

ABSTRACT

Title of Document: LINKING DETRITUS AND PRIMARY PRODUCER BASED COMMUNITIES

Jessica Hines, PhD, 2008

Directed By: Professor, Robert F. Denno, Department of Entomology

Terrestrial food-web theory has been developed largely by examining species interactions in primary producer food webs. However, the decomposer subsystem can have strong influences on aboveground communities and ecosystem functioning. Here I examine, at several spatial scales, the complexity of terrestrial food-web interactions by considering interactions between species in detritivore and primary-producer food webs. I focused on *Spartina alterniflora* marshes and interactions among the numerically dominant herbivore *Prokelisia dolus*, its major spider predator *Pardosa littoralis*, and several detritivores (*Littorophiloscia vittata*, *Orchestia grillus*, *Melampus bidentatus* and *Littoraria irrorata*). I found that predator-detritivore interactions have weak indirect effects on plant growth and decomposition (Chapter 1). Furthermore, by serving as alternative prey, detritivores can influence the strength of predator-herbivore interactions. However, the strength of predator-herbivore-detritivore interactions was species-specific and depended on habitat structure (leaf litter - Chapter 1) and detritivore identity (Chapter 2). Although detritivore species

are often functionally redundant in soil communities, changes in detritivore species composition can have divergent influences on aboveground predator-herbivore interactions (Chapter 2). Whereas some detritivores (*Littorophiloscia vittata*) promote herbivore and predator survival, other detritivores (*Littoraria irrorata*) reduce predator and herbivore densities. Moreover, the geographic distribution of detritivores influences the relative strength of predator-herbivore interactions across broader spatial scales (Chapter 3). I found a shift in the relative abundance of dominant detritivore, herbivore, and predator species across a 1660 km latitudinal gradient. Detritivorous *Littoraria* snails that abound on low-latitude marshes modify *Spartina* vegetation structure and create an unfavorable habitat for *Pardosa* spiders. *Pardosa* exert stronger predation pressure on *Prokelisia* planthoppers on high-latitude marshes where spiders are abundant. Changes in global carbon cycles may influence the strength of linkages between primary production and decomposition food webs. I examined how changes in the detritivore food chain influenced the growth of two plant species (*Scirpus olneyi* and *Spartina patens*) under elevated and ambient CO₂ conditions. I found limited and species-specific support for the increased importance of the decomposition pathway under elevated CO₂ conditions. Overall, detritivores modified predator-herbivore interactions, live plant growth, and decomposition. The strength of these interactions changed with the composition of the detritivore community, latitude, and atmospheric CO₂ conditions.

LINKING DETRITUS AND PRIMARY PRODUCER BASED COMMUNITIES

By

Jessica Hines

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2008

Advisory Committee:
Professor Robert F. Denno, Chair
Dr. Galen Dively
Dr. Bert Drake
Dr. Charles Mitter
Dr. Margaret Palmer
Dr. Irwin Forseth

© Copyright by
Jessica Hines
2008

Table of Contents

Table of Contents	ii
List of Tables	iii
List of Figures	v
Chapter 1: Detritivores mediate predator-herbivore interactions	1
Abstract	1
Introduction	2
Methods	4
Results	9
Discussion	12
Literature Cited	15
List of Figures	22
Tables	27
Chapter 2: Detritivore identity influences interactions between generalist predators and their herbivore prey	28
Abstract	28
Introduction	29
Methods	32
Results	37
Discussion	41
Literature Cited	45
List of Figures	52
Tables	57
Chapter 3: Latitudinal change in the trophic structure of a salt marsh food web	58
Abstract	58
Introduction	59
Methods	65
Results	67
Discussion	69
Literature Cited	75
List of Figures	82
Tables	88
Chapter 4: Detritivore food chain length influences plant growth response to elevated CO ₂	92
Abstract	92
Introduction	93
Methods	96
Results	98
Discussion	98
Literature Cited	100
List of Figures	106
Tables	108
Bibliography	110

List of Tables

Chapter 1: Detritivores mediate predator-herbivore interactions

Table 1. ANOVA results for the main and interactive effects of the detritivorous isopod *Littorophiloscia vittata* (I), the herbivorous planthopper *Prokelisia dolus* (H), the predaceous spider *Pardosa littoralis* (P), and leaf litter (L) on the abundance of the isopod *L. vittata* and the planthopper *P. dolus* prey, as well as on the dry mass of remaining leaf litter (g) and dry biomass (g) of *Spartina alterniflora* plants in outdoor mesocosms. Significant F and *p*-values are bolded for emphasis.

Chapter 2: Detritivore identity influences interactions between generalist predators and their herbivore prey.

Table 1. ANOVA results show the main and interactive effects of the detritivore identity and predator-addition treatments on *Spartina alterniflora* root biomass and soil inorganic nitrogen availability in common garden mesocosms after 60 days' exposure to treatments.

Chapter 3: Latitudinal change in the trophic structure of a salt marsh food web.

Table 1. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on species richness and diversity of three trophic groups: detritivores, herbivores, predators. Significant F and *p*-values are bolded for emphasis.

Table 2. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on plant structure and quality as indexed by live *Spartina alterniflora* biomass, %N content, plant height, culm density, and dead leaf litter biomass. Significant F and *p*-values are bolded for emphasis.

Table 3. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on the densities of invertebrate herbivores (*Prokelisia sp.* and *Trigonotylus uhleri*), and the omnivorous snail (*Littoraria irrorata*). Significant F and *p*-values are bolded for emphasis.

Table 4. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on the densities of invertebrate predators. Significant F and *p*-values are bolded for emphasis.

Chapter 4. Detritivore food chain length influences plant growth response to elevated CO₂

Table 1. ANOVA results showing the direct and interactive influences of CO₂ (elevated or ambient) and 4 detritus food web treatments (control, litter addition, litter and isopod addition, or litter, isopod, and spider addition) on *Scirpus olneyi* root biomass, leaf area index (LAI) and aboveground shoot biomass. Treatments with *p* values equal to or less than 0.1 are bolded for emphasis.

Table 2. ANOVA results showing the direct and interactive influences of CO₂ (elevated or ambient) and 4 detritus food web treatments (control, litter addition, litter and isopod addition, or litter, isopod, and spider addition) on *Spartina patens* root biomass, number of aboveground shoots and aboveground shoot biomass.

List of Figures

Chapter 1: Detritivores mediate predator-herbivore interactions.

Figure 1. Functional response of *Pardosa* spiders to increasing prey density: the number of the amphipod *Orchestia grillus* (●) or the isopod *Littorophiloscia vittata* (○) killed per 48 hours.

Figure 2. Effect of food-web treatment combinations on the density (# per mesocosm) of (A) the detritivorous isopod *Littorophiloscia vittata* and (B) the herbivorous planthopper *Prokelisia dolus*, as well as (C) the dry mass (g) of leaf litter remaining and (D) the dry mass (g) of live *Spartina alterniflora*. Treatment combinations in experimental mesocosms were the presence of: (I) the detritivorous isopod *Philoscia vittata*, (H) the herbivorous planthopper *Prokelisia dolus*, (P) the predaceous spider *Pardosa littoralis*, (L) leaf litter, and (O) the unmanipulated control treatment. Open and hatched bars indicate the absence and presence of leaf litter respectively. Means (+ SEM, n=5) with different letters within each panel are significantly different ($p < 0.05$).

Figure 3. Conceptual model of a salt-marsh, arthropod food web describing the direct (solid arrow) and indirect (dashed arrow) interactions among predators (the spider *Pardosa littoralis*), herbivores (the planthopper *Prokelisia dolus*), detritivores (the isopod *Philoscia vittata*), and plants (*Spartina alterniflora*) in the (A) absence and (B) presence of leaf litter. (A) In simple-structured habitats devoid of leaf litter, species interactions are less reticulate, and predators predominantly consume herbivores. (B) In structurally-diverse habitats with leaf litter, species interactions are more complex. Predators directly suppress populations of both herbivores and detritivores, and the presence of detritivores results in an indirect positive effect on herbivore growth due to relaxed predation pressure. The pathway through the detrital food web and rather than predator-herbivore interactions results in a trophic cascade and enhanced plant growth.

Chapter 2: Detritivore identity influences interactions between generalist predators and their herbivore prey

Figure 1. Effect of detritivore identity and *Pardosa* predator addition on the density of *Prokelisia dolus* herbivores in common garden mesocosms. Mean *Prokelisia dolus* density (\pm SEM) over the season in response to A) detritivore absence (control) and the presence of one of the four detritivores B) *Orchestia grillus* C) *Littorophiloscia vittata* D) *Melampus bidentatus* and E) *Littoraria irrorata* in *Spartina alterniflora* mesocosms when *Pardosa littoralis* predators were either added (●) or withheld (○). Mean seasonal densities (\pm SEM) are shown to the right of each panel. Significant

differences ($p < 0.05$) due to spider predation at each time period are indicated by (*). F) Final *Prokelisia dolus* density in *Spartina alterniflora* mesocosms after 60 days exposure to detritivore and predator addition treatments. Significant treatment differences ($p < 0.05$) are indicated with different letters.

Figure 2. *Pardosa* predator density (mean \pm SE) in common garden mesocosms containing *Spartina alterniflora*, *Prokelisia dolus* herbivore prey and one of five detritivore-addition treatments: *Littorophiloscia vittatta* (\blacktriangledown), *Orchestia grillus* (\bullet), *Melampus bidentatus* (\square), *Littoraria irrorata* (∇), or no detritivore addition (\circ).

Spider densities in response to detritivores that serve as alternative prey are shown as solid symbols and spider densities in response to detritivore treatments that do not serve as alternative prey are displayed as open symbols. Significant detritivore treatment differences ($p < 0.05$) are shown as different letters above seasonal means shown in bars to the right.

Figure 3. *Spartina alterniflora* live biomass A) and *Spartina alterniflora* leaf litter mass remaining B) in common garden mesocosms after 60 days exposure to one of 5 detritivore addition treatments (*Littoraria irrorata*, *Melampus bidentatus*, *Littorophiloscia vittatta*, *Orchestia grillus*) when *Pardosa littoralis* predators either were added (\bullet) or withheld (\circ). Significant treatment differences ($p < 0.05$) are indicated with different letters.

Chapter 3: Latitudinal change in the trophic structure of a salt marsh food web

Figure 1. Biogeographic A) and food web B) predictions regarding the relative importance of predation, herbivory, and plant structure for salt marsh food web structure across a latitudinal gradient.

Figure 2. A) Map showing 13 *Spartina alterniflora* salt marshes sites where invertebrates and plants were sampled in 2004 and 2005. B) Cluster dendrogram based on a Bray-Curtis similarity index using $\log_{10}(x+1)$ transformed abundance data of invertebrates sampled from sites shown in panel A.

Figure 3. Relationship between latitude and the species richness (A,C,E) and diversity (B,D,F) of invertebrate detritivores (A,B), herbivores (C,D), and predators (E,F) sampled on Atlantic coastal *Spartina alterniflora* salt marshes in 2004 (\circ) and 2005 (\bullet).

Figure 4. Relationship between latitude and the structure and quality of *Spartina* (A-E), herbivore density (F-G), and predator density (H-J) on Atlantic coastal salt marshes sampled during 2004 (\circ) and 2005 (\bullet). All invertebrate densities are reported as $\log_{10}x+1$ number individuals/m². Lines in all panels indicate best fit linear regression in 2004 (dashed) and 2005 (solid).

Figure 5. Relationship between the density ($\log_{10}x+1$ number individuals/m²) of *Littoraria irrorata* on Atlantic coastal salt marshes and latitude (A), *Spartina* leaf

litter (B), culm density (C), and *Pardosa* wolf spider density (D). The solid line indicates the exponential decay regression.

Chapter 4. Detritivore food chain length influences plant growth response to elevated CO₂

Figure 1. The influence of atmospheric carbon dioxide and increases in detritivore food chain length on three measures of plant growth (shoot biomass, leaf area index and root biomass) of the C₃ sedge *Scirpus olneyi* (A-C) and the C₄ grass *Spartina patens* (D-E) in chambered mesocosms. Bars show treatment means (\pm SE) in response to ambient (\circ) or elevated (ambient + 345ppm: \bullet) CO₂ treatments. Detritivore food chain length is shown on the x-axis as control (C), litter addition (L), litter and isopod addition (LI), and litter, isopod, and spider addition (LIS).

Chapter 1: Detritivores mediate predator-herbivore interactions

Abstract

Linkages between primary producer and detritus based food webs can strongly influence ecosystem processes and trophic structure. To investigate the influence of detritivores on the strength of predator-herbivore interactions, and the cascading consequences of species interactions on plant growth and decomposition, I conducted a factorial mesocosm experiment. In my experiment, although predators suppressed both herbivore and detritivore populations, herbivores experienced reduced predation pressure in the presence of detritivores. By consuming detritivores, predators indirectly limited decomposition. Notably, detritivores enhanced plant biomass when herbivores and predators were excluded. Thus in this experiment, the pathway through the decomposition food web and not a trophic cascade due to predation on herbivores, enhanced plant biomass. These results emphasize that not only can changes in detritivore abundance influence rates of decomposition, but they can also impact live plant biomass and predator-herbivore interactions.

Keywords: aboveground-belowground, predation, alternative prey, food web, detritivore, decomposition

Introduction

There has been much interest in the extent to which trophic dynamics influence ecosystem functioning in terrestrial systems (Laakso and Setälä 1999; Polis 1999; Silliman and Bertness 2002; Chase 2003). Although traditional trophic models examine predators consuming herbivores (Polis 1999; Halaj and Wise 2001), generalist predators are known to consume both herbivores and detritivores in many systems (Ferguson and Joly 2002; Miyashita *et al.* 2003). The strength of predator-herbivore interactions and potential for cascading effects that alter plant productivity have been reviewed extensively and can be influenced by features of the environment such as habitat complexity (Rypstra *et al.* 2007), physical disturbance (Elderl 2006), and patch size (Greze and Prado 2000) as well as species-specific characteristics of plants (Stiling and Moon 2005), herbivores (Denno and Peterson 1995), and predators (Chalcraft and Resatarits 2003; Casula *et al.* 2006). Additionally, many studies have also examined the strength and consequences of predator-detritivore interactions and their cascading effects on decomposition (Mikola and Setälä 1998; Hedlund and Öhrn 2000; Moore *et al.* 2004). Thus, there is growing interest in the potential for generalist predators to serve as links between detritivore and primary producer food webs (Halaj and Wise 2002; Wardle 2002; Wise *et al.* 2006) and we can now consider how predator-detritivore interactions might influence herbivore abundance and plant growth (Rypstra and Marshall 2005), and reciprocally how interactions between predators and herbivores can trickle down to impact the soil community (Wardle *et al.* 2005).

Generalist spiders are the dominant arthropod predators in many terrestrial ecosystems (Shimazaki and Miyashita 2005). Spiders often aggregate in habitats rich in leaf litter-detritus in many grassland and forest biomes (Uetz 1991; Miyashita *et al.* 2003; Langellotto and Denno 2004). In these litter-rich habitats, detritus serves as a structural refuge for spiders from cannibalism and intraguild predation (Langellotto and Denno 2006). Moreover, due to a refuge from antagonistic predator-predator interactions in litter-rich habitats, there can be enhanced suppression of herbivore prey (Finke and Denno 2002). By serving as alternative prey for predators, invertebrate detritivores have the potential to dampen predation on herbivores when herbivores are abundant or to enhance herbivore suppression by maintaining predator populations in habitats during times of low herbivore prey availability (Settle *et al.* 1996; Halaj and Wise 2002; Wise *et al.* 2006). Alternatively, detritivores may influence predator-herbivore interactions via non-trophic pathways such as by altering habitat structure or nutrient availability for plants (Bertness 1985).

In this study, I explored diverse food web interactions using a natural assemblage of the dominant arthropods inhabiting coastal salt marshes, namely predaceous spiders, herbivorous planthoppers and detritivorous isopods. I addressed the following questions: 1) does the presence of isopod detritivores alter interactions between spiders and herbivore prey, and 2) can spiders regulate rates of decomposition and plant growth by consuming isopods? This study provides strong support for a recent emphasis in community ecology, to include detritivores when seeking to identify key biotic drivers of primary producer food web interactions (Wardle 2002; Miyashita *et al.* 2003).

Methods

Study System

Atlantic coastal salt marshes are dominated by large, monospecific stands of the smooth cordgrass *Spartina alterniflora*. *S. alterniflora* structure varies across an elevation gradient from short-form plants growing in high marsh meadows that are rarely inundated by tides to tall-form plants growing along tidal creeks that are regularly flooded (Bertness 1985). Due to differences in decomposition, tidal inundation, and plant structure there is extensive variation in the amount of leaf litter, which accumulates at the base of *S. alterniflora* plants and contributes greatly to the architectural complexity of the system (Brewer *et al.* 1998; Denno *et al.* 2005).

The architectural complexity of *Spartina* grasses strongly influences the density and feeding behavior of spider predators (Döbel and Denno 1994; Langellotto and Denno 2006). The community of generalist spiders in Atlantic salt marshes includes a diversity of hunting spiders and web builders. The most numerically dominant spider is *Pardosa littoralis* (Araneae: Lycosidae), which reaches densities as high as 600 individuals/m² (Denno *et al.* 2002; Finke and Denno 2005). *Pardosa* wolf spiders aggregate in litter-rich habitats where they effectively reduce populations of herbivorous insects due to relaxed cannibalism and intraguild predation (Finke and Denno 2002; Langellotto and Denno 2004). Additionally, *Pardosa* spiders have been reported to consume detritivores such as amphipods and collembolans in intertidal habitats (Morse 1997).

The dominant herbivorous arthropods in the salt marsh system are phloem-feeding planthoppers (Denno *et al.* 2005; Stiling and Moon 2005). The congeners

Prokelisia dolus and *P. marginata* (Hemiptera: Delphacidae) are by far the most abundant herbivores on the marsh where they are frequently consumed by *Pardosa* spiders (Denno *et al.* 2002; Denno *et al.* 2003). Although both *Prokelisia* species co-occur on the same marsh, *Prokelisia dolus* is found more consistently in high marsh habitats where *Pardosa* spiders abound (Denno *et al.* 1991).

Decomposition of standing dead *Spartina alterniflora* is initiated primarily by ascomycete fungi (Newell *et al.* 1989; Newell and Porter 2000), though macrofaunal shredders and grazers also contribute greatly to the decomposition process. For example, *Littorophiloscia vittata* (Isopoda: Philosciidae) and *Venezillo parvus* (Isopoda: Armadillidae), are grazing isopods that shred *Spartina alterniflora* leaf litter in high marsh habitats (Newell and Porter 2000). Because of its spatial co-occurrence with *Pardosa*, its vulnerability to spider predation, and its ability to shred leaf litter and promote microbial decomposition, I used *Littorophiloscia vittata* for this study (Newell and Porter 2000). Other important detritivores include the talitrid amphipods (*Uhlorchestia spartinophila*, *Orchestia grillus*) (Amphipoda: Talitridae) that graze on both decaying cordgrass and associated fungus (Newell and Porter 2000).

Functional response of *Pardosa* spiders to detritivore prey

To determine if *Pardosa* spiders consume salt marsh detritivores and to examine the functional response of *Pardosa* to varying densities of detritivores in a simple habitat, single *Pardosa* wolf spiders (medium-sized immatures with a 2-3mm wide prosoma) were collected from the field, starved for 24 hours and placed in

mesocosms containing 1, 5, 10, 15, or 20 individuals of either the amphipod *Orchestia grillus* or the isopod *Littorophiloscia vittata* for 48 hours. Each mesocosm consisted of a 180.6 cm³ clear plastic cup (8.5 cm tall x 5.0 cm diameter) filled with damp sand to a height of 3.0 cm and capped with a plastic lid. Each detritivore species (2) by density (5) treatment combination was replicated 5 times for a total of 50 mesocosms. Control mesocosms were also established to examine density effects (same 5 densities) on isopod and amphipod survival in the absence of spider predation. Mixed model ANOVA was used to assess the effect of prey species (categorical variable) and prey density (continuous variable) on the number of prey killed (Proc Mixed, SAS v 9.1).

Effect of detritivores on predator-herbivore interactions, litter decomposition and plant biomass

To examine the direct and interactive effect of detritivores on predator-herbivore interactions as well as their cascading effects on rates of decomposition and plant growth, I conducted a randomized incomplete block (2x2x2x2) factorial experiment in outdoor mesocosms. Treatments included factorial combinations of two levels of predators (3 *Pardosa* present or absent), two levels of herbivores (20 *Prokelisia dolus* nymphs present or absent), two levels of detritivores (20 *Littorophiloscia vittata* present or absent), and two levels of detritus (25 g of dried *Spartina alterniflora* detritus present or absent). These densities were chosen in order to closely mimic field densities (Denno *et al.* 2002; Finke and Denno 2002; Zimmer *et al.* 2002, 2004), and maintain equal initial densities of detritivore and herbivore

prey. Because *Spartina* marshes are naturally simplified systems with low plant species diversity this system lends well to rigorous tests of ecological theory using a mesocosm approach (Benton *et al.* 2007). Similarly designed mesocosms have closely paralleled findings from field manipulations (Finke and Denno 2005). However, due to logistical difficulty simultaneously including naturally high densities of detritivore populations and excluding spiders, a field component was not included in this study.

To allow species time to settle, the leaf litter treatment was applied one day before herbivores and detritivores were added to mesocosms, and the spider treatment was applied the following day. Treatment combinations that involved a spider predator without any prey were excluded from the experiment. Thus, there were 14 treatment combinations, each replicated 5 times for a total of 70 mesocosms. Each mesocosm consisted of a sand-filled pot (23cm diameter x 15.5cm deep) with 5 transplants of *S. alterniflora* collected from a marsh near Tuckerton, NJ and grown to the height of 10 cm before the start of the experiment. Potted plants were enclosed in clear plastic tube cages (21.5 cm diameter x 30 cm tall), capped with a mesh top, and placed in large plastic wading pools (120 cm diameter and 15 cm deep) filled with water. Treatments were blocked by wading pools which were located outside under 30% shade cloth (Gempler®) at the Smithsonian Environmental Research Center in Edgewater, MD. Because the isopods were often hidden in the leaf litter it was not possible to visually monitor detritivore populations throughout the experiment. Instead I focused on the influence of detritivores on aboveground predator-herbivore dynamics and experiment was run for 75 days (approximately 2 planthopper

generations), and the experiment was terminated when herbivores showed initial signs of decline before they overwinter in leaf litter as nymphs (Denno *et al.* 2002). *Pardosa* molted to adults but did not reproduce over the course of the experiment.

To determine treatment effects on the density of detritivores and herbivores I collected all arthropods in each mesocosm at the end of the experiment using a Shopvac® vacuum sampler (Williamsport, PA, USA). Arthropods were killed using ethyl acetate and were transferred into glass jars containing 70% ethanol before they were returned to the laboratory where they were sorted and counted. To determine the cascading effects of the treatment combinations on plant growth and decomposition, I measured dry weight of aboveground plant biomass and dry weight of leaf litter remaining at the end of the experiment.

The survival and population growth of *L.vittata* isopods, and *P. dolus* herbivores, was assessed in the treatments where these factors were added. For example, variation in isopod density was assessed in response to main and interactive effects of herbivore, predator, and leaf litter addition. However, the influence of isopod addition was not included in the model as a factor that influenced isopod survival. Arthropod density data was $\log_{10}(x+1)$ transformed before analysis to meet assumptions of normality of residuals. Untransformed data are reported in figures. Four way ANOVA was used to assess the main and interactive effects of food-web composition (presence or absence of *L. vittata* detritivores, *P. dolus* herbivores, and *P. littoralis* predators) and leaf litter addition on live plant biomass and litter mass remaining (Proc Mixed, SAS v 9.1). Following significant ANOVA results, I used

contrasts and pairwise comparisons to determine treatment differences caused by interactive effects.

Results

Functional response of *Pardosa* spiders to detritivore prey

There was a significant effect of prey density ($F_{4,20}=8.20$, $p=0.0004$) and detritivore species (isopod and amphipod: $F_{1,20}=9.73$, $p=0.005$) on the number of individuals killed by *Pardosa* wolf spiders; the interaction was not significant ($F_{4,20}=1.06$, $p=0.40$). This result suggests a type II functional response with homogenous slopes for both prey species but with different intercepts (Figure 1). Thus, both detritivores were susceptible to spider predation, but amphipods were generally more at risk than isopods. Differences in the number of individuals surviving between spider-free controls and spider-containing mesocosms indicated that >95% of amphipod mortality was attributable to spider predation, whereas all isopods died from spider predation.

Effect of detritivores on predator-herbivore interactions, decomposition, and plant biomass

Isopod density was positively influenced by the presence of leaf litter in their habitat ($F_{1,28}=37.76$, $p<0.0001$) (compare hatched to open bars; Figure 2A). In the presence of leaf litter, isopod populations grew significantly from initial densities (20 *L. vittata*/mesocosm) such that there were six to eight fold increases in the isopod alone treatments (125 ± 35.3 *L. vittata*/mesocosm, mean \pm SEM, $n=5$; Figure 2A). *P. dolus* herbivores did not directly ($F_{1,28}=0.81$, $p=0.38$), or interactively (herbivore x

leaf litter: $F_{1,28}=0.25$, $p=0.62$; herbivore x predator: $F_{1,28}=0.47$, $p=0.50$) influence isopod density (Figure 2A). However, there was an interactive effect of leaf litter and spider predation on isopod abundance ($F_{1,28}=4.55$, $p=0.04$). Predation had a relatively larger adverse effect on the density of isopods in habitats that contained leaf litter, where isopods were also more abundant overall. In mesocosms with leaf litter, *Pardosa* wolf spiders suppressed isopod abundance by almost 50 percent (65 ± 12.5 , mean \pm SEM, $n=5$) compared to the spider-free control (125 ± 35.3 , mean \pm SEM, $n=5$). In contrast, in mesocosms devoid of leaf litter, isopods densities were roughly the same as initial densities after two month's time (22 ± 3.8 , mean \pm SEM, $n=20$; open bars Figure 2A). Neither predation by spiders, the presence of *Prokelisia* herbivores, nor any interactive effects influenced isopod abundance in litter-free mesocosms (open bars, Figure 2A).

In contrast to isopods, *Prokelisia* herbivores, which feed on the phloem of live plants, were not directly affected by the presence of leaf litter ($F_{1,28}=0.18$, $p=0.67$), and their populations grew rapidly either in the presence of leaf litter (159 ± 17.4 , mean \pm SEM, $n=20$; hatched bars) or when it was absent (172.4 ± 19.92 , mean \pm SEM, $n=20$; open bars Figure 2B). Also, there was no direct effect of detritivore presence on planthopper density ($F_{1,28}=0.01$, $p=0.97$; Figure 2B). However, there was an interactive effect of spider predation and the presence of isopods on *Prokelisia* herbivore abundance (spider x isopod: $F_{1,28}=9.26$, $p=0.005$; spider x isopod x leaf litter: $F_{1,28}=3.54$, $p=0.07$). In habitats that contained leaf litter, *Pardosa* predation on *Prokelisia* herbivores was reduced in the presence of isopods (121 ± 5.6 , mean \pm SEM, $n=5$) compared to when isopods were absent (83 ± 8.4 , mean \pm SEM, $n=5$)

(Figure 2B hatched bars compare HPL and IHPL). However, in habitats devoid of leaf litter, *Pardosa* predation had consistent influence on *Prokelisia* herbivores independent of the presence (90 ± 8.8 , mean \pm SEM, n=5) or absence (87 ± 6.5 , mean \pm SEM, n=5) of isopods (Figure 2B open bars compare HP and IHP).

Treatment effects, explicitly through the detrital pathway, had cascading consequences for both litter decomposition and plant biomass (Figure 2C-D). Specifically, litter decomposition was influenced by the presence of *L. vittata* isopods ($F_{1,24}=27.30$, $p=0.0001$), such that the greatest reduction of leaf litter biomass, the least amount of leaf litter remaining in the isopod-addition treatment (treatment IL: 1.04 ± 0.39 g, mean \pm SEM, n=5). However there was an interactive effect of isopods and *Prokelisia* herbivores ($F_{1,24}=8.23$, $p=0.009$). Thus, there was reduced decomposition, resulting in more litter remaining when both isopods and *Prokelisia* were present (4.72 ± 0.22 g, mean \pm SEM, n=5) (IHL: Figure 2C), a treatment where there were non-significant trends toward reduction in isopod abundance (IL compared to IHL Figure 2A). There was no direct influence of *Prokelisia* herbivores on decomposition ($F_{1,24}=0.31$, $p=0.58$). *Pardosa* spiders diminished the influence of isopods on leaf litter decomposition resulting in more leaf litter remaining when *Pardosa* were present (treatments IPL and IHPL Figure 2C; $F_{1,24}=13.34$, $p=0.001$). Notably, over the course of the experiment, live *Spartina* grew the most, and exhibited the largest final biomass when only isopods were present (5.81 ± 0.75 g; Figure 2D), the same treatment where isopods were the most abundant (Figure 2A: bar IL), and leaf litter decomposition was also greatest (Figure 2C: treatment IL).

The positive effect of isopods on live plant biomass was eliminated by the addition of either spiders, herbivores or both (Figure 2D).

Discussion

Results of this study indicate that detritivores can influence interactions in the primary producer based food web. The influence of salt marsh isopods on plant growth and predator-herbivore interactions is contingent upon habitat structure, as isopod populations are greatly reduced in the absence of leaf litter (Figure 2A). The presence of leaf litter enhances isopod reproduction, but leaves them more vulnerable to spider predation (Figure 2A). Spider predators also reduce herbivore populations in simple habitats devoid of leaf litter (Figure 2B). However in more complex habitats rich in leaf litter, the direct negative effect of predators on detritivores can result in an indirect positive effect of relaxed predation pressure on herbivores (Figure 2B). This experiment suggests that the presence of leaf litter and detritivores can reduce the suppression of herbivores by predators.

I found that in more structurally complex habitats species interactions were also more complex (Figure 3). Species interactions in this experiment had relatively stronger effects on decomposition, which was either directly or indirectly influenced by isopods, herbivores, and predators (Figure 2C; Figure 3), than on live plant biomass, which was only affected by isopods when they were in habitats rich in leaf litter (Figure 2D; Figure 3). Notably, it was the pathway through the decomposition-based food web (spiders consuming isopods which feed on leaf litter) that affected live plant biomass and not a trophic cascade due to predation on herbivores that ultimately affected live plant biomass (Figure 2D; Figure 3).

Even though I found that predator presence reduced rates of decomposition by decreasing the impact of macrofaunal detritivores on detritus, several studies have found positive indirect effects of predator removal on rates of decomposition (Lawrence and Wise 2000). Furthermore, the exclusion of macroinvertebrate predators (mainly spiders and ants) from litterbags resulted in altered leaf litter chemistry (total phenolics and condensed tannins), but did not regularly translate to increased litter mass loss during decomposition despite a 34% increase in detritivore (Collembola) populations in riparian forest habitat (Hunter *et al.* 2003). Inconsistent results among the above studies may be due to the indirect effects of relaxed predation pressure on macrofauna that either consume or stimulate changes in the abundance or activity of microbial decomposers (Hedlund and Öhrn 2000), which I did not measure.

In a summary of 24 studies, Mikola and colleagues found that arthropods stimulated decomposition through their variable effects on microbes comparatively more than by their direct effects on leaf litter consumption (Mikola *et al.* 2002). Thus, both the age of the leaf litter, which influences microbial colonization (Wensem *et al.* 1993), as well as changes in the community composition of macrofaunal detritivores (Postma-Blaauw *et al.* 2006) will likely have strong impacts on the relative importance of microbial and macrofaunal decomposers (Huhta *et al.* 1998). Therefore, changes in the detritivore community and its influence on microbial activity can influence feedbacks to primary producers via altered N-mineralization (Setälä *et al.* 1998).

My results are consistent with recent studies that emphasize the importance of detritivores in the diet of generalist predators (Settle *et al.* 1996; Ishijima *et al.* 2006; Park and Lee 2006). However, changes in the size distribution of the generalist predator assemblage will also likely influence the strength of predator-detritivore interactions. Although I found a fairly strong negative influence of medium-sized *Pardosa* wolf spiders on isopods in my study, research in cucurbit gardens indicates that smaller spiders feed on detritivores, but that larger spiders consume predominantly herbivore prey (Wise *et al.* 2006).

Furthermore, the relative proportion of a predator's diet that is composed of detritivores as opposed to herbivores may shift throughout the growing season, an interaction that I did not examine in this study. For example, spiders in rice paddies feed on detritivores early in the season and shift to feed on herbivorous planthoppers later in the season (Settle *et al.* 1996; Ishijima *et al.* 2006; Park and Lee 2006). Thus, leaf litter and associated detritivores can be critical for maintaining predators in a habitat at high enough densities that they are able to more effectively suppress herbivore populations later in the season.

In conclusion, detritivores play multiple roles in food web interactions and ecosystem processes. Most notably, detritivores serve as alternative prey (Lawrence and Wise 2000, 2004), litter mineralizers (Càcamo *et al.* 2000), and ecosystem engineers (Lavelle 2002). Specifics of the functional group of detritivores, the voracity in which they consume leaf litter, their classification as a fungivores, shredders, grazers, and deposit feeders, as well as those that are vulnerable or resistant to predation will determine the extent to which detritivores influence

predator-herbivore interactions. Furthermore, there is likely to be a significant temporal component to the strength of interactions among predators, herbivores, and detritivores. This study emphasizes that changes in detritivore abundance are likely to have widespread influences, not only on rates of decomposition, but also for primary production and feedback loops that affect aboveground food-web interactions between predators and herbivores.

Literature Cited

- Benton T.G., Solan M., Travis J.M.J. and Sait S.M. (2007) Microcosm experiments can inform global ecological problems. *Trends in ecology and evolution*, 22, 516-521
- Bertness M.D. (1985) Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology*, 66, 1042-1055
- Brewer J.S., Levine J.M. and Bertness M.D. (1998) Interactive effects of elevation and burial with wrack on plant community structure in some Rhode Island salt marshes. *Journal of Ecology*, 86, 125-136
- Càcamo H.A., Abe T.A., Prescott C.E., Holl F.B. and Chanway C.P. (2000) Influence of millipedes on litter decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. *Canadian Journal of Forest Research*, 30, 817-826
- Casula P., Wilby A. and Thomas M.B. (2006) Understanding biodiversity effects on prey in multi-enemy systems. *Ecology Letters*, 9, 1-10
- Chalcraft D.R. and Resatarits W.J. (2003) Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology*, 84, 2407-2418

- Chase J.M. (2003) Strong and weak trophic cascades along a productivity gradient. *Oikos*, 101, 187-195
- Denno R., F., Lewis D. and Gratton C. (2005) Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Annales Zoologici Fennici*, 42, 295-311
- Denno R.F., Gratton C., Dobel H.G. and Finke D.L. (2003) Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology*, 84, 1032-1044
- Denno R.F., Gratton C., Peterson M.A., Langellotto G.A., Finke D.L. and Huberty A.F. (2002) Bottom-up forces mediate natural enemy impact in a phytophagous insect community. *Ecology*, 83, 1443-1458
- Denno R.F. and Peterson M.A. (1995) Density-dependent dispersal and its consequences for population dynamics. In: *Population Dynamics*, pp. 113-130. Academic Press, Inc.
- Denno R.F., Roderick G.K., Olmstead K.L. and Dobel H.G. (1991) Density-related migration in planthoppers (Homoptera, Delphacidae) - the role of habitat persistence. *American Naturalist*, 138, 1513-1541
- Döbel H.G. and Denno R.F. (1994) Predator-Planthopper Interactions. In: *Planthoppers, their ecology and management* (eds. Denno RF and Perfect IT), pp. 325-399. Chapman and Hall, London
- Elderl B.D. (2006) Disturbance-mediated trophic interactions and plant performance. *Oecologia*, 147, 261-271

- Ferguson S.H. and Joly D.O. (2002) Dynamics of springtail and mite populations: the role of density dependence, predation, and weather. *Ecological Entomology*, 27, 565-573
- Finke D.L. and Denno R.F. (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology*, 83, 643-652
- Finke D.L. and Denno R.F. (2005) Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*, 8, 1299-1306
- Greze A.A. and Prado E. (2000) Effect of plant patch shape and surrounding vegetation on the dynamics of predatory coccinellids and their prey *Brevicoryne brassicae* (Hemiptera : Aphididae). *Environmental Entomology*, 29, 1244-1250
- Halaj J. and Wise D.H. (2001) Terrestrial trophic cascades: How much do they trickle? *American Naturalist*, 157, 262-281
- Halaj J. and Wise D.H. (2002) Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *ecology*, 83, 3141-3151
- Hedlund K. and Öhrn M.S. (2000) Tritrophic interactions in a soil community enhance decomposition rates. *Oikos*, 88, 585-591
- Huhta V., Persson T. and Setälä H. (1998) Functional implications of soil fauna diversity in boreal forests. *Applied Soil Ecology*, 10, 277-288
- Hunter M.D., Adl S., Pringle C.M. and Coleman D.C. (2003) Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia*, 47, 101-115

- Ishijima C., Taguchi A., Takagi M., Motobayashi T., Nakai M. and Kunimi Y. (2006) Observational evidence that the diet of wolf spiders (Araneae : Lycosidae) in paddies temporarily depends on dipterous insects. *Applied Entomology and Zoology*, 41, 195-200
- Laakso J. and Setälä H. (1999) Population-and ecosystem-level effects of predation on microbial-feeding nematodes. *Oecologia*, 120, 279-286
- Langellotto G.A. and Denno R.F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, 139, 1-10
- Langellotto G.A. and Denno R.F. (2006) Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. *Ecological Entomology*, 31, 575-581
- Lavelle P. (2002) Functional domains in soils. *Ecological Research*, 17, 441-450
- Lawrence K.L. and Wise D.H. (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia*, 44, 33-39
- Lawrence K.L. and Wise D.H. (2004) Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia*, 48, 149-157
- Mikola J., Bardgett R.D. and Hedlund K. (2002) Biodiversity, ecosystem functioning and soil decomposer food webs. In: *Biodiversity and ecosystem functioning- Synthesis and perspectives* (eds. Loreau M, Naeem S and Inchausti P), pp. 169-180. Oxford University Press, Oxford
- Mikola J. and Setälä H. (1998) No evidence of trophic cascades in an experimental microbial-based soil food web. *Ecology*, 79, 153-164

- Miyashita T., Takada M. and Shimazaki A. (2003) Experimental evidence that aboveground predators are sustained by underground detritivores. *Oikos*, 103, 31-36
- Moore J.C., Berlow E.L., Coleman D.C., De Ruiter P.C., Dong Q., Hastings A., Johnson N.C., McCann K.S., Melville K., Morin P.J., Nadelhoffer K., Rosemond A.D., Post D.M., Sabo J.L., Scow K.M., Vanni M.J. and Wall D.H. (2004) Detritus, trophic dynamics and biodiversity. *Ecology Letters*, 7, 584-600
- Morse D.H. (1997) Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae: Lycosidae). *Journal of Arachnology*, 25, 1-10
- Newell S.Y., Fallon R.D. and Miller J.D. (1989) Decomposition and microbial dynamics for standing, naturally positioned leaves of the salt-marsh grass *Spartina alterniflora*. *Marine Biology*, 101, 471-481
- Newell S.Y. and Porter D. (2000) Microbial secondary production from salt marsh-grass shoots, and its known and potential fates. In: *Concepts and Controversies in Tidal Marsh Ecology* (eds. Weinstein MP and Kreeger DA), pp. 159-185. Kluwer Academic Publishers, Boston
- Park H.H. and Lee J.H. (2006) Arthropod trophic relationships in a temperate rice ecosystem: A stable isotope analysis with delta C-13 and delta N-15. *Environmental Entomology*, 35, 684-693
- Polis G.A. (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, 86, 3-15

- Postma-Blaauw M.B., Bloem J., Faber J.H., van Groenigen J.W., de Goede R.G.M. and Brussaard L. (2006) Earthworm species composition affects the soil bacterial community and net nitrogen mineralization. *Pedobiologia*, 50, 243-256
- Rypstra A.L. and Marshall S.D. (2005) Augmentation of soil detritus affects the spider community and herbivory in a soybean agroecosystem. *Entomologia Experimentalis Et Applicata*, 116, 149-157
- Rypstra A.L., Schmidt J.M., Reif B.D., DeVito J. and Persons M.H. (2007) Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos*, 116, 853-863
- Setälä H., Laakso J., Mikola J. and Huhta V. (1998) Functional diversity of decomposer organisms in relation to primary production. *Applied Soil Ecology*, 9, 25-31
- Settle W.H., Ariawan H., Astuti E.T., Cahyana W., Hakim A.L., Hindayana D., Lestari A.S. and Pajarningsih (1996) Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology*, 77, 1975-1988
- Shimazaki A. and Miyashita T. (2005) Variable dependence on detrital and grazing food webs by generalist predators: aerial insects and web spiders. *Ecography*, 28, 485-494
- Silliman B.R. and Bertness M.D. (2002) A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Science*, 99, 10500-10505

- Stiling P. and Moon D.C. (2005) Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia*, 142, 413-420
- Uetz G.W. (1991) Habitat structure and spider foraging. In: *Habitat structure: the physical arrangement of objects in space*. (eds. Bell S, McCoy E and Mushinsky H), pp. 325-348. Chapman and Hall, New York, NY
- Wardle D.A. (2002) *Communities and ecosystems: Linking the aboveground and belowground components*. Princeton University Press, Princeton, NJ.
- Wardle D.A., Williamson W.M., Yeates G.W. and Bonner K.I. (2005) Trickle-down effects of aboveground trophic cascades on the soil food web. *Oikos*, 111, 348-358
- Wensem J.V., Verhoef H.A. and Van Straalen N.M. (1993) Litter degradation stage as a prime factor for isopod interaction with mineralization processes. *Soil Biology and Biochemistry*, 25, 1175-1183
- Wise D.H., Moldenhauer D.M. and Halaj J. (2006) Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*, 16, 865-876
- Zimmer M., Pennings S.C., Buck T.L. and Carefoot T.H. (2002) Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. *Functional Ecology*, 16, 596-607
- Zimmer M., Pennings S.C., Buck T.L. and Carefoot T.H. (2004) Salt marsh litter and detritivores: A closer look at redundancy. *Estuaries*, 27, 753-769

List of Figures

Figure 1. Functional response of *Pardosa* spiders to increasing prey density: mean (\pm SEM; n=5) number of amphipods *Orchestia grillus* (●) or isopods *Littorophiloscia vittata* (○) killed per 48 hours.

Figure 2. Effect of food-web treatment combinations on the density (# per mesocosm) of (A) the detritivorous isopod *Littorophiloscia vittata* and (B) the herbivorous planthopper *Prokelisia dolus*, as well as (C) the dry mass (g) of leaf litter remaining and (D) the dry mass (g) of live *Spartina alterniflora*. Treatment combinations in experimental mesocosms were the presence of: (I) the detritivorous isopod *Philoscia vittata*, (H) the herbivorous planthopper *Prokelisia dolus*, (P) the predaceous spider *Pardosa littoralis*, (L) leaf litter, and (O) the unmanipulated control treatment. Open and hatched bars indicate the absence and presence of leaf litter respectively. Means (+ SEM, n=5) with different letters within each panel are significantly different ($p < 0.05$)

Figure 3. Conceptual model of a salt-marsh, arthropod food web describing the direct (solid arrow) and indirect (dashed arrow) interactions among predators (the spider *Pardosa littoralis*), herbivores (the planthopper *Prokelisia dolus*), detritivores (the isopod *Philoscia vittata*), and plants (*Spartina alterniflora*) in the (A) absence and (B) presence of leaf litter. (A) In simple-structured habitats devoid of leaf litter, species interactions are less reticulate, and predators predominantly consume herbivores. (B) In structurally-diverse habitats with leaf litter, species interactions are more complex. Predators directly suppress populations of both herbivores and detritivores, and the presence of detritivores results in an indirect positive effect on herbivore growth due

to relaxed predation pressure. The pathway through the detrital food web and rather than predator-herbivore interactions results in a trophic cascade and enhanced plant growth.

Figure 1.

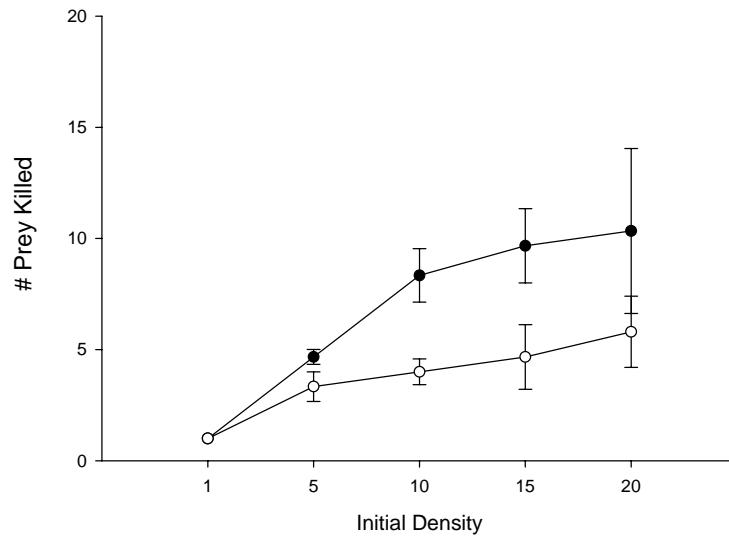


Figure 2.

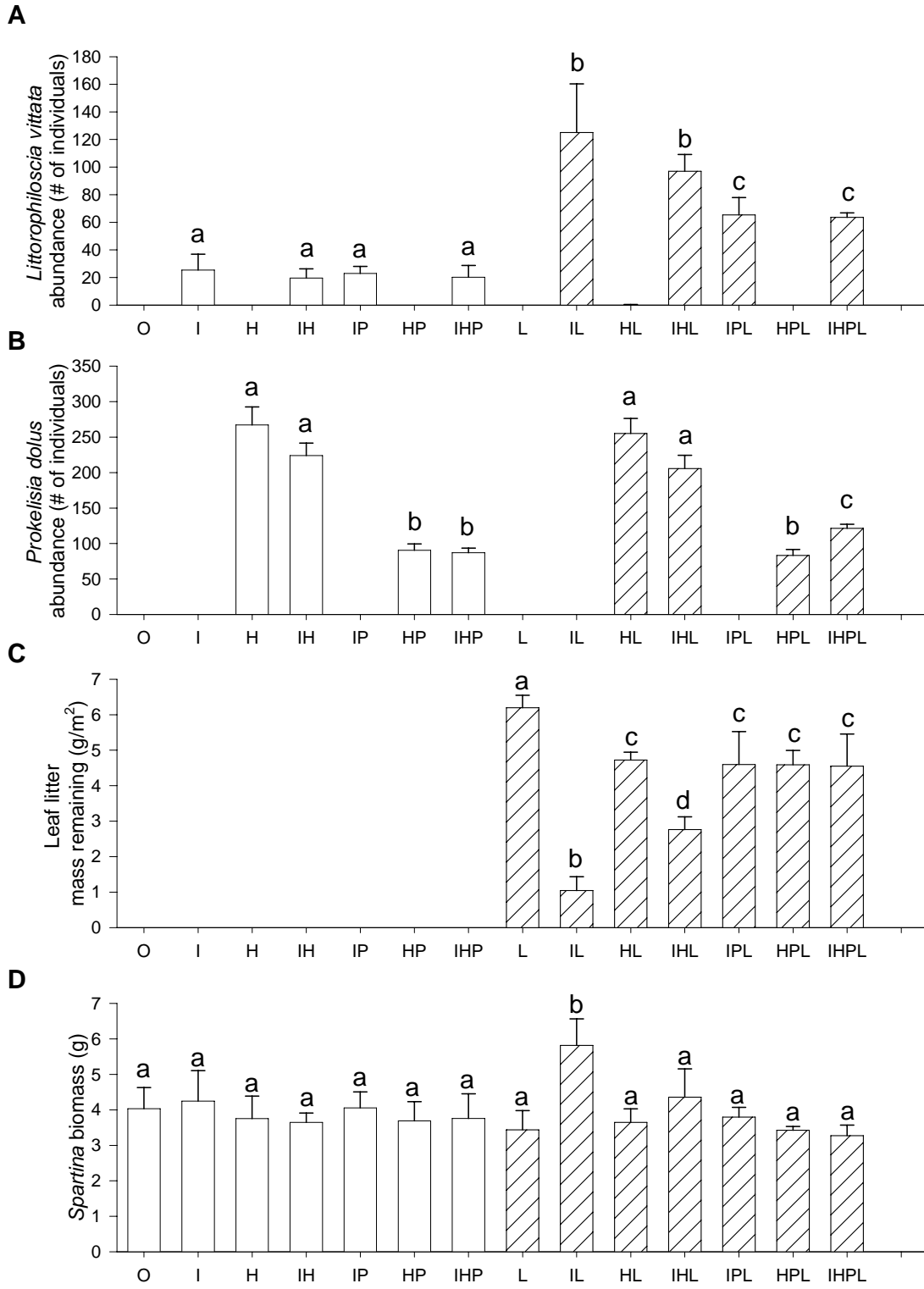
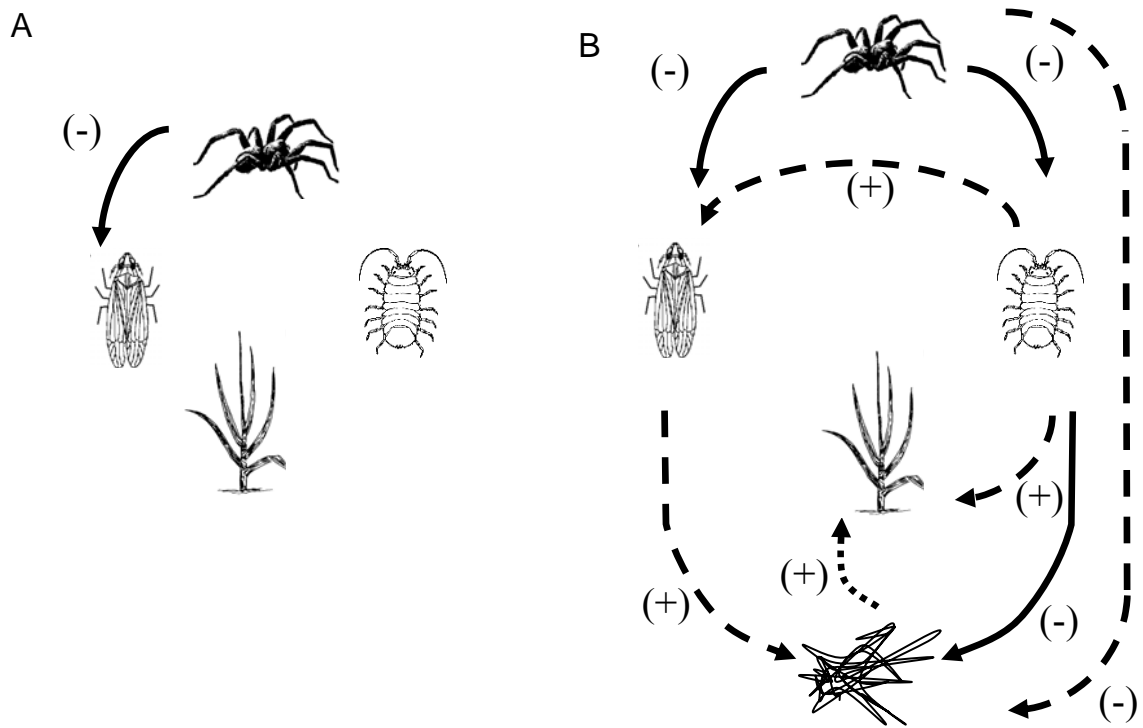


Figure 3.



Tables Table 1. ANOVA results for the main and interactive effect of the detritivorous isopod *Littorophiloscia vittata* (I), the herbivorous planthopper *Prokelisia dolus* (H), the predaceous spider *Pardosa littoralis* (P), and leaf litter (L) on the abundance of the isopod *L. vittata* and the planthopper *P. dolus* prey, as well as on the dry mass of remaining leaf litter (g) and dry mass (g) of *Spartina alterniflora* plants in mesocosms. Significant F and *p*-values are **bolded** for emphasis.

Source of variation	<i>L. vittata</i> Detritivore			<i>P. dolus</i> Herbivore			Leaf litter Mass remaining			<i>S. alterniflora</i> Live biomass		
	<i>df</i> *	F	<i>P</i>	<i>df</i> *	F	<i>P</i>	<i>df</i> *	F	<i>P</i>	<i>df</i> *	F	<i>p</i>
I				1,28	0.01	0.97	1,24	27.30	<0.0001	1,52	3.09	0.09
H	1,28	0.81	0.38				1,24	0.31	0.58	1,52	0.93	0.34
P	1,28	4.91	0.03	1,28	224.2	<0.0001	1,24	13.34	0.001	1,52	3.18	0.08
L	1,28	37.76	<0.0001	1,28	0.18	0.67				1,52	0.00	0.99
I*H							1,24	8.23	0.009	1,52	1.75	0.19
I*P				1,28	9.26	0.005	1,24	2.97	0.09	1,52	0.21	0.65
I*L				1,28	2.45	0.13				1,52	1.88	0.17
H*L	1,28	0.25	0.62							1,52	0.03	0.87
P*L	1,28	4.55	0.04	1,28	2.63	0.11				1,52	2.21	0.14
H*P	1,28	0.47	0.50				1,24	2.51	0.13	1,52	0.68	0.42
I*H*L										1,52	0.62	0.43
I*P*L				1,28	3.54	0.07				1,52	3.89	0.05
I*H*P*L										1,52	0.18	0.67

* *degrees of freedom*: numerator, denominator

Chapter 2: Detritivore identity influences interactions between generalist predators and their herbivore prey

Abstract

There is growing awareness that aboveground food-web dynamics are strongly dependent on the composition and activity of the associated detritivore community. However, gradients in abiotic stress can differentially influence the distribution of species in these two linked subsystems. On *Spartina alterniflora* salt marshes the relative abundance of the numerically dominant detritivore species (the isopod *Littorophiloscia vittata*, the amphipod *Orchestia grillus*, and the snails *Melampus bidentatus* and *Littoraria irrorata*) changes across an elevation gradient, but there is spatial overlap of all species in mid-elevation habitats. In order to determine whether the identity of these detritivores influences the ability of *Pardosa* wolf spiders to suppress their herbivore prey in the aboveground assemblage I conducted a 5x2 factorial mesocosm study designed to mimic the variety of species interactions that can be found in mid-elevation *Spartina alterniflora* meadow habitats. I measured the direct and interactive response of aboveground-feeding *Prokelisia* herbivores to one of five detritivore treatments in the presence and absence of generalist *Pardosa* predators. In the absence of detritivores, *Pardosa* spiders effectively suppressed *Prokelisia* prey populations. However, by serving as alternative prey some detritivores (*Littorophiloscia vittata*) but not others (*Orchestia grillus*) dampened the influence of *Pardosa* on *Prokelisia* populations and acted to

maintain both herbivores and predators in the aboveground subsystem. Detritivores also generated non-trophic influences on predator-herbivore interactions. Voracious grazing detritivores that were invulnerable to spider predation (the snail *Littoraria irrorata*) altered the structure and biomass of the *Spartina* habitat and limited both herbivore and predator abundance. In contrast, *Melampus bidentatus* mineralized *Spartina* leaf litter, but had no influence on aboveground food-web interactions. These results underscore the multiple pathways by which changes in the identity and species composition of the detritivore community can alter the strength of aboveground predator-herbivore interactions.

Keywords: aboveground-belowground, predation, alternative prey, food web dynamics, detritivore, ecosystem engineer, herbivore suppression, species identity

Introduction

Live plants and their associated leaf litter serve as biotic links between aboveground and detritivore communities (Wardle 2002, Wardle et al. 2004). However, abiotic gradients that constrain species distributions and thus influence realized species interactions differ between aboveground and belowground communities (De Deyn and Van Der Putten 2005). Aboveground herbivore communities that depend upon live plant production can be constrained by ambient climate, host plant quality, and predators (Hunter et al. 1997). In contrast, detritivore communities that rely on leaf-litter subsidies are more directly influenced by litter quality, soil chemistry, and water availability (Wall 2004). Thus, even though the

primary producer and decomposer subsystems are interdependent, there is growing recognition that species identity and changes in community composition within the two subsystems may be somewhat decoupled (Wolters et al. 2000, De Deyn and Van Der Putten 2005, Wall 2007). Here I focus on several pathways by which changes in detritivore species identity can alter aboveground predator-herbivore interactions and food-web dynamics. Notably, reciprocal feedback mechanisms are also possible, and changes in aboveground community composition can also indirectly influence detritivore communities (Wardle et al. 2005), but I do not explore such interactions here.

Detritivores can influence aboveground food web structure and ecosystem processes via multiple pathways. First, by functioning as ecosystem engineers, soil moving detritivores can alter the physical environment for plant roots which in turn can result in changes to plant growth, quality, and architecture (Lavelle 2002, Boyer and Fong 2005, Jouquet et al. 2006). Soil engineering is a trait found in many groups of soil invertebrate macrofauna such as earthworms, ants, termites, and fiddler crabs (Bertness 1985, Jouquet et al. 2006, Holdsworth et al. 2007). Secondly, by mineralizing leaf litter, detritivores can alter nutrient availability for plant uptake (Càcamo et al. 2000). By directly grazing leaf litter or by consuming microbial decomposers, macrofauna detritivores can both enhance or suppress rates of decomposition (Hättenschwiler et al. 2005). Considering the important role that host plant nutrition plays for plant-herbivore interactions, it is surprising that only recently have herbivore population dynamics begun to be linked to the detritivore species influencing nutrient cycling (Scheu et al. 1999, Bonkowski et al. 2001, Hines et al.

2006). Finally, by serving as a food resource for generalist predators, detritivores can indirectly influence trophic interactions in the aboveground food web. Augmentation of detritivore prey densities have resulted in mixed consequences for aboveground predator-herbivore interactions (Halaj and Wise 2002, Wise et al. 2006). Alternative detritivore prey can maintain high predator densities in a habitat, resulting in enhanced suppression of herbivore prey (Settle et al. 1996). In contrast, the presence and abundance of preferred detritivore prey can reduce predation pressure on less vulnerable herbivore prey (Wise et al. 2006). Ultimately, changes in soil conditions that influence detritivore species composition can change the functional pathway by which detritivores influence aboveground food web interactions (Wardle 2002). Therefore, although pairs of species in the aboveground food web may coexist across environmental gradients in soil conditions, the strength and consistency of their interactions may be contingent upon changes to the detritivore sub system due to the identity of the dominant detritivore species.

The aim of my study was to examine if the identity of the abundant detritivores found on a North Atlantic salt marsh influences the strength of aboveground, predator-herbivore interactions. There have been intensive investigations into the ability of aboveground salt marsh predators to limit their herbivorous prey (Denno et al. 2002, Denno et al. 2005, Finke and Denno 2005). Additional studies have investigated the ability of detritivores to influence salt-marsh plant growth (Bertness 1985) and litter decomposition (Zimmer et al. 2004). I predict that 1) by serving as alternative prey detritivores can maintain predators in the system, but that 2) by mineralizing leaf litter detritivores may subsidize plant quality

and enhance herbivore population growth, and that 3) by engineering habitat structure detritivores can influence both herbivore and predator populations. Because some predicted detritivore influences on the aboveground community can differentially promote predator populations (prediction 1), subsidize herbivore populations (prediction 2), or potentially destabilize predator-herbivore dynamics (prediction 3) the extent to which each prediction attenuates or cascades to influence all trophic levels likely depends on the identity of the numerically dominant detritivores in the system.

Methods

Study System

Along the Atlantic coast of North America, the single cordgrass species, *Spartina alterniflora*, can form expansive monospecific stands that extend across natural gradients in soil conditions created by changes in elevation, tidal inundation, soil porosity, and nitrogen availability (Valiela et al. 1976, Mendelsohn 1979, Mendelsohn et al. 1981, Bradley and Morris 1991). A short form of *S. alterniflora* grows in high marsh meadows habitats that are characterized by high salinity, and irregular tidal inundation. At the low end of the elevation gradient a tall form of *S. alterniflora* grows in creek-side habitats that are regularly flooded and thus are highly subsidized with tidal nutrients. Variation in live plant structure and leaf litter accumulation and decomposition create a patchy mosaic of habitats at intermediate elevations (Brewer et al. 1998, Denno et al. 2005).

The aboveground food web is numerically dominated by the phloem-feeding herbivore *Prokelisia dolus* (Delphacidae: Hemiptera) and the generalist spider

predator *Pardosa littoralis* (Araneae: Lycosidae). *Prokelisia* herbivores are sensitive to changes in host plant nitrogen, and can reach densities as high as 50,000 individuals/m² in patches of high-quality *Spartina* plants (Denno et al. 2002). *Pardosa* wolf spiders display a positive numerical response to increases in prey density, and they also aggregate in habitats with abundant leaf litter where they gain refuge from cannibalism and intraguild predation (Denno et al. 2002, Finke and Denno 2002, Langellotto and Denno 2004). Additionally, *Pardosa* have been reported to consume detritivore prey such as isopods, amphipods, and collembolans that abound in habitats with ample *Spartina* leaf litter (Morse 1997; Chapter 1). Therefore, leaf litter and the specific composition of the associated detritivore community have a strong potential to influence the ability of *Pardosa* spiders to suppress their herbivore prey (Chapter 1).

Across the elevation gradient on the marsh there is a characteristic zonation in the abundance of particular detritivore species, but there is overlap of all species in expansive mid-elevation habitats. Moreover, macrofauna shredder/grazers vary in their vulnerability to spider predation, even though they all consume the fungi that initiate decomposition (Newell et al. 1989, Newell and Porter 2000). Due to their hard shells, the dominant snails *Littoraria irrorata* and *Melampus bidentatus* are invulnerable to spider predation. *Littoraria*, the salt marsh periwinkle, selectively consumes portions of *S. alterniflora* that are rich in fungus while it aggressively consumes both live and decaying leaf tissue (Graça et al. 2000). *Littoraria* are prolific consumers in low and mid elevation habitats, where they typically range from 21 to 70 individuals/m² (Schindler et al. 1994). Coffeebean snails, *Melampus*

bidentatus, graze standing-decaying cord grass, and their feeding activity can stimulate rather than limit fungal growth (Graça et al. 2000). *Melampus* (8-10 mm) are much smaller than *Littoraria* (22-24 mm) and they can be found in patches with densities as high as 3,000 individuals/m² in high and mid elevation habitats, but densities less than 400 individuals/m² are more common (Graça et al. 2000).

In contrast to grazing snails, other dominant macrofauna detritivores such as isopods and amphipods are susceptible to spider predation (Morse 1997). The isopods *Littorophiloscia vittata* and *Venezillo parvus*, are grazing crustaceans that shred *Spartina alterniflora* leaf litter in high and mid elevation habitats, with variable impact on microbial activity and decomposition rates (Newell and Porter 2000, Zimmer et al. 2004). In contrast, talitrid amphipods (*Uhlorchestia spartinophila*, *Orchestia grillus*) are more evenly distributed across the elevation gradient where they graze on fungus and decaying cord grass (Graça et al. 2000). Although the feeding rates per mg individual have been found to be over seven times that of *Littoraria* their smaller size makes their per capita grazing capacity much less than that of *Littoraria* (Graça et al. 2000).

Despite their high densities, overlap in spatial distribution and general trophic position between microbes and higher order consumers, I anticipate that differences in vulnerability to predation and feeding style among the detritivore species (*Littoraria irrorata*, *Melampus bidentatus*, *Littorophiloscia vittata*, and *Orchestia grillus*) will contribute to differences in the way they influence interactions with members of the aboveground food web. Thus, I examined the unique ability of each of these detritivore species to influence the aboveground food web structure by N-

mineralization, habitat modification, and by serving as prey for invertebrate consumers such as spider predators. Although I do not deny the potential importance of the interactive effects of multiple detritivore species on predator-herbivore interactions, this question was beyond the logistical scope of this study.

Mesocosm study

To determine the influence of detritivore identity on predator-herbivore interactions I conducted a randomized complete block, 5x2 factorial experiment in mesocosms. Treatment combinations consisted of the addition of one of 5 detritivore treatments (no detritivore, 50 *Littorophiloscia vittata*, 50 *Orchestia grillus*, 50 *Melampus bidentatus*, or 5 *Littoraria irrorata*) crossed with two levels of spider predation (4 *Pardosa littoralis* present or absent). This design resulted in 10 treatment combinations, each replicated 9 times for a total of 90 mesocosms.

Mesocosms were placed outside at the Smithsonian Environmental Research Center in Edgewater, MD and blocked by location in a common garden habitat. Each mesocosm consisted of a sand-filled pot (22 cm diameter x 21 cm deep) with 5 transplants of *S. alterniflora*, 25 g *S. alterniflora* leaf litter, and 30 adult *Prokelisia dolus* herbivores (25 females and 5 males). Potted plants were enclosed in clear plastic tube cages (21.5 cm diameter x 30 cm tall), capped with a mesh top, and pots were placed in plastic pans (30 cm diameter x 10 cm deep) filled with water.

Treatments were applied in a sequential fashion that approximated the phenology of field interactions. Detritivore species which remain in meadow habitats year round were applied 7 June 2007 and were allowed settle and feed before herbivores emerged. *Prokelisia dolus* herbivores, which overwinter as nymphs in leaf

litter and emerge as adults by mid June, were added to mesocosms on 25-27 June 2007 and allowed to settle for 4 days before 4 juvenile *Pardosa* spiders were added. In order to closely replicate field conditions, all plant and animal material was collected from an expansive *Spartina alterniflora* salt marsh meadow near Tuckerton, NJ. Species densities were chosen in an effort to mimic typical field densities (Graça et al. 2000, Zimmer et al. 2002, 2004) and also to establish a fairly consistent influence of detritivore biomass on *Spartina* leaf litter. Results of species manipulations in similarly designed mesocosms have been found to closely parallel findings in field manipulations (Finke and Denno 2005). However, because of the logistical difficulty of consistently maintaining healthy detritivore treatments but excluding spiders from habitats rich in leaf litter, I did not include a field manipulation in this study.

To determine the influence of the detritivore treatments on the strength of predator-herbivore interactions, *Pardosa* spider predators and *Prokelisia* herbivores were visually counted in each mesocosm after the experiment ran for 0, 15, 20, 40, 50, and 60 days. Because detritivores were often hidden in the leaf litter, it was not possible to obtain a visual assessment of the detritivore densities throughout the course of the experiment. However on 27 August 2007 after the experiment had run for 2 months, final invertebrate densities were obtained by collecting all animals from mesocosms using a Shop-vac® vacuum (Williamsport, PA, USA) fitted with mesh bags. Arthropods were killed using ethyl acetate, transferred into plastic bags, and frozen before they were returned to the laboratory and counted. To determine the cascading effects of the treatment combinations on plant growth I harvested and

recorded dry weight of aboveground *Spartina* biomass. To determine if leaf litter mineralization influenced nitrogen availability for plant roots, I collected and weighed leaf litter, extracted inorganic soil nitrogen (NH_4^+ and NO_3^-) using 2.0 M KCL (Mulvaney 1996), and sieved roots through 1.7 mm sieves. All plant material was freeze-dried (Labconco freezezone 6) and weighed.

The main and interactive effects of detritivore and predator treatments on *Spartina* roots, shoots, leaf litter, and soil inorganic nitrogen availability at the end of the experiment were assessed using two-way ANOVA. Survival of *Prokelisia dolus* and *Pardosa littoralis* was assessed using repeated measures two-way ANOVA with first order autoregressive covariance structure, which was selected due to best fit according to Akaike's Information Criterion. Following significant ANOVA results, I compared treatment means using Tukey's adjustment for multiple means comparison.

Results

Herbivore density

Prokelisia herbivore populations were influenced by detritivore identity ($F_{4,78}=3.40, p=0.01$) and *Pardosa* spiders ($F_{1,78}=10.73, p=0.001$) (Figure 1A-E). By the end of the experiment on the last sample date there was an interactive effect of detritivore and predator addition treatments indicating that the ability of *Pardosa* spiders to suppress *Prokelisia* is dependent upon both the presence and identity of detritivore species ($F_{4,80}=2.55, p=0.04$; Fig. 1F). In all mesocosms, *Prokelisia* populations experienced an initial decline from day 0-15 as the original planthoppers died of natural causes (Figure 1 A-E). Subsequently, *Prokelisia* populations grew

rapidly between days 20 to 50 as nymphs from the second generation emerged and developed. The experiment was terminated on day 60 when planthopper populations were again showing a slight natural decline. In the absence of detritivores, *Pardosa* spiders suppressed *Prokelisia* to low densities by day 50 (Figure 1A). *Pardosa* predators molted to adults by the end of the experiment but did not reproduce during the time course of the experiment.

The two detritivorous snail species, which were both invulnerable to spider predation, differentially influenced the strength of aboveground predator-herbivore interactions (Figure 1 B, C). In the absence of *Pardosa* spider predators, *Littoraria* snail addition reduced *Prokelisia* populations (Figure 1B), whereas *Melampus* snails did not significantly influence herbivore abundance (Figure 1C). Notably, *Pardosa* predation did not reduce planthopper populations beyond the negative influence of *Littoraria* (Figure 1B), and by the end of the experiment there was no difference in planthopper abundance between the spider predator-addition and *Littoraria* snail-addition treatments (Figure 1F). In contrast, spiders were able to suppress *Prokelisia* populations slightly earlier (day 40) in the *Melampus* addition treatment (Figure 1C) compared to the *Melampus*-free control treatment in which spiders did not suppress planthoppers until day 50 (Figure 1A). However, by the end of the experiment this difference did not enhance the overall spider suppression of *Prokelisia* herbivores compared to habitats devoid of detritivores (compare control and *Melampus* treatments in Figure 1F).

The detritivorous isopods and amphipods that were more vulnerable to predation also had differential effects on the strength of spider-herbivore interactions

(Figure 1D, E). In the absence of predators, neither *Littorophiloscia vittata* isopods (Figure 1D) nor *Orchestia grillus* (Figure 1E) amphipods directly influenced *Prokelisia* herbivore populations compared to control treatments. However, when *L. vittata* isopods were present, predation pressure on *Prokelisia* was relaxed (Figure 1D), such that after 60 days there were no significant differences between *Prokelisia* treatments that were exposed to spider predation, and those that were not (Figure 1F). Although *Orchestia grillus* initially reduced predation pressure on *Prokelisia* herbivores (Figure 1E), by the end of the experiment, *Pardosa* had suppressed *Prokelisia* populations as effectively as in habitats devoid of the detritivorous amphipod (Figure 1F).

Detritivore density

All snails survived but none reproduced during the experiment which resulted in final densities that were consistent with the initial densities stocked in the mesocosms (*Littoraria*: 70 individuals/m²; *Melampus* 700 individuals/m²). Similarly, *Orchestia grillus* populations were only weakly suppressed by the presence of spiders (524 ± 36 individuals/m²; mean \pm SE) compared to the spider-free control (601 ± 52 individuals/m²; mean \pm SE). In contrast, *Littorophiloscia vittata* populations were limited by *Pardosa* predators (424 ± 278 individuals/m²; mean \pm SE) and even grew beyond initial densities in the absence of spider predation (1157 ± 392 individuals/m²; mean \pm SE).

Predator density

Pardosa spider survival was differentially influenced by the detritivore species addition treatments ($F_{4,40}=7.67$, $p=0.0001$; Figure 2). The presence of

Littoraria irrorata snails adversely influenced *Pardosa* ($7.08 \pm 1.41/\text{m}^2$ mean \pm SE) compared to the control ($9.9 \pm 1.55/\text{m}^2$ mean \pm SE). However, the presence of *Melampus* snails did not affect spider survival. *Pardosa* exhibited the highest survivorship in the presence of *Littorophiloscia vittata* isopods ($20.18 \pm 2.12/\text{m}^2$ mean \pm SE), but was uninfluenced by the presence of *Orchestia grillus* ($15.2 \pm 1.84/\text{m}^2$ mean \pm SE) (Figure 2). Overall, treatment differences remained fairly consistent throughout the course of the experiment, suggesting that initial habitat conditions and detritivore prey the inter-generation gap in herbivore populations (day 0-15) strongly influenced spider survival and treatment differences. Spider densities increased on the last sampling date, indicating that vacuum sampling more effectively measured actual spider density than did visual counts.

Spartina plant biomass and litter decomposition: Aboveground *Spartina* biomass was influenced by changes in detritivore identity ($F_{4,72}=3.82, p=0.007$), but was not influenced by the presence of spiders ($F_{1,72}=0.09, p=0.77$). *Littoraria* snails limited live plant biomass due to their grazing activity (Figure 3A), but they did not influence leaf litter decomposition (Figure 3B). In contrast, *Melampus bidentatus* snails had little effect on *Spartina* biomass (Figure 3A), but they enhanced rates of decomposition as evidenced by the least amount of *Spartina* leaf litter remaining of all the detritivore species treatments (Figure 3B). Neither *Littorophiloscia vittata* nor *Orchestia grillus* influenced *Spartina* live plant biomass or *Spartina* decomposition (Figure 3A-B). Additionally, none of the detritivore addition treatments influenced *Spartina* root biomass ($F_{4,72}=1.04, p<0.39$), or inorganic soil nitrogen availability (NH_4^+ $F_{4,72}=0.39, p=0.81$; NO_3^- $F_{4,72}=0.30, p=0.87$; Table 1).

Discussion

Defining species' functional characteristics has been a useful technique for assessing the influence of species identity on ecosystem processes (Lavorel and Garnier 2002, Hooper et al. 2005). Within a trophic level such as detritivores, a high degree of continuity among functional traits between species can minimize the influence of species loss on the functioning of a system (Chapin et al. 1997). In contrast, loss of species with more unique functional characteristics can potentially have more severe consequences for productivity or rates of decomposition (Tilman et al. 1997, Eviner and Chapin 2003). Notably, species do not interact in isolated feeding guilds, and community dynamics generally involve feedbacks between soil resources and multi-trophic interactions, including those within and between soil and aboveground consumers (Bardgett and Wardle 2003, De Deyn and Van Der Putten 2005). Thus, much of the apparent conflict involving the role of species identity, diversity, and functional complementarity can be resolved by taking a more holistic approach that considers not only detritivore influence on individual ecosystem processes, but also linkages between detrital and primary producer subsystems (Wardle et al. 2000, Wardle et al. 2004).

Predator-herbivore-detritivore interactions: Detritivore identity in this study had very divergent influences on aboveground predator-herbivore interactions that could not be predicted from a simple extension of whether or not detritivores were vulnerable to predation. Although *Littoraria* itself was invulnerable to spider predation, this snail strongly limited both herbivore and predator populations (Figure 1B) by extensively grazing live *Spartina* plants (Figure 3A). Despite grazing

pressure, *Spartina* plants continued to grow throughout the experiment which partially offset the effect of this voracious snail on live plant biomass by the end of the experiment. Here I look beyond the relatively stronger influence of *Littoraria* as opposed to *Prokelisia* herbivory on *Spartina* plant growth (Gustafson et al. 2006) and find that *Littoraria* feeding enhanced resource competition and led to declines in *Prokelisia* densities (Figure 1A, B) as well as to a cascading reduction in *Pardosa* predator density due to both reductions in prey density and habitat structure (Figure 2). In contrast *Melampus* snails that were also invulnerable to spider predation did not impose significant grazing pressure on live *Spartina* (Figure 3A) and this detritivorous snail had little influence on the density of *Prokelisia* herbivores (Figure 1C) or their spider predator (Figure 2).

Although feeding trials and observations revealed that the two crustaceans *Littorophiloscia vittata* and *Orchestia grillus* were both vulnerable to predation (Chapter 1), behavioral differences between the two species resulted in a divergent influence of these two detritivores on *Pardosa*-planthopper interactions. *Orchestia grillus* avoided *Pardosa* predators by burrowing under the soil surface, while *Littorophiloscia vittata* foraged across the surface of the leaf litter and up into the *Spartina alterniflora* canopy where it was more adversely influenced by the presence of *Pardosa* predators. The vulnerability of *L. vittata* to *Pardosa* attack led to relaxed spider predation on co-occurring *Prokelisia* planthoppers (Figure 1D), an effect that did not occur when the less vulnerable *O. grillus* was the focal detritivore (Figure 1E).

Decomposition: Both gastropods and crustaceans (amphipods and isopods) are known to contribute to decomposition processes and have species-specific effects on litter chemistry and microbial activity (Zimmer et al. 2002, 2004). The two gastropods in this study had different effects on litter mass loss (Figure 3B). *Melampus bidentatus* enhanced rates of decomposition, whereas *Littoraria irrorata* had a negligible influence on litter mass loss. Detritivore influences on litter mass loss could not be attributed to differences in biomass or the density of any of the detritivore species. Although *Spartina* leaf litter provided the nutritional resources necessary for isopod populations to grow, and when they were present spider predation suppressed final isopod densities, neither of the crustaceans (*Littorophiloscia vittata* and *Orchestia grillus*) influenced *Spartina* decomposition. Thus, three of the four detritivores had no influence on litter mass loss. Despite the rapid (hours to days) fluctuations in activity of litter microbes that can be seen in response to predation by soil fauna, seasonal dynamics and recalcitrant litter can temper ecosystem level responses (Bardgett et al. 2005a). All decomposition effects in this study attenuated, and did not cascade to influence soil nitrogen availability, or growth of plant roots or shoots. Changes in litter chemistry (phenolics, lignin, cellulose) and microbial activity (respiration, community composition) have been revealed during decomposition even when there was no change in litter mass loss (Hunter et al. 2003). Nonetheless, if such changes in litter quality occurred in this study, they were not strong enough to feedback and influence live plant biomass (Figure 3A), or herbivore population density (Figure 3 A, E).

Conclusions: Plant species composition, and the quantity or quality of plant organic matter input can, in part, drive the species composition of the soil food web (Wardle 1992, Bardgett et al. 2005b). However, especially in ecosystems with low plant diversity, abiotic constraints also contribute to changes in detritivore species composition (Wall 2007). Therefore changes in detritivore species composition that are not paralleled by changes in plant communities can potentially have unique influences on the aboveground food web. Although most soil food webs are characterized by high consumer diversity, the functional diversity of species in soil detrital food webs is often described as being low as many species serve multiple overlapping functions (Laakso and Setälä 1999, Jouquet et al. 2006). I found that while changes in detritivore functional traits led to diminutive differences in rates of decomposition, the detritivore species identity had a dramatic influence on the strength of aboveground predator-herbivore interactions. In fact, the presence of some detritivore species such as the snail, *L. irrorata*, can destabilize predator-herbivore interactions by engineering the structure of the aboveground plants, whereas other detritivores such as the isopod, *L. vittata*, can maintain predators and herbivores in habitats by serving as alternative prey. Therefore, changes in the identity of the dominant detritivores in the soil assemblage and thus the functional composition of the detritivore community across habitats may be essential in determining the strength of interactions and spatial dynamics between aboveground generalist predators and their herbivore prey.

Literature Cited

- Bardgett, R. D., W. D. Bowman, R. Kaufmann, and S. K. Schmidt. 2005a. A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution* **20**:634-631.
- Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* **84**:2258-2268.
- Bardgett, R. D., G. W. Yeates, and J. M. Anderson. 2005b. Patterns and determinants of soil biological diversity. Pages 100-118 in R. D. Bardgett, M. D. Usher, and D. W. Hopkins, editors. *Biological diversity and function in soils*. Cambridge University Press, Cambridge, UK.
- Bertness, M. D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology* **66**:1042-1055.
- Bonkowski, M., I. E. Geoghegan, B. A. N. E., and B. S. Griffiths. 2001. Effects of soil decomposer invertebrates (protozoa and earthworms) on an above-ground phytophagous insect (cereal aphid) mediated through changes in the host plant. *Oikos* **95**:441-450.
- Boyer, K. E., and P. Fong. 2005. Co-occurrence of habitat-modifying invertebrates: effects on structural and functional properties of a created salt marsh. *Oecologia* **143**:619-628.
- Bradley, P. M., and J. T. Morris. 1991. The influence of salinity on the kinetics of NH_4^+ uptake in *Spartina alterniflora*. *Oecologia* **85**.

- Brewer, J. S., J. M. Levine, and M. D. Bertness. 1998. Interactive effects of elevation and burial with wrack on plant community structure in some Rhode Island salt marshes. *Journal of Ecology* **86**:125-136.
- Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* **277**:500-504.
- De Deyn, G. B., and W. H. Van Der Putten. 2005. Linking aboveground and belowground diversity. *Trends in ecology and evolution* **20**:625-633.
- Denno, R. F., D. Lewis, and C. Gratton. 2005. Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Annales Zoologici Fennici* **42**:295-311.
- Denno, R. F., C. Gratton, M. A. Peterson, G. A. Langellotto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces mediate natural enemy impact in a phytophagous insect community. *Ecology* **83**:1443-1458.
- Eviner, V. T., and F. S. Chapin. 2003. Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology Evolution and Systematics* **34**:455-485.
- Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* **83**:643-652.
- Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* **8**:1299-1306.

- Graça, M. A., S. Y. Newell, and R. T. Kneib. 2000. Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt marsh invertebrates. *Marine Biology* **136**:281-289.
- Gustafson, D. J., J. Kilheffer, and B. R. Silliman. 2006. Relative effects of *Littoraria irrorata* and *Prokelisia marginata* on *Spartina alterniflora*. *Estuaries and Coasts* **29**:639-644.
- Halaj, J., and D. H. Wise. 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology* **83**:3141-3151.
- Hättenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics* **36**:191-218.
- Hines, J., J. P. Megonigal, and R. Denno, F. 2006. Nutrient subsidies to belowground microbes impact aboveground foodweb interactions. *Ecology* **87**:1542-1555.
- Holdsworth, A. R., L. E. Frelich, and P. B. Reich. 2007. Regional extent of an ecosystem engineer: Earthworm invasion in northern hardwood forests. *Ecological Applications* **17**:1666-1677.
- Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* **75**:3-35.

- Hunter, M. D., S. Adl, C. M. Pringle, and D. C. Coleman. 2003. Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia* **47**:101-115.
- Hunter, M. D., G. C. Varley, and G. R. Gradwell. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Science* **94**:9176-9181.
- Jouquet, P., J. Dauber, J. Lagerlof, P. Lavelle, and M. Lepage. 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* **32**:153-164.
- Laakso, J., and H. Setälä. 1999. Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos* **87**:57-64.
- Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139**:1-10.
- Lavelle, P. 2002. Functional domains in soils. *Ecological Research* **17**:441-450.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**:545-556.
- Mendelssohn, I. A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. *Ecology* **60**:574-584.

- Mendelssohn, I. A., K. L. McKee, and W. H. Patrick. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* **214**:439-441.
- Morse, D. H. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae: Lycosidae). *Journal of Arachnology* **25**:1-10.
- Mulvaney, R. L. 1996. Nitrogen - Inorganic Forms. Pages 1183-1184 in J. M. Bigham, editor. *Methods of Soil Analysis*. Soil Science Society of America, Madison, Wisconsin.
- Newell, S. Y., R. D. Fallon, and J. D. Miller. 1989. Decomposition and microbial dynamics for standing, naturally positioned leaves of the salt-marsh grass *Spartina alterniflora*. *Marine Biology* **101**:471-481.
- Newell, S. Y., and D. Porter. 2000. Microbial secondary production from salt marsh-grass shoots, and its known and potential fates. Pages 159-185 in M. P. Weinstein and D. A. Kreeger, editors. *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publishers, Boston.
- Scheu, S., A. Theenhaus, and T. H. Jones. 1999. Links between the detritivore and the herbivore system: effects of earthworms and Collembola on plant growth and aphid development. *Oecologia* **119**:541-551.
- Schindler, D. E., B. M. Johnson, N. A. MacKay, N. Bouwes, and J. F. Kitchell. 1994. Crab:snail size structure interactions and salt marsh predation gradients. *Oecologia* **97**:49-61.

- Settle, W. H., H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, A. S. Lestari, and Pajarningsih. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* **77**:1975-1988.
- Tilman, D., J. M. H. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300-1302.
- Valiela, I., J. M. Teal, and N. Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation. *Limnology and Oceanography* **21**:245-252.
- Wall, D. H. 2004. Sustaining biodiversity and ecosystem services in soil and sediments. Island Press, Washington D.C.
- Wall, D. H. 2007. Global change tipping points: above- and below-ground biotic interactions in a low diversity ecosystem. *Philosophical Transactions of the Royal Society B* **362**:2291-2306.
- Wardle, D. A. 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biological Reviews* **67**:321-358.
- Wardle, D. A. 2002. *Communities and ecosystems: Linking the aboveground and belowground components*. Princeton University Press, Princeton, NJ.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. Van Der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**:1629-1633.

- Wardle, D. A., K. I. Bonner, and G. M. Barker. 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos* **89**:11-23.
- Wardle, D. A., W. M. Williamson, G. W. Yeates, and K. I. Bonner. 2005. Trickle-down effects of aboveground trophic cascades on the soil food web. *Oikos* **111**:348-358.
- Wise, D. H., D. M. Moldenhauer, and J. Halaj. 2006. Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications* **16**:865-876.
- Wolters, V., W. L. Silver, D. E. Bignell, D. C. Coleman, P. Lavelle, W. H. Van Der Putten, P. C. De Ruiter, J. Rusek, D. H. Wall, D. A. Wardle, L. Brussaard, J. M. Dangerfield, V. K. Brown, K. E. Giller, D. U. Hooper, O. Sala, J. M. Tiedje, and J. A. Van Veen. 2000. Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: Implications for ecosystem functioning. *Bioscience* **50**:1089-1098.
- Zimmer, M., S. C. Pennings, T. L. Buck, and T. H. Carefoot. 2002. Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. *Functional Ecology* **16**:596-607.
- Zimmer, M., S. C. Pennings, T. L. Buck, and T. H. Carefoot. 2004. Salt marsh litter and detritivores: A closer look at redundancy. *Estuaries* **27**:753-769.

List of Figures

Figure 1. Effect of detritivore identity and *Pardosa* predator addition on the density of *Prokelisia dolus* herbivores in common garden mesocosms. Mean *Prokelisia dolus* density (\pm SEM) over the season in response to A) detritivore absence (control) and the presence of one of the four detritivores B) *Orchestia grillus* C) *Littorophiloscia vittata* D) *Melampus bidentatus* and E) *Littoraria irrorata* in *Spartina alterniflora* mesocosms when *Pardosa littoralis* predators were either added (\bullet) or withheld (\circ). Mean seasonal densities (\pm SEM) are shown to the right of each panel. Significant differences ($p < 0.05$) due to spider predation at each time period are indicated by (*). F) Final *Prokelisia dolus* density in *Spartina alterniflora* mesocosms after 60 days exposure to detritivore and predator addition treatments. Significant treatment differences ($p < 0.05$) are indicated with different letters.

Figure 2. *Pardosa* predator density (mean \pm SE) in common garden mesocosms containing *Spartina alterniflora*, *Prokelisia dolus* herbivore prey and one of five detritivore-addition treatments: *Littorophiloscia vittata* (\blacktriangledown), *Orchestia grillus* (\bullet), *Melampus bidentatus* (\square), *Littoraria irrorata* (∇), or no detritivore addition (\circ).

Spider densities in response to detritivores that serve as alternative prey are shown as solid symbols and spider densities in response to detritivore treatments that do not serve as alternative prey are displayed as open symbols. Significant detritivore treatment differences ($p < 0.05$) are shown as different letters above seasonal means shown in bars to the right.

Figure 3. *Spartina alterniflora* live biomass A) and *Spartina alterniflora* leaf litter mass remaining B) in common garden mesocosms after 60 days exposure to one of 5 detritivore addition treatments (*Littoraria irrorata*, *Melampus bidentatus*, *Littorophiloscia vittata*, *Orchestia grillus*) when *Pardsoa littoralis* predators either were added (●) or withheld (○). Significant treatment differences ($p < 0.05$) are indicated with different letters.

Figure 1.

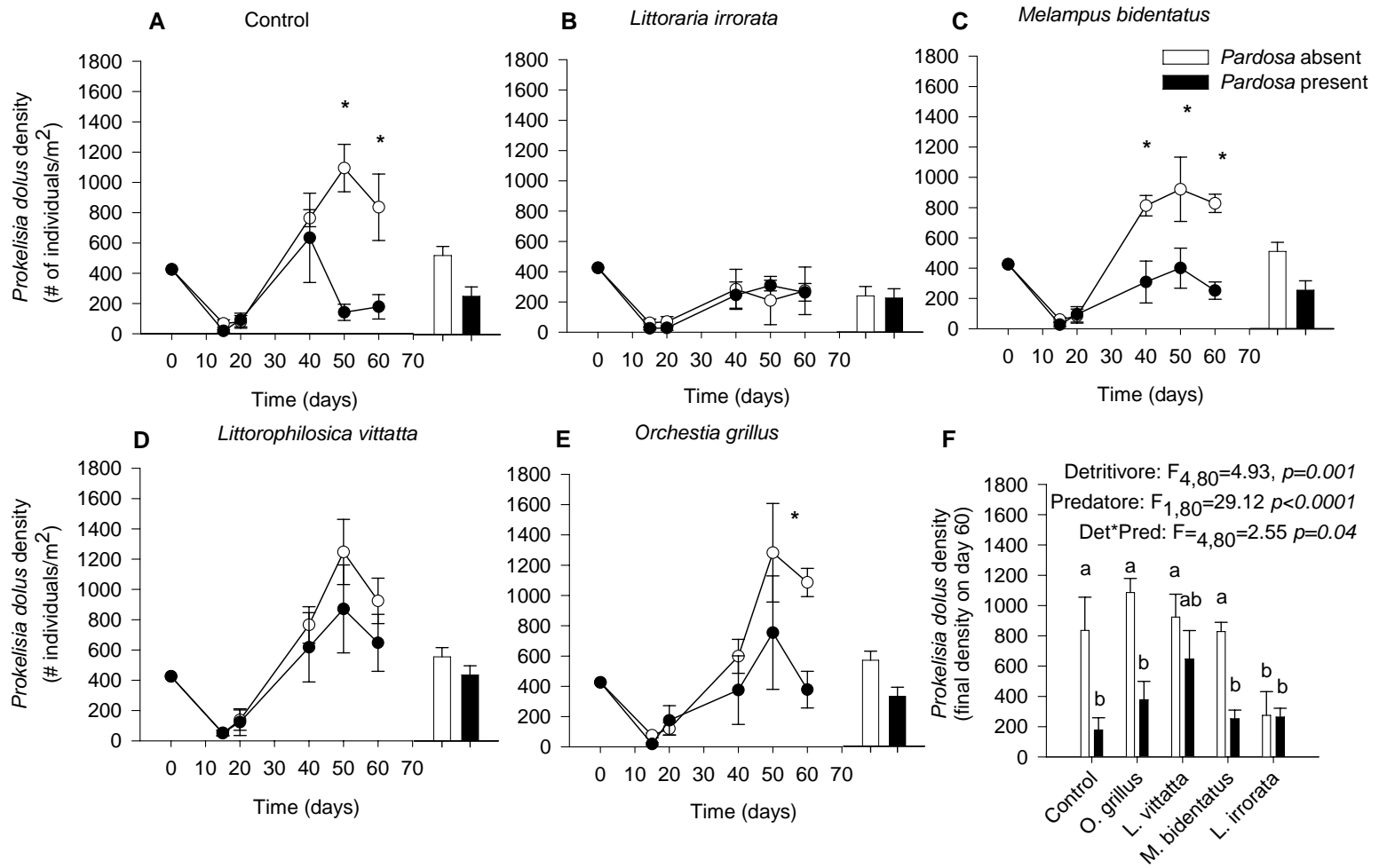


Figure 2.

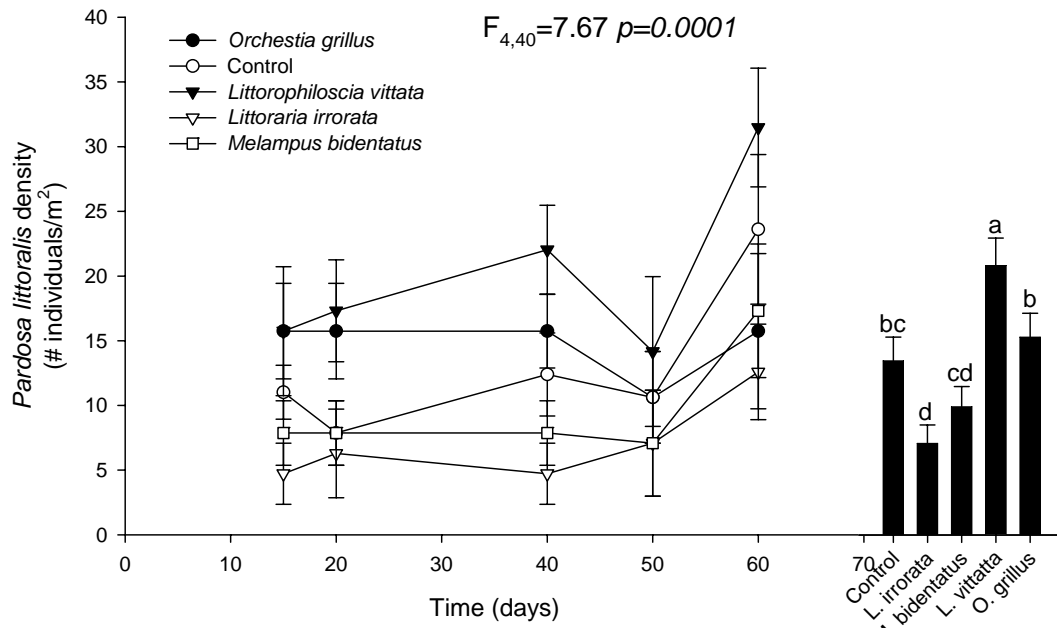
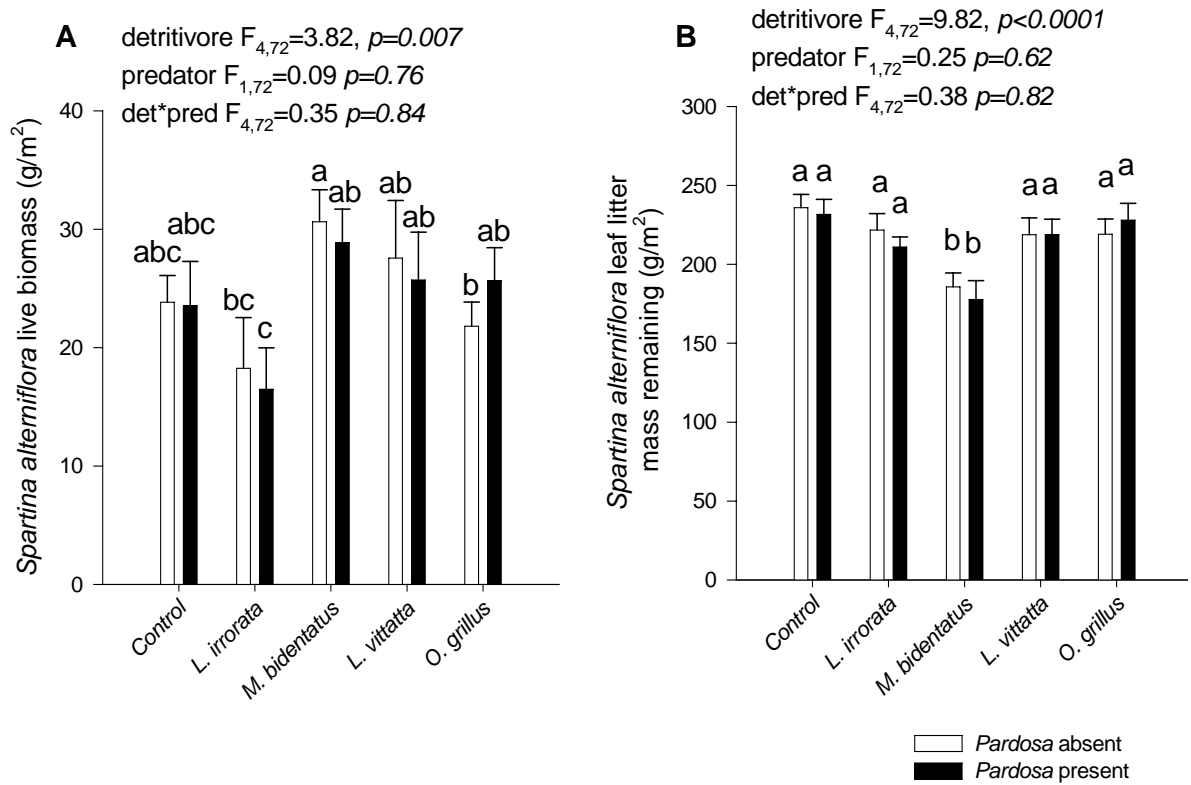


Figure 3.



Tables

Table 1. ANOVA results show the main and interactive effects of the detritivore identity and predator-addition treatments on *Spartina alterniflora* root biomass and soil inorganic nitrogen availability in common garden mesocosms after 60 days exposure to treatments.

Source of Variation	Root biomass (g)		NH_4 ($\mu\text{g/g}$)		NO_3 ($\mu\text{g/g}$)		
	<i>df</i> [*]	F	<i>P</i>	F	<i>p</i>	F	<i>p</i>
Detritivore	4,72	1.04	0.39	0.39	0.81	0.30	0.87
Predator	1,72	1.36	0.24	0.67	0.42	0.00	0.98
Det*Pred	4,72	1.48	0.22	0.13	0.97	0.39	0.81

*degrees of freedom (numerator, denominator)

Chapter 3: Latitudinal change in the trophic structure of a salt marsh food web

Abstract

Classic biogeography theory posits that species diversity increases at lower latitudes. However, very few studies have examined changes in the trophic structure of food webs across broad-scale latitudinal gradients. I examined the abundance of insect herbivores and their invertebrate predators in *Spartina alterniflora* marshes at 13 sites along a 1660 km stretch of the Atlantic coast of North America ranging in latitude from 43° 20' (Wells, ME) to 31° 05' (Jekyll Island, GA). The invertebrate community composition can be clustered into three main zones defined by a high, mid, and low latitude assemblage. However, neither the diversity nor density of the dominant herbivore species varied consistently with latitude. Notably, I found that predator density increased dramatically at higher latitudes. Overall, predatory spider density was positively correlated with complex-structured marsh vegetation and leaf litter biomass, and negatively correlated with the abundance of *Littoraria*, a detritivorous grazing snail. This finding suggests that by modifying vegetation structure *Littoraria* functions as an ecosystem engineer that alters the habitat structure for spiders and may indirectly influence spider ability to suppress their herbivorous prey across broad-scale latitudinal gradients. These results indicate that there is a dramatic geographic shift in food-web structure on North Atlantic salt marshes as

evidenced by the altered relative densities of dominant predators, herbivores, and detritivores across a latitudinal gradient. Although changes in food web composition were coupled with changes in habitat complexity, contrary to expectation vegetation complexity increased on high rather than low latitude marshes.

Keywords: latitudinal gradient, ecosystem engineer, food web structure, habitat complexity

Introduction

Increasing awareness of global change has inspired interest in larger-scale perspectives in understanding biodiversity and food web interactions (Raffaelli 2006). One of the most consistent broad-scale patterns in ecology is the latitudinal diversity gradient whereby species diversity increases at lower latitudes (Willig et al. 2003, Hillebrand 2004). However, our understanding of large-scale geographic patterns such as the latitudinal diversity gradient are not always compatible with the current understanding of food-web ecology and community assembly at a local scale (Brose et al. 2004, Kneitel and Chase 2004, Menge et al. 2004). For example, although a single causal mechanism underlying the latitude diversity gradient has not been identified, it has been suggested that most species interactions, including herbivory (Coley and Aide 1991, Pennings et al. 2001), predation (Stachowicz and Hay 2000) and competition (Pennings et al. 2003) are more intense at lower latitudes. Moreover, simple trophic models do not allow for simultaneous increases in the intensity of interactions at all trophic levels (Hairston et al. 1960, Oksanen et al. 1981). More complex food web models that include habitat complexity and omnivory can help relax the assumptions of the strict trophic level perspective (Polis 1991, Thompson et

al. 2007), but they have not yet been applied in the context of understanding broad scale geographic distribution of species interactions.

Across large-scale latitudinal gradients, increased habitat structural complexity is often associated with increases in density or diversity of species in all trophic levels (MacArthur 1972). Species in tropical habitats are thought to have decreased niche breadth and increased niche diversity due to increased complexity and diversity of vegetation (MacArthur 1972, Vázquez and Stevens 2004). However, intensive experimental investigations at a more local scale have revealed that habitat complexity can influence food web structure by modifying foraging behavior (Schmitz 2005), providing differential refuge for predators and prey (Langellotto and Denno 2004), or by altering community composition (Beals 2006). Habitat complexity can both enhance (Finke and Denno 2002) and dampen the strength of predator-prey interactions (Borer et al. 2005), making simultaneous increases in the densities of species at neighboring trophic levels in complex habitats difficult to predict (Moore et al. 2004). Habitat complexity can also be modified by the local species assemblage. Species can create (Cardinale et al. 2002, Badano and Cavieres 2006) or reduce (Jones et al. 1994) structural complexity and thus engineer their environment (Crooks 2002). Thus, pairs of interacting species can be confronted by ecosystem engineers that modify their interaction strength. Therefore, over broad geographic ranges, environmental thresholds that limit the geographic range of ecosystem engineers may decouple species interactions within a portion of the pairs range (Crooks 2002, Peacor and Werner 2004). Notably, despite the large number of studies that examine patterns of biodiversity as they relate to changes in habitat

complexity, few studies have examined patterns in multi-trophic communities or food web structure across latitudinal gradients (Buckley et al. 2003, Menge et al. 2004).

I surveyed geographical variation in diversity and trophic structure in an Atlantic coastal salt-marsh food web. Environmental gradients across latitude provide a natural means to explore patterns in food-web structure and how complex communities might respond to changes in climate and abiotic stress (Helmuth et al. 2002). However, for most species, lack of detailed knowledge about life history and local species interactions restricts our ability to predict and monitor how species respond to environmental change. Here, I overcome those limitations and eliminate several possible confounding variables by selecting comparable sites and by using standardized sampling of invertebrate communities that exist on a single host plant that spans both large-scale latitudinal and local elevation gradients. Life-history characteristics and food web interactions of these species have been intensively studied for the last 30 years, and have more recently begun to be placed in a larger spatial context (Denno et al. 2005, Pennings and Silliman 2005).

Intertidal salt marshes along the Atlantic coast of North America are dominated by monospecific stands of *Spartina alterniflora*, a perennial cord grass which grows across both elevation and latitudinal gradients. Due to differences in tidal inundation and pore-water chemistry across an elevation gradient, *Spartina* varies in structure from large, tall-form plants that grow in low marsh tidal creek-side habitats to small short-form plants that grow in higher elevation salt-stressed habitats (Mendelssohn 1979, Mendelssohn et al. 1981). Along the Atlantic coast, low-latitude

S. alterniflora has been found to be tougher and less palatable to herbivores than high latitude *S. alterniflora* (Pennings et al. 2001).

I am unaware of any studies that have shown how reductions in *S. alterniflora* quality across a latitudinal gradient influence food web structure. Sap-feeding insects (*Prokelisia dolus*, *Prokelisia marginata*, and *Trigonotylus uhleri*) are the most abundant herbivores throughout the geographic range of *Spartina*, with densities often exceeding several thousand individuals per m² (Denno et al. 2002).

Trigonotylus (Miridae: Hemiptera) however, are less susceptible to predation than are *Prokelisia* planthoppers (Delphacidae: Hemiptera) (Denno et al. 2003). The principle predators of *Prokelisia* herbivores are an assemblage of predatory spiders, dominated by *Pardosa littoralis*, a ground-foraging hunting spider, and *Grammonota trivitata*, a web spinning spider.

Although there has been a recent emphasis on the intense herbivore pressure exerted on *S. alterniflora* by the mollusk *Littoraria irrorata* (Silliman et al. 2005), much of the published work on the *S. alterniflora* food web has focused on the life history and dispersal ability of the herbivorous sap-feeders (Denno et al. 1989, Hines et al. 2005). These experiments have shown that sap-feeder populations increase rapidly in high-quality (increased %N) patches of *S. alterniflora* (Denno et al. 2002). Predatory spiders that feed on the sap-feeders show strong numerical response to increases in both prey density, and increased structural complexity provided by the matrix of leaf litter detritus surrounding live *S. alterniflora* (Denno et al. 2002). In habitats rich in leaf litter *Pardosa* spiders gain refuge from cannibalism and show enhanced suppression of their planthopper prey (Langellotto and Denno 2006).

Several species of detritivores are also abundant in habitats rich in leaf litter.

Orchestia grillus (Amphipoda) and *Littorophiloscia vittata* (Isopoda) are commonly found in high marsh habitat where they graze leaf litter (Graça et al. 2000), and also serve as prey for *Pardosa* spiders (Morse 1997; Chapter 1).

Thus, understanding latitudinal patterns of live *Spartina* quality and leaf-litter accumulation in marsh habitats is critical because these factors act synergistically to mediate the strength of top-down predator effects on herbivores (Denno et al. 2002). Here, I use a latitudinal survey approach to determine if factors that are known to influence herbivore populations at a local scale (*Spartina* quality, vegetation structure, and predator density) are associated with larger scale biogeographic patterns in food web structure.

Theories developed in the biogeography (Figure 1A) (Coley and Aide 1991, Stachowicz and Hay 2000, Pennings and Silliman 2005) as opposed to the food-web literature (Figure 1B)(Polis 1991, Hunter et al. 1997, Denno et al. 2002) provide two unique sets of predictions regarding the *Spartina* system. Biogeographic theory predicts that as latitude decreases 1) *S. alterniflora* plants will have increased productivity, structural complexity, and allocation to defensive compounds, but will exhibit lower nutritional quality, 2) herbivores will exert increased feeding pressure on their host plant as evidenced by increases in herbivore density, diversity, or feeding damage, 3) predation intensity will be intensified as demonstrated by increases in predator density, diversity, or consumption.

In contrast, if food-web theory that has been developed from small-scale manipulative experiments can be extended to have a large-scale influence on species

distributions, then 1) *Spartina* plant quality will be influenced predominantly by bottom-up factors, such as pore water chemistry and tidal inundation (nutrient subsidy), and there will likely be larger differences across local elevation gradients and no distinct relationship between plant nitrogen and large-scale latitudinal changes. 2) Herbivores will be more abundant on high-quality host plants independent of latitude. 3) Predator abundance will be positively associated with both increases in *S. alterniflora* structural complexity and increased abundance of prey. Therefore, 4) in habitats with high-quality, structurally-complex plants, herbivores will respond to increases in plant quality, and herbivores that are not as susceptible to predation (*Trigonotylus*) will exhibit population increases that will not be paralleled by herbivores that are susceptible to predation (*Prokelisia sp.*). Notably consistent predictions regarding the role of detritivore populations in ecology are glaringly absent from both traditional biogeographic and food-web theory. Although a more mechanistic approach would involve manipulating species densities simultaneously across large geographic gradients, there are logistical difficulties associated with conducting such experiments. By examining the distribution of dominant herbivore, predator, and detritivore species across a latitudinal gradient, I reveal a pattern in food web structure, which suggests that 1) the scope of small-scale manipulative experiments can be extended to predict large-scale species distributions, and 2) the relative influence of resource quality and predation on herbivore population regulation may shift across broad scale geographic gradients.

Methods

To examine changes in *Spartina* quality and structural complexity across a latitudinal gradient, I collected plant samples from 13 Atlantic salt marshes that span 1660 km of coastline and 12 degrees latitude from 43° 20' (Wells, ME) to 31° 05' (Jekyll Island, GA) (Figure 2A). Samples were taken from late June to mid July in both 2004 and 2005 at a time that coincides with peak-season biomass of *Spartina* plants. By sampling at this peak in each of two years, I gained insight into annual variation in the spatial patterns. Plant structure and quality change across a local elevation gradient due to differences in tidal inundation and soil chemistry (Mendelsohn 1979, Mendelsohn et al. 1981). In order to capture variation in *Spartina* structure at each marsh location, I sampled three sites along each of two transects that spanned an elevation gradient: 5 meters from upland, a mid elevation meadow habitat, and a low elevation creek-side habitat. Because of the different spatial configurations of the marshes, not all transects were the same length, but each marsh experienced equal sampling effort in the three habitat types. For each sample, I collected all plant material within a quarter meter square quadrat frame. Samples were frozen and returned to the laboratory where plant height, stem density, dry biomass of live and dead vegetation (index of vegetation structure), and plant quality (N content, determined by Exeter CE-440 CHN analyzer) were recorded.

To capture variation in the structure of the associated invertebrate food web (herbivores, predators and detritivores) across marsh habitats (Denno et al. 1996, Denno et al. 2005) and determine if broad-scale patterns in invertebrate abundance and diversity were associated with changes in latitude, density of neighboring trophic

group, or habitat complexity, I sampled invertebrates at low tide at each plant sample location along elevation and latitude gradients. I obtained samples using a vacuum suction sampler (10 standard sampling units, D-vac company: Ventura, CA) and a sweep net (10 standard sweeps). All arthropods sampled were killed with ethyl acetate and transferred into jars containing 95% ethyl alcohol and returned to the laboratory. To minimize the possible influence of phenological variation among sites in herbivore density I pooled all age classes of sap-feeding herbivores as they were identified to species and counted. To quantify *Littoraria* snail density at each sample location, I randomly placed a plastic hoop (0.9 m diameter) on the marsh surface and counted the total number of snails present within the boundary. Thus, there were a total of 6 plant samples (2004, 2005), 12 arthropod samples (D-vac + sweep net; 2004, 2005), and 6 snail counts (2005 only) per marsh location.

To assess how the invertebrate community composition changed across the latitudinal gradient, I used a hierarchical cluster analysis based on group averages of $\log_{10}(x+1)$ transformed invertebrate species abundance data derived from a Bray-Curtis Similarity Index (Primer 6). Ninety-six invertebrate species were identified to species or morphospecies and were included in the multivariate community analysis. To examine underlying factors behind multivariate community patterns, mixed model analysis of variance was used to assess the direct and interactive effect of year (2004, 2005: categorical variable) and latitude (continuous variable) on species richness, species diversity- H' , plant quality (% N) and four components of plant architectural complexity (culm density, plant height, live biomass, and dead biomass), as well as density of the dominant invertebrates (*Prokelisia* sp., *Trigonotylus uhleri*, *Pardosa*

littoralis, *Grammonota trivittata*, *Tythus vagus*) (Proc mixed, SAS v 9.1). An exponential decay regression model was used to assess the influence of latitude on *Littoraria irrorata* density due to lack of fit (Akaike's Information Criteria) and non-random patterns in residuals using a linear regression for this species. Invertebrate densities were $\log_{10}(x+1)$ transformed to meet assumptions of normality of residuals, and homogeneity of variance. Because small-scale manipulative experiments indicate that the densities of *Pardosa*, *Grammonota*, and *Littoraria* are associated with changes in plant structure (Denno et al. 2002, Silliman et al. 2005), correlation was used to evaluate the latitudinal association between plant structure and density of these species.

Results

Invertebrate community structure: Community composition of invertebrate salt marsh species was influenced by variation in latitude (Figure 2B). Low (31-33°), mid (34-39°), and high (41-43°) latitude invertebrate communities form three distinct community assemblage groups with over 70% similarity (Figure 2B). Inconsistent with biogeographic theory, species richness and diversity were relatively low and uninfluenced by latitude despite the spatial extent of the 1660 km survey (Table 1). Thus, although detritivore species richness and diversity (H') were slightly increased at higher latitudes (Figure 3 A-B; Table 1), these patterns were not exhibited by all trophic levels and there was no distinct influence of latitude on the species richness or diversity of either herbivores (Figure 3 C-D) or predators (Figure 3 E-F; Table 1).

Plant structure and quality: The structure of *Spartina alterniflora* (height, culm density, dead biomass) changed across the latitudinal gradient, although there

was no change in standing crop of live *Spartina* biomass ($F_{1,24}=-0.74$, $p=0.46$; Figure 4A-E; Table 2). High-latitude plants were shorter ($F_{1,24}=-2.88$, $p<0.0001$; Figure 4B) and provided more structural complexity at the marsh surface as they exhibited increased culm density ($F_{1,24}=5.44$, $p=0.0001$; Figure 4C) and an accumulated matrix of dead biomass (leaf litter) ($F_{1,24}=2.75$, $p=0.01$; Figure 4D) compared to low-latitude *Spartina* plants which were taller but had culms that were more sparsely spaced and were not surrounded by a matrix of leaf litter on the marsh surface (Table 2).

Spartina host plant quality (%N) did not vary consistently across the latitudinal gradient ($F_{1,24}=0.87$, $p=0.40$; Figure 4E; Table 2). Notably, there was no main or interactive effect of inter-annual variation (2004-2005) on patterns of *Spartina* quality or any measure of plant structure across the latitudinal gradient (Table 2).

Herbivore versus predator abundances: *Prokelisia sp.* herbivore density did not vary consistently with latitude (Figure 4F); *Prokelisia sp.* were more abundant on high latitude marshes in 2005, but were similarly abundant on marshes across the latitudinal gradient in 2004 ($F_{1,24}=2.43$, $p=0.02$; Table 3). In contrast *Trigonotylus uhleri* was consistently more abundant on high latitude marshes ($F_{1,24}=5.05$, $p<0.0001$; Figure 4G; Table 3). Predation intensity on insect herbivores increases at higher latitudes, as the density of all three dominant predators consistently increased on high latitude marshes (Figure 4 H-J), where there was also enhanced vegetation complexity (culm density and leaf litter biomass) (Figure 4 C-D). However, the two dominant spiders were influenced by separate aspects of vegetation structure; populations of *Pardosa littoralis*, a ground foraging hunting spider, were positively associated with increases in culm density ($r=0.63$, $p=0.02$), and

Grammononta trivittata, a web spinning spider, was positively associated with increased accumulation of leaf litter on the marsh surface ($r=0.61$, $p=0.02$). *Tythus vagus*, a specialized predator of *Prokelisia* planthopper eggs, was also more abundant at higher latitudes ($F_{1,24}=6.74$, $p<0.0001$; Figure 4J; Table 4), which suggests that all stage classes of *Prokelisia* herbivores face higher densities of invertebrate predators at higher latitudes.

Detritivorous grazing snails: Although the presence of *Littoraria* has been reported on more northern marshes, I found that *Littoraria irrorata* abundance decreased exponentially across the latitudinal gradient ($F_{1,12}=21.8$, $p=0.0007$), whereby *Littoraria* were not found on the marshes above 37° N latitude (Figure 5A, Table 3). With one exception, *Littoraria* were only found in high densities on marshes with less than 56g/m² of leaf litter biomass (Figure 5B), and they were always found on marshes with low *Spartina* culm density, i.e., those that averaged less than 120 culms/m² (Figure 5C). Across all marshes there was a negative association between *Littoraria* and *Pardosa*, such that when *Littoraria* was abundant, *Pardosa* were consistently absent (Figure 5D).

Discussion

A recent drive in food-web ecology has been to extend the scope of experiments and to evaluate how food webs change across space. By reconciling longstanding debates regarding the system-specific, local-scale importance of top-down and bottom-up factors in controlling animal population dynamics (Hunter et al. 1997, Denno et al. 2002), ecologists are now able to ask how these factors vary

synergistically to impact food-web dynamics across systems and across larger spatial gradients (Denno et al. 2005, Post 2005). Consistent with biogeographic theory, previous studies have shown that Atlantic coast salt marsh plants possess increased defenses (increased lignin, decreased nitrogen) and are subjected to increases in herbivore pressure from grazing invertebrates at lower latitudes (Pennings et al. 2001, Siska et al. 2002). Data presented here extend the results of experiments regarding *Spartina* nutritional quality and plant-herbivore interactions, and suggest that latitudinal gradients in plant structure have more comprehensive effects for food web structure and the intensity of predation.

Notably, the most consistent latitudinal patterns in “plant quality” involved aspects of plant structural complexity (Figure 4 B-D). I sampled monospecific expanses of *Spartina alterniflora*, and thus there were no changes in plant species diversity. However, there was a reverse latitudinal gradient in the complexity of the vegetation on the marsh surface, whereby both culm density and dead biomass increased in high-latitude habitats (Figure 4 C-D). Moreover, I did not find consistent increases in *Spartina* nitrogen content across the latitudinal gradient (Figure 4E). This was inconsistent with previous studies (Siska et al. 2002) and suggests that while high latitude *Spartina* near the end of its distribution may have increased nitrogen content compared to low latitude marshes, an explicit linear relationship between latitude and plant nitrogen does not adequately explain this variation. Moreover, my data indicate no change in live *Spartina* biomass across the latitudinal gradient (Figure 4A). This too, contradicts previous trends that have repeatedly demonstrated increased plant production at lower latitudes. However, my estimates of standing

crop biomass probably underestimate net primary production especially in low-latitude marshes because they do not account for turnover of plant shoots throughout the season, or plant biomass lost to herbivory (Silliman and Bortolus 2003).

In contrast to distinct changes in plant structural complexity, I found little variation in herbivore species richness or diversity (Figure 3 C,D) across the latitudinal gradient. Because the herbivore community was so strongly dominated by the *Prokelisia* planthopper species, I focused the examination of food-web structure on these herbivores, whose density did not vary consistently across the latitudinal gradient (Figure 4F). *Prokelisia* herbivores were faced with substantially higher densities of their three dominant predators (*Pardosa littoralis*, *Grammonota trivittata*, and *Tythus vagus*) on high-latitude marshes (Figure 1 H-J). For many systems there is strong evidence that the relative impact of predators on herbivore population growth is mediated by plant structure (Hunter et al. 1997, Polis et al. 1998). Therefore, in addition to the increased abundance of predators at higher latitudes (Figure 4 H-J), the habitat complexity provided by increases in *Spartina* culm density and leaf litter (Figure 4 C,D) have been demonstrated to provide a refuge for predators from cannibalism and intraguild predation resulting in enhanced suppression of herbivore prey (Denno et al. 2002, Langellotto and Denno 2006). Thus, I contend that plant structure has the strong potential to intensify top-down predator influences on *Prokelisia* herbivores in high latitude habitats (Denno et al. 2002).

Increases in predator abundance (Figure 4 H-J) and parallel increases in abundance of herbivores that are less susceptible to predation (*Trigonotylus*; Figure 4

G) suggest that predation plays a relatively more important role in suppressing *Prokelisia* populations at higher latitudes, and alternatively that both *Prokelisia* and *Trigonotylus* herbivores are controlled by some factor other than predation at lower latitudes where predator densities were much reduced. Because neither plant quality nor predators were manipulated in these habitats, an explicit mechanistic explanation underlying these patterns of herbivore abundance is not yet possible. However, interspecific variation in herbivore life histories and vulnerability to predation are consistent with the view that predation intensity is higher at high latitudes.

In contrast to consistent latitudinal patterns in predation intensity, the role of latitude on herbivory may depend upon feeding guild. Previous work on *Spartina* has indicated that per capita feeding pressure from grazing snails increase at lower latitudes independent of herbivore density (Pennings and Silliman 2005). Because phloem-feeding *Prokelisia* do not leave noticeable scars on leaf tissue except at population outbreak densities I was not able to directly assess the influence of *Prokelisia* herbivory on host plant quality in this study. It is possible that phloem feeders also increase their feeding rates in low latitude marshes. Additionally, sap feeding herbivores exert more pressure on their low-latitude host plants by feeding for a longer period of time each year due to differences in growing season length. Low-latitude plants are typically subjected to four or more generations of planthoppers per growing season, whereas high-latitude plants are only exposed to three or two generations per year. However, regardless of the change in planthopper voltinism due to differences in degree-day accumulation across their geographic range, *Spartina* plants are exposed to planthoppers throughout the entire duration of their growing

season. Therefore, while *Spartina* seems to be under more intense feeding pressure from grazing invertebrates at lower latitudes, the role of sap-feeder pressure in increased *Spartina* defense seems somewhat equivocal.

The influence of some grazers likely extends past simple two-species plant-herbivore interactions. The omnivorous salt marsh snail, *Littoraria irrorata*, is a prolific grazing consumer that can greatly alter the structure of marsh vegetation by consuming both live and dead *Spartina* leaf tissue on low latitude marshes (Silliman and Bertness 2002, Silliman et al. 2005). Thus, as snails graze *Spartina*, they potentially engineer an environment that is far different than the litter-rich habitat that spiders prefer on high-latitude marshes (Denno et al. 2002). Notably, the entire invertebrate community is sensitive to changes in latitude and can be clustered into three distinct communities that are also consistent with changes in snail densities and habitat structure (Figure 2B). On the low latitude marshes where *Littoraria* are abundant (Figure 5A), *Spartina* leaf litter and culm density are reduced (Figure 4C-D, 5B-C) and spiders are rare (Figure 4H-I, 5D). There is a mid latitude transition assemblage (Figure 2B) that is found toward the northern limit of *Littoraria* distribution (Figure 5A) where there is intermediate structural complexity (Figure 4C-D, 5B-C) and slightly increased spider density (Figure 4 H-I, 5D). Lastly, there is a high latitude assemblage (Figure 2B) where *Littoraria* are absent (Figure 5A), there are strong increases in habitat complexity of the marsh surface (Figure 4 C-D, 5B-C) and there are high densities of invertebrate predators (Figure 4 H-J, 5D).

In addition to the biotic pressure placed on *Spartina* by *Littoraria* at lower latitudes, physical factors associated with changes in latitude may also contribute to

altered *Spartina* structure and leaf litter accumulation. Differences in tidal inundation and warmer temperatures probably contribute to faster decomposition and removal of loose leaf litter on low-latitude marshes. Furthermore, the salt-marsh soil microbial community responsible for decomposition of leaf litter varies across the latitudinal gradient (Newell et al. 2000, Blum et al. 2004). Consistent with patterns of increased leaf litter accumulation at higher latitudes I found slight increases in detritivore species richness and diversity (Figure 3 A,B). Therefore, although I identify a distinct break in the latitudinal distribution of *Littoraria* (Figure 5A), there is a more continuous linear increase in *Spartina* structural complexity (Figure 4D), suggesting that factors in addition to the abundance of *Littoraria* contribute to patterns of vegetation structure and its extended effects on the invertebrate community assemblage.

Seasonal plant growth and decomposition as well as density of omnivorous snails result in overall changes in community composition that are closely coupled to increases in habitat complexity. Thus, rather than strong latitudinal patterns in species diversity, I found an overall shift in trophic structure. Increases in vegetation complexity and the niche space provided by leaf litter accumulation promote increased density of predators and diversity of detritivores, but do not directly influence sap feeding *Prokelisia* herbivores. In comparison to forest systems (Novotny et al. 2006), herbivores in systems with low plant diversity such as salt marshes (this study) and pitcher plants (Buckley et al. 2003) may be particularly sensitive to shifts in trophic structure. Realized species interactions in multi-trophic

communities may result in large scale changes in the influence of top-down, bottom-up and detritivore-mediated influences on herbivore population dynamics.

Literature Cited

- Badano, E. I., and L. A. Cavieres. 2006. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography* **33**:304-313.
- Beals, M. L. 2006. Understanding community structure: a data-driven multivariate approach. *Oecologia* **150**:484-495.
- Blum, L. K., M. S. Roberts, J. L. Garland, and A. L. Mills. 2004. Distribution of microbial communities associated with the dominant high marsh plants and sediments of the United States east coast. *Microbial Ecology* **48**:375-388.
- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* **86**:528-537.
- Brose, U., A. Ostling, K. Harrison, and N. D. Martinez. 2004. Unified spatial scaling of species and their trophic interactions. *Nature (London)* **428**:167-171.
- Buckley, H. L., T. E. Miller, A. M. Ellison, and N. J. Gotelli. 2003. Reverse latitudinal trends in species richness of pitcher-plant food webs. *Ecology Letters* **6**:825-829.

- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* **415**:426-429.
- Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pages 25–49 in P. W. Price, editor. *Plant–animal interactions: evolutionary ecology in tropical and temperate regions*. John Wiley and Sons, New York, New York, USA.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* **97**:153-166.
- Denno, R., F., D. Lewis, and C. Gratton. 2005. Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Annales Zoologici Fennici* **42**:295-311.
- Denno, R. F., C. Gratton, H. G. Dobel, and D. L. Finke. 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* **84**:1032-1044.
- Denno, R. F., C. Gratton, M. A. Peterson, G. A. Langellotto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces mediate natural enemy impact in a phytophagous insect community. *Ecology* **83**:1443-1458.
- Denno, R. F., K. L. Olmstead, and E. S. McCloud. 1989. Reproductive Cost of Flight Capability - a Comparison of Life-History Traits in Wing Dimorphic Planthoppers. *Ecological Entomology* **14**:31-44.
- Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Dobel, M. D. Eubanks, J. E. Losey, and G. A. Langellotto. 1996. Habitat persistence

- underlies intraspecific variation in the dispersal strategies of planthoppers. Ecological Monographs **66**:389-408.
- Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology **83**:643-652.
- Graça, M. A., S. Y. Newell, and R. T. Kneib. 2000. Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt marsh invertebrates. Marine Biology **136**:281-289.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **XCIV**:421-424.
- Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. Science **298**:1015-1017.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. American Naturalist **163**:192-211.
- Hines, J., M. E. Lynch, and R. Denno, F. 2005. Sap-feeding insect communities as indicators of habitat fragmentation and nutrient subsidies. Journal of Insect Conservation **9**:261-280.
- Hunter, M. D., G. C. Varley, and G. R. Gradwell. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. Proceedings of the National Academy of Science **94**:9176-9181.
- Jones, C., J. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373-386.

- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* **7**:69-80.
- Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139**:1-10.
- Langellotto, G. A., and R. F. Denno. 2006. Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. *Ecological Entomology* **31**:575-581.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York, New York, USA.
- Mendelssohn, I. A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. *Ecology* **60**:574-584.
- Mendelssohn, I. A., K. L. McKee, and W. H. Patrick. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* **214**:439-441.
- Menge, B. A., C. A. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: Testing model predictions along an upwelling gradient. *Ecological Monographs* **74**:663-684.
- Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. De Ruiter, Q. Dong, A. Hastings, N. C. Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni, and D. H. Wall. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* **7**:584-600.

- Morse, D. H. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae: Lycosidae). *Journal of Arachnology* **25**:1-10.
- Newell, S. Y., L. K. Blum, R. E. Crawford, T. Dai, and M. Dionne. 2000. Autumnal biomass and potential productivity of salt marsh fungi from 29° to 43° North latitude along the United States Atlantic Coast. *Applied and Environmental Microbiology* **66**:180-185.
- Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313**:1115-1118.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation Ecosystems in Gradients of Primary Productivity. *American Naturalist* **118**:240-261.
- Peacor, S. D., and E. E. Werner. 2004. How dependent are species-pair interaction strengths on other species in the food web? *Ecology* **85**:2754-2763.
- Pennings, S. C., E. R. Selig, L. T. Houser, and M. D. Bertness. 2003. Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* **84**:1527-1538.
- Pennings, S. C., and B. R. Silliman. 2005. Linking biogeography and community ecology: Latitudinal variation in plant-herbivore interaction strength. *Ecology* **86**:2310-2319.
- Pennings, S. C., E. L. Siska, and M. D. Bertness. 2001. Latitudinal differences in plant palatability in Atlantic coast salt marshes. *Ecology* **82**:1344-1359.

- Polis, G. A. 1991. Complex trophic interactions in deserts an empirical critique of food-web theory. *American Naturalist* **138**:123-155.
- Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Piñero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California islands. *Ecology* **79**:490-502.
- Post, E. 2005. Large-scale spatial gradients in herbivore population dynamics. *Ecology* **86**:2320-2328.
- Raffaelli, D. G. 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Marine Ecology-Progress Series* **311**:285-294.
- Schmitz, O. J. 2005. Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management. *Oecologia (Berlin)* **145**:225-234.
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Science* **99**:10500-10505.
- Silliman, B. R., and A. Bortolus. 2003. Underestimation of *Spartina* productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus. *Oikos* **101**:549-554.
- Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelsohn. 2005. Drought, snails, and large-scale die-off of southern US salt marshes. *Science* **310**:1803-1806.

- Siska, E. L., S. C. Pennings, T. L. Buck, and M. D. Hanisak. 2002. Latitudinal variation in palatability of salt-marsh plants: which traits are responsible? *Ecology* **83**:3369–3381.
- Stachowicz, J. J., and M. E. Hay. 2000. Geographic variation in camouflage specialization by a decorator crab. *American Naturalist* **156**:59-71.
- Thompson, R. M., M. Hemberg, B. M. Starzomski, and J. B. Shurin. 2007. Trophic levels and trophic tangles: The prevalence of omnivory in real food webs. *Ecology* **88**:612-617.
- Vázquez, D. P., and R. D. Stevens. 2004. The latitudinal gradient in niche breadth: Concepts and evidence. *The American Naturalist* **164**:E1-19.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology and Systematics* **34**:273-309.

List of Figures

Figure 1. Biogeographic (A) and food web (B) predictions regarding the relative importance of predation, herbivory, and plant structure for salt marsh food web structure across a latitudinal gradient.

Figure 2. A) Map showing 13 *Spartina alterniflora* salt marshes sites where invertebrates and plants were sampled in 2004 and 2005. B) Cluster dendrogram based on a Bray-Curtis similarity index using $\log_{10}(x+1)$ transformed abundance data of invertebrates sampled from sites shown in panel A.

Figure 3. Relationship between latitude and the species richness (A,C,E) and diversity (B,D,F) of invertebrate detritivores (A,B), herbivores (C,D), and predators (E,F) sampled on Atlantic coastal *Spartina alterniflora* salt marshes in 2004 (o) and 2005 (●).

Figure 4. Relationship between latitude and the structure and quality of *Spartina* (A-E), herbivore density (F-G), and predator density (H-J) on Atlantic coastal salt marshes sampled during 2004 (o) and 2005 (●). All invertebrate densities are reported as $\log_{10}x+1$ number individuals/m². Lines in all panels indicate best fit linear regression in 2004 (dashed) and 2005 (solid).

Figure 5. Relationship between the density ($\log_{10}x+1$ number individuals/m²) of *Littoraria irrorata* on Atlantic coastal salt marshes and latitude (A), *Spartina* leaf litter (B), culm density (C), and *Pardosa* wolf spider density (D). The solid line indicates the exponential decay regression.

Figure 1.

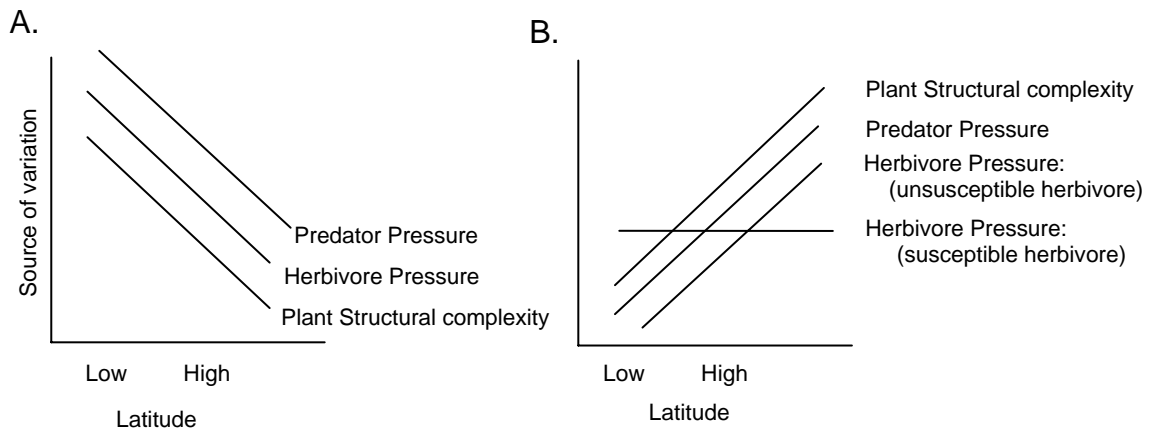
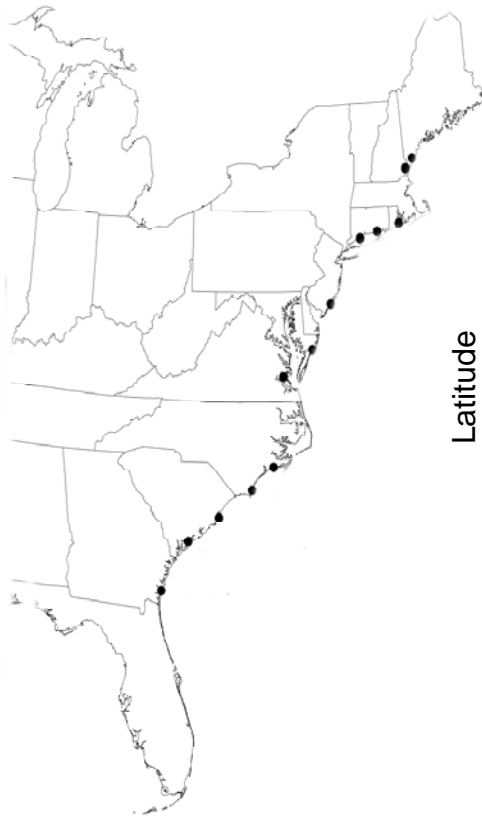


Figure 2.

A.



B.

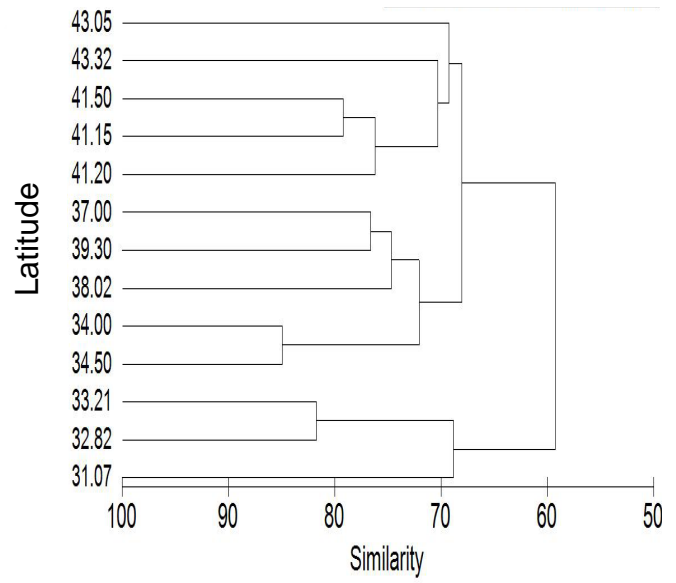


Figure 3.

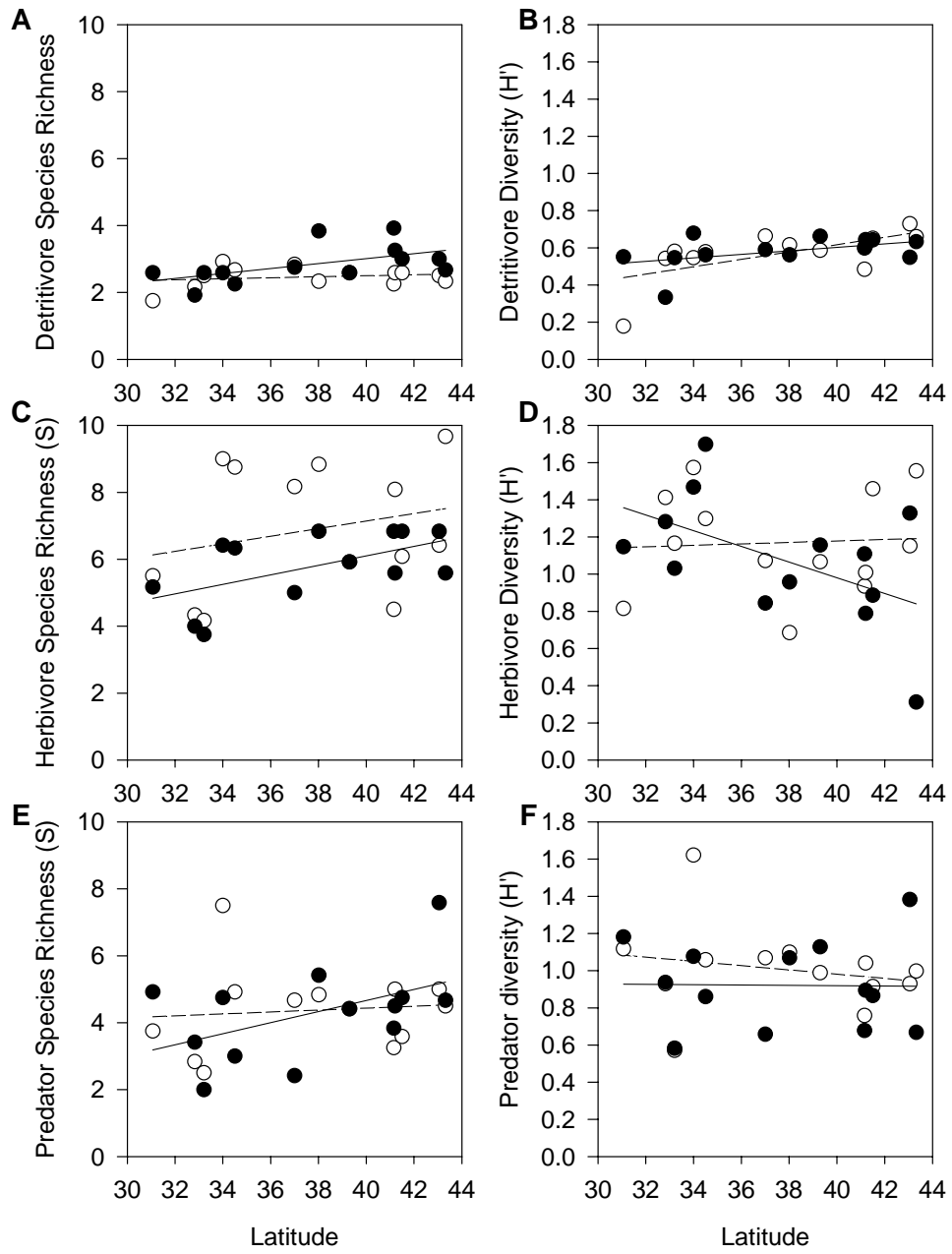


Figure 4.

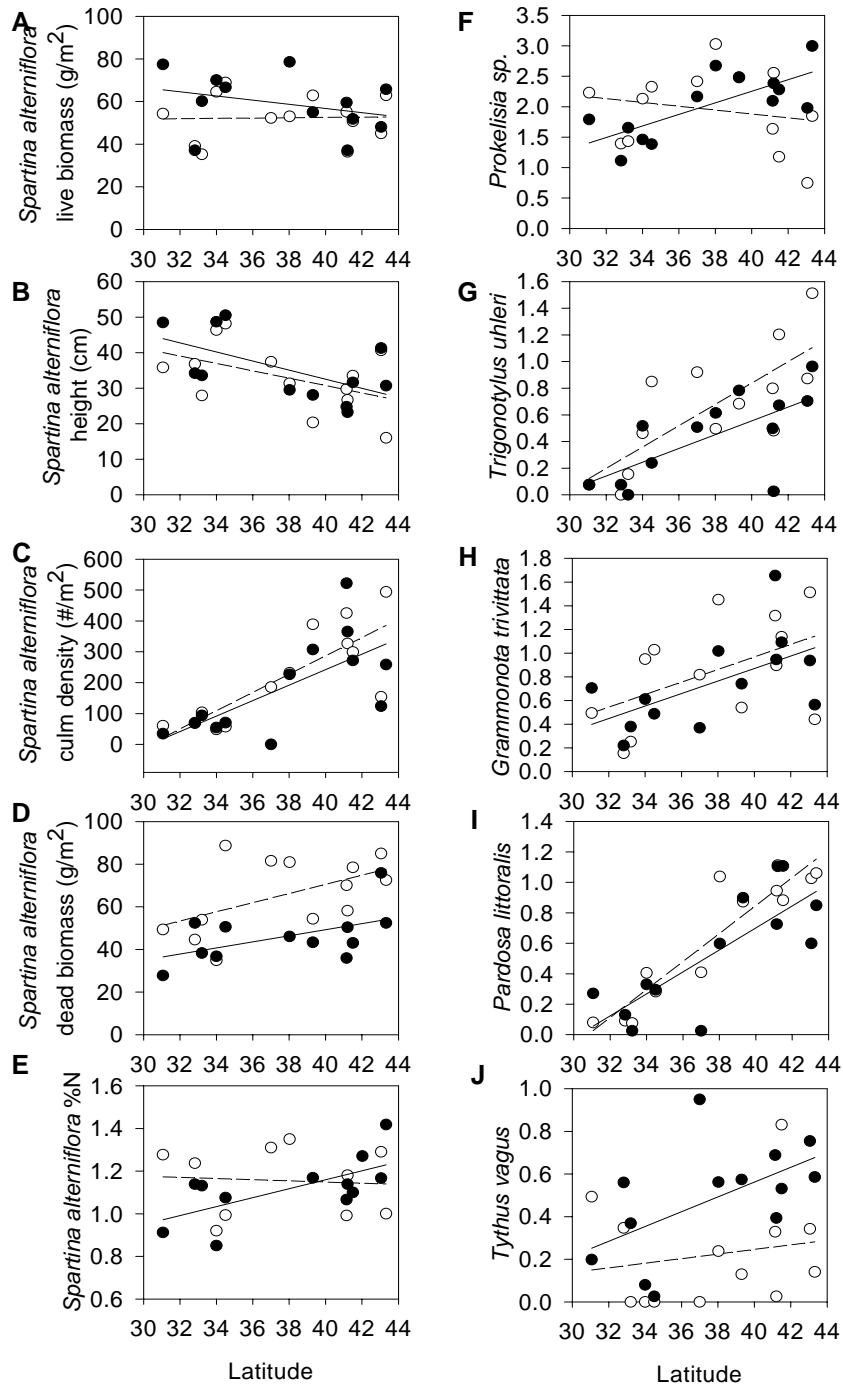
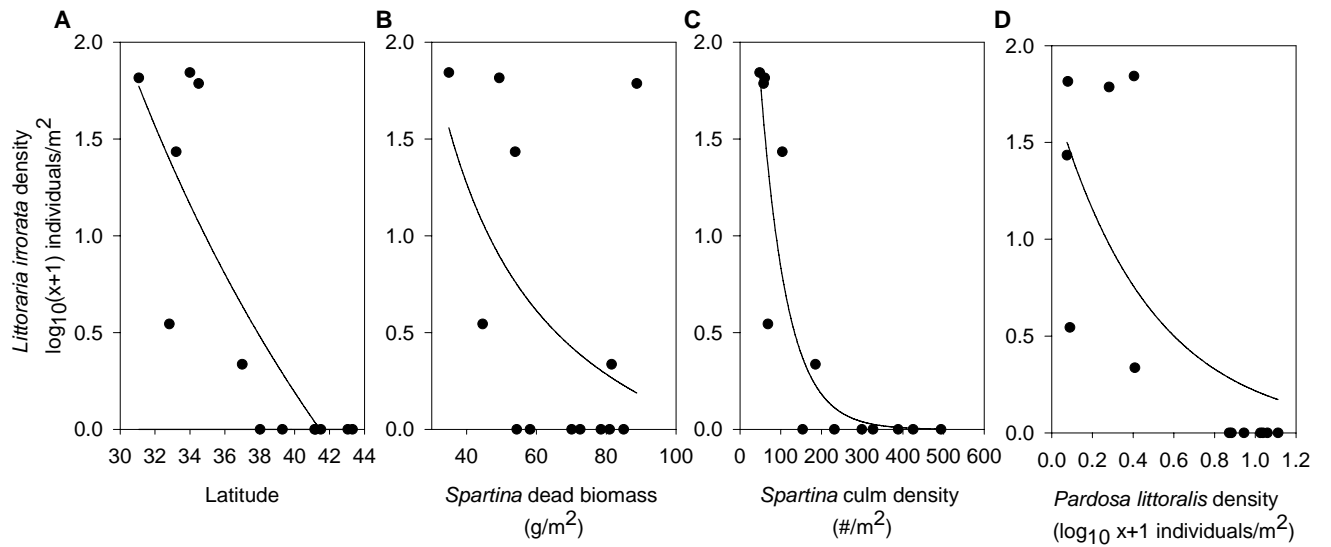


Figure 5.



Tables

Table 1. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on species richness and diversity of three trophic groups: detritivores, herbivores, and predators. Significant F and *p*-values are bolded for emphasis.

	Detritivore		Detritivore		Herbivore		Herbivore		Predator		Predator	
	Richness		Diversity		Richness		Diversity		Richness		Diversity	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>P</i>	F	<i>P</i>	F	<i>p</i>
Latitude	2.22	0.03	3.13	0.004	1.71	0.10	1.32	0.20	1.53	0.14	0.52	0.61
Year	1.22	0.23	1.13	0.27	0.38	0.70	1.50	0.14	1.08	0.29	0.53	0.59
Latitude*Year	1.48	0.15	1.15	0.26	0.19	0.85	1.59	0.12	1.09	0.28	0.44	0.66

Table 2. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on plant structure and quality as indexed by live *Spartina alterniflora* biomass, %N content, plant height, culm density, and dead leaf litter biomass. Significant F and *p*-values are bolded for emphasis.

Source of variation	Live biomass		%N		Height		Culm density		Dead biomass	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>	F	<i>P</i>	F	<i>p</i>
Latitude	0.74	0.46	0.87	0.39	2.88	0.009	5.44	<0.0001	2.75	0.01
Year	1.00	0.32	1.36	0.19	0.37	0.72	0.46	0.65	0.15	0.88
Latitude*Year	0.86	0.39	1.25	0.23	0.29	0.77	-0.52	0.61	0.55	0.58

Table 3. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on the densities of invertebrate herbivores (*Prokelisia sp.* and *Trigonotylus uhleri*), and the omnivorous snail (*Littoraria irrorata*). Significant F and *p*-values are bolded for emphasis.

Source of variation	<i>Prokelisia sp.</i>		<i>Trigonotylus uhleri</i>		<i>Littoraria irrorata</i>	
	F	<i>p</i>	F	<i>p</i>	F	<i>P</i>
Latitude	1.22	0.23	5.05	<0.0001	21.8	0.0007
Year	2.37	0.03	0.86	0.39		
Latitude*Year	2.43	0.02	1.09	0.29		

Table 4. ANOVA results for the main and interactive effects of year (2004, 2005) and latitude on the densities of invertebrate predators. Significant F and *p*-values are bolded for emphasis.

<i>Source of variation</i>	<i>Grammonota trivittata</i>		<i>Pardosa littoralis</i>		<i>Tythus vagus</i>	
	F	<i>p</i>	F	<i>p</i>	F	<i>p</i>
Latitude	2.99	0.007	8.20	<0.0001	6.74	<0.0001
Year	0.07	0.95	0.85	0.41	1.18	0.25
Latitude*Year	0.00	0.99	0.99	0.33	1.38	0.18

Chapter 4: Detritivore food chain length influences plant growth response to elevated CO₂

Abstract

Changes in the global carbon cycle may influence the strength of linkages between primary production and decomposition food webs. I examined how changes in detritivore food chain length (litter/isopod/spider) influenced the growth of two different plant species, the C₃ sedge *Scirpus olneyi* and the C₄ grass *Spartina patens*, under elevated and ambient CO₂ conditions. Increases in atmospheric carbon dioxide have been shown to result in sustained increases of biomass and subsequent leaf litter production in the C₃ sedge *Scirpus olneyi* but not in the C₄ grass *Spartina patens*. Macrofauna detritivores fragment and mineralize leaf litter, affect decomposition, and can influence nutrient availability for plant uptake and growth. I found preliminary evidence suggesting that changes in detritivore food chain length may have a relatively stronger influence on *Scirpus* growth under elevated compared to ambient CO₂ conditions. In contrast, increases in atmospheric CO₂ have diminished direct influences on *Spartina patens* primary production, and I found no evidence that changes in the detritivore food chain length modifies the growth response of this C₄ grass to elevated CO₂ conditions. The distribution of leaf litter and the density of detritivore macrofauna and their predators could contribute to variation in plant response to elevated CO₂ conditions.

Keywords: elevated CO₂, detritivore, food chain length, leaf litter

Introduction

Increasing atmospheric carbon dioxide (CO₂) is likely to influence ecosystem processes such as primary production (Drake et al. 1997, Rasse et al. 2003). Plants growing in habitats where nitrogen is not limiting are more likely to increase production in response to CO₂ enrichment (Nowak et al. 2004). Therefore, the feedback loop between aboveground plant growth, and mineralization of nutrients from leaf litter, is a critical component to understanding plant response to elevated CO₂ and ecosystem carbon sequestration. Notably, most studies examine the influence of elevated CO₂ on separate ecosystem functions such as primary production (Rasse et al. 2003), litter decomposition (Couteaux and Bolger 2000, David et al. 2001, Norby et al. 2001), and soil microbial processes (Hungate et al. 2000, Pinay et al. 2007). This approach has likely led to a distorted perspective regarding the relative importance of linkages between these ecosystem components (Wolters et al. 2000, Wall 2007).

It stands to reason that detritivore food webs should be sensitive to changes in net primary productivity due to increasing CO₂ because it can alter the quantity and quality of leaf litter resource input (Wardle 2002). Saprophagous macrofauna such as isopods fragment and mineralize leaf litter and they play an important role in the decomposition process (Hattenschwiler et al. 1999, David et al. 2001). Isopods can adjust their feeding rates to compensate for poor-quality litter (high lignin concentration, low nitrogen content) (Hattenschwiler et al. 1999), but low resource quality can also lead to reduced isopod survivorship (David et al. 2001). Macrofauna

consumers can both stimulate (Hattenschwiler and Bretscher 2001), and suppress (Mikola et al. 2002) the activity of microbial decomposers that are also responsible for leaf litter decomposition. Thus, although changes in detritivore abundance and food chain length can potentially influence decomposition rates and subsequent nutrient availability for plant uptake (Kajak 1995, Wardle et al. 1998b, Hunter et al. 2003, Lawrence and Wise 2004), a high degree of omnivory in detritivore food webs suggests that indirect interactions between non-adjacent trophic groups do not always cascade to basal resources (Mikola and Setälä 1998, Mikola et al. 2002, Scheu and Setälä 2002).

Because elevated CO₂ can reduce the nitrogen content and enhance the biomass of live aboveground leaf tissue (Cotrufo et al. 1998), there has been much interest in the resulting influences of elevated CO₂ on leaf litter chemistry and subsequent decomposition rates (Strain and Bazzaz 1983, King et al. 2001, Norby et al. 2001). The “litter quality hypothesis” suggests that elevated CO₂ will result in poor quality litter (low N content, high C:N) and reduced rates of decomposition (Strain and Bazzaz 1983). This in turn, should provide a negative feedback for live plant growth by reducing nitrogen availability for plant uptake. More recent reviews of elevated CO₂ influences on litter chemistry and decomposition have suggested that plants are able to translocate most nitrogen to roots before senescence, and that elevated CO₂ has more limited influence on litter decomposition rates than originally projected (Norby et al. 2001). However, increases in both live plant demand for nitrogen (Norby and Iversen 2006), and increases in litter production (Liu et al. 2007) may counter response of litter chemistry (C:N) and decomposition rates. Thus

understanding of aboveground CO₂ response must consider the decomposer food web responsible for driving plant-litter feedbacks (Wardle et al. 1998a, David et al. 2001).

Notably, not all plant species respond equally to changes in atmospheric CO₂ conditions (Cotrufo et al. 1998, Goverde et al. 2002, Nowak et al. 2004). The extent to which plant demand for nitrogen is influenced by increasing CO₂, may be mitigated by increased root production (Jongen et al. 1995), water availability (Roth et al. 1997, Rasse et al. 2005) and plant photosynthetic pathway (Cotrufo et al. 1998, Goverde et al. 2002, Nowak et al. 2004). For example, aboveground leaf biomass and nutrient content of plants with C₃ photosynthetic pathways are on average more responsive to elevated CO₂ than plants with a C₄ pathway (Cotrufo et al. 1998). However, there is little consensus about how variation in litter quantity, detritivore feeding preferences, and changes in plant functional group synergistically influence plant response to elevated CO₂.

In this study, I examine the impact of changes in detritivore food chain length on the growth response of two wetland plant species (*Scirpus olneyi*, and *Spartina patens*) to elevated CO₂ conditions. For plants that display a positive growth response to elevated CO₂ (*Scirpus olneyi*), I predict that an increased demand for nitrogen will result in an interaction between detritivore and CO₂ treatments, such that litter decomposition should be more important under elevated compared to ambient CO₂ conditions. In contrast, when aboveground plant growth is not directly influenced by elevated CO₂ (*Spartina patens*) the relative influence of litter decomposition on live plant growth should also be less influenced by elevated CO₂. Thus I predict that litter mineralization by detritivorous isopods will enhance plant

growth, that the addition of invertebrate spider predators will dampen any positive influence of detritivores, and that the relative effect of these treatments will be contingent upon both atmospheric CO₂ concentrations and plant photosynthetic pathway.

Methods

Study System

This study was conducted at the Smithsonian Environmental Research Center on a brackish wetland located on the Rhode River inlet of the Chesapeake Bay (38°53'N, 76°33'W). Plant communities at this site are dominated by *Scirpus olneyi* (a C₃ sedge), and *Spartina patens* (a C₄ grass). A long-term open topped chamber experiment was established in 1987 (Drake et al. 1989) and results to date show that *S. olneyi* has a sustained increase in primary production and reduced N content under elevated CO₂ conditions (Rasse et al. 2005). In contrast, the nitrogen content and biomass of *S. patens* are relatively unaffected by elevated CO₂ conditions (Arp et al. 1993). Although there has been an intensive investigation into plant physiological responses to elevated CO₂ in this system, there has been little investigation into litter decomposition, the activity of the invertebrate community, or interactive feedbacks between the two subsystems.

Generalist wolf spiders forage broadly across the surface of the marsh in both plant communities. The dominant hunting spider is *Pardosa littoralis* (Araneae: Lycosidae), which can occur in densities up to 600 individuals/m². *Pardosa* consume a broad variety of invertebrate prey. Detritivorous isopods such as *Littorophiloscia*

vittatta (Isopoda: Philosciidae) are vulnerable to spider predation, and they occur in high densities in wetland habitats where they shred and mineralize leaf litter.

The influence of detritivore food chain on the plant growth response to elevated CO₂

To examine if changes in detritivore food chain are relatively more important for live plant growth under elevated atmospheric CO₂ concentrations, I conducted a 2x4 split plot chambered mesocosm experiment. Each main plot CO₂ treatment (ambient CO₂ at 365 ppm and elevated CO₂ at 705 ppm) was replicated three times for a total of 6 greenhouse chambers (1.5 m long x 1 m wide x 1.5 m tall, wooden enclosures surrounded by Melinex® clear plastic sheeting). Nested within each chamber, plants were exposed to one of four treatments representing increasing detritus food chain length: 1) control litter withheld, 2) litter addition (400 g/m²), 3) litter and 20 *Littorophiloscia vittatta* isopod addition, and 4) litter, isopod and 2 *Pardosa littoralis* spider addition. Litter addition treatments were established using leaf litter that was air dried after it was collected from plants that were grown and allowed to completely senesce under either elevated or ambient conditions during the previous year. All plants were grown in sand filled pots (11 cm diameter x 16 cm deep) exposed to constant moisture by seating them within water filled pots (16 cm diameter x 16 cm deep). Clear plastic tube cages 15 cm diameter x 1 m tall were sunk in to the soil of all mesocosms to enclose the litter community. I replicated the entire experiment using species from two plant functional groups (*Scirpus olneyi* a C₃ sedge grown from field collected rhizomes, and *Spartina patens* a C₄ grass propagated from field collected seeds) for a total of 48 experimental units (2 plant species, 4 detritivore treatments, 2 CO₂ levels, with 3 replicate chambers for each

treatment combination). Throughout the experiment I recorded changes in plant height and leaf area and I harvested all live plant material after 50 days.

The main and interactive effects of atmospheric CO₂ and detritivore food chain treatments on C₃ and C₄ plant growth (change in leaf area, shoot biomass, and root biomass) were assessed using ANOVA with CO₂ chamber as a random block factor. Due to a combination of replication constraints associated with using CO₂ chambers, and high variation in growth response I decided to accept ($p < 0.10$) as indicative statistical significance.

Results

There was an interactive effect of elevated CO₂ and detritivore food chain treatments on plant growth response of *Scirpus olneyi* (Table 1), but not *Spartina patens* (Table 2). Detritivore food chain treatments had no influence on *Scirpus* aboveground shoot, leaf area, or root production under ambient CO₂ conditions (Figure 1 A-C). However, under elevated CO₂ conditions the addition of isopods enhanced *Scirpus* leaf area and root production in both the presence and absence of spiders (Figure 1 B,C; Table 1). Neither *Spartina* aboveground biomass, shoot production, nor root production responded to the CO₂ or detritivore food-chain treatments (Figure 1 D-F; Table 2).

Discussion

The results of this study suggest that plant growth response to elevated CO₂ may depend in part on the presence of macrofauna detritivores. Consistent with predictions, I found that C₃ *Scirpus* was relatively more sensitive to changes in

detritivore food chain length under elevated compared to ambient conditions (Figure 1). However, contrary to expectation, addition of leaf litter and subsequent feeding activity of isopods did not result in enhanced plant production in either the ambient *Scirpus* treatments or the *Spartina* plants growing under either ambient or elevated CO₂ conditions. This suggests that plant uptake of nutrients released from decomposing leaf litter was moderated by isopod influence on microbial processes, or that factors other than nitrogen release (i.e. water use efficiency) limited plant growth in these treatments.

Little is known about how multiple environmental factors interactively influence the response of plant growth to changes in CO₂ conditions. Still less is known about how food-web interactions will contribute to ecosystem level response to climate change. The few studies that have examined isopod feeding behavior under elevated and ambient CO₂ conditions provide mixed results (Hattenschwiler et al. 1999, David et al. 2001). Leaf litter produced under ambient and elevated CO₂ conditions can directly influence detritivore feeding preferences (Adams et al. 2003) and consumption rates (David et al. 2001). However these effects may be moderated by detritivore food web structure. For instance, Couteaux *et al.* (1991) found that increasing the complexity of detritivore food webs can reverse the negative effects on elevated CO₂ on decomposition rates. In contrast, I found that predation did not moderate the indirect influence of detritivorous isopods on either aboveground or belowground plant growth. Notably, CO₂ can have mixed effects on rhizodeposition (Paterson 1996, Rouhier 1996), fine root production and root:shoot ratios (Jongen et al. 1995, Salt et al. 1996, Parsons et al. 2003). Therefore, detritivore influences on

litter mineralization and nitrogen availability may be attenuated by microbial activity and root growth in the soil subsystem. Taken together these results emphasize the need for studies that adopt a combined aboveground-belowground perspective to understanding food web and ecosystem response to elevated CO₂.

Literature Cited

- Adams, J. A., N. C. Tuchman, and P. A. Moore. 2003. Atmospheric CO₂ enrichment alters leaf detritus: impacts on foraging decisions of crayfish (*Orconectes virilis*). *Journal of the North American Benthological Society* **22**:410-422.
- Arp, W. J., B. G. Drake, W. T. Pockman, P. S. Curtis, and D. F. Whigham. 1993. Interactions between C-3 and C-4 salt-marsh plant-species during four years of exposure to elevated atmospheric CO₂. *Vegetatio* **104**:133-143.
- Cotrufo, M. F., P. Ineson, and A. Scott. 1998. Elevated CO₂ reduces the nitrogen concentration of plant tissues. *Global Change Biology* **4**:43-54.
- Couteaux, M. M., and T. Bolger. 2000. Interactions between atmospheric CO₂ enrichment and soil fauna. *Plant and Soil* **224**:123-134.
- David, J. F., N. Malet, M. M. Couteaux, and J. Roy. 2001. Feeding rates of the woodlouse *Armadillidium vulgare* on herb litters produced at two levels of atmospheric CO₂. *Oecologia* **127**:343-349.
- Drake, B. G., M. A. Gonzalez Meler, and S. P. Long. 1997. More efficient plants: A consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology* **48**:609-639.

- Drake, B. G., P. W. Leadley, W. J. Arp, D. Nassiry, and P. S. Curtis. 1989. An open top chamber for field studies of elevated atmospheric CO₂ concentration on saltmarsh vegetation. *Functional Ecology* **3**:363-371.
- Goverde, M., J. A. Arnone, and A. Erhardt. 2002. Species-specific reactions to elevated CO₂ and nutrient availability in four grass species. *Basic and Applied Ecology* **3**:221-227.
- Hattenschwiler, S., and D. Bretscher. 2001. Isopod effects on decomposition of litter produced under elevated CO₂, N deposition and different soil types. *Global Change Biology* **7**:565-579.
- Hattenschwiler, S., S. Buhler, and C. Korner. 1999. Quality, decomposition and isopod consumption of tree litter produced under elevated CO₂. *Oikos* **85**:271-281.
- Hungate, B. A., C. H. Jaeger, G. Gamara, F. S. Chapin, and C. B. Field. 2000. Soil microbiota in two annual grasslands: responses to elevated atmospheric CO₂. *Oecologia* **124**:589-598.
- Hunter, M. D., S. Adl, C. M. Pringle, and D. C. Coleman. 2003. Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia* **47**:101-115.
- Jongen, M., M. B. Jones, T. Hebeisen, H. Blum, and G. Hendrey. 1995. The Effects of elevated CO₂ concentrations on the root growth of *Lolium perenne* and *Trifolium repens* grown in a FACE system. *Global Change Biology* **1**:361-371.

- Kajak, A. 1995. The role of soil predators in decomposition processes. *European Journal of Entomology* **92**:573-580.
- King, J. S., K. S. Pregitzer, D. R. Zak, M. E. Kubiske, and W. E. Holmes. 2001. Correlation of foliage and litter chemistry of sugar maple, *Acer saccharum*, as affected by elevated CO₂ and varying N availability, and effects on decomposition. *Oikos* **94**:403-416.
- Lawrence, K. L., and D. H. Wise. 2004. Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia* **48**:149-157.
- Liu, L. L., J. S. King, and C. P. Giardina. 2007. Effects of elevated atmospheric CO₂ and tropospheric O₃ on nutrient dynamics: decomposition of leaf litter in trembling aspen and paper birch communities. *Plant and Soil* **299**:65-82.
- Mikola, J., R. D. Bardgett, and K. Hedlund. 2002. Biodiversity, ecosystem functioning and soil decomposer food webs. Pages 169-180 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning- Synthesis and perspectives*. Oxford University Press, Oxford.
- Mikola, J., and H. Setälä. 1998. No evidence of trophic cascades in an experimental microbial-based soil food web. *Ecology* **79**:153-164.
- Norby, R. J., M. F. Cotrufo, P. Ineson, E. G. O'Neill, and J. G. Canadell. 2001. Elevated CO₂, litter chemistry, and decomposition: a synthesis. *Oecologia* **127**:153-165.
- Norby, R. J., and C. M. Iversen. 2006. Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂-enriched sweetgum forest. *Ecology* **87**:5-14.

- Nowak, R. S., D. S. Ellsworth, and S. S. Smith. 2004. Tansley review: Functional responses of plants to elevated atmospheric CO₂- do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* **162**:253-280.
- Parsons, W. F. J., B. J. Kopper, and R. L. Lindroth. 2003. Altered growth and fine root chemistry of *Betula papyrifera* and *Acer saccharum* under elevated CO₂. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **33**:842-846.
- Paterson, E. 1996. Effect of elevated atmospheric CO₂ concentration on C-partitioning and rhizosphere C-flow for three plant species. *Soil Biology and Biochemistry* **28**:195-201.
- Pinay, G., P. Barbera, A. Carreras-Palou, N. Fromin, L. Sonie, M. M. Couteaux, J. Roy, L. Philippot, and R. Lensi. 2007. Impact of atmospheric CO₂ and plant life forms on soil microbial activities. *Soil Biology and Biochemistry* **39**:33-42.
- Rasse, D. P., J.-H. Li, and B. Drake. 2003. Carbon dioxide assimilation by a wetland sedge canopy exposed to ambient and elevated CO₂ measurements and model analysis. *Functional Ecology* **17**:222-230.
- Rasse, D. P., G. Peresta, and B. Drake. 2005. Seventeen years of elevated CO₂ exposure in a Chesapeake Bay wetland: sustained but contrasting responses of plant growth and CO₂ uptake. *Global Change Biology* **11**:369-377.

- Roth, S., E. P. McDonald, and R. L. Lindroth. 1997. Atmospheric CO₂ and soil water availability: consequences for tree-insect interactions. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **27**:1281-1290.
- Rouhier, H. 1996. Carbon fluxes in the rhizosphere of sweet chesnut (*Castanea sativa*) grown under two atmospheric CO₂ concentrations: ¹⁴C partitioning after pulse labelling. *Plant and Soil* **180**:101-111.
- Salt, D. T., P. Fenwick, and J. B. Whittaker. 1996. Interspecific herbivore interactions in a high CO₂ environment: Root and shoot aphids feeding on Cardamine. *Oikos* **77**:326-330.
- Scheu, S., and H. Setälä. 2002. Multitrophic interactions in decomposer food-webs. Pages 223-266 in T. Tscharrntke and B. A. Hawkins, editors. *Multitrophic Level Interactions*.
- Strain, B. R., and F. Bazzaz. 1983. Terrestrial plant communities. Pages 177-222 in E. R. Lemon, editor. *CO₂ and plants*, Boulder, CO.
- Wall, D. H. 2007. Global change tipping points: above- and below-ground biotic interactions in a low diversity ecosystem. *Philosophical transactions of the royal society B* **362**:2291-2306.
- Wardle, D. A. 2002. *Communities and ecosystems: Linking the aboveground and belowground components*. Princeton University Press, Princeton, NJ.
- Wardle, D. A., H. A. Verhoef, and M. Clarholm. 1998a. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. *Global Change Biology* **4**:713-727.

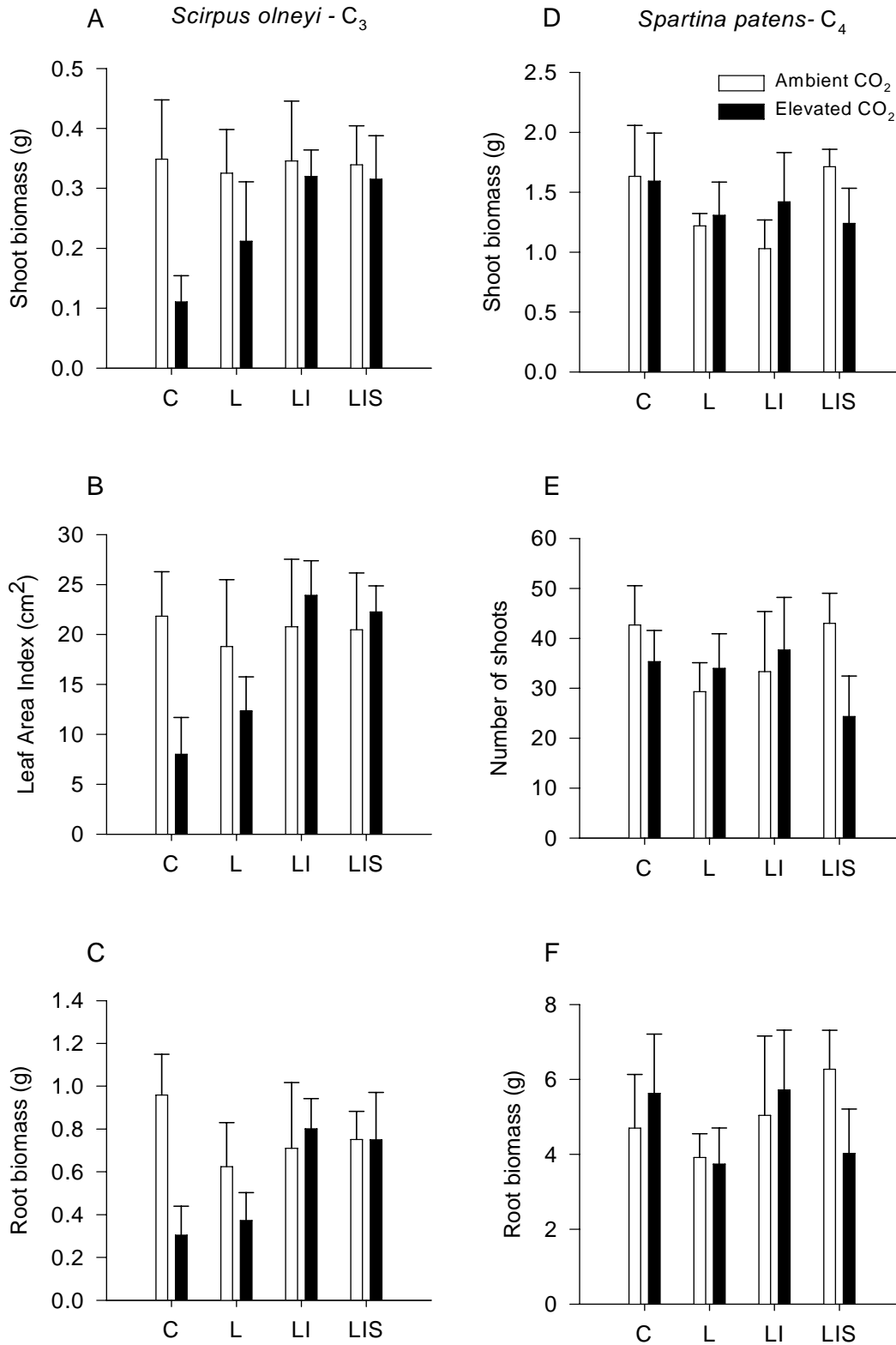
Wardle, D. A., H. A. Verhoef, and M. Clarholm. 1998b. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. *Global Change Biology* **4**:713-727.

Wolters, V., W. L. Silver, D. E. Bignell, D. C. Coleman, P. Lavelle, W. H. Van Der Putten, P. C. De Ruiter, J. Rusek, D. H. Wall, D. A. Wardle, L. Brussaard, J. M. Dangerfield, V. K. Brown, K. E. Giller, D. U. Hooper, O. Sala, J. M. Tiedje, and J. A. Van Veen. 2000. Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: Implications for ecosystem functioning. *Bioscience* **50**:1089-1098.

List of Figures

Figure 1. The influence of atmospheric carbon dioxide and increases in detritivore food chain length on three measures of plant growth (shoot biomass, leaf area index and root biomass) of the C₃ sedge *Scirpus olneyi* (A-C) and the C₄ grass *Spartina patens* (D-E) in chambered mesocosms. Bars show treatment means (\pm SE) in response to ambient (\circ) or elevated (ambient + 345ppm: \bullet) CO₂ treatments. Detritivore food chain length is shown on the x-axis as control (C), litter addition (L), litter and isopod addition (LI), and litter, isopod, and spider addition (LIS).

Figure 1.



Tables

Table 1. ANOVA results showing the direct and interactive influences of CO₂ (elevated or ambient) and 4 detritus food web treatments (control, litter addition, litter and isopod addition, or litter, isopod, and spider addition) on *Scirpus olneyi* root biomass, leaf area index (LAI) and aboveground shoot biomass. Treatments with *p* values equal to or less than 0.1 are bolded for emphasis.

<i>Scirpus olneyi</i> -C ₃	<i>df</i>	Root biomass		LAI		<i>df</i>	Aboveground Shoot biomass	
		F	<i>p</i>	F	<i>p</i>		F	<i>p</i>
CO ₂	1,4	1.01	0.37	0.50	0.51	1,16	3.34	0.08
Det	3,12	1.37	0.29	2.57	0.10	3,16	0.81	0.50
CO ₂ *det	3,12	2.59	0.10	2.70	0.09	3,16	0.85	0.48

Table 2. ANOVA results showing the direct and interactive influences of CO₂ (elevated or ambient) and 4 detritus food web treatments (control, litter addition, litter and isopod addition, or litter, isopod, and spider addition) on *Spartina patens* root biomass, number of aboveground shoots and aboveground shoot biomass.

<i>Spartina patens</i> -C ₄	Root biomass			Number of Aboveground Shoots			Aboveground Shoot biomass		
	<i>df</i>	F	<i>p</i>	<i>df</i>	F	<i>p</i>	<i>df</i>	F	<i>p</i>
CO ₂	1,4	0.02	0.88	1,16	0.54	0.47	1,4	0.00	0.97
Det	3,12	0.70	0.56	3,16	0.29	0.83	3,12	0.87	0.48
CO ₂ *det	3,12	0.73	0.55	3,16	0.92	0.45	3,12	0.83	0.50

Bibliography

Adams, J. A., N. C. Tuchman, and P. A. Moore. 2003. Atmospheric CO₂ enrichment alters leaf detritus: impacts on foraging decisions of crayfish (*Orconectes virilis*). *Journal of the North American Benthological Society* 22:410-422.

Arp, W. J., B. G. Drake, W. T. Pockman, P. S. Curtis, and D. F. Whigham. 1993. Interactions between C-3 and C-4 salt-marsh plant-species during four years of exposure to elevated atmospheric CO₂. *Vegetatio* 104:133-143.

Badano, E. I., and L. A. Cavieres. 2006. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography* 33:304-313.

Bardgett, R. D., W. D. Bowman, R. Kaufmann, and S. K. Schmidt. 2005a. A temporal approach to linking aboveground and belowground ecology. *Trends in ecology and evolution* 20:634-631.

Bardgett, R. D., and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258-2268.

Bardgett, R. D., G. W. Yeates, and J. M. Anderson. 2005b. Patterns and determinants of soil biological diversity. Pages 100-118 in R. D. Bardgett, M. D. Usher, and D. W. Hopkins, editors. *Biological diversity and function in soils*. Cambridge University Press, Cambridge, UK.

- Beals, M. L. 2006. Understanding community structure: a data-driven multivariate approach. *Oecologia* 150:484-495.
- Benton, T. G., M. Solan, J. M. J. Travis, and S. M. Sait. 2007. Microcosm experiments can inform global ecological problems. *Trends in ecology and evolution* 22:516-521.
- Bertness, M. D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a new england salt marsh. *Ecology* 66:1042-1055.
- Blum, L. K., M. S. Roberts, J. L. Garland, and A. L. Mills. 2004. Distribution of microbial communities associated with the dominant high marsh plants and sediments of the United States east coast. *Microbial Ecology* 48:375-388.
- Bonkowski, M., I. E. Geoghegan, B. A. N. E., and B. S. Griffiths. 2001. Effects of soil decomposer invertebrates (protozoa and earthworms) on an above-ground phytophagous insect (cereal aphid) mediated through changes in the host plant. *Oikos* 95:441-450.
- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528-537.
- Boyer, K. E., and P. Fong. 2005. Co-occurrence of habitat-modifying invertebrates: effects on structural and functional properties of a created salt marsh. *Oecologia* 143:619-628.
- Bradley, P. M., and J. T. Morris. 1991. The influence of salinity on the kinetics of NH_4^+ uptake in *Spartina alterniflora*. *Oecologia* 85.

- Brewer, J. S., J. M. Levine, and M. D. Bertness. 1998. Interactive effects of elevation and burial with wrack on plant community structure in some Rhode Island salt marshes. *Journal of Ecology* 86:125-136.
- Brose, U., A. Ostling, K. Harrison, and N. D. Martinez. 2004. Unified spatial scaling of species and their trophic interactions. *Nature (London)* 428:167-171.
- Buckley, H. L., T. E. Miller, A. M. Ellison, and N. J. Gotelli. 2003. Reverse latitudinal trends in species richness of pitcher-plant food webs. *Ecology Letters* 6:825-829.
- Càcamo, H. A., T. A. Abe, C. E. Prescott, F. B. Holl, and C. P. Chanway. 2000. Influence of millipedes on litter decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. *Canadian Journal of Forest Research* 30:817-826.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426-429.
- Casula, P., A. Wilby, and M. B. Thomas. 2006. Understanding biodiversity effects on prey in multi-enemy systems. *Ecology Letters* 9:1-10.
- Chalcraft, D. R., and W. J. Resatarits. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? *Ecology* 84:2407-2418.
- Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* 277:500-504.

- Chase, J. M. 2003. Strong and weak trophic cascades along a productivity gradient. *Oikos* 101:187-195.
- Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pages 25–49 in P. W. Price, editor. *Plant–animal interactions: evolutionary ecology in tropical and temperate regions*. John Wiley and Sons, New York, New York, USA.
- Cotrufo, M. F., P. Ineson, and A. Scott. 1998. Elevated CO₂ reduces the nitrogen concentration of plant tissues. *Global Change Biology* 4:43-54.
- Couteaux, M. M., and T. Bolger. 2000. Interactions between atmospheric CO₂ enrichment and soil fauna. *Plant and Soil* 224:123-134.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153-166.
- David, J. F., N. Malet, M. M. Couteaux, and J. Roy. 2001. Feeding rates of the woodlouse *Armadillidium vulgare* on herb litters produced at two levels of atmospheric CO₂. *Oecologia* 127:343-349.
- De Deyn, G. B., and W. H. Van Der Putten. 2005. Linking aboveground and belowground diversity. *Trends in ecology and evolution* 20:625-633.
- Denno, R., F., D. Lewis, and C. Gratton. 2005. Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Annales Zoologici Fennici* 42:295-311.

- Denno, R. F., C. Gratton, H. G. Döbel, and D. L. Finke. 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* 84:1032-1044.
- Denno, R. F., C. Gratton, M. A. Peterson, G. A. Langellotto, D. L. Finke, and A. F. Huberty. 2002. Bottom-up forces mediate natural enemy impact in a phytophagous insect community. *Ecology* 83:1443-1458.
- Denno, R. F., K. L. Olmstead, and E. S. McCloud. 1989. Reproductive cost of flight capability - a comparison of life-history traits in wing dimorphic planthoppers. *Ecological Entomology* 14:31-44.
- Denno, R. F., and M. A. Peterson. 1995. Density-dependent dispersal and its consequences for population dynamics. Pages 113-130 in *Population Dynamics*. Academic Press, Inc.
- Denno, R. F., G. K. Roderick, K. L. Olmstead, and H. G. Döbel. 1991. Density-Related Migration in Planthoppers (Homoptera, Delphacidae) - the Role of Habitat Persistence. *American Naturalist* 138:1513-1541.
- Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Döbel, M. D. Eubanks, J. E. Losey, and G. A. Langellotto. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecological Monographs* 66:389-408.
- Döbel, H. G., and R. F. Denno. 1994. Predator-Planthopper Interactions. Pages 325-399 in R. F. Denno and I. T. Perfect, editors. *Planthoppers, their ecology and management*. Chapman and Hall, London.

- Drake, B. G., M. A. Gonzalez Meler, and S. P. Long. 1997. More efficient plants: A consequence of rising atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology* 48:609-639.
- Drake, B. G., P. W. Leadley, W. J. Arp, D. Nassiry, and P. S. Curtis. 1989. An open top chamber for field studies of elevated atmospheric CO₂ concentration on saltmarsh vegetation. *Functional Ecology* 3:363-371.
- Elder, B. D. 2006. Disturbance-mediated trophic interactions and plant performance. *Oecologia* 147:261-271.
- Eviner, V. T., and F. S. Chapin. 2003. Functional matrix: A conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology Evolution and Systematics* 34:455-485.
- Ferguson, S. H., and D. O. Joly. 2002. Dynamics of springtail and mite populations: the role of density dependence, predation, and weather. *Ecological Entomology* 27:565-573.
- Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* 83:643-652.
- Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8:1299-1306.
- Goverde, M., J. A. Arnone, and A. Erhardt. 2002. Species-specific reactions to elevated CO₂ and nutrient availability in four grass species. *Basic and Applied Ecology* 3:221-227.

- Graça, M. A., S. Y. Newell, and R. T. Kneib. 2000. Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt marsh invertebrates. *Marine Biology* 136:281-289.
- Grez, A. A., and E. Prado. 2000. Effect of plant patch shape and surrounding vegetation on the dynamics of predatory coccinellids and their prey *Brevicoryne brassicae* (Hemiptera : Aphididae). *Environmental Entomology* 29:1244-1250.
- Gustafson, D. J., J. Kilheffer, and B. R. Silliman. 2006. Relative effects of *Littoraria irrorata* and *Prokelisia marginata* on *Spartina alterniflora*. *Estuaries and Coasts* 29:639-644.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* XCIV:421-424.
- Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: How much do they trickle? *American Naturalist* 157:262-281.
- Halaj, J., and D. H. Wise. 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology* 83:3141-3151.
- Hattenschwiler, S., and D. Bretscher. 2001. Isopod effects on decomposition of litter produced under elevated CO₂, N deposition and different soil types. *Global Change Biology* 7:565-579.
- Hattenschwiler, S., S. Buhler, and C. Korner. 1999. Quality, decomposition and isopod consumption of tree litter produced under elevated CO₂. *Oikos* 85:271-281.

- Hättenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics* 36:191-218.
- Hedlund, K., and M. S. Öhrn. 2000. Tritrophic interactions in a soil community enhance decomposition rates. *Oikos* 88:585-591.
- Helmuth, B., C. D. G. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298:1015-1017.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* 163:192-211.
- Hines, J., M. E. Lynch, and R. Denno, F. 2005. Sap-feeding insect communities as indicators of habitat fragmentation and nutrient subsidies. *Journal of Insect Conservation* 9:261-280.
- Hines, J., J. P. Megonigal, and R. Denno, F. 2006. Nutrient subsidies to belowground microbes impact aboveground foodweb interactions. *Ecology* 87:1542-1555.
- Holdsworth, A. R., L. E. Frelich, and P. B. Reich. 2007. Regional extent of an ecosystem engineer: Earthworm invasion in northern hardwood forests. *Ecological Applications* 17:1666-1677.
- Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on

- ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3-35.
- Huhta, V., T. Persson, and H. Setälä. 1998. Functional implications of soil fauna diversity in boreal forests. *Applied Soil Ecology* 10:277-288.
- Hungate, B. A., C. H. Jaeger, G. Gamara, F. S. Chapin, and C. B. Field. 2000. Soil microbiota in two annual grasslands: responses to elevated atmospheric CO₂. *Oecologia* 124:589-598.
- Hunter, M. D., S. Adl, C. M. Pringle, and D. C. Coleman. 2003. Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia* 47:101-115.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders - Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724-732.
- Hunter, M. D., G. C. Varley, and G. R. Gradwell. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Science* 94:9176-9181.
- Ishijima, C., A. Taguchi, M. Takagi, T. Motobayashi, M. Nakai, and Y. Kunimi. 2006. Observational evidence that the diet of wolf spiders (Araneae : Lycosidae) in paddies temporarily depends on dipterous insects. *Applied Entomology and Zoology* 41:195-200.

- Jones, C., J. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373-386.
- Jongen, M., M. B. Jones, T. Hebeisen, H. Blum, and G. Hendrey. 1995. The effects of elevated CO₂ concentrations on the root-growth of *Lolium perenne* and *Trifolium repens* grown in a FACE System. *Global Change Biology* 1:361-371.
- Jouquet, P., J. Dauber, J. Lagerlof, P. Lavelle, and M. Lepage. 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* 32:153-164.
- Kajak, A. 1995. The role of soil predators in decomposition processes. *European Journal of Entomology* 92:573-580.
- King, J. S., K. S. Pregitzer, D. R. Zak, M. E. Kubiske, and W. E. Holmes. 2001. Correlation of foliage and litter chemistry of sugar maple, *Acer saccharum*, as affected by elevated CO₂ and varying N availability, and effects on decomposition. *Oikos* 94:403-416.
- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7:69-80.
- Laakso, J., and H. Setälä. 1999. Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos* 87:57-64.
- Laakso, J., and H. Setälä. 1999. Population-and ecosystem-level effects of predation on microbial-feeding nematodes. *Oecologia* 120:279-286.

- Langellotto, G. A., and R. F. Denno. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139:1-10.
- Langellotto, G. A., and R. F. Denno. 2006. Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. *Ecological Entomology* 31:575-581.
- Lavelle, P. 2002. Functional domains in soils. *Ecological Research* 17:441-450.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545-556.
- Lawrence, K. L., and D. H. Wise. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia* 44:33-39.
- Lawrence, K. L., and D. H. Wise. 2004. Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia* 48:149-157.
- Liu, L. L., J. S. King, and C. P. Giardina. 2007. Effects of elevated atmospheric CO₂ and tropospheric O₃ on nutrient dynamics: decomposition of leaf litter in trembling aspen and paper birch communities. *Plant and Soil* 299:65-82.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York, New York, USA.
- Mendelsohn, I. A. 1979. Nitrogen metabolism in the height forms of *Spartina alterniflora* in North Carolina. *Ecology* 60:574-584.

- Mendelssohn, I. A., K. L. McKee, and W. H. Patrick. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* 214:439-441.
- Menge, B. A., C. A. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: Testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663-684.
- Mikola, J., R. D. Bardgett, and K. Hedlund. 2002. Biodiversity, ecosystem functioning and soil decomposer food webs. Pages 169-180 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning- Synthesis and perspectives*. Oxford University Press, Oxford.
- Mikola, J., and H. Setälä. 1998. No evidence of trophic cascades in an experimental microbial-based soil food web. *Ecology* 79:153-164.
- Miyashita, T., M. Takada, and A. Shimazaki. 2003. Experimental evidence that aboveground predators are sustained by underground detritivores. *Oikos* 103:31-36.
- Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. De Ruiter, Q. Dong, A. Hastings, N. C. Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni, and D. H. Wall. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7:584-600.

- Morse, D. H. 1997. Distribution, movement, and activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (araneae, lycosidae). *Journal of Arachnology* 25:1-10.
- Mulvaney, R. L. 1996. Nitrogen--Inorganic Forms. Pages 1183-1184 in J. M. Bigham, editor. *Methods of Soil Analysis*. Soil Science Society of America, Madison, Wisconsin.
- Newell, S. Y., L. K. Blum, R. E. Crawford, T. Dai, and M. Dionne. 2000. Autumnal biomass and potential productivity of salt marsh fungi from 29° to 43° North latitude along the United States Atlantic Coast. *Applied and Environmental Microbiology* 66:180-185.
- Newell, S. Y., R. D. Fallon, and J. D. Miller. 1989. Decomposition and microbial dynamics for standing, naturally positioned leaves of the salt-marsh grass *Spartina alterniflora*. *Marine Biology* 101:471-481.
- Newell, S. Y., and D. Porter. 2000. Microbial secondary production from salt marsh-grass shoots, and its known and potential fates. Pages 159-185 in M. P. Weinstein and D. A. Kreeger, editors. *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publishers, Boston.
- Norby, R. J., M. F. Cotrufo, P. Ineson, E. G. O'Neill, and J. G. Canadell. 2001. Elevated CO₂, litter chemistry, and decomposition: a synthesis. *Oecologia* 127:153-165.
- Norby, R. J., and C. M. Iversen. 2006. Nitrogen uptake, distribution, turnover, and efficiency of use in a CO₂-enriched sweetgum forest. *Ecology* 87:5-14.

- Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why are there so many species of herbivorous insects in tropical rainforests? *Science* 313:1115-1118.
- Nowak, R. S., D. S. Ellsworth, and S. S. Smith. 2004. Tansley review: Functional responses of plants to elevated atmospheric CO₂- do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist* 162:253-280.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation Ecosystems in Gradients of Primary Productivity. *American Naturalist* 118:240-261.
- Park, H. H., and J. H. Lee. 2006. Arthropod trophic relationships in a temperate rice ecosystem: A stable isotope analysis with delta C-13 and delta N-15. *Environmental Entomology* 35:684-693.
- Parsons, W. F. J., B. J. Kopper, and R. L. Lindroth. 2003. Altered growth and fine root chemistry of *Betula papyrifera* and *Acer saccharum* under elevated CO₂. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 33:842-846.
- Paterson, E. 1996. Effect of elevated atmospheric CO₂ concentration on C-partitioning and rhizosphere C-flow for three plant species. *Soil Biology and Biochemistry* 28:195-201.
- Peacor, S. D., and E. E. Werner. 2004. How dependent are species-pair interaction strengths on other species in the food web? *Ecology* 85:2754-2763.

- Pennings, S. C., E. R. Selig, L. T. Houser, and M. D. Bertness. 2003. Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* 84:1527-1538.
- Pennings, S. C., and B. R. Silliman. 2005. Linking biogeography and community ecology: Latitudinal variation in plant-herbivore interaction strength. *Ecology* 86:2310-2319.
- Pennings, S. C., E. L. Siska, and M. D. Bertness. 2001. Latitudinal differences in plant palatability in Atlantic coast salt marshes. *Ecology* 82:1344-1359.
- Pinay, G., P. Barbera, A. Carreras-Palou, N. Fromin, L. Sonie, M. M. Couteaux, J. Roy, L. Philippot, and R. Lensi. 2007. Impact of atmospheric CO₂ and plant life forms on soil microbial activities. *Soil Biology and Biochemistry* 39:33-42.
- Polis, G. A. 1991. Complex Trophic Interactions in Deserts an Empirical Critique of Food-Web Theory. *American Naturalist* 138:123-155.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86:3-15.
- Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Piñero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California islands. *Ecology* 79:490-502.
- Post, E. 2005. Large-scale spatial gradients in herbivore population dynamics. *Ecology* 86:2320-2328.

- Postma-Blaauw, M. B., J. Bloem, J. H. Faber, J. W. van Groenigen, R. G. M. de Goede, and L. Brussaard. 2006. Earthworm species composition affects the soil bacterial community and net nitrogen mineralization. *Pedobiologia* 50:243-256.
- Raffaelli, D. G. 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Marine Ecology-Progress Series* 311:285-294.
- Rasse, D. P., J.-H. Li, and B. Drake. 2003. Carbon dioxide assimilation by a wetland sedge canopy exposed to ambient and elevated CO₂ measurements and model analysis. *Functional Ecology* 17:222-230.
- Rasse, D. P., G. Peresta, and B. Drake. 2005. Seventeen years of elevated CO₂ exposure in a Chesapeake Bay wetland: sustained but contrasting responses of plant growth and CO₂ uptake. *Global Change Biology* 11:369-377.
- Roth, S., E. P. McDonald, and R. L. Lindroth. 1997. Atmospheric CO₂ and soil water availability: consequences for tree-insect interactions. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 27:1281-1290.
- Rouhier, H. 1996. Carbon fluxes in the rhizosphere of sweet chesnut (*Castanea sativa*) grown under two atmospheric CO₂ concentrations: ¹⁴C partitioning after pulse labelling. *Plant and Soil* 180:101-111.
- Rypstra, A. L., and S. D. Marshall. 2005. Augmentation of soil detritus affects the spider community and herbivory in a soybean agroecosystem. *Entomologia Experimentalis et Applicata* 116:149-157.

- Rypstra, A. L., J. M. Schmidt, B. D. Reif, J. DeVito, and M. H. Persons. 2007. Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos* 116:853-863.
- Salt, D. T., P. Fenwick, and J. B. Whittaker. 1996. Interspecific herbivore interactions in a high CO₂ environment: Root and shoot aphids feeding on Cardamine. *Oikos* 77:326-330.
- Scheu, S., and H. Setälä. 2002. Multitrophic interactions in decomposer food-webs. Pages 223-266 in T. Tschamntke and B. A. Hawkins, editors. *Multitrophic Level Interactions*.
- Scheu, S., A. Theenhaus, and T. H. Jones. 1999. Links between the detritivore and the herbivore system: effects of earthworms and Collembola on plant growth and aphid development. *Oecologia* 119:541-551.
- Schindler, D. E., B. M. Johnson, N. A. MacKay, N. Bouwes, and J. F. Kitchell. 1994. Crab:snail size structure interactions and salt marsh predation gradients. *Oecologia* 97:49-61.
- Schmitz, O. J. 2005. Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management. *Oecologia (Berlin)* 145:225-234.
- Setälä, H., J. Laakso, J. Mikola, and V. Huhta. 1998. Functional diversity of decomposer organisms in relation to primary production. *Applied Soil Ecology* 9:25-31.

- Settle, W. H., H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, A. S. Lestari, and Pajarningsih. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77:1975-1988.
- Shimazaki, A., and T. Miyashita. 2005. Variable dependence on detrital and grazing food webs by generalist predators: aerial insects and web spiders. *Ecography* 28:485-494.
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Science* 99:10500-10505.
- Silliman, B. R., and A. Bortolus. 2003. Underestimation of *Spartina* productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus. *Oikos* 101:549-554.
- Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelsohn. 2005. Drought, snails, and large-scale die-off of southern US salt marshes. *Science* 310:1803-1806.
- Siska, E. L., S. C. Pennings, T. L. Buck, and M. D. Hanisak. 2002. Latitudinal variation in palatability of salt-marsh plants: which traits are responsible? *Ecology* 83:3369-3381.
- Stachowicz, J. J., and M. E. Hay. 2000. Geographic variation in camouflage specialization by a decorator crab. *American Naturalist* 156:59-71.

- Stiling, P., and D. C. Moon. 2005. Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia* 142:413-420.
- Strain, B. R., and F. Bazzaz. 1983. Terrestrial plant communities. Pages 177-222 in E. R. Lemon, editor. *CO₂ and plants*, Boulder, CO.
- Thompson, R. M., M. Hemberg, B. M. Starzomski, and J. B. Shurin. 2007. Trophic levels and trophic tangles: The prevalence of omnivory in real food webs. *Ecology* 88:612-617.
- Tilman, D., J. M. H. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300-1302.
- Uetz, G. W. 1991. Habitat structure and spider foraging. Pages 325-348 in S. Bell, E. McCoy, and H. Mushinsky, editors. *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, New York, NY.
- Valiela, I., J. M. Teal, and N. Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnology and Oceanography* 21:245-252.
- Vázquez, D. P., and R. D. Stevens. 2004. The latitudinal gradient in niche breadth: Concepts and evidence. *The American Naturalist* 164:E1-19.
- Wall, D. H. 2004. *Sustaining biodiversity and ecosystem services in soil and sediments*. Island Press, Washington D.C.

- Wall, D. H. 2007. Global change tipping points: above- and below-ground biotic interactions in a low diversity ecosystem. *Philosophical transactions of the royal society B* 362:2291-2306.
- Wardle, D. A. 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. *Biological Review* 67:321-358.
- Wardle, D. A. 2002. *Communities and ecosystems: Linking the aboveground and belowground components*. Princeton University Press, Princeton, NJ.
- Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. Van Der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304:1629-1633.
- Wardle, D. A., K. I. Bonner, and G. M. Barker. 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. *Oikos* 89:11-23.
- Wardle, D. A., H. A. Verhoef, and M. Clarholm. 1998a. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. *Global Change Biology* 4:713-727.
- Wardle, D. A., H. A. Verhoef, and M. Clarholm. 1998b. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. *Global Change Biology* 4:713-727.
- Wardle, D. A., W. M. Williamson, G. W. Yeates, and K. I. Bonner. 2005. Trickle-down effects of aboveground trophic cascades on the soil food web. *Oikos* 111:348-358.

- Wensem, J. V., H. A. Verhoef, and N. M. Van Straalen. 1993. Litter degradation stage as a prime factor for isopod interaction with mineralization processes. *Soil Biology and Biochemistry* 25:1175-1183.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics* 34:273-309.
- Wise, D. H., D. M. Moldenhauer, and J. Halaj. 2006. Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications* 16:865-876.
- Wolters, V., W. L. Silver, D. E. Bignell, D. C. Coleman, P. Lavelle, W. H. Van Der Putten, P. C. De Ruiter, J. Rusek, D. H. Wall, D. A. Wardle, L. Brussaard, J. M. Dangerfield, V. K. Brown, K. E. Giller, D. U. Hooper, O. Sala, J. M. Tiedje, and J. A. Van Veen. 2000. Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: Implications for ecosystem functioning. *Bioscience* 50:1089-1098.
- Zimmer, M., S. C. Pennings, T. L. Buck, and T. H. Carefoot. 2002. Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. *Functional Ecology* 16:596-607.
- Zimmer, M., S. C. Pennings, T. L. Buck, and T. H. Carefoot. 2004. Salt marsh litter and detritivores: A closer look at redundancy. *Estuaries* 27:753-769.