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IN FOCUS

Disentangling multiple predator effects in biodiversity and ecosystem functioning research

A diver observes a school of small predators interacting on fringing reefs off the west coast of Barbados. The heterogeneous reef habitat enables spatial separation of different predator species. Here, juvenile and sub-adult french (diagonal stripes) and smallmouth (horizontal stripes) grunts (*Haemulon flavolineatum* and *Haemulon chrysargyreum*) swim in open water habitat, while glassy sweepers (*Pempheris schomburgki*) use caves. Interactions among multiple predator species affect their impact on ecosystem processes and services. To gain a better understanding of these effects in marine ecosystems, the spatial extent of biodiversity and ecosystem functioning experiments will have to increase to accommodate the larger foraging spectrum of most predators.
Photo credit: K. Turgeon.

M. O'Connor & J. Bruno (2009) Predator richness has no effect in a diverse marine food web. *Journal of Animal Ecology*, **78**, 732–740.

Disentangling the effects of predator loss can be complex as predators exert a suite of direct and indirect effects in ecosystems. O'Connor & Bruno manipulated predator abundance, richness, and composition in experiments with and without prey dispersal in an estuarine ecosystem. They observed effects of predator presence and composition on prey assemblages, particularly in experiments without prey dispersal, but they found no effect of predator richness on prey assemblage. Here, we discuss the role of non-additive, antagonistic, and spatial effects of predators in biodiversity and ecosystem functioning experiments, with a particular focus on the results of O'Connor & Bruno.

Predators are disproportionately threatened by human activities relative to other trophic groups (Pauly *et al.* 1998; Duffy 2003) and predator extinctions can have cascading effects in ecosystems (e.g. Terborgh *et al.* 2001; Duffy 2003). The strength of these effects varies among ecosystems (Shurin *et al.* 2002) and depends on the assemblage of predators present (Bruno & Cardinale 2008). Given current rates of biodiversity loss, there is a sense of urgency to develop a better understanding of the functional consequences of biodiversity loss in different ecosystems. Most biodiversity and ecosystem functioning studies, however, focus on sessile organisms because mobile organisms, like predators, are much more difficult to control, like herbaceaus plants (Duffy *et al.* 2007). Studies that investigate the effects of predators in ecosystems

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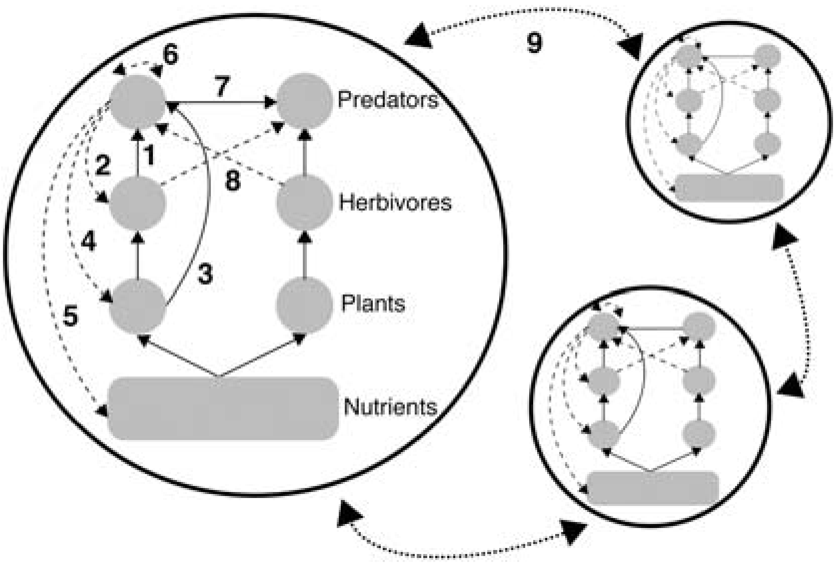

Fig. 1. Conceptual diagram of the multiple effects of predators in ecosystems. Consumptive effects are represented with solid lines, nonconsumptive effects are represented with dashed lines, and spatial effects are represented with dotted lines. 1, Direct consumption; 2, trait-mediated, nonlethal interactions; 3, omnivory; 4, trophic cascades; 5, nutrient recycling; 6, intraspecific interference; 7, intraguild predation; 8, competition; and 9, spatial subsidies. O'Connor & Bruno (2009) measured direct consumption (1) and partially controlled for intraguild predation (7).

usually focus on the direct effects of a single predator species on prey and the subsequent indirect or cascading effects on producers (Hairston, Smith, & Slobodkin 1960; Oksanen *et al.* 1981; Carpenter, Kitchell, & Hodgson 1985). A growing number of studies are now investigating the effects of predator richness in ecosystems (reviewed in Duffy *et al.* 2007), but these studies are often limited to small spatial scales and few species. Natural ecosystems are complex (Polis & Strong 1996) and presently, we have resolved the complete web of trophic interactions in only a few cases. Consequently, we currently lack a synthetic understanding of the multiple effects of predators in ecosystems (Fig. 1). In this issue of the *Journal of Animal Ecology*, O'Connor & Bruno (2009) designed field and mesocosm experiments to disentangle the effects of predator abundance, diversity, and composition on diverse prey assemblages in a subtidal estuarine food web in Bogue Sound, North Carolina, USA.

O'Connor & Bruno's (2009) study system is ideal for experimental manipulation because it harbours a diverse predator assemblage (10 species) and a high diversity of amphipod, isopod, and gastropod prey species (52), which have rapid demographic responses to changes in predation and habitat quality. O'Connor & Bruno (2009) designed two field experiments where prey species were able to disperse and one mesocosm experiment that was closed to prey dispersal. Their study is one of the few experiments to vary prey dispersal and predator diversity and composition simultaneously, although they did not control prey dispersal. Predator presence reduced prey density by at least half and reduced prey richness by one to six species but both effects depended on the predator species present. Overall, shrimp presence had the strongest effects on prey density and richness. In two of the experiments predator presence also significantly shifted prey composition. For example, in the presence of shrimp the relative abundance of the amphipod, *Elasmopus levis*, more than doubled whereas the relative abundance of the isopod, *Paracerceis caudata*, decreased by threefold. These effects were strongest in the mesocosm experiment, where prey dispersal did not occur. This suggests that prey dispersal may dampen the effects of multiple predators on prey, although these results are confounded by the fact that prey diversity was also lowest in the mesocosm experiment. O'Connor & Bruno (2009) did not find a significant effect of predator richness on prey density, richness, or composition. Here we explore two potential reasons why O'Connor & Bruno (2009) did not observe an effect of predator richness on prey assemblages: (i) non-additive, antagonistic interactions between predators, and (ii) spatial effects.

Sih, Englund, & Wooster (1998) defined three categories of multiple-predator effects: linear (i.e. substitutable and additive), risk enhancing (i.e. synergistic) or risk reducing (i.e. antagonistic). Non-additive, antagonistic interactions between predators are frequent (Finke & Denno 2005; Schmitz 2007; Bruno & Cardinale 2008), and theory demonstrates that these interactions can decrease the per capita capture rates of predator species and dampen the effects of multiple predators on prey assemblages (Ives, Cardinale, & Snyder 2005; Casula, Wilby & Thomas 2006). Interference, intraguild predation, and nonlethal interactions are common non-additive, antagonistic interactions (Schmitz 2007). For example, Finke & Denno (2005) observed that intraguild predation dampened the effects of predators (i.e. spiders, beetles) on herbivores (i.e. planthoppers) and producers (i.e. cordgrass) in a salt-marsh mesocosm study. O'Connor & Bruno (2009) held predator density constant in all their experiments and to limit the effects of intraguild predation, they checked each enclosure at least twice during the experiments and replaced missing predators. They were able to estimate the potential magnitude of density-mediated intraguild predation but they were not able to quantify the trait-mediated, nonlethal effects of intraguild predators in experimental cages. Shrimps were the most common victim of intraguild predation but they also had the strongest, negative effects on prey density relative to other predators in monoculture and they significantly reduced prey richness, evenness, and composition as described above. As a result, intraguild predation on shrimps may have played the same role as an additional trophic level controlling the most efficient consumers in this system, i.e., it generated a negative selection effect that opposed any complementarity effect among predators (Loreau & Hector 2001; Thébault & Loreau 2003). Furthermore, predators can have both density- and trait-mediated effects on prey species (e.g. Schmitz 2003); therefore, we should expect that the presence of an intraguild predator may also have the potential to cause trait-mediated indirect effects on the predators they consume. The presence of nonlethal interactions between predators in the O'Connor & Bruno (2009) experiments, however, may have been limited because prey did not have access to refuge area. Conversely, the potential for intraguild predation to dampen the effects of predator richness on prey assemblages appears to be strong in this ecosystem.

The flow of energy, material, and organisms across ecosystems, most commonly referred to as allochthonous inputs or spatial subsidies, is ubiquitous (Polis, Anderson & Holt 1997; Loreau, Mouquet & Holt 2003). Theory and experiments that incorporate spatial flows can be complex but offer new insights into the relationship between biodiversity and ecosystem functioning. For example, McCann, Rasmussen, & Umbanhowar (2005) provided empirical data and theoretical analysis to demonstrate that mobile predators can couple distinct patches and stabilize complex ecosystems. Similarly, Nakano & Murakami (2001) demonstrated a strong reliance of aquatic (i.e. fish) and terrestrial (i.e. birds) consumers on subsidies during different times of the year. O'Connor & Bruno (2009) found limited differences between the experiments that allowed prey dispersal and the one that did not. In the field experiments, prey were able to disperse to and from the regional species pool; therefore, we would expect dampened effects of caged predators because of quick replacement of lost prey within the inclusion cages.

A thorough understanding of who eats whom, who affects whom in other ways, and the dispersal abilities of different species is critical to predicting the effects of diversity in natural ecosystems, particularly for the top of the food chain where indirect effects are common (Fig. 1). O'Connor & Bruno (2009) is part of a group of biodiversity and ecosystem functioning studies that have manipulated predator diversity. Results from these studies demonstrate that multiple predators may have null, additive, antagonistic, or synergistic effects on prey assemblages (Cardinale *et al.* 2006; Duffy *et al.* 2007; Bruno & Cardinale 2008). The habitat domain of predator and prey (i.e. spatial movement) and hunting mode of the predator interact to shape the outcome of multiple-predator effects in ecosystems (Schmitz 2007). O'Connor & Bruno's (2009) experiments are limited because they artificially reduced the habitat domain of the predators by preventing predator dispersal. Experiments with spatially constrained designs, such as small enclosures, may facilitate antagonistic effects between predators because predators in constrained habitats may hunt each other (Schmitz 2007). Predator dispersal may create spatial heterogeneity in predator–prey dynamics because predators will be able to actively select areas with preferred food and abandon areas with undesirable food (France & Duffy 2006). This will also enable intraguild prey to find spatial refuges. Densities of prey in these refuge areas may decrease as a result of increased predation pressure (e.g. Schmitz 2003). Natural ecosystems are open to spatial flows at all trophic levels, therefore, future experiments should explicitly test for the effects of predator mobility on prey assemblages. To incorporate predator mobility effectively, the spatial extent of biodiversity and ecosystem functioning experiments will likely have to increase to accommodate the larger foraging spectrum of most predators.

Diverse predator assemblages are becoming increasingly rare both on land and at sea. Biodiversity loss at the top of food chains can have strong cascading effects but we still have a rudimentary understanding of these effects in diverse, spatially extended ecosystems. Future studies on the effects of predator diversity in ecosystems should simultaneously consider non-additive and nontrophic interactions and spatial effects of predators in addition to their direct trophic effects through local prey consumption. Schmitz (2007) provides a theoretical framework for incorporating multiple-predator effects in biodiversity and ecosystem functioning experiments. A more thorough understanding of the multiple effects of predator in ecosystems is required to inform conservation and management of biodiversity in our rapidly changing world.

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