ABSTRACT

Title:	PREDATOR DIVERSITY, HABITAT COMPLEXITY AND THE STRENGTH OF TERRESTRIAL TROPHIC CASCADES
	Deborah L. Finke, Doctor of Philosophy, 2005
Directed By:	Professor Robert F. Denno, Department of Entomology

Food web complexity is thought to weaken the strength of terrestrial trophic cascades whereby strong natural enemy impacts on herbivores cascade to indirectly influence primary production. Predator diversity can enhance food web complexity by promoting the occurrence of intraguild predation, wherein predators feed on each other and on shared prey. In such cases, theory suggests that the impact of predation on herbivores relaxes and cascading effects on basal resources are dampened. In a terrestrial marsh community, I compared arthropod predator impacts 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. I found that enhancing predator diversity dampened enemy effects on herbivores and weakened trophic cascades. The role of intraguild predators in dampening such trophic cascades was determined by factorially manipulating predator species richness (1, 2, or 3 species) and predator trophic composition (strict predators, intraguild predators, or a mixture of both) and measuring their effects on prey suppression and plant productivity. I found that the impact of predator richness on the strength of trophic cascades was dependent on the trophic composition of the predator complex present. Specifically, strict predators additively enhanced planthopper suppression and increased plant productivity with an increase in species richness. However, intraguild predators interacted antagonistically, resulting in greater herbivore abundance and lower plant productivity at the highest levels of species richness. An investigation of the influence of habitat complexity on cascading predator effects revealed that complex habitats with cordgrass leaf litter provided a refuge for predators from intraguild predation and elevated planthopper suppression by the diverse predator assemblage. However, reducing the antagonistic predator-predator interactions and increasing prey suppression did not enhance the conductance of predator effects through the food web to impact positively primary producers, although there was a trend towards greater plant biomass in the complex-structured habitat. Therefore, the possibility exists that changes in habitat complexity might enhance trophic cascades and impact positively productivity by mediating trophic interactions among predators. Overall, interactions between species diversity at higher trophic levels and habitat structure can significantly alter ecosystem function in natural systems.

PREDATOR DIVERSITY, HABITAT COMPLEXITY AND THE STRENGTH OF TERRESTRIAL TROPHIC CASCADES

By

Deborah L. Finke

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Advisory Committee:
Professor Robert F. Denno, Chair
Professor Pedro Barbosa
Professor Galen Dively
Associate Professor William Fagan
Professor Charles Mitter

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CHAPTER 1: Predator diversity dampens trophic cascades

ABSTRACT

Food web complexity is thought to weaken the strength of terrestrial trophic cascades (Strong 1992; Halaj and Wise 2001; Shurin, Borer et al. 2002) whereby strong natural enemy impacts on herbivores cascade to indirectly influence primary production (Carpenter, Kitchell et al. 1985). Predator diversity can enhance food web complexity by promoting the occurrence of intraguild predation, wherein predators feed on each other and on shared prey (Polis, Myers et al. 1989; Rosenheim, Kaya et al. 1995; Crooks and Soulé 1999). In such cases, theory suggests that the impact of predation on herbivores relaxes and cascading effects on basal resources are dampened (McCann, Hastings et al. 1998; Hart 2002). Despite this view, no empirical studies have explicitly investigated the role of predator diversity in mediating primary productivity in a natural terrestrial system (Loreau, Naeem et al. 2001; Duffy 2003). In a coastal marsh community, I compare arthropod predator impacts 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. I 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.

INTRODUCTION

Studies investigating the impact of biodiversity on ecosystem functions such as primary production have become widespread given concern over the rapid rate of species extinctions (Naeem and Li 1997; Loreau, Naeem et al. 2001; Tilman, Reich et al. 2001). However, many studies in this area have focused specifically on the role of producer diversity while the consequences of biodiversity loss at higher trophic levels have been often ignored (Hooper and Vitousek 1997; Tilman, Reich et al. 2001; Duffy 2003), despite evidence that top trophic levels can be more susceptible to extinction than their basal resources (Pauly, Christensen et al. 1998; Petchey, McPherson et al. 1999; Duffy 2003). Studies that do incorporate trophic interactions into investigations of the link between biodiversity and ecosystem function have manipulated herbivore or filter-feeder diversity only (Mulder, Koricheva et al. 1999; Norberg 2000; Cardinale, Palmer et al. 2002), consumer diversity at several trophic levels simultaneously (McGrady-Steed, Harris et al. 1997; Naeem and Li 1997; Downing and Leibold 2002), or the overall presence and absence of predators (Gutiérrez et al. 1997, Fraser and Grime 1998, Halaj and Wise 2001, Schmitz 2003). Few studies have independently manipulated predator diversity (Morin and Lawler 1995; Cardinale, Harvey et al. 2003) 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.

METHODS

Study system and general methods

I investigated the consequences of the loss of predator diversity for the occurrence of trophic cascades and its impact on primary productivity using a natural assemblage of arthropods inhabiting the *Spartina alterniflora* 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* (Finke and Denno 2002; Langellotto 2002; Denno, Mitter et al. 2004) (Fig. 1.1). Because *Grammonota*, *Tytthus*, and *Pardosa* are susceptible to intraguild predation in this system (Finke and Denno 2002; Langellotto 2002; Denno, Mitter et al. 2004), the opportunity exists for antagonistic interactions among predators with cascading consequences for primary production.

In the context of this coastal marsh community, I constructed replicated food webs with varying 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 using 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 with *Hogna* as well only in mesocosms). I manipulated predator diversity using an additive treatment design to hold intra-specific interactions among *Tytthus* constant across levels of diversity (Jolliffe 2000) 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). Since I 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 independently reduce planthopper population sizes as compared to no-predator controls (Finke and Denno 2002; Langellotto 2002; Denno, Mitter et al. 2004). Therefore, while 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 since the experiment spanned more than two herbivore generations from July to October 2002.

Greenhouse mesocosms

Greenhouse mesocosms consisted of 10 field-collected *Spartina* culms transplanted into sand-filled pots (30 cm diameter, 0.04 m^2) and caged within a clear plastic cylinder (cellulose butyrate, 22 cm diameter x 30 cm 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 10 separate watering pools in groups of four (1 replication of each treatment per pool) for a total of 10 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 m^2 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 into groups of four for a total of six replications.

Assessment of arthropod population density

Herbivore and predator densities were censused 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 censused using an insect vacuum. One sample consisted of eight 10-s placements of the sampling head on the marsh surface such that 0.8 m^2 of *Spartina* was vacuumed.

Assessment of 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 $0.047m^2$ wire frame. Vegetation was dried in an oven for three days at 55º C and then weighed. The number of tillers produced was determined visually by counting all tillers in mesocosms and counting all tillers within the $0.047m^2$ sampling quadrat for the field enclosures.

Statistical Analyses

The effects of the food web complexity treatments on final planthopper population size, number of *Spartina* tillers, and the aboveground biomass of *Spartina* were each analysed independently using mixed model analyses of variance in which block was modelled as a random source of variation. Subsequently, pair-wise comparisons of treatment means were done 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.

RESULTS

In greenhouse mesocosms, a trophic cascade occurred in the simple-structured food web with low predator diversity. Notably, 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 dramatically reduced compared to the density of planthoppers when no predators were present ($F_{3, 27} = 25.67$, $P < 0.0001$, $t = 6.27$, $P < 0.0001$, Fig. 1.2a). However, when predator diversity was high, planthopper density was intermediate and greater than when predator diversity was low ($t = 5.34$, $P < 0.0001$, Fig. 1.2a). Predator effects on herbivore populations cascaded down to affect primary productivity, both tiller production ($F_{3, 27} = 5.83$, $P < 0.01$, Fig. 1.2b) and aboveground live biomass ($F_{3, 27} = 4.83$, $P < 0.01$, Fig. 1.2c). In the simple food web with a single predator species, the dramatic reduction in planthopper population size resulted in a trophic cascade, increasing both the number of tillers ($t = 3.52$, $P < 0.01$, Fig. 1.2b) and aboveground biomass ($t = 2.83$, $P < 0.05$, Fig. 1.2c) compared to 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. 1.2b) compared to 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. 1.2c). Thus, predator diversity precluded a trophic cascade on *Spartina* biomass due to the occurrence of intraguild 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 intraguild predation since spiders left small pellets of exsanguinated mirid exoskeletons following feeding (Finke and Denno 2002). Therefore, when predator diversity was high, the occurrence of intraguild 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. 1.3a), which increased the number of *Spartina* tillers ($F_{3, 15} = 5.45$, $P < 0.01$; $t = 2.75$, $P < 0.05$, Fig. 1.3b) when compared to the predator-free herbivore treatment. Treatment effects on aboveground biomass were not significant ($t = 1.10$, $P > 0.05$, Fig. 1.3c). In the complex food web with high predator diversity, the trophic cascade was dampened. Planthopper densities were no different when all predators were present than when no predators were present ($t = 0.29$, $P > 0.05$, Fig. 1.3a) and the density of tillers was also not different ($t = 0.92$, $P > 0.05$, Fig. 1.3b). Again, the dampening of the trophic cascade in the complex food web was due to the occurrence of intraguild predation since the density of *Tytthus* was significantly reduced in the presence of other predators ($t = 2.92$, $P < 0.01$). It is important to note, however, that the strength of the cascade was weaker in the field than in mesocosms. This is likely the result of planthopper contamination of the field treatments (Fig 1.3a) due to the small size (3 mm) and high ambient density of planthoppers (~11,000 individuals per m^2 during this study). Thus, this study underscores the view that it may be more difficult to demonstrate trophic cascades in open versus closed systems.

DISCUSSION

My results show that increasing arthropod predator diversity promotes intraguild interactions among predators, diminishes enemy impacts on herbivores, and dampens cascading effects on basal resources. Therefore, given the widespread occurrence of intraguild predators in natural systems (Polis, Myers et al. 1989), a decline in predator species diversity may positively affect ecosystem function. Thus, a management conflict arises since maximizing productivity, rather than preserving diversity, may be beneficial in certain contexts (Schmitz 2003). For example, in agricultural systems the goal of biological-control programs 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, my study highlights how conservation biologists whose goal is to maintain diversity and biological-control practitioners who aim to maximize productivity can reach ultimately conflicting conclusions about the importance of biodiversity as it relates to ecosystem function.

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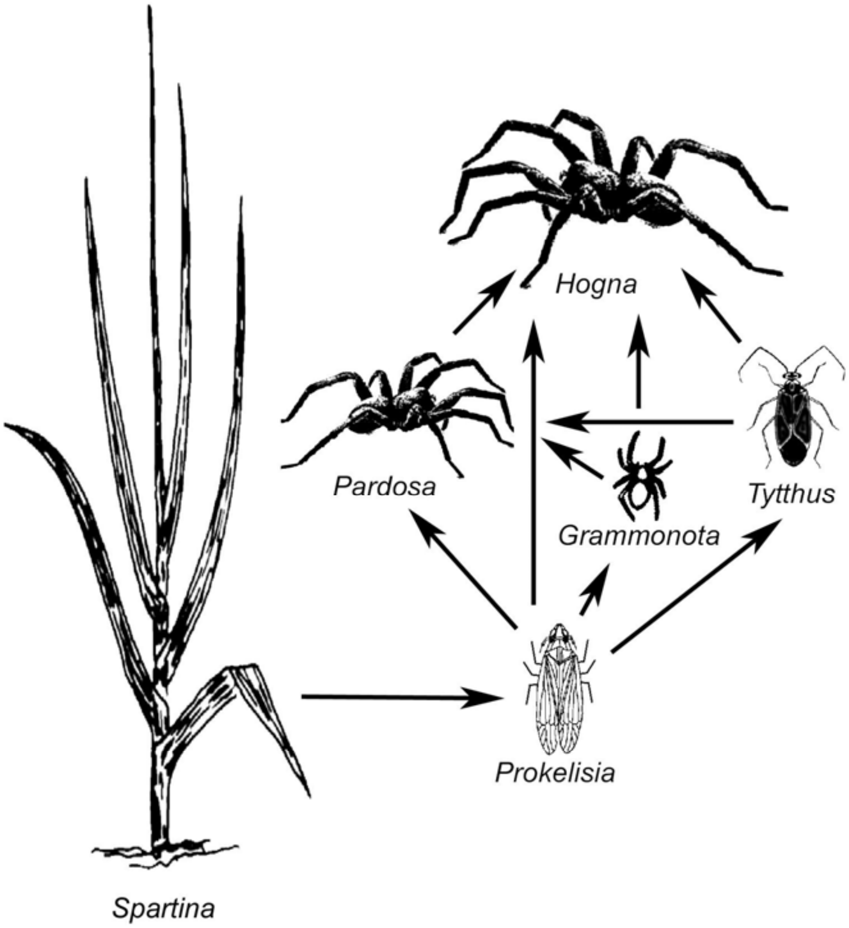

Figure 1.1. Component of salt marsh food web used in experimental design. Arrows indicate the flow of energy from the source to the consumer.

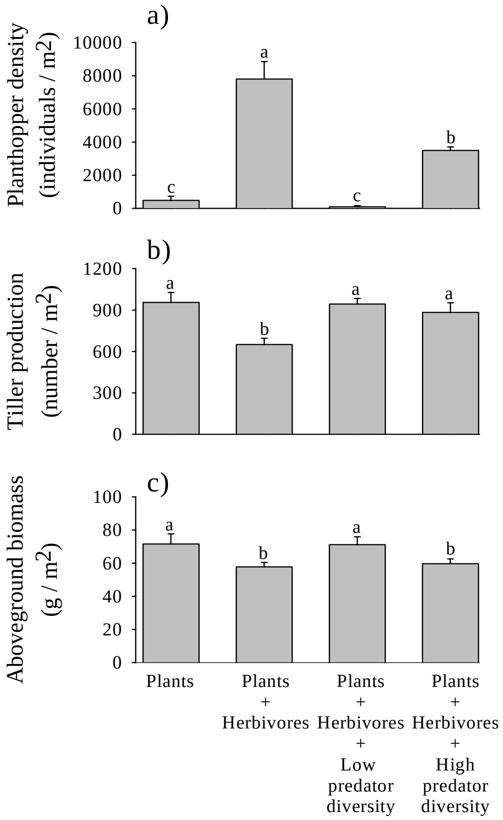

Figure 1.2. Effect of predator diversity on the occurrence of trophic cascades in greenhouse mesocosms. Means (± 1 SEM) with different letters are significantly different ($P < 0.05$). (a) Herbivore (*Prokelisia* planthopper) population size. Low predator diversity dramatically reduces planthopper population 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 ($t = 2.44$, $P < 0.05$).

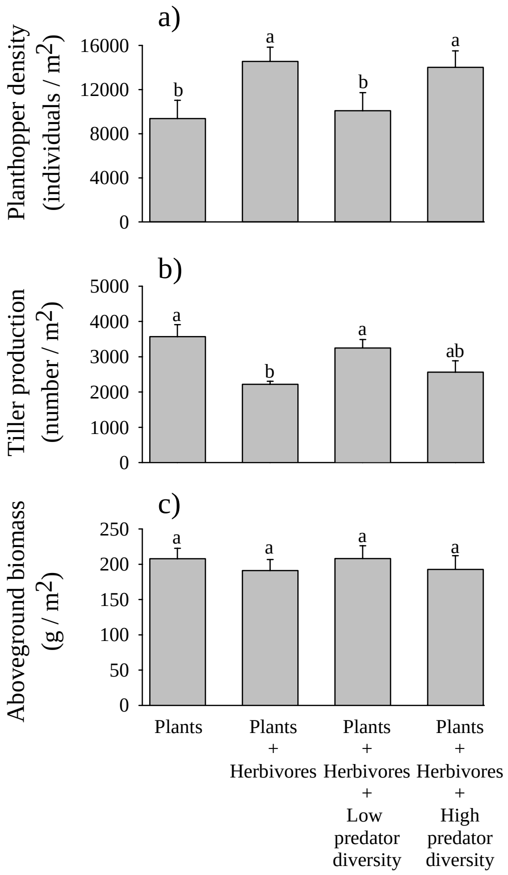

Figure 1.3. Effect of predator diversity on the occurrence of trophic cascades in field enclosures. Means (± 1 SEM) with different letters are significantly different ($P < 0.05$). (a) Herbivore (*Prokelisia* planthopper) population size. High predator diversity results in a population size no different than when predators are absent ($t = 0.29$, $P > 0.05$). (b) Number of tillers produced by *Spartina*. Low predator diversity enhances tiller number as compared to no predators ($t = 2.75$, $P < 0.05$). Tiller production is no different when predator diversity is high versus when predators are absent ($t = 0.92$, $P > 0.05$). (c) Aboveground biomass of *Spartina*. Predator diversity treatments did not impact biomass ($F = 0.72$, $P > 0.05$).

CHAPTER 2: Predator diversity and the functioning of ecosystems: The role of intraguild predation in dampening trophic cascades

ABSTRACT

Single trophic-level studies of the relationship between biodiversity and ecosystem functioning highlight the importance of mechanisms such as complementary resource use, facilitation, and sampling effect. In a multi-trophic context, trophic interactions may also be an important mediator of this relationship. Here I investigate the impact of intraguild predation on ecosystem functions such as prey suppression and primary production via trophic cascades. Using a salt-marsh food web, the interactive effects of predator species richness (1, 2, or 3 species) and predator trophic composition (strict predators, intraguild predators, or a mixture of the two) on the occurrence of trophic cascades were determined by factorially manipulating both aspects of predator diversity. I found that the impact of predator diversity on the strength of trophic cascades was dependent upon the trophic composition of predator complex present. Specifically, the occurrence of intraguild predation when predator diversity was high diminished cascading predator effects on herbivore suppression and reduced primary productivity. Therefore, trophic interactions among predators can play an important role in determining the nature of the relationship between predator diversity and ecosystem function.

INTRODUCTION

Studies investigating the importance of biodiversity for ecosystem functioning have become widespread due to concern over the currently unprecedented rate of biodiversity loss (Loreau, Naeem et al. 2001). Many studies in this area have focused specifically on the role of producer diversity (Tilman, Knops et al. 2002), whereas the consequences of biodiversity loss at higher trophic levels have been often overlooked (Duffy 2002; Duffy 2003); but see (Naeem and Li 1998; Norberg 2000; Paine 2002; Duffy 2003; Hillebrand and Cardinale 2004). As a result, the commonly implicated mechanisms by which changes in biodiversity can influence ecosystem functioning, such as complementary resource use, facilitation, and sampling effect, have emerged primarily from single trophic-level investigations of plant assemblages (Tilman, Knops 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 (Wilby and Thomas 2002; Cardinale, Harvey et al. 2003; Montoya, Rodríguez et al. 2003; Finke and Denno 2004; Snyder, Chang 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, Cardinale et al. 2005).

Impacts of the predator trophic level as a whole on critical ecosystem functions such as prey suppression and primary production via the occurrence of trophic cascades have been documented. Predators are capable of reducing herbivore populations (DeBach and Rosen 1991; Symondson, Sunderland et al. 2002) and these top-down effects can propagate through the food web to positively influence primary producers, resulting in a trophic cascade (Carpenter, Kitchell et al. 1985; Schmitz, Hamback et al. 2000; Halaj and Wise 2001). However, diversity within the predator trophic level is likely to have significant consequences for the occurrence of trophic cascades as well, since individual predator species can vary substantially in their impacts on prey populations (Chalcraft and Resetarits 2003). The importance of predator diversity 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 (Wilby and Thomas 2002; Cardinale, Harvey et al. 2003; Finke and 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 (Snyder, Chang et al. 2005). Increasing predator diversity could promote trophic cascades if predator species act additively (Chang 1996; Snyder and Ives 2003) or synergistically (Losey and Denno 1998; Cardinale, Harvey et al. 2003), trophic mechanisms that are analogous to complementary resource use and facilitation among producers (Fridley 2001), or hinder trophic cascades if these species engage in intraguild predation (Polis and McCormick 1987; Rosenheim, Wilhoit et al. 1993; Finke and Denno 2002; Finke and Denno 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 additively enhance predator effects on prey suppression as predator diversity is enhanced (Polis, Myers et al. 1989; Rosenheim 1998).

Intraguild predation is a widespread phenomenon in a variety of ecosystems (Polis, Myers et al. 1989; Rosenheim 1998; Arim and Marquet 2004) and the potential role of intraguild predation in inhibiting trophic cascades has been documented, both empirically and theoretically (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, Cardinale et al. 2005)). In a previous study, I showed that increasing predator diversity dampens the occurrence of trophic cascades in a terrestrial salt marsh system (Finke and 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 and 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 due to 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.

In this study, I test the hypothesis that predator diversity dampens trophic cascades because intraguild predation is more likely to occur in diverse predator assemblages. I tested this hypothesis in mesocosms using the natural assemblage of arthropods inhabiting coastal salt marshes, an assemblage which has striking compositional similarity to other agricultural and natural systems (Heong, Aquino et al. 1992; Cronin, Haynes et al. 2004). I 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 and tillering). I 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, predator trophic composition also influences the strength of the trophic cascade (the presence of intraguild predators dampened cascading predator effects), but this effect is independent of changes in predator species richness.

METHODS

Study System

This experiment was conducted using the assemblage of arthropods that inhabit the cordgrass (*Spartina alterniflora*)-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* and *Prokelisia marginata* (Hemiptera: Delphacidae), the most common herbivores on these marshes (Denno, Schauff et al. 1987). Both planthoppers are extremely abundant in a variety of marsh habitats. However, *Prokelisia dolus* is the predominant planthopper found in meadow habitats, a habitat where predators abound (Denno, Roderick et al. 1996). Therefore, my study focused specifically on the impact of predator diversity on *Prokelisia dolus* populations.

Prokelisia planthoppers are consumed by a variety of invertebrate predators including the hunting spiders *Pardosa littoralis* (Araneae: Lycosidae), *Clubiona saltitans* (Araneae: Clubionidae), and *Marpissa pikei* (Araneae: Salticidae), the web-building spider *Grammonota trivitatta* (Araneae: Linyphiidae), the lady beetle *Naemia seriata* (Coleoptera: Coccinellidae), and the mirid bug *Tytthus vagus* (Hemiptera: Miridae) (Döbel and Denno 1994, Denno and Peterson 2000, Finke and 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 and Denno 1994, Finke and 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). Therefore, the opportunity exists for a diversity of interactions among predators. These predators were assigned to trophic groups (strict or intraguild predators) based on previous studies investigating the occurrence of intraguild predation among a subset of these predators and accumulated knowledge of the natural history of the marsh food web (Döbel and Denno 1994, Finke and Denno 2002, Denno et al. 2004). However, for the purposes of this study, these trophic assignments will be verified (see ‘Verification of trophic identity’ below).

Verification of the trophic identity of predators: strict vs. intraguild predators

Before investigating the importance of intraguild predation for the dampening of trophic cascades, the trophic identity of each predator was verified. Predators were classified as either 'strict predators' (predators which feed only on planthoppers) or 'intraguild predators' (predators which consume other predators as well as planthoppers) (Polis, Myers et al. 1989) by performing a variety of feeding trials in the laboratory using field-collected arthropods from my major study site at Tuckerton, Ocean Co., New Jersey, USA (for detailed site description, see Denno et al. 2002).

Consumption of planthoppers by each predator species (with the exception of *Tytthus* mirids which consume planthopper eggs) was assessed in laboratory mesocosms containing 10 *Prokelisia dolus* planthopper adults. Mesocosms were constructed by transplanting three *Spartina* plants (25cm in height) from the field into sand-filled pots (6.3 cm diameter). Potted transplants were enclosed in a 30 cm high x 7.5 cm diameter plastic tube cage (cellulose butyrate) topped with an organdy-mesh cover. One of six predator treatments was randomly assigned to each mesocosm and replicated ten times. The predator treatments included: 1) a no-predator control, 2) a single *Naemia* larvae or adult, 3) a single *Grammonota* adult, 4) a single *Pardosa* adult, 5) a single *Clubiona* adult, or 6) a single *Marpissa* adult. Predators foraged within the mesocosms for 48 hours and at the end of this time the number of living planthoppers remaining was counted. The number of planthoppers consumed by each predator in 48 hours was determined by subtracting the number of living planthoppers remaining when the predator was present from the number of planthoppers surviving in the no-predator control. A one-way analysis of variance (PROC MIXED, (SAS 1999) was performed to determine the effect of predator species identity on the number of planthoppers consumed in 48 hours. Differences of treatment means from zero (indicating significant predation effects) and pair-wise comparisons of treatment means were determined by t-test with Bonferroni correction for multiple comparisons where appropriate.

Consumption of the herbivore by *Tytthus* mirids was more difficult to quantify since *Tytthus* mirids consume planthopper eggs that are embedded within leaf blades of *Spartina*. Therefore, consumption of planthoppers by *Tytthus* was documented by counting the number of planthopper nymphs that emerged in mesocosms with *Tytthus* mirid bugs present and comparing that to the number of planthopper nymphs that emerged in mesocosms where *Tytthus* were absent. Ten planthopper adults (5 gravid females and 5 males) were released into 20 mesocosms containing *Spartina* cordgrass (mesocosms were identical to those described above). After a three-day oviposition period, all planthoppers were removed from the mesocosms and a single *Tytthus* mirid bug was added to half of the cages. After 72 hours, *Tytthus* was removed. Subsequently, the number of planthopper nymphs emerging from the two treatment combinations were counted. The impact of the presence of *Tytthus* on the number of planthopper nymphs emerging was determined by one-way analysis of variance (PROC MIXED, (SAS 1999) and means were compared by t-test.

The intraguild predation of *Tytthus* by *Naemia* and *Grammonota* (probable strict predators) and *Pardosa, Clubiona,* and *Marpissa* (probable intraguild predators) was also assessed in laboratory mesocosms. The plants used in this experiment contained planthopper eggs, since *Tytthus* do not survive in the absence of plants containing planthopper eggs (D. Finke, personal observation). Importantly, by virtue of its piercing mouthparts, *Tytthus* is the only predator that can feed on embedded eggs. One of six predator treatments was randomly assigned to each mesocosm and replicated ten times. The predator treatments included: (1) a no-predator control, (2) a single *Naemia* larva or adult, (3) a single *Grammonota* adult, (4) a single *Pardosa* adult, (5) a single *Clubiona* adult, or (6) a single *Marpissa* adult. Predators foraged within the mesocosms for 48 hours and at the end of this time the number of living *Tytthus* remaining was counted. The number of *Tytthus* consumed by the predator was determined by subtracting the number of living *Tytthus* remaining when the predator was present from the number of *Tytthus* surviving in the no-predator control. Analysis of variance (PROC MIXED, (SAS 1999) was performed to determine the effect of predator species identity on the number of *Tytthus* consumed in 48 hours. Significant differences of treatment means from zero (indicating the occurrence of intraguild predation) and pair-wise comparisons of treatment means were determined by t-test with Bonferroni correction for multiple comparisons where appropriate.

Feeding linkages among intraguild predators and intraguild prey that did not include *Tytthus* were determined by pairing individual predators of different species within a petri dish until a predation event occurred and recording the “winning intraguild predator” for each interaction. All pair-wise combinations of an individual *Naemia* adult or larva, *Grammonota* adult, *Pardosa* adult, *Clubiona* adult, or *Marpissa* adult were released into petri dishes with moistened plaster-of-paris covering the bottom (moist plaster-of-paris provides moisture for predators without promoting mold). Predator treatment combinations containing at least one suspected strict predator (*Grammonota* / *Naemia*, *Pardosa* / *Naemia*, *Clubiona* / *Naemia*, *Marpissa* / *Naemia*, *Pardosa* / *Grammonota*, *Clubiona* / *Grammonota*, *Marpissa* / *Grammonota*) were each replicated 6 times. Pairings of suspected intraguild predators (*Clubiona* / *Pardosa*, *Marpissa* / *Pardosa*, and *Marpissa* / *Clubiona*) were replicated 10, 15, and 9 times respectively. There were too few data points to perform a chi-square test (Sokal and Rohlf 1987; SAS 1999), therefore, data are presented as the number of predation events ('wins') by each predator for each treatment combination.

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

I 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). Each mesocosm contained ten field-collected *Spartina* culms transplanted into sand-filled pots (30 cm diameter, 0.04 m^2). Plants were enclosed in a clear plastic cage (cellulose butyrate cylinder, 22 cm diameter x 30 cm height) sunk into the sand and covered by a screened lid (0.6 x 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 pool of 6 predator species, 3 strict predators (*Tytthus*, *Grammonota*, and *Naemia*) and 3 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). The experiment was an incomplete factorial design since it was not possible to create a mixture of both strict and intraguild predators when the level of species richness was one. Replicates were created by drawing (with replacement) from the pool of 6 predator species. 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. These individual predator treatments were used to verify that no single predator species had impacts large enough to disproportionately influence the results (i.e. exhibit a sampling effect) (Huston 1997). 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*, 5 *Pardosa*, 5 *Clubiona*, and 5 *Marpissa* per mesocosm). An additive treatment design was used so that predator diversity was not confounded with changes in the abundance of individual predator species (Jolliffe 2000). As a result, departures from the null hypothesis of independent additive effects among predators were more confidently attributed to changes in interspecific interactions among predators, such as intraguild predation, rather than intraspecific effects (Sih, Englund et al. 1998; 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 and tiller production 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 55ºC, and weighing it. The number of *Spartina* tillers produced was determined by visually counting all tillers present within each mesocosm. The density of planthoppers, *Spartina* biomass, and the number of tillers per cage were scaled up to units per m^2.

Since the experiment was designed as an incomplete factorial, the analyses of the direct and interactive effects of predator species richness and trophic composition on herbivore suppression and plant productivity were done using the levels of species richness for which all trophic combinations were possible, the 2-species level of richness and the 3-species level of richness. The interactive and main effects of predator species richness (2 species versus 3 species) and trophic composition (strict predators only, intraguild predators only, or a mixture of both) on planthopper population density, *Spartina* biomass, and the number of *Spartina* tillers was assessed by performing a separate mixed model one-way analyses of variance for each response variable with blocks included as a random source of variation (SAS 1999). To account for differences within and among treatments in total predator abundance, initial predator density was incorporated into the ANOVA model as a covariate.

The effect of predator species richness (2 versus 3 species for the mixture of both strict and intraguild predators; 1, 2, or 3 species for both strict predators alone and intraguild predators alone) on prey suppression and plant productivity was also assessed within each trophic-composition category independently. For each trophic-composition category, separate mixed model ANOVAs were performed to investigate the impact of predator species richness on planthopper population density, *Spartina* biomass, and the number of *Spartina* tillers with blocks modeled as a random source of variation (SAS 1999). Initial predator density was included as a covariate for the analysis of the mixture of both strict and intraguild predators. However, including initial predator density as a covariate was not possible for the analyses of either the strict predators alone or the intraguild predators alone, since there was only a single predator density represented at each level of species richness for both of these trophic composition categories. Therefore, for strict predators alone and intraguild predators alone, the expected proportion of planthoppers surviving predators with independent effects were generated using the multiplicative risk model (Soluk and Collins 1988; Sih, Englund et al. 1998). The expected number of planthoppers surviving was determined by multiplying the expected proportion surviving by the actual observed number of planthoppers present in the no-predator control. Observed and predicted planthopper densities were compared by performing a two-way analysis of variance with value type (observed versus predicted values) and predator species richness as predictor variables in the model. A significant interactive effect of value type and predator species richness on planthopper density indicated non-additivity of predator effects. An observed planthopper population size that was greater than the expected population size based on the multiplicative risk model indicated the occurrence of antagonistic interactions, such as intraguild predation, among predators.

The impacts of trophic composition (strict predators only, intraguild predators only, or a mixture of both) on prey suppression and plant productivity within the two and three levels of species richness were also determined independently. For each level of species richness, consecutive mixed model ANOVAs were performed to assess the effect of trophic composition on planthopper population density, *Spartina* biomass, and the number of *Spartina* tillers with blocks modeled as a random source of variation (SAS 1999). Once again, including initial predator density as a covariate was not possible. Therefore, for each trophic composition the expected number of planthoppers surviving was generated using the multiplicative risk model (Soluk and Collins 1988; Sih, Englund et al. 1998) and value type (observed versus predicted) and its interaction with predator trophic composition were included as predictor variables in the analysis of variance model.

For all analyses, means were compared by performing t-tests with Bonferroni adjustment of p-values to account for multiple comparisons (Sokal and Rohlf 1987). Data were log-transformed when necessary to meet assumptions of analysis of variance including normality and homogeneity of variances (Sokal and Rohlf 1987).

RESULTS

Verification of the trophic identity of predators: strict vs. intraguild predators

Laboratory feeding trials confirmed that my initial assignment of predators to trophic groups (*Tytthus*, *Naemia*, and *Grammonota* as strict predators; *Pardosa, Clubiona,* and *Marpissa* as intraguild predators) was accurate. All predators consumed significant numbers of planthoppers over the 48 hour exposure period. Consumption of the active stages of planthoppers by the predators *Naemia, Grammonota, Pardosa, Clubiona*, and *Marpissa* was significantly greater than zero, indicating significant predation effects of these predators on the herbivores (t = 4.89, 4.16, 4.99, 3.85, and 4.78, respectively; $P < 0.01$) (Fig. 2.1). In addition, there was no difference in the number of adult planthoppers consumed by a single individual of any of these predator species ($F_{4, 45} = 0.25$, $P > 0.05$) (Fig. 2.1). *Tytthus* also consumed significant numbers of planthopper eggs, reducing the number of emerging planthopper nymphs compared to *Tytthus*-free controls ($F_{1, 15} = 11.59$, $P < 0.05$) (Fig. 2.2). These data suggest a single *Tytthus* bug kills on average 28 ± 8 planthopper eggs per day.

There was a significant effect of predator species identity on the intraguild predation of *Tytthus* ($F_{4, 95} = 7.33$, $P < 0.01$) (Fig. 2.3). The number of *Tytthus* consumed by either *Naemia* or *Grammonota* was not significantly different from zero (t = 0.97 and 0.57, respectively; $P > 0.05$) (Fig. 2.3), suggesting that these predators did not engage in the intraguild predation of *Tytthus*. However, *Pardosa, Clubiona,* and *Marpissa* did engage in intraguild predation, consuming significant numbers of *Tytthus* (t = 2.57, 3.26, and 2.88, respectively; $P < 0.05$) (Fig. 2.3). Pairing predators in petri dishes confirmed that both *Naemia* and *Grammonota* are strict predators since neither was a successful predator of *Pardosa, Clubiona, Marpissa,* or each other (Table 2.1). *Grammonota* did fall prey to *Pardosa, Clubiona,* and *Marpissa*, whereas *Naemia* appeared immune to intraguild predation (Table 2.1). All intraguild predators were capable of consuming all other intraguild predators, however, *Clubiona* appeared to be the most voracious predator of other spiders followed by *Marpissa* and then *Pardosa* (Table 2.1).

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

Differences in planthopper suppression among individual predator species were not large suggesting that the occurrence of a sampling effect was unlikely with these predators (Fig. 2.4). After correcting for differences in the initial abundance of predators, there was a significant effect of predator treatment on planthopper density when the no-predator control was included in the analysis ($F_{6, 19} = 3.81$, $P < 0.05$). However, the significant effect of predator treatment disappeared when the no-predator control was omitted and only the individual predator treatments were compared ($F_{5, 16} = 0.25$, $P > 0.05$). Comparisons of individual treatment means revealed that the impact of *Tytthus* on planthopper suppression was no different from that of *Pardosa* (t = 1.81, $P > 0.05$), but significantly greater than that of *Naemia, Grammonota, Clubiona,* and *Marpissa* (t = 2.61, 2.41, 2.66, and 3.26, respectively; $P < 0.05$) (fig 2.4).

There was a significant interactive effect of predator species richness and trophic composition on planthopper density ($F_{2, 50} = 3.78$, $P < 0.05$), indicating that the impact of increasing predator richness on prey suppression depended on the trophic composition of the predator complex present. An examination of the main effect of predator species richness on the occurrence of trophic cascades showed that increasing species richness from two to three diminished planthopper suppression and enhanced planthopper density ($F_{1, 115} = 33.87$, $P < 0.01$) (Fig. 2.5a), but this effect did not cascade down to impact either *Spartina* biomass ($F_{1, 115} = 0.80$, $P > 0.05$) (Fig. 2.5b) or tiller production ($F_{1, 115} = 2.05$, $P > 0.05$) (Fig. 2.5c). However, predator species richness had idiosyncratic effects on the strength of trophic cascades within individual trophic-composition categories. Planthopper suppression was additively enhanced when the richness of strict predators was increased from one to three (non-significant ‘value type’ x ‘predator species richness’ interaction; $F_{2, 32} = 1.10$, $P > 0.05$) (Fig. 2.6a), an effect that propagated down and resulted in increased *Spartina* biomass ($F_{2, 20} = 3.43$, $P = 0.05$) (Fig. 2.6b) and tiller production ($F_{2, 20} = 3.62$, $P < 0.05$) (Fig. 2.6c). By contrast, intraguild predators interacted antagonistically, resulting in diminished planthopper suppression as predator richness was enhanced (significant ‘value type’ x ‘predator species richness’ interaction; $F_{2, 37} = 3.67$, $P < 0.05$) (Fig. 2.7a). As a result, any trophic cascade on plant productivity was dampened and there was no change in either *Spartina* biomass ($F_{2, 26} = 0.05$, $P > 0.05$) (Fig. 2.7b) or tiller production ($F_{2, 26} = 0.04$, $P > 0.05$) (Fig. 2.7c) with an increase in the number of intraguild predator species. When 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 ($F_{1, 82} = 6.78$, $P < 0.05$)

(Fig. 2.8a). However, this dampened level of suppression resulted in an unexpected increase in *Spartina* biomass ($F_{1, 82} = 13.02$, $P < 0.05$) (Fig. 2.8b), whereas tiller production remained unchanged ($F_{1, 82} = 0.38$, $P > 0.05$) (Fig. 2.8c). 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, Gratton et al. 2002; Finke and Denno 2004). It appears that the treatments comprising a mixture of strict and intraguild predators may have been randomly assigned to mesocosms with greater initial *Spartina* biomass, despite the fact that treatments were blocked by visual assessment of biomass. Unfortunately, no data is available on the pre-treatment biomass of *Spartina* within mesocosms.

The main effect of the trophic composition of the predator complex (averaged across levels of species richness) significantly affected the occurrence of the trophic cascade. Specifically, as the proportion of intraguild predator species in the assemblage increased (and thus the opportunity for the occurrence of intraguild predation), suppression was relaxed and planthopper populations were enhanced ($F_{2, 115} = 14.63$, $P < 0.01$) (Fig. 2.9a). This resulted in a dampened trophic cascade. Although there was no difference in *Spartina* biomass among trophic composition treatments ($F_{2, 115} = 0.36$, $P > 0.05$) (Fig. 2.9b), tiller production was negatively impacted by an increase in the proportion of intraguild predators in the assemblage ($F_{2, 115} = 3.06$, $P = 0.05$) (Fig. 2.9c).

For each level of species richness independently, increasing the proportion of intraguild predators in the complex also dampened the trophic cascade. For instance, increasing the proportion of intraguild predators from 0 to 100% when the level of species richness was two resulted in antagonistic interactions among predators and diminished planthopper suppression (significant ‘value type’ x ‘predator trophic composition’ interaction; $F_{2, 49} = 4.07$, $P < 0.05$) (Fig. 2.10a). *Spartina* biomass was unaffected by this increase in planthopper density ($F_{2, 37} = 1.73$, $P > 0.05$) (Fig. 2.10b), but tiller production was significantly diminished ($F_{2, 37} = 4.87$, $P < 0.05$) (Fig. 2.10c). Likewise, when the level of species richness was three, enhancing the proportion of intraguild predators in the assemblage resulted in reduced planthopper suppression (greater planthopper population size) (significant ‘value type’ x ‘predator trophic composition’ interaction; $F_{3, 81} = 7.48$, $P < 0.05$) (Fig. 2.11a), decreased *Spartina* biomass ($F_{3, 65} = 3.26$, $P < 0.05$) (Fig. 2.11b), and diminished tiller production ($F_{3, 65} = 2.51$, $P = 0.06$) (Fig. 2.11c).

DISCUSSION

Results show that intraguild predation is the mechanism by which predator diversity dampens trophic cascades in this salt marsh food web. I found that increasing predator species richness influenced the occurrence of trophic cascades (Fig. 2.5), but that the magnitude and the direction of the effect depended on the trophic composition (proportion of intraguild predators) of the predator complex. Specifically, with an increase in the number of strict predator species, there was an additive decrease in planthopper abundance and an increase in *Spartina* productivity (Fig. 2.6). By contrast, a commensurate increase in the number of intraguild predators promoted antagonistic interactions and resulted in a higher density of herbivores and lower plant productivity at the highest level of predator species richness (Fig. 2.7). Predator trophic composition also influenced the strength of the trophic cascade independent of changes in predator species richness (Fig. 2.9). Increasing the proportion of intraguild predator species present within the predator assemblage diminished the ability of predators to suppress planthopper populations and decreased plant productivity. This effect occurred consistently both across and within individual levels of predator species richness (Figs. 2.10 and 2.11). Therefore, my results show that the trophic composition of the predator complex may be equally or even more important than the number of predator species *per se* in determining the relationship between predator diversity and ecosystem function, as indexed by herbivore suppression and the strength of the trophic cascade.

It could be argued that this relationship between predator trophic composition and the occurrence of a trophic cascade was not due to the occurrence of intraguild predation, but to the reduced probability of including *Tytthus* (a strict predator with relatively large impacts on herbivore populations, Fig. 2.4) 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*, since the probability of including *Pardosa* was increased as the probability 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 is enhanced was due 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 (Wilby and Thomas 2002; Cardinale, Harvey et al. 2003; Montoya, Rodríguez et al. 2003; Finke and Denno 2004; Snyder, Chang et al. 2005). Likewise, this study demonstrates that a 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. Increasing predator diversity when only strict predators are present will additively enhance prey suppression and positively impact plants, whereas increasing predator diversity when intraguild predators are present will have negative effects on prey suppression and plant productivity due to the enhanced opportunity for intraguild predation. I 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, Myers et al. 1989; Rosenheim 1998; Arim and Marquet 2004).

Understanding the importance of predator trophic identity 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, Naeem et al. 2001). However, little is known about the consequences of biodiversity loss at higher trophic levels (Duffy 2002; 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 programs in agricultural systems is to initiate trophic cascades by manipulating predator complexes that result in enhanced crop yield (DeBach and Rosen 1991; Snyder, Chang et al. 2005). My results suggest that diverse predator assemblages will optimally suppress herbivore pests and maximize productivity in systems where intraguild predators are rare. When intraguild predators abound, promoting a diverse predator assemblage will 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 and Denno 2002), may be necessary in order to maximize productivity while simultaneously encouraging predator diversity in agricultural systems.

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Table 2.1. Intraguild predation events recorded between individual predators in petri dishes. The number of successful predation events (wins) by each species and the total number of trials (n) are shown. The difference between the total number of trials and the total number of wins for any given pair is the number of trials in which a predation even did not occur.

#wins : #wins
n = # trials
	Strict predators		***Intraguild predators***		

	Naemia	**Grammonota**	**Pardosa**	**Clubiona**	**Marpissa**
Naemia					
Grammonota	*Gramm* : *Naemia* 0 : 0 n = 6				
Pardosa	*Pard* : *Naemia* 0 : 0 n = 6	*Pard* : *Gramm* 3 : 0 n = 6			
Clubiona	*Club* : *Naemia* 0 : 0 n = 6	*Club* : *Gramm* 4 : 0 n = 6	*Club* : *Pard* 5 : 2 n = 10		
Marpissa	*Marp* : *Naemia* 0 : 0 n = 6	*Marp* : *Gramm* 3 : 0 n = 6	*Marp* : *Pard* 9 : 1 n = 15	*Marp* : *Club* 2 : 7 n = 9	

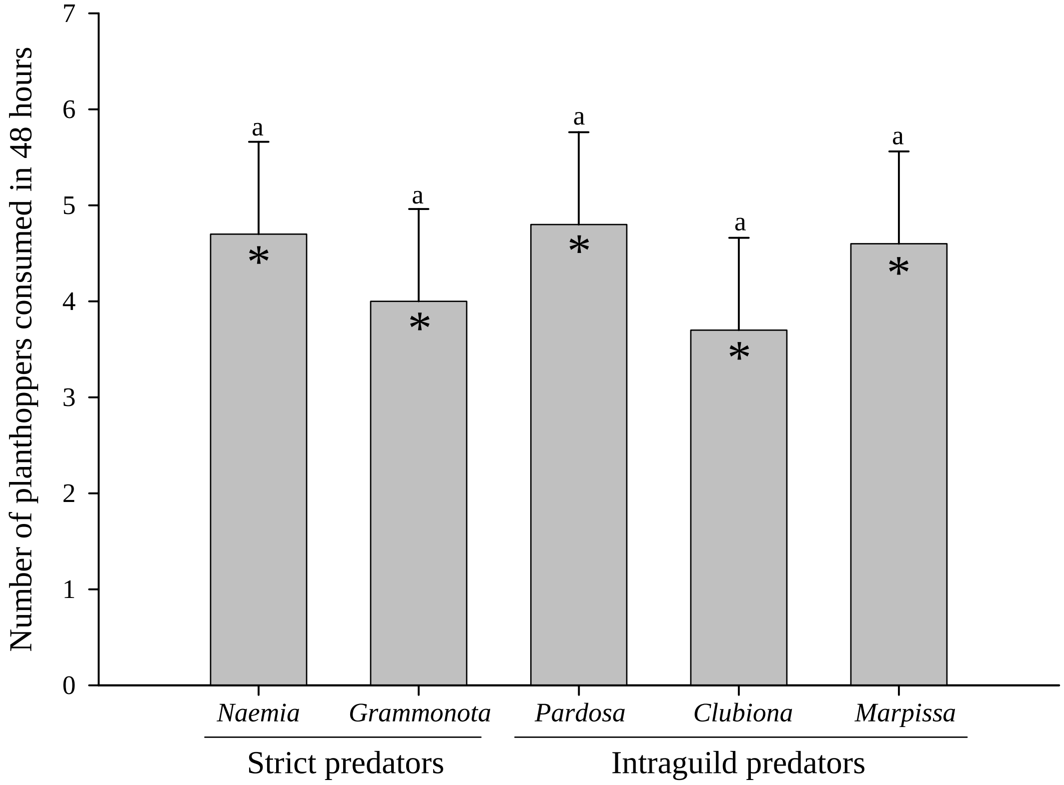

Figure 2.1. The effect of predator species identity (*Naemia, Grammonota*, *Pardosa, Clubiona*, or *Marpissa*) on the number of *Prokelisia* planthopper adults consumed by an individual predator over 48 h (the number of planthoppers remaining in the no-predator control - the number of planthoppers remaining in the presence of the predator). There was no difference among predators in the number of planthoppers consumed ($F_{4,\,45}$ = 0.25, $P > 0.05$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$). Asteriks (*) indicate means that are significantly different from zero (i.e. there was a significant effect of predation).

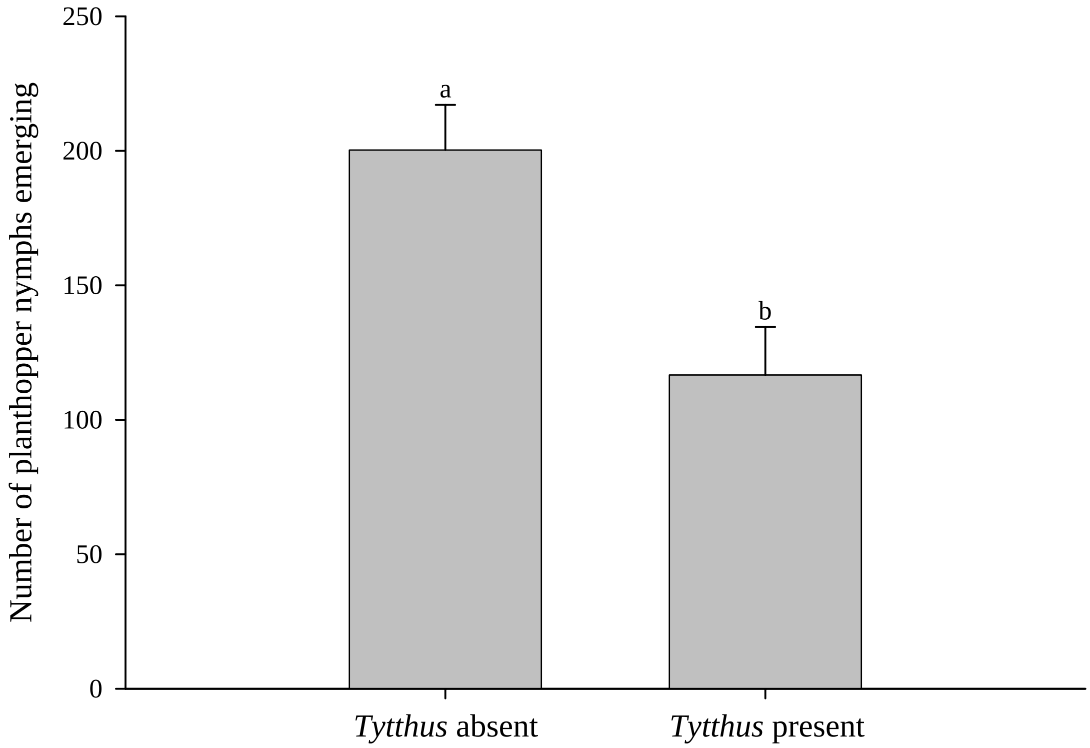

Figure 2.2. The effect of *Tytthus* predation (present or absent) on the number of planthopper nymphs ultimately emerging from plants into which female planthoppers have oviposited and on which *Tytthus* has fed over 72 h. The number of planthopper nymphs emerging was significantly reduced in the presence of *Tytthus* ($F_{1,15} = 11.59$, $P < 0.05$), evidence for the predation of planthopper eggs by *Tytthus*. Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

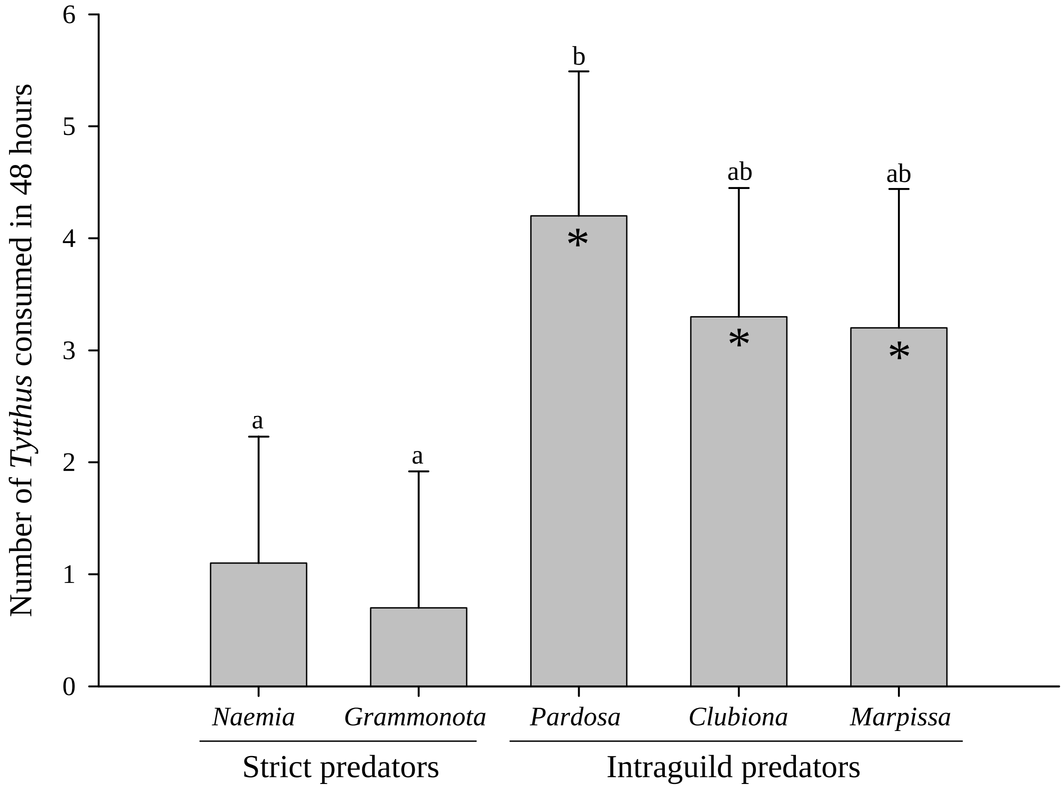

Figure 2.3. The effect of predator species identity (*Naemia*, *Grammonota*, *Pardosa*, *Clubiona*, or *Marpissa)* on the number of *Tytthus* consumed by an individual predator over 48 hours (the number of *Tytthus* remaining in the no-predator control - the number of *Tytthus* remaining in the presence of the predator). Predator identity had a significant effect on predation of *Tytthus*, whereby the hypothesized strict predators (*Naemia* and *Grammonota*) did not consume *Tytthus*, but the hypothesized intraguild predators (*Pardosa*, *Clubiona*, and *Marpissa*) did engage in intraguild predation of *Tytthus* ($F_{4,\,95} = 7.33$, $P < 0.01$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$). Asteriks (*) indicate means that are significantly different from zero (i.e. intraguild predation occurred).

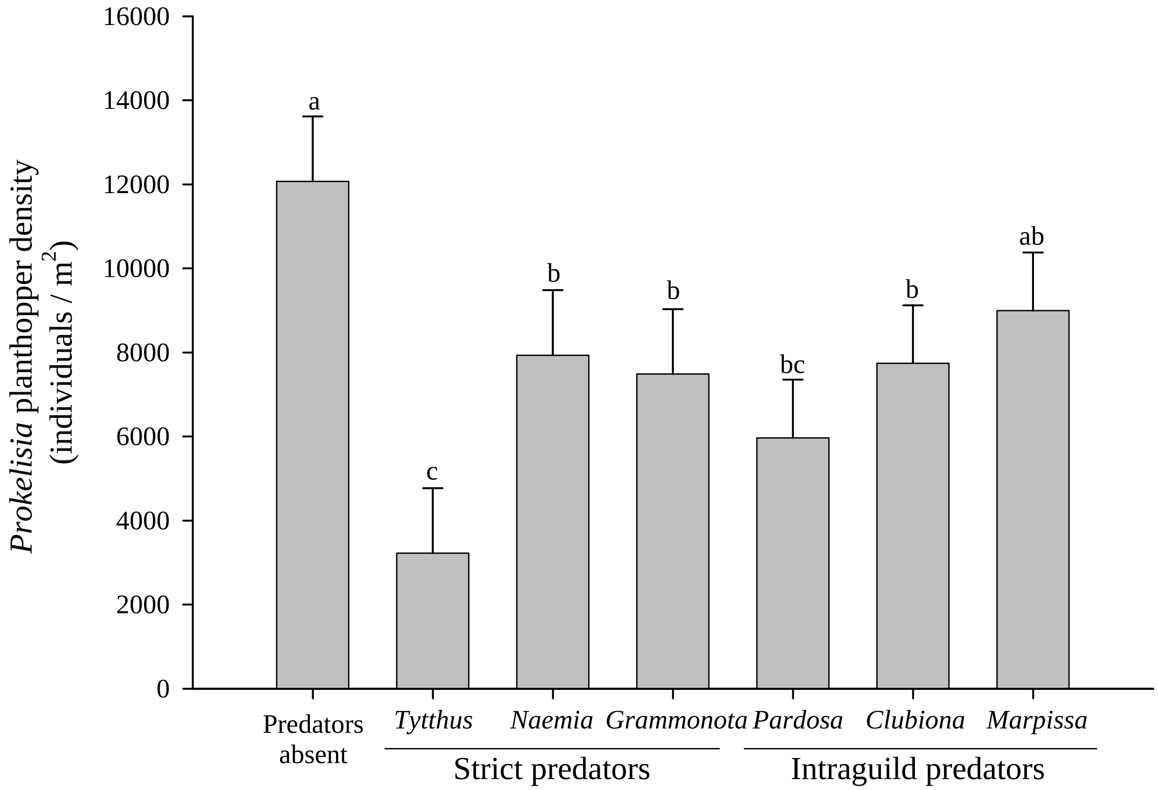

Figure 2.4. The effect of predator species identity (no predators, *Tytthus, Naemia, Grammonota*, *Pardosa, Clubiona,* or *Marpissa*) on the density of *Prokelisia* planthopper adults and nymphs present in mesocosms after a 68-d interaction period. There was a significant effect of predator treatment on planthopper density ($F_{6, 19} = 3.81$, $P < 0.05$). However, differences in planthopper suppression among individual predator species were not large suggesting that the occurrence of a sampling effect was unlikely with these predators. Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

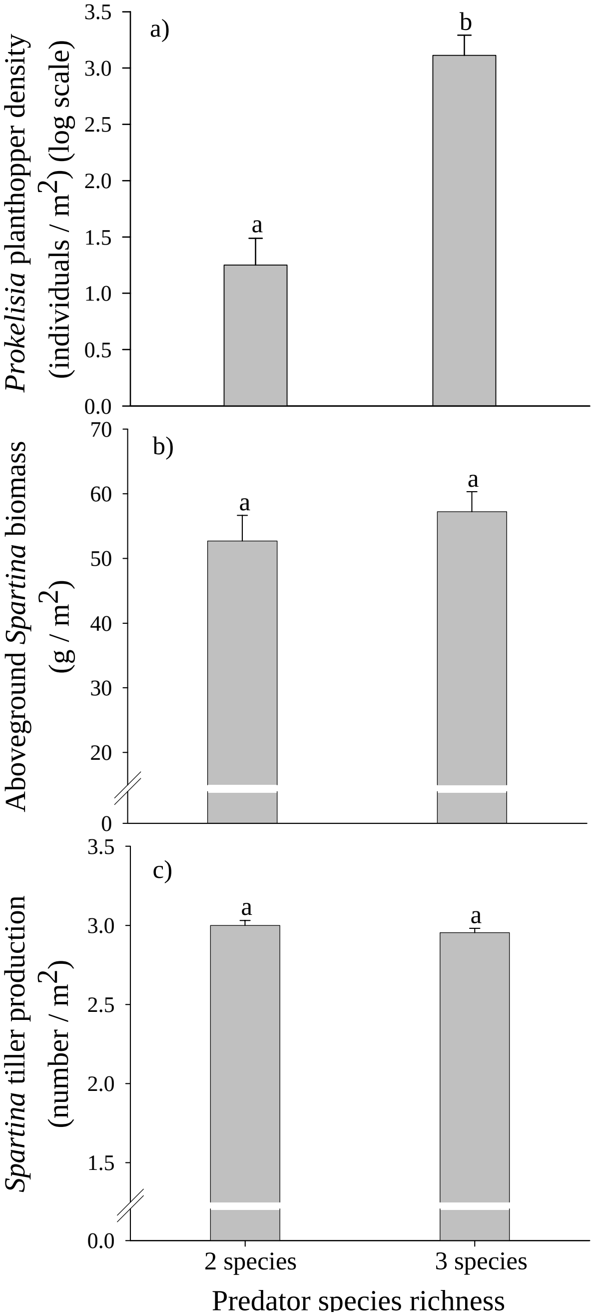

Figure 2.5. The main effect of predator species richness (2 species or 3 species) on (a) *Prokelisia* planthopper density, (b) aboveground *Spartina* biomass, and (c) *Spartina* tiller production in mesocosms after a 68-d interaction period. Increasing species richness enhanced planthopper density ($F_{1,\,115} = 33.87$, $P < 0.01$), but this effect did not cascade down to impact either *Spartina* biomass ($F_{1,\,115} = 0.80$, $P > 0.05$) or tiller production ($F_{1,\,115} = 2.05$, $P > 0.05$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

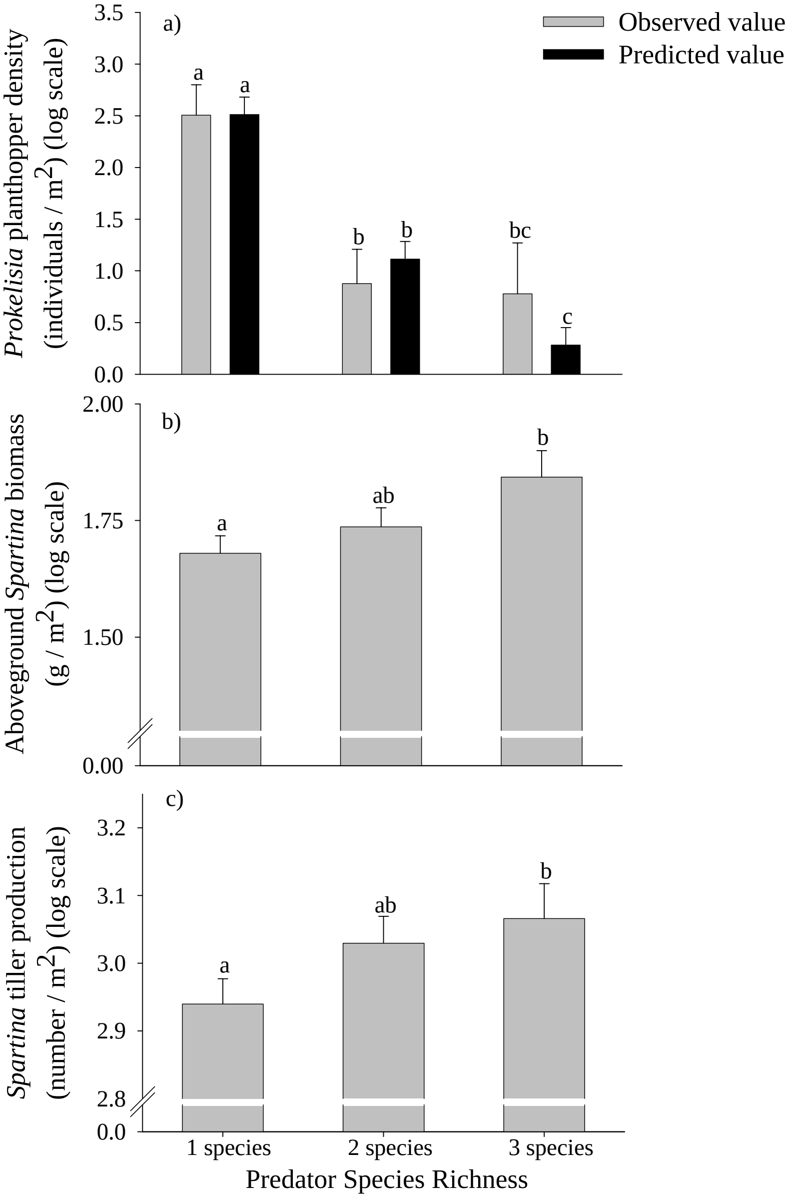

Figure 2.6. The effect of strict predator species richness (1, 2, or 3 species) on (a) *Prokelisia* planthopper density, (b) aboveground *Spartina* biomass, and (c) *Spartina* tiller production in mesocosms after a 68-d interaction period. Observed values (gray bars) indicate the actual measured response at the end of the experiment, whereas predicted values (black bars) indicate the number of planthoppers estimated to survive if predators had independent additive effects. Strict predators additively enhanced planthopper suppression [there was a non-significant 'value type' (observed value or predicted value) x 'predator species richness' (1, 2, or 3 species) interaction on planthopper density ($F_{2, 32} = 1.10$, $P > 0.05$)] and this effect cascaded down to increase *Spartina* biomass ($F_{2, 20} = 3.43$, $P = 0.05$) and tiller production ($F_{2, 20} = 3.62$, $P < 0.05$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

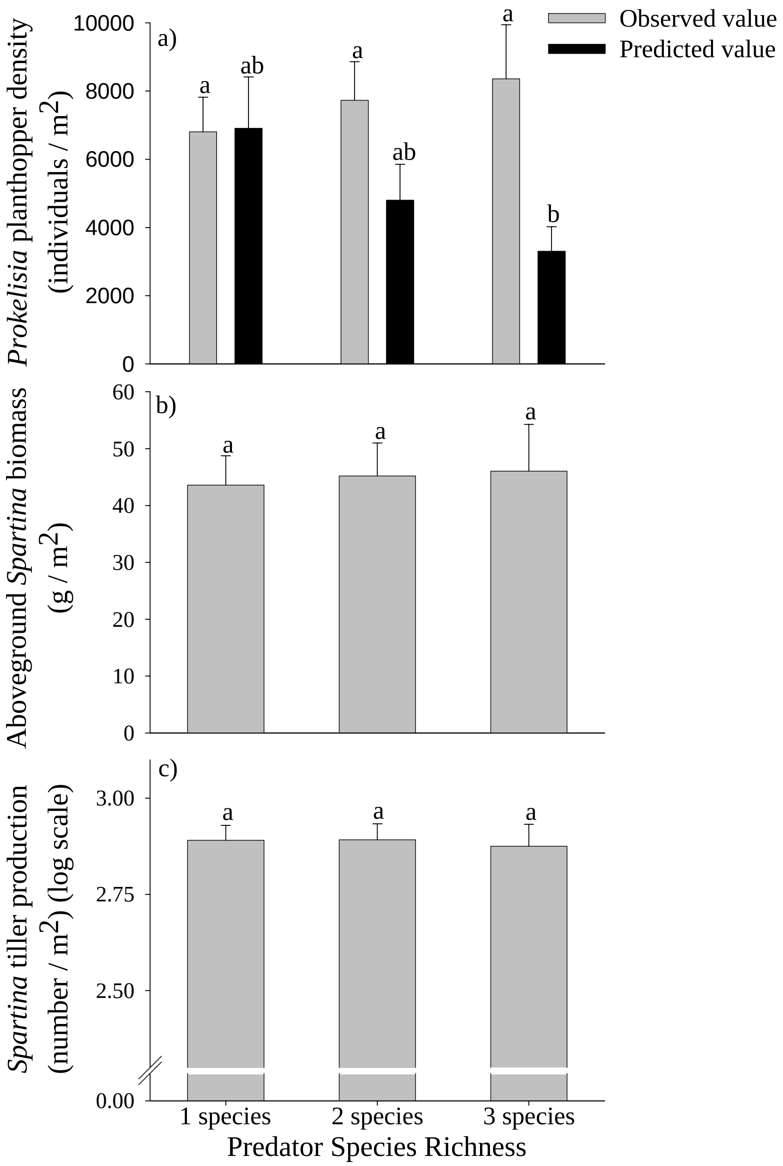

Figure 2.7. The effect of predator species richness (1, 2, or 3 species) when only intraguild predators are present on (a) *Prokelisia* planthopper density, (b) aboveground *Spartina* biomass, and (c) *Spartina* tiller production in mesocosms after a 68-d interaction period. Observed values (gray bars) indicate the actual measured response at the end of the experiment, whereas predicted values (black bars) indicate the number of planthoppers estimated to survive if predators had independent additive effects. Intraguild predators interacted antagonistically with an increase in species richness [there was a significant ‘value type’ (observed value or predicted value) x ‘predator species richness’ (1, 2, or 3 species) interaction on planthopper density ($F_{2, 37} = 3.67$, $P < 0.05$)] and the trophic cascade was dampened. There was no change in *Spartina* biomass ($F_{2, 26} = 0.05$, $P > 0.05$) or tiller production ($F_{2, 26} = 0.04$, $P > 0.05$) with an increase in predator species richness. Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

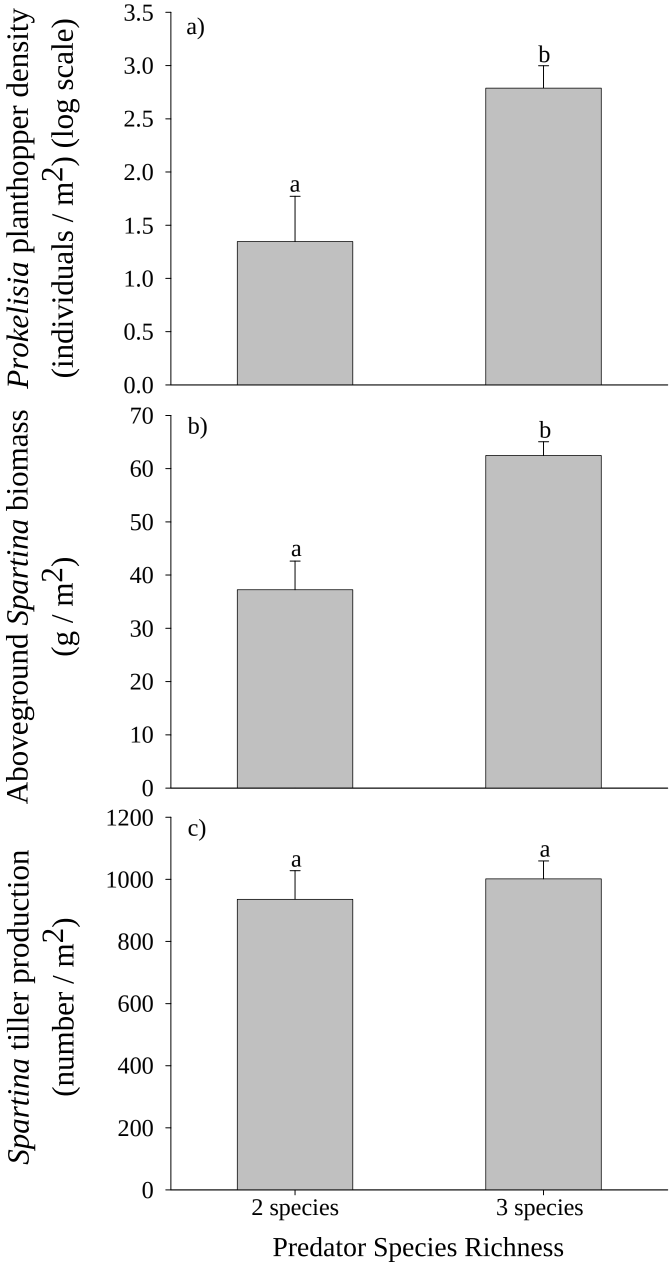

Figure 2.8. The effect of predator species richness (2 species or 3 species) when a mixture of both strict and intraguild predators are present on (a) *Prokelisia* planthopper density, (b) aboveground *Spartina* biomass, and (c) *Spartina* tiller production in mesocosms after a 68-d interaction period. Predators interacted antagonistically with an increase in species richness when both strict and intraguild predators were present, resulting in significantly more planthoppers surviving ($F_{1,\,82} = 6.78$, $P < 0.05$). This dampened planthopper suppression with an increase in predator species richness resulted in an unpredicted increase in *Spartina* biomass ($F_{1,\,82} = 13.02$, $P < 0.05$) and did not affect tiller production ($F_{1,\,82} = 0.38$, $P > 0.05$).

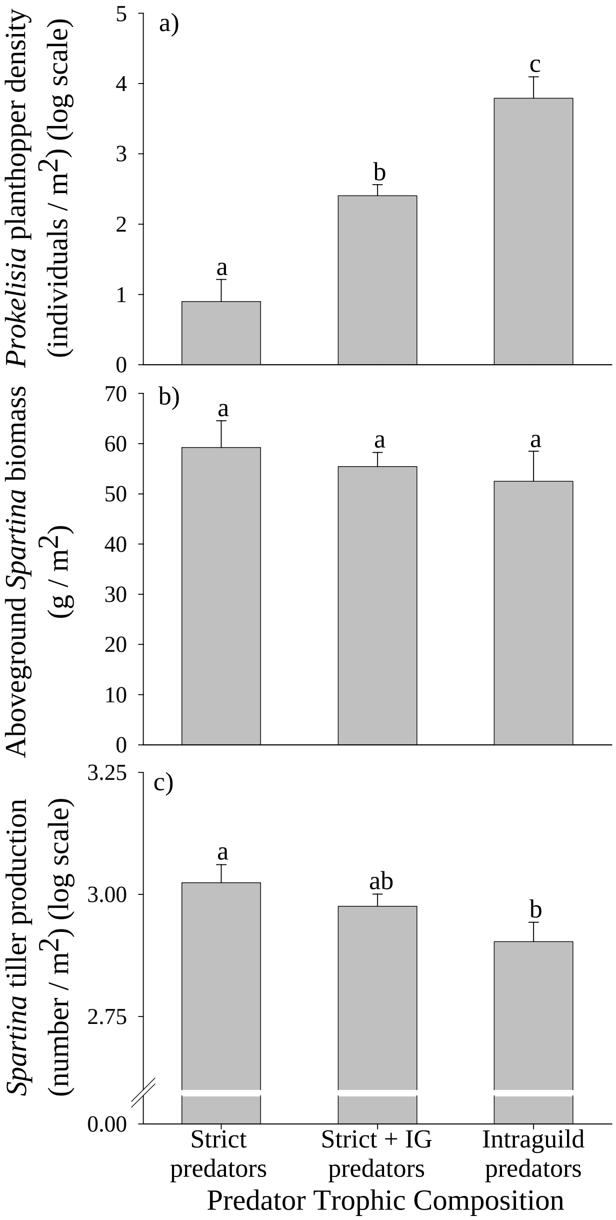

Figure 2.9. The main effect of predator trophic composition (strict predators only, a mixture of strict and intraguild predators, or intraguild predators only) on (a) *Prokelisia* planthopper density, (b) aboveground *Spartina* biomass, and (c) *Spartina* tiller production in mesocosms after a 68-d interaction period. Predator trophic compositions are arranged along the x-axis sequentially in the order of increasing proportion of intraguild predator species present within the predator assemblage. Increasing the proportion of intraguild predator species present within the predator assemblage diminished planthopper suppression ($F_{2,\,115} = 14.63$, $P < 0.01$) and dampened the trophic cascade. There was no difference in *Spartina* biomass among trophic composition treatments ($F_{2,\,115} = 0.36$, $P > 0.05$), but tiller production was negatively impacted by an increase in the proportion of intraguild predator species present ($F_{2,\,115} = 3.06$, $P = 0.05$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

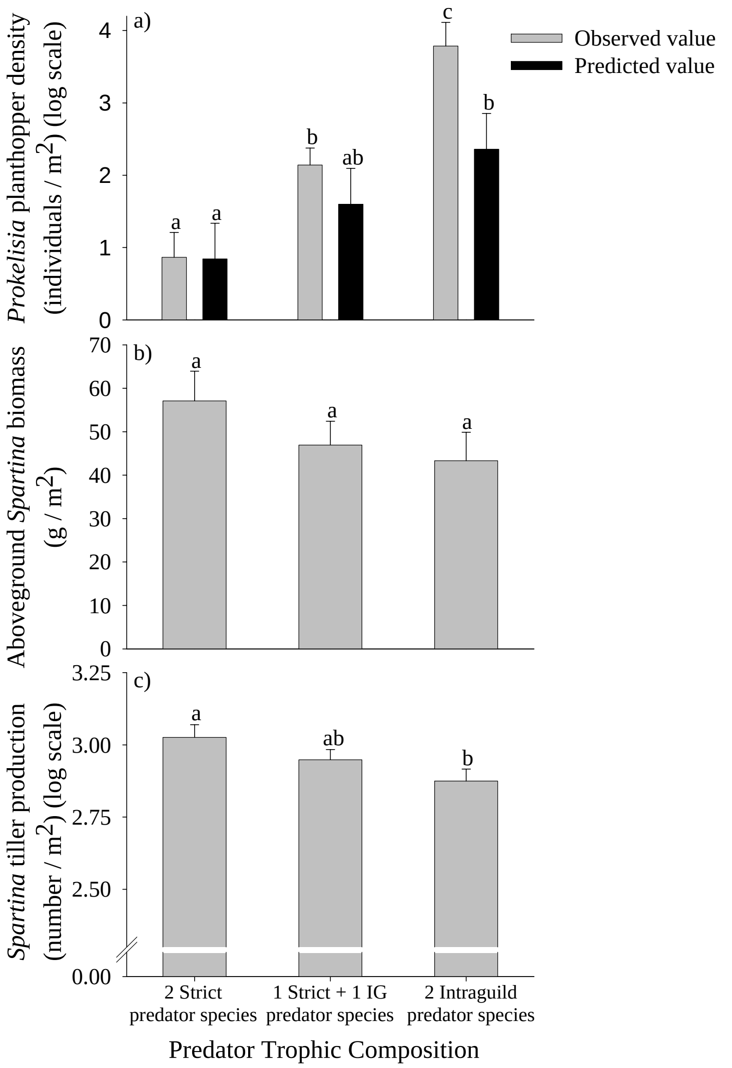

Figure 2.10. The effect of predator trophic composition (2 strict predator species, 1 strict and 1 intraguild predator species, or 2 intraguild predator species) when the level of predator species richness is 2 on (a) *Prokelisia* planthopper density, (b) aboveground *Spartina* biomass, and (c) *Spartina* tiller production in mesocosms after a 68-d interaction period. Predator trophic compositions are arranged along the x-axis sequentially in the order of increasing proportion of intraguild predator species present within the predator assemblage. Observed values (gray bars) indicate the actual measured response at the end of the experiment, whereas predicted values (black bars) indicate the number of planthoppers estimated to survive if predators had independent additive effects. Increasing the proportion of intraguild predator species present within the predator assemblage when the level of species richness was 2 resulted in diminished planthopper suppression [there was a significant ‘value type’ (observed value or predicted value) x ‘predator trophic composition’ (2 strict predator species, 1 strict and 1 intraguild predator species, or 2 intraguild predator species) interaction on planthopper density ($F_{2, 49} = 4.07$, $P < 0.05$)], no change in *Spartina* biomass ($F_{2, 37} = 1.73$, $P > 0.05$), and a decrease in tiller production ($F_{2, 37} = 4.87$, $P < 0.05$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

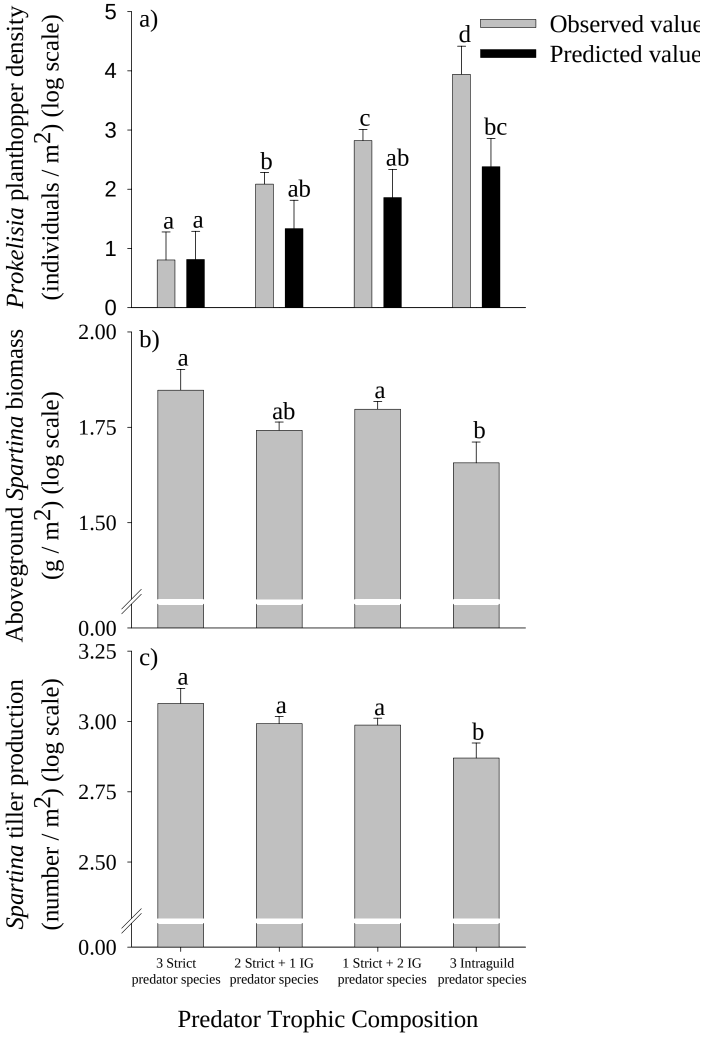

Figure 2.11. The effect of predator trophic composition (3 strict predator species, 2 strict and 1 intraguild predator species, 1 strict and 2 intraguild predator species, or 2 intraguild predator species) when the level of predator species richness is 3 on (a) *Prokelisia* planthopper density, (b) aboveground *Spartina* biomass, and (c) *Spartina* tiller production in mesocosms after a 68-d interaction period. Predator trophic compositions are arranged along the x-axis sequentially in the order of increasing proportion of intraguild predator species present within the predator assemblage. Observed values (gray bars) indicate the actual measured response at the end of the experiment, whereas predicted values (black bars) indicate the number of planthoppers estimated to survive if predators had independent additive effects. Increasing the proportion of intraguild predator species present within the predator assemblage when the level of species richness was 3 resulted in diminished planthopper suppression [there was a significant 'value type' (observed value or predicted value) x 'predator trophic composition' interaction on planthopper density ($F_{3, 81} = 7.48$, $P < 0.05$), decreased *Spartina* biomass ($F_{3, 65} = 3.26$, $P < 0.05$), and reduced tiller production ($F_{3, 65} = 2.51$, $P = 0.06$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

CHAPTER 3: A refuge from intraguild predation in complex-structured habitats: Implications for prey suppression and the strength of terrestrial trophic cascades

ABSTRACT

Habitat structure has been shown to enhance the strength of cascading predator effects on plants due to the accumulation of predators in complex habitats, but the ability of architecturally complex habitats to influence primary producers by mediating predator-predator interactions is unclear. Complex-structured habitats can alter trophic interactions among predators and their combined impact on herbivore populations, but an investigation of the influence of habitat complexity on the cascading effects of diverse predator assemblages on primary productivity is lacking. The objective of this study was to determine if habitat complexity, by providing a refuge for predators from intraguild predation, might enhance the collective ability of predators to limit herbivore populations and thus increase the overall strength of the trophic cascade.

I investigated the ability of habitat complexity to mediate predator-predator interactions and the strength of cascading predator effects on basal resources using an assemblage of terrestrial arthropods inhabiting Atlantic coastal salt marshes. To determine the direct and interactive effects of predator diversity and habitat complexity for the occurrence of trophic cascades, I conducted a full factorial experiment in laboratory mesocosms containing *Spartina* cordgrass transplants and herbivorous *Prokelisia* planthoppers. Five predator diversity manipulations (no predators, *Pardosa* only, *Grammonota* only, *Tytthus* only, or a combination of all three predator species)

were crossed with two levels of habitat complexity (thatch absent or present) to determine the effects of the various treatment combinations on intraguild predation (predator density), herbivore (*Prokelisia* planthopper) population size, and the productivity (biomass) of *Spartina* cordgrass after two planthopper generations.

I found that complex habitats with thatch tempered antagonistic predator-predator interactions and enhanced planthopper suppression by the diverse predator assemblage. This resulted because complex-structured habitats provided a refuge for predators from intraguild predation (including cannibalism). However, reducing antagonistic interactions among predator species and increasing prey suppression did not enhance the conductance of predator effects through the food web to positively impact primary producers. Notably, there was a trend towards greater *Spartina* biomass in the complex-structured habitat, despite the fact that this experiment was initiated late in the *Spartina* growing season after most plant growth occurred. Therefore, the possibility exists that changes in habitat complexity might enhance trophic cascades and impact productivity positively by mediating trophic interactions among predators.

INTRODUCTION

Habitat destruction is generally cited as the primary cause of the currently rapid rate of species extinctions (Myers et al. 2000, Pimm and Raven 2000, Melián and Bascompte 2002, Nakagiri and Tainaka 2004). Therefore, incorporating habitat quality into studies investigating the relationship between biodiversity and ecosystem functioning is essential for gaining a complete understanding of the consequences of biodiversity loss (Srivastava 2002). Many studies have documented that ecosystem functions, such as primary productivity, are altered by a decline in species diversity (Hughes and Petchey 2001; Loreau, Naeem et al. 2001). However, an investigation of the links between habitat quality, biodiversity loss, and ecosystem functioning would provide additional insight into the direct effects of biodiversity loss versus the habitat destruction itself for the functioning of ecosystems (Petchey, McPherson et al. 1999; Srivastava 2002).

Habitat structure, the number of different physical elements per unit habitat volume, is one aspect of habitat quality that could impact ecosystem functioning due to its ability to mediate trophic interactions (McCoy and Bell 1991; Langellotto and Denno 2004). Trophic interactions are emerging as an important element of the relationship between biodiversity and ecosystem functioning (Spiller and Schoener 1994; Wilby and Thomas 2002; Cardinale, Harvey et al. 2003; Montoya, Rodríguez et al. 2003; Finke and Denno 2004; Hillebrand and Cardinale 2004; Ives, Cardinale et al. 2005; Snyder, Chang et al. 2005). For example, predator diversity can have significant consequences for prey suppression and primary production via the occurrence of trophic cascades, but the magnitude and direction of the effect is dependent on the trophic identities of the predators. Specifically, the occurrence of intraguild predation when predator diversity is high diminishes cascading predator effects on prey and reduces primary productivity (Finke and Denno 2004), Chapters 1 and 2).

In multi-trophic systems, data suggests that habitat structure can mediate trophic interactions and affect the probability for trophic cascades. Predator species diversity and individual predator abundance are often elevated in complex-structured habitats (Greenstone 1984; Riechert and Bishop 1990; Rypstra, Carter et al. 1999; Langellotto and Denno 2004). In addition, the structural complexity of habitats has been shown to influence predator-prey, host-parasitoid, and predator-predator interactions (Root 1973; Kareiva 1987; Hunter and Price 1992; Bottrell, Barbosa et al. 1998; Clark and Messina 1998; Denno, Gratton et al. 2002; Finke and Denno 2002; Cronin 2003; Harvey and Eubanks 2003; Langellotto and Denno 2004). Notably, there is widespread evidence that intraguild predation (including cannibalism) is reduced when predators co-occur in complex-structured habitats (Crowder and Cooper 1982; Gunnarsson 1990; Agrawal and Karban 1997; Roda, Nyrop et al. 2000; Norton, English-Loeb et al. 2001; Langellotto 2002; Grabowski 2004), which in turn enhances the suppression of shared prey populations (Finke and Denno 2002); but see (Grabowski 2004). Therefore, habitat structural complexity might mediate the extent to which predator effects on prey propagate down to influence primary productivity when predator diversity is high. However, the consequences of such complex interactions between predator diversity, trophic interactions, and habitat complexity for ecosystem functioning (e.g. trophic cascades) are largely unknown.

I investigated the ability of habitat complexity to mediate predator-predator interactions and the strength of cascading predator effects on basal resources using an assemblage of terrestrial arthropods inhabiting Atlantic coastal salt marshes. In this system, *Prokelisia* planthoppers are the most common herbivores and they are consumed by a variety of invertebrate predators including hunting spiders (*Pardosa littoralis*), web-building spiders (*Grammonota trivitatta*), and mirid bugs (*Tytthus vagus*). This predator complex includes both intraguild predators (the hunting spider) that consume other predators as well as strict predators (the web-building spiders and the mirid bug) that do not engage in intraguild predation (Finke and Denno 2002; Denno, Mitter et al. 2004), Chapter 2). Therefore, the opportunity exists for a diversity of trophic interactions among predators (Denno, Gratton et al. 2002; Finke and Denno 2002; Denno, Mitter et al. 2004), Chapters 1 and 2). In addition, the structural complexity of the vegetation varies tremendously across the marsh due to the differential accumulation of leaf litter (thatch) (Denno, Roderick et al. 1996).

Previous studies of this system have shown that in structurally-simple habitats an increase in predator diversity can negatively affect prey suppression and dampen the strength of a trophic cascade, due to the increased probability for intraguild predation when predator diversity is high (Finke and Denno 2004), Chapters 1 and 2). However, the indirect effects of habitat structure on primary productivity were not assessed, even though the ability of habitat complexity to mediate trophic interactions in this system has been documented. Specifically, the presence of thatch provides refuge for *Tytthus* mirid bugs from intraguild predation by *Pardosa* hunting spiders, increasing the combined impact of these predators on the planthopper population (Finke and Denno 2002). In addition, complex habitats with thatch intensify the impact of *Pardosa* predation on planthopper populations by enhancing the numerical response of spiders to planthopper prey (Döbel and Denno 1994), encouraging predator aggregation (Denno, Gratton et al. 2002), diminishing cannibalism (Langellotto 2002), and increasing capture efficiency (Denno, Gratton et al. 2002; Langellotto 2002). The objective of this study was to determine if habitat complexity, by providing a refuge for multiple predators from intraguild predation, might enhance the collective ability of predators to limit planthopper populations and thus increase the overall strength of the trophic cascade when predator diversity is high.

An investigation of the links between habitat complexity, predator diversity, and the strength of trophic cascades would provide additional insight into important issues concerning biological control. The simplification of habitats due to agricultural intensification could diminish the potential for diverse predator assemblages to control pest populations and increase yield via trophic cascades due to frequent intraguild predation (Rosenheim, Kaya et al. 1995; Snyder, Chang et al. 2005). However, complex habitats may mitigate such antagonistic predator-predator interactions and thus enhance overall pest suppression and the strength of trophic cascades (Polis and Strong 1996; Denno, Gratton et al. 2002; Finke and Denno 2002). Therefore, control of economically important pests might be achieved through the targeted use of habitat modification in association with the manipulation of predator assemblages (Bottrell, Barbosa et al. 1998; Landis, Wratten et al. 2000). Using the assemblage of arthropod predators inhabiting mid-Atlantic coastal marshes as a model system, this research aims to elucidate how habitat complexity might impact the relationship between predator diversity and the occurrence of trophic cascades by moderating antagonistic interactions among predators.

METHODS

Study System

Research was conducted using the terrestrial food web associated with intertidal salt marshes along the Atlantic coast of North America. The perennial cordgrass *Spartina alterniflora* is the most abundant plant species found within the intertidal zone of mid-Atlantic marshes where it often grows as extensive monocultures (Blum 1968; Redfield 1972; Gallagher, Somers et al. 1988; Denno, Roderick et al. 1996). Within this zone, the structural complexity of *Spartina* varies tremendously with elevation due to differences in the frequency of tidal flooding, nutrient subsidy, and litter decay (Blum 1968; Redfield 1972; Denno, Roderick et al. 1996). One of the major contributors to variation in structural complexity along this elevational gradient is the accumulation of dead *Spartina* leaf litter (thatch) at higher elevations (Denno, Roderick et al. 1996). As a result, the structural complexity of the *Spartina* vegetation varies across habitats from architecturally-complex meadows where thatch is abundant to the structurally-simple vegetation of mud flats that is devoid of thatch (Blum 1968; Redfield 1972; Gallagher, Somers et al. 1988; Denno, Roderick et al. 1996).

Spartina cordgrass is the only host plant for the most abundant herbivores on the marsh, the phloem-feeding planthoppers *Prokelisia dolus* and *Prokelisia marginata* (Hemiptera: Delphacidae) (Denno, Douglass et al. 1986; Cook and Denno 1994). These small insects (3 mm in body length) frequently exceed 1000 adults/m^2 (Denno, Schauff et al. 1987). *Prokelisia* planthoppers are trivoltine on mid-Atlantic marshes with peaks of adult abundance occurring in May, July, and September, and overwintering occurs during the nymphal stage (Denno, Schauff et al. 1987). *Prokelisia* eggs are deposited within the

Spartina leaf blades and hatch after two weeks. Nymphs pass through five instars before molting to adults (Denno, Schauff et al. 1987).

Generalist wolf spiders (Araneae: Lycosidae), particularly *Pardosa littoralis*, are the major predators of planthopper nymphs and adults on mid-Atlantic coastal marshes (Döbel et al. 1990, Döbel and Denno 1994). *Pardosa* spiders are known to aggregate in complex-structured habitats with large amounts of thatch (Döbel and Denno 1994, Langellotto 2002). *Pardosa* is also a documented intraguild predator of other common predators of planthoppers in the field including the mirid bug *Tytthus vagus* (Hemiptera: Miridae), that feeds exclusively on planthopper eggs, and the web-building spider *Grammonota trivitatta* (Araneae: Linyphiidae) (Finke and Denno 2002; Finke and Denno 2003; Denno, Mitter et al. 2004), Chapter 2). Intraguild predation is completely asymmetric in these cases since both *Tytthus* and *Grammonota* consume only planthoppers and do not feed on other predators (Chapter 2). Importantly, thatch provides a refuge for *Tytthus* from intraguild predation by *Pardosa* (Finke and Denno 2002).

Experimental Design

To determine the direct and interactive effects of predator diversity and habitat complexity for the occurrence of trophic cascades, I conducted a full factorial experiment in laboratory mesocosms containing *Spartina* transplants and *Prokelisia* planthoppers. Five predator diversity manipulations (no predators, *Pardosa* only, *Grammonota* only, *Tytthus* only, or a combination of all three predator species) were crossed with two levels of habitat complexity (thatch absent or present) and the impact of these treatment combinations on the occurrence of intraguild predation (predator density), *Prokelisia* planthopper population size, and *Spartina* cordgrass productivity was assessed.

Each mesocosm contained ten greenhouse-reared *Spartina* culms (Environmental Concern; Saint Michael's, Maryland) transplanted into sand-filled pots (30 cm diameter, 0.04 m^2) and caged within a clear plastic cylinder (cellulose butyrate, 22 cm diameter x 30 cm height) sunk into the sand. Each mesocosm was covered by a screened lid (0.6 x 0.6 mm holes, 85% light transmission). Mesocosms were divided among 7 watering pools maintained in the laboratory under 1000-w sodium-vapor lamps suspended 2 meters above. Treatments were randomly assigned to mesocosms within watering pools in a randomized complete block design.

Habitat-complexity treatments were applied by placing either 25 g or 0 g (dry weight) of field-collected *Spartina* thatch onto the bottom of each mesocosm, interdigitated among the live culms of *Spartina* to mimic the natural situation. On 23 August 2004, 20 field-collected planthoppers (adults of *Prokelisia dolus*) were released into each mesocosm and predator treatments were established the following day. Predator treatments consisted of each predator species alone and in combination with all other species (5 *Pardosa* only, 10 *Grammonota* only, 10 *Tytthus* only, and a combination of 5 *Pardosa*, 10 *Grammonota,* and 10 *Tytthus*) and two predator-free controls (*Spartina* plants with planthoppers present and *Spartina* plants alone). Each of the 12 treatment combinations was replicated 7 times for a total of 84 mesocosms. All herbivores and predators for this experiment were obtained at my major study site in Tuckerton, Ocean Co., New Jersey, USA (for detailed site description, see Denno et al. 2002).

Field-collected predators were released into the mesocosms in an additive treatment design (i.e. the treatment 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 abundances. An additive treatment design was used so that predator diversity was not confounded with changes in the abundance of individual predator species (Jolliffe 2000). As a result, departures from the null hypothesis of independent additive effects among predators were more confidently attributed to changes in interspecific interactions among predators, such as intraguild predation, rather than intraspecific effects (Sih, Englund et al. 1998; Jolliffe 2000).

On 23 November 2004, after more than two planthopper generations, the size of the planthopper population, *Spartina* biomass, and predator density were assessed. Herbivore and predator densities were determined by visually counting all living planthoppers (nymphs and adults), *Pardosa, Grammonota,* and *Tytthus* in each mesocosms. *Spartina* biomass was determined by harvesting all live aboveground vegetation from each mesocosm, drying the vegetation in an oven for 3 days at 55ºC, and weighing it. Density of planthoppers, *Spartina* biomass, and number of predators per mesocosm were scaled up to units per m^2.

I tested for the direct and interactive effects of predator diversity and habitat complexity on planthopper population size and *Spartina* biomass by performing two-way mixed model analyses of variance (PROC MIXED) with predator diversity treatment (no predators, *Pardosa* only, *Grammonota* only, *Tytthus* only, or a combination of all three predator species), habitat complexity treatment (thatch absent versus present), and their interaction as fixed effects and block as a random source of variation in the model (SAS

1999). The ability of habitat complexity to provide a refuge from intraguild predation was assessed by performing a separate two-way analysis of variance on the density of each predator species (*Pardosa*, *Grammonota*, or *Tytthus*) remaining at the end of the experiment with predator diversity treatment (the focal predator species alone versus the focal predator in combination with other predators), habitat complexity treatment (thatch absent versus present), and their interaction as fixed effects and block as a random source of variation in the model (PROC MIXED, (SAS 1999)).

For all analyses, means were compared by performing t-tests with Bonferroni adjustment of p-values to account for multiple comparisons (Sokal and Rohlf 1987). Data were log-transformed when necessary to meet assumptions of analysis of variance including normality and homogeneity of variances (Sokal and Rohlf 1987).

RESULTS

Habitat complexity mediated the impact of the predator diversity treatments on the *Prokelisia* planthopper population, as indicated by the significant predator diversity treatment by habitat complexity treatment interaction ($F_{4, 44} = 2.65$, $P < 0.05$) (Fig. 3.1). In the structurally-simple habitat, predators interacted antagonistically and planthopper suppression was diminished. Specifically, in the absence of thatch, predation by each individual predator species resulted in planthopper densities that were equal to (*Pardosa*, $t_{1,44} = 1.16$, $P > 0.05$; *Grammonota*, $t_{1,44} = 0.79$, $P > 0.05$) or less than (*Tytthus*, $t_{1,44} = 3.05$, $P < 0.05$) the density of planthoppers when predator diversity was high (all three predators present in combination) (Fig. 3.1). This result occurred despite the greater initial predator density in the high predator diversity treatment due to the additive treatment design. By contrast, in the complex-structured habitat, antagonism among predators was dampened (but not eliminated) and planthopper suppression was enhanced. Specifically, planthopper population density was significantly lower when predator diversity was high in the presence of thatch than when thatch was absent ($t_{1,44} = 3.29$, $P < 0.05$). However, the level of suppression by the predator complex at large was no greater in the presence of thatch than the level that resulted from predation by *Tytthus* alone ($t_{1,44} = 0.55$, $P > 0.05$) (Fig. 3.1). Notably, habitat complexity did not have a direct effect on planthopper suppression since the presence of thatch did not influence planthopper population size in the absence of predators ($t_{1,44} = 0.04$, $P > 0.05$), nor did thatch influence the suppression of planthopper populations by *Pardosa*, *Grammonota*, or *Tytthus* individually ($t_{1,44} = 1.00, 0.29, 0.25$, respectively; $P > 0.05$) (Fig. 3.1). Therefore, the significant reduction in planthopper density when predator diversity was high and thatch was present was due to the indirect effect of habitat complexity moderating antagonistic interactions among predators.

The impact of the predator diversity treatments on the planthopper population cascaded down to differentially impact *Spartina* biomass (significant main effect of predator diversity treatment; $F_{5, 66} = 10.54$, $P < 0.0001$). However, this effect was not mediated by the complexity of the habitat (non-significant predator diversity treatment x habitat complexity treatment interaction; $F_{5, 66} = 0.64$, $P > 0.05$) (Fig. 3.2). For example, the presence of predators resulted in a trophic cascade on *Spartina* biomass, but the strength of the cascade was similar across predator diversity treatments and for both levels of habitat complexity. In treatments where predators were present (*Pardosa* only, *Grammonota* only, *Tytthus* only, and the combination of all three predator species present), *Spartina* biomass was significantly enhanced as compared to the case when predators were absent and planthoppers were present (Fig. 3.2). However, this effect occurred independently of the specific combination of predators present or the complexity of the habitat. Therefore, significant differences in planthopper suppression among predator treatments were not great enough to differentially influence *Spartina* biomass. However, there was a trend towards greater *Spartina* biomass when predator diversity was high and thatch was present as opposed to when predator diversity was high and thatch was absent.

There was evidence that habitat complexity diminished the occurrence of intraguild predation (including cannibalism) for some predators. *Pardosa* was not susceptible to intraguild predation by *Grammonota* or *Tytthus*, therefore *Pardosa's* survival was unaffected by the presence of other predator species (non-significant main effect of predator diversity; $F_{1,\,18} = 0.02$, $P > 0.05$) or its interaction with habitat complexity ($F_{1,\,18} = 2.84$, $P > 0.05$) (Fig. 3.3a, Table 3.1). However, habitat complexity provided a refuge for *Pardosa* from cannibalism, resulting in significantly greater *Pardosa* survival in the presence of thatch (significant main effect of habitat complexity treatment; $F_{1,\,18} = 5.29$, $P < 0.001$) (Fig. 3.3b, Table 2.1). *Grammonota* was susceptible to intraguild predation, resulting in lower *Grammonota* survival in the presence of other predators ($F_{1,\,18} = 67.46$, $P < 0.0001$) (Fig. 3.4b) (Table 3.1). However, thatch provided a refuge for *Grammonota* from *Pardosa* predation as evidenced by its higher density in mesocosms with thatch than those without it ($F_{1,\,18} = 18.51$, $P < 0.001$) (Fig. 3.4c, Table 3.1). Surprisingly, the survival of *Tytthus* was not affected by the predator diversity treatment ($F_{1, 18} = 0.45$, $P > 0.05$), the habitat complexity treatment ($F_{1, 18} = 0.30$, $P > 0.05$), or their interaction ($F_{1, 18} = 1.29$, $P > 0.05$) (Fig 3.5). However, final *Tytthus* density was extremely low (less than 2 per mesocosm for all treatments) and only nymphs were recovered, suggesting that the majority of mirids may have been in the egg stage at the time that *Tytthus* densities were assessed. An earlier assessment of *Tytthus* densities may have captured differences in *Tytthus* survival among treatments.

DISCUSSION

Intraguild predation is a widespread phenomenon in a variety of natural and managed ecosystems (Polis, Myers et al. 1989; Rosenheim, Kaya et al. 1995; Arim and Marquet 2004), and its role in the dampening of trophic cascades when predator diversity is high has been documented (Finke and Denno 2004), Chapters 1 and 2). Complex-structured habitats have been shown to alter predator-predator interactions (Crowder and Cooper 1982; Gunnarsson 1990; Agrawal and Karban 1997; Roda, Nyrop et al. 2000; Norton, English-Loeb et al. 2001; Langellotto 2002; Grabowski 2004) with extended impacts on herbivore populations (Finke and Denno 2002); but see (Grabowski 2004). However, an investigation of the influence of habitat complexity on the cascading effects of diverse predator assemblages on primary productivity is lacking.

I found that complex habitats with thatch tempered antagonistic predator-predator interactions and enhanced planthopper suppression by the diverse predator assemblage (Fig. 3.1). This resulted because the complex-structured habitat provided a refuge for predators from intraguild predation (including cannibalism) (Figs. 3.3 and 3.4). However, predator effects on herbivores attenuated as they cascaded down to the basal trophic level. The strength of the trophic cascade on *Spartina* biomass did not vary among treatments where predators were present (either alone or in combination) or across levels of habitat complexity, despite the significant differences in the size of the planthopper populations (Fig. 3.2). Therefore, the indirect effect of habitat structure on the planthopper population when predator diversity was high did not cascade down to affect positively *Spartina* cordgrass biomass.

The attenuation of cascading predator effects on plant biomass has been documented in other systems (Schmitz, Hamback et al. 2000; Halaj and Wise 2001). Three meta-analytical syntheses of trophic cascades in terrestrial systems have found that the indirect impact of predators on plant biomass is often weaker than the direct effect of predators on herbivores (Schmitz, Hamback et al. 2000; Halaj and Wise 2001). However, the commonly cited mechanisms for attenuation, including the presence of anti-herbivore mechanisms in plants, low plant nutritional quality resulting in exploitative competition among herbivores, and an averaging of effects across plant species with opposing responses (Schmitz, Hamback et al. 2000; Halaj and Wise 2001), do not appear to be important in the *Spartina* cordgrass system. *Spartina* is relatively devoid of allelochemicals that adversely affect the performance of phloem-feeding herbivores such as planthoppers (Cook and Denno 1994). In addition, contemporaneous and delayed intraspecific competition does occur among individuals of *Prokelisia dolus*, but is of minor consequence to its population dynamics (Denno, Roderick et al. 1996; Denno and Peterson 2000). Finally, *Spartina* grows virtually as a monoculture within the intertidal zone, therefore multiple plant species with opposing responses were not considered in this study (Blum 1968; Redfield 1972; Gallagher, Somers et al. 1988; Denno, Roderick et al. 1996).

Interestingly, predator effects on the basal trophic level did not attenuate in previous investigations of the impact of predator diversity on the strength of trophic cascades in this *Spartina* system (Finke and Denno 2004), Chapters 1 and 2). In these studies, variation in planthopper abundance among predator diversity treatments was found to have significant effects on *Spartina* biomass (Finke and Denno 2004), Chapters 1 and 2), such that primary productivity was enhanced when predator diversity was low. However, these prior studies were initiated much earlier in the *Spartina* growing season (July) than the current study, suggesting that the strength of cascading predator effects on plants may vary with time. In the current study, plants were free of herbivores for most of the growing season and likely accumulated the majority of their biomass before treatments were imposed. As a result, it is no surprise that differences in *Spartina* biomass were not found, despite significant differences in planthopper abundance. Notably, there was a trend towards greater *Spartina* biomass when predator diversity was high and thatch was present as opposed to when thatch was absent. Therefore, the possibility remains that habitat complexity might impact productivity positively by mediating predator-predator interactions if their impacts are assessed earlier in the season when *Spartina* is growing more rapidly.

There was an interactive effect of habitat complexity and predator diversity on planthopper suppression, despite the lack of a trophic cascade on plant productivity. This interaction resulted from the moderating effects of habitat complexity on predator-predator interactions (intraguild predation) and not from any direct effect of habitat complexity on planthopper population growth or an indirect effect of habitat complexity on planthopper suppression by individual predators. In fact, the overall abundance of predators in the diverse predator assemblage when thatch was present (9.01 ± 0.67 individuals per mesocosm) was nearly twice that in thatch-poor habitats (4.91 ± 0.67 individuals per mesocosm).

The hunting spider *Pardosa*, the largest of the three predators, was not susceptible to intraguild predation by either *Grammonota* or *Tytthus*. However, the abundance of *Pardosa*, averaged across predator diversity treatments, was significantly higher in the presence of thatch (Fig. 3.3). The increase in *Pardosa's* abundance in the complex-structured habitat is likely attributable to a decrease in cannibalism (Langellotto 2002), since *Pardosa* did not reproduce during the timeframe of this study. Despite the higher density of *Pardosa* in the thatch-containing treatment (Fig. 3.3b), planthopper suppression was not affected by the presence of thatch when only *Pardosa* was present (Fig 3.1). Previously, thatch was found to intensify the impact of *Pardosa* predation on planthopper populations in the field (Denno, Gratton et al. 2002). In light of my results, this effect is likely attributable to an aggregation of *Pardosa* spiders in thatch-rich habitats rather than increased capture efficiency (Denno, Gratton et al. 2002; Langellotto and Denno 2004), because immigration was precluded in the current mesocosm study.

Grammonota density was reduced in the presence of other predators, indicating that this web-building spider was susceptible to intraguild predation by *Pardosa.* However, intraguild predation was diminished and the survival of *Grammonota* was enhanced in the complex habitat with thatch (Fig 3.4). Because G*rammonota* did not reproduce during this study, the impact of thatch on *Grammonota's* abundance was attributable to the spatial refuge thatch provides from intraguild predation. Other studies have shown that elevated web-spider densities in complex-structured habitats result from an increase web attachment sites (McNett and Rypstra 2000). Here I found that a decrease in antagonistic interactions with other predators, specifically *Pardosa*, occurred in the presence of thatch, thus providing an alternative explanation for the accumulation of web-building spiders in complex-structured habitats.

Surprisingly, the density of *Tytthus* did not differ across treatments (Fig. 3.5). Previous studies have documented that *Tytthus* is extremely susceptible to intraguild predation by *Pardosa* (Finke and Denno 2002; Finke and Denno 2003) and that it finds refuge from intraguild predation in thatch-rich habitats (Finke and Denno 2002). The lack of a significant treatment effect on *Tytthus* abundance in this study was likely due to the timing of the predator assessment relative to the life cycle of *Tytthus*. *Tytthus* nymphs were present at the end of the study, suggesting that adults reproduced and deposited eggs earlier during the experiment. The extremely low density of nymphs when the experiment was terminated (< 2 nymphs per mesocosm) suggests that emergence had just begun and that the majority of *Tytthus* were still in the egg stage. As a consequence, treatment effects were likely masked.

Habitat complexity differentially affected predator-predator and predator-prey interactions, highlighting the importance of individual predator and prey behavior in mediating the refuge effect of thatch. Thatch provided a refuge from predation for predators but not herbivores. The lack of a spatial refuge for planthoppers in complex-structured habitats may be due to the fact that planthoppers restrict their position to living plants where they feed predominantly on leaf blades located above the thatch layer and thus do not make use of the potential cover provided by thatch. On the contrary, *Tytthus* bugs are active foragers that scurry along leaves in search of planthopper eggs. These mobile predators wander from living plants and are often found within the thatch layer (D. Finke unpublished data). Therefore, the scaffold-like structure of thatch may provide hiding sites and pathways of escape for mirids from the visually-orienting *Pardosa*. Likewise, *Grammonota* spiders, which build sheet webs that are suspended close to the marsh surface (Döbel et al. 1990), may also find refuge from *Pardosa* predation within the thatch layer. Therefore, the mediating effect of habitat complexity on the intensity of predator-predator interactions and prey suppression likely depends on the foraging behavior and microhabitat of individual predator and prey species in the system (Schmitz 2003; Almany 2004; Grabowski 2004; Rosenheim, Glik et al. 2004; Schmitz, Krivan et al. 2004; Warfe and Barmuta 2004).

Complex food webs with high species diversity are thought to buffer communities against trophic cascades because enemy impacts often attenuate through a reticulate network of species interactions (Strong 1992; Polis and Strong 1996; McCann, Hastings et al. 1998). Intraguild predators, by feeding from multiple trophic levels, could further enhance the reticulate nature of the food web and thus reduce the potential for predator effects to cascade down to lower trophic levels (Polis, Myers et al. 1989; Fagan 1997; McCann, Hastings et al. 1998; Rosenheim 1998). However, structurally complex habitats may provide a refuge for predators from intraguild predation, weakening the intensity of antagonistic interactions among predators and enhancing prey population suppression (Finke and Denno 2002). Therefore, by reducing reticulate interactions among predators, habitat structure has the potential to promote trophic cascades, even in species-rich ecosystems. Habitat structure has been shown to enhance the strength of cascading predator effects on plants due to the accumulation of predators in complex habitats (Riechert and Bishop 1990; Denno, Gratton et al. 2002), but the ability of architecturally complex habitats to influence primary producers by mediating predator-predator interactions remains less clear. I found that habitat complexity did reduce the occurrence of reticulate interactions among predators. The presence of thatch diminished intraguild predation and enhanced prey suppression by a diverse predator complex. However, reducing antagonistic predator-predator interactions and increasing prey suppression did not enhance the conductance of predator effects through the food web to primary producers. Notably, there was a trend towards greater *Spartina* biomass in the complex-structured habitat, despite the fact that this experiment was initiated late in the *Spartina* growing season when growth is slow. Therefore, the possibility remains that changes in habitat complexity might enhance trophic cascades and impact productivity positively by mediating trophic interactions among predators. If this were the case, preserving the structural complexity of habitats, both natural and managed, would contribute to greater suppression of herbivores and elevated rates of primary production by simultaneously encouraging the accumulation of natural enemies (Greenstone 1984; Riechert and Bishop 1990; Denno, Gratton et al. 2002; Langellotto and Denno 2004) and by damping antagonistic interactions among them (Crowder and Cooper 1982; Gunnarsson 1990; Agrawal and Karban 1997; Roda, Nyrop et al. 2000; Norton, English-Loeb et al. 2001; Finke and Denno 2002; Langellotto 2002).

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Table 3.1. Analysis of variance results (*F* values and significance levels) for the effects of predator diversity treatment (individual predator species alone vs. a combination of *Pardosa*, *Grammonota*, and *Tytthus*), habitat complexity treatment (thatch present vs. absent), and their interaction on the density (no. per m^2) of *Pardosa*, *Grammonota*, and *Tytthus* remaining after a 2-mo interaction period.

Source	df	*Pardosa*	*Grammonota*	*Tytthus*
Predator diversity treatment	1	0.02	67.46***	0.45
Habitat complexity treatment	1	5.29*	18.51**	0.30
Predator x Habitat	1	2.84	2.87	1.29
Error	18			

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$

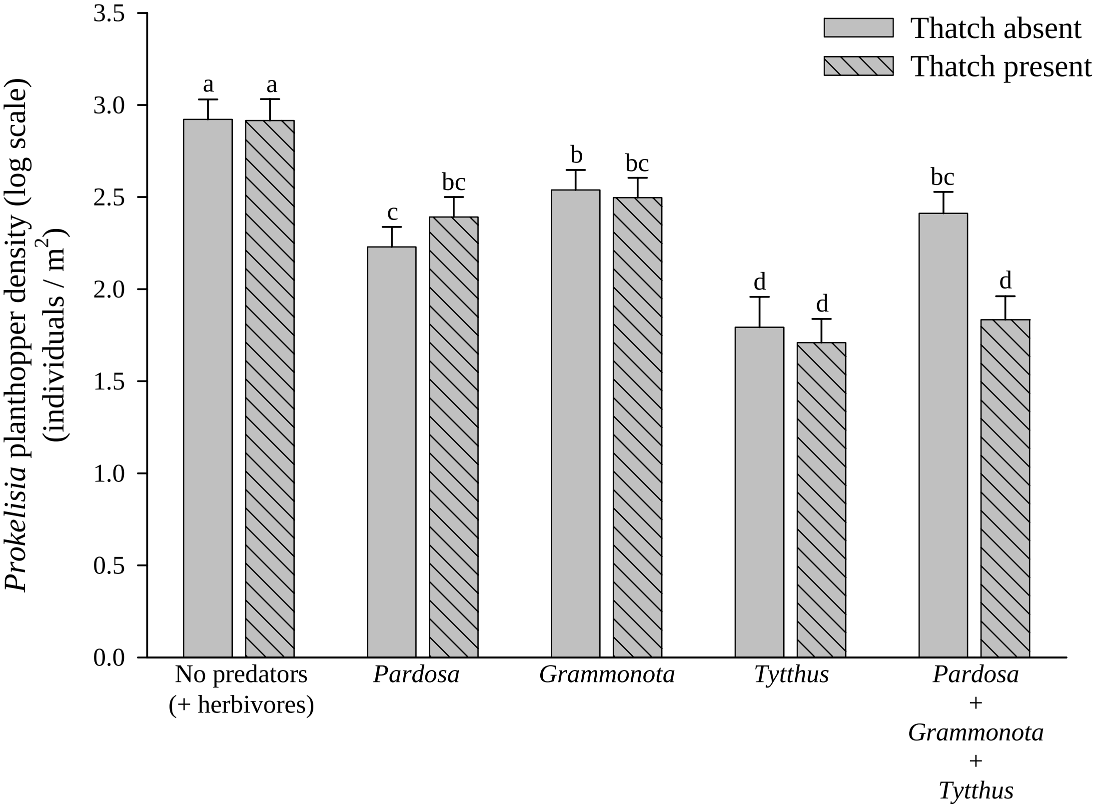

Figure 3.1. The effects of predator diversity treatment (no predators, 5 *Pardosa* only, 10 *Grammonota* only, 10 *Tytthus* only, or a combination of 5 *Pardosa*, 10 *Grammonota*, and 10 *Tytthus*) and habitat complexity treatment (thatch present vs. absent) on the density of *Prokelisia dolus* planthoppers (no. per m^2) present in laboratory mesocosms after a 2-mo interaction period. Analysis of planthopper densities showed a significant predator diversity treatment x habitat complexity treatment interaction ($F_{4, 44} = 2.65$, $P < 0.05$), indicating that planthopper suppression by the diverse predator assemblage is enhanced in the presence of thatch. Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

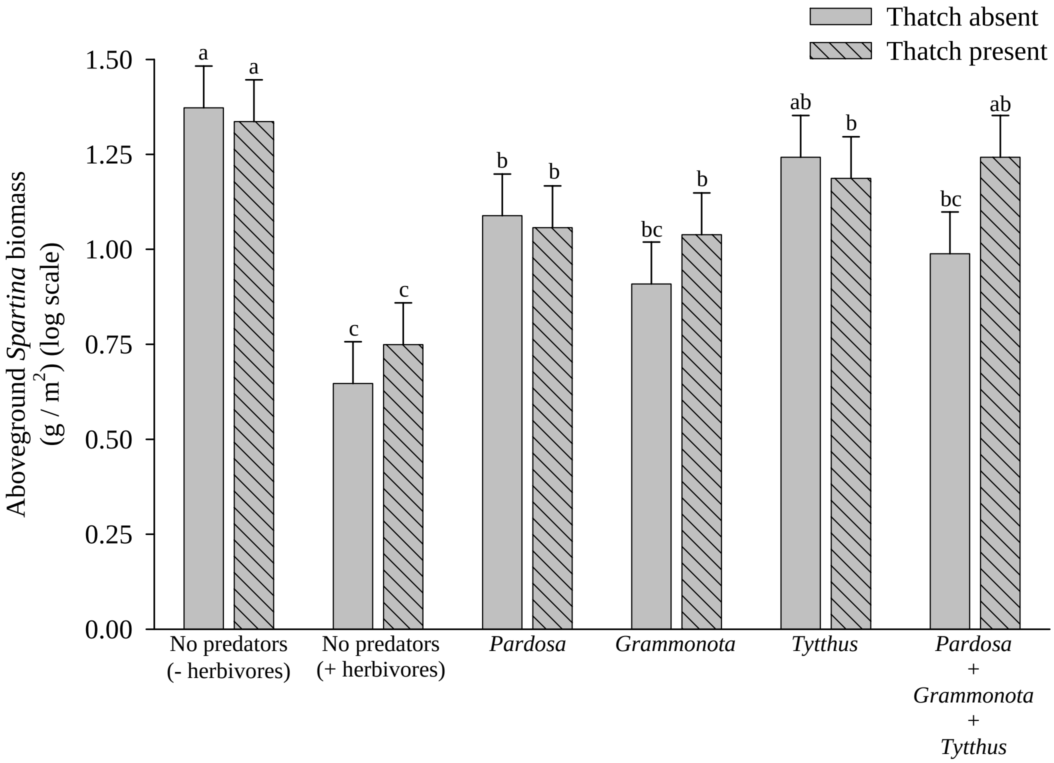

Figure 3.2. The effects of predator diversity treatment (no predators without planthoppers present, no predators with planthoppers present, 5 *Pardosa* only, 10 *Grammonota* only, 10 *Tytthus* only, or a combination of 5 *Pardosa*, 10 *Grammonota*, and 10 *Tytthus*) and habitat complexity treatment (thatch present vs. absent) on the living aboveground *Spartina* biomass present in laboratory mesocosms after a 2-mo interaction period. A non-significant predator diversity treatment x habitat complexity treatment interaction ($F_{5, 66} = 0.64$, $P > 0.05$), indicates that habitat complexity did not mediate cascading predator effects on primary producers. Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

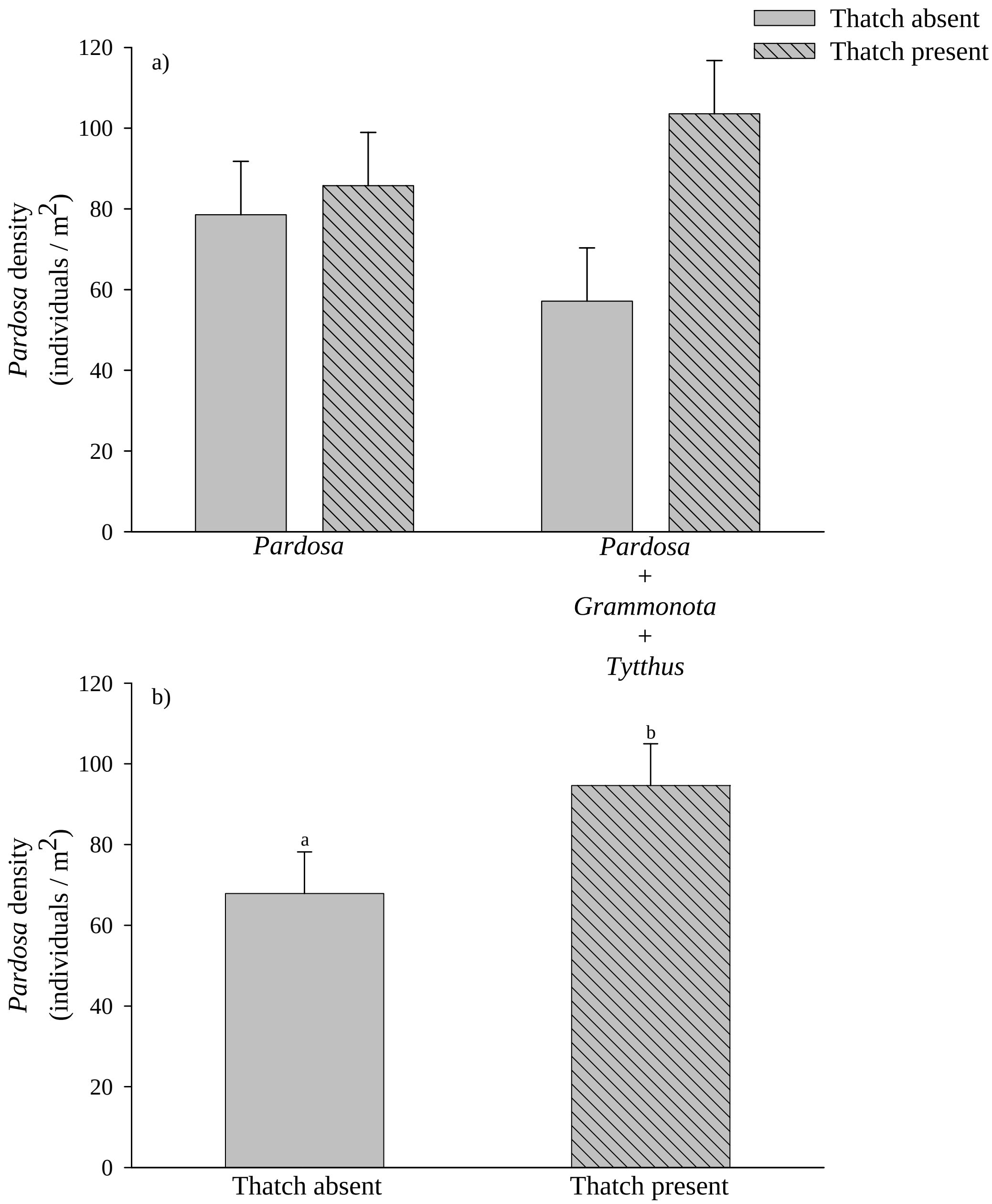

Figure 3.3. The effects of predator diversity treatment (5 *Pardosa* only vs. a combination of 5 *Pardosa*, 10 *Grammonota*, and 10 *Tytthus*) and habitat complexity treatment (thatch present vs. absent) on the density (no. per m^2) of *Pardosa* remaining after a 2-mo interaction period. (a) The interactive effect of predator diversity and habitat complexity on *Pardosa* survival was non-significant ($F_{1, 18} = 2.84$, $P > 0.05$). (b) There was a significant main effect of habitat complexity treatment ($F_{1, 18} = 5.29$, $P < 0.001$), indicating that the presence of thatch provided a refuge for *Pardosa* from cannibalism. Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

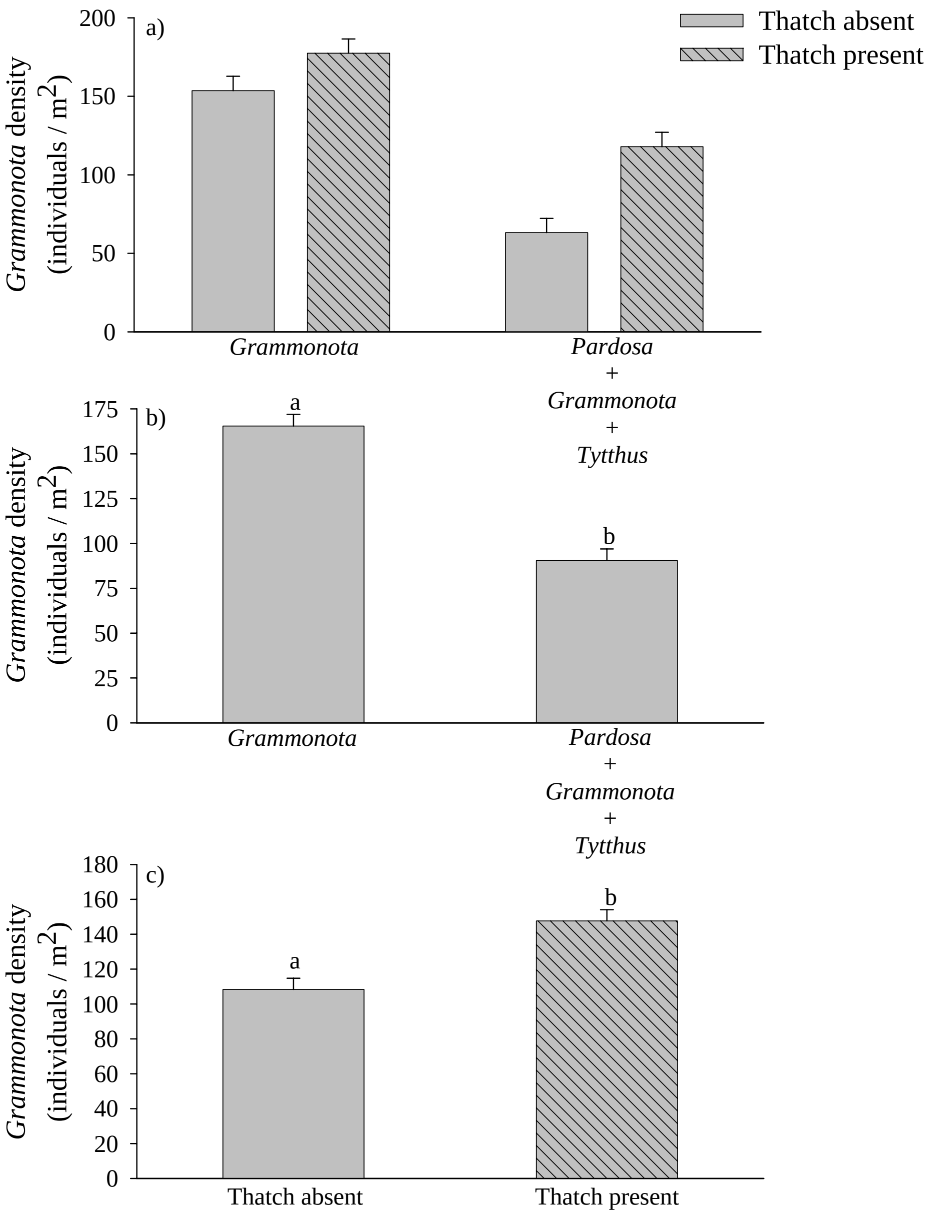

Figure 3.4. The effects of predator diversity treatment (10 *Grammonota* only vs. a combination of 5 *Pardosa*, 10 *Grammonota*, and 10 *Tytthus*) and habitat complexity treatment (thatch present vs. absent) on the density (no. per m^2) of *Grammonota* remaining after a 2-mo interaction period. (a) The interactive effect of predator diversity and habitat complexity on *Grammonota* survival was non-significant ($F_{1,18} = 2.87$, $P > 0.05$). (b) There was a significant main effect of predator diversity treatment ($F_{1,18} = 67.46$, $P < 0.0001$), indicating that *Grammonota* was susceptible to intraguild predation. (c) There was a significant main effect of habitat complexity treatment ($F_{1,18} = 18.51$, $P < 0.001$), indicating that the presence of thatch provided a refuge for *Grammonota* from intraguild predation. Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

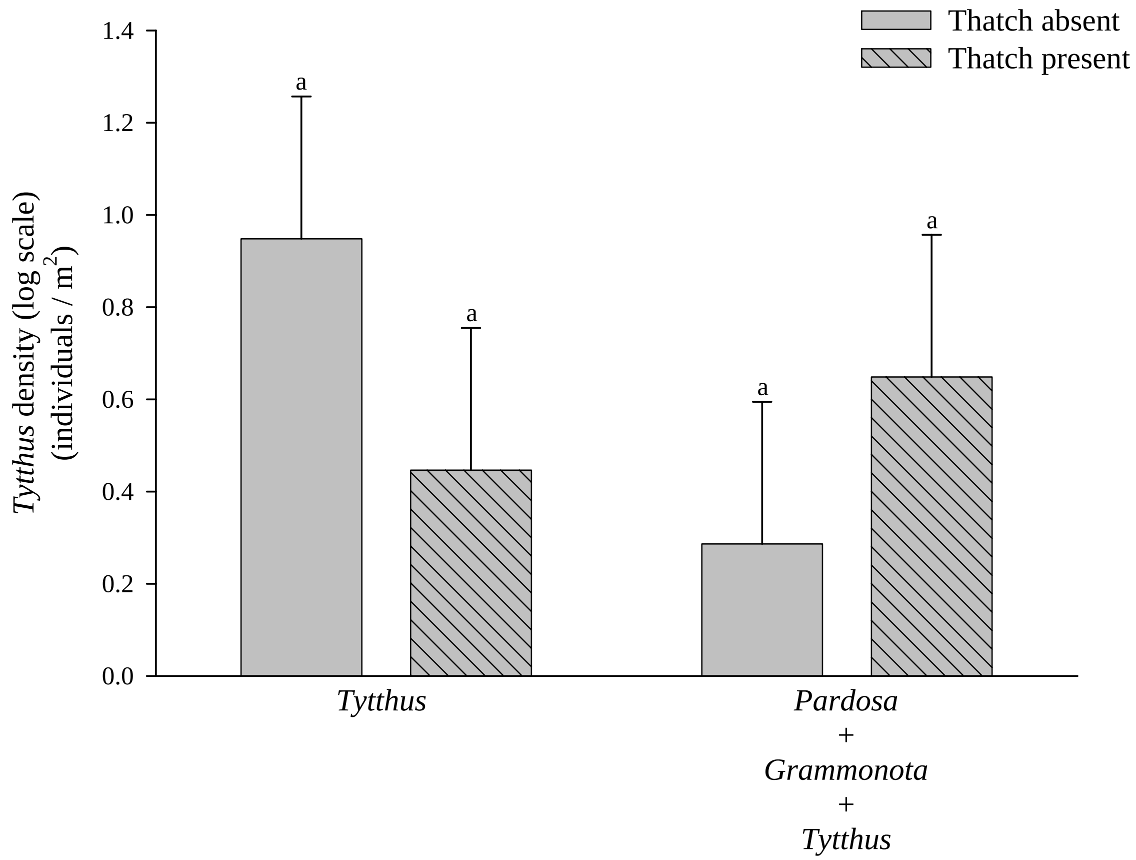

Figure 3.5. The effects of predator diversity treatment (10 *Tytthus* only vs. a combination of 5 *Pardosa*, 10 *Grammonota*, and 10 *Tytthus*) and habitat complexity treatment (thatch present vs. absent) on the density (no. per m^2) of *Tytthus* remaining after a 2-mo interaction period. *Tytthus* survival was not affected by predator diversity treatment ($F_{1,\,18} = 0.45$, $P > 0.05$), habitat complexity treatment ($F_{1,\,18} = 0.30$, $P > 0.05$), or their interaction ($F_{1,\,18} = 1.29$, $P > 0.05$). Means ± 1 SEM with different letters are significantly different ($P < 0.05$).

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