

More Than Muck Munchers: Detritivores Impact Primary Producer Food Webs

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INTRODUCTION

There has been much interest in the role that biodiversity and trophic dynamics play in mediating productivity and decomposition rates of plants in terrestrial systems (Laakso and Setälä 1999, Polis 1999, Adams and Wall 2000, Chase 2003, Hooper et al. 2005). Although generalist predators consume both herbivores and detritivores in many systems, traditional trophic models focus on predators consuming herbivores that feed on plants (Halaj and Wise 2001, Silliman and Bertness 2002). Thus, very few studies have explicitly examined the complexity of food web interactions provided by including detritivore diversity in primary producer food webs (Hooper et al. 2000, Hättenschwiler et al. 2005). Because predatory spiders aggregate in habitats rich in leaf litter-detritus in salt marsh systems (Langellotto and Denno 2004, Hines et al. 2006), invertebrate detritivores that consume leaf litter have the potential to enhance predator populations by serving as a food resource for spiders, or to diminish predator populations by rapidly consuming leaf litter, the preferred spider habitat (Moore et al. 2004). Therefore, the role of detritivores in mediating predator-herbivore interactions is three-fold: 1) by mineralizing nutrients during decomposition detritivores can indirectly affect host plant quality (biomass, %N) (Seastedt 1984, Wensem et al. 1993), which is important for herbivore population growth and host plant selection (Hines et al. 2005), 2) by acting as ecosystem engineers and modifying detritus structure, detritivores can transform refuges for predators and prey (Jones et al. 1994, Finke and Denno 2002, Lavelle 2002), and 3) by serving as alternative prey detritivores can increase food web complexity and stability (Polis 1998, McCann 2000, Wardle et al. 2000). Notably, the composition of the detritivore community (relative proportion of vulnerable and unsusceptible prey, or voracious and weak consumers) and interactions between and among detritivore species (competitive, synergistic, null) will affect the relative impact of this trophic level on food-web dynamics. In the context of examining the influence of community interactions on wetland ecosystem function, I propose to investigate the influence of detritivore community composition on: 1) decomposition and primary production of *Spartina alterniflora* and, 2) the ability of predators to exert top-down control on primary production, decomposition, and herbivore population growth.

STUDY SYSTEM

The proposed work will be conducted using species collected from mid-Atlantic salt marshes dominated by large monospecific stands of the smooth cord grass *Spartina alterniflora* (Teal 1962). *S. alterniflora* productivity is sensitive to changes in resource availability (Boyer and Zedler 1998). Plant quality (biomass, structure, %N) changes across an elevation gradient due to differences in tidal inundation, soil porosity, and nitrogen availability (Valiela et al. 1976, Bradley and Morris 1991). Due to changes in plant productivity and tidal inundation across the elevation gradient there is also variation in the amount of nutrients and structure of provided by leaf litter detritus (Marinucci et al. 1983, Brewer et al. 1998, Denno et al. 2005).

Decomposition of standing dead *S. alterniflora* is initiated primarily by ascomycetes fungi such as *Phaeosphaeria spartinicola*, *Mycosphaerella* sp., and *Buergenerula spartinae* (Newell et al. 1989, Newell and Porter 2000). Macrofauna shredder/grazers also contribute to decomposition on mid-Atlantic marshes and can be categorized into two broad functional groups: 1) microbivores, such as collembolans (*Isotoma viridis*) (Witteveen and Joosse 1987)

and talitrid amphipods (*Uhlorchestia spartinophila*, *Orchestia grillus*) (Kneib et al. 1997, Graça et al. 2000), and 2) omnivores such as coffee bean snails *Melampus bidentatus*, isopods (*Philoscia vittata*), and periwinkle snails *Littoraria irrorata* (Newell and Porter 2000, Silliman and Bertness 2002). Microbivores suppress fungal populations growing on senescent *Spartina* leaves and have comparatively weaker direct effects on *Spartina* decomposition through grazing (Witteveen and Joosse 1987, Graça et al. 2000), whereas omnivores have strong direct grazing effect on senescent leaf litter in the presence or absence of fungal colonization (Newell and Porter 2000, Wardle 2002, Hättenschwiler et al. 2005). Preliminary feeding trials indicate that these 6 detritivores differ in both their voracity and vulnerability to predation by spiders.

The dominant arthropod herbivores in the salt marsh system are phloem-feeding planthoppers in the genus *Prokelisia* (Denno et al. 2005, Stiling and Moon 2005). *Prokelisia* planthoppers show positive numerical response to increases in the quality of their only host plant *Spartina alterniflora* (Hines et al. 2005, Hines et al. 2006). The hunting spider, *Pardosa littoralis*, is by far the numerically dominant predator on the salt marsh and it can reach densities as high as 600 individuals/m² (Denno et al. 2002, Denno et al. 2004). Wolf spiders in the genus *Pardosa* have been reported to consume amphipods, collembolans, and planthoppers in low intertidal habitats (Morse 1997). *Pardosa* wolf spiders aggregate in thatchy habitats where they show enhanced suppression of herbivore prey due to relaxation of cannibalism and intraguild predation (Finke and Denno 2002).

OBJECTIVES AND EXPERIMENTAL METHODS

Objective 1: To determine the influence of detritivore diversity on wetland ecosystem function.

Rationale: Relatively little is known about the consequences of biodiversity and species interactions in donor controlled detritivore food webs (Mikola et al. 2002, Moore et al. 2004) compared to primary producer food webs (Grime 1997, Finke and Denno 2005) (Hooper et al. 2005). Although decomposition and primary production are necessarily linked there has been little investigation into how changes in detritivore community composition will indirectly feed back to influence primary production via altered leaf litter mineralization (Wardle 2002).

Methods: To examine how changing detritivore community composition influences rates of decomposition and primary production, combinations of 6 dominant detritivores species (microbivores: *Orchestia grillus*, *Uhlorchestia spartinophila* and *Isotoma viridis*, and omnivores *Philoscia vittata*, *Melampus bidentatus*, and *Littoraria irrorata*) will be added to mesocosms containing 25g senescent *Spartina alterniflora* leaves and 5 live *S. alterniflora* culms grown in pots (23cm diameter x 15.5cm deep) enclosed by a clear plastic tube cages (21.5 cm diameter x 30 cm tall), capped with an organdy mesh top, and placed in large plastic wading pools filled with water. Each treatment combination will be replicated ten times and blocked by plastic wading pool. I will establish detritivore diversity treatments by initially establishing fixed detritivore community biomass while crossing 3 species richness treatments (1, 3, 6) with 3 functional group compositions (microbivores, omnivores, or mixed communities of both). After two months mesocosms will be broken down and treatment effects will be assess on leaf litter decomposition (mass loss, C:N), microbial biomass [ergosterol content (Newell 2001) and fumigation extraction *sensu* (Hines et al. 2006)) and plant productivity (aboveground and belowground biomass, C:N].

Analysis: Treatment affects will be assessed using MANOVA followed by ANOVAs for individual variables, followed by a-priori means comparisons. Data will be transformed as necessary to meet assumptions of normality and heterogeneity of variance before analysis. My

laboratory working group at the University of Maryland has had success conducting and analyzing this type of experimental design (Finke and Denno 2004, Finke and Denno 2005). I predict that detritivore communities that synergistically graze leaf litter and promote microbial decomposition will positively influence primary production. Furthermore, detritivore communities dominated by species that consume and limit microbial decomposition without directly grazing leaf litter will also limit plant primary production because nutrient resources will be retained in leaf litter rather than being mineralized for plant uptake.

Objective 2: To determine the influence of detritivore diversity on ability of predators to exert top-down control on decomposition, primary production, and herbivore abundance.

Rationale: Predators can have a broad range of indirect effects on rates of decomposition; previous studies have reported positive (Kajak 1995, Lawrence and Wise 2000), null (Hunter et al. 2003), and negative (Lawrence and Wise 2004) effects of predator removal on decomposition rates. Inconsistencies in the above studies may be due to indirect effects of relaxed predation on different detritivore functional groups (microbivores vs. omnivores) (Hedlund and Öhrn 2000, Mikola et al. 2002), or differences in vulnerability of detritivores to predation. Detritivores that serve as alternative prey for predators may relax predation pressure on herbivores and indirectly alter primary production via top-down (herbivore pressure) or bottom-up (litter mineralization) pathways. Previous studies have examined effects of changing density of single detritivore populations, but very few studies have examined how diversity of the detritivore community can mediate predator-herbivore interactions as well as primary production and decomposition.

Methods: To examine the effect of detritivore community composition on the ability of predators to exert top-down control on the rate of decomposition, the above experiment (objective 1) will be crossed with predators (5 *Pardosa* wolf spiders present, or absent) and herbivores (30 *Prokelisia* herbivores present, or absent). Direct and interactive treatment effects on decomposition and primary production (see objective 1 for methods) as well as survival of herbivores and predators will be assessed after two months.

Analysis: Analysis will be consistent with objective 1, additionally treatment effects on predator and herbivore survival will be assessed. I predict that predators will influence rates of decomposition relatively more when detritivore communities are composed of species that are vulnerable to predation (amphipods, collembolans). Predation will increase decomposition in communities dominated by microbivores, but decrease decomposition in communities dominated by omnivorous detritivores. Reciprocally, vulnerable detritivores will decrease predation on herbivores by serving as alternative prey, while unsusceptible detritivores will alter predator-herbivore interactions by modifying the structure of leaf litter habitat.

SIGNIFICANCE AND FUTURE DIRECTIONS

Little is known about competition, resource partitioning, and/or synergistic effects between salt marsh detritivores, or their community level impact on wetland function. Therefore, this proposed research will provide information for conservation of salt marsh biodiversity and restoration of salt marsh food web interactions. The proposed studies will improve upon traditional conservation and restoration efforts which have focused on monitoring biodiversity rather than a specific assessment of the strength and influence of species interactions. Funding from the Garden Club of America will contribute to a broader understanding of salt marsh food web interactions, and support my career goal of being a field

ecologist who focuses on excellence in education, research and outreach (see attached CV) while focusing on community ecology and ecosystem processes of coastal wetland systems.

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