

BIOTIC AND ABIOTIC FACTORS INFLUENCING STREAM ECOSYSTEM
FUNCTIONING: TWO EXPERIMENTAL CASE STUDIES

THESIS

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by

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CHAPTER I

EFFECTS OF NATIVE AND INTRODUCED SPECIES ON STREAM ECOSYSTEM FUNCTION

INTRODUCTION

Ecosystem function is linked to community composition and the functional roles of the taxa in the community (Tilman et al. 1997). Native consumers can affect or maintain ecosystem functions such as production, nutrient cycling, decomposition and community metabolism, by mediating the processes which influence these functions. This may occur via trophic interactions such as top-down effects on primary production (eg. Wiegert and Owen 1971, Power 1992), decomposition (Webster and Benfield 1986) and consumer-driven nutrient recycling (Vanni et al. 1997). Organisms may maintain ecosystem functioning processes by the non-trophic modification of abiotic ecosystem properties as well. These organisms, termed ecosystem engineers, create habitat and alter the abiotic drivers of ecosystem processes, such as temperature, salinity, pH, turbidity and sediment movement; altering the availability of resources to other organisms within the community (Jones et al. 1994, Gutierrez and Jones 2006). Sediment movement by crayfish for example, decreases primary productivity and alters invertebrate abundances (Statzner et al. 2003). Alteration of a system's abiotic properties alters the resources by which community members influence ecosystem function.

While native consumers may maintain ecosystem function, the presence of invasive ecosystem engineers may alter ecosystem function properties via the same mechanisms (Crooks 2002). The modifications made to abiotic resources by invasive ecosystem engineers alter the availability of these resources to native organisms, provoking changes in resource utilization and ecosystem function (Parker et al. 1999). The density at which biological invaders often establish themselves within systems can dilute the effects of native organisms performing similar abiotic alterations as well (Crooks 2002). For instance, introduced populations of common carp populate ecosystems in such high densities that they fundamentally alter the habitats to which they are introduced, by increasing chl *a* concentrations, turbidity and decreasing macrophyte biomass. These modifications increase in magnitude with increases in carp biomass (Chumchal et al. 2005).

Many studies have investigated the mechanisms and influence of native and non-native ecosystem engineers on resource availability within systems (see reviews in Crooks 2002, Moore 2006, Wright and Jones 2006, Hastings et al. 2007). While there have been several comparison studies of the effects of native and invasive ecosystem engineers (e.g. Posey 1988, Hahn 2003, Brusati and Grosholz 2006), few studies have investigated both the individual and interactive effect of native and invasive ecosystem engineers (but see Berkenbusch and Rowden 2007 and Statzner et al. 2008). It is likely that when native and invasive ecosystem engineers coexist within systems the influence and intensity by which each alters the abiotic environment may be altered (Jones et al. 1997). However, it remains unclear how these interactions alter or change the effect of each consumer on environmental conditions.

Riverine ecosystems are particularly susceptible to the dispersal and establishment of introduced species, due to human perturbations and the inherent interconnectivity of river systems (Lodge et al. 1998). This makes them important systems for the study of the individual and interactive effects of native and invasive consumers on ecosystem function. Spring fed river systems are unique in that they have high occurrences of endemism and taxa with geographical limitations (Erman and Erman 1995). These systems are especially susceptible to invasion, due to their high hydrological predictability and low physiochemical variability (Moyle and Light 1996). These characteristics provide a relatively benign environment for the establishment of invasive species.

In a spring dominated system such as the headwaters of the San Marcos River (Hayes Co., Texas, USA), the invasive population of suckermouth armored catfish (*Hypostomus* sp., Loricariidae; hereafter referred to as catfish or armored catfish) is of particular concern. Loricariid catfishes are efficient algavores (Power et al. 1989), which leads to overgrazing of periphyton standing stock (Power 1984b). This invasive consumer has the potential to interact with native taxa which may serve as ecosystem engineers, such as large bodied crustaceans. One of these potential native ecosystem engineers is the big claw river shrimp (*Macrobrachium carcinus* Decapoda: Palaemonidae; hereafter referred to as shrimp), the largest species of freshwater shrimp in North America (Bowles et al. 2000). The big claw river shrimp is omnivorous, but known to be an aggressive predator (Covich et al. 1996). We suspected these shrimp due to its morphological and behavioral similarities to crayfish. This species of river shrimp has been reported to eat small fish, decomposing leaf litter, algae, mollusks, other shrimp and

macrophytes (Covich and McDowell 1996), and is considered the top predator in some tropical streams (Covich et al. 1996).

Here, I present the results of a replicated stream experiment in which I investigated the individual and interactive effects of the presence of shrimp and catfish on ecosystem function and invertebrate community composition. I used the San Marcos River as my model system. I hypothesize that native and non-native consumers differently influence ecosystem processes and benthic community assemblages via biotic and abiotic interactions. I used the native big claw river shrimp and the invasive armored catfish as my model species (Figure 1.1a-d). I predicted that (a) in the absence of shrimp and catfish periphyton standing stocks will be high and organic matter decomposition will be relatively low. Periphyton will be the dominant food source of macroinvertebrate scrapers, while shredders and collectors will predominantly rely on leaf litter as a food source. Due to the lack of large, mobile organisms, benthic sediment movement will be low (Figure 1.1a). (b) In the presence of omnivorous shrimp, organic matter decomposition will be enhanced and periphyton standing stocks will be enhanced due to sediment removal via shrimp foraging activities. Invertebrate communities will be negatively impacted by the presence of shrimp. Downstream transport of benthic sediments will also be higher in the presence of shrimp due to its large size and foraging activities (Figure 1.1b). (c) The presence of invasive catfish will directly reduce periphyton standing stocks, thereby indirectly negatively affecting invertebrate scraper and collector communities. Downstream sediment movement will also be increased due to their foraging activities (Figure 1.1c). (d) When both shrimp and catfish are present their large body size will lead to interference competition, thereby decreasing the direct

and indirect impacts of both species on invertebrate communities. However, downstream sediment movement should be highest when both species are present (Figure 1.1d).

MATERIALS AND METHODS

Description of the study system and species

The San Marcos River is characterized by clear water, abundant macrophytes, and exhibits little seasonal variation in temperature, flow and water quality (Groeger et al. 1997). Like many spring fed river systems in the western US, the San Marcos River is habitat for many endemic and endangered species (USFWS 1996, Bowles et al. 2000). One of these species is the big claw river shrimp. This species of shrimp is currently designated with a “high priority” status for conservation by the Comprehensive Wildlife Conservation Strategy. Populations of this shrimp have been extirpated from much of their historic range and remaining populations are undergoing a decline, because of over harvesting, habitat degradation and competition with non-indigenous species (Bowles et al. 2000). Armored catfish were introduced to central Texas rivers in the 1960’s. Originally imported from their native South America, as aquarium fishes, they have successfully established themselves in North American freshwaters, due to escapes and releases (Nico and Martin 2001).

Experimental Design and Stream Channel Description

I investigated the individual and interactive effects of the native shrimp and invasive catfish on ecosystem processes and benthic invertebrate communities in a replicated stream channel experiment which consisted of a 2×2 factorial design in which the presence and absence of shrimp was cross-classified with the presence and absence of

armored catfish. Shrimp presence treatments consisted of one shrimp and catfish presence treatments consisted of two individual catfish. Due to the low densities of shrimp in the upper San Marcos River, I limited the number of replicates of each treatment to four. Shrimp and catfish used in the experiment were collected from the upper San Marcos River by hand capture or nets. Shrimp and catfish were added to experimental stream channels after a three week period to allow stream channels systems to equilibrate after the addition of periphyton and macroinvertebrates (see below). Shrimp lengths (tip of rostrum to tail) ranged from 19.5 - 25.0 cm ($\bar{x} (\pm 1 \text{ SE}) = 20.9 (\pm 1.9) \text{ cm}$), with wet mass ranging from 126.0 - 299.0 g ($184.9 (\pm 57.8) \text{ g}$). Catfish total lengths ranged from 23.0 cm to 33.0 cm, ($28.2 (\pm 3.6) \text{ cm}$). Wet mass for catfish ranged from 130.0 g to 382.0 g and ($250.1 (\pm 90.9) \text{ g}$). Due to the conservation status of the big claw river shrimp, all individuals used in the experiment were released back into the San Marcos River at the end of the experiment, with the exception of one shrimp from one of the shrimp only treatments, which died on day 15 of the experiment. I chose not to replace this individual because of the threatened status of the shrimp and instead, removed all data concerning that replicate from analysis. The experiment was conducted for 28 days after the addition of shrimp and catfish.

Artificial stream channels were created by modifying eight existing concrete raceways located in a covered outdoor facility at the Freeman Aquatic Biology Building on the Texas State University-San Marcos campus (San Marcos, Texas, U.S.A.). In order to create the stream channels, the original eight raceways were divided in half with a PVC frame and fully lined (sides and bottom) with 6-mil black polyethylene, creating 16 separate channels. The PVC frame and plastic lining ensured that there was no exchange

of water between the stream channels. Each original raceway had a single valve that discharged water into it; in order to ensure equal flow from the single valve to each of the two stream channels within each raceway, we created a single PVC and plastic reservoir that discharged equal amounts of water over a small spillway into each stream channel. Channel dimensions were $3.9 \times 0.3 \times 0.3$ m (length \times width \times depth). All channels were fenced off on each end, as well as over the top of the channel, with 3 cm aperture mesh to prevent escape of shrimp or catfish. Forty watt full spectrum florescent lights were hung 68 cm above each stream channel, in an orientation parallel to flow. Lights were kept on a 16/8 h light/dark cycle via timers throughout the experiment. Mean light intensity just above the water surface, below stream channel protective coverings was $21.9 \pm 0.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the upstream section of the channel, $19.5 \pm 0.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the downstream section of the channel, and $20.7 \pm 0.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the entire stream channel. Each stream channel bottom was covered with 9.5 L of sand, 5.8 L of cobble (for 50% cover of the benthos) and 1 L of gravel, in comparable proportions to the upper San Marcos River. Water feeding stream channels came from an outdoor artesian well fed from the Edwards Aquifer, providing the water to stream channels with the same water chemistry properties to that of the upper San Marcos River. One cinderblock was added to all stream channels as a refuge site for shrimp and catfish; cinderblocks were typically occupied during daytime because both species are more active during night (S. Scott, pers. obs.). Additionally, stream channels were checked at least once daily to note the location and status of each of catfish and/or shrimp.

Prior to the start of the experiment, periphyton from the San Marcos River was collected by scrubbing rocks with a brush with soft nylon bristles into a bucket of river

water and creating periphyton slurry. Equal 550 – 700 ml aliquots of this periphyton slurry were added to each stream channel four times over a three week period prior to the initiation of the experiment. The rocks used to obtain periphyton were also added to stream channels in equal densities as well, to promote periphyton growth.

Before the initiation of the experiment and the addition of shrimp and catfish, macroinvertebrates placed into stream channels were collected using a kick net from the upper San Marcos River; collected macroinvertebrates were placed into a bucket of river water. Bucket contents were then divided into nineteen 550 ml volume subsamples and one subsample was added to each of the 16 stream channels; the three remaining samples were kept to determine baseline densities of taxon added to the stream channels. Because the source water was from the underground aquifer (containing very few invertebrates) and macroinvertebrates were allowed to ‘drift’ out of stream channels, the addition of river macroinvertebrates using the above procedure was repeated on a weekly (every 7 d) basis to simulate incoming drift of macroinvertebrates.

Big claw river shrimp are considered an omnivorous species, ingesting invertebrates and periphyton (Covich and McDowell 1996). The shrimp in the San Marcos River occupy a fairly high trophic position (predators in trophic level ~ 4; Cohen et al., *in prep*) and the shrimp in the river have been observed eating live and dead fish (S. Scott, *pers. obs.*). Thus, to ensure that the shrimp in our stream channels occupied a similar trophic role as in the San Marcos River, we added one small dead fish (*Lepomis* sp. 70-120 mm total length) to each stream channel once a week, as a potential food source. Fish were added to all 16 stream channels each week, to prevent differences associated with the fish from arising between shrimp present and shrimp absent

treatments. Fish were collected from the San Marcos River with seines or cast nets, immediately pithed, submerged and weighted down within the stream channel so as to allow shrimp access to them. Remaining fish material was removed from each stream channel after a 24-h period and weighed (wet mass) and measured to determine the amount of fish consumed. Fish in channels containing shrimp were entirely consumed in all but four instances; each instance involved a separate shrimp. On two of these occurrences all but 5.0 g of the fish was consumed, and on two feeding dates one shrimp did not consume its fish.

Ecosystem-level Responses

In order to assess ecosystem-level responses to the presence and absence of shrimp and catfish, I quantified several response variables, including periphyton standing stock, organic matter decomposition and sediment and organic matter transport and accumulation. All ecosystem-level response variables were measured twice after the initiation of the experiment on days 14 and 28.

To quantify treatment effects on periphyton standing stock, ($\text{Chl } a \cdot \text{m}^{-2}$) four unglazed ceramic tiles ($16.2 \text{ cm} \times 16.2 \text{ cm}$) were placed at the downstream section of each stream channel. Two tiles were open to grazing and two were enclosed within a wire cage with 2-cm aperture mesh. All tiles were allowed to grow periphyton for three weeks prior to the experiment. One grazed, and one caged tile was pulled from each stream channel on each sampling date. Upon being pulled from the stream channel, tiles were cleaned with a nylon-bristled brush and rinsed with Milli-Q water into acid-washed high-density polyethylene (HDPE) cups. A portion of this slurry was filtered onto a Pall A/E

filter and filters were frozen at -4°C . Chl *a* was extracted from these filters using 99% HPLC grade acetone for 4 h in the dark and measured on a Turner TrilogyTM Lab Fluorometer (Turner Designs Inc. Sunnyvale California). The remaining slurry was used to estimate organic and inorganic matter on tiles by filtration onto pre-ashed and pre-weighed Pall A/E filters. Concentration of organic and inorganic matter on tiles ($\text{mg}\cdot\text{m}^{-2}$) was determined by determining filter dry mass after drying at 60°C for 48 h and after ignition at 500°C for 4 h.

To quantify treatment effects on the decomposition of organic matter, I measured leaf litter breakdown rates. Four leaf packs, each containing ten leaves of Texas Oak (*Quercus texana*), a common riparian tree species in Central Texas, were placed in each stream channel. Two leaf packs were enclosed within bags consisting of 3-cm aperture plastic mesh, and two were left open, with the petioles tied together with monofilament fishing line. All leaf packs were weighted to ensure submersion. One bagged and one open leaf pack were pulled on each sampling date. Coarse particulate organic matter (CPOM, $>1\text{ mm}$) was gently washed from leaves with DI water and dried for 48 h at 60°C and weighed to obtain dry mass. Leaf packs were dried at 60°C for 48 h and weighed.

To assess the downstream movement and accumulation of sediments in stream channels, sediment traps were placed mid-channel, and allowed to accumulate sediments (Statzner and Peltret 2006). Sediment traps consisted of $12.7 \times 12.7\text{ cm}$ shallow plastic trays and 2 sediment traps were placed mid channel 2.3 m from the down stream end of the channel. One sediment trap was pulled from each stream channel on each sampling date. Each sediment trap was washed with DI water into an aluminum weigh boat and allowed to dry at 60°C for at least 48 hours, to a constant dry mass. Dry mass of samples

within each sediment trap was measured. Samples were then homogenized, ashed at 500° C for 4 hours, and percent organic matter (% OM) was determined by difference in the two measurements.

Community-level Responses

To investigate effects of shrimp and catfish at the community level, I examined invertebrate communities in stream channels. Invertebrate densities and composition in leaf packs and in the benthos of the stream channels were examined. When open leaf packs were removed on each sampling date (see above), all invertebrates were removed via rinsing with DI water and picking with forceps and preserved in 95% EtOH. To assess the influence of shrimp and catfish on benthic invertebrate communities, basket samplers were placed within the substrate 20 cm from the end of the stream channel and randomly selected for sampling. Basket samplers were constructed with 15.2 cm diameter, 3.8 cm depth plastic baskets. Baskets were filled with cobble and gravel substrate and buried in the substrate with the upper lip of the basket was flush with the stream channel substrate. The entire contents of each basket sampler were preserved in 95% EtOH. Invertebrates from leaf packs and benthic basket samplers were identified to the family level in the lab (Merritt et al. 2007).

Data Analysis

For ecosystem-level response variables where time may be a factor (organic matter decomposition and sediment and organic matter transport and accumulation), I performed a two-way analysis of covariance (ANCOVA) comparisons between

treatments, using sampling date as the covariate. To analyze all other ecosystem-response level variables (periphyton standing stock), means of each variable were taken across both sampling dates and analyzed via two-way analysis of variance (ANOVA) with cross classified factors.

All community-level response variables (open leaf packs and basket samplers) were analyzed for total abundance, taxa abundance, taxa richness, functional feeding group abundance and functional feeding group richness. Means were taken across both sampling dates for each response variable and analyzed using ANOVAs.

Due the loss of two replicates, resulting in a different number of replicates per treatment, Type III sums of squares were used. Data not meeting assumptions of normality and homoscedasticity were log transformed prior to analysis. All data were analyzed with SPSS15.0 for Windows (SPSS[®] Inc.).

RESULTS

Ecosystem-level Response

Chl *a* concentration on the ceramic tiles was significantly reduced in treatments containing armored catfish (Fig. 1.2a; Table 1.1), with the greatest reduction in concentration occurring in catfish treatments, followed by the shrimp and catfish treatments, and a non-significant decrease in chl *a* concentration, relative to the control in the shrimp treatments. Catfish treatments averaged an 82% reduction in concentration from controls, shrimp treatments averaged a 27% reduction and S+C treatments averaged a 67% reduction. Biomass for organic matter and inorganic matter ($\text{mg}\cdot\text{m}^{-2}$) on periphyton standing stock followed the same general trend (Fig. 1.2b, c). Periphyton

standing stock in all three different treatments was significantly lower than that in the control.

Open leaf packs showed a trend of increased organic matter decomposition for all treatments containing armored catfish (Fig. 1.3a, see Table 1.2). Mean percent leaf mass remaining on day 28 for open leaf packs was 60.5% for catfish, 66.1% for shrimp, 54.3% for the combined catfish and shrimp, and 65.2% for the control. Leaf breakdown rates for leaf packs enclosed in mesh bags show no significant difference between treatments for either day 14 or day 28. CPOM accumulation on open leaf packs showed little difference between treatments, but with a significant difference over time as all treatments increased in the mass of CPOM accumulated (Fig. 1.3b). Leaf packs enclosed in mesh showed a similar trend, with no significant difference between treatments, but a significant increase in CPOM over time (Table 1.2).

The presence of armored catfish significantly increased the amount of sediment accumulation (Table 1.1), with treatments containing armored catfish accumulating at least two times as much sediment as control and shrimp treatments (Fig. 1.4a). Rates of organic matter deposition remained constant for the control and shrimp treatment, but significantly increased over time in all treatments containing catfish (Fig. 1.4b). The increased quantities of matter in sediment traps of catfish treatments were not entirely due to organic matter deposition. Mass of inorganic matter in traps was significantly higher in treatments containing catfish. By day 28, catfish had moved approximately 3 times more inorganic sediment into sediment traps than shrimp, and 5.8 times as much inorganic sediment than accumulated in the control (Fig. 1.3c).

Community-level response

Mean total abundance of invertebrates added to stream channels were (145.73 ± 31.88) ind/channel, and mean taxa richness added to each channel was $8.6 (\pm 0.47)$ taxon/channel. Dominant taxa included amphipoda, coleoptera, diptera, ephemeroptera and gastropoda. Less abundant taxa added to stream channels included ostrocooda, lepidoptera, hemiptera and bivalves, all with mean abundances of less than 1 ind/channel addition. Shredders were the dominant functional feeding group constituting 37.39% of the individuals added to stream channels. Collector gatherers made up 32.6 % of the added population. Scraper and predator densities amounted to 17.42 % and 12.04 % of the added population respectively.

Dominant taxa in both open and mesh leaf packs consisted of amphipoda, gastropoda, ostracoda, ephemeroptera and trichoptera. There was no significant treatment effect on taxa richness or taxa abundance (Table 1.2). Catfish treatments elicited a significant community response in collector gatherer abundance in open leaf packs. Mean abundance of collector gatherers were significantly lower in treatments containing catfish ($F_{1,10} = 9.061$, $P = 0.013$, Fig. 1.5a). There was no significant influence of treatments on other functional feeding groups present. However, there was an interaction effect between shrimp and catfish which reduced taxa richness of scrapers in the presence of both shrimp and catfish ($F_{1,10} = 6.353$, $P = 0.030$).

In general, there were low densities of invertebrates in basket samplers. Dominant taxa were chironomidae, amphipoda and ostrocooda (Table 1.3). There was a significant interaction effect between shrimp and catfish for abundances of ostrocooda, but no significant main effects (Table 1.3). All treatment abundances of ostrocooda were

significantly lower than the control. Treatment effects for all other taxa abundance were non-significant, as was taxa richness. When all treatments were pooled, average abundance per basket was 4.786 ± 0.820 . There were no significant differences between treatments in abundance or richness within functional feeding groups (Table 1.3, Fig. 1.5b).

DISCUSSION

The presence of the invasive armored suckermouth catfish had an effect on multiple ecosystem processes. Armored catfish significantly reduced the periphyton standing stock and facilitated decomposition, altering energy and carbon pathways in stream channels. These changes provoked a community response by reducing abundances of macroinvertebrate collector gatherers in leaf packs. Presence of armored catfish produced ecosystem engineering effects as well, by nearly tripling the amount of sediment moving downstream. In contrast, the presence of the native shrimp produced minimal changes in ecosystem function; only affecting periphyton organic matter and inorganic matter on tiles.

Ecosystem-level Response

One of the major findings of this experiment was the interactive effect of shrimp and catfish on the biomass of periphyton organic matter and inorganic matter on tiles in our stream channels. While both the presence of each consumer had effect on biomass of these parameters, these affects were altered when both species occurred together. Consumption of periphyton by catfish was significant, though lessened in treatments containing catfish and shrimp. During the course of the experiment, I observed

antagonistic interactions toward catfish by shrimp. The interaction between shrimp and catfish decreasing catfish reduction of periphyton on tiles suggests that the presence of shrimp ameliorates some grazing pressure by catfish, possibly through interference competition. It is unknown if this was competition for space or periphyton as a resource, as we did not test for consumption of periphyton, merely biomass differences between treatments.

The effects of shrimp and catfish on decomposition did not follow my predictions (Fig. 1.1). In this experiment, treatments containing catfish had the highest rates of decomposition. There are several possible mechanisms for increased leaf litter decomposition by catfish. One potential mechanism for the unexpected increase in decomposition rate in treatments containing catfish is grazing by catfish on leaf litter biofilm. Biofilm will grow on leaf litter during decomposition process (Webster and Benfield 1986) and the grazing of this biofilm can facilitate the fragmentation of detritus. However, increased decomposition could also be attributed to incidental contact by catfish while foraging.

In contrast to catfish effects on decomposition, shrimp did not influence the decomposition of leaf litter. It is widely thought that these shrimp are omnivores that consume some detritus (Covich and McDowell 1996), but a lack of effect of shrimp on leaf litter in the current experiment could be a result of the subsidies of fish we added to the stream channels. Although shrimp have been observed to consume leaf litter (Covich and McDowell 1996), fish are presumably a higher quality and potentially a preferred food source. Fish were added to the diets of shrimp only once per week, and this subsidy seems to have been a sufficient quantity to reduce the utilization of leaf detritus by

shrimp in stream channels. In tropical streams, the big claw river shrimp is often considered a top predator (Covich et al. 1996), and aggressive interactions of shrimp with other decapod detritivores can reduce decomposition of leaf litter in streams (March et al. 2001). This kind of interaction did not occur in this study, where the mean mass of leaf litter remaining for treatments containing both shrimp and catfish, though non-significant, was lower than all other treatments.

As active, benthic foragers, I predicted both shrimp and catfish would increase sediment movement due to direct contact with the benthic substrate (Fig. 1.1b-d). However, only armored catfish increased sediment movement, producing ecosystem engineering effects. Ecosystem engineering via sediment movement, known as bioturbation, by aquatic organisms affects multiple aspects of ecosystem functioning and biodiversity. Bioturbation alters habitat heterogeneity (Flecker 1992) eliciting either positive or negative effects on the distribution and abundance of resources. Statzner et al. (2003) found that bioturbation by crayfish decreased biofilms, decreasing grazer abundance, while Flecker (1996) found that the exclusion of a benthic detritivore increased the accrual of sediments, and increased both algal biomass and invertebrate densities.

Armored catfishes increase the sediment load in streams through several likely mechanisms. They resuspend benthic sediment via foraging activities (Power 1990), thereby increasing turbidity (Hoover et al. 2004). Catfish also burrow in to clay banks to build nests (Burgess 1989, Power 2003), releasing sediments into the stream system. This may cause an increase in turbidity in riverine systems. Increased turbidity as a result of particle suspension can potentially reduce the food value and abundance of periphyton

via light reduction (Cline et al. 1982, Van Nieuwenhuysen and LaPierriere 1986, Graham 1990). It may also impair filter feeding by macroinvertebrates (Aldridge et al. 1987), and increase macroinvertebrate drift downstream to more suitable habitat (Culp et al. 1986). However, the removal of sediment from periphyton beds has been shown to have positive effects as well. Grazing by the Loricariid armored catfish, *Ancistrus spinosus*, in tropical streams has been shown to increase primary productivity in periphyton due to the removal of sediment from the substrate (Power 1990). Periphyton net primary productivity is lower when covered in sediment relative to periphyton free of sediment. Grazing activity of *A. spinosus* clears areas of sediment, facilitating periphyton growth (Power 1990).

Community-level Response

Presence of catfish yielded a community response by decreasing abundances of collector-gatherers in leaf packs in our stream channels. Few studies have investigated the effects of grazing fish on invertebrate community composition. Flecker (1992) found that grazing tropical fishes reduced abundances of ephemeropterans (Baetis, Tricorythodes and Leptohyphidae), all collector gatherers, as well as chironomidae larvae. Rosemond et al. (1998) also found that presence of macroconsumers (including shrimp and fish) in a tropical stream decreased collector-gatherer abundance on leaf packs, but were unable to separate the individual impacts of macroconsumer species.

I predicted that the presence of shrimp would negatively alter invertebrate community structure (Fig. 1.1b), but did not find this pattern in this experiment. In contrast to my results, several studies have shown that the presence of freshwater

crustaceans can alter invertebrate assemblages, leading to an increase in densities of mobile grazers such as ephemeroptera, and a decrease in the more sessile invertebrates, such as chironomids (Pringle et al. 1993, March et al. 2001, 2002). Moulton et al. (2004) found an increase in benthic ephemeropteran densities in *Macrobrachium olfersi* inhabited areas during the day, when *Macrobrachium* foraging activity was reduced, and a subsequent decrease at night, when *Macrobrachium* shrimps are more active. The stream channels gave macroinvertebrates the opportunity to drift out of the system but all drift into the system was artificial, through weekly inputs. However, if shrimp were influencing drift out of the system, it would be expected that there would be higher densities of ephemeropterans in all treatments excluding shrimp, and this was not the case.

Implications

The role of shrimp in ecosystem functioning in stream channels was minimal. Densities of shrimp in stream channels were far higher than natural densities in the San Marcos River (*S. Scott pers. obs.*, ongoing snorkel surveys). It can be assumed that the maximum effect by shrimp was observed in this study. Historically however, densities in the San Marcos River were much higher, to the extent that populations were commercially harvested (Bowles et al. 2000). Most studies involving shrimp have been conducted in tropical streams, where shrimp are often present in high densities (Covich 1988), and it is unknown whether there is a behavioral or ecological difference between tropical populations of shrimp and those that live in temperate streams. For instance, shrimp are considered top predators in many tropical streams (Covich et al. 1996). This

experiment did not include an assessment of the role of shrimp as predators, so the extent of the role shrimp might play in this regard cannot be ascertained.

Armored catfish were the major producers of ecosystem effects in this experiment. Experimental densities in our stream channels ($0.585/\text{m}^2$) were comparable to natural densities in the San Marcos River ($0.516 \pm 0.050/\text{m}^2$) (*S. Scott pers. obs.*, ongoing snorkel surveys). As invasive species, armored catfish have only been residents in the San Marcos River for approximately than 50 years (Nico and Martin 2001). There are a number of possible reasons why armored catfishes have successfully established themselves in the San Marcos River. (i) Constant flows and temperatures provide a relatively benign habitat, with little mortality due to stochastic events. (ii) There is little evidence that armored catfishes have any natural predators in the San Marcos River. It is possible that catfish fall subject to predation from wading birds, as they do in South American rivers (Power 1984a, Power et al. 1989), but again, there is little evidence for this, and it is questionable that avian predation would impact the current population much. (iii) It is very likely that armored catfishes face little in the way of competition. The San Marcos River has few native large bodied grazers, so armored catfishes are effectively filling a niche that did not previously exist to the extent that it does with the current population of armored catfishes. The degree to which armored catfishes consume basal resources and the hypothesized lack of predation on armored catfish may place them at a trophic dead end, severely altering natural trophic flows in the river.

Although observed interference by shrimp on catfish grazing effect is encouraging, populations of catfish far outnumber shrimp. Armored catfishes now represent approximately 50% of the upper San Marcos River ichthyomass, and range

from 20-450 cm in total body length (T. Bonner, Texas State University-San Marcos, Dept. of Biology, unpubl data. 2005). Shrimp populations in the upper reaches of the San Marcos River, where most observations have been made, number less than a dozen (*S. Scott, pers. obs.*, ongoing snorkel surveys). Clear water systems such as the San Marcos River are reliant on primary productivity as a source of carbon and nutrients, and significant reductions in this energy source could severely impair biological processes. As a stable, spring-fed system, the San Marcos River is highly susceptible to the long term impacts of the disturbance created by the ecosystem engineering effects of armored catfish as well. The manner by which ecosystem engineers impact their environment is a function of behavior, body size, and population density. Larger organisms and organisms at high densities will have a more substantial impact than the converse. In aquatic systems, this is mediated by the stability of the system. In streams dominated by frequent floods, ecosystem engineering effects of animals are greatly reduced and abiotic alterations are ephemeral (Moore 2006). In a relatively consistent system, such as the San Marcos River, high densities of catfish, coupled with their large body sizes, could result in large cumulative ecosystem engineering effects.

Invasive armored catfishes negatively affected periphyton biomass, reduced collector gatherer abundances and exhibited ecosystem engineering effects by increasing sediment movement in this experiment. However, the role of additional environmental variables still need to be teased out concerning the roles and interactions of shrimp and catfish, and more generally, the individual and interactive effects of native and invasive species. We chose not to perform these experiments with the remaining community of the San Marcos River, omitting the presence of other fish species and larger

macroinvertebrates, such as crayfish, in order to tease apart the specific contributions of our model species to ecosystem functioning. This prevented direct investigation of ecosystem and community effects of taxa extirpation and species invasion on my model system. However more inclusive mesocosm experiments should be the next step in determining the influence of these species within the context of the entire river community.

Invasive species introductions pose a serious threat to freshwater ecosystems and are a major concern for freshwater conservation and management (Naiman et al. 1995, Mooney and Hobbs 2000). Invasive species frequently result in losses to biodiversity, loss of ecosystem function, and extinction of native taxa (Gurevitch and Padilla 2004, Clavero and García-Berthou 2005). The high densities at which invaders may populate new ecosystems have the potential to alter the effects of native organisms performing similar alterations (Crooks 2002). Globally, there are currently few systems that are not composed of both native and invasive species (Didham et al. 2005). While it is important to determine the individual effects each has on ecosystem functioning and community structure, we must also investigate their interactive effects, as these interactions may mitigate or alter individual effects.

Table 1.1: Summary of *F*-values from ANOVA (Type III sums of squares) for Chl *a* on tiles, inorganic matter on tiles (IM) and organic matter on tiles (OM). Lower panel contains *F* values from ANCOVAs for sediment accumulation data, including total sediment accumulated in traps (total), inorganic matter accumulated in traps (mg), and the rate of inorganic matter accumulation ($\text{mg}\cdot\text{day}^{-1}$). * $P < 0.05$.

Treatment	d.f.	Tiles - Open			Tiles – Closed
		Chl <i>a</i>	IM	OM	Chl <i>a</i>
Shrimp (S)	1	1.482	14.04*	10.616*	3.144
Catfish (C)	1	27.582*	24.864*	24.669*	1.863
S×C	1	5.003*	19.773*	15.675*	0.620
Error	10				

Sediment Accumulation				
	d.f.	Total (mg)	IM (mg)	OM ($\text{mg}\cdot\text{day}^{-1}$)
Time	1	22.034*	10.277*	3.254
Shrimp (S)	1	1.298	0.321	2.567
Catfish (C)	1	9.412*	7.297*	5.827*
S×C	1	0.096	0.006	4.221
Error	23			

Table 1.2: Summary of *F*-values from ANCOVAs (Type III sums of squares) measuring the net effects of catfish and shrimp on leaf break-down (LR (%)) and accumulation of CPOM on open and mesh enclosed leaf packs (g), as well as *F*-values for ANOVAs for influence of treatments on abundance (Abund., individual number) and richness (Rich., number of taxa) of invertebrate colonization on open leaf packs. Ephemeroptera (Ephem), Diptera, Amphipoda (Amph), Trichoptera (Trichop) and Gastropoda (Gast). No ANOVA data is available for shredder richness, as shredders richness equaled 1 for all replicates of all treatments. **P*>0.05.

Treatment	d.f	Open		Mesh		Total invertebrates Open Leaf Packs		
		LR (%)	CPOM	LR (%)	CPOM	d.f	Abun.	Rich
Time	1	15.139*	31.365*	26.675*	4.814*			
Shrimp (S)	1	0.613	1.063	1.045	1.541	1	0.029	2.595
Catfish (C)	1	6.716*	0.000	0.258	0.379	1	4.134	2.188
S×C	1	0.799	0.043	0.369	1.131	1	1.183	0.312
Error	23					10		

	d.f.	Shredders		Scrapers		Predators		Collector-Gatherers	
		Abund	Rich	Abund	Rich	Abund.	Rich	Abund.	Rich
Shrimp (S)	1	0.002		0.003	0.940	2.121	3.259	0.941	0.265
Catfish (C)	1	0.684		0.00	3.045	0.820	1.507	9.061*	0.265
S×C	1	1.989		2.397	6.353*	0.559	0.255	1.370	0.510
Error	10								

	d.f.	Ephem.	Diptera	Amph	Trichop	Gast
Shrimp (S)	1	0.481	0.048	0.003	0.624	0.378
Catfish (C)	1	0.407	1.552	0.813	0.050	0.008
S×C	1	0.038	0.048	2.365	0.033	0.165
Error	10					

Table 1.3: Summary of *F*-values from ANOVAs (Type III sums of squares) analyzing the influence of shrimp and catfish on benthic invertebrate abundance from basket samplers (individual number) and richness (number of taxa). Ephemeroptera (Ephem), Coleoptera (Coleop), Diptera, Apmhipoda (Amph), Trichoptera (Trichop), Gastropoda (Gast), and Ostrocodas. **P* < 0.05.

	d.f.	Total Invertebrates		Shredders		Scrapers		Predators		Collector-Gatherers	
		Abund	Rich	Abund	Rich	Abund	Rich	Abund	Rich	Abund	Rich
Shrimp (S)	1	2.921	0.613	0.210	0.066	0.005	0.011	1.750	0.596	1.391	1.181
Catfish (C)	1	0.783	0.055	0.706	0.184	4.032	3.176	0.036	0.044	0.001	0.714
S×C	1	0.700	1.202	1.889	3.247	0.235	0.538	0.036	0.123	0.517	1.181
Error	10										

	d.f.	Ephem	Coleop.	Diptera	Amph	Trichop	Gast	Ostrocodas
Shrimp (S)	1	1.631	0.306	2.287	1.305	1.623	0.039	0.765
Catfish (C)	1	0.013	2.755	1.117	1.112	0.065	3.861	5.104*
S×C	1	0.337	0.306	1.259	2.232	0.065	0.965	0.765
Error	10							

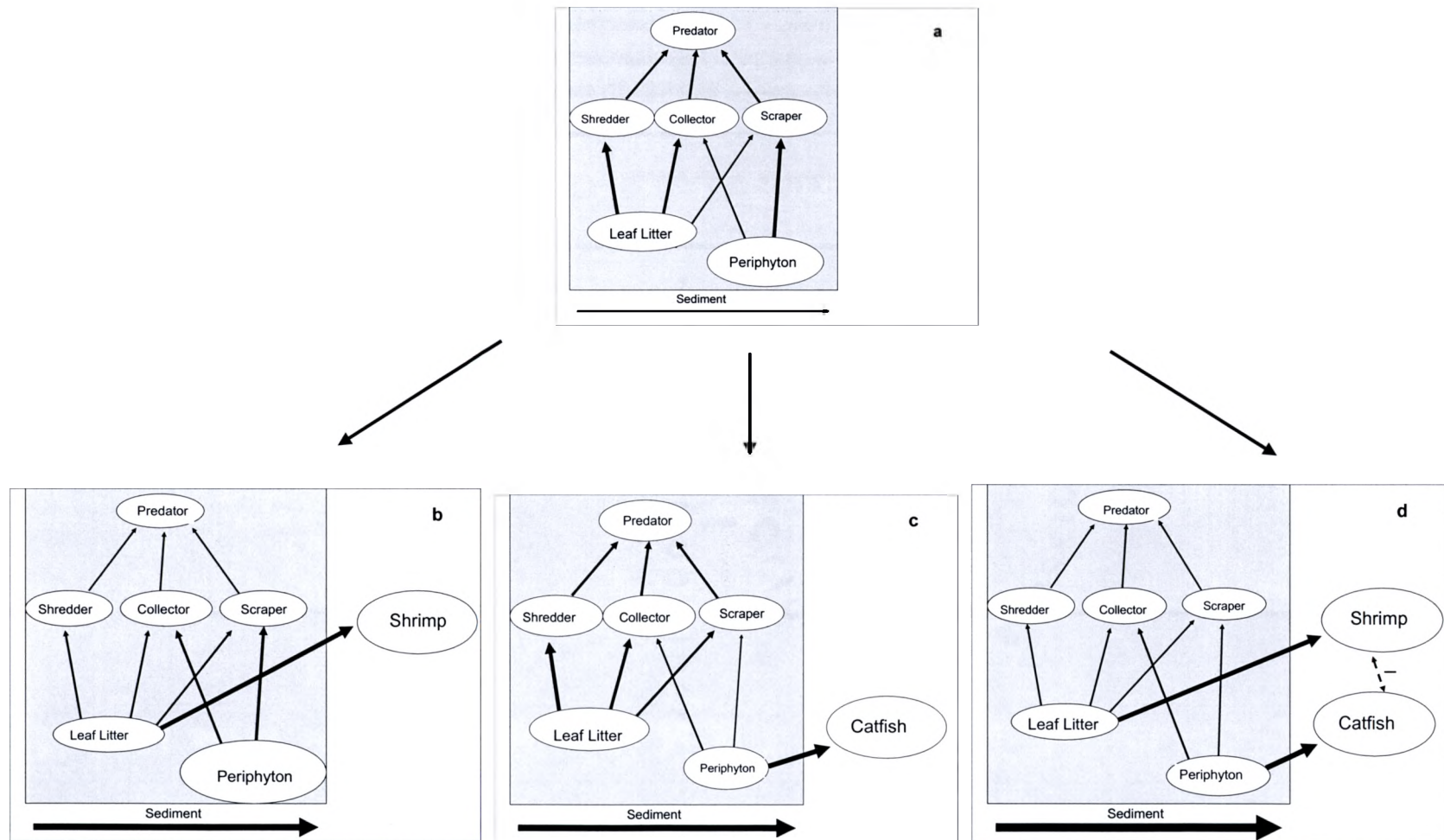


Figure 1.1: Hypothetical relationship and interactions of exotic armored catfishes and native river shrimp and their effects on community. Arrow thickness indicates strength of interaction of significant trophic links. Solid lines indicate direct interactions and dashed lines indicate indirect interactions. Sediment box indicates instances when sediment would be more actively transported downstream. Four treatments a) Control b) Shrimp, c) Catfish and d) Shrimp + Catfish.

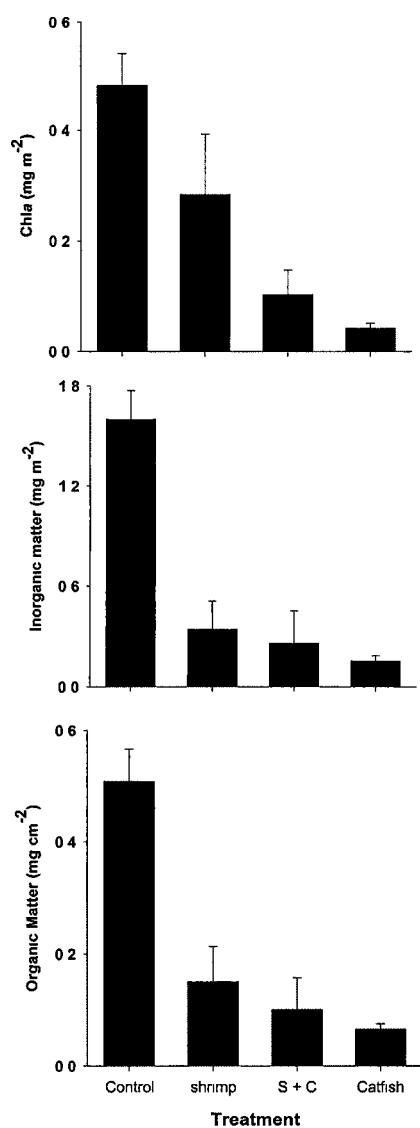


Figure 1.2: Composition of matter accumulating on tiles in stream channels per treatment. S+C is Shrimp + Catfish treatment. a) Mean concentration of periphyton (Chl a) ± 1 Standard error; b) mean mass of inorganic matter in the periphyton on tiles ± 1 Standard error, c) mean mass organic matter on tiles ± 1 Standard error

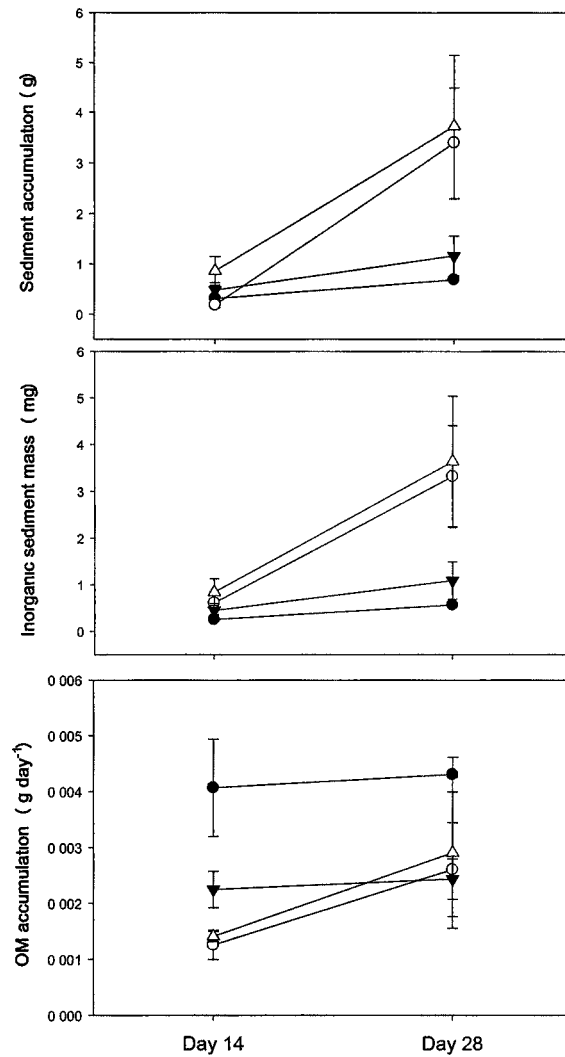


Figure 1.3: Detrital breakdown rates in open leaf packs for four treatments. Closed circles represent control, open circles represent catfish, closed triangles represent shrimp and open triangles represent shrimp + catfish (S+C). **A)** mean percent leaf mass remaining for day 14 and 28 \pm 1 SE. **b)** mean mass (g) of coarse particulate organic matter (CPOM) on leaf packs \pm 1 SE for each treatment.

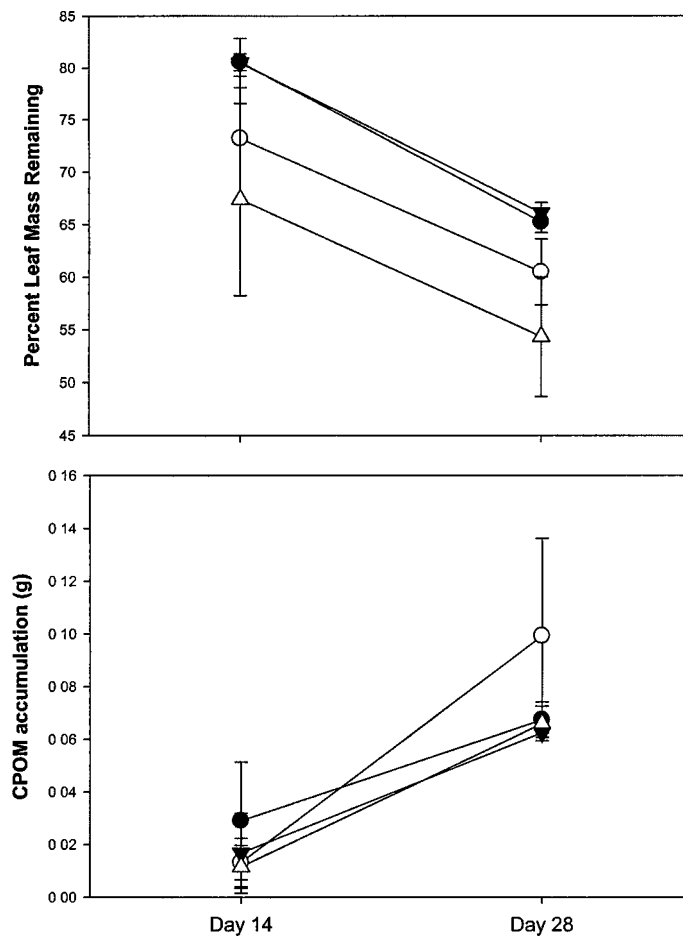


Figure 1.4: Deposition of sediment in traps (g) on days 14 and 28. for treatments: Closed circles represent control treatments, open circles represent catfish, closed triangles represent shrimp treatments and open triangles represent Shrimp + Catfish (S+C) treatments. Top panel contains dry mass (g) of sediment accumulation ± 1 Standard error. Middle panel depicts rates of organic matter deposited in sediment ± 1 Standard error. Bottom panel contains mean mass of inorganic sediment deposited in traps ± 1 Standard error.

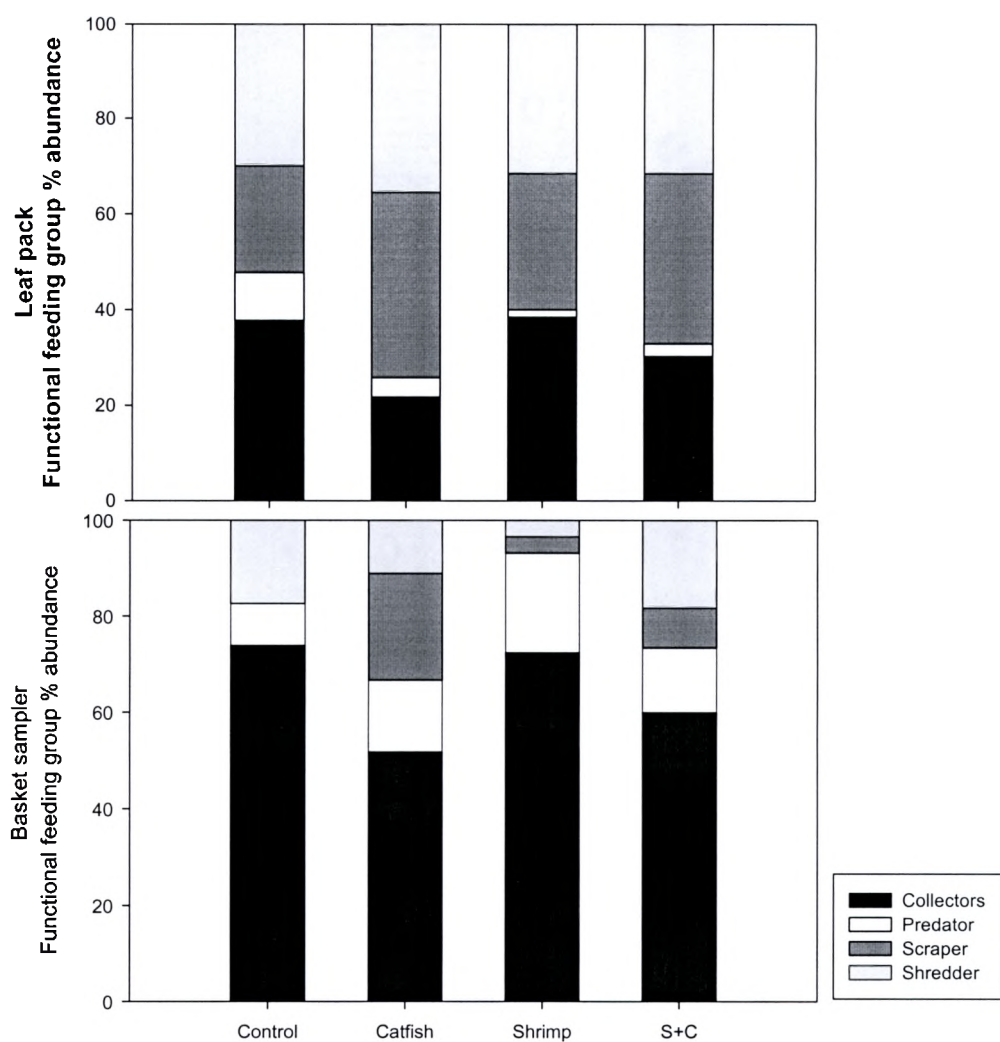


Figure 1.5: Percent abundances of functional feeding groups for a) leaf packs and b) basket samplers. Abundances used were means of days 14 and 28.

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CHAPTER II

THE EFFECT OF SAND-SEDIMENT MOVEMENT ON BENTHIC COMMUNITY COLONIZATION OF LEAF DETRITUS IN A SANDY BOTTOMED STREAM

INTRODUCTION

In flowing waters, the unidirectional movement of currents carrying materials and energy downstream poses a unique problem concerning the retention of resources (Wallace and Merritt, 1980). Unless locally retained, organic matter and energy are transported to downstream reaches out of the local system. Ecosystem structural properties, including substrate and woody debris, affect the dynamics of organic matter retention and processing, which influences biotic interactions (Bunn and Davies 2000). Low gradient sandy-bottomed streams often have little structure for primary production, and thus, may be reliant on detrital inputs as a basal nutrient resource (Roeding and Smock 1989, Metzler and Smock 1990) and as habitat (Johnson et al. 2003). Our understanding on the relationship between detrital process and benthic invertebrate colonization in sandy-bottom streams is still limited (Metzler and Smock 1990, Yammamuro and Lamberti 2007).

The classic model of energy transport in rivers states that allochthonous inputs of materials, such as detrital matter, constitute one of the major sources of nutrients, energy and habitats in streams (Vannote et al. 1980, Wallace et al. 1997, 1999). Here, leaf litter

provides a substantial component of the nitrogen, phosphorous and carbon entering the system. Primary productivity is often low in headwater streams in forests due to heavy shading by dense riparian vegetation (Vannote et al. 1980). Leaf litter becomes available as a food source through a series of processes which enhance palatability and accessibility to consumers. When leaf litter falls into streams, a substantial portion of leaf mass is lost through the leaching of soluble organic and inorganic compounds out of the leaf (Webster and Benfield 1986). Mechanical processes, such as hydrodynamic force on leaves and abrasion by sand and substrate particles, facilitate fragmentation of leaves (Boling et al. 1975, Webster and Benfield 1986, Heard et al. 1999). As leaf litter is fragmented and decomposed, the resulting particulate matter becomes available for other invertebrate functional feeding groups. Course particulate organic matter (CPOM > 1mm) resulting from leaf breakdown becomes available for collector gathers (Cummins 1974, Heard and Richardson 1995), while fine particulate organic matter (FPOM < 1mm) and dissolved organic matter (DOM) from leached nutrients and partially digested fecal material provides a food source for filter feeders within the system (Cummins 1974, Wallace and Merritt 1980).

The role of leaf litter as a food source and the structure it provides when trapped on instream structures creates a patch of high habitat complexity and nutrient availability (Anderson et al. 1978, Triska et al. 1984). This resource-rich patch increases macroinvertebrate diversity and organic matter processing (e.g. Richardson and Neill 1991, Lemly and Hildebrand 2000). Amalgamations of retained leaf litter become hotspots for local diversity within the stream channel. This not only due to its role in

creating nutrient-rich patch, but the structure supplied by the amalgamation itself, which provides habitat and refugia from predators (Johnson et al. 2003).

Much research has been conducted concerning the processing of leaf litter in high-gradient, cobble- and gravel- dominated streams (Peterson and Cummings 1974, Kobayashi and Kagaya 2005), but low gradient sandy-bottomed streams have garnered considerably less attention (but see Herbst 1980, Mayack et al. 1989, Metzler and Smock 1990, Tilman et al. 2003 and Yamamuro and Lamberti 2007). While cobble- and gravel- dominated stream bottoms provide physical structure for organic matter retention and influence breakdown (Hoover et al. 2006) and substrate for primary production (Uehlinger 1991), sand-dominated stream beds provide little structure for these processes.

The lack of organic matter- retaining substrate in the benthos reduces the capacity of the whole system to retain organic matter (Webster et al. 1994, Jones 1997). However, the dynamic shifting of sandy substrate through burying and espousing CPOM does provide a unique mechanism for organic matter storage and retention. Disturbance events, such as storms and anthropogenic activities are the primary movers of large bedload quantities through the benthos, covering stream detritus and preventing its export out of the system (Smock 1990, Schofield et al. 2004). This mechanism can be especially important for retaining CPOM in channels when these events are coupled with large pulses of leaf fall into streams. However, when spates do not coincide with leaf fall, the movement of sand results in a net release of CPOM into the water column (Metzler and Smock 1990). It is thought that leaf litter stored in the sandy hyporheic zone decomposes more slowly than that exposed to the water column, due to lower dissolved oxygen and fewer shredders within the substrate (Strommer and Smock 1989), as well as less

mechanical impact. This pool of nutrients can persist in the hyporheic zone for years before reintroduction to the water column (Metzler and Smock 1990). This mechanism for retention of nutrients is less spatially and temporally variable than storage in debris dams, which provide a patchy distribution of organic matter (Smock 1990).

The low gradient, sandy bottomed streams on Texas's Gulf Coastal Plane have little primary production, and are reliant upon allochthonous inputs of leaf detritus as a basal food source. Shifting sands in the benthos periodically cover and uncover CPOM stored in the hyporheic zone, but it is unknown how these changes in the burial status influences leaf litter utilization by invertebrates. This study aimed to test the consequences of the temporal dynamics of detrital availability on benthic invertebrate communities. I investigated how the periodic covering and uncovering of leaf litter by sandy sediments, which I am calling burial regime shift, influences the colonizing invertebrate community structure on the leaf litter. I hypothesize that burial regime will influence the detrital decomposition and invertebrate colonization dynamics on these resource patches.

To test these hypotheses, I conducted an experiment in a natural sandy bottomed stream to examine the effect of dynamic burial processes by sand movement on benthic invertebrate colonization on leaf litter. Treatments include experimental leaf packs that were buried within the sandy substrate or exposed in the water column for the duration of the experiment, as well as leaf packs exposed to burial regime shift to determine how such a shift influences leaf breakdown rate and invertebrate colonization (Fig. 2.1). I determined the influence of temporal variations in detrital burial by comparing leaf litter breakdown rates and invertebrate colonization on leaf packs between the treatments. I

predicted burial in the sand sediment would slow breakdown of detritus and decrease macroinvertebrate densities on leaf litter habitats.

MATERIALS AND METHODS

Study stream

This study took place in Clear Creek (30.054433° N, -96.0580244°W), a tributary of the Brazos River (Waller County, Texas). This stream is approximately 3-5 meters wide and is characterized by highly mobile, sandy substrates and highly variable flow. The riparian vegetation is dominated by American elm (*Ulmus americana*), Sycamore (*Plantus occidentalis*), Sweet Gum (*Liquidamber styraciflua*), Loblolly pine (*Pinus taeda*), and herbaceous vegetation.

Depth at the sampling site ranged from 15.33 cm to 32.00 cm with an mean depth of 22.09 ± 1.81 cm (mean \pm 1 SE). Water velocity ranged from $17.00 \text{ cm} \cdot \text{s}^{-1}$ to $36.00 \text{ cm} \cdot \text{s}^{-1}$ and averaged $26.40 (\pm 1.24) \text{ cm} \cdot \text{s}^{-1}$. Dissolved oxygen in Clear Creek ranged from $6.33 \text{ mg} \cdot \text{L}^{-1}$ to $10.14 \text{ mg} \cdot \text{L}^{-1}$ and averaged $8.83 (\pm 1.28) \text{ mg} \cdot \text{L}^{-1}$. Mean pH in Clear Creek is 7.63. Specific conductivity at the site is $406 \mu\text{S} \cdot \text{cm}^{-1}$.

Dominant invertebrate taxa in Clear Creek are diptera (chironomidae and simuliidae), ephemeroptera (baetidae and leptohyphidae), trichoptera (hydropsychidae) and corbicula bivalves. Collector-gatherers are the most abundant functional feeding group in Clear Creek, with densities of $5608.8 (\pm 1076.0) \text{ ind.} \cdot \text{m}^{-2}$. Scrapers and filter feeders number $284.6 (\pm 158.4) \text{ ind.} \cdot \text{m}^{-2}$ and $260.0 (\pm 160.5) \text{ ind.} \cdot \text{m}^{-2}$. Shredders are the least abundant functional feeding group in Clear Creek, with only $4.7 (\pm 4.7) \text{ ind.} \cdot \text{m}^{-2}$.

Experimental design

This study was conducted in January of 2009. At this time, American elm (*Ulmus americana*) leaves were collected on sight from a sandy bank for leaf pack construction. Leaves were transported back to the lab and dried at 60 °C to a constant weight, to obtain initial dry mass. Leaf packs were constructed with large mesh (3 cm mesh, measuring 20 cm × 20 cm total area) and contained 2-3 elm leaves.

This experiment consisted of six treatments (Fig. 2.1). Treatment 1 contained leaf packs completely buried approximately 15 cm within the stream substratum for 1 week (B). Treatment 2 contained unburied leaf packs, which were exposed to the water column for 1 week (U). Treatment 3 contained leaf packs completely buried for the entire duration of the experiment (BB). Treatment 4 consisted of leaf packs left exposed in the water column for the duration of the experiment (UU). Treatment 5 contained leaf packs left exposed for the first half of the experiment, and buried for the second half of the experiment (UB). Treatment 6 contained leaf packs buried for the first half of the experiment, and uncovered and exposed for the second half of the experiment (BU). Leaf packs for each treatment were tied to planks of wood measuring 1.5 m in length, which were staked to the substrate, with flow moving horizontally over each leaf pack, to minimize variation of the influence of water velocity on leaf packs. Each plank of wood contained 1 treatment with five replicates. Water velocities on exposed leaf packs ranged from 19 cm·s⁻¹ to 34 cm·s⁻¹, ($\bar{x} \pm 1$ SE: 27.25 ± 2.11 cm·s⁻¹). Water temperature at sampling times ranged from 18.4 °C to 8.0 °C (13.26 ± 3.01). Sand temperature at the time of sampling ranged from 9.0 °C to 12.0 °C, (11.01 ± 1.00).

This experiment took place over a two week period, and burial regime shifts for treatments UB and BU took place after one week. Data were collected on days 7 and 14. On each sampling date, water current velocity was measured at each leaf pack, as well as water temperature and temperature within the substrate. Depth of buried leaf packs was approximately 15 cm below the surface of the substrate surface. Leaf packs collected at each sampling date were preserved on ice in individual bags and transported back to the lab for analysis.

Leaf packs were collected individually, with a 250 μm sieve positioned immediately downstream of the leaf pack, to capture any invertebrates knocked loose during the removal of the leaf pack. To collect treatments buried in sand, the top layer of sand was first gently brushed away from the leaf pack before using the methods mentioned above. All leaf packs were transferred on ice in separate containers back to the lab for processing. Leaf packs were gently washed with tap water over a 250 μm sieve, and all invertebrates were removed and preserved for identification. All invertebrates were identified to the lowest practical taxonomic level for the determination of functional feeding group (Merritt et al. 2007). Leaves collected from each treatment were dried at 60 °C for at least 48 hours, and reweighed to determine percent mass reduction.

Data Analysis

Data analyzed included percent leaf mass remaining (dry mass reduction) and all invertebrate data. To fully investigate the influence of burial regime shift on invertebrate community composition, we looked at taxa composition, which included total abundances in all leaf packs, abundances of all the dominant taxa and total taxa richness,

as well as functional feeding group abundances and richness in all leaf packs. Because invertebrate densities were not normally distributed, Kruskal-Wallis Nonparametric Tests, which is the analogue to the F-test in ANOVA, were used to determine the influence of treatment on invertebrate abundance and richness for functional feeding groups and taxa groups (Zar 1999). Percent leaf mass remaining was analyzed with a one-way analysis of covariance (ANCOVA) using sampling date as a covariate, in order to examine the influence of time in our analysis. Data with significantly different treatment effects were then analyzed post hoc with a Tukey's HSD test to determine similarity among treatment means.

RESULTS

For the two week period, there was no detectable difference of effects of treatments on leaf litter breakdown and the leaf remaining percentages were similar between treatments (ANCOVA, $F_{3,24} = 1.223$, $P = 0.323$). However, there was a significant effect of experimental time ($F_{1,24} = 6.110$, $P = 0.021$) on percent leaf litter remaining (Fig 2.2). Leaf packs lost an average of 11.2 % dry mass after 7 days and an average of 17.7 % dry mass after 14 days.

Dominant invertebrate taxa inhabiting leaf packs included diptera (chironomidae and simuliidae), ephemeroptera (baetidae, heptageniidae, isonychiidae and leptophlebiidae), plecoptera (perlidae) and trichoptera (hydropsychidae and hydroptiliidae). Other less dominant taxa included coleoptera (elmidae larvae and gyrinidare larvae), amphipoda, and gastropoda. Experimental treatments provoked significant effects of sand burial process on invertebrate community composition in leaf

packs. The results of the experimental manipulation show significant differences in total abundance and total richness of all invertebrates, taxa abundance, and all categories of functional feeding group abundance and richness, with the exception of shredder abundance (Table 2.1). Total abundance of invertebrate individuals on leaf packs ranged from the lowest at ($\bar{x} \pm 1 \text{ SE}$: $15.4 \pm 1.53 \text{ ind}$) for the UB treatment to the most abundant for the UU treatment at ($2057.8 \pm 387.18 \text{ ind}$) (Fig 2.4a). This pattern shift in abundance was primarily driven by abundances of chironomidae larvae, with a maximum average of (1874.2 ± 258.4) in UU leaf packs, and a minimum average of $13.8 (\pm 1.6) \text{ ind.}$ in UB leaf packs (Figure 2.4b).

Analysis of invertebrate functional feeding groups yielded similar trends (Figure 2.5). Collector-gatherer abundances were by far the highest in all leaf packs, primarily due to the abundances of collector-gatherer chironomidae (Chironominae and Orthocladiinae). Filter feeder abundances were surprisingly high, due to high abundances of simuliidae in treatments exposed to the water column. Predator abundances were low in buried leaf packs, but increased in leaf packs exposed to the water column. Again, this was due in part to the presence of predator chironomidae (Tanypodinae). Scraper abundances were low as well. Dominant scrapers in Clear Creek were gastropods, and likely did not colonize quickly. Shredder densities were low as well. Only three shredders were found among all leaf packs, all amphipoda. However, this is unsurprising, as overall abundances of shredders in Clear Creek were low.

Tukey's HSD tests revealed that invertebrate colonization on leaf packs was heavily dependant on buried status of the leaf pack at the time of collection, meaning buried leaf packs tended to group together and unburied leaf packs tended to do the same

(Fig 2.3 and 2.4, Table 2.2). Leaf pack treatment for the first week of the experiment had little influence on invertebrate colonization of leaf packs.

DISCUSSION

For this experiment, densities of primary consumers shifted dramatically in response to burial status of leaf packs upon time of collection. Specifically, buried leaf packs had low abundances of invertebrates and unburied leaf packs had high abundances of invertebrates. Shift in burial regime had no detectable influence on leaf breakdown rate or invertebrate community composition. Instead, the status of the leaves, whether buried or unburied, at the time of collection was the primary factor influencing invertebrate community composition. This concurs with the prediction that burial in sandy sediment influences and decreases invertebrate community composition. However, this also leads to the preliminary conclusion that for leaf litter suspended in the water column, prior status of the leaves, whether buried or unburied, makes no difference in invertebrate colonization dynamics.

Detrital breakdown rates were comparable between all treatments. This experiment was conducted in January, and it is possible that our results were influenced by the season, and the effect of stream temperature at which it was conducted. Mayacke et al. (1989) found that during the winter portion of a leaf burial experiment, buried leaf litter breakdown rate did not differ significantly from exposed leaf litter. However, their spring findings showed a significant difference in leaf breakdown rates of buried and unburied sweetgum (*Liquidamber styraciflua*) leaf litter during the spring months, when the breakdown of buried leaf litter was retarded. Metzler and Smock (1990) however,

found higher decay rates for organic matter buried within sandy sediments between January and March, when organic matter exhibited a 10% greater mass reduction than other months. It is possible that a longer treatment time for our experiment would have yielded different results. Most detrital breakdown experiments are conducted for at least one month or longer, to determine breakdown rates of leaf litter. However, our experiment was performed in the winter, so it is possible that our streams are following the same seasonal trend. During the fall prior to our study we performed a pilot study with buried and unburied leaf packs over a two week period of time. Leaf breakdown rates between buried and unburied treatments after 14 days were significantly different, with B treatments losing 31.1 % of the original dry mass and U treatments losing 58.6% of the original dry mass. However, without a longer comparison time, it is difficult to be sure if our winter experiment would have followed the same trend as we observed during the 14 days the experiment was run. It is highly probable that the short duration of the January experiment, in conjunction with the cooler winter temperatures was a factor in determining the influence of burial regime on leaf breakdown rate.

Invertebrate colonization was significantly influenced by the burial status of leaf packs at the time of sampling, but not to first week's treatment of leaves. There was virtually no difference in taxa and functional feeding group abundance and richness in leaves that had been buried and subsequently unburied and leaves that remained unburied. This suggests that colonization rates of unburied leaf litter are relatively rapid, and that invertebrate densities are low within the sandy substratum. Several studies have examined the vertical distributions of invertebrates in sandy hyporheic zones. These hyporheic communities in sandy streams have lower densities and diversity than the

surface (e.g. benthic) community, due to small pore space and low dissolved oxygen (Whitman and Clark 1984, Strommeyer and Smock 1989). Few invertebrates are adapted to these conditions, but chironomids, nematodes and crustaceans are usually the dominant taxa found in sandy hyporheic zones (Poole and Stewart 1976, Jeffery et al. 1986, Strommeyer and Smock 1989, Tilman et al. 2003, Yamamuro and Lamberti 2007). Buried leaf litter in this study was primarily colonized by chironomids as well as few simuliids and baetid ephemeropterans. I was unable to measure dissolved oxygen in the sandy subsurface of our experiment, but we can infer that this was the case due to the low diversity of taxa present on buried leaf litter.

We were unable to test the effect of leaf burial in sand on leaf quality in this experiment, although there seemed to be no difference in preference by invertebrates when colonizing leaf packs between litter that had been buried, and that which had not. It is possible that had our treatments been conducted over a longer period of time, treatments would have yielded different results. Herbst (1980) found that invertebrate shredders consumed greater amounts of surface incubated leaf litter over leaf litter buried in sand. This was not reflective of the nutrient quality of the leaf litter however. Leaves buried in sand generally had higher caloric and organic content than leaf litter incubated in the water column. This may be variable with leaf species and season however. C:N ratios of sweetgum litter did not differ between litter buried in sand and litter in the water column during winter months, but did during the spring when burial slowed the reduction of C:N ratios (Mayack et al. 1989).

Leaf litter inputs often occur in large pulse events, with high temporal variability (Moore et al. 2004). Moreover, sandy bottomed streams generally have little substrate

with which to retain organic inputs, resulting in a reduction in the capacity of the entire system to retain organic matter (Webster et al. 1994, Jones 1997). Metzler and Smock (1990) estimated that over 20% of the annual litter fall entering sandy bottomed streams were covered and retained by sand. Because sediment movement is very dynamic, this periodic covering and uncovering of leaf litter by sand affects the temporal scale of energy utilization. This may influence nutrient spiraling lengths (Newbold 1998), decrease the spatial and temporal variability of carbon availability (Metzler and Smock 1990), and influence biodiversity and ecosystem function (Yamamuro and Lamberti 2007). It is necessary to conduct further experiments to investigate the trophic consequences of prolonged burial period of leaf litter in sandy sediments, and its effects on ecosystem function.

In summary, I found that the burial of leaf litter in sand sediments influenced the invertebrate community colonizing leaf packs. I found no difference in the community composition in leaf packs that had been buried than unburied and leaf packs that had never been buried (BU and UU); leading to the preliminary conclusion that the shift from burial to exposing for leaf litter had no bearing on the colonization dynamics of invertebrate community. This suggests that colonization rate of benthos on newly exposed leaf pack can be fast, which may be due to the lack of habitat structure in the stream and the available leaf litter on the channel bed can offer refugia habitat for drifting invertebrates. This study supplies us the ecological understanding of community-scale consequences of sediment movement in a sandy bottomed stream ecosystem.

Table 2.1: Summary of H values from Kruskal-Wallis Test for all invertebrate data. All abundance data was analyzed as number of individuals in each leaf pack. Taxa richness was analyzed at the family level.

	<i>df</i>	H	<i>P</i>
Total Abundance	5	23.627	<0.001*
Total Taxon Richness	5	24.657	<0.001*
Collector-gatherer Abundance	5	23.844	<0.001*
Filter-feeder Abundance	5	24.063	<0.001*
Predator Abundance	5	24.929	<0.001*
Scraper Abundance	5	25.157	<0.001*
Shredder Abundance	5	3.229	0.665
Collector-gatherer Richness	5	24.688	<0.001*
Filter-feeder Richness	5	24.314	<0.001*
Predator Richness	5	26.609	<0.001*
Scraper Richness	5	24.394	<0.001*
Shredder Richness	5	24.395	<0.001*
Diptera Abundance	5	23.395	<0.001*
Ephemeroptera Abundance	5	23.688	<0.001*
Trichoptera Abundance	5	27.765	<0.001*
Plecoptera Abundance	5	23.171	<0.001*

$\alpha = 0.05$

Table 2.2: Summary of homogeneous subsets from Tukey HSD test for all invertebrate data. All treatments for all data are grouped in 1, 2 or 3 subsets based on similarity of means. Treatments belonging to the same subset have similar means. Numbers 1, 2 and 3 denote which subset each treatment belongs to. Treatments are grouped at $\alpha = 0.05$.

	B	BB	UB	BU	U	UU
Total Abundance	1	1	1	2	2	2
Total Taxon Richness	1	1	1	2	2, 3	3
Collector-gatherer Abundance	1	1	1	2	2	2
Filter-feeder Abundance	1	1	1, 2	1, 2	1, 2	2
Predator Abundance	1	1	1	1, 2	2	1, 2
Scraper Abundance	1	1	1	2, 3	1, 2, 3	3
Shredder Abundance	1	1	1	1	1	1
Collector-gatherer Richness	1	1	1	2	2	2
Filter-feeder Richness	1	1	1	2	2	2
Predator Richness	1	1	1	2	2	3
Scraper Richness	1	1	1	2	2	2
Shredder Richness	1	1	1	2	2	2
Diptera Abundance	1	1	1	2	2	2
Ephemeroptera Abundance	1	1	1	2	2	2
Trichoptera Abundance	1	1	1	2	2	3
Plecoptera Abundance	1	1	1	1	1	2

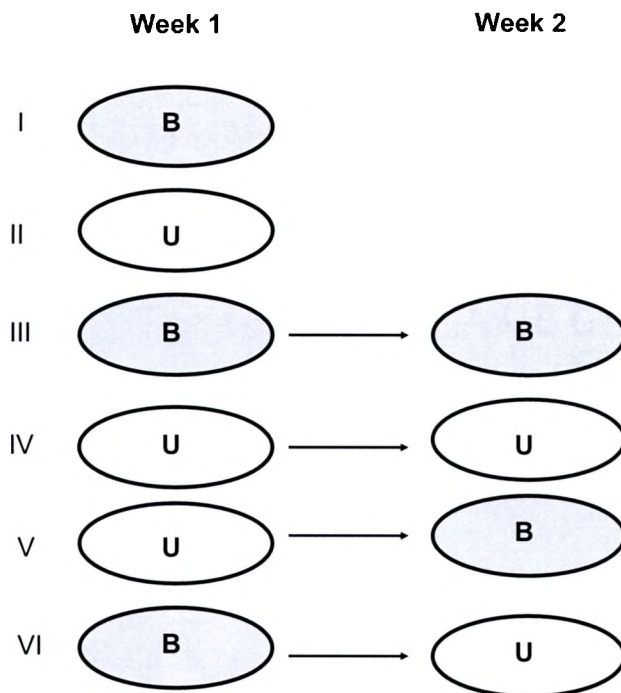


Figure 2.1: Illustration of treatments for sand burial experiments 2 and 3 in Chapter 2. B indicates treatments where leaf packs are buried. U indicated unburied leaf packs. Treatments I and II (B and U) are to be collected after week 1. Treatment III will remain buried for the duration of the experiment, and treatment IV will remain unburied for the entire experiment. Treatments V and VI will undergo burial regime shift, from U to B (V) and from B to U (VI). Treatments III – VI will be collected for analysis after two weeks.

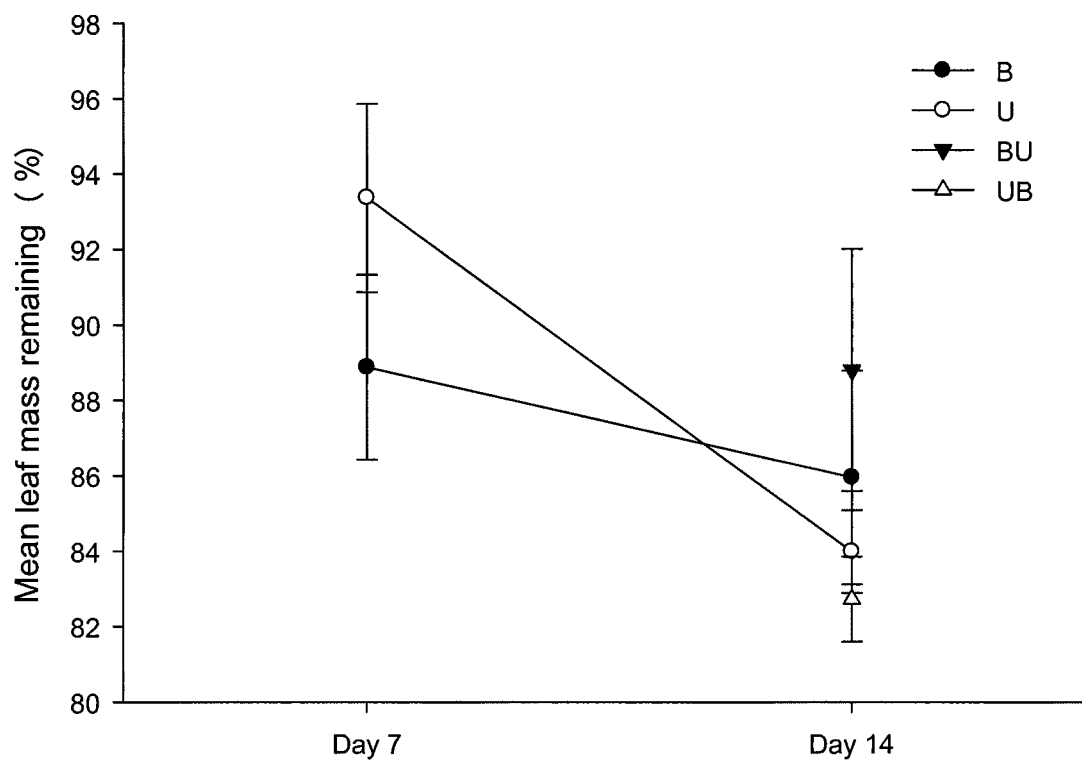


Figure 2.2: Leaf litter remaining (%) for all treatments. Mean percent leaf mass remaining ± 1 SE for days 7 and 14. Treatments B and U on Day 14 represent treatments BB and UU respectively.

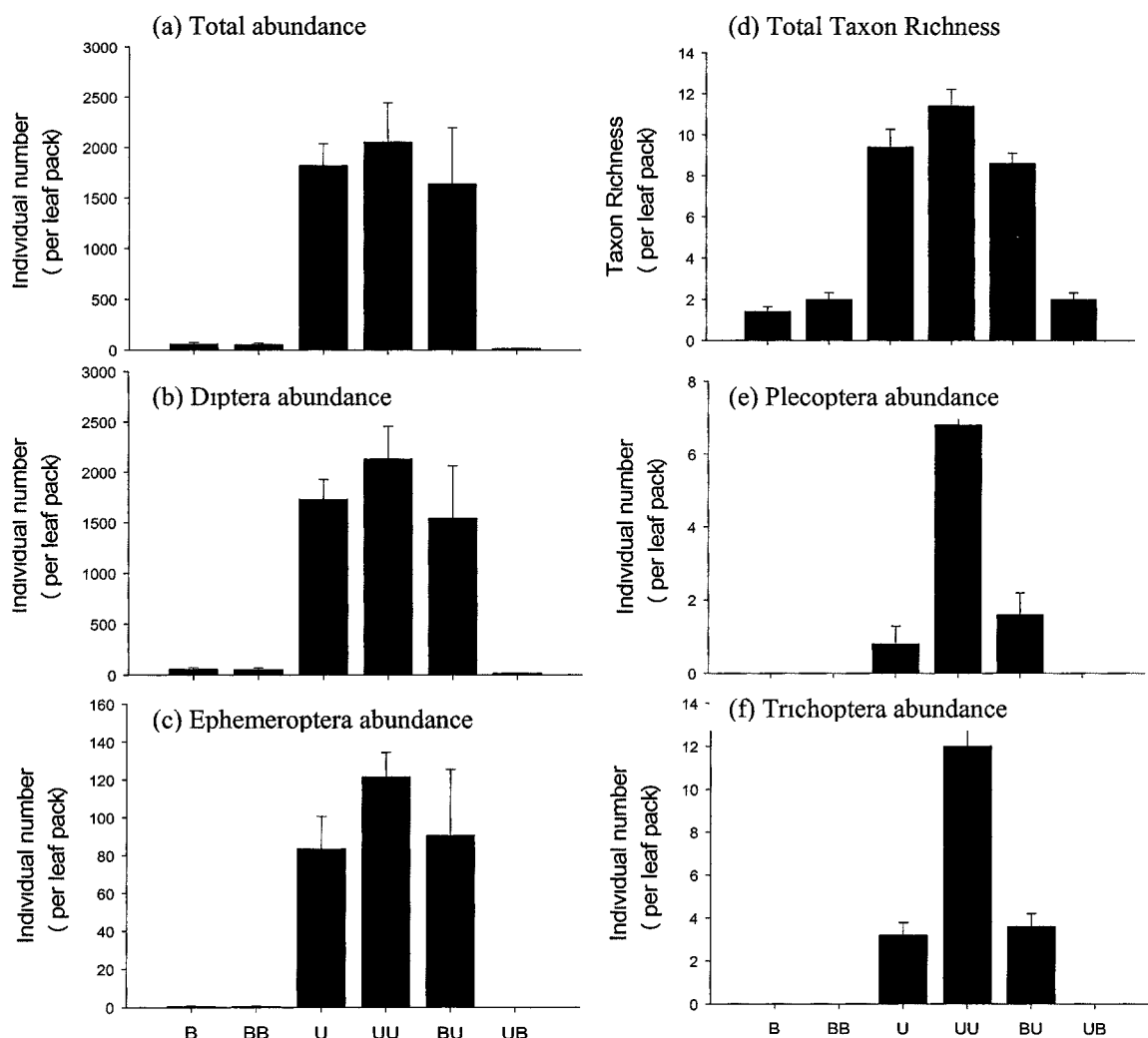


Figure 2.3: Invertebrate data for **A**) Total abundance (individual number), **B**) Total taxon richness (number of taxa present), **C-D**) Taxa abundance (individual number) \pm 1 SE, for all treatments. Treatment averages derived from mean abundance or richness per leaf pack. B= buried for 1 week; BB= buried for 2 weeks; U= unburied for 1 week; UU= unburied for 2 weeks; BU= buried for 1 week, then unburied for 1 week; UB= unburied for 1 week then buried for 1 week. Error bars are standard errors.

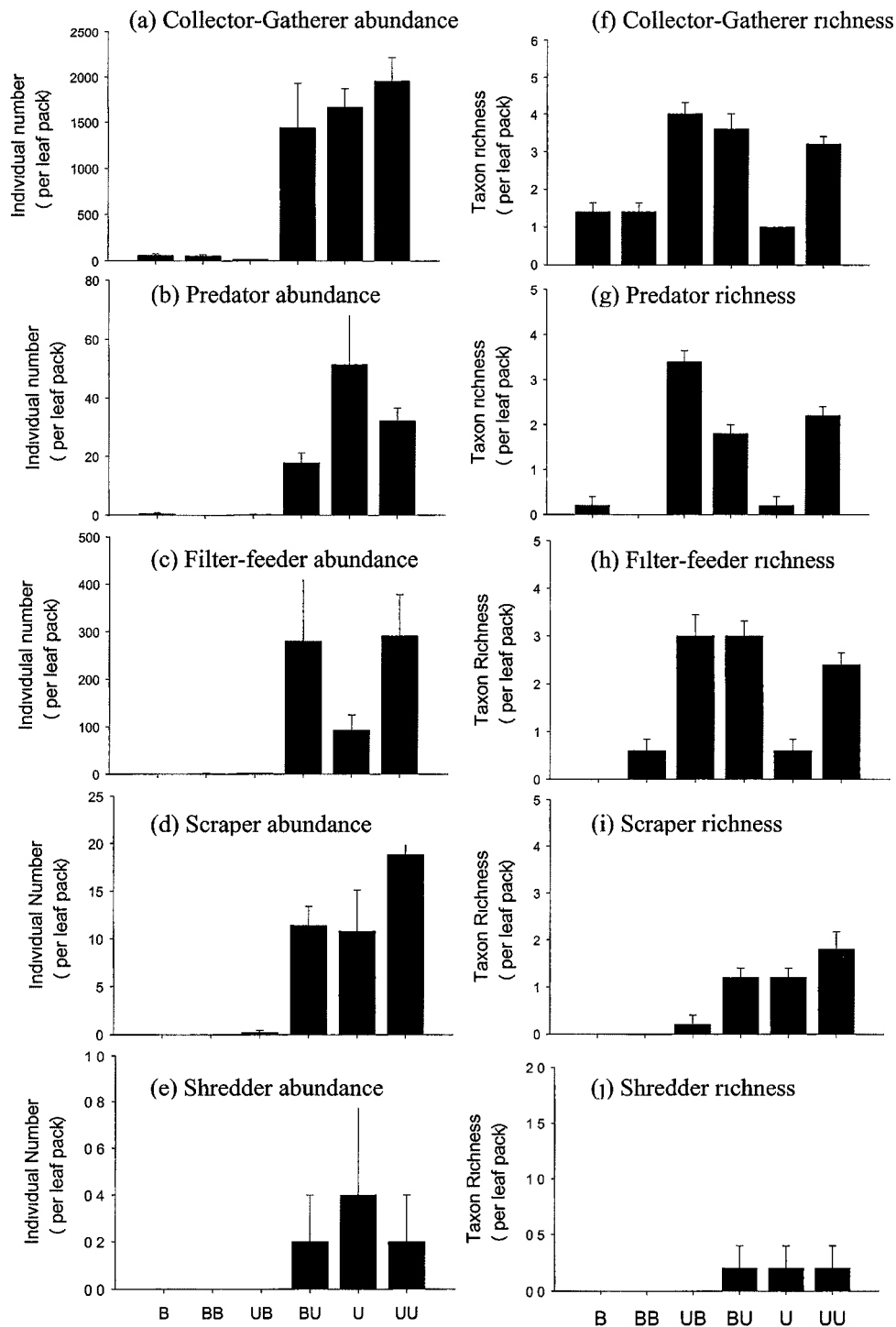


Figure 2.4: Invertebrate functional feeding group abundance (A-E) and richness (F-J) per leaf pack. Error bars denote standard errors (± 1 SE). Treatment averages derived from mean abundance or richness in leaf packs. B= buried for 1 week; BB= buried for 2 weeks; U= unburied for 1 week; UU= unburied for 2 weeks; BU= buried for 1 week, than unburied for 1 week; UB= unburied for 1 week than buried for 1 week.

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