

# Top predators suppress rather than facilitate plants in a trait-mediated tri-trophic cascade

John N. Griffin\*, Jack Butler, Nicole N. Soomdat, Karen E. Brun, Zachary A. Chejanovski and Brian R. Silliman

Department of Biology, University of Florida, Gainesville, FL, USA

\*Author for correspondence ([johngriffin@ufl.edu](mailto:johngriffin@ufl.edu)).

Classical ecological theory states that in tri-trophic systems, predators indirectly facilitate plants by reducing herbivore densities through consumption, while more recent work has revealed that predators can generate the same positive effect on plants non-consumptively by inducing changes in herbivore traits (e.g. feeding rates). Based on observations in US salt marshes dominated by vast monocultures of cordgrass, we hypothesized that sit-and-wait substrate-dwelling predators (crabs) could actually strengthen *per capita* impacts of potent grazers (snails), by non-consumptively inducing a vertical habitat shift of snails to their predation refuge high on canopy leaves that are vulnerable to grazing. A two-month field experiment supported this hypothesis, revealing that predators non-consumptively increased the mean climbing height of snails on grasses, increased grazing damage per leaf and ultimately suppressed cordgrass biomass, relative to controls. While seemingly counterintuitive, our results can be explained by (i) the vulnerability of refuge resources to grazing, and (ii) universal traits that drove the vertical habitat shift—i.e. relative habitat domains of predator and prey, and the hunting mode of the top predator. These results underline the fact that not only should we continue to incorporate non-consumptive effects into our understanding of top-down predator impacts, but we should do so in a spatially explicit manner.

**Keywords:** non-consumptive; grazing; salt marsh

## 1. INTRODUCTION

Trophic cascades occur when predators suppress the densities or activities of their prey and thereby indirectly influence the success of lower trophic levels. Where plants are the basal species in trophic cascades with three feeding levels, top predators often strongly affect ecosystem functioning by exerting indirect control over their production [1]. Classical theory [2] holds that trophic cascades are mediated exclusively through consumptive effects of predators

on herbivore population density. However, more recent work (reviewed by Werner & Peacor [3]) has highlighted the fact that trophic cascades can also be governed by non-consumptive effects of predators on their prey's traits (e.g. feeding rates). Theory states these trait changes are driven by a foraging–predation risk trade-off, in which herbivores exhibit risk-reducing traits at a cost of compromised rates and/or patterns of foraging [4]. Consistent with this trade-off, numerous studies have shown that the 'fear' of predation reduces *per capita* impacts of herbivores on plants, producing a positive trait-mediated indirect interaction (TMII), and therefore reinforces consumptive predation in the indirect facilitation of plants in tri-trophic systems (reviewed by Schmitz *et al.* [5]).

Spatial refuge-seeking behaviour of grazers can, however, actually generate the opposite effect and increase their impacts on plant resources in refuges [6], complicating predictions of the strength and even sign of the TMII on overall health and productivity of plants. Indeed, TMII may well become negative, as opposed to the predicted positive values, if basal species in the refuge habitat make a dominant contribution to primary productivity [6]. Negative TMII challenge the classical three-level trophic cascade paradigm and potentially fundamentally shift the perceived roles of top predators in those ecosystems in which they occur, but they have rarely been documented (see [5] and references therein) and have not been known to occur in natural marine ecosystems.

We report here on field observations and experimentation that revealed a negative TMII between top predators and the dominant vascular plants in southeastern US salt marshes. In the high reaches of these intertidal ecosystems, extensive monocultures of *Spartina alterniflora* are grazed by the abundant marsh periwinkle (*Littoraria irrorata*). This grazer has a broad vertical habitat domain—it can be found from the marsh surface, where it feeds on microscopic algae, to the top of the *Spartina* canopy. In the marsh canopy it inflicts longitudinal wounds on green leaves that, together with ensuing fungal infection, suppress *Spartina* productivity [7] and can even contribute to extensive community die-off [8]. *Littoraria* are consumed by sit-and-wait predatory crabs (*Panopeus obesus* and *Eurytium limosum*) that reside in burrows in the marsh substrate [9,10]. This generates a classical three-level food chain, with this system's potent grazer, *Littoraria*, forming the link between top predators and the single dominant plant, *Spartina*.

Preliminary field observations indicated that climbing height of snails on *Spartina* plants is positively influenced by infaunal predator concentrations. We found that snails climbed approximately 50 per cent higher in the local presence of predators (electronic supplementary material, 1), suggesting that predators non-consumptively induce a functionally significant microhabitat shift in *Littoraria* as it moves from lower stem heights and the marsh surface, to the elevated yet vulnerable canopy leaves of *Spartina*, ostensibly in a bid to reduce risk from substrate-dwelling predators. We therefore hypothesized that, contrary to the traditional conceptualization of top-predator effects in a three-level food chain, the non-consumptive effects of predators in this system could increase *per capita*

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2011.0166> or via <http://rsbl.royalsocietypublishing.org>.

impacts of grazers on plants; i.e. predators induce a negative TMII.

## 2. MATERIAL AND METHODS

We conducted this study in the intermediate intertidal zone of a salt marsh on Sapelo Island, GA, USA (31°23' N, 81°16' W). To test the hypothesis that non-consumptive predator effects result in reduced *Spartina* height and productivity, we manipulated the presence/absence of predatory crabs in a field experiment over two months in summer 2010 (June–August), using 70 × 70 × 100 cm galvanized wire mesh field enclosures (electronic supplementary material, 2) as experimental units.

### (a) Experimental set-up

We selected a naturally predator-free area of marsh, allowing us to spatially isolate the presence of predators (and their cues). We thus established a predator addition treatment ( $n = 8$ ), adding eight individuals (a naturally occurring density [9]) that included a range of body sizes of the two species of predatory mud crab found in this system. Prior to addition, we secured crab claws with non-toxic super glue, preventing prey killing and thus strictly isolating non-consumptive effects [11]. All predators were replaced every 10 days to ensure that they did not die of starvation. For direct comparison, we also established control enclosures ( $n = 8$ ) to which no predators were added, but were otherwise treated identically. Replicates of the treatments (predator addition, control) were randomly assigned to field enclosures separated by 3 m (greater than the predator cue travel distance of <1 m, as indicated by preliminary field trials). All field enclosures were stocked with 300 *Littoraria*, a naturally occurring high density [8].

### (b) Measurement of response variables

#### (i) Grazer habitat use

In each replicate, we estimated the heights of all *Littoraria* on 10 randomly selected plants (using 70 cm vertical measuring poles placed in the centre of all plots as a guide) during tidal emersion at both day and night ( $n = 3$  for both; sampling dates predetermined, i.e. not selected on the basis of observed snail behaviour). Night versus day did not influence the non-consumptive effect; thus data were pooled for final analysis. We also made observations of climbing height during high tide (approx. 10 cm depth) on a single daytime occasion when conditions allowed (replication was not possible owing to the specific tidal and water visibility conditions required). Finally, to estimate benthic habitat use by *Littoraria*, we noted the total number foot-down on the benthos (replicated as described for snail heights).

#### (ii) Leaf damage and plant biomass

As an indication of direct snail impact on *Spartina* leaves, we measured longitudinal grazing scars (radulations—*sensu* [7]) on all leaves of each of 10 randomly chosen plants in each replicate. We performed this after one month, before extensive grazer damage precluded the identification and measurement of individual radulations. Plants were harvested upon experiment termination, oven-dried and weighed [7].

### (c) Statistical analysis

We compared the means of response variables in predator additions with controls by using *t*-tests, except for the use of snail benthos that required a generalized linear model ( $\gamma$  distribution). All analyses were one-tailed, following our mechanistic directional hypothesis.

## 3. RESULTS

Predators induced striking non-consumptive effects on grazer habitat use. Presence of predators more than doubled the mean snail height observed during tidal emersion in comparison with controls (figure 1a,  $t = 14.29$ ,  $p < 0.001$ ). This vertical shift in grazer habitat domain was also evident at high tide, when snails were driven higher than controls and above water level with the presence of predators (electronic supplementary material, 3;  $t = 3.08$ ,  $p = 0.005$ ). Predators also non-consumptively reduced snail abundance on the benthos observed during low tide (figure 1b;  $\chi^2 = 10.21$ ,  $p < 0.001$ ).

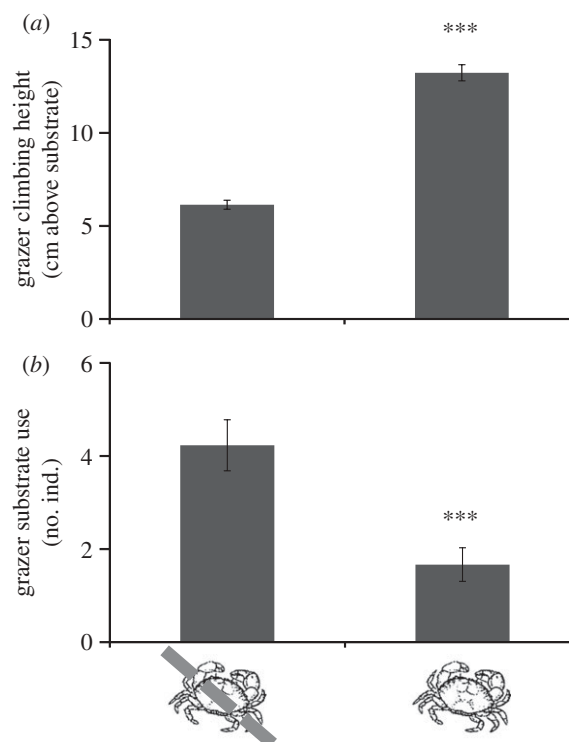


Figure 1. Non-consumptive effects of predatory crabs on (a) mean grazer climbing height at low tide and (b) mean number of snails on the marsh substrate. Crab with line denotes control treatment; crab with no line denotes non-consumptive predator treatment. Error bars show  $\pm 1$  s.e. \*\*\* $p < 0.001$ .

Consistent with our hypothesis, the non-consumptive effect increased destructive snail foraging on *Spartina* leaves relative to controls, as the grazing intensity per leaf (radulations) increased by 38 per cent (figure 2a;  $t = 3.06$ ,  $p = 0.004$ ). This intensified grazing suppressed the overall biomass of *Spartina* (figure 2b;  $t = -0.83$ ,  $p = 0.046$ ), thereby generating a negative TMII between top-predators and basal plants.

## 4. DISCUSSION

Current empirical evidence overwhelmingly supports the theory that foraging–risk trade-offs should result in predator presence weakening *per capita* impacts of grazers on plants in three-level food chains (reviewed by Schmitz *et al.* [5]). On the contrary, our field observations and subsequent experimentation in a salt marsh revealed that the non-consumptive effects of top predators can act to strengthen the *per capita* impacts of grazing snails on *Spartina*—the vascular plant that forms vast monocultures in this highly productive and valuable intertidal ecosystem.

Our results indicate that the negative effect of top predators on *Spartina* was driven by the vertical habitat shift undertaken by *Littoraria* (figure 1), which in turn increased the *per capita* impacts of this grazer on leaves and overall plant biomass (figure 2). The predator-induced habitat shift of *Littoraria* probably reflects a trade-off between the multiple benefits of remaining close to the substrate (e.g. minimal investment in climbing activity, reduced risk from avian predators

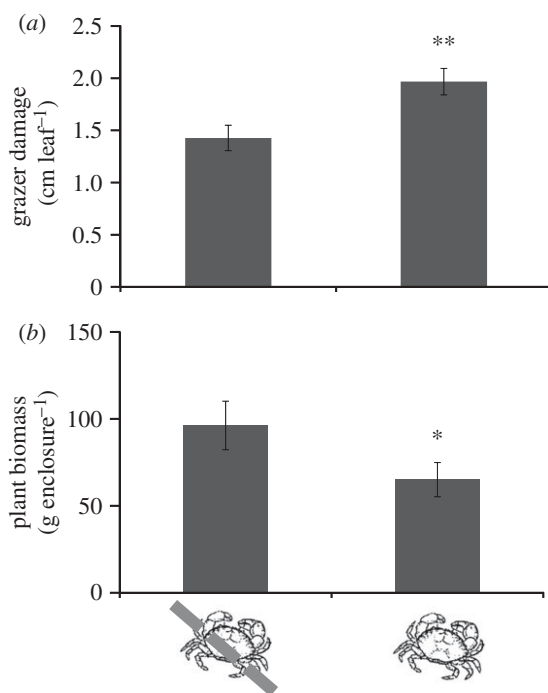


Figure 2. Trait-mediated indirect effects of predators on (a) grazer-inflicted leaf damage and (b) plant biomass. Treatments and error bars as in figure 1. \* $p < 0.05$ ; \*\* $p < 0.01$ .

and proximity to energy-rich substrate microalgae) and the risk of predation from substrate-dwelling predators. The vertical habitat shift of *Littoraria* can be further explained in terms of both predator foraging mode, and predator and prey habitat domains [5]. Firstly, the sit-and-wait predatory crabs provide spatially consistent point source cues, and are thus potentially effectively avoided by prey. Secondly, the broad vertical habitat domain of *Littoraria* relative to its predators allowed it to respond to these spatially consistent cues, reducing predation risk with a chronic shift in foraging activity from the risky benthos and lower *Spartina* stems, to the canopy of *Spartina* plants, beyond the reach of ground-dwelling predatory crabs. Thus, the perpendicular orientation of risk (horizontal, across the substrate) and refuge (vertical, away from the substrate) habitats predictably drove grazers vertically (figure 1), to the vulnerable and important canopy leaves of *Spartina*, and consequently strengthened the negative *per capita* grazer–plant interactions (figure 2).

Although this study is the first experimental demonstration of a negative TMII generated by contrasting predator (horizontal) and prey (vertical) habitat domains, we predict that similar, but yet undetected, effects may occur in many other systems because of how common this perpendicular movement contrast is in nature. For example, across temperate and tropical forests and in savannahs with dotted tree cover, facultatively leaf-eating prey (e.g. baboons, other monkeys, small mammals) often find refuge from ground-dwelling predators (lions, hyenas, canines) by climbing up trees [1]. Similarly, in mangroves and kelp beds around the world, snails are thought to maintain high climbing heights in the canopies of dominant plants to

reduce predation by substrate-bound carnivores (e.g. crabs, lobsters [12,13]).

By experimentally preventing prey capture, we revealed a negative TMII between predators and plants in our study system. Under natural field conditions however, these predators also consume *Littoraria*, and many exert substantial control on their densities [9,10]. This system thus probably exhibits opposing trait-mediated (negative) and density-mediated (positive) indirect interactions between top predators and plants, with the net effect of predators being determined by the relative strengths of these indirect interactions. Notably, while we focus here on the negative TMII between predators and the biomass of the single habitat-forming vascular plant species in this system (*Spartina*), future studies must additionally quantify the potentially positive effect of *Littoraria*'s habitat shift on substrate microalgae to ascertain the sign of the TMII on the overall community primary production.

Despite the bewildering complexity of species interactions, non-consumptive effects of top predators on herbivores may be explained (and ultimately predicted) in terms of simple, universal traits—hunting mode of the top predators and the relative orientation of the habitat domains of both top predator and herbivores (this study [5]). This information, combined with explicit consideration of the functional importance of resources in refuge habitats, probably explains our findings and provides a powerful tool to predict the direction of trait-mediated indirect effects of predators in other important ecosystems dominated by three-dimensional, canopy-generating plants.

This study was funded by grant no. 1030822 from NSF BIO-OCE to B.R.S.

- 1 Terborgh, J. & Estes, J. A. 2010 *Trophic cascades: predators, prey and the changing dynamics of nature*. Washington, DC: Island Press.
- 2 Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960 Community structure, population control and competition. *Am. Nat.* **94**, 421–425. (doi:10.1086/282146)
- 3 Werner, E. E. & Peacor, S. D. 2003 A review of trait-mediated indirect interactions. *Ecology* **84**, 1083–1100. (doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2)
- 4 Abrams, P. A. 1984 Foraging time optimization and interactions in food webs. *Am. Nat.* **124**, 80–96. (doi:10.1086/284253)
- 5 Schmitz, O. J., Krivan, V. & Ovadia, O. 2004 Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* **7**, 153–163. (doi:10.1111/j.1461-0248.2003.00560.x)
- 6 Schmitz, O. J. 2008 Effects of predator hunting mode on grassland ecosystem function. *Science* **319**, 952–954. (doi:10.1126/science.1152355)
- 7 Silliman, B. R. & Zieman, J. C. 2001 Top-down control of *Spartina alterniflora* growth by periwinkle grazing in a Virginia salt marsh. *Ecology* **82**, 2830–2845.
- 8 Silliman, B. R., Van de Koppel, J., Bertness, M. D., Stanton, L. & Mendelsohn, I. 2005 Drought, snails, and large-scale die-off of southern US salt marshes. *Science* **310**, 1803–1806. (doi:10.1126/science.1118229)
- 9 Silliman, B. R., Layman, C. A., Geyer, K. & Zieman, J. C. 2004 Predation by the black-clawed mud crab,

- Panopeus herbstii*, in mid-Atlantic salt marshes: further evidence for top-down control of community structure. *Estuaries* **27**, 188–196. (doi:10.1007/BF02803375)
- 10 Griffin, J. N. & Silliman, B. R. 2011 Predator diversity stabilizes and strengthens trophic control of a keystone grazer. *Biol. Lett.* **7**, 79–82. (doi:10.1098/rsbl.2010.0626)
  - 11 Trussell, G. C., Ewanchuk, P. J., Bertness, M. D. & Silliman, B. R. 2004 Trophic cascades in rocky shore tide pools: distinguishing lethal and nonlethal effects. *Oecologia* **139**, 427–432. (doi:10.1007/s00442-004-1512-8)
  - 12 Byrnes, J. E., Stachowicz, J. J., Hultgren, K. M., Hughes, A. R., Olyarnik, S. V. & Thornber, C. 2006 Predator diversity enhances trophic cascades in kelp forests by modifying herbivore behavior. *Ecol. Lett.* **9**, 61–71. (doi:10.1111/j.1461-0248.2005.00842.x)
  - 13 McGuinness, K. A. 2006 The climbing behaviour of *Cerithidea anticipata* (Mollusca: Gastropoda): the roles of physical and biological factors. *Aust. J. Ecol.* **91**, 283–289.