3 from x_4 to x_1.

4.5. *Effects of single-species ID on net responses*

The effects on prediction matrices of adding IDs (in anyone species) to basal (with no ID) trophic chains are summarized in Fig. 5. Arcs with sign equal to that of their corresponding one in the basal model (Fig. 4) represent a reinforcement of the basal effect, whereas opposite signs represent weakening. When the reference (basal) effect remains unchanged no arc is displayed, denoting zero effect.

Among the non-zero interaction modifications (see Fig. 5), single ID acts reinforcing all the direct effects (DE) exhibited by the basal system, with the exception of the negative DE exerted by a predator on its defended prey which is weakened. The ID acts reinforcing the length-2 top–down indirect effect (IE) from the induced prey, but weakening all other lengths-2 and -3 top–down IE. Only one bottom–up IE is affected (reinforced) by single ID.

The specific effects of adding cost to a trophic chain with a single ID are shown in Fig. 6. Most of IEs affected by the ID are

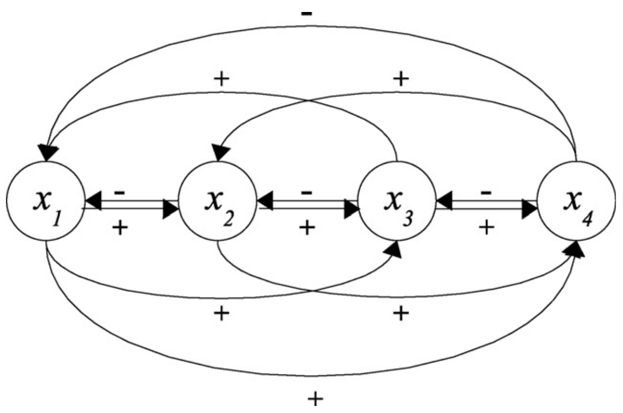

Fig. 4 – Graphic representation of four-species net response matrices. This graph summarizes responses of all nested trophic chains. Signs on each arc indicate the sign of the change in equilibrium density of a species after a sustained increase in the growth rate of another.

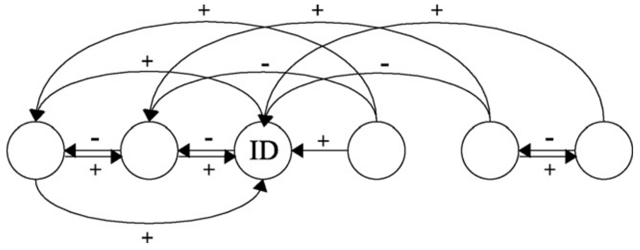

Fig. 5 – Graphic representation of response modification matrices for B- and S-models (see text or Figs. A1 and A2 for explanation) with inducible defenses (ID) exhibited by a single species. This graph summarizes response modification matrices for all nested trophic chains. Modification matrices are $\Delta P^{m-r} = P^m - P^r$, where P^m is a net response matrix for models with single ID and P^r is a basal net response matrix (for models with no ID). Positive and negative sign in each arc indicates that positive or negative cycles are added to the basal net response matrix with the inclusion of single ID under stability assumptions. Only non-diagonal (i.e. only interspecific responses) and non-zero effects are shown. Note that the set of possible effects is constrained by the models' architecture.

weakened by the addition of costs. That means that the costs of ID let the net effect structure of the system closer to its basal state. Regarding the DE resulting from adding costs, it is noticeable the reinforcement of the ID-driven effects at trophic levels which are distant from the focal species, and has a weakening or null effect on the DE directly related to the defended species. Note also the sign of three links is dependent on the model type in use.

4.6. *Incorporating a second defended species*

If ID is incorporated to a species in a trophic chain which already had one defended species, the modification effects are completely consistent respect to incorporating ID on the basal system (see Figs. 5 and 7). Therefore, the modification of net effects after incorporating a second ID are the same as previously described for a single ID. For further details see Appendix 2.

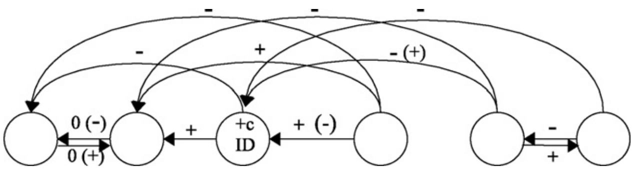

Fig. 6 – Graphic representation of response modification matrices for B- and S-models (see text or Figs. A1 and A2 for explanation) with inducible defenses (ID) and costs exhibited by a single species. This graph summarizes response modification matrices for all nested trophic chains. Modification matrices are $\Delta P^{m-r} = P^m - P^r$, where P^m is a net response matrix for models with single ID and costs, and P^r is a net response matrix for the corresponding model with single ID (with no costs). Symbols and assumptions are the same as in the previous figure. Differences in the response modification matrix for S-models are indicated in parenthesis.

5. Discussion

Most of previous theoretical work on ID at a population level assumes that the response of prey to cues released by natural enemies is instantaneous (Frank, 1993; Abrams and Walters, 1996; Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto et al., 2002; Ramos-Jiliberto, 2003). Although the delay between the increase of predation risk and the exhibition of the defense by the prey could be considered negligible in some cases, it is also true that the effects of the ID on the system dynamics could depend strongly on the timing of that response (DeWitt et al., 1998; Underwood, 1998, 1999;

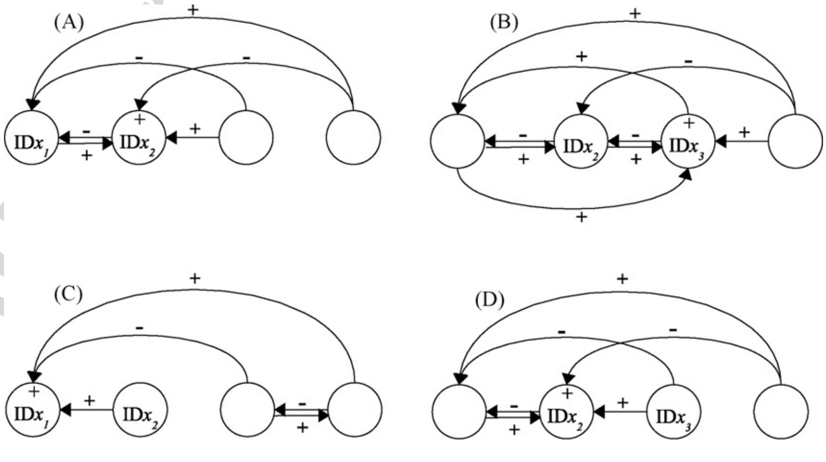

Fig. 7 – Graphic representation of response modification matrices for B- and S-models (see text or Figs. A1 and A2 for explanation) resulting after adding a second defended species. Here $\Delta P^{m-r} = P^m - P^r$, where P^m is a net response matrix for models with inducible defenses (ID) in two trophic levels, P^r is a net response matrix for models with single ID. In (A) are shown the response modifications after incorporating ID in the second-level species on a trophic chain that previously had ID in the basal species. Other graphs follow the same logic.

Verschoor et al., 2004; Miner et al., 2005). Here we include the concentration of the cue in the environment as a state variable, and thus we incorporate time delays in the prey response through the path connecting predator, cue, and prey.

Current theory about population/community effects of ID states that ID promote stability over a fraction of the parameter space, as verified by modeling (Ives and Dobson, 1987; Sih, 1987; Ruxton, 1995; Krivan, 1998; Ramos-Jiliberto, 2003; Rinaldi et al., 2004; Vos et al., 2004b; Kopp and Gabriel, 2006) and experiments (Verschoor et al., 2004; Van der Stap et al., 2006). On the other hand, ID can destabilize the system under a number of specific assumptions embodied in the parameter values (McNair, 1986; Ramos-Jiliberto et al., 2002; Ramos-Jiliberto, 2003; Kopp and Gabriel, 2006). Therefore, the current evidence support that the effects of ID and associated costs on the community stability are rather complex when viewed on a broad parameter space. Since numerical analyses of quantitative (i.e. completely specified) models as well as experimental results are both dependent on the specific assumptions or conditions, testing the robustness of results requires more evidence to be developed in the field of dynamic consequences of ID. Here we use a qualitative approach in order to assess the most likely effects of ID on trophic chains, regardless of parameter values. This helps for knowing the expected properties of a system lacking specific assumptions about both functional relationships and parameter values, and serves as a source of null hypotheses to be tested by experiments or other modeling techniques.

In line with previous studies, our results show that the inclusion of ID in trophic chains drives changes in the qualitative stability of the system. Broadly speaking, adding ID in multiple species makes an initially stable trophic chain more susceptible to unstable dynamics, and this is more noticeable when ID is exhibited at lower trophic levels. Conversely, the studied systems are always stable whenever all but the basal prey species exhibit ID. On the other hand, an addition of costs exerts influences on the system stability mostly when two species exhibit ID simultaneously.

The derived feedback conditions for stability (see Eqs. (9)–(13) and Fig. 3) appears to be reasonable for real ecological systems, and they show that trophic chains are likely to be stable if (a) the positive indirect self-effect of the predator driven by an increase of prey growth as a consequence of reduced predation, should be weaker than the negative predator self-effect driven by reduced prey consumption, weighted by the prey self-effect. Another condition is (b) the positive non-lethal indirect effect of the predator on the defended prey should be weaker than the negative lethal direct effect, weighted by the kairomone self-effect. Regarding the effects of costs in the more realistic S-models, the corresponding stability condition is that the positive indirect effect of the infochemical on the prey storage should be weaker than the accompanying negative direct effect weighted by the prey's resource self-effect. Overall, inclusion of ID generates multiple positive and negative paths among the variables connected to the defended prey, and stability is more likely whenever the negative paths dominate over the positive ones. Note that the reported changes in the stability of trophic chains are drawn over all possible parameter values, but biological constraints are expected to increase the likelihood of stability.

How the net responses of the species change after including ID? Adding ID to a given prey species modifies all net effects exerted on itself by the other community members. Conversely, an ID does not modify any of the effects entering the predator species. Regarding the entire trophic chain, ID reinforces most of the DEs, whereas most of the top–down IEs are weakened and most of the bottom–up IEs are not modified. Some specific results of including ID are worthy for noting: (a) the DE of the predator on the defended prey is weakened due to decreased predation, (b) the DE of the defended prey on its resource is reinforced, but costs suppress this effect, (c) the lenght-2 top–down IE (trophic cascade) from the defended prey is also reinforced, but cost suppress this effects, (d) the DE of the defended prey on its predator remains unchanged, (e) the DE of the resource on its defended consumer is reinforced, and (f) the lenght-2 bottom–up IE on the defended prey is reinforced. It is important also to note that ID reinforces direct interactions between trophic levels that are most distant from the focal species, and this tends to be more pronouncing when costs exist. On the other hand, the inclusion of costs tends to counterbalance the effects exerted by ID on the DE around the focal species, and the top–down IE. The effects resulting from adding a second species exhibiting ID and/or costs does not alter substantially the effects of single-species ID.

Our results suggests that the dominant view of ID and other forms of antipredator behavior as a stabilizing force is valid only for a biologically constrained set of parameter values, and that the net responses among community members can be strongly affected by this kind of trait-mediated effects.

Acknowledgements

We thank Jaime Mena-Lorca for his help on various math topics, and Jeff Dambacher for numerous helpful comments to a first version of this work. This work was supported by grants FONDECYT 1040821/2004 and DI ENL 06/1 to RRJ.

Appendix A

A.1. *Two-species models*

When the infochemical does not induce antipredator responses two Jacobian matrices are obtained for each model type, represented by the digraphs in Fig. A1A and C for B-models and in Fig. A2A and D for S-models.

Direct density-dependence was either excluded (i.e. $\lambda_i = 0$, Fig. A1A and B for B-models; and Fig. A2A–C for S-models) or included in all trophic levels (i.e. $\lambda_i > 0$, Fig. A1C and D for B-models; and Fig. A2D–F for S-models). As it is shown in Figs. A1B and A2B and C, a self-regulation link is generated in the basal trophic level as a consequence of the inclusion of ID. In S-models costs are explicitly represented as a negative effect on the storage of the defended basal trophic level (Fig. A2C and F).

A.2. *Three-species models*

In tri-trophic chains, there are two prey species and therefore ID can be exhibited by any one or by both of them.

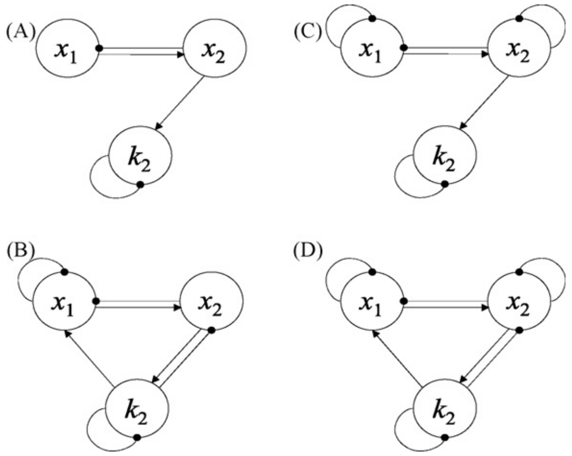

Fig. A1 – Digraphs representing Jacobian matrices of two-species B-models (for this and following figures, models that include population size and infochemical concentration as state variables). A and B for models with no direct density-dependence ($\lambda_i = 0$). C and D for models with direct density-dependence ($\lambda_i > 0$) in all trophic levels. Models with the prey exhibiting inducible defenses (ID) are B and D. As shown in B, a self-regulation link arises in the defended species as an effect of the ID.

Jacobian matrices for models with ID in the basal trophic level are equivalent to the Jacobian matrices in Figs. A1B for B-models and A2B and C for S-models, plus the addition of a top undefended predator.

In systems with ID in the second trophic level, Jacobian matrices are equivalent to the matrices shown in Fig. A3, after deleting the top predator. As it is shown in Fig. A3C and D, a self-regulation link in the basal trophic level arises by the inclusion of costs. Therefore, self-regulation arises in both the defended prey (when ID is included) and its resource (when a cost is included).

For any trophic level exhibiting ID except the basal one, the costs are explicitly represented in S-models by two links outgoing from the predator's infochemical: a negative effect on the storage of the induced prey and a positive effect on the resource of the induced prey. In B-models costs are represented by a positive effect on the resource of the induced prey. These links account for the self-regulation of basal species in system with ID in the second trophic level.

A.3. Four-species models

The existence of a fourth trophic level (see Fig. A3) allows for new combinations of species displaying ID and costs. As in the previous cases, the inclusion of ID and costs form self-regulation terms as well as other negative and positive

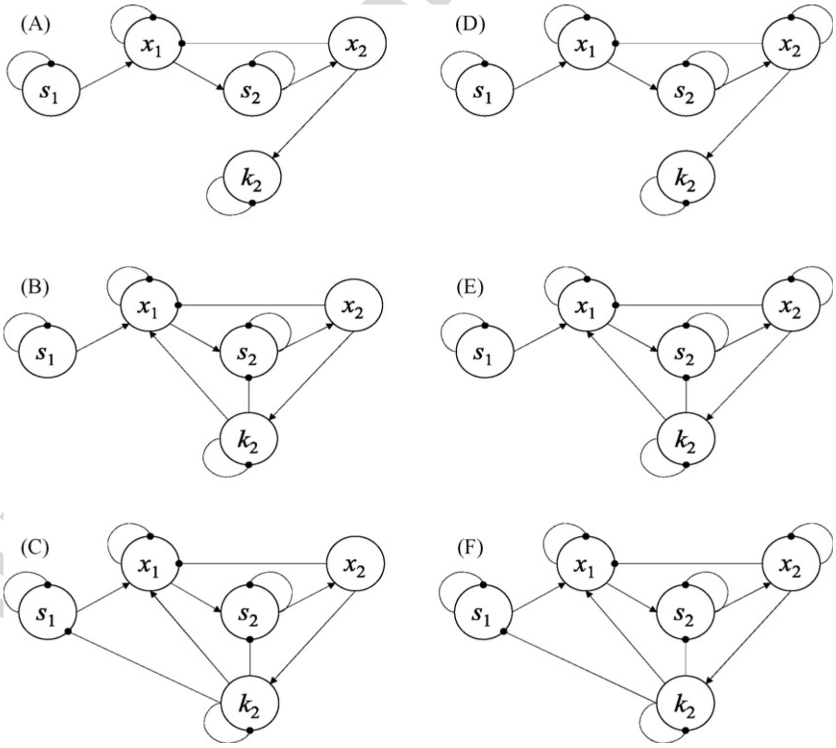

Fig. A2 – Digraphs representing Jacobian matrices of two-species S-models (for this and following figures, models that include population size, infochemical concentration, and energy storage as state variables). A–C for models with no direct density-dependence ($\lambda_i = 0$). D–F for models with direct density-dependence in all trophic levels. Models with the prey exhibiting inducible defenses (ID) are B and C and E and F. Models C and F include costs of ID. As it is shown in B and C, a self-regulation link arises in the defended species as an effect of the ID.

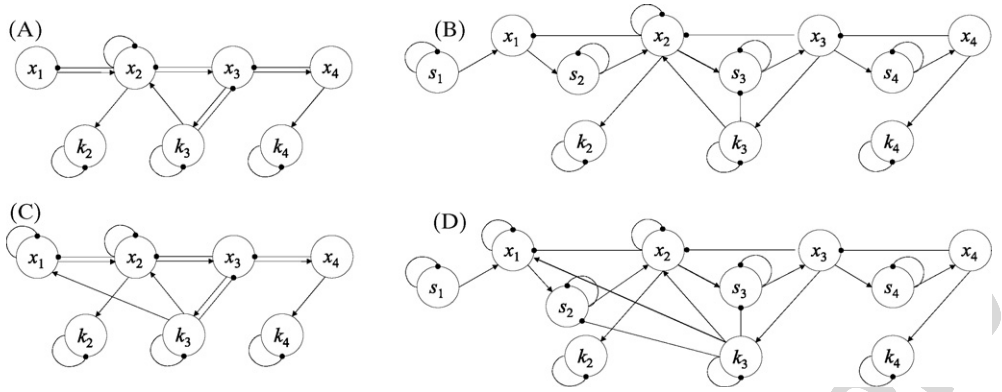

Fig. A3 – Digraphs representing Jacobian matrices of systems of four species with single inducible defenses (ID) in the second trophic level, for B- and S-models (see text or Figs. A1 and A2 for explanation) with no direct density-dependence ($\lambda_i = 0$). C and A represent Jacobian matrices for B-models with and with no associated costs, respectively, and D and B represent Jacobian matrices for S-models with and with no associated costs, respectively. The cost for the B-model (C) is represented by the link from k_3 to x_1. Two links, the one from k_3 to x_1, and the other from k_3 to s_2 represent the cost for the S-model (D). As it is shown in C and D, two self-regulation links arise as an effect of ID and associated costs, one in the defended prey and the other in its resource.

feedback cycles. This feedback structure will determine whether the systems are stable or not.

Appendix B

B.1. *Effect of incorporating a second defended species on net responses*

Finally, we examine the effect of including costs in systems with two species exhibiting ID simultaneously. In Fig. A4 it is shown the effect of adding a single cost on a community structure lacking any previous cost, and Fig. A5 shows that effect of adding a cost on a trophic chain where one species already had a cost. Twelve out of 60 possible interspecific effects (i.e. 23%) found in models that are represented by the two forms (S and B, Figs. A4A, B and D and A5B and D) are model-dependent. Nevertheless we assume that S-models better capture the nature of costs, at a price of larger dimension.

Overall, the effects of adding costs in S-models are similar to adding costs in single ID systems. That is to say, adding costs to double ID systems weakened the effects of adding ID, except for (a) the effects exerted on the species with added cost by its resource remains unaltered, (b) the cost reinforces the basal trophic links of model of Figs. A4B and A5B; (c) the cost reinforces the top trophic link of Figs. A4C and A5C.

By comparing Figs. A4A and A5C it becomes clear that the addition of a cost in x_1 on a system where x_2 had a preexisting cost, exert a change in three of the DE and two IE. The effect $\Delta P_{1,2}$ (i.e. the elements 1, 2 of the matrix ΔP) weaken the

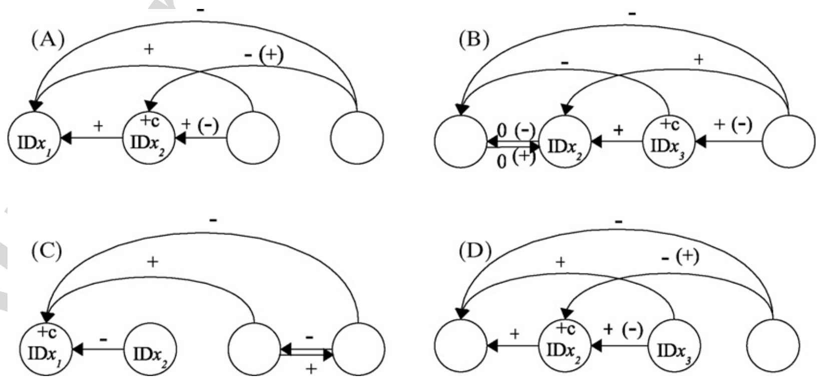

Fig. A4 – Graphic representation of response modification matrices for B- and S-models (see text or Figs. A1 and A2 for explanation) with inducible defenses (ID) exhibited by two species, resulting after adding costs to one of the defended species. Here $\Delta P^{m-r} = P^m - p^r$, where P^m is a net response matrix for models with ID in two trophic levels and costs in one of them, and P^r is a net response matrix for models with ID in two trophic levels and no costs. In (A) are shown the response modifications after incorporating costs in the second-level species on a trophic chain that previously had ID in the two lower levels. Other graphs follow the same logic. In parenthesis are shown results of S-models that are different from that of the B-models. In C, the results belong only to S-models since its structure in not allowed by B-models.

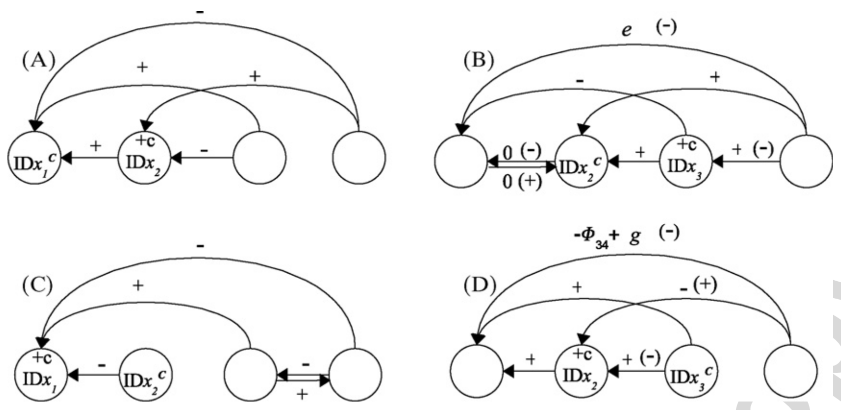

Fig. A5 – Graphic representation of response modification matrices for B and S-models (see text or Figs. A1 and A2 for explanation) with inducible defenses (ID) exhibited by two species, resulting after adding costs to a second defended species. Here $\Delta P^{m-r} = P^m - p^r$, where P^m is a net response matrix for models with ID and costs in two trophic levels, and P^r is a net response matrix for models with ID in two trophic levels and costs in one of them. In (A) are shown the response modifications after incorporating costs in the second-level species on a trophic chain that previously had ID in the two lower levels and costs in the first-level species. Other graphs follow the same logic. In parenthesis are shown results of S-models that are different from those of the B-models. In A and C, the results belong only to S-models since the assumed feedback structure in not allowed by B-models. Here we found some sign ambiguities defined by $e = -\alpha_{x_1x_2}\alpha_{x_3x_3}\alpha_{k_3k_3} - \alpha_{x_1x_2}\alpha_{x_3k_3}\alpha_{k_3x_3} + \alpha_{x_1k_3}\alpha_{x_3x_2}\alpha_{k_3x_3}$ **and** $g = \alpha_{x_2k_4}\alpha_{x_3x_2}\alpha_{k_4x_4}$.

corresponding effect of adding a first cost in x_2, whereas the effects $\Delta P_{1,3}$ and $\Delta P_{1,4}$ are enhanced. Furthermore, there appear two new DE of opposite sign: $\Delta P_{3,4}$ and $\Delta P_{4,3}$. Other effects can be read directly from Figs. A4 and A5.

REFERENCES

Abrams, P.A., Walters, C.J., 1996. Invulnerable prey and the paradox of enrichment. Ecology 77, 1125–1133.

Agrawal, A.A., 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294, 321–326.

Arditi, R., Michalski, J., Herzel, A.H., 2005. Rheagogies: modeling non-trophic effects in food webs. Ecol. Complex. 2, 249–258.

Bender, E.A., Case, T.J., Gilpin, M.E., 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65, 1–13.

Bernard, M.F., 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. Ann. Rev. Ecol., Evolut., System. 35, 651–673.

Brönmark, C., Miner, J.G., 1992. Predator-induced phenotypical change in body morphology in crucian carp. Science 258, 1348–1350.

Burks, R.L., Lodge, D.M., 2002. Cued in: advances and opportunities in freshwater chemical ecology. J. Chem. Ecol. 28, 1901–1917.

Dambacher, J.M., Li, H.W., Rossignol, P.A., 2003a. Qualitative predictions in model ecosystems. Ecol. Modell. 161, 79–93.

Dambacher, J.M., Luh, H., Li, H.W., Rossignol, P.A., 2003b. Qualitative stability and ambiguity in model ecosystems. Am. Nat. 161, 876–888.

Dambacher, J.M., Ramos-Jiliberto, R., 2007. Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. Q. Rev. Biol., in press.

DeWitt, T.J., Sih, A., Wilson, D.S., 1998. Costs and limits of phenotypic plasticity. Trends Ecol. Evolut. 13, 77–81.

Dicke, M., Grostal, P., 2001. Chemical detection of natural enemies by arthropods: an ecological perspective. Ann. Rev. Ecol. System. 32, 1–23.

Frank, S.A., 1993. A model of inducible defense. Evolution 47, 325–327.

Gilbert, J.J., 1966. Rotifer ecology and embryological induction. Science 151, 1234–1237.

Harvell, C.D., 1990. The ecology and evolution of inducible defenses. Q. Rev. Biol. 65, 323–340.

Harvell, C.D., Tollrian, R., 1999. Why inducible defenses? In: Tollrian, R., Harvell, C.D. (Eds.), The Ecology and Evolution of Inducible Defenses. Princeton University Press, Princeton, NJ, pp. 3–9.

Hay, M.E., Kubanek, J., 2002. Community and ecosystem level consequences of chemical cues in the plankton. J. Chem. Ecol. 28, 2001–2016.

Hessen, D.O., Van Donk, E., 1993. Morphological changes in *Scenedesmus* induced by substances released from *Daphnia*. Arch. für Hydrobiol. 127, 129–140.

Ives, A.R., Dobson, A.P., 1987. Antipredator behavior and the population dynamics of simple predator–prey systems. Am. Nat. 130, 431–447.

Kopp, M., Gabriel, W., 2006. The dynamic effect of an inducible defense in the Nicholson–Bailey model. Theor. Populat. Biol. 70, 43–55.

Krivan, V., 1998. Effects of optimal antipredator behavior of prey on predator–prey dynamics: the role of refuges. Theor. Populat. Biol. 53, 131–142.

Krueger, D.A., Dodson, S.I., 1981. Embryological induction and predation ecology in *Daphnia pulex*. Limnol. Oceanogr. 26, 219–223.

Kuhlmann, H.W., Heckmann, K., 1985. Interspecific morphogens regulating prey-predator relationships in protozoa. Science 227, 1347–1349.

Lampert, W., 1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3, 21–27.

Lass, S., Spaak, P., 2003. Chemically induced anti-predator defences in plankton: a review. Hydrobiologia 491, 221–239.

Levins, R., 1966. The strategy of model building in population biology. Am. Scientist 54, 421–431.

Levins, R., 1974. The qualitative analysis of partially specified systems. Ann. NY Acad. Sci. 231, 123–138.

Levins, R., 1975. Evolution of communities near equilibrium. In: Cody, M., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA, pp. 16–50.

McNair, J., 1986. The effects of refuges on predator-prey interactions: a reconsideration. Theor. Populat. Biol. 29, 38–63.

Miller, T.E., Kerfoot, W.C., 1987. Redefining indirect effects. In: Kerfoot, W.C., Sih, A. (Eds.), Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover, NH, pp. 33–37.

Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K., Relyea, R.A., 2005. Ecological consequences of phenotypic plasticity. Trends Ecol. Evol. 20, 685–692.

Puccia, C.J., Levins, R., 1985. Qualitative Modeling of Complex Systems. An Introduction to Loop Analysis and Time Averaging. Harvard University Press, Cambridge, p. 259.

Ramos-Jiliberto, R., 2003. Population dynamics of prey exhibiting inducible defenses: the role of associated costs and density-dependence. Theor. Populat. Biol. 64, 221–231.

Ramos-Jiliberto, R., González-Olivares, E., 2000. Relating behaviour to population dynamics: a predator–prey metaphysiological model emphasizing zooplankton diel vertical migration as an inducible response. Ecol. Modell. 127, 221–233.

Ramos-Jiliberto, R., González-Olivares, E., Bozinovic, F., 2002. Population-level consequences of antipredator behavior: a metaphysiological model based on the functional ecology of the leaf-eared mouse. Theor. Populat. Biol. 62, 63–80.

Rinaldi, S., Gragnanic, A., De Monte, S., 2004. Remarks on antipredator behavior and food chain dynamics. Theor. Populat. Biol. 66, 277–286.

Ruxton, G.D., 1995. Short term refuge use and stability of predator–prey models. Theor. Populat. Biol. 47, 1–17.

Sih, A., 1987. Prey refuges and predator–prey stability. Theor. Populat. Biol. 31, 1–12.

Skelly, D.K., Werner, E.E., 1990. Behavioral and life historical responses of larval American toads to an odonate predator. Ecology 71, 2313–2322.

Smith, D.C., Van Buskirk, J., 1995. Phenotypic design, plasticity, and ecological performance in two tadpole species. Am. Nat. 145, 211–233.

Tollrian, R., Harvell, C.D., 1999. The Ecology and Evolution of Inducible Defenses. Princeton University Press, Princeton, NJ, p. 383.

Underwood, N., 1998. The timing of induced resistance and induced susceptibility in the soybean-Mexican bean beetle system. Oecologia 114, 376–381.

Underwood, N., 1999. The influence of plant and herbivore characteristics on the interaction between induced resistance and herbivore population dynamics. Am. Nat. 153, 282–294.

Van der Stap, I., Vos, M., Mooij, W., 2006. Linking herbivore-induced defences to population dynamics. Freshwater Biol. 51, 424–434.

Verschoor, A.M., Vos, M., Van der Stap, I., 2004. Inducible defences prevent strong population fluctuations in bi- and tritrophic food chains. Ecol. Lett. 7, 1143–1148.

Vos, M., Kooi, B.W., DeAngelis, D.L., Mooij, W.M., 2004a. Inducible defences and the paradox of enrichment. Oikos 105, 471–480.

Vos, M., Verschoor, A.M., Kooi, B.W., Wäckers, F.L., DeAngelis, D.L., Mooij, W.M., 2004b. Inducible defenses and trophic structure. Ecology 85, 2783–2794.

Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions. Ecology 84, 1083–1100.

Wootton, J.T., 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. Am. Nat. 141, 71–89.