

Determining the amount of DD ingested by copepods

Samples of 40 ml of PRO (8.0×10^4 cells per ml) were incubated in sea water with $1.5 \mu\text{g ml}^{-1}$ of DD. After different incubation times, the cells were filtered onto GF/C filter (21 mm, Whatman) under reduced pressure until dry. The filter was rinsed with 1 ml 25 mM pentafluorobenzylhydroxylamine in 100 mM Tris-HCl, pH 7.0. After addition of benzaldehyde (5 μl of a 1 mM solution in methanol) as an internal standard, the cell suspension was sonicated in an ice bath with pulses of a B. Braun 10001 Sonicator for 1 min. Afterwards, the sample was incubated at room temperature for 30 min. Extraction was performed with hexane³¹. Each treatment was replicated three times. Triplicate controls, consisting of sea water and DD without PRO, were conducted to determine the filter adsorption of DD. Detection was performed with gas chromatography/mass spectrometry (GC/MS) (GC Q; equipped with a 30 m RTX-200 column, 0.25 mm internal diameter, 0.25 μm film thickness). The analyses were performed by negative ion chemical ionization electron-capture mass spectrometry with methane as the reagent gas. For quantification of DD, the ion at m/z 327 $[\text{M}-\text{HF}]^-$ was chosen. A calibration curve shows linearity ($r^2 > 0.98$) in the measurement range (see Supplementary Information 2).

Assessment of Apoptosis

Egg hatching success and number of teratogenic nauplii were also monitored daily with the two diets. Procedures to determine egg-hatching success are described elsewhere²⁴. Apoptosis in teratogenic nauplii was verified using TdT-mediated dUTP nick end labelling (TUNEL) (Roche Diagnostics). *C. helgolandicus* nauplii were fixed overnight in 4% paraformaldehyde and 0.2 M NaCl in PBS, pH 7.4, rinsed in PBS, and frozen in liquid nitrogen to fracture the carapace. Samples were incubated for 24 h in 1 unit ml^{-1} chitinase enzyme (Sigma) at 25 °C, and rendered permeable according to the TUNEL manufacturer's instructions. They were then incubated for 90 min at 37 °C in TUNEL reaction mix and for 30 min in 0.5 $\mu\text{g ml}^{-1}$ propidium iodide at room temperature. Nauplii were observed with a confocal laser-scanning microscope, Zeiss LSM-410, in which TUNEL-positive areas appear yellow because of the superimposition of the green fluorescence of TUNEL and the red fluorescence of propidium iodide. Complementary tests with a mammalian cell line (A1 mes c-myc cells), generated from mouse mesencephalon primary cultures, suggest that DD is potentially a neutral compound for somatic but not for embryonic development, affecting undifferentiated proliferating rather than differentiated non-proliferating cells (see Supplementary Information 3).

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Predator diversity dampens trophic cascades

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Food web complexity is thought to weaken the strength of terrestrial trophic cascades^{1–3} in which strong impacts of natural enemies on herbivores cascade to influence primary production indirectly⁴. Predator diversity can enhance food web complexity because predators may feed on each other and on shared prey^{5–7}. In such cases, theory suggests that the impact of predation on herbivores relaxes and cascading effects on basal resources are dampened^{8,9}. Despite this view, no empirical studies have explicitly investigated the role of predator diversity in mediating primary productivity in a natural terrestrial system^{10,11}. Here we compare, in a coastal marsh community, impacts of arthropod predators on herbivores and plant productivity between a simple food web with a single predator species and a complex food web with a diverse predator assemblage. We show that enhancing predator diversity dampens enemy effects on herbivores and weakens trophic cascades. Consequently, changes in diversity at higher trophic levels can significantly alter ecosystem function in natural systems.

Studies investigating the impact of biodiversity on ecosystem functions such as primary production have become widespread as a result of concern over the rapid rate of species extinctions^{10,12,13}. However, many studies in this area have focused specifically on the role of producer diversity, whereas the consequences of biodiversity loss at higher trophic levels have been often ignored^{11,13,14}, despite evidence that top trophic levels can be more susceptible to extinction than their basal resources^{11,15,16}. Studies that do incorporate trophic interactions into investigations of the link between biodiversity and ecosystem function have manipulated only the diversity of herbivores or filter-feeders^{17–19}, the diversity of consumers at several trophic levels simultaneously^{12,20,21}, or the overall presence or absence of predators^{2,22–24}. Few studies have independently manipulated predator diversity^{25,26} and none have done so in a natural terrestrial community. This study specifically examines the

importance of predator diversity for maintaining ecosystem function, and it does so in a native terrestrial salt marsh community that is vulnerable to human impacts.

We investigated the consequences of the loss of predator diversity for the occurrence of trophic cascades and its impact on primary productivity by using a natural assemblage of arthropods inhabiting the *Spartina* cordgrass-dominated salt marshes along the Atlantic coast of North America. Phloem-feeding *Prokelisia* planthoppers, the most abundant herbivores on the marsh, are consumed by a diversity of invertebrate predators including the hunting spiders *Pardosa littoralis* and *Hogna modesta*, the web-building spider *Grammonota trivitatta* and the mirid bug *Tytthus vagus*^{27–29} (Fig. 1). Because *Grammonota*, *Tytthus* and *Pardosa* are susceptible to intra-guild predation^{27–29}—in which predators at the same trophic level feed on each other—the opportunity exists for antagonistic interactions among predators with cascading consequences for primary production.

In the context of this coastal marsh community, we constructed replicated food webs with various levels of predator species diversity (0, 1 or multiple predators) and measured the resulting impacts on herbivore population size and primary production. This study was conducted concurrently in the controlled setting of greenhouse mesocosms and under real-world conditions with the use of field enclosures at a marsh in Ocean County, New Jersey, USA. The species richness component of predator diversity was manipulated to create four food-web complexity treatments: (1) *Spartina* plants only, (2) *Spartina* plants and *Prokelisia* herbivores with no predators present, (3) *Spartina* plants, *Prokelisia* herbivores and a low-predator-diversity treatment (*Tytthus* only), and (4) *Spartina* plants, *Prokelisia* herbivores and a high-diversity predator assemblage (*Tytthus*, *Grammonota* and *Pardosa* in both mesocosms and field enclosures, and also with *Hogna* in mesocosms only). We manipulated predator diversity by using an additive treatment design to hold intraspecific interactions among *Tytthus* constant across levels of diversity³⁰ and to provide densities of predators that were equivalent to those found in the field (*Tytthus* 250 m⁻², *Grammonota* 250 m⁻², *Pardosa* 125 m⁻² and *Hogna* 25 m⁻²). Because we did not include treatments containing each predator individually, this treatment design does not allow a test of the null hypothesis of additive predator effects. However, *Tytthus*, *Grammonota*, *Pardosa* and *Hogna* are known to reduce planthopper population sizes independently in comparison with no-predator

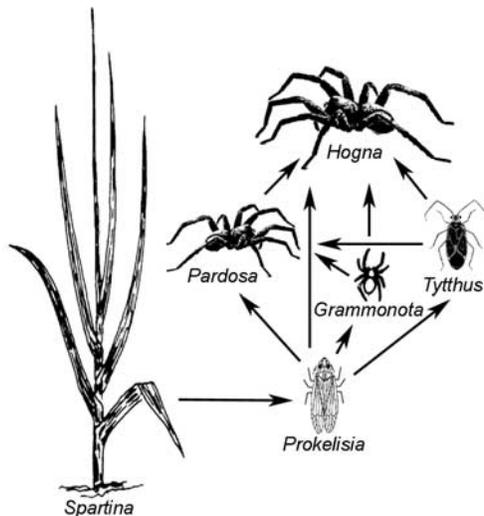


Figure 1 Component of salt marsh food web used in experimental design^{27–29}. Arrows indicate the flow of energy from the source to the consumer.

controls^{27–29}. Therefore, although no conclusions can be made about the nature of predator interactions if planthopper populations decrease when predator diversity is high, an increase in planthopper populations in the presence of the predator complex would indicate unequivocally that antagonistic interactions among predators occur. To determine the influence of these predator diversity treatments on the strength of top-down effects, planthopper population density and plant productivity were assessed at the end of the study. Aboveground biomass and the number of tillers produced (an indirect measure of biomass in the following year) were determined as a proxy for primary productivity. Results are the consequences of longer-term food-web dynamics because the experiment spanned more than two herbivore generations from July to October 2002.

In greenhouse mesocosms, a trophic cascade occurred in the simple-structured food web with low predator diversity. This trophic cascade was diminished in the complex food web with a diverse predator assemblage. Planthopper density in the presence of the single predator was markedly reduced in comparison with the density of planthoppers when no predators were present ($F_{3,27} = 25.67$, $P < 0.0001$; $t = 6.27$, $P < 0.0001$; Fig. 2a). However, when predator diversity was high, planthopper density was

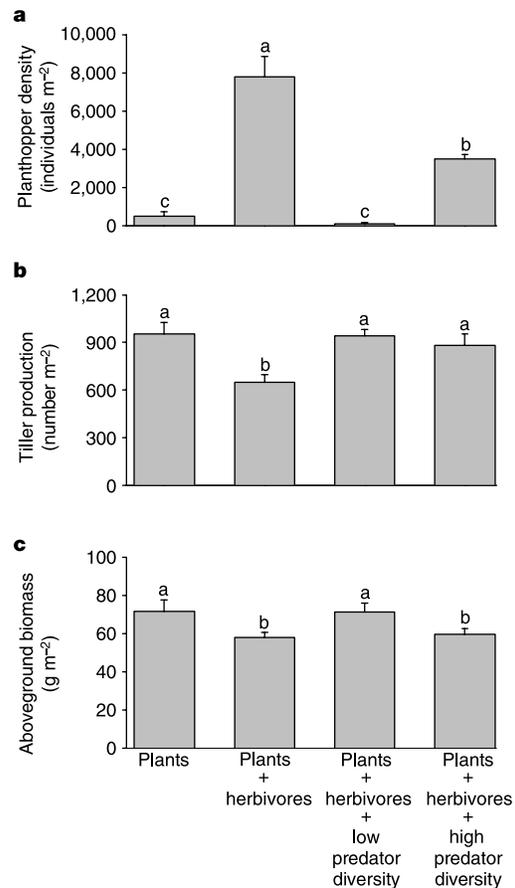


Figure 2 Effect of predator diversity on the occurrence of trophic cascades in greenhouse mesocosms. Means \pm s.e.m. with different letters are significantly different ($P < 0.05$). **a**, Herbivore (*Prokelisia* planthopper) population size. Low predator diversity markedly reduces planthopper population size ($t = 6.27$, $P < 0.01$), but planthopper suppression is diminished when diversity is high ($t = 5.34$, $P < 0.01$). **b**, Number of tillers produced by *Spartina* cordgrass. In the absence of predators, planthoppers reduce the number of tillers ($t = 3.67$, $P < 0.01$). **c**, Aboveground biomass of *Spartina*. Low predator diversity enhances biomass relative to the high-predator-diversity treatment ($t = 2.44$, $P < 0.05$).

intermediate and greater than when predator diversity was low ($t = 5.34, P < 0.0001$; Fig. 2a). Predator effects on herbivore populations cascaded down to affect primary productivity, both tiller production ($F_{3,27} = 5.83, P < 0.01$; Fig. 2b) and aboveground live biomass ($F_{3,27} = 4.83, P < 0.01$; Fig. 2c). In the simple food web with a single predator species, the marked reduction in planthopper population size resulted in a trophic cascade, increasing both the number of tillers ($t = 3.52, P < 0.01$; Fig. 2b) and the aboveground biomass ($t = 2.83, P < 0.05$, Fig. 2c) in comparison with the predator-free herbivore treatment. In the high-predator-diversity treatment, the intermediate level of planthopper suppression was still sufficient to cascade down and increase the number of tillers ($t = 2.80, P < 0.05$; Fig. 2b) in comparison with the predator-free herbivore treatment. However, the intermediate control of the planthopper population by the predator complex did not cascade to affect aboveground biomass positively. Plant biomass in the complex food web with a diverse predator community was not different from that in the predator-free herbivore treatment ($t = 0.39, P > 0.05$; Fig. 2c). Thus, predator diversity precluded a trophic cascade on *Spartina* biomass because of the occurrence of intra-guild predation when predator diversity was high. Specifically, the population size of the *Tytthus* mirid predator was much lower in the presence of other predators in the high-diversity treatment than

when alone in the low-predator-diversity treatment ($t = 4.07, P < 0.01$). This decline in density is attributed to intra-guild predation because spiders left small pellets of exsanguinated mirid exoskeletons after feeding²⁸. Therefore, when predator diversity was high, the occurrence of intra-guild predation resulted in an attenuation of enemy impacts on herbivores and dampened the strength of the trophic cascade on *Spartina* biomass.

Results of the field experiment were consistent with those from mesocosms. In the simple food web, predation by the single predator resulted in a trophic cascade. Planthopper density was reduced by *Tytthus* predation ($F_{3,15} = 3.85, P < 0.05$; $t = 2.34, P < 0.05$; Fig. 3a), which increased the number of *Spartina* tillers ($F_{3,15} = 5.45, P < 0.01$; $t = 2.75, P < 0.05$; Fig. 3b) in comparison with the predator-free herbivore treatment. Treatment effects on aboveground biomass were not significant ($t = 1.10, P > 0.05$; Fig. 3c). In the complex food web with high predator diversity, the trophic cascade was dampened. There was no difference in planthopper densities when all predators were present and when no predators were present ($t = 0.29, P > 0.05$; Fig. 3a) and the density of tillers was also not different ($t = 0.92, P > 0.05$; Fig. 3b). Again, the dampening of the trophic cascade in the complex food web was due to the occurrence of intra-guild predation because the density of *Tytthus* was significantly reduced in the presence of other predators ($t = 2.92, P < 0.01$). However, it is important to note that the strength of the cascade was weaker in the field than in mesocosms. This is probably the result of contamination of the field treatments by planthoppers (Fig. 3a) because of the latter's small size (3 mm) and high ambient density (about 11,000 individuals per m² during this study). This study therefore underscores the view that it might be more difficult to demonstrate trophic cascades in open systems than in closed systems.

Our results show that increasing the diversity of arthropod predators promotes intra-guild interactions among predators, diminishes enemy impacts on herbivores, and dampens cascading effects on basal resources. Therefore, given the widespread occurrence of intra-guild predators in natural systems⁶, a decline in predator species diversity might positively affect ecosystem function. A management conflict therefore arises because maximizing productivity, rather than preserving diversity, might be beneficial in certain contexts²⁴. For example, in agricultural systems the goal of biological-control programmes is to initiate trophic cascades by manipulating predator complexes to enhance crop yield, a circumstance that can arise when predator diversity is low or when antagonistic interactions among predators are minimal. By specifically examining the role of predator diversity, our study highlights how conservation biologists, whose goal is to maintain diversity, and biological-control practitioners, who seek to maximize productivity, can reach ultimately conflicting conclusions about the importance of biodiversity as it relates to ecosystem function. □

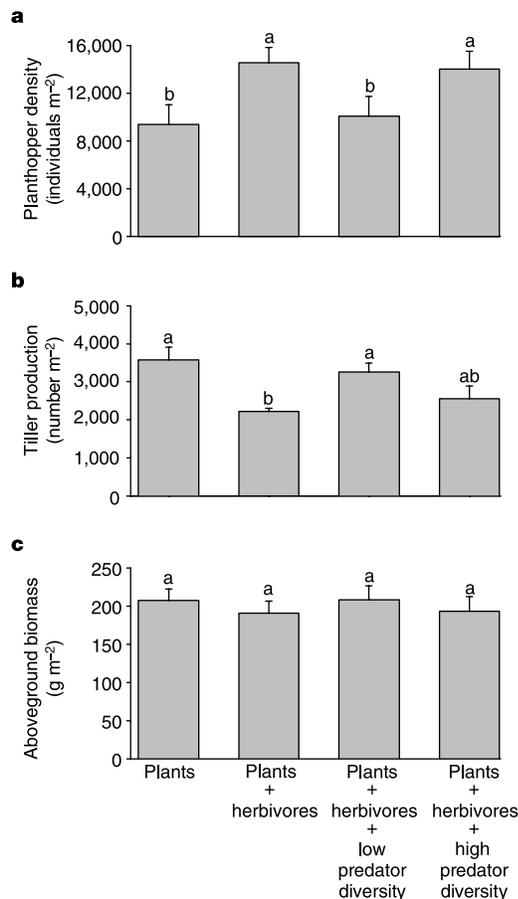


Figure 3 Effect of predator diversity on the occurrence of trophic cascades in field enclosures. Means \pm s.e.m. with different letters are significantly different ($P < 0.05$). **a**, Herbivore (*Prokelisia* planthopper) population size. High predator diversity results in a population size no different from that when predators are absent ($t = 0.29, P > 0.05$). **b**, Number of tillers produced by *Spartina*. Low predator diversity enhances tiller number in comparison with the absence of predators ($t = 2.75, P < 0.05$). There is no difference in tiller production when predator diversity is high and when predators are absent ($t = 0.92, P > 0.05$). **c**, Aboveground biomass of *Spartina*. Predator diversity treatments did not impact biomass ($F = 0.72, P > 0.05$).

Methods

Greenhouse mesocosms

Greenhouse mesocosms consisted of ten field-collected *Spartina* culms transplanted into sand-filled pots (30 cm diameter, 0.04 m²) and caged within a clear plastic cylinder (cellulose butyrate, 22 cm in diameter and 30 cm in height) sunk into the sand. Each mesocosm was covered by a screened lid (0.6 mm mesh, 85% light transmission). Forty mesocosms were placed into ten separate watering pools in groups of four (one replication of each treatment per pool) for a total of ten replications.

Field enclosures

Field enclosures were established in a *Spartina* meadow on an intertidal salt marsh in the Great Bay–Mullica River estuarine system in Tuckerton, Ocean County, New Jersey, USA. Circular enclosures (1.6 m² in area and 40 cm high) were constructed of PVC plastic sheeting covered with a screened lid (0.6 mm mesh, 85% light transmission) and sunk 10 cm into the marsh surface. To control for differences in elevation and grass height, the 24 enclosures were blocked in groups of four for a total of six replications.

Arthropod population density

Herbivore and predator densities were measured once at the end of each experiment. Densities within greenhouse mesocosms were determined by visually counting all

herbivores and predators. Densities within field enclosures were measured with an insect suction device. One sample consisted of eight 10-s placements of the sampling head on the marsh surface such that 0.8 m² of *Spartina* was subjected to suction.

Plant productivity

Two measures of plant productivity, aboveground biomass and the number of tillers produced (vegetative reproduction), were measured once at the end of the study. Aboveground biomass was determined for mesocosms by harvesting all live aboveground vegetation and for field enclosures by sampling all live aboveground biomass within a 0.047 m² wire frame. Vegetation was dried in an oven for 3 days at 55 °C and then weighed. The number of tillers produced was determined visually by counting all tillers in mesocosms and counting all tillers within the 0.047 m² sampling quadrat for the field enclosures.

Statistical analyses

The effects of the food web complexity treatments on final planthopper population size, the number of *Spartina* tillers and the aboveground biomass of *Spartina* were each analysed independently with mixed-model analyses of variance in which a block was modelled as a random source of variation. Subsequently, pairwise comparisons of treatment means were performed by using a *t*-test with a Bonferroni correction for multiple comparisons. Data were log-transformed when necessary to meet assumptions of normality and homogeneity of variances.

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Object-based attention determines dominance in binocular rivalry

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A question of long-standing interest to philosophers, psychologists and neuroscientists is how the brain selects which signals enter consciousness^{1,2}. Binocular rivalry and attention both involve selection of visual stimuli, but affect perception quite differently. During binocular rivalry, awareness alternates between two different stimuli presented to the two eyes. In contrast, attending to one of two different stimuli impairs discrimination of the ignored stimulus, but without causing it to disappear from consciousness. Here we show that despite this difference, attention and rivalry rely on shared object-based selection mechanisms. We cued attention to one of two superimposed transparent surfaces and then deleted the image of one surface from each eye, resulting in rivalry. Observers usually reported seeing only the cued surface. They were also less accurate in judging unpredictable changes in the features of the uncued surface. Our design ensured that selection of the cued surface could not have resulted from spatial, ocular or feature-based mechanisms. Rather, attention was drawn to one surface, and this caused the other surface to be perceptually suppressed during rivalry. These results raise the question of how object representations compete during these two forms of perceptual selection, even as the features of those objects change unpredictably over time.

The relationship between attention and rivalry has been debated from the late nineteenth century^{1,2} to the present^{3,4}. The question of what is selected in attention and rivalry has also been disputed. It is well established that spatial locations can be selectively attended^{5,6}, but it is now recognized that objects can be selected as well^{7,8}. For rivalry, the debate has been whether competition is stimulus-based, eye-based or some combination of the two⁹. Using the paradigm illustrated in Fig. 1, we asked whether selection of an object by attention causes that object to be dominant during rivalry. Observers viewed two superimposed patterns of dots presented to both eyes at the start of each trial. The patterns rotated rigidly in opposite directions around a fixation point, yielding a percept of two superimposed transparent surfaces. After a period of dual rotation, one surface was briefly translated in one of eight directions, and the observer reported the perceived direction. Such brief translations are known to cue attention to the translated surface^{10–13}. Hence, we refer to the translated surface as the ‘cued surface’.

After translation, the image of the cued surface was removed from one eye and the image of the uncued surface was removed from the other eye (see Methods). Because the surfaces differed in rotation direction, this dichoptic presentation produced rivalry. To determine whether rivalry favoured the cued surface, we asked observers to report whether one surface was clearly dominant at the end of