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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

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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.

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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: roram@uchile.cl (R. Ramos-Jiliberto).

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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

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

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

$$wF_n = \frac{F_n}{F_n^*} \tag{2}$$

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

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

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:

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

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.

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