

Experimental evidence that induced defenses promote coexistence of zooplanktonic populations

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Theoretical predictions suggest that adaptive phenotypic plasticity, and induced defenses in particular, exert a stabilizing effect on ecological systems and increase the likelihood of species coexistence. Nonetheless, up to now, there is little empirical support for this hypothesized mechanism of diversity preservation. We experimentally assessed the effects of induction of plastic morphological responses triggered by a predator kairomone, on patterns of co-occurrence of two herbivore populations of rotifers (*Brachionus calyciflorus* and *B. havanaensis*) sharing resources (*Chlorella vulgaris*) and predators (*Asplanchna brightwelli*). To our knowledge, this is the first experimental work conducted at the population level where non-induced and induced states of same prey species are obtained through manipulating the level of predator signal. Our objective was to assess the consequences of induced defenses on the mean population density, population variability, evenness and likelihood of persistence of competitor populations. Our results show that induced defenses promote species coexistence through increasing the likelihood of persistence and evenness of competing populations, over a gradient of resource availability.

KEYWORDS: Non-lethal effects; phenotypic plasticity; stability; rotifers; persistence

INTRODUCTION

Since the pioneering work of Gardner and Ashby (Gardner and Ashby, 1970) and May (May, 1972), ecologists have increasingly accepted that the persistence of populations embedded in natural multispecific assemblages cannot be understood without considering biological stabilizing mechanisms. Adaptive predator and prey responses to changes in the abundance or behavior of interacting species have been postulated as important

stabilizing factors in food webs of different complexity (Ives and Dobson, 1987; Abrams, 2000; Kondoh, 2003, 2007).

Inducible antipredator defenses (Harvell, 1990) constitute a type of adaptive prey response that decreases predation success via shifts in behavioral, morphological or life-history traits of prey perceiving predator cues (see Tollrian and Harvell, 1999). A number of theoretical studies have explicitly addressed the effects of inducible

defenses on the local stability and persistence probability of model systems consisting of a few interacting populations (Ives and Dobson, 1987; Ramos-Jiliberto *et al.*, 2002; Ramos-Jiliberto, 2003; Rinaldi *et al.*, 2004; Vos *et al.*, 2004a,b; Yamauchi and Yamamura, 2005; Ramos-Jiliberto *et al.*, 2008a,b), up to large complex communities (Kondoh, 2003, 2007). These theoretical results support the conclusion that the presence of induced defenses exerts a stabilizing effect on the model systems and increase the likelihood of species coexistence.

The suggested mechanism underlying the stabilizing effect of induced defenses is as follows. At low predator abundances, prey exhibits an inexpensive basic undefended state, which favors their growth and indirectly that of their predators. A consequent increase in predator density induces prey to exhibit modified traits that reduce their vulnerability (e.g. longer spines relative to those present in the basic morph), decreasing predators' feeding and per capita growth. In addition, the growth of the prey decreases, due to the costs of carrying their arms. Therefore, adaptive prey defenses are expected to create negative feedback loops that prevent strong population oscillations, enhancing community stability and persistence (Abrams, 1984; Kopp and Gabriel, 2006; Dambacher and Ramos-Jiliberto, 2007). Nevertheless, when more than a single species per trophic level is considered to exhibit inducible defenses, the dynamic outcome and underlying mechanisms are little understood (van der Stap *et al.*, 2008; Garay-Narváez and Ramos-Jiliberto, 2009).

Despite the extensive evidence on the prevalence of induced defenses across many taxa and ecosystems (Harvell and Tollan, 1999), and the soundness of modeling developments, there is still a wide gap between data and theory regarding the role played by adaptive prey responses in the puzzle of biodiversity maintenance. The empirical validation of theoretical proposals has not been fully convincing, mainly due to the inherent difficulties in manipulating the level of responses of the experimental organisms to inductor signals (Underwood and Rausher, 2002; Verschoor *et al.*, 2004; van der Stap *et al.*, 2006, 2007, 2008). Previous studies have found difficulties in maintaining a control consisting of a population composed of basic non-induced organisms under predation pressure, in order to contrast its properties with the population of organisms displaying an induced response.

In this work, we advance our understanding of the relationship between phenotypic plasticity and community stability. This is done by performing a controlled experiment to evaluate the effects of induction of morphological responses triggered by predator kairomones,

on the coexistence of two competing zooplankton species (each as a single clone) in populations that share predators and resources. We developed a tritrophic experimental model system with four species: two herbivorous rotifers (*Brachionus calyciflorus* and *B. havanaensis*), a single resource (*Chlorella vulgaris*) and a common predator (*Asplanchna brightwelli*) that is able to induce morphological defenses in the two herbivores. To isolate the impact of the induced defenses, we were able to separate the lethal effect of predators from the net effect, by manipulating the level of inducing signal (kairomone) in the simple experimental communities. Our results present experimental evidence that induced defenses promote species coexistence, increasing the evenness and likelihood of persistence of animal populations.

METHOD

Experimental organisms

Predator *Asplanchna brightwelli* and the herbivores *B. calyciflorus* and *B. havanaensis* were isolated from two temperate lakes from central Chile: Pitama (33°27'S–70°49'W) and Rapel (34°09'S–71°26'W). Clonal cultures were initiated from a single amictic female and kept under laboratory conditions for 2 months prior to experiments. To maintain the cultures and carry out the experiments, we used artificial freshwater (U.S. EPA) enriched with vitamins: thiamine (100 mg L⁻¹), biotin (0.5 mg L⁻¹) and cyanocobalamine (0.5 mg L⁻¹).

Prey rotifers in the stock cultures were fed daily with the green alga *Chlorella vulgaris* at a density of 0.5×10^6 cells mL⁻¹, which was grown in axenic 2 L glass bottles with Bold basal medium (Borowitzka and Borowitzka, 1988). The algae were harvested in the exponential growth phase, centrifuged at 3000 rpm for 5 min and re-suspended in EPA water prior to presenting it as food. Algal density was estimated by cell counting in a Neubauer chamber.

The predator *A. brightwelli* was cultured in 500 mL glasses and fed daily *ad libitum* with a *Brachionus* mixture (*B. calyciflorus*, *B. caudatus*, *B. havanaensis* and *B. patulus*). The culture media were replaced daily.

Standard culture and experimental conditions were: pH 7.5 ± 0.1 , temperature $25 \pm 0.5^\circ\text{C}$ and diffuse fluorescent lighting with 12:12 (light:dark) photoperiod.

Plastic response to predator kairomones

An independent assay was run in order to measure the morphological response of prey to low and high kairomone concentrations. Signal concentrations of 5 and

100 *Asplanchna* per liter were chosen as the low and high conditions, respectively, based on previous laboratory measurements and reported field abundances (Nandini, 1999). In this test, *B. calyciflorus* and *B. havanaensis*, at an initial density of 1 ind. mL⁻¹ in 150 mL, were exposed to low and high kairomone levels, in addition to a control (without signal) level. Control and treatment media were prepared daily as follows. The control medium consisted of EPA freshwater pre-conditioned with the mixture of rotifers used as prey for *Asplanchna*. Kairomone treatments were carried out with predator-conditioned medium, which was prepared daily with EPA water, containing the corresponding *Asplanchna* densities. *Asplanchna* was fed with a mixture of brachionids at a density of 4 ind. mL⁻¹. Every 24 h, all rotifers were removed, the media were filtered through a 0.45 µm membrane and the pH adjusted to 7.5 ± 0.1 through addition of 1N HCl when required. Once the control and treatment media had been set up, *C. vulgaris* at a density of 10⁶ cells mL⁻¹ was added as food. The media were distributed into 18 experimental jars, consisting of six treatments (2 rotifer species × 3 kairomone levels) × 3 replicates. Rotifers were transferred daily to freshly prepared medium. After 6 days, 50 egg-bearing prey individuals were sampled from each experimental jar and fixed in 5% formalin. Digital images of each animal were obtained under a dissecting microscope, from which the lengths of the anterior and posterior spines were measured.

Differences between morphological measures among treatments were evaluated, for each species, by means of *t*-test after verification of parametric assumptions.

Coexistence experiments

Levels of morphological induction were set from the results of the experiment described in the previous section (5 and 100 *Asplanchna* per liter), following the same procedures for the preparation and renewal of treatment media. At the “low kairomone concentration” level, predators were presented at a fixed low density (5 *Asplanchna* per liter). The concentration of kairomones resulting from such a predator density did not induce morphological defenses in the clones tested, but lethal effects occurred (see results). At the “high kairomone concentration” level, predators are present at the same low density (5 *Asplanchna* per liter), but the medium was conditioned with a predator density of 100 *Asplanchna* per liter. This allowed us to evaluate lethal effects of predation together with the induction of morphological defenses. The experimental design consisted of 2 (kairomone levels) × 4 (food densities: 0.5, 1, 2 and 4 × 10⁶ cells mL⁻¹ of

C. vulgaris) × 4 (replicates), resulting in 32 experimental units. Every beaker containing 200 mL of medium was initiated with 200 individuals of each prey species and on individual *Asplanchna*. The initial groups of brachionids used in the induction treatments were grown in the predator-conditioned medium for a period of 7 days prior to beginning the experiment. This ensured that founder individuals exhibited defenses from the first experimental day.

Predator density was maintained constant, through replacing dead or inactive individuals and removing each newborn, after an exhaustive search of each beaker performed each 12 h. Maintaining a constant predator density during the experiment allows a clearer separation of the net effect of predation between lethal and non-lethal effects.

Herbivorous rotifers from each experimental beaker were counted every 24 h, using three to four 10 mL aliquots. After this, all the rotifers were transferred to new medium using a flame-narrowed pipette. Coexistence experiments were terminated after 16 days, when brachionid populations in most replicates began to stabilize.

Population density of brachionids was analyzed based on their mean values and population variability of de-trended density over time (excluding an initial transient phase of 6 days) by means of one-way ANOVA and Bonferroni *post hoc* tests. Raw data were log-transformed in order to satisfy parametric assumptions.

Pielou's evenness index \mathcal{J}' was estimated daily, as $\mathcal{J}' = H' / \ln S$, where H' is Shannon's diversity index and S the number of species (Pielou, 1966). Pielou's index was estimated based on the densities of both brachionid species in order to obtain a measure of the homogeneity of herbivore densities. This index was considered adequate due to its symmetry, sensitivity and range of variation, and because it is comparable with many other evenness indices (Biesel *et al.*, 2003). Finally, a population viability analysis (PVA) was performed following Dennis *et al.* (Dennis *et al.*, 1991) for the estimation of mean and variance of the growth rate. This analysis was developed in order to roughly assess the probability of population persistence from the observed variation of rotifers' abundances, and not for calculating the viability of endangered populations. Under this approach, the extinction probability $P(e)$ of each replicate was estimated on a 60-day time horizon. A population was considered extinct when its density dropped below 0.002 ind. mL⁻¹, corresponding to <0.5% of initial densities. The calculated persistence probabilities $1 - P(e)$ were analyzed using two-way ANOVA, after arcsine transformation, with resource density and defense induction as factors.

RESULTS

Spine elongation in both prey species was effectively induced by the high kairomone level (100 *Asplanchna* per liter), reaching 40% of elongation of anterior spines relative to the control (without kairomone) in both species, and 100 and 60% of elongation of posterior spines in *B. calyciflorus* and *B. havanaensis*, respectively. On the other hand, anterior and posterior spines of *B. calyciflorus* exposed to a low kairomone level (5 *Asplanchna* per liter) showed a slight increase of less than 20%. In the case of *B. havanaensis*, spines were marginally lower (anterior spines) or of similar length as those measured in control individuals (Fig. 1). We considered induction of morphological defenses as a significant elongation of both spines relative to measures obtained from control individuals, and not a novo formation of spines. From these results, it was considered that at the low kairomone level, the organisms were not induced to exhibit morphological defenses, and at the high kairomone level the organisms were effectively induced. Although body sizes were measured in both species, no

significant differences were observed between treatments and control.

Without induction of morphological defenses at the low kairomone level, mean population density of *B. calyciflorus* increased with resource density, while *B. havanaensis* reached its highest mean density at a low resource level (Fig. 2 and Supplementary data, Fig. S1). Also, population densities of *B. calyciflorus* showed larger variations at highest resource levels, unlike *B. havanaensis* whose densities were more variable at lowest resource densities. With induced defenses at the high kairomone level, mean density values of both species were homogeneous over the entire resource gradient (at about 0.5 ind. mL⁻¹, see Supplementary data, Fig. S1), and interspecific differences were only significant at the highest level of resource. In addition, where defenses were induced, variability of density trajectories decreased consistently in both species and did not differ between species over the resource gradient (Supplementary data, Fig. S1).

A higher evenness among population densities of the herbivores was observed in the induction treatments, as revealed by the dynamics of the Pielou's index \mathcal{J} (Fig. 3). In the absence of induction at the low kairomone level, evenness declined over time and more abruptly at lower resource densities. With induced defenses at the highest kairomone level, \mathcal{J} remained virtually constant over time for all resource densities.

Finally, the results of the PVA (Fig. 4) show that induced defenses promoted a significant increase in the persistence probability of herbivores. This applies to *B. calyciflorus* across the entire resource gradient and to *B. havanaensis* at all but the lowest resource level, where the persistence probability remained quite high (Fig. 4). Homogenization of abundances between species, on the gradient of resources and along trajectories of each species (Figs 2 and 3) was translated into a homogenization of the values of r , which render the results of the PVA.

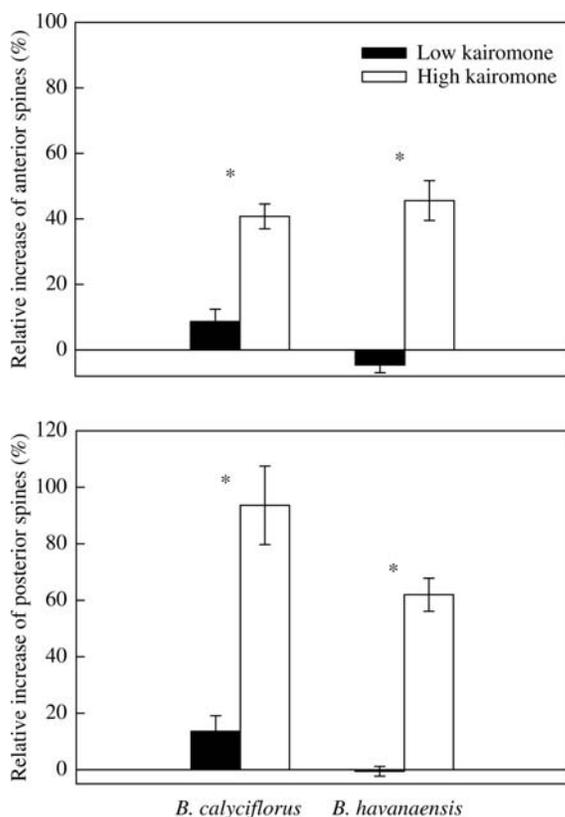


Fig. 1. Relative increase (mean \pm 95% CI) of anterior spines (upper), and posterior spines (lower), of the prey *Brachionus calyciflorus* and *B. havanaensis* exposed to medium with the “low kairomone concentration” and the “high kairomone concentration”. * $P < 0.05$, N.S., non-significant.

DISCUSSION

Induced defenses of *B. calyciflorus* and *B. havanaensis*, in response to the kairomone of *A. brightwelli*, produced a homogenization between herbivore population densities and the decreased variability of their dynamics: high densities decreased, low densities increased, while temporal oscillations were dampened, so that both species were nearly equally abundant and less variable over time. This competitive equivalence promoted by phenotypic plasticity led to either maintaining or increasing the persistence probability of herbivores over all tested

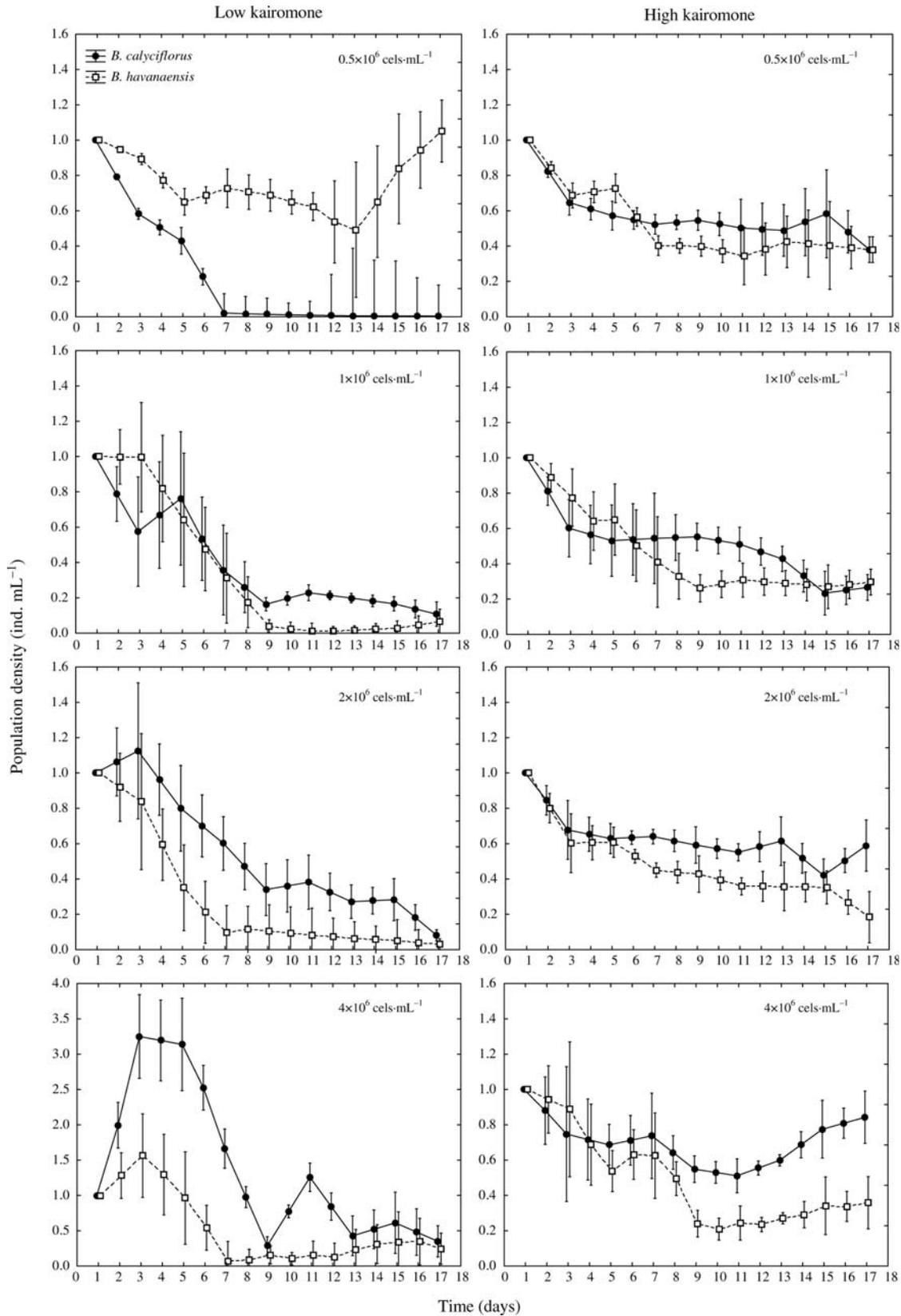


Fig. 2. Population trajectories (mean density \pm 95% CI) of *B. calyciflorus* and *B. havanaensis* in media with the low (left column) and high (right column) kairomone concentration. Prey was subjected to predation by *Aplanchna* and was competing for a single resource (*C. vulgaris*). Resource densities are given within the plots.

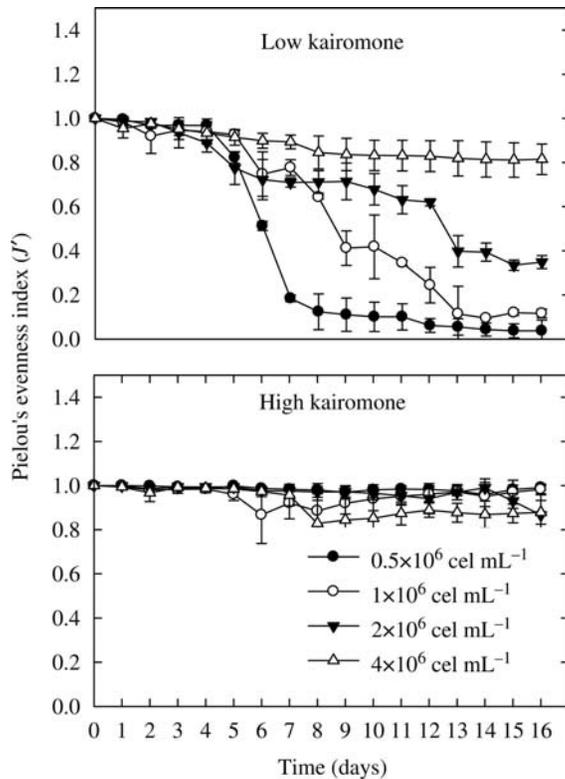


Fig. 3. Pielou's evenness index J' of prey rotifers over time (mean \pm 95% CI). Prey was exposed to predation with the low or high kairomone level. Resource densities are given within the plots.

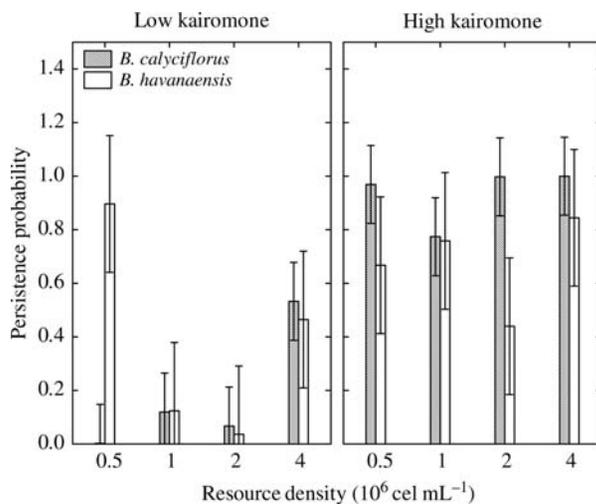


Fig. 4. Persistence probability (mean \pm 95% CI), estimated in a community experiment, of *B. calyciflorus* (filled bars) and *B. havanaensis* (open bars) as a function of the resource level. Prey was exposed to predation with the low (left) or high (right) kairomone level.

resource levels. Furthermore, the induction of antipredator defenses suppressed the resource-dependence that, in the absence of antipredator response effects,

exhibited the mean abundance, stability and persistence of herbivore populations.

Rotifers show large interspecific and even interclonal variability in the development of spines in response to the presence of predatory zooplankton. Postero-lateral spines of non-induced *B. calyciflorus* have been reported to be absent (Halbach, 1971), of 20 μm long (Stemberger, 1990), or 40 μm long (present work). Although the clones used in our experiments exhibit posterior or postero-lateral spines even without being exposed to an inducing signal, the incorporation of a high kairomone concentration caused a significant increase in length of the structures, which can be considered an effective induction. Other experiments performed with the same isolated herbivores (Aránguiz-Acuña *et al.*, 2010) indicated that induced morphs of both *B. calyciflorus* as *B. havanaensis* were less attacked by *Asplanchna*, and more time was required by predators to handle induced prey. This supports the fact that the morphological changes observed in both clones exposed to the high level of kairomones are effective defenses against predation by *Asplanchna*.

Although uncovering the precise mechanisms by which induced defenses promote biodiversity maintenance requires dedicated experiments, our results could be explained by means of current ecological knowledge about differential abilities in resource use (Leibold, 1996), interacting with differential abilities and costs of predator avoidance tactics (Chesson and Kuang, 2008). At a low kairomone density, where only consumption effects took place, *B. havanaensis* was able to reach higher densities at low resource levels, as compared with its congeneric *B. calyciflorus*. Conversely, higher resource levels favored the growth of *B. calyciflorus*. Previous experiments conducted with non-induced clones of both competing species showed that this trend held also in the absence of predators (Supplementary data, Fig. S2). Thus, the incorporation of predation decreases the mean abundances of the two prey over the resource gradient due to consumption, without changing the pattern of dominance. On the other hand, when defenses were induced by the addition of the kairomone to the predation treatments (Fig. 2, right column), dominant prey decreased their mean abundance, while the subordinate competitor increases or maintains its abundance.

We propose that at the low resource level, the induction of defenses drove the density increase in *B. calyciflorus* due to diminished mortality as a consequence of effective antipredator responses (e.g. Gilbert, 1966, 1999). This can be seen by comparing the top left and right plots in Fig. 2. The density increase in *B. calyciflorus* led to a decrease in *B. havanaensis* likely due

to stronger food limitation. This process promoted the equalization of the abundances of both herbivores (see Fig. 2, top right, and Supplementary data, Fig. S1, top right). On the other hand, at the highest food level, *B. havanaensis* did not change its mean abundance with the addition of kairomones (Supplementary data, Fig. S1, top plots). This suggests that the costs of defenses observed in Supplementary data, Fig. S2 (bottom plots) were not overwhelmed by the net benefits of decreased mortality. Therefore, the defense effectiveness of *B. havanaensis* appears to be relatively weak, especially at the highest food level. Since there was no significant change in the abundance of *B. havanaensis* at the highest food level, the effects of the treatments on the dynamics of its competitor allow us to discard changes in resource availability. The species *B. calyciflorus* showed evidence of high costs at intermediate and high food levels (compare bottom left and right plots of Supplementary data, Fig. S2). Therefore, the addition of the kairomone promoted the homogenization of trajectories at the initial phase of population growth (left column of Fig. 2) and sustained higher abundances in later phases as a product of their defenses. Similar to *B. havanaensis*, the effectiveness of defenses of *B. calyciflorus* decreases at the highest resource level. This could be explained because higher resources sustain higher herbivore density, which offers a protection by numbers given the saturating (i.e. type II) functional response of *Asplanchna* (Nandini and Sarma, 1999; Sarma and Nandini, 2007). Costs of defenses in isolated populations of rotifer prey can be explained by reduced fertility or delayed reproduction (Gilbert, 1980, 2009; Epp and Lewis, 1984; Stemberger, 1988; Zagarese and Marinone, 1992; Relyea, 2002). In interacting populations, ecological costs (such as reduced competitive ability) could also take place (Strauss *et al.*, 2002; Garay-Narváez and Ramos-Jiliberto, 2009). The results of this study suggest that induced defenses of herbivores in competition, promote evenness of their abundances over a gradient of resource availability. This pattern is arguably driven by diminished mortality acquired from antipredator protection, together with the release of resources and the costs of exhibiting defenses. This results in the suppression of numerical dominance between the herbivores, at all resource levels, which increases the persistence probability of both rotifer populations.

Prior experimental work suggested that induced defenses in primary producers enhance a herbivore's density dependence (Underwood and Rausher, 2002), preventing population fluctuations in herbivores (Verschoor *et al.*, 2004; van der Stap *et al.*, 2006), and could increase the persistence probability of competing

herbivores and their predators (van der Stap *et al.*, 2008). Nonetheless, those studies did not compare the dynamics among systems including the same species/strain of plant in induced versus non-induced states. Overcoming this drawback, our work introduces a methodological improvement based on an appropriate manipulation of *Asplanchna* densities, adjusted for discrimination between induction (non-lethal) effects and net effects of the predator. To our knowledge, this is the first experimental work where the population dynamics consequences of induced defenses are assessed after manipulating the level of phenotypic response in the same animal populations. As with any experimental system, which is necessarily a simplification of nature, our results cannot be directly extended to natural conditions. In the wild, rotifer species are composed of many clones, and density of predators fluctuates, linked with kairomone dynamics. Nevertheless, our interest in this study was not focused on explaining species-specific reactions, but rather on identifying the potential relevance of plastic defensive responses as a driving mechanism of coexistence between competitors.

Our results support the hypothesis that induced antipredator defenses promote stability of populations and thus facilitate biodiversity maintenance. These findings help explain the prevalence of complex communities in nature, and give empirical support to the incorporation of biological realism, and adaptive individual responses in particular, into theoretical ecological models as useful tools for understanding nature.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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REFERENCES

- Abrams, P. A. (1984) Foraging time optimization and interactions in food web. *Am. Nat.*, **124**, 80–96.
- Abrams, P. A. (2000) The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.*, **31**, 79–105.
- Aránguiz-Acuña, A., Ramos-Jiliberto, R., Nandini, S. *et al.* (2010) Benefits, costs and reactivity of inducible defences: an experimental test with rotifers. *Freshwater Biol.*, **55**, 2114–2122.
- Biesel, J. N., Usseglio-Polatera, P., Bachmann, V. *et al.* (2003) A comparative analysis of evenness index sensitivity. *Internat. Rev. Hydrobiol.*, **88**, 3–15.
- Borowitzka, M. A. and Borowitzka, L. J. (1988) *Micro-Algal Biotechnology*. Cambridge University Press, London.
- Chesson, P. and Kuang, J. J. (2008) The interaction between predation and competition. *Nature*, **456**, 235–238.
- Dambacher, J. M. and Ramos-Jiliberto, R. (2007) Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. *Q. Rev. Biol.*, **82**, 227–250.
- Dennis, B., Munholland, P. L. and Scott, J. M. (1991) Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.*, **61**, 115–143.
- Epp, R. W. and Lewis, W. M. (1984) Cost and speed of locomotion for rotifers. *Oecologia*, **61**, 289–292.
- Garay-Narváez, L. and Ramos-Jiliberto, R. (2009) Induced defenses within food webs: the role of community trade-offs, delayed responses, and defense specificity. *Ecol. Complex.*, **6**, 383–391.
- Gardner, M. R. and Ashby, W. R. (1970) Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature*, **228**, 784.
- Gilbert, J. J. (1966) Rotifer ecology and embryological induction. *Science*, **151**, 1234–1237.
- Gilbert, J. J. (1980) Further observations on developmental polymorphism and its evolution in the rotifer *Brachionus calyciflorus*. *Freshwater Biol.*, **10**, 281–294.
- Gilbert, J. J. (1999) Kairomon-induced morphological defenses in rotifers. In Tollrian, R. and Harvell, C. D. (eds), *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, New Jersey, pp. 127–141.
- Gilbert, J. J. (2009) Predator-specific inducible defenses in the rotifer *Keratella tropica*. *Freshwater Biol.*, **54**, 1933–1946.
- Halbach, U. (1971) The adaptive value of cyclomorphic spine production in *Brachionus calyciflorus* Pallas (Rotatoria). *Oecologia*, **6**, 267–288.
- Harvell, C. D. (1990) The ecology and evolution of inducible defenses. *Q. Rev. Biol.*, **65**, 323–340.
- Harvell, C. D. and Tollrian, R. (1999) Why inducible defenses?. In Tollrian, R. and Harvell, C. D. (eds.), *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, New Jersey, pp. 3–9.
- Ives, A. R. and Dobson, A. P. (1987) Antipredator behavior and the population dynamics of simple predator-prey systems. *Am. Nat.*, **130**, 431–447.
- Kondoh, M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science*, **299**, 1388–1391.
- Kondoh, M. (2007) Anti-predator defense and the complexity–stability relationship of food webs. *Proc. R. Soc. B Biol. Sci.*, **274**, 1617–1624.
- Kopp, M. and Gabriel, W. (2006) The dynamic effects of an inducible defense in the Nicholson–Bailey model. *Theor. Popul. Biol.*, **70**, 43–55.
- Leibold, M. A. (1996) A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.*, **147**, 784–812.
- May, R. M. (1972) Will a large complex system be stable? *Nature*, **238**, 413–414.
- Nandini, S. (1999) Variations in physicochemical parameters and plankton community structure in a series of sewage stabilization ponds. *Rev. Biol. Trop.*, **47**, 149–156.
- Nandini, S. and Sarma, S. S. S. (1999) Effect of starvation time on the prey capture behaviour, functional response and population growth of *Asplanchna sieboldi* (Rotifera). *Freshwater Biol.*, **42**, 121–130.
- Pielou, E. C. (1966) The measurement of diversity in different types of biological collections. *J. Theor. Biol.*, **13**, 131–144.
- Ramos-Jiliberto, R. (2003) Population dynamics of prey exhibiting inducible defenses: the role of associated costs and density-dependence. *Theor. Popul. Biol.*, **64**, 221–231.
- Ramos-Jiliberto, R., González-Olivares, E. and Bozinovic, F. (2002) Population-level consequences of antipredator behavior: a metaphysiological model based on the functional ecology of the Leaf-Eared Mouse. *Theor. Popul. Biol.*, **62**, 63–80.
- Ramos-Jiliberto, R., Duarte, H. and Frodden, E. (2008a) Dynamic effects of inducible defenses in a one-prey two-predators system. *Ecol. Model.*, **214**, 242–250.
- Ramos-Jiliberto, R., Mena-Lorca, J., Flores, J. D. *et al.* (2008b) Role of inducible defenses in the stability of a tritrophic system. *Ecol. Complex.*, **5**, 183–192.
- Relyea, R. A. (2002) Costs of phenotypic plasticity. *Am. Nat.*, **159**, 272–282.
- Rinaldi, S., Gragnani, A. and De Monte, S. (2004) Remarks on anti-predator behavior and food chain dynamics. *Theor. Popul. Biol.*, **66**, 277–286.
- Sarma, S. S. S. and Nandini, S. (2007) Small prey size offers immunity to predation: a case study on two species of *Asplanchna* and three brachionid prey (Rotifera). *Hydrobiologia*, **593**, 67–76.
- Stemberger, R. S. (1988) Reproductive costs and hydrodynamic benefits of chemically induced defenses in *Keratella testudo*. *Limnol. Oceanogr.*, **33**, 593–606.
- Stemberger, R. S. (1990) Food limitation, spination, and reproduction in *Brachionus calyciflorus*. *Limnol. Oceanogr.*, **35**, 33–44.
- Strauss, S. Y., Rudgers, J. A., Lau, J. A. *et al.* (2002) Direct and ecological costs of resistance to herbivory. *Trends Ecol. Evol.*, **17**, 278–285.
- Tollrian, R. and Harvell, C. D. (eds) (1999) *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, New Jersey.
- Underwood, N. and Rausher, M. (2002) Comparing the consequences of induced and constitutive plant resistance for herbivore population dynamics. *Am. Nat.*, **160**, 20–30.

- van der Stap, I., Vos, M. and Mooij, W. M. (2006) Linking herbivore-induced defenses to population dynamics. *Freshwater Biol.*, **51**, 424–434.
- van der Stap, I., Vos, M., Verschoor, A. M. *et al.* (2007) Induced defenses in herbivores and plants differentially modulate a trophic cascade. *Ecology*, **88**, 2474–2481.
- van der Stap, I., Vos, M., Tollrian, R. *et al.* (2008) Inducible defenses, competition and shared predation in planktonic food chains. *Oecologia*, **157**, 697–705.
- Verschoor, A. M., Vos, M. and van der Stap, I. (2004) Inducible defenses prevent strong population fluctuations in bi- and tritrophic food chains. *Ecol. Lett.*, **7**, 1143–1148.
- Vos, M., Verschoor, A. M., Kooi, B. W. *et al.* (2004a) Inducible defenses and trophic structure. *Ecology*, **85**, 2783–2794.
- Vos, M., Kooi, B. W., DeAngelis, D. L. *et al.* (2004b) Inducible defenses and the paradox of enrichment. *Oikos*, **105**, 471–480.
- Yamauchi, A. and Yamamura, N. (2005) Effects of defense evolution and diet choice on population dynamics in a one-predator-two-prey system. *Ecology*, **86**, 2513–2524.
- Zagarese, H. E. and Marinone, M. C. (1992) Induction and inhibition of spine development in the rotifer *Keratella tropica*: evidence from field observations and laboratory experiments. *Freshwater Biol.*, **28**, 289–300.