

LETTER

Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades

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Abstract

Single trophic-level studies of the relationship between biodiversity and ecosystem functioning highlight the importance of mechanisms such as resource partitioning, facilitation, and sampling effect. In a multi-trophic context, trophic interactions such as intraguild predation may also be an important mediator of this relationship. Using a salt-marsh food web, we investigated the interactive effects of predator species richness (one to three species) and trophic composition (strict predators, intraguild predators, or a mixture of the two) on ecosystem functions such as prey suppression and primary production via trophic cascades. We found that the trophic composition of the predator assemblage determined the impact of increasing predator species richness on the occurrence of trophic cascades. In addition, increasing the proportion of intraguild predator species present diminished herbivore suppression and reduced primary productivity. Therefore, trophic composition of the predator assemblage can play an important role in determining the nature of the relationship between predator diversity and ecosystem function.

Keywords

Biocontrol, biodiversity, food webs, herbivore suppression, indirect interactions, omnivory, predator–predator interactions, predator–prey interactions, salt marsh, trophic dynamics.

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INTRODUCTION

Studies investigating the importance of biodiversity for ecosystem functioning have become widespread because of concern over the currently unprecedented rate of biodiversity loss (Loreau *et al.* 2001). Many studies, in this area, have focused specifically on the role of producer diversity (Tilman *et al.* 2002), whereas the consequences of biodiversity loss at higher trophic levels have been often overlooked (Duffy 2003; but see Naeem & Li 1998; Norberg 2000; Paine 2002; Duffy *et al.* 2003; Hillebrand & Cardinale 2004; Downing 2005). As a result, the commonly implicated mechanisms by which changes in biodiversity can influence ecosystem functioning, such as resource use partitioning, facilitation, and sampling effect, have emerged primarily from single trophic-level investigations of plant assemblages (Tilman *et al.* 1997; Hooper 1998; Fridley 2001). Little is known about the impact of trophic interactions, particularly predator–predator and predator–prey interactions, on the

relationship between biodiversity and ecosystem functioning in natural systems (Morin 1995; Wilby & Thomas 2002; Cardinale *et al.* 2003; Montoya *et al.* 2003; Finke & Denno 2004; Snyder *et al.* 2005). Incorporating such a multi-trophic perspective will necessitate the consideration of additional mechanisms by which changes in biodiversity might influence ecosystem functioning, including the occurrence of intraguild predation (Ives *et al.* 2005).

Impacts of the entire predator trophic level on critical ecosystem functions such as prey suppression and primary production via the occurrence of trophic cascades have been documented. The predator trophic level as a whole is capable of reducing herbivore populations and these top-down effects can propagate through the food web to positively influence primary producers, resulting in a trophic cascade (Carpenter *et al.* 1985; Schmitz *et al.* 2000; Halaj & Wise 2001; Shurin *et al.* 2002). However, diversity within the predator trophic level is likely to have significant consequences for the occurrence of trophic cascades as well,

because individual predator species can vary substantially in their impacts on prey populations (Chalcraft & Resatarits 2003). The importance of diversity within higher trophic levels for prey suppression and trophic cascades has been explored only recently and evidence is emerging that changes in natural enemy diversity can, in fact, influence the functioning of ecosystems (Morin 1995; Cardinale *et al.* 2003; Finke & Denno 2004).

Predator–prey studies of herbivore suppression by multiple predator species suggest that there are a variety of mechanisms by which changes in predator diversity could impact the occurrence of trophic cascades (Sih *et al.* 1998; Snyder *et al.* 2005). Increasing predator diversity could promote trophic cascades if predator species act additively (Snyder & Ives 2003; Straub & Snyder *in press*) or synergistically (Losey & Denno 1998; Cardinale *et al.* 2003), trophic mechanisms that are analogous to resource use partitioning and facilitation among producers (Fridley 2001), or hinder trophic cascades if these species engage in intraguild predation (Polis *et al.* 1989; Rosenheim *et al.* 1993; Finke & Denno 2002, 2003). The exact mechanism that emerges with changes in predator diversity may be mediated by the trophic composition of the predator complex present. For example, increasing the diversity of intraguild predators (predators which consume other predators with which they compete for shared prey resources) may reduce the collective impact of predators on prey and dampen indirect effects on herbivores and plants, whereas strict predators (predators which do not engage in intraguild predation, for example, predators which feed only on herbivores) may be more likely to enhance predator effects on prey suppression as predator diversity is enhanced (Polis *et al.* 1989; Rosenheim 1998).

Intraguild predation is a widespread phenomenon in a variety of ecosystems (Polis *et al.* 1989; Rosenheim 1998; Arim & Marquet 2004) and the potential role of intraguild predation in inhibiting trophic cascades has been documented, both empirically (Finke & Denno 2004) and theoretically (McCann *et al.* 1998; Hart 2002). Despite this fact, the importance of intraguild predation in mediating relationships between biodiversity and ecosystem function has been rarely addressed (but see Ives *et al.* 2005). In a previous study, we showed that increasing predator diversity dampens the occurrence of trophic cascades in a terrestrial salt-marsh system (Finke & Denno 2004). Specifically, the presence of predatory *Tytthus* bugs alone reduced herbivorous planthopper populations and resulted in greater plant biomass and enhanced tiller production, but this strong top-down effect was diminished in the presence of a diverse predator assemblage containing *Tytthus*, the hunting spiders *Pardosa* and *Hogna*, and the web-building spider *Grammonota* (Finke & Denno 2004). The susceptibility of *Tytthus* to intraguild predation from *Pardosa* and *Hogna* was

documented in this study. Therefore, it was concluded that the dampening of top-down effects in the diverse predator treatment arose because of the occurrence of intraguild predation. However, the importance of intraguild predation as the ultimate mechanism by which predator diversity impacted ecosystem function was not tested explicitly because species richness and composition were confounded.

In this study, we test the hypothesis that predator diversity dampens trophic cascades because intraguild predation is more likely to occur in diverse predator assemblages. We tested this hypothesis in mesocosms using the natural assemblage of arthropods inhabiting coastal-salt marshes. We manipulated predator diversity (predator species richness and trophic composition) using six of the most common predators of herbivorous planthoppers, including both strict and intraguild predators, and measured the strength of the cascading predator effects as changes in planthopper population size and plant productivity (biomass). We found that increasing predator species richness impacts the occurrence of trophic cascades, but that the magnitude and direction of the effect is a function of the trophic composition of the predator complex present. Likewise, increasing the proportion of intraguild-predator species present within the predator assemblage dampens cascading predator effects on herbivore populations and plant productivity.

METHODS

Study system

This experiment was conducted using the assemblage of arthropods that inhabit *Spartina alterniflora* Loisel (cordgrass)-dominated salt marshes along the mid-Atlantic coast of North America. *Spartina* cordgrass is the only host plant of the phloem-feeding planthoppers *Prokelisia dolus* Wilson and *P. marginata* (Van Duzee) (Hemiptera: Delphacidae), the most common herbivores on these marshes (Denno *et al.* 1996). Both planthoppers are extremely abundant in a variety of marsh habitats. However, *P. dolus* is the predominant planthopper found in meadow habitats, a habitat where predators abound (Denno *et al.* 1996). Therefore, this study focused specifically on the impact of predator diversity on *P. dolus* populations.

Prokelisia planthoppers are consumed by a variety of invertebrate predators including the hunting spiders *Pardosa littoralis* Banks (Araneae: Lycosidae), *Clubiona saltitans* Emerton (Araneae: Clubionidae), and *Marpissa pikei* (Peckham) (Araneae: Salticidae), the web-building spider *Grammonota trivittata* Banks (Araneae: Linyphiidae), the lady beetle *Naemia seriata* (Melsheimer) (Coleoptera: Coccinellidae), and the mirid bug *Tytthus vagus* (Knight) (Hemiptera: Miridae) (Döbel & Denno 1994; Finke & Denno 2002).

All of these predators attack planthopper adults and nymphs, with the exception of *Tytthus*, which is a specialist on planthopper eggs that have been oviposited within the leaf blade (Döbel & Denno 1994; Finke & Denno 2002). This predator complex includes predators that have been identified as intraguild predators (the hunting spiders) as well as strict predators (the web-building spider, the coccinellid, and the mirid bug) (Finke & Denno 2002; Denno *et al.* 2004; Finke 2005). Therefore, the opportunity exists for a diversity of interactions among predators.

Intraguild predation and the relationship between predator diversity and the occurrence of trophic cascades

We investigated the importance of intraguild predation as a mechanism by which predator diversity dampens the occurrence of trophic cascades by factorially manipulating predator species richness (1, 2, or 3 species) and predator trophic composition (strict predators only, intraguild predators only, or a mixture of both strict and intraguild predators) in mesocosms and then assessing the impact of these predator diversity treatments on planthopper suppression and *Spartina* cordgrass productivity.

Mesocosms were located outside at the University of Maryland greenhouse facility (College Park, MD, USA). Each mesocosm contained 10 field-collected *Spartina* culms transplanted into sand-filled pots (30 cm diameter, 0.04 m²). Plants were enclosed in a clear plastic cage (cellulose butyrate cylinder, 22 cm diameter × 30 cm height) sunk into the sand and covered by a screened lid (0.6 × 0.6 mm holes, 85% light transmission). A total of 186 mesocosms were divided among 10 watering pools and treatments were randomly assigned to mesocosms within watering pools in a blocked design.

On 30 July 2003, 20 field-collected planthopper adults were released into each mesocosm and predator diversity treatments were established the following week. Using a species pool of six predator species, three strict predators (*Tytthus*, *Grammonota*, and *Naemia*) and three intraguild predators (*Pardosa*, *Clubiona*, and *Marpissa*), predator diversity treatments were created by crossing predator species richness (1, 2 or 3 species) with trophic composition (strict predators only, intraguild predators only, or a mixture of both strict and intraguild predators). Replicates were created by drawing with replacement from the species pool of six predator species (see Table 1 for specific species compositions used). As a result, predator diversity treatments were not confounded with predator species identity (the two exceptions being that there was only one possible combination of three strict predators and only one possible combination of three intraguild predators). This treatment design included six treatments assessing the individual impacts of each of the predator species on planthopper

suppression and plant productivity. In addition, there were also two no-predator controls, *Spartina* plants with planthoppers present and *Spartina* plants alone.

Field-collected predators were released into mesocosms in an additive treatment design (i.e. treatments with multiple predator species contained the summed number of individuals used in each of the single predator treatments) and at densities that approximated natural field densities (10 *Tytthus*, 10 *Grammonota*, 10 *Naemia*, five *Pardosa*, five *Clubiona*, and five *Marpissa* per mesocosm). An additive design was appropriate in this case because the overall abundance of predators on the marsh increases with predator species richness (correlation between total predator abundance and predator species richness from 41 samples taken throughout the growing season in four major habitat types across the Tuckerton marsh, $r^2 = 0.598$, $P < 0.001$; H.G. Döbel, D. Lewis, and R.F. Denno, unpublished data). In addition, intraspecific antagonistic interactions have been documented for some of the predator species used (Langellotto 2002; Denno *et al.* 2004). The additive treatment design ensured that predator diversity effects were not confounded with changes in the intensity of any intraspecific interactions by controlling the initial abundance of individual predator species (Jolliffe 2000). Therefore, departures from the null hypothesis of independent effects among predators were more confidently attributed to changes in interspecific interactions among predators, such as intraguild predation, rather than intraspecific effects (Jolliffe 2000).

On 6 October 2003, after two planthopper generations, the effects of the predator diversity treatments on the size of the herbivore population and *Spartina* biomass were assessed. Herbivore densities were determined by visually counting all living planthoppers (nymphs and adults) within the mesocosms. *Spartina* biomass was determined by harvesting all live aboveground vegetation from each mesocosm, drying it in an oven for 3 days at 55 °C, and weighing it. The density of planthoppers and *Spartina* biomass per cage were scaled up to units per m².

The direct and interactive effects of predator species richness (1, 2 or 3 species) and trophic composition (strict predators only, intraguild predators only, or a mixture of both) on planthopper population size and *Spartina* biomass were assessed by performing an analysis of covariance for each response variable with trophic composition modelled as a class variable and species richness as a continuous variable (both variables fixed). To account for differences within and among treatments in total predator abundance because of the additive treatment design, initial predator density was incorporated into the model as a covariate. Blocking effects were also included as a class variable with a random source of variation (SAS 2002). Treatment means were compared by performing *t*-tests with Tukey–Kramer adjustment of *P*-values to account for multiple comparisons.

Table 1 Identity of predator species, trophic composition of treatments, number of replicates, initial density of predators, and per capita impact of predators on the herbivore population [$\ln(\text{herbivore density in absence of predators}/\text{herbivore density in presence of predators})/\text{initial predator density}$] at three levels of species richness (1–3)

Predator species identity	Trophic category	Number of replicates	Initial predator abundance	Per capita impact
Species richness 1				
<i>G. trivittata</i>	S	4	10	0.214 ± 0.062^b
<i>N. seriata</i>	S	5	10	0.241 ± 0.056^b
<i>T. vagus</i>	S	5	10	0.439 ± 0.056^a
<i>C. saltitans</i>	I	6	5	0.250 ± 0.051^b
<i>M. pikei</i>	I	6	5	0.203 ± 0.051^b
<i>P. littoralis</i>	I	6	5	0.353 ± 0.051^{ab}
Species richness 2				
<i>G. trivittata</i> + <i>T. vagus</i>	S	6	10 + 10	0.313 ± 0.051
<i>G. trivittata</i> + <i>N. seriata</i>	S	6	10 + 10	0.375 ± 0.051
<i>N. seriata</i> + <i>T. vagus</i>	S	5	10 + 10	0.437 ± 0.056
<i>N. seriata</i> + <i>P. littoralis</i>	S + I	4	10 + 5	0.310 ± 0.062
<i>G. trivittata</i> + <i>P. littoralis</i>	S + I	5	10 + 5	0.251 ± 0.056
<i>M. pikei</i> + <i>T. vagus</i>	S + I	5	5 + 10	0.448 ± 0.051
<i>P. littoralis</i> + <i>T. vagus</i>	S + I	6	5 + 10	0.422 ± 0.051
<i>C. saltitans</i> + <i>T. vagus</i>	S + I	6	5 + 10	0.195 ± 0.056
<i>C. saltitans</i> + <i>P. littoralis</i>	I	6	5 + 5	0.042 ± 0.051
<i>C. saltitans</i> + <i>M. pikei</i>	I	6	5 + 5	0.045 ± 0.051
<i>M. pikei</i> + <i>P. littoralis</i>	I	6	5 + 5	0.048 ± 0.051
Species richness 3				
<i>G. trivittata</i> + <i>N. seriata</i> + <i>T. vagus</i>	S	5	10 + 10 + 10	0.257 ± 0.056
<i>G. trivittata</i> + <i>T. vagus</i> + <i>P. littoralis</i>	S + I	6	10 + 10 + 5	0.077 ± 0.051
<i>G. trivittata</i> + <i>T. vagus</i> + <i>C. saltitans</i>	S + I	5	10 + 10 + 5	0.195 ± 0.056
<i>G. trivittata</i> + <i>T. vagus</i> + <i>M. pikei</i>	S + I	5	10 + 10 + 5	0.135 ± 0.056
<i>T. vagus</i> + <i>N. seriata</i> + <i>P. littoralis</i>	S + I	4	10 + 10 + 5	0.170 ± 0.062
<i>T. vagus</i> + <i>N. seriata</i> + <i>C. saltitans</i>	S + I	6	10 + 10 + 5	0.214 ± 0.051
<i>T. vagus</i> + <i>N. seriata</i> + <i>M. pikei</i>	S + I	6	10 + 10 + 5	0.215 ± 0.051
<i>C. saltitans</i> + <i>P. littoralis</i> + <i>G. trivittata</i>	S + I	6	5 + 5 + 10	0.002 ± 0.051
<i>C. saltitans</i> + <i>P. littoralis</i> + <i>N. seriata</i>	S + I	6	5 + 5 + 10	0.104 ± 0.051
<i>C. saltitans</i> + <i>P. littoralis</i> + <i>T. vagus</i>	S + I	6	5 + 5 + 10	0.205 ± 0.051
<i>P. littoralis</i> + <i>M. pikei</i> + <i>G. trivittata</i>	S + I	6	5 + 5 + 10	-0.003 ± 0.051
<i>P. littoralis</i> + <i>M. pikei</i> + <i>N. seriata</i>	S + I	6	5 + 5 + 10	0.190 ± 0.051
<i>P. littoralis</i> + <i>M. pikei</i> + <i>T. vagus</i>	S + I	6	5 + 5 + 10	0.256 ± 0.051
<i>C. saltitans</i> + <i>M. pikei</i> + <i>P. littoralis</i>	I	5	5 + 5 + 5	0.019 ± 0.056

S, strict predator species only; S + I, both strict and intraguild predator species; I, intraguild predator species only. Mean per capita impacts (± 1 SEM) with different letters are significantly different ($P < 0.05$).

Planthopper population data were log-transformed to meet assumptions of analysis of variance including normality and homogeneity of variances.

The per capita predator impact on the planthopper population, $\ln(\text{herbivore density in absence of predators}/\text{herbivore density in presence of predators})/\text{initial predator density}$, was calculated for each of the 31 different predator species compositions. Per capita predator impacts were used to correct for differences in the initial abundance of predators across predator compositions because of the additive design. To examine possible sampling effects, the per capita impacts of each predator species in monoculture

were compared by performing *t*-tests with Tukey–Kramer adjustment of *P*-values to account for multiple comparisons.

To verify the occurrence of intraguild predation, all predators surviving at the end of the study were counted by visually inspecting each mesocosm. For intraguild predators and strict predators individually, the impact of increasing predator species richness on the proportion of predators surviving was assessed by regression analysis [$\text{proportion surviving} = \beta_0 + \beta_1 (\text{species richness}) + \text{error}$]. In addition, the influence of intraguild predators (present vs. absent) on the densities of each of the three strict predator species (*Grammonota*, *Naemia*, and *Tytthus*) was assessed by

performing a separate analysis of variance for each species with the presence of intraguild predators as a fixed factor and block modelled as a random source of variation in the model.

RESULTS

Intraguild predation and relationship between predator diversity and the occurrence of trophic cascades

Differences in the per capita impact of individual predator species on planthopper suppression were not large (Table 1). Comparisons among predator species revealed that *Tytthus* was no more effective than *Pardosa* in suppressing planthopper populations ($t_{1,9} = 1.14$, $P = 0.25$), but was better able to do so than *Naemia*, *Grammonota*, *Clubiona*, and *Marpissa* ($t_{\text{NDF,DDF}} = 2.51_{1,8}$, $8.51_{1,7}$, $2.49_{1,9}$, and $3.51_{1,9}$, respectively; $P < 0.05$) (Table 1).

There was a significant interactive effect of predator species richness and trophic composition on planthopper density ($F_{2,143} = 3.12$, $P = 0.047$) and plant biomass ($F_{2,143} = 3.07$, $P = 0.049$) (Table 2), indicating that the impact of increasing predator richness on trophic levels beneath depended on the trophic composition of the predator complex present. Predator impacts on planthopper suppression were independent when the species richness of strict predators was increased from one to three (Fig. 1a), an effect that propagated down and resulted in increased *Spartina* biomass with an increase in predator density (Fig. 1b). By contrast, intraguild predators interacted antagonistically, resulting in diminished planthopper suppression as predator richness was enhanced (Fig. 1a). As a result, any trophic cascade on plant productivity was dampened and there was no change in *Spartina* biomass (Fig. 1b) with an increase in the number of intraguild predator species. When

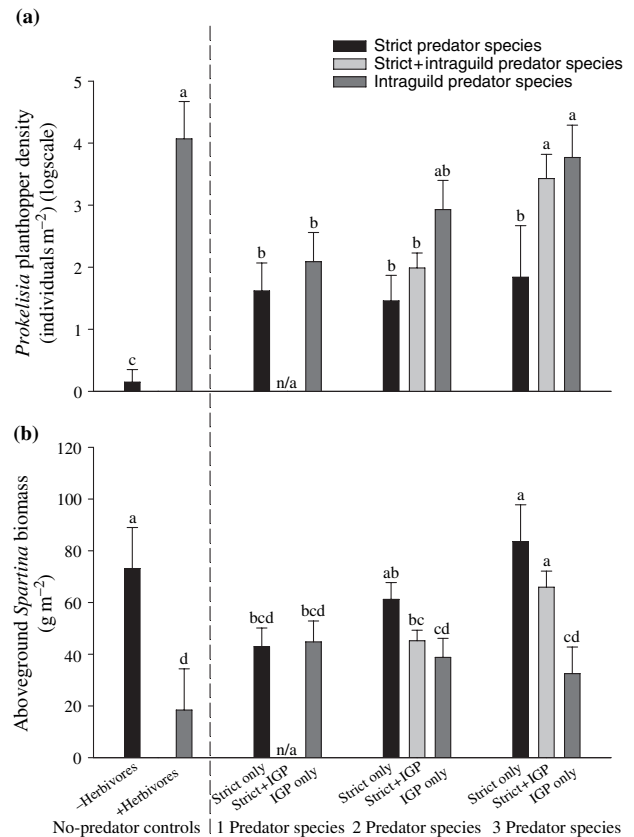


Figure 1 The interactive effects of predator species richness (1, 2, or 3 species) and predator trophic composition (strict predator species only, both strict and intraguild predator species, or intraguild predator species only) on (a) *Prokelisia* planthopper density; and (b) aboveground *Spartina* biomass in mesocosms after a 68-day interaction period. Mean values \pm 1 SEM with different letters are significantly different ($P < 0.05$).

Table 2 Mixed model analysis of covariance results for the effects of predator species richness (1, 2, or 3 species) and predator trophic composition (strict predator species only, both strict and intraguild predator species, or intraguild predator species only) on (a) *Prokelisia* planthopper density and (b) aboveground *Spartina* biomass, with initial predator density as a covariate

Source of variation	NDF	DDF	F	P-value
(a) Herbivore population response				
Species richness	1	143	4.21	0.042
Trophic composition	2	143	3.13	0.047
Richness \times composition	2	143	3.12	0.047
Initial predator density	1	143	6.94	0.009
(b) Plant biomass response				
Species richness	1	143	5.5	0.020
Trophic composition	2	143	1.51	0.225
Richness \times composition	2	143	3.07	0.049
Initial predator density	1	143	1.27	0.262

a mixture of both strict and intraguild predators were present, increasing predator richness from two to three resulted in an antagonistic interaction, diminishing planthopper suppression (Fig. 1a). However, this dampened level of suppression resulted in an unexpected increase in *Spartina* biomass (Fig. 1b). An increase in plant productivity is not consistent with other results from this study or with the results of previous studies of this marsh system which have all shown a consistent decrease in *Spartina* productivity with an increase in planthopper abundance (Denno *et al.* 2002; Finke & Denno 2004).

Within each level of predator species richness, altering predator trophic composition such that the proportion of intraguild predators in the assemblage increased from 0 (strict predators only) to 100% (intraguild predators only) resulted in antagonistic interactions among predators and diminished planthopper suppression (compare planthopper densities between 'strict' and 'intraguild' treatments within

richness levels of 2 and 3) (Fig. 1a). As a result, *Spartina* biomass was significantly diminished (Fig. 1b) and the trophic cascade was dampened as the relative abundance of intraguild predators increased.

There was physical evidence for the occurrence of intraguild predation in those treatment combinations containing intraguild predators, because spiders left small pellets of exsanguinated exoskeletons following feeding. Additionally, in treatments where only intraguild predators were present, the proportion of predators surviving at the end of the study declined with an increase in intraguild predator species richness [for treatments composed only of intraguild predators, proportion of predators surviving = $11.35 - 0.11 (\text{species richness}) + 0.53$, $r^2 = 0.27$, $P = 0.0034$, $n = 30$]. However, when only strict predators were present, predator survival remained constant as the richness of strict predator species increased [for treatments composed only of strict predators, proportion of predators surviving = $0.28 - 0.05 (\text{species richness}) + 0.24$, $r^2 = 0.13$, $P = 0.08$, $n = 25$]. Moreover, the abundances of both *Tytthus* and *Grammonota* (strict predator species) were reduced in the presence of intraguild predators ($F_{1,69} = 6.89$, $P = 0.011$ and $F_{1,37} = 32.44$, $P < 0.0001$, respectively). However, the abundance of the third strict predator species (*Naemia*) was unaffected by the addition of intraguild predators ($F_{1,35} = 0.77$, $P = 0.39$), a finding that is consistent with the results of a previous feeding trial which confirmed that *Naemia* adults and larvae are not susceptible to predation by the intraguild predator species used in this study (Finke 2005).

DISCUSSION

Our results show that the trophic composition of the predator assemblage can play an important role in determining the nature of the relationship between predator diversity and ecosystem function, as indexed by herbivore suppression and the strength of the trophic cascade on plant productivity. We found that increasing predator species richness influenced the occurrence of trophic cascades, but the magnitude and the direction of the effect depended on the trophic composition of the predators present. Specifically, the impacts of strict predators were independent, resulting in no change in planthopper abundance with an increase in the richness of strict predator species (Fig. 1a). By contrast, a commensurate increase in the number of intraguild predator species promoted antagonistic interactions and resulted in a higher density of herbivores and lower plant productivity at the highest level of predator species richness (Fig. 1a and b). Additionally, increasing the proportion of intraguild predator species present within the predator assemblage diminished the ability of predators to suppress planthopper populations, which then led to

decreased plant productivity (Fig. 1a,b). Therefore, the occurrence of antagonistic interactions when predator diversity is high dampens trophic cascades in this salt-marsh food web.

We attribute this antagonism among predators to the occurrence of intraguild predation, for which evidence does exist. However, in addition to the direct consumptive effects of predators (e.g. predation, intraguild predation, or cannibalism), indirect non-consumptive effects (e.g. trait-mediated effects such as anti-predator behaviour or interference phenomena) may also contribute to the strength of cascading effects at high levels of predator diversity. Such behavioural modifications in response to predation risk could also explain the unexpected increase in *Spartina* biomass with dampened planthopper suppression that was documented in the mixture of both strict and intraguild predators. Planthoppers have been shown to reduce their mobility in the presence of the *Pardosa* hunting spider (D.L. Finke and R.F. Denno, unpublished data), although the behavioural response of planthoppers to other combinations of predators is unknown. Such risk-avoiding behaviours, while enabling planthoppers to avoid predation and enhance survival, could lead to reductions in planthopper feeding and thus may explain the greater *Spartina* biomass in mixed predator treatments where planthopper suppression was diminished. Though not investigated explicitly in this study, trait-mediated cascading effects have been documented in a variety of systems (Schmitz *et al.* 2004).

It could be argued that the relationship between predator trophic composition and the occurrence of a trophic cascade was not because of the occurrence of intraguild predation, but to the reduced probability of including *Tytthus* (a strict predator with relatively large impacts on herbivore populations, Table 1) in the predator assemblage as the proportion of intraguild predators increased (i.e. a sampling effect) (Huston 1997). However, *Pardosa*, an intraguild predator, had adverse effects on the herbivore population that were similar in magnitude to those of *Tytthus*. Therefore, the impact of *Tytthus* on the strength of the trophic cascade was balanced by the effect of *Pardosa*, as the probability of including *Pardosa* was increased and that of including *Tytthus* was reduced. In addition, increasing predator species richness dampened the cascading impact of intraguild predators on lower trophic levels in the absence of strict predator species. Therefore, the dampened trophic cascade on *Spartina* productivity when predator diversity was enhanced and was attributed to the increased opportunity for the occurrence of intraguild predation and not the species-specific effects of *Tytthus*.

The few studies that have explicitly incorporated natural enemy diversity into an investigation of the linkages between biodiversity and ecosystem functioning have highlighted the importance of complex trophic interactions

in mediating this relationship (Morin 1995; Wilby & Thomas 2002; Cardinale *et al.* 2003; Montoya *et al.* 2003; Finke & Denno 2004). Likewise, this study demonstrates that knowledge of the trophic role of predator species is necessary to accurately predict the impact of changes in predator diversity on the occurrence of trophic cascades. Strict predator species may independently affect prey suppression and the strength of trophic cascades, whereas increasing predator diversity when intraguild predators are present could negatively impact prey suppression and plant productivity because of the enhanced opportunity for intraguild predation. We argue that intraguild predation is likely to be a common mechanism mediating the impact of changes in predator diversity on the occurrence of trophic cascades because intraguild predation is a ubiquitous interaction in a wide diversity of systems (Polis *et al.* 1989; Rosenheim 1998; Arim & Marquet 2004).

Understanding the importance of predator trophic composition for the relationship between predator diversity and the occurrence of trophic cascades has important implications for both conservation biology and agriculture. Significant progress has been made concerning the importance of biodiversity at lower trophic levels for the functioning of ecosystems (Loreau *et al.* 2001). However, little is known about the consequences of biodiversity loss at higher trophic levels (Duffy 2003), despite evidence that top trophic levels can be more susceptible to extinction than their basal resources (Petchey *et al.* 1999). Such insights will help aid policy makers with important decisions regarding which kinds of species need the greatest conservation in order to protect valuable ecosystem services such as primary productivity. Moreover, the goal of biological control programmes in agricultural systems is to initiate trophic cascades by manipulating predator complexes that result in enhanced crop yield (Snyder *et al.* 2005). Our results suggest that diverse predator assemblages may optimally suppress herbivore pests and maximize productivity in systems where intraguild predators are rare. When intraguild predators abound, promoting a diverse predator assemblage could weaken trophic cascades and reduce productivity. In such cases, additional control measures, such as the inclusion of physical refuges for predators from intraguild predation by other predators (Finke & Denno 2002), may be necessary in order to maximize productivity while simultaneously encouraging predator diversity in agricultural systems.

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