ABSTRACT

Title of Document: TERRESTRIAL-AQUATIC LINKAGES IN HUMAN-ALTERED LANDSCAPES

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Streams and adjacent riparian zones are intimately linked by the flow of resource subsidies between terrestrial and aquatic habitats. Landscape-level changes in land use can have profound impacts on riparian structure and stream health, and may alter the flow of resource subsidies across the stream-riparian boundary. Yet, terrestrial-aquatic linkages have not been well-studied in human-impacted landscapes. Here, I examine energy flows across the stream-riparian boundary in agricultural and suburban landscapes in Maryland. I study the effects of terrestrial resource subsidies (grass and herbaceous vegetation, periodical cicada detritus) on stream ecosystem processes and consumers and the effects of one aquatic subsidy (emerging aquatic insects) on agriculturally important consumers, wolf spiders (Lycosidae).

I present strong evidence for terrestrial-aquatic linkages where large quantities of high quality, allochthonous resources subsidize stream ecosystems. Herbaceous vegetation and grasses growing along the edges of agricultural headwater streams

provide significant quantities of organic matter that are rapidly decomposed and support a diverse macroinvertebrate community. Further, the dense vegetation appears to limit light to algae growing on the stream bottom. Detritus from 17-year periodical cicadas (*Magicicada* spp.) that falls into forested suburban streams provides an intense pulse of terrestrial resources that is unusual for the summer, but is locally utilized and causes dramatic increases in whole-stream community respiration.

I provide weak evidence for a terrestrial-aquatic linkage between emerging aquatic insects and lycosid wolf spiders inhabiting agro-ecosystems in central Maryland. Results from field studies indicate that wolf spiders are generally more abundant in the riparian buffers adjacent to corn fields, and exhibit neither alternating abundance nor net movement between the field and buffer habitats throughout the year. While wolf spiders consume adult aquatic insects in the lab, I could not resolve the specific contribution aquatic insects make to the diets of field-collected wolf spiders.

Terrestrial-aquatic linkages are important in human-altered ecosystems, and have significant implications for the conservation and restoration of impacted habitats and ecosystem services. The relative strength of these linkages, however, depends on the species involved, the direction of the subsidy flux, the nature of the land-water boundary, and the temporal context in which they occur.

TERRESTRIAL-AQUATIC LINKAGES IN HUMAN-ALTERED LANDSCAPES

By

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Dissertation submitted to the Faculty of the Graduate School of the
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Preface

This dissertation contains a single introduction section, three research chapters, and a conclusion. Chapters I, II, and III are presented in manuscript form with abstract, introduction, methods, results, and discussion, followed by tables, figure legends, and figures. A single reference section occurs at the end for literature cited throughout the dissertation.

Dedication

For my grandparents, Robert and Jean Bertsch and Frances Menninger

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Table of Contents

List of Tables

Chapter I: The role of herbaceous plants and grasses as a food resource in open-canopy headwater streams of the Maryland Piedmont.

Chapter II: Periodical cicada detritus impacts stream ecosystem function.

Chapter III: Weak terrestrial-aquatic linkage in central Maryland agro-ecosystems.

List of Figures

Chapter I: The role of herbaceous plants and grasses as a food resource in open-canopy headwater streams of the Maryland Piedmont.

Chapter II: Periodical cicada detritus impacts stream ecosystem function.

Chapter III: Weak terrestrial-aquatic linkage in central Maryland agro-ecosystems.

Introduction

While traditionally food webs have been described for communities with spatially discrete habitat or ecosystem boundaries (Elton 1927, Lindeman 1942), ecologists have recently shifted their focus towards the effects of energy flows across these boundaries on food webs and ecosystem processes (Polis et al. 1997, Polis et al. 2004). Resource subsidies – prey, nutrients or detritus exchanged between habitats – have been shown to have direct, measurable consequences on the consumer dynamics and productivity of recipient habitats (Polis et al. 1997). The importance of resource subsidies is particularly evident at the terrestrial-aquatic interface where subsidy fluxes between terrestrial systems and oceans, lakes, and streams have been well-studied (Polis and Hurd 1995, Pace et al. 2004, Power et al. 2004, Baxter et al. 2005).

Streams and adjacent riparian zones are intimately linked by the flow of resource subsidies between the two habitats (Gregory et al. 1991, Naiman and Decamps 1997). In particular, the exchange of leaf litter, woody debris, and nutrients has long been recognized as critical to the functioning of stream ecosystems (Likens and Bormann 1974, Hynes 1975, Vannote et al. 1980). Allochthonous organic matter provides the energy base for forested stream food webs (Webster et al. 1995, Wallace et al. 1997), and nutrients such as nitrogen and phosphorous are critical to stream metabolism and microbial processes (Allan 1995). Additionally, recent research has emphasized the exchange of prey subsidies across the stream-riparian zone boundary: terrestrial insects falling into streams that provide food for fish (Mason and MacDonald 1982, Cloe and Garman 1996, Baxter et al. 2005) and the emergence of aquatic insects that provide prey resources for riparian arthropod and vertebrate predators (Nakano and Murakami 2001, Sabo and Power 2002, Sanzone et al. 2003, Paetzold et al. 2005). In addition to contributing significantly to consumer diets and increasing consumer abundance, prey subsidies also have, in some cases, cascading effects on ecosystem processes in the recipient habitats (Nakano et al. 1999, Henschel et al. 2001).

As topographic low points in the landscape, stream ecosystems integrate the effects of environmental processes occurring at multiple scales (Hynes 1975, Harding et al. 1998, Brooks et al. 2002, Gessner and Chauvet 2002). Landscape-level changes in land use can have profound impacts on riparian buffer structure and stream health (Dance and Hynes 1980, Paul and Meyer 2001, Allan 2004, Walsh et al. 2005), and consequently may alter the flow of resource subsidies across the terrestrial-aquatic boundary. For example, England and Rosemond (2004) report that riparian deforestation, a practice that frequently accompanies urban development, reduces the subsidy of terrestrial plant resources to stream consumers. Similarly, where agricultural practices extend to the stream margin and the natural riparian forest is removed or replaced with a vegetated buffer, stream macroinvertebrate consumers shift from relying on deciduous litter inputs to relying largely on autochthonous algal production, and shredding macroinvertebrates are frequently lost from the aquatic community (Delong and Brusven 1998). Yet, beyond this examination of the loss of basal food resources with different land use practices, terrestrial-aquatic linkages have not been well-studied in human-impacted landscapes.

Given that human modification of the planet will only continue to increase with time, understanding the processes that occur in altered ecosystems has become an important ecological research priority (Palmer et al. 2004). Studying the exchange of subsidies across the terrestrial-aquatic interface may ultimately lead to useful insights regarding the conservation and restoration of impacted habitats and ecosystem services. In this dissertation, I use a case-study approach to examine energy flows across the stream-riparian zone boundary in agricultural and suburban landscapes in Maryland. Specifically, I examine the effects of two types of terrestrial resource subsidies (grass and herbaceous vegetation, periodical cicada detritus) on stream ecosystem processes and consumers and the effects of one aquatic subsidy (emerging aquatic insects) on agriculturally important terrestrial consumers, wolf spiders. A brief description of each chapter follows below.

In Chapter I, I examine the resource dynamics of open-canopy streams with riparian buffers dominated by grasses and herbaceous plants, an increasingly common feature of agricultural and suburban landscapes. Previous studies of treeless streams have focused on algae as a primary food resource of the food web (Delong and Brusven 1998), providing little evidence for terrestrial-aquatic linkage in these systems. However, a recent study of Mid-Atlantic Piedmont streams suggests that diverse communities of invertebrates, including detritivores, are supported in small streams with herbaceous riparian buffers (Moore and Palmer 2005). I hypothesize that the herbaceous plants and grasses growing along small open-canopy stream edges, by falling over and into the channel, provide an important source of organic matter and limit light to the stream bed for algal production. I quantify the herbaceous plant and grass material overhanging the edges of three open-canopy, agricultural streams and report standing stocks similar to the amount of course particulate organic matter measured in Eastern deciduous forest streams. In a decomposition experiment, I find that two common herbs and two common grasses decompose more quickly than rates generally reported for tree leaf litter and are rapidly colonized by macroinvertebrate shredders. Results of an edge vegetation removal experiment indicate that the dense growth of herbs and grasses along the stream edge indeed limits algal production. I conclude that herbaceous plants and grasses may, in fact, provide an important allochthonous food resource to the food webs of open-canopy headwater streams.

In Chapter II, I take advantage of the emergence of Brood X 17-year periodical cicadas (*Magicicada* spp.) in 2004 to study the effect of a large, temporally limited resource pulse of terrestrial arthropod detritus on stream ecosystem function. Given the large quantity and high nutrient quality of cicada detritus entering streams, I hypothesize that the pulsed subsidy would be readily consumed by heterotrophic microbes and invertebrates, resulting in an increase in whole-stream respiration. I compare emergence dynamics, cicada detritus input, retention, decomposition, and community respiration at two sites: one with a wide, undisturbed riparian forest and the other with a narrow riparian forest that had experienced significant habitat modification in the year prior to cicada emergence. While emergence is greater at the intact forest site, the overall cicada detritus input rate is actually higher at the disturbed site. At both sites, cicada detritus that falls into the streams is retained within a short distance of entry and rapidly decomposes. Daily whole-stream community respiration increases dramatically compared to pre-cicada measurements at both the intact and disturbed sites following cicada detritus input, although the specific pattern of increase varies between the sites. Understanding how the stream ecosystem responds to this intense, natural resource pulse provides insight into how stream ecosystems will respond to unnatural resource pulses that could accompany human-induced environmental change.

In Chapter III, I shift my focus from the impact of terrestrial subsidies on stream ecosystems to examine the reciprocal flux of an aquatic subsidy to terrestrial consumers, wolf spiders (Araneae: Lycosidae), in riparian buffers adjacent to agricultural fields. I predict that wolf spiders, an agriculturally important natural enemy, are more abundant in riparian buffers at times when fields are less hospitable due to farming practices or low terrestrial prey abundance. Recent research in unmanaged systems has established a strong terrestrial-aquatic linkage between riparian arthropod predators and emerging aquatic insects (Sanzone et al. 2003, Paetzold et al. 2005), but this has not been tested in an agro-ecosystem. I hypothesize that riparian buffers adjacent to crop fields provide important habitat for the wolf spiders as well as alternative prey, emerging aquatic insects. To test these predictions I collect seasonal activity data in riparian buffers and adjacent corn fields at three sites and find a general trend of increased wolf spider abundance in the riparian buffer. However, I find no evidence of a significant habitat by time interaction, where the abundance of spiders alternates between the two habitats at different times of the year. Additionally, the adult aquatic insect abundance and emergence biomass is concurrent with terrestrial prey abundance, which does not differ between the field and buffer habitats at any time of the year. Wolf spiders readily consume adult aquatic prey in feeding trials, but I am unable to identify the specific contribution of aquatic insects to field-collected wolf spider diets with stable isotope analyses. Further, no patterns of seasonal movement between riparian buffers and corn fields are detected with directional pitfall trapping. Thus, these results provide only weak evidence for a terrestrial-aquatic linkage between emerging aquatic insects and wolf spiders in riparian buffers adjacent to agricultural fields. The strength of terrestrial-aquatic linkages in agro-ecosystems may be highly species-specific, reflecting individual predators' habitat and prey preferences, behavior and phenology.

I conclude from this body of research that terrestrial-aquatic linkages are important in human-altered ecosystems, and have significant implications for the conservation and restoration of impacted habitats and ecosystem services. I suggest that the relative strength of these linkages depends on a number of factors including the direction of the subsidy flux, the nature of the land-water boundary, and the temporal context in which they occur.

Chapter I: The role of herbaceous plants and grasses as a food resource in open-canopy headwater streams of the Maryland Piedmont

Abstract

The organic matter dynamics of open-canopy streams with buffers dominated by herbaceous plants and grasses are largely unstudied despite the fact that such streams are common worldwide, particularly in agricultural and suburban landscapes. Streams densely vegetated with herbs and grasses may receive significant amounts of detritus that could have important consequences on stream food webs. Further, if the streams are small, the herbaceous and grassy vegetation often hangs over or completely across the channel, thereby reducing light levels and perhaps limiting in-stream primary production. The standing crop of edge vegetation and associated macroinvertebrate communities were quantified along three headwater streams on agricultural land in the Maryland Piedmont. The decomposition rates of four common species of herbs and grasses were measured using experimental leafpacks, and an edge vegetation removal experiment was used to determine the effect of edge plant shading on benthic algal production. Large standing crops of plant material (average range: 68 – 276 g AFDM m^{-2}), composed largely of monocots, were found at all three study streams and were similar to standing stocks of coarse particulate organic matter that have been reported for nearby Eastern deciduous headwater streams. In addition, diverse assemblages of shredding macroinvertebrates were observed at all three study sites. The decomposition rates of the herbaceous species were faster than the rates for the grass species, and both had higher rates of decomposition than rates generally reported for deciduous leaf litter. The decomposition rates of the herbs and grasses were significantly related to leaf quality as measured by leaf nitrogen content ($p < 0.05$). Macroinvertebrate shredders colonized all experimental leafpacks, and the colonization rate was also significantly affected by plant species ($p < 0.05$). Removal of edge vegetation along an experimental reach resulted in a dramatic increase in chlorophyll *a* accrual compared to the accrual rates measured prior to removal in the experimental reach as well as in an unmanipulated reference reach ($p < 0.05$). Given that the large standing crops of organic matter measured in the herbaceous and grass buffer study streams are similar to those measured in nearby deciduous forest streams, that the organic matter is rich in nitrogen and is used by detritivores, and that the dense edge vegetation appears to limit algal growth, I suggest that herbaceous and grass plant material may be an important food resource in such systems.

Introduction

Forest canopy removal due to logging, urbanization, and agriculture has well-known impacts on stream ecosystems (Gregory et al. 1991, Sweeney 1993, Allan 2004). The removal of shade trees results in an increase in solar radiation to the streambed with concomitant increases in algal production and water temperature (Hetrick et al. 1998b, Bourque and Pomeroy 2001). These, in turn, have been shown to affect invertebrate community structure (Hetrick et al. 1998a, Kelly et al. 2003), and recent work by Sweeney et al. (2004) suggests that deforestation may have dramatic impacts on organic matter processing and nitrogen uptake per length of stream. Today, open-canopy streams with edges dominated by herbs and grasses are particularly common in suburban and agricultural regions throughout the world. Understanding ecosystem function, particularly organic matter dynamics, in these open-canopy streams is of particular importance given that agricultural streams represent the major form of undeveloped land in temperate regions experiencing urbanization pressure and are frequently the focus of conservation efforts (Jacobs 1999, Moore and Palmer 2005).

Research on the roles played by herbs and grasses growing along open-canopy streams has been limited largely to describing the ability of the vegetation to mitigate the effects of agricultural land use (Montgomery 1997, Lyons et al. 2000). The decomposition dynamics of herbaceous plants and grasses and their availability to stream consumers are poorly studied (but see Mackay et al. 1992, Young et al. 1994) compared to the dynamics of deciduous tree leaf litter (Webster and Benfield 1986, Ostrofsky 1997). In fact, studies of treeless streams have suggested that algae is the primary basal food resource fueling the stream food web (Delong and Brusven 1998). Yet, work by Moore and Palmer (2005) in mid-Atlantic Piedmont streams has shown that the diversity and abundance of invertebrates, including detritivores, can be extremely high in headwater streams with riparian vegetation dominated by herbs and grasses.

While rooted on the bank, herbs and grasses tend to fall over into the active stream channel during the growing season and after senescence and may, in fact, provide a significant source of organic matter to small streams (Figure 1). Further, because many open-canopy headwater streams have narrowed channels (< 1m), herbaceous vegetation and grasses growing along the edges may actually function as a low-level 'canopy' over the stream, reducing light penetration and limiting algal growth. Thus, herbaceous and grassy vegetation growing along treeless stream edges may provide an allochthonous source of organic matter *and* limit the degree of primary production.

In this study, I seek to understand the role of herbaceous plants and grasses as food resources in headwater streams within agricultural watersheds. First, I quantified the standing crop of herbaceous vegetation and grasses and the associated assemblages of macroinvertebrates along the edges of three open-canopy headwater streams in Maryland. Second, I performed a leaf decomposition study using four common riparian herbaceous and grass species. Finally, through a vegetation removal experiment, I examined the effect of herbaceous and grass edge plant shading on benthic algal growth. Where deciduous, tree-derived organic matter may not be available, detritus from herbaceous plants and grasses growing along the edges of headwater streams may be a critical resource for the stream food web.

Methods

Study Sites

The study was conducted in three headwater streams with riparian vegetation dominated by herbaceous plants and grasses in the Piedmont physiographic province of Maryland, U.S.A. (Table 1). Cattail Creek (CC) (39.322°N, 77.067°W), a tributary of the Hawlings River, drains a 3.37-km^2 watershed that is dominated by row-crop and pasture agricultural land use (61%). Reddy Branch (RB) (39.182°N, 77.067°W), also a tributary of the Hawlings River, drains a 5.15-km^2 watershed that has substantial agricultural land use (56%) and forest (32%). Folly Quarter Creek (FQC) (39.253°N, 76.929°W), a tributary of the Middle Patuxent River, drains a 0.98- km^2 watershed that is largely composed of row-crop agriculture (81%) with some forest (17%). All three streams have at least a 3-m wide riparian buffer composed entirely of herbaceous forbs and grasses (no tree cover).

Edge vegetation standing crop and associated fauna

The edge vegetation along a 75-m reach within each site was sampled 22 October – 6 November 2001. The open-end frame of a large 0.25-m^2 Surber sampler (150 μm mesh size) was placed over a randomly selected 0.5-m length of stream edge. All overhanging and submerged vegetation inside the frame was clipped and collected in plastic bags. Vegetation consisted of both detritus and live plant material (at time of collection, 2:1 ratio of detritus:live vegetation, unpublished data). A total of eight replicate samples per reach was collected. Vegetation in each sample was sorted in the laboratory and identified to lowest taxonomic level. Vegetation was dried at 60°C for at least three days, weighed, and then ashed at 550°C for one hour to determine ash-free dry mass (AFDM) of plant material per meter stream length. I assumed that in addition to the submerged vegetation, all vegetation overhanging the edge would also become in-stream detrital material. Initial per-length estimates taken from a single-side of the stream were doubled to account for inputs from both vegetated banks. I then divided that number by average stream width for each site to determine g AFDM m^{-2} so that the reported results were comparable to those of other studies that measured inputs and standing crops of detritus on a per-area basis.

I was also interested in the stream macroinvertebrates that were associated with the submerged portion of overhanging edge vegetation. Prior to drying clipped vegetation, all macroinvertebrates from each sample were washed from the vegetation and stored in 70% ethanol. They were then identified to lowest practical taxonomic level and assigned to functional feeding groups (Merritt and Cummins 1996, Thorp and Covich 2001).

Decomposition experiment

Four herbaceous and grass species that dominated the study sites and many other open-canopy streams were collected from local streambanks in September 2001. Two of the species were dicots and included one native species, *Impatiens capensis* Meerb. (Jewelweed), and one invasive, *Polygonum perfoliatum* L. (Tearthumb). The other two species were monocots and also included one native species, *Panicum dichotomiflorum* Michx. (Spreading witchgrass), and one invasive species, *Microstegium vimineum* Trin. (Asian stiltgrass). For each species, fresh cut leaves and stems were wet-weighed and placed into seven replicate mesh-bag packs. A regression of wet-mass to AFDM was developed for each species and used to determine initial AFDM of leaf packs (Range: 0.36-1.41 g). Dried samples of each species were also analyzed for C:H:N content (Research Environmental Analysis Lab, University of Maryland).

On 15 September 2001 (Day 0), all mesh-bag leaf packs were attached to the bottom of a 10-m reach of Folly Quarter Creek (discharge = 4.58 L s^{-1}) with tent stakes and cable ties such that packs were suspended in flow. Packs were arranged in seven groups of four packs with one pack from each species per group. Leaf pack groups were collected from the most downstream to upstream positions on days 2, 9, 16, 23, 30, 37, and 44. Packs were collected underwater in a Ziplock© bag (S.C. Johnson & Son, Racine, WI, USA) and placed on ice. In the lab, bag contents were rinsed through a 500µm sieve and the leaf pack and mesh bag were thoroughly rinsed to collect macroinvertebrates and remaining leaf contents. Leaf contents were placed in pre-weighed tins, dried for 24 hours at 60°C, and combusted at 550 °C for one hour to determine AFDM (g) remaining. Macroinvertebrates were stored in 70% ethanol, identified to lowest practical taxonomic level, and assigned to functional feeding groups (Merritt and Cummins 1996, Thorp and Covich 2001).

Data Analysis

The decomposition rate (*k*) of each species was determined using the exponential decay model, $W_t = W_0 e^{-kt}$, where W_0 is the intial mass, W_t is the mass remaining after time t and *k* is the decomposition rate (Petersen and Cummins 1974, Webster and Benfield 1986). To estimate decomposition rates for each species, an ANCOVA was used to analyze $\ln(W_t - W_0)$ as a function of day, species, and the interaction between day and species (Proc Mixed, SAS v. 8.2, SAS Institute Inc., Cary, NC, USA). Initial dry mass was fixed so no intercept was fit for the decay models. Residuals were examined to ensure the assumptions of normality and homogeneity of variance were met. An ANCOVA was used in order to make pairwise comparisons between the decomposition rates of each leaf species, *i.e.*, to test for differences among the slopes of the regression lines for each species (Day x Species interaction, Littell et al. 2006). Adjustments for multiple comparisons were made using the Bonferroni correction. Simple linear regression was then used to analyze decomposition rate as a function of leaf quality (% N) (Proc Reg, SAS v. 8.2).

Similar to the calculation and analysis of leaf decomposition rates, an ANCOVA was used to calculate shredder colonization rates and then compare colonization rates among the four leaf species treatments.

Benthic algal growth

In July 2002, two 25-m reaches (upper, lower) were established at Folly Quarter Creek, separated by a 50-m length of stream. No side tributaries entered the stream within the study length, and no significant differences among the upper and lower reaches were measured in water chemistry, ambient light input, channel width, depth or flow ($p > 0.05$). On 18 July 2002, unglazed ceramic tile sets were deployed in three transects (upstream, midstream, downstream) across the width of the stream in the upper and lower reaches. Each tile set consisted of 12, 5.29-cm^2 individual tiles connected to one another in a 3 x 4 rectangular array. Tile sets were staked to the streambed in a consecutive line across the width of the stream (two - five sets/transect depending on stream width) and were oriented perpendicular to flow. On 31 July 2002 (13 days later), all tile sets were collected from the three transects in each reach. On 1 August 2002, the herbaceous and grass vegetation growing along the stream edge of the lower reach was trimmed to a width of 1-m on each side. Vegetation clippings were carefully removed by hand to avoid leaf litter inputs to the stream. The clipped treatment was maintained with bi-weekly hand-trimming. On 14 September 2002, three tile transects were re-deployed in both the unclipped upper reach and lower clipped reach as above. Tiles were collected on 28 September 2002 (14 days later).

Following removal from the stream, tile sets were immediately wrapped in aluminum foil to prevent degradation of chlorophyll *a* due to ambient light, placed on ice, and returned to the lab for processing. Six individual tiles from each component set comprising each transect were processed for chlorophyll *a*. To dislodge algae, tiles were submerged in a shallow bath of distilled water and scrubbed with a stiff-bristled brush under low-light conditions. This water, as well as that used to rinse the brush and aluminum foil, were filtered through a 0.70µm Whatman® GF/F filter (Whatman, Brentford, Middlesex, UK). Chlorophyll *a* for each tile set in each transect was extracted by placing filters in 15-mL 90% ethanol for at least 48 hours. Concentrations of chlorophyll *a* were determined with a spectrophotometer (Steinman and Lamberti 1996), substituting the absorption coefficient for ethanol extraction derived from Nusch (1980). Chlorophyll *a* values for each set were standardized by tile area and by day to determine accumulation rates (mg m^{-2} d^{-1}).

Data analysis

Mean chlorophyll *a* accrual rates were calculated for each transect in upper and lower reaches, before and after vegetation removal. A two-factor ANOVA (Proc Mixed, SAS v.8.2) was used, weighting transect means by the number of tile sets in each transect, to determine differences in chlorophyll *a* accrual rates between upper and lower reaches before and after vegetation removal (Smith 2002). Recognizing the design limitations because I did not replicate the control and vegetation removal reaches across multiple stream sites (Hurlbert 1984), I urge caution that the scope of inference for the results of the vegetation removal experiment is limited to this study site.

Results

Edge vegetation standing crop and associated fauna

The standing crop of vegetation overhanging the edge of Cattail Creek averaged 276.4 g AFDM m^{-2} (SE = 81.8, n = 8) (Table 2). Monocots, namely grasses (Poaceae), dominated the edge, comprising 93.7% of the total edge crop. Identification of grasses and other monocots to species was difficult as many of the plants lacked flowers, a key feature for correct identification. Dicots at Cattail Creek included smartweed (*Polygonum* L. sp.: Polygonaceae), goldenrod (*Solidago* L. sp.: Compositae) and other members of the Compositae. Reddy Branch averaged 214.2 g AFDM m^{-2} (SE = 51.0, n = 8), where monocots similarly dominated the edge vegetation (95.2%) and included rice cutgrass (*Leersia oryzoides* L.: Poaceae), rush (*Juncus* L. sp.: Juncaceae) and sedge (*Carex* L. sp.: Cyperaceae). Dicots identified at Reddy Branch also included smartweed (*Polygonum* L. sp.: Polygonaceae) and goldenrod (*Solidago* L. sp.: Compositae) as well as jewelweed (*Impatiens capensis* Meerb.: Balsaminaceae). While Folly Quarter Creek had a much smaller average total crop of edge vegetation than the other two sites, 67.7 g AFDM m^{-2} (SE = 20.2, n = 8), dicots, namely jewelweed (*I. capensis*), comprised a much larger portion of the crop (26.3%). The dominant monocot at this site was the invasive reed canary grass (*Phalaris arundinacea* L.: Poaceae).

Average macroinvertebrate density ranged from 7.4 individuals g^{-1} AFDM edge vegetation at Reddy Branch to 63.7 individuals g^{-1} AFDM edge vegetation at Folly Quarter Creek (Table 3). Ephemeroptera (mostly Leptophlebiidae and Heptageniidae) and Diptera (mostly Chironomidae) were the two most dominant taxa at Cattail Creek and Reddy Branch whereas Diptera (again mostly Chironomidae), Amphipoda (Hyalellidae, Crangonyctidae), and Isopoda (Asellidae) dominated macroinvertebrate density at Folly Quarter Creek. With respect to functional feeding group composition, collector-gatherers represented the largest proportion of individuals across all sites (CC: 74.3%, RB: 34.7%, FQC: 64.6%) (Table 4). Shredders were the second most numerically dominant group (CC: 10.0%, RB: 29.7%, FQC: 19.8%), followed by predaceous invertebrates (CC: 9.3%, RB: 14.3%, FQC: 14.2%). Each stream site had a diverse assemblage of shredder macroinvertebrates, and Plecoptera (Capniidae, Leuctridae), Trichoptera (Limnephilidae, Phryganeidae), and Diptera (Tipulidae) were commonly found at all sites. Folly Quarter Creek was the only site where crustaceans, Isopoda (Asellidae) and Amphipoda (Crangonyctidae, Hyalellidae), numerically dominated the shredder community.

Decomposition experiment

The exponential decay model explained leaf decomposition dynamics in herbaceous plants and grasses well (Figure 2). All curves were highly significant ($p < 0.0001$) and had r^2 values ≥ 0.95. There was a significant effect of species on the leaf decomposition rate, k (ANCOVA, Day x Species, $F_{3,24} = 54.20$, $p < 0.0001$). Jewelweed ($k = 0.082$ day^{-1}) decomposed the fastest, followed by tearthumb ($k = 0.047$ day^{-1}), stiltgrass ($k = 0.027$ day^{-1}), and witchgrass ($k = 0.021$ day^{-1}) (Table 5). The decomposition rates of witchgrass and stiltgrass were not significantly different ($p = 0.32$).

Leaf nutritional quality as measured by nitrogen content varied among the four plant species. Jewelweed had the highest leaf nitrogen content followed by tearthumb, stiltgrass, and witchgrass, respectively (Table 5). A regression of decomposition rate as a function of nitrogen content suggests that decomposition rate was significantly related to leaf nutritional quality ($p = 0.013$, $r^2 = 0.97$) (Figure 3).

Shredding macroinvertebrates including *Caecidotea communis* Cole & Minkley (Isopoda: Asellidae), *Hyalella* S.I. Smith sp. (Amphipoda: Hyalellidae), *Crangonyx* Bate sp. (Amphipoda: Crangonyctidae) and tipulid fly larva (Diptera: Tipulidae) colonized experimental leafpacks linearly over time. As with leaf decomposition, there was a significant effect of leaf species on shredder colonization rate (ANCOVA, Day x Species, $F_{3,\,13.6} = 24.70$, $p < 0.0001$). Similarly, the rates of colonization mirrored the decomposition rates whereby shredders colonized jewelweed the fastest (4.9 shredders g^{-1} AFDM remaining day^{-1}), followed by tearthumb (2.0 shredders g^{-1} AFDM remaining day^{-1}), stiltgrass (0.8 shredders g^{-1} AFDM remaining day^{-1}), and witchgrass (0.6 shredders g^{-1} AFDM remaining day^{-1}) (Table 5, Figure 4). The shredder colonization rates of witchgrass and stiltgrass did not significantly differ ($p = 0.13$).

Benthic algae

Vegetation removal resulted in a dramatic increase in the chlorophyll *a* accumulation rate in the lower reach (1.61 ± 0.14 mg m^{-2} d^{-1}) of Folly Quarter Creek compared to rates measured before clipping within the same reach and during both time periods in the upper reference reach (ANOVA, Reach x Time, $F_{1,8} = 29.75$, $p = 0.0006$). Chlorophyll *a* accrued at similar mean rates in the upper control reach for both time periods (before = 0.02 ± 0.12 mg m^{-2} d^{-1}, after = 0.02 ± 0.14 mg m^{-2} d^{-1}) as well as in the lower treatment reach prior to clipping (0.03 ± 0.17 mg m^{-2} d^{-1}).

Discussion

Large standing crops of plant material (average range: 68 – 276 g AFDM m^{-2}), composed largely of monocots, were found submerged or overhanging the edges at all three open-canopy, agricultural stream study sites. This standing crop was composed of submerged and detrital plant material as well as overhanging vegetation that would eventually enter the stream after plant senescence. Herbaceous plants and grasses fall into the stream while still attached to plants rooted on the bank and remain locally at the site of input. In contrast, the leaves and stems of deciduous trees completely detach from the trees when they enter the stream and are often transported downstream from the site of input. Thus, I found it useful to compare measurements from this study to published estimates of both standing stocks of coarse particulate organic matter (CPOM) (g AFDM m^{-2}) collected locally within stream reaches as well as yearly inputs of leaf litter (g AFDM m^{-2} $year^{-1}$). Estimates of herbaceous plant and grass material at the study sites were similar to standing stocks of CPOM reported for nearby Eastern deciduous streams but slightly less than their yearly litterfall estimates. For example, a CPOM standing crop of 118 g AFDM m^{-2} and litterfall of 313 g AFDM m^{-2} $year^{-1}$ were reported for White Clay Creek (Pennsylvania) (Minshall et al. 1983, Newbold et al. 1997), and 175 g AFDM m^{-2} standing crop CPOM and 459 g AFDM m^{-2} $year^{-1}$ litterfall were reported for the West Fork of Walker Branch (Tennessee) (Mulholland et al. 1985, Mulholland 1997).

Only a few previous studies have examined organic matter in open-canopy streams, and they emphasized algal production as the primary source of organic matter (Matthews 1988, Campbell et al. 1992, Delong and Brusven 1994). These studies reported smaller quantities of coarse particulate organic matter and generally lower litter inputs than I quantified in the edge samples. For example, in treeless reaches of Kings Creek, a North American tallgrass prairie stream, the standing crop of non-woody coarse benthic organic matter (which included grasses, aquatic macrophytes, moss, and algae) ranged from 38 – 43 g AFDM m^{-2} while direct and lateral litter inputs ranged from 118 - 128.1 g AFDM m^{-2} (Gurtz et al. 1988, Gray 1997, Stagliano and Whiles 2002). Similarly, in three southern Illinois agriculturally impacted streams, Stone et al. (2005) reported mean estimates of non-woody coarse benthic organic matter (which included grass, leaves, and corn residues) ranging from

20.9 - 49.2 g AFDM m^{-2}. In the herbaceous plant-lined reaches of Lapwai Creek in northern Idaho, mean input of non-woody organic matter ranged between 1.33 – 112.42 g AFDM m^{-2} for the entire year (Delong and Brusven 1994). In montane tussock grassland streams in New Zealand, Scarsbrook and Townsend (1994) report litterfall generally <12 g AFDM m^{-2}.

The larger quantity of herbaceous and grass organic matter reported in this study may reflect significant differences in the land-water interface between eco-regions. Downstream of their wetland-like headwaters, prairie streams are typically incised and the riparian plants do not necessarily intersect the stream edge nor do they block light to the channel (Whiles, pers. comm.). Inputs of herbaceous material in prairie streams occur seasonally after senescence as a result of lateral blow-in or overland flow during rainstorms (Matthews 1988, Stagliano and Whiles 2002). In the braided stream channels of the New Zealand tussock grasslands, senesced grasses enter the streams following floods (Scarsbrook and Townsend 1994). In contrast, herbaceous vegetation and grasses at the sites used in this study grow so densely along the edges that they fall into the stream while still rooted on the bank (Figure 1). Additionally, evidence from the vegetation removal study suggests that edge vegetation can shade narrow stream channels and limit primary production.

Consistent with the large standing crops of herbaceous and grass organic matter in this study's open-canopy streams, diverse macroinvertebrate shredder assemblages were found living in the submerged edge vegetation, including representatives of the more sensitive orders, Plecoptera (stoneflies) and Trichoptera (caddisflies). These results suggest that herbaceous and grass edge vegetation may be an integral food resource in small streams in non-forested watersheds and directly contrast with observations from other studies of agriculturally impacted streams that found very few shredding invertebrates associated with coarse particulate organic matter (Stone et al. 2005, Hagen et al. 2006). In addition, shredders appeared to respond to differences in leaf nutritional quality in the decomposition experiment; the highest shredder densities and fastest colonization rates occurred on the two dicot species with the fastest decomposition rates (jewelweed and tearthumb) and the highest nitrogen contents. The other two plant species, spreading witchgrass and Asian stiltgrass, have lower leaf quality than the dicots (C:N ratios of the monocots were almost two times higher) and, like other grasses, probably have a high silica content (Lanning and Eleuterius 1987), contributing to their slower rates of decomposition and lower colonization rates by shredders.

Perhaps one of the most interesting findings is that all of the decomposition rates reported here are generally much faster than published rates for tree leaf litter (Webster and Benfield 1986), aquatic macrophytes, and other grasses (e.g., tussock grass in New Zealand; Young et al. 1994, Niyogi et al. 2004). In addition, the herbaceous plants and grasses used in this study have higher percent leaf nitrogen than has been reported for common eastern deciduous tree species (Ostrofsky 1997) (Figure 5). One reason for this difference is that studies of deciduous leaf decomposition typically use autumn-shed litter collected after the trees have reabsorbed nutrients from the leaves. However, I measured decomposition rates on fresh leaves/grass because I frequently observed green plant material trailing into the stream at the field sites. Additionally, elevated nutrient levels, as regularly observed in agricultural streams, may also lead to increased leaf decomposition rates via increased shredder (Robinson and Gessner 2000) and microbial activity (Suberkropp 1998).

While forested buffers are often the preferred condition and restoration endpoint, herbaceous and grassy stream buffers are increasingly common and may have value not only as part of best management practices to decrease erosion and reduce nutrient loads (Maryland Department of Agriculture 1996, Lyons et al. 2000, Wigington et al. 2003), but may promote higher macroinvertebrate diversity in agricultural versus urban streams (Moore and Palmer 2005). While other studies suggest that small reductions in forest cover reduce terrestrial-aquatic linkages via a decline in deciduous tree leaf litter inputs (England and Rosemond 2004), I suggest that inputs of leaf material from herbaceous plants and grasses growing along small stream edges may provide significant organic matter to stream ecosystems. The fact that the herbaceous and grass organic matter measured in this study were similar in magnitude to standing crops and inputs in nearby small deciduous forest streams and that this organic matter is rich in nitrogen suggests that herbaceous and grass leaf material may be an important food resource in small, open-canopy streams where algal growth can be limited by the low-level canopy created by the dense edge vegetation. Certainly the high rates of decomposition I report suggest that stream macroinvertebrates and microbes readily use herbaceous plant and grass material as an energy source. The extent to which this detritus makes its way to higher trophic levels remains an open question. The use of stable isotopes would be one method to confirm the potential contribution of herbaceous plant and grass material to food webs in open-canopy headwater streams (Mulholland et al. 2000, Huryn et al. 2001, Finlay et al. 2002).

Given the rampant and extensive conversion of forested watersheds to agricultural and residential land use, ‘classic’ forested headwater streams, where much of our understanding of stream organic matter and food web dynamics was developed (Hynes 1975, Vannote et al. 1980, Wallace et al. 1997), are becoming less and less common (Meyer and Wallace 2001, Meyer et al. 2003). Indeed in many regions, urbanization pressures are so great that agricultural watersheds with headwater streams with riparian vegetation dominated by herbaceous plants and grasses are viewed as the primary form of undeveloped land. In fact, land preservation programs have been implemented to promote their conservation (Jacobs 1999, Moore and Palmer 2005). Thus, I encourage the continuation of basic ecological research on streams with edges of herbaceous plants and grasses as they will only become more important over time. Understanding the organic matter dynamics in open-canopy headwater streams is particularly critical because these dynamics may exert important control over food webs in open-canopy lotic ecosystems.

Tables

Table 1. Characteristics of stream study sites; CC = Cattail Creek, RB = Reddy Branch, FQC = Folly Quarter Creek.

Site	Watershed size (km^2)	Mean width (m)	Mean depth (m)	Mean bank height (m)	Mean baseflow discharge ($L\ s^{-1}$)
CC	3.37	0.83	0.18	0.78	4.16
RB	5.15	1.16	0.20	0.62	14.57
FQC	0.98	0.61	0.19	0.51	3.32

Table 2. Biomass per m^2 of edge vegetation found at three open-canopy study streams. Means ± 1 SE and median are presented for monocots, dicots, and total g ash-free dry mass (AFDM) m^{-2} per site (n = 8 samples per site).

	Monocot (g AFDM m^{-2})		**Dicot (g AFDM m^{-2})**		**Total (g AFDM m^{-2})**	
Site	**Mean (SE)**	**Median**	**Mean (SE)**	**Median**	**Mean (SE)**	**Median**
CC	259.0 (83.7)	193.9	17.4 (6.8)	11.8	276.4 (81.8)	213.7
RB	203.9 (50.9)	177.3	10.3 (3.5)	6.7	214.2 (51.0)	178.0
FQC	49.9 (20.3)	18.8	17.8 (13.9)	4.5	67.7 (20.2)	40.3

Table 3. Average density (± 1 SE) of macroinvertebrate taxa collected in vegetation from edge samples at three open-canopy streams. Density is reported as number of individuals per gram AFDM of herbaceous and grass vegetation collected from stream edge (n = 8 samples per site).

		Site	
Taxon	**CC**	**RB**	**FQC**
Insects			
Ephemeroptera	6.7 (5.1)	3.1 (1.9)	0.1 (0.1)
Odonata	0.2 (0.1)	0.1 (0.1)	0.6 (0.2)
Hemiptera	0	<0.1 (<0.1)	0.2 (0.1)
Plecoptera	0.3 (0.2)	0.7 (0.3)	0.2 (0.1)
Megaloptera	0	<0.1 (<0.1)	<0.1 (<0.1)
Trichoptera	1.6 (0.9)	0.9 (0.6)	0.8 (0.2)
Lepidoptera	0	<0.1 (<0.1)	0.1 (0.1)
Coleoptera	2.9 (2.3)	0.4 (0.3)	2.2 (0.7)
Diptera	4.0 (2.0)	1.2 (0.8)	49.7 (16.1)
Non-insects			
Isopoda	0	0	4.8 (3.0)
Amphipoda	0	0.2 (0.2)	5.0 (2.8)
Nematomorpha	0	0.1 (0.1)	0.1 (0.1)
Oligochaeta	<0.1 (<0.1)	0.7 (0.4)	0.1 (0.1)
Total	**15.7 (10.3)**	**7.4 (4.1)**	**63.7 (18.8)**

Table 4. Average density # (± 1 SE) and percent contribution to total % for each macroinvertebrate functional feeding group collected in vegetation from edge samples. Density is reported as number of individuals per gram AFDM of herbaceous and grass vegetation collected from stream edge (n = 8 samples per site).

	Site					
	CC		**RB**		**FQC**	
Functional Feeding Group	**#**	**%**	**#**	**%**	**#**	**%**
Collector-gatherer	12.6 (8.8)	74.3	4.1 (2.8)	34.7	46.3 (15.0)	64.6
Collector-filterer	0.5 (0.4)	4.1	0.1 (0.1)	4.1	0.2 (0.1)	1.3
Shredder	1.4 (0.8)	10.0	1.7 (0.8)	29.7	10.8 (5.8)	19.8
Scraper	0.1 (<0.1)	1.0	0.3 (0.2)	8.4	0	0
Predator	1.0 (0.6)	9.3	0.4 (0.2)	14.3	6.1 (1.7)	14.2
Deposit feeder	<0.1 (<0.1)	1.3	0.7 (0.4)	8.7	0.1 (0.1)	0.1

Table 5. Results from decomposition experiment using four common species of herbs and grasses found at study sites. Decomposition rates *k* (± 1 SE) and shredder colonization rates (± 1 SE) were estimated using ANCOVA and are all significantly different from 0 ($p < 0.0001$). Different letters indicate significantly different ($p < 0.05$) decomposition and shredder colonization rates determined using multiple comparisons tests with the Bonferroni correction.

Species	***k* (day^{-1})** **(SE)**	***r*^{2}**	**% C**	**% N**	**C:N**	**Colonization rate** **(Individuals g^{-1} AFDM remaining day^{-1})** **(SE)**
Jewelweed	0.082 **a** (0.004)	0.97	46.59	4.02	11.59	4.9 **a** (0.74)
Tearthumb	0.047 **b** (0.004)	0.95	46.43	2.87	16.18	2.0 **b** (0.2)
Witchgrass	0.021 **c** (0.004)	0.95	43.77	1.77	24.73	0.6 **c** (0.2)
Stiltgrass	0.027 **c** (0.004)	0.98	47.30	2.33	20.30	0.8 **c** (0.1)

Figure legends

Figure 1. Contrasting the edge of an open-canopy headwater stream, Cattail Creek, surrounded by agricultural fields (left), and a Piedmont stream with a "classic" deciduous forest edge (right). Photo credits: Left, H.L. Menninger; Right, L.S. Craig.

Figure 2. Fraction of initial AFDM remaining over the course of the decomposition experiment (44 days). Filled shapes indicate dicots (circle = jewelweed, JW; triangle = tearthumb, TH). Open shapes indicate monocots (circle = witchgrass, WG; triangle = stiltgrass, SG). Circles indicate native plant. Triangles indicate invasive plant.

Figure 3. Linear regression showing a positive relationship between decomposition rate (*k*) and leaf nitrogen content ($p = 0.013$, $r^2 = 0.97$). Symbols as in Figure 2. Error bars represent ± 1 SE calculated from ANCOVA.

Figure 4. Colonization of shredders (individuals g^{-1} AFDM remaining) over the course of the decomposition experiment (44 days). Symbols as in Figure 2. All slopes (representing the colonization rate) are significantly different from 0 ($p < 0.05$), and different letters indicate significantly different shredder colonization rates ($p < 0.05$) for each plant species.

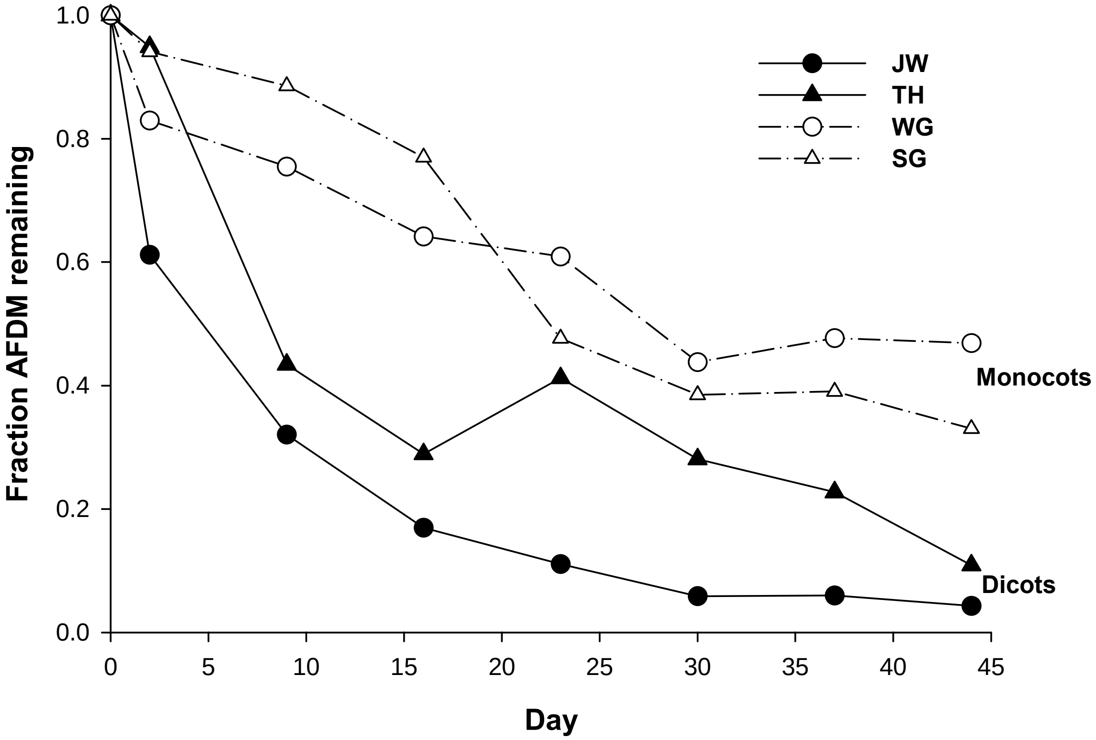
Figure 5. (a) The leaf nitrogen content and (b) the decomposition rate, k ± 1 SE

(day $^{-1}$), of herbaceous plants and grasses used in this study compared to published values (Ostrofsky 1997; Swan & Palmer 2004) for common deciduous riparian trees in the eastern Piedmont, U.S.A.: black willow (*Salix nigra* Marshall), box elder (*Acer negundo* L.), silver maple (*Acer saccharinum* L.), sycamore (*Platanus occidentalis* L.) and slippery elm (*Ulmus rubra* Muhl.) Dark bars represent herbaceous dicots, open bars represent grasses, and hatched bars represent deciduous riparian tree species.

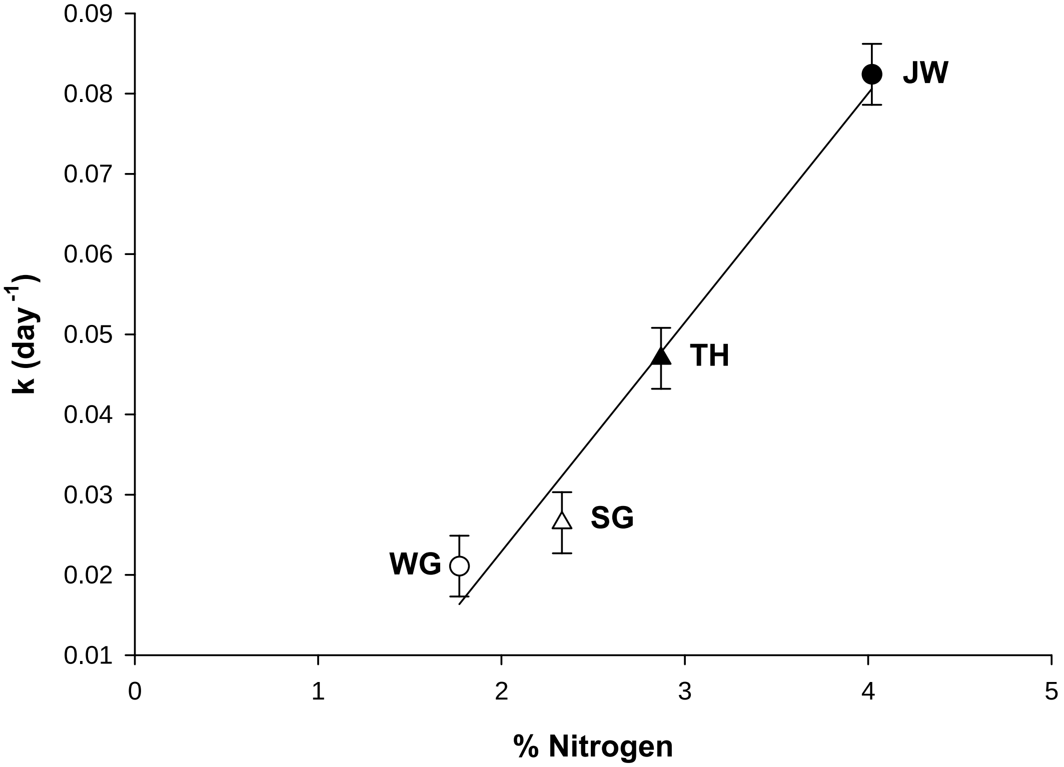
Figures

(Figure 1)

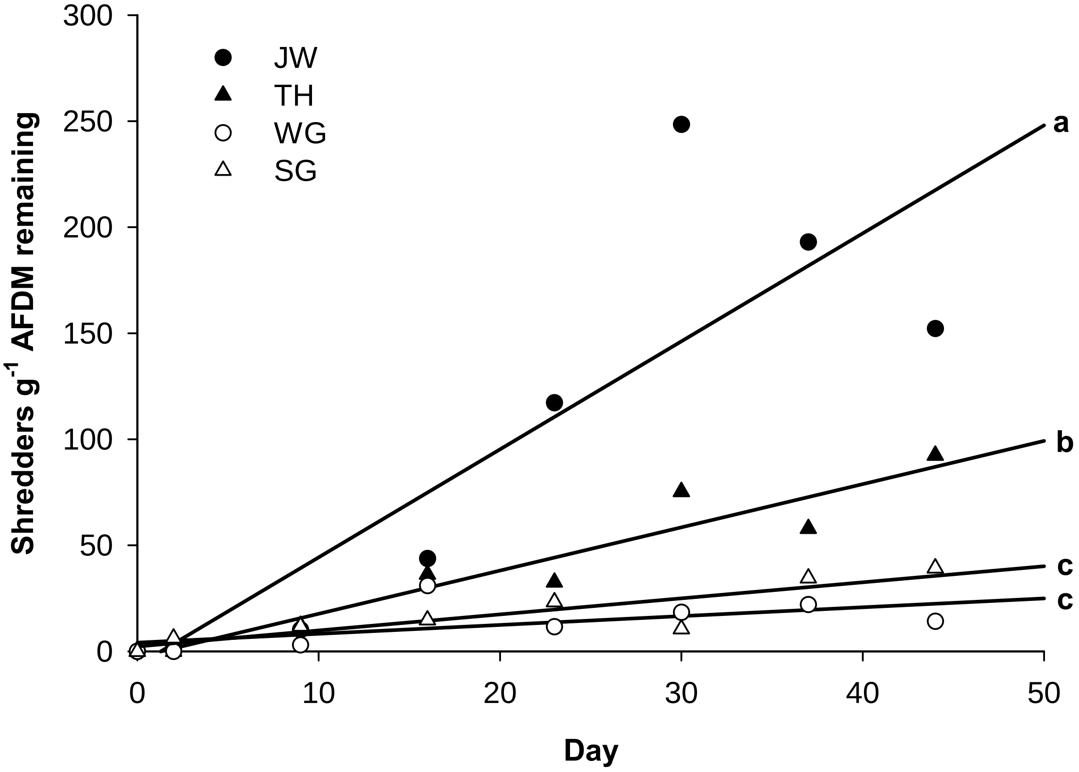
(Figure 2)


1.0
0.8
0.6
0.4
0.2
0.0
Fraction AFDM remaining
0
5
10
15
20
25
30
35
40
45
Day
JW
TH
WG
SG
Monocots
Dicots

(Figure 3)

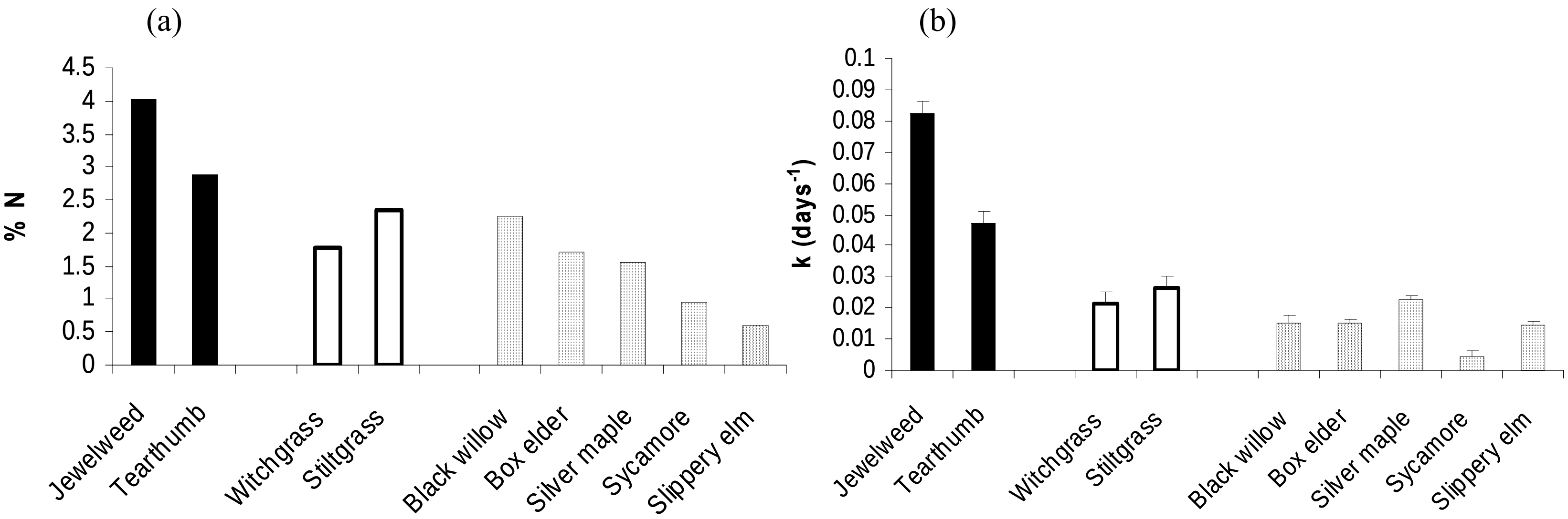

0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
k (day^{-1})
0
1
2
3
4
5
% Nitrogen
JW
TH
SG
WG

(Figure 4)



300
250
200
150
100
50
0
0
10
20
30
40
50
Day
Shredders g^{-1} AFDM remaining
● JW
▲ TH
○ WG
△ SG
a
b
c
c

(Figure 5)


(a)
% N
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
Jewelweed
Tearthumb
Witchgrass
Stiltgrass
Black willow
Box elder
Silver maple
Sycamore
Slippery elm
(b)
k (days-1)
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
Jewelweed
Tearthumb
Witchgrass
Stiltgrass
Black willow
Box elder
Silver maple
Sycamore
Slippery elm

Chapter II: Periodical cicada detritus impacts stream ecosystem function

Abstract

In May 2004, the emergence of the Brood X seventeen-year periodical cicadas (Cicadidae: *Magicicada* sp.) provided a unique opportunity to study the effect of a large, but temporally limited, resource pulse of arthropod detritus on ecosystem function in two small streams in Maryland. I hypothesized, given the large quantity and high quality of cicada detritus entering streams, that this multi-annual resource pulse would be readily consumed by heterotrophic microbes and invertebrates, resulting in an increase in whole-stream respiration. Cicada emergence dynamics were quantified in the riparian forests adjacent to two small streams, where one site had not been disturbed in the 17 years prior to the 2004 emergence (Intact) and the other had experienced recent habitat modification (Disturbed). I estimated the input of cicada detritus to the streams, described the subsequent retention and in-stream decomposition dynamics of cicada detritus, and measured whole-stream community respiration over the course of the adult cicada flight season (55 days, May-July 2004). Average emergence density was greater in the Intact riparian forest (25 cicadas m^{-2}) compared to the Disturbed (5 cicadas m^{-2}), but average cicada detritus input rates to the stream were greater at the Disturbed site ($p < 0.05$). Significant cicada detritus input rates occurred 13-35 days after the onset of emergence, and at peak (Intact: 0.349 g m^{-2} d^{-1}; Disturbed: 0.575 g m^{-2} d^{-1}), were an order of magnitude greater than other terrestrial arthropod input rates. Experiments suggested that a dead cicada falling into the stream was transported only 12.64 m, before being locally retained by debris dams, root wads, and overhanging edge vegetation in the stream. Cicadas decomposed very quickly ($k = 0.03$ day^{-1}), compared to leaf litter, and were colonized by both microbes and invertebrate detritivores. Daily whole-stream community respiration at both sites responded dramatically to the cicada pulse, doubling pre-cicada baseline measurements following the time period of greatest cicada input (Intact: 12.82 → 23.78 g O_2 m^{-2} d^{-1}; Disturbed: 2.76 → 5.77 g O_2 m^{-2} d^{-1}). Respiration returned to baseline levels when cicada input decreased at the Intact site, but more than doubled again at the Disturbed site (13.14 g O_2 m^{-2} d^{-1}), despite a decline in cicada input rate. I posit that differences in the respiration response of the Intact and Disturbed streams to the cicada pulse may be a function of differences in cicada input rates over the cicada flight season as well as differences in microbial community activity. The short but intense input of periodical cicada detritus to streams following the Brood X emergence appears to have exerted strong effects on stream ecosystem function, providing a unique example of a terrestrially-derived resource pulse affecting an adjacent aquatic system.

Introduction

Inputs of nutrients, detritus or prey from an adjacent donor ecosystem (Polis et al. 1997) are critical to the ecosystem dynamics of a number of recipient systems, including systems as diverse as desert islands (Polis and Hurd 1995, Anderson and Polis 1999), intertidal zones (Menge et al. 2003), and freshwater lakes (Pace et al. 2004, Carpenter et al. 2005). Most well known in eastern deciduous forests of North America, leaf litter entering streams each autumn provides an *annual* pulse of detritus and nutrients that fuels stream ecosystem processes (Fisher and Likens 1972, Webster and Meyer 1997, Gessner and Chauvet 2002) and structures stream food webs (Wallace et al. 1997). Recently, it has been found that fluxes of terrestrial invertebrates to streams, occurring annually but particularly in the summer months, are important to fish predator diets and lead to trophic interactions that influence stream ecosystem function (Cloe and Garman 1996, Nakano et al. 1999, Baxter et al. 2004, Baxter et al. 2005).

Pulses occurring irregularly or at time scales greater than one year may also have major consequences for food web and ecosystem dynamics (Ostfeld and Keesing 2000). Acorn masting by oak trees, for example, has been linked to outbreaks of white-footed mice populations that in turn may affect the dynamics of the gypsy moth as well as the incidence of Lyme disease (Ostfeld et al. 1996, Jones et al. 1998b, a). Recently, Yang (2004) examined the effect of the 17-year periodical cicadas on forest processes; cicada detritus falling to the forest floor decomposed, resulting in an increase in microbial biomass and nitrogen availability, which then positively affected the growth and reproduction of understory plants.

Periodical cicadas (Cicadidae: *Magicicada* sp.) emerge synchronously and in such incredibly dense numbers that they have been reported as among the most abundant (in number and biomass) of all forest insects (Dybas and Davis 1962). Adult periodical cicadas quickly satiate predators such as birds and small mammals (Karban 1982, Williams et al. 1993), and thus most die of natural causes two to six weeks after emergence and fall from trees as detritus. In riparian forests, periodical cicada density has been reported as high as 370 individuals m^{-2} (Dybas and Davis

1962). I hypothesized that a portion of the cicada detritus would fall from riparian trees into nearby streams, providing a terrestrially derived resource pulse to stream organisms that may be quite different from the live terrestrial arthropod and leaf litter subsidies that occur annually to streams. Indeed, periodical cicadas as well as other terrestrial arthropods have a much lower carbon:nitrogen (C:N) ratio than the leaves of common riparian tree species (Figure 1), and are considered a high quality resource for heterotrophic organisms.

I quantified the 2004 emergence dynamics of Brood X periodical cicadas in the forests adjacent to two streams, estimated the input of cicada detritus to the streams, and described their subsequent retention and in-stream decomposition dynamics. I hypothesized that the large pulse of high resource quality (low C:N) periodical cicada detritus would be readily consumed by in-stream heterotrophs. Consequently, I measured whole-stream community respiration over the course of the adult cicada flight season and predicted that respiration would increase following the input of cicadas. The input of periodical cicadas offers an extraordinary opportunity to record the effect of a large terrestrial arthropod resource pulse on stream ecosystems.

Methods

Study organism

Seventeen-year periodical cicadas in Brood X (Cicadidae: *Magicicada* sp.) emerged throughout the Midwest and Mid-Atlantic in May 2004. The immature cicada nymphs had spent the previous 17 years below the forest floor feeding on xylem fluid in tree roots (Marlatt 1907, Brown and Chippendale 1973, White and Strehl 1978, Williams and Simon 1995). In early May, nymphs tunneled up to the soil surface where they were consequently cued by light, temperature, and soil conditions to emerge en masse from their individual underground chambers (Heath 1968, Williams and Simon 1995). Their emergence leaves distinct 13-17 mm diameter holes that are often surrounded by mud turrets (Dybas and Davis 1962). After molting into winged, sexually mature adults on nearby vertical surfaces (e.g. tree trunks), males and females flew to tree tops and shrubs where they engaged in boisterous courtship behavior. Males sing loud, species-specific choruses to attract females (Alexander and Moore 1958, Dunning et al. 1979). Following mating, females oviposited in small twigs and branches (Marlatt 1907). Small nymphs hatched from the eggs within several weeks and fell to the forest floor where they burrowed into the soil and began feeding on root xylem for the next 17 years (Cory and Knight 1937, Williams and Simon 1995).

Study sites

This study took place along two suburban streams near Washington, D.C., in the Piedmont physiographic province of Montgomery County, Maryland, USA. Both streams are first-order tributaries of the Northwest Branch, a larger stream in the Chesapeake Bay watershed. The first study site, hereafter the “Intact” site (39° 4’ 57” lat, 77° 1’ 26.04” long) drains a 3.24 km^2 watershed (Table 1). The Intact site has an extensive riparian forest that has been undisturbed for at least the last 17 years due to proactive conservation efforts (Moore and Palmer 2005). It is mature secondary forest with a tree density of 11 trees per 100 m^2, dominated by sycamore (*Platanus occidentalis* L.) and tulip poplar (*Liriodendron tulipifera* L.), with a thick under-story of sassafras (*Sassafras albidum* Nutt.). After leaf-out, canopy cover above the stream is ~97%.

The "Disturbed" site (39° 7' 12" lat, 77° 0' 32.40" long) drains a slightly larger watershed (4.01 km^2), but has a much narrower riparian zone, limited largely to one side of the stream and consisting of tulip poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrh.), and pin oak (*Quercus palustris* Muenchh.) in a low density of 0.3 trees per 100 m^2. Despite the narrow riparian zone, the stream is ~94% covered by the forest canopy after leaf-out. Portions of the riparian zone were removed in 2002 to create a vehicle access point for nearby construction. In addition, in 2003, as part of a wetland mitigation project, much of the soil adjacent to one side of the narrow riparian forest was excavated and transported offsite. Young riparian trees including green ash (*Fraxinus pennsylvanica* Marsh.), sycamore (*Platanus occidentalis* L.), red maple (*Acer rubrum* L.), box elder (*Acer negundo* L.), pin oak (*Quercus palustris* Muenchh.), swamp white oak (*Quercus bicolor* Willd.), black willow (*Salix nigra* Marsh.), red osier dogwood (*Cornus sericea* L.), speckled alder (*Alnus rugosa* L.), and tulip poplar (*Liriodendron tulipifera* L.) were planted on the site (Joe Berg, Biohabitats Inc., pers. comm.).

Two sites with very different riparian forest characteristics and histories of disturbance were chosen to compare in-stream dynamics between sites that differed in expected cicada emergence densities. Intensive sampling of more than two streams was impossible because of the short cicada flight season and rigorous methods necessary to measure stream ecosystem function. My results technically only apply to these two streams (Hurlbert 1984), within which I do have replicated sampling over time.

Emergence density

In April 2004, prior to periodical cicada emergence, four linear transects were randomly established at each site that extended perpendicularly from the stream bank into the riparian forest. Transects extended into the forest on both sides of the stream, and points were marked at 1, 5, 10 and 20 m from the stream (n = 32) (Figure 2). Twelve emergence cages were randomly set throughout the riparian forest at each site and were used to determine that periodical cicada emergence commenced 12 May (hereafter, Day 0), and was completed by 24 May 2004 (Day 12). The density of emergence holes in a $0.16m^2$ area was then measured at each transect point. Evidence from the emergence traps corroborated data from other studies that only one cicada emerges from each hole (Dybas and Davis 1962, Whiles et al. 2001); thus, density of emergence holes accurately represents emergence density of cicadas.

Greater cicada emergence at the Intact site versus the Disturbed site was predicted and tested by comparing emergence density between sites, with distance from the stream as a covariate, using an ANCOVA (Proc Mixed, SAS v. 8.2, SAS Institute Inc., Cary, NC, USA). Emergence data were transformed using a square-root (x + 0.5), as recommended by Sokal & Rohlf (1995) for count data, ensuring assumptions of normality and homogeneity of variance.

Allochthonous inputs

Prior to cicada emergence, four litter traps, one per transect, were deployed in each stream (Figure 2). Traps were constructed from plastic baskets (0.24 m^2) that were cable-tied to rebar supports, and elevated approximately 1m above the water. Traps collected allochthonous inputs (plant and arthropod) falling into the channel from adjacent banks or overhanging forest canopy. Litter traps were emptied every five to nine days through Day 55 (6 July 2004). Contents were sorted as periodical cicada, other terrestrial arthropod, or plant material, dried at 60˚C, and weighed to determine rate of allochthonous input (g DM m^{-2} day^{-1}) over eight roughly similar time intervals (Average: 7 days, Range: 5-9).

Allochthonous input rates of cicadas, other terrestrial arthropods, and deciduous tree leaf litter were compared between sites over the eight time intervals using mixed model repeated measures ANOVA (Proc Mixed). A spatial power covariance error structure was used for cicada input rates to account for correlations among errors declining exponentially with distance in time and unequal time intervals, and a compound symmetry covariance error structure was used for other terrestrial arthropod and leaf litter input rates (Littell et al. 2006). Rates were transformed using a log(x) or log(x+1), depending on the presence of 0 values, to ensure assumptions of normality and homogeneous variance.

Retention

Field observations suggested that periodical cicadas that fell into the stream, whether dead or alive, floated. Often they became trapped in the shallow sediments and rocks on the edges of the stream and in riffles, or were retained in leaf packs, root wads, and debris dams. To estimate the retention rate of cicadas at the two sites, I employed methods previously used by stream ecologists to determine leaf litter retention rates (Speaker et al. 1988, Webster et al. 1994, Brookshire and Dwire 2003). Using wetted corks (density 0.203 g/cm^3) as a surrogate for periodical cicadas (density 0.487g/cm^3), batches of corks (n = 800/release) were released into a 60 m length of stream at each site. After one hour, the distance traveled by each cork retained in the length was measured.

The cork retention rate was calculated from the negative exponential decay equation:

$$T_d = T_0 e^{-kd}$$

where T_d is the proportion of corks still in transport (not retained) at some distance (d) below the release point, $T_0 = 1$, and k is the instantaneous rate of removal of corks from transport per meter, or the retention rate (Young et al. 1978, Brookshire and Dwire 2003). The mean transport distance S_p was then calculated by taking the inverse of k ($1/k$). The cork retention rate k was compared between streams using an ANCOVA to analyze $\ln(T_d - T_o)$ as a function of distance as well as the interaction between distance and site (Proc Mixed). T_o was fixed to 1 so no intercept was fit for the decay models. Residuals were examined to ensure the assumptions of normality and homogeneity of variance.

Decomposition dynamics

To quantify the in-stream breakdown of cicada detritus, "packs" of known-masses of dead cicadas were assembled, and the mass loss of the packs over time was measured (Petersen and Cummins 1974, Swan and Palmer 2004). Dead periodical cicadas were collected from Prince George's, Anne Arundel and Montgomery counties, Maryland, during peak emergence in late May 2004 and were immediately frozen. Approximately 10 g of cicadas (~20 cicadas on average) were wet-weighed and placed in double-bagged mesh produce bags (8 mm x 3 mm effective mesh size), secured closed with cable-ties. At each site, ten rows of four cicada packs were attached with tent stakes and cable ties to areas of the stream bottom with similar flow environments (mean = 0.19 m s^{-1}; SD = 0.07) on 16 June 2004 (Decomp day 0).

To calculate the initial mass for cicada packs, ten samples of cicadas were wet-weighed, dried at 60°C, and re-weighed for dry biomass to determine a wet:dry mass conversion factor (0.46). Four cicada packs were collected on decomp days 1, 3, 5, 12, 20, 26, 33, 43, 62, and 98, beginning with the most downstream rows. Packs were placed immediately on ice and returned to the lab where contents were gently washed and sorted. Cicada pieces were dried at 60°C and weighed to determine dry mass remaining.

The decomposition rate (*k*) was determined using the exponential decay model:

$$W_t = W_0 e^{-kt}$$

where W_0 is the intial mass, W_t is the mass remaining after time t and *k* is the decomposition rate (Petersen & Cummins 1974; Webster & Benfield 1986). To estimate and compare decomposition rates between sites, I used an ANCOVA to analyze $\ln(W_t - W_o)$ as a function of day, site, and the interaction between day and site (Proc Mixed). Initial dry mass was fixed so no intercept was fit for the decay models. Residuals were examined to ensure the assumptions of normality and homogeneity of variance. In addition, I calculated the average biological turnover time T_b (days) by taking the inverse of k ($1/k$).

Community respiration

At each site, community respiration over a 24 hour period was measured once prior to cicada emergence (Day -14) and three times throughout the cicada flight season (Day 12, 26, 40) at each site. The single-station diel oxygen method described by Bott (1996) was used. Dissolved oxygen (DO) concentrations were measured every hour with a MiniSonde multiprobe (Hydrolab, Austin, TX, USA) for 24 hours. The net rate of oxygen change due to metabolism was calculated for each 1-hour interval, accounting for exchange of oxygen from the stream to the atmosphere. The surface renewal model was used to empirically derive the reaeration coefficient, k, using stream velocity and depth (Owens et al. 1964). Daily rate of community respiration (CR_{24}) was calculated by multiplying the average hourly rate of oxygen change over the nighttime hours (22:00 – 6:00 hrs) by 24.

Changes in CR_{24} were compared on the three dates following cicada emergence to pre-cicada CR_{24} within each site. Pearson correlation analyses were performed between CR_{24} and cicada input rate in the time interval just prior to respiration measurements as well as physical factors known to affect respiration (water flow and temperature). Additionally, CR_{24} at the two focal sites was compared to similar measurements collected in the spring of a non-cicada year (May 2001) from nearby small, forested streams.

Results

Emergence

As predicted, the emergence density in the Intact riparian forest was significantly higher than the Disturbed forest (*site*: $F_{1,60} = 19.05$, $p < 0.0001$). On average, there were 25.3 (95% CI: 18.2-33.4) emergence holes m^{-2} at the Intact site compared to 5.1 (95% CI: 2.1-9.1) holes m^{-2} at the Disturbed site (Figure 3). There was no effect of distance from the stream on emergence density at each individual site (*site x distance*: $F_{1,60} = 2.16$, $p = 0.15$) or when considering data from both sites combined (*distance*: $F_{1,60} = 0.08$, $p = 0.78$).

Allochthonous inputs

The pattern and rate of input of allochthonous material to the Intact and Disturbed sites varied greatly, depending largely on the type of resource. Significant cicada detritus input rates at each site occurred between 13 and 35 days after the onset of emergence (*day*: $F_{7,40.2} = 21.41$, $p <.0001$) (Figure 4, Table 2), with maximum input rates occurring between Day 21 and 26 at both the Intact site, with 0.349 g m^{-2} d^{-1}(95% CI: 0.223 – 0.488), and the Disturbed site with 0.575 g m^{-2} d^{-1} (95% CI: 0.447 – 0.714). Allochthonous input of cicada detritus to the streams ceased by Day 55. Across all time intervals combined, the Disturbed site had significantly greater cicada input rates than the Intact site (*site*: $F_{1,28.9} = 5.15$, $p = 0.03$), contrasting the observations of lower emergence density at this site compared to the Intact site.

The mean input rates of other terrestrial arthropods to the Intact and Disturbed sites ranged from 0.001 – 0.042 g m^{-2} d^{-1}, an order of magnitude lower than peak cicada input rates (Figure 5, Table 2) While input rates generally increased over time (*day*: $F_{7,39.3} = 3.01$, $p = 0.01$), there were no differences in rates between the two sites on each sampling date (*site x day*: $F_{7,39.3} = 1.28$, $p = 0.29$) nor were there overall differences between the two sites (*site*: $F_{1,5.1} = 1.19$, $p = 0.33$).

The mean input rates of deciduous tree leaf litter to the Intact and Disturbed sites ranged from 0.114 – 1.162 g m^{-2} d^{-1} (Table 2). Leaf litter input rates varied little between sites over the course of cicada emergence (*site*: $F_{1,5.95} = 1.42$, $p = 0.28$; *site x day*: $F_{7,40} = 1.32$, $p = 0.27$) and did not change significantly through time (*day*: $F_{7,40} = 1.20$, $p = 0.32$).

Retention

Observed patterns of the retention of cicada-surrogate corks conformed well to the negative exponential decay model with $r^2 \geq 0.90$ for both sites. The cork retention rate *k* did not differ between the Intact and Disturbed sites (*site x distance*: $F_{1,62} = 0.35$, $p = 0.56$) (Table 3), and data from both sites were combined into a single regression to obtain a mean cork transport distance S_p of 12.64m (1/*k*, *k* ± SE = 0.079 ± 0.003). Confirming previous field observations of cicadas at each site, corks were commonly retained within short distances by debris dams, root wads, and overhanging edge vegetation.

Cicada decomposition

The exponential decay model explained cicada decomposition dynamics well. Decay curves for both sites were highly significant ($p < 0.0001$) and had r^2 values $\geq$ 0.79, but did not differ in the cicada decomposition rate k (*day x stream*: $F_{1,58} = 0.36$, $p = 0.55$) (Table 3). Data from both sites were combined into a single regression to calculate a mean cicada biological turnover time T_b ($1/k$, $k = 0.029 \pm 0.002$) of 34.61 days.

Community respiration

Prior to cicada emergence, there daily whole stream community respiration (CR_{24}) was four times greater at the Intact site compared to the Disturbed site (Intact: 12.82 g O_2 m^{-2} d^{-1}, Disturbed: 2.76 g O_2 m^{-2} d^{-1}). The respiration rate measured at the Disturbed site fell within the range of rates measured at similarly sized streams in nearby watersheds during a non-cicada spring (0.33 - 5.08 g O_2 m^{-2} d^{-1}) (Table 4).

Despite initial, pre-cicada differences between respiration rates at the Intact versus the Disturbed site, both sites had dramatic increases in CR_{24} during the cicada flight season (Figure 6). These increases were not correlated with changes in mean stream velocity or average daily temperature ($p >> 0.05$). Respiration peaked at 23.78 g O_2 m^{-2} d^{-1} at the Intact site on Day 26, increasing nearly two times the pre-cicada rate, but then declined to similarly low pre-cicada rates by Day 40 (11.48 g O_2 m^{-2} d^{-1}) (Figure 6A). When considered in the context of cicada detritus input rates, CR_{24} at the Intact site appeared to peak immediately following the interval of greatest input (Day 21-26), and then declined by Day 40. Consequently, there was a significant correlation between the cicada input rate in the interval immediately prior to respiration measurement and CR_{24} at the Intact site ($r = 0.98$, $p = 0.02$).

Whole stream community respiration at the Disturbed site also increased following cicada input, but in a different manner than respiration at the Intact site (Figure 6B). Respiration increased exponentially from the pre-cicada measurement over the course of the cicada flight season, with the highest CR_{24} on Day 40 (13.14 g O_2 m^{-2} d^{-1}), over four times the pre-cicada rate. Similar to the Intact site response, CR_{24} at the Disturbed site increased two-fold over the pre-cicada rate following the interval of greatest cicada input (Day 21-26). However, in contrast to the Intact site, CR_{24} more than doubled again on Day 40, despite a lower cicada input rate. Thus, there was not a significant correlation between cicada input rate and respiration at the Disturbed site ($p = 0.95$).

Discussion

The emergence of Brood X periodical cicadas from Mid-Atlantic riparian forests in May 2004 and their subsequent fall from the canopy as detritus offered a unique opportunity to study the effects of an intense, nutrient rich terrestrial arthropod pulse on stream ecosystem processes. In this study, periodical cicadas were followed from time of emergence into the stream as detritus where they were found to have a direct, measurable effect on whole stream community respiration. In fact, community respiration during the cicada flight season was two to four times greater than respiration measured prior to cicada emergence or at other sites during non-cicada years. Moreover, results from a decomposition experiment showed that cicadas were quickly decomposed and colonized by microbes, suggesting that cicada detritus is indeed a readily used resource for stream organisms.

Given cicada detritus was locally retained within streams (~ 13 m) and had a biological turnover time of approximately 35 days, the larger pulse of cicada detritus spread over a longer period of time at the Disturbed site may have promoted the exponential response in respiration that continued even as cicada input rates there declined. This pattern at the Disturbed site was very different from that observed at the Intact site where community respiration peaked immediately after the period of greatest cicada detritus input and then declined back to pre-cicada levels. While physical factors like water flow and temperature may affect stream metabolic processes (Webster et al. 1995, Mulholland et al. 2001), neither variation in flow nor temperature explained the pattern in community respiration observed at the Intact or Disturbed site. Further, the input rates of other allochthonous resources, terrestrial arthropods and leaf litter, did not differ between the two sites and, thus, could not explain inter-site variation in respiration.

Differences in organic matter resources prior to cicada emergence at the Intact and Disturbed site may have led to initial differences between the sites in microbial community activity that, in turn, mediated the community respiration response to the cicada pulse. Specifically, the standing crop of benthic organic matter (BOM) or inputs of dissolved organic carbon (DOC) may have been greater at the Intact site than the Disturbed site and may explain the different pre-cicada respiration rates (Intact: 12.82 g O_2 m^{-2} d^{-1} vs. Disturbed: 2.76 g O_2 m^{-2} d^{-1}). Studies of subsurface microbes in wetlands have suggested that ‘priming,’ or exposure to pulses of resources (e.g., nitrate) over time, results in a subsequent increase in microbial dentrifying activity (Addy et al. 2002, Addy et al. 2005, Kellogg et al. 2005). Thus, differences in background environment and prior exposure to dissolved organic matter may have led to different microbial respiration responses to the cicada pulse at the two sites (Findlay et al. 2003).

Despite differences in the pattern of respiration response, it is apparent that stream microbes at the Intact and Disturbed sites rapidly responded to the novel, large pulse of high-quality cicada detritus. Previous research by Judd et al. (2006) supports these results by suggesting that stream microbial communities are quick to adapt to new sources of organic matter, via shifts in both community composition and productivity. Cicada detritus provided a much higher quality resource than the low levels of leaf litter that also entered the stream during the study period; the C:N ratio of cicada detritus (4.71) was much lower than published ratios for the common riparian trees at the Intact and Disturbed sites (29.8 - 64.7, Ostrofsky 1997). Consequently, cicada detritus decomposed more rapidly (~ 0.03 d^{-1}) than deciduous tree leaf litter (Webster and Benfield 1986, Ostrofsky 1997). In addition, colonization by the water mold, *Saprolegnia*, as well as detritivorous invertebrates (e.g., chironomid and tipulid larvae) were observed when cicada packs were collected and returned to the laboratory, further suggesting that cicadas were used as an in-stream food resource. Future studies should consider using stable isotopes as a tool to trace the fate of this terrestrial-derived cicada detritus into the aquatic food web (Yang 2004).

The emergence densities of periodical cicadas from suburban Maryland riparian forests in 2004 (Intact: 25 m^{-2}, Disturbed: 5 m^{-2}) were much lower than observations of previous Brood X emergences in Maryland; these ranged from approximately 76 – 356 cicadas m^{-2} (Andrews 1921, Cory and Knight 1937, Graham and Cochran 1954). However, these historical estimates were based on density measurements from areas where emergence holes indicated large populations, rather than random sampling of habitat as was performed in this study. Estimates presented here do fall within the range of periodical cicada emergence randomly sampled from riparian forests in Kansas (Whiles et al. 2001), but are much lower than the 370 m^{-2}, recorded from random samples in floodplain habitat in a forest preserve in Illinois (Dybas and Davis 1962). These comparisons as well as the large differences in emergence found between the Intact and Disturbed sites, located within just a few miles of one another, suggest that a great deal of variability and patchiness exists in emergence density.

Significantly lower emergence density at the Disturbed site compared to the Intact site was likely the result of riparian forest modification following construction and mitigation in 2002-2003 that would have destroyed critical cicada nymph habitat. Historical records of periodical cicada emergence in New Jersey (Schmitt 1974) and Connecticut (Maier 1982) have indicated that some populations have actually gone extinct as a result of habitat loss inflicted by urbanization. In addition to the direct consequences of deforestation, urbanization contributes to a number of other processes that have profound impacts on forest ecosystems, including the deposition of air pollutants (ozone, sulfur dioxide, nitrogen), the delivery of excess nutrients and chemicals via surface runoff, and the invasion of native floras by plant and pest species. Given the cicada nymphal stage is directly tied to the health of trees, these other stresses on forest ecosystems may also have significant effects on the emergence and stream input dynamics of the 17-year periodical cicada.

Interestingly, despite lower emergence at the Disturbed site, greater cicada detritus input rates were observed there than at the Intact site. There are several possible explanations for this observation. First, adult periodical cicadas may have been more attracted to the edge habitat provided by the narrow riparian forest at the Disturbed site, as observed by Rodenhouse et al. (1997) where males tended to aggregate in the edges of forest fragments to chorus and attract females. Second, the presence of recently planted young trees in the high light mitigation area at the Disturbed site may also have provided preferred oviposition habitat (White 1980, Yang 2006), recruiting females from other nearby areas. A third possibility is that terrestrial predation pressure may have been higher at the Intact site, resulting in fewer adult cicadas falling into the stream as detritus.

In conclusion, the pulse of periodical cicada detritus that entered Maryland streams in May-June 2004 was quite unlike other terrestrial resources known to subsidize forested stream ecosystems, namely deciduous tree leaf litter and other live arthropods, in terms of its timing, quantity, and resource quality. Indeed, the large pulse of high quality cicada detritus that fell into the Intact and Disturbed streams resulted in dramatic increases in whole stream community respiration. By expanding the spatial scope of this study in the future to include riparian forests throughout other brood ranges of periodical cicadas in the eastern U.S., one would be able to evaluate how common and widespread the effects of this cicada pulse are on stream ecosystems. Moreover, while the Brood X periodical cicada emergence and input represented an irregular, but natural pulse event, it is reasonable to think that this and future studies may provide insight into how stream ecosystems will respond to unnatural resource pulses that accompany global change and continued human impact on the landscape, including those resulting from the spread of pests and pathogens and increased nutrient subsidies (Riley and Jefferies 2004).

Tables

Table 1. Characteristics of stream and adjacent riparian forest at Intact and Disturbed sites. Where listed, mean ± standard error measured during study period, May – July 2004.

Site	Watershed size (km^2)	Stream discharge ($m^3 s^{-1}$)	Stream Width (m)	Stream Depth (m)	Riparian tree density (# /100 m^2)	Canopy Cover (%)
Intact	3.24	0.014 (± 0.002)	1.54 (± 0.09)	0.08 (± 0.01)	11	97.42 (± 0.59)
Disturbed	4.01	0.044 (± 0.004)	2.00 (± 0.14)	0.20 (± 0.01)	0.3	94.01 (± 1.23)

Table 2. Least-square mean (95% confidence intervals) input rates of cicadas, other terrestrial arthropods, and leaf litter (g dry mass m^{-2} d^{-1}) collected in litter traps at the Intact and Disturbed sites (n = 4 traps per site) over eight time intervals.

	Allochthonous input rate (g DM m^{-2} d^{-1})					
Collection interval	**Cicada**		**Other terrestrial arthropods**		**Leaf litter**	
Day since emergence (Dates)	**Intact**	**Disturbed**	**Intact**	**Disturbed**	**Intact**	**Disturbed**
0 – 7	0	0.029	0.004	0.001	0.638	0.278
(12 May – 19 May)	(-0.081 – 0.088)	(-0.055 – 0.119)	(-0.015 – 0.024)	(-0.019 – 0.020)	(0.17 9– 2.270)	(0.078 – 0.991)
8 – 12	0.007	0.001	0.002	0.017	0.333	0.304
(20 May – 24 May)	(-0.088 – 0.111)	(-0.080 – 0.089)	(-0.020 – 0.025)	(-0.002 – 0.037)	(0.084 – 1.322)	(0.085 – 1.082)
13 – 20	0.120	0.115	0.014	0.004	0.700	0.242
(25 May – 2 June)	(0.029 – 0.219)	(0.025 – 0.214)	(-0.006 – 0.033)	(-0.015 – 0.024)	(0.197 – 2.492)	(0.068 – 0.860)
21 – 26	0.349	0.575	0.015	0.003	0.783	0.114
(3 June – 7 June)	(0.223 – 0.488)	(0.447 – 0.714)	(-0.005 – 0.034)	(-0.016 – 0.022)	(0.197 – 3.114)	(0.032 – 0.405)
27 – 35	0.184	0.403	0.014	0.004	0.546	0.226
(8 June – 16 June)	(0.088 – 0.289)	(0.289 – 0.527)	(-0.005 – 0.034)	(-0.015 – 0.024)	(0.153 – 1.945)	(0.064 – 0.806)
36 – 40	0	0.020	0.010	0.012	0.753	1.162
(17 June – 21 June)	(-0.081 – 0.088)	(-0.063 – 0.109)	(-0.012 – 0.033)	(-0.007 – 0.032)	(0.212 – 2.683)	(0.326 – 4.136)
41 – 47	0.041	0.024	0.038	0.042	0.796	0.198
(22 June – 28 June)	(-0.044 – 0.133)	(-0.059 – 0.114)	(0.018 – 0.058)	(0.022 – 0.062)	(0.224 – 2.836)	(0.056 – 0.704)
48 – 55	0	0	0.039	0.001	0.554	0.498
(29 June – 6 July)	(-0.081 – 0.088)	(-0.081 – 0.088)	(0.019 – 0.059)	(-0.018 – 0.021)	(0.155 – 1.972)	(0.140 – 1.775)

Table 3. Ecosystem processes measured at the Intact and Disturbed sites. Where applicable, mean ± standard error.

	Site	
	Intact	**Disturbed**
Cicada retention, expressed as transport distance S_p (m)	12.35 ± 0.76	12.99 ± 0.84
Cicada decomposition rate *k* (d^{-1})	0.030 ± 0.003	0.028 ± 0.002
Community respiration CR_{24} (g O_2 m^{-2})		
Day -14	12.82	2.76
Day 12	14.13	3.70
Day 26	23.78	5.77
Day 40	11.48	13.14

Table 4. Community respiration, average daily temperature, and discharge at the Intact and Disturbed sites, prior to cicada emergence (28 April 2004), and at three nearby headwater streams during a non-cicada spring (May 2001).

Site	**CR_{24} ($g\ O_2\ m^{-2}$)**	**Daily temperature (ºC)**	**Discharge ($m^3\ s^{-1}$)**
Intact	12.82	16.5	0.021
Disturbed	2.76	13.9	0.055
Northwest Br 01	0.33	18	0.005
Northwest Br 18	5.08	17	0.019
Paint Br 20	4.20	17.4	0.003

Figure legends

Figure 1. Carbon:Nitrogen ratio (± SE) of *Magicicada* sp. and other terrestrial arthropods compared to common deciduous leaf litter that enters streams. *Magicicada* C:N ratio measured in this study and other terrestrial arthropods C:N ratio from Matsumura et al. (2004). Deciduous tree C:N ratios from Ostrofsky (1997).

Figure 2. Sampling design for cicada emergence and allochthonous inputs. Circles indicate points (0.16 m^2) along each transect where density of emergence holes measured (n = 32 per site). Rectangles indicate location of in-stream litter traps (0.24 m^2) for collecting allochthonous inputs (n = 4 per site).

Figure 3. Mean emergence density of *Magicicada* sp. per m^2 based on abundance of emergence holes (n = 32 per site). Vertical bars indicate 95% confidence limits.

Figure 4. Least-square mean input rates of cicada detritus over time. Rates are calculated over a five to nine day time interval (See Table 2) and plotted at the mid-point of that time interval. Dark circles indicate the Intact site, open circles represent the Disturbed site. Vertical bars indicate 95% confidence limits. Mean based on n = 4 litter traps per site.

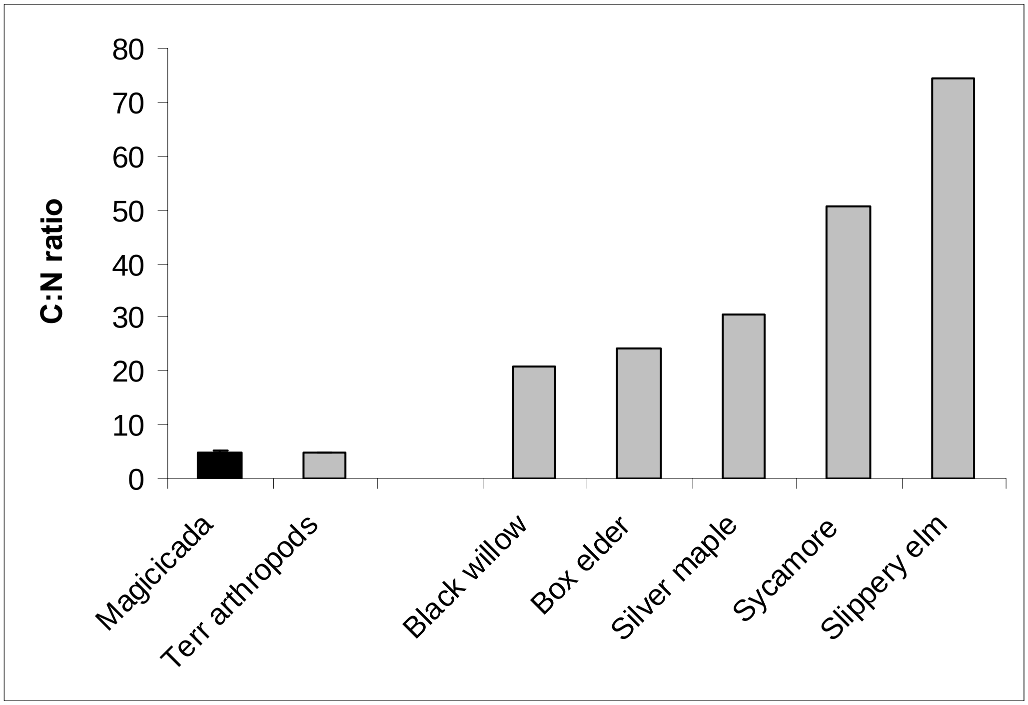
Figure 5. Least-square mean input rates of arthropod dry mass over time at A) Intact site (dark shapes) and B) Disturbed site (open shapes). Rates are calculated over a

five to nine day time interval (See Table 2) and plotted at the mid-point of that time interval. Circles represent cicada detritus and squares represent other terrestrial arthropods. Vertical bars indicate 95% confidence limits. ** indicates significant difference between cicada and other terrestrial arthropod input rates in t-test at $p < 0.05$, * indicates $p < 0.10$.

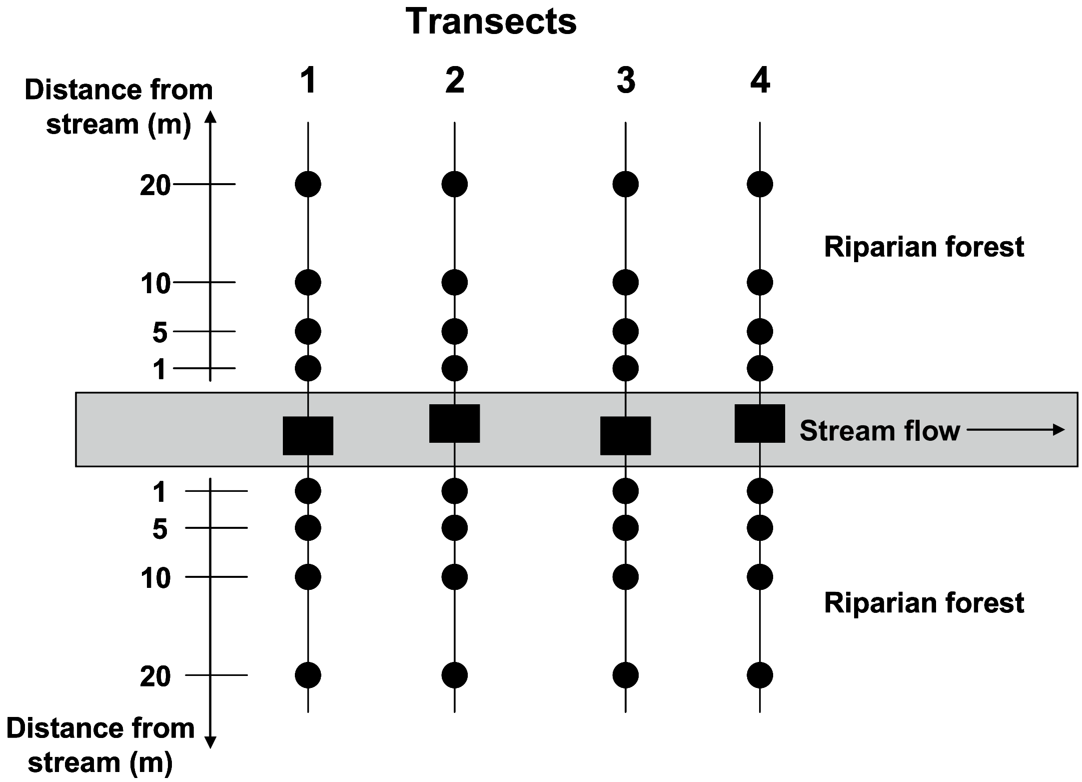
Figure 6. Community respiration (CR_{24}) and cicada input rates at the A) Intact (dark shapes) and B) Disturbed (open shapes) sites. Triangles represent CR_{24} measurements (left axis) and circles represent cicada input rate (right axis). Horizontal bars indicate the time interval over which cicada input rate was calculated (Table 2).

Figures

(Figure 1)



(Figure 2)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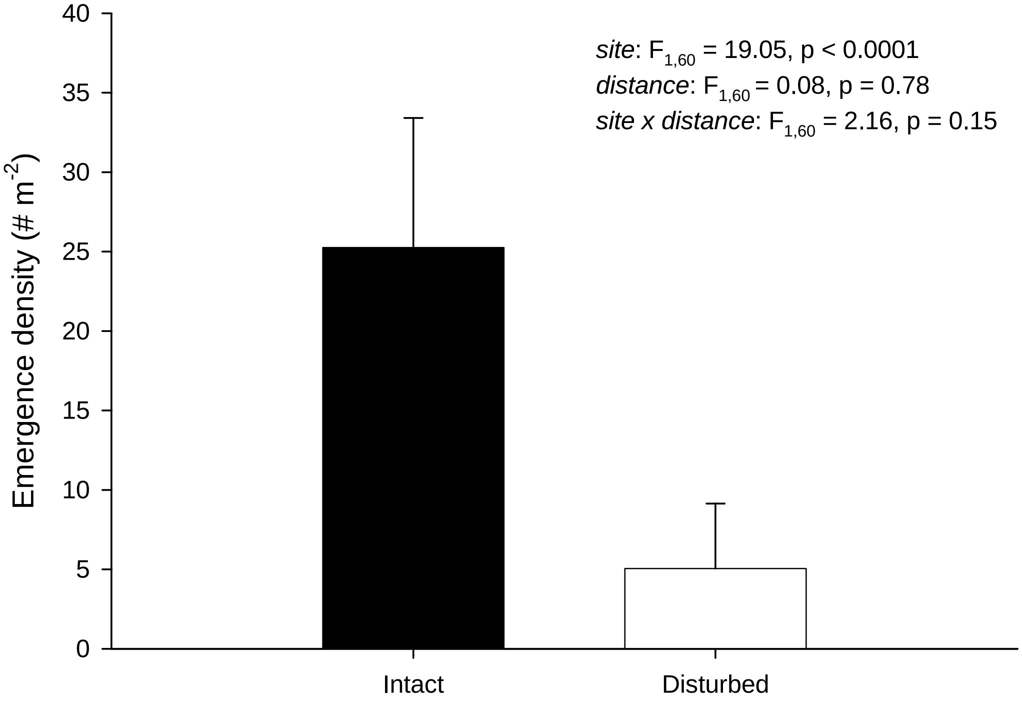
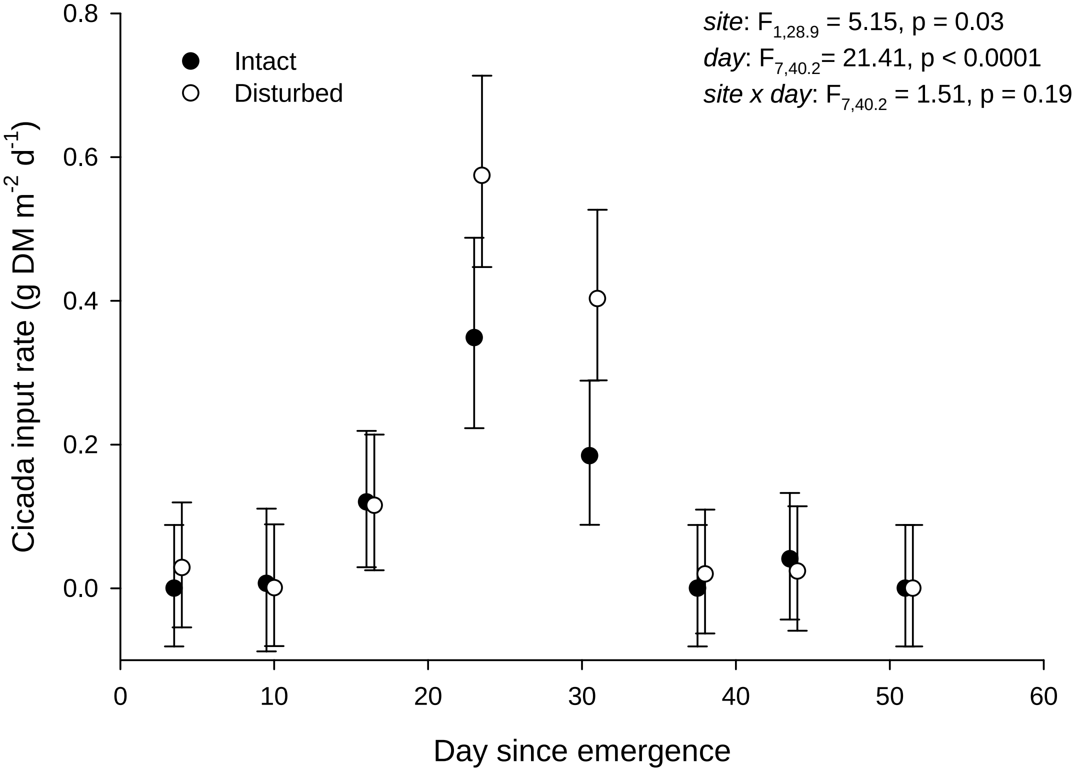
3
4
Distance from stream (m)
20
10
5
1
Riparian forest
Stream flow
1
5
10
20
Riparian forest
Distance from stream (m)

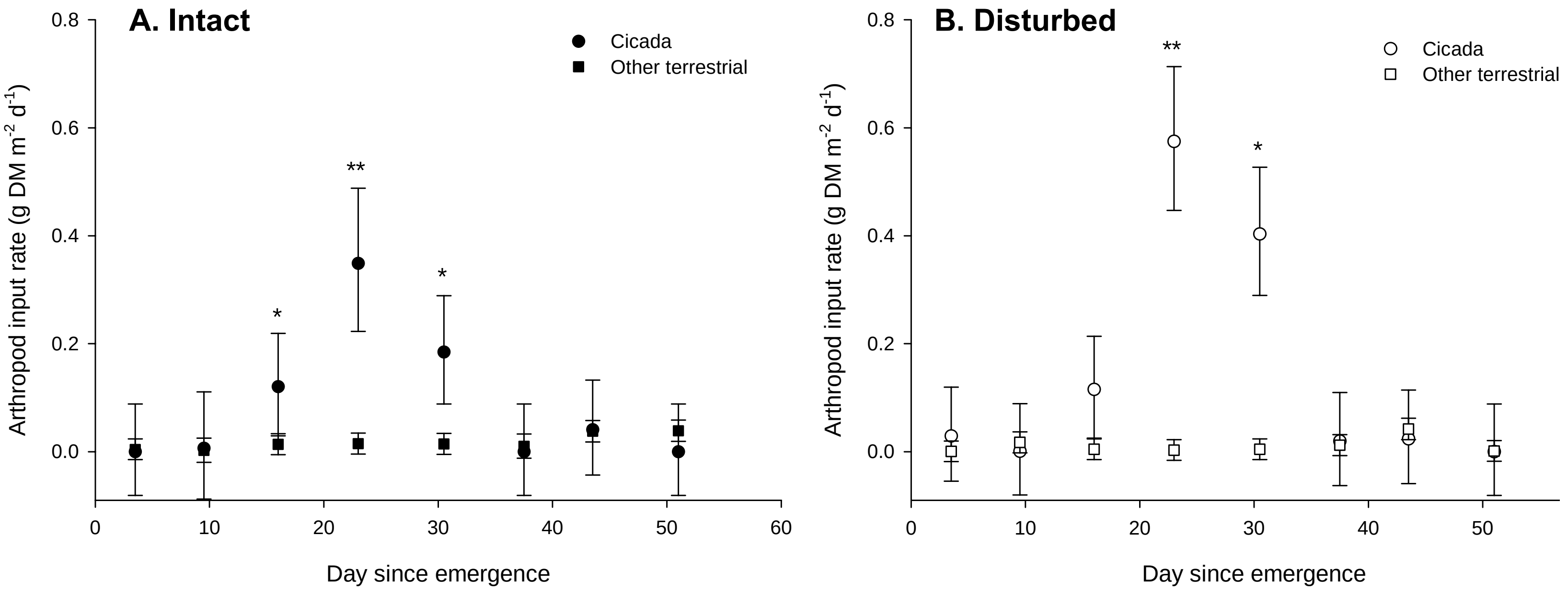
(Figure 3)


site: F1,60 = 19.05, p < 0.0001
distance: F1,60 = 0.08, p = 0.78
site x distance: F1,60 = 2.16, p = 0.15
Emergence density (# m-2)
0
5
10
15
20
25
30
35
40
Intact
Disturbed

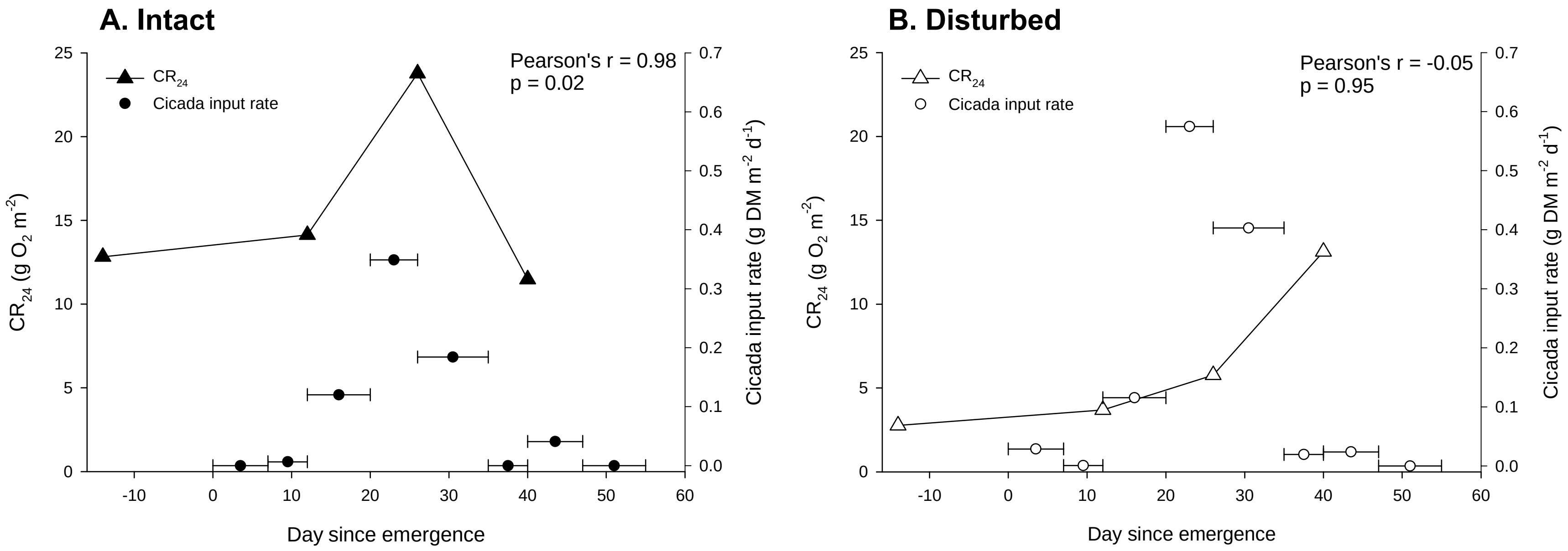
(Figure 4)


site: $F_{1,28.9}$ = 5.15, p = 0.03
day: $F_{7,40.2}$= 21.41, p < 0.0001
site x day: $F_{7,40.2}$ = 1.51, p = 0.19
● Intact
○ Disturbed
Cicada input rate (g DM m^{-2} d^{-1})
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
60
Day since emergence

(Figure 5)


A. Intact
Cicada
Other terrestrial
Arthropod input rate (g DM m-2 d-1)
0.8
0.6
0.4
0.2
0.0
*
**
*
0
10
20
30
40
50
60
Day since emergence
B. Disturbed
Cicada
Other terrestrial
Arthropod input rate (g DM m-2 d-1)
0.8
0.6
0.4
0.2
0.0
**
*
0
10
20
30
40
50
Day since emergence

(Figure 6)


A. Intact
CR24
Cicada input rate
Pearson's r = 0.98
p = 0.02
CR24 (g O2 m-2)
Cicada input rate (g DM m-2 d-1)
Day since emergence
0
5
10
15
20
25
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
-10
0
10
20
30
40
50
60
B. Disturbed
CR24
Cicada input rate
Pearson's r = -0.05
p = 0.95
CR24 (g O2 m-2)
Cicada input rate (g DM m-2 d-1)
Day since emergence

Chapter III: Weak terrestrial-aquatic linkage in central Maryland agro-ecosystems

Abstract

Riparian buffers of herbaceous plants and grasses are commonly employed as a best management practice to mitigate the negative effects of agriculture on stream ecosystems. Additionally these landscape features may provide complex habitat structure, favorable microclimate, and alternative food resources to agriculturally important predators. Previous research in unmanaged systems has established a strong terrestrial-aquatic linkage between terrestrial arthropod predators and emerging aquatic insects, but this has remained untested in an agro-ecosystem. In this study, I use field and laboratory methods to evaluate the function of riparian buffers for ground-dwelling wolf spiders (Araneae, Lycosidae), common generalist predators in corn fields, to determine if emerging aquatic insects provide an important alternative prey resource to the spiders. Seasonal pitfall sampling of the activity-abundance of lycosid spiders and their terrestrial and aquatic prey in corn fields and adjacent riparian buffer habitats at three locations in central Maryland, USA, revealed a general trend of greater adult activity-abundance in the buffer compared to the corn field, but no specific seasonal patterns in either habitat. Across all sites, patterns of aquatic insect emergence mirrored seasonal patterns of abundance in terrestrial prey, and the abundance of ground-dwelling terrestrial prey varied little between riparian and corn field habitats. In laboratory feeding trials the consumption of aquatic prey

varied by wolf spider genus while analysis of the natural abundance of ^{13}C and ^{15}N in field-collected lycosids suggested that individuals captured in both riparian and field habitats in March had consumed prey that fed on plants in the riparian buffer or that had emerged from the stream. However, the inability to separate the isotopic signatures of in-stream and riparian primary producers precluded the identification of the specific contribution of aquatic insects to lycosid diets. Intensive directional pitfall trap sampling at the field edge and in the riparian buffer interior at one site was unable to detect any patterns of seasonal movement of lycosids between the riparian buffer and the corn field. Taken together, evidence from these studies suggest that only a weak terrestrial-aquatic linkage exists between streams and lycosid spiders in neighboring agricultural fields. I suggest that the strength of terrestrial-aquatic linkages in agro-ecosystems may be highly species-specific, reflecting each individual predator's habitat and prey preferences, behavior, and phenology.

Introduction

Riparian conservation buffers are frequently employed as a best management practice to mitigate the negative effects of agriculture on stream ecosystems (Lovell and Sullivan 2006). These vegetated buffers can lead to measurable improvements in stream water quality by trapping sediments (Karr and Schlosser 1978), reducing excess nitrate and phosphorous from fertilizers (Osborne and Kovacic 1993, Lee et al. 2003, Mayer et al. 2006), and removing pesticides (Radkins et al. 1998), all common constituents of field run-off. Additionally, riparian buffers in agricultural areas provide important wildlife habitat and promote biological diversity (Maisonneuve and Rioux 2001, Chapman and Ribic 2002, Boutin et al. 2003, Henningsen and Best

2005). Given the intense disturbance that occurs in neighboring agricultural fields during tilling and harvest (Wissinger 1997, Landis et al. 2000), conservation buffers may also provide refuge habitat for agriculturally important natural enemies (French et al. 2001).

Generalist arthropod predators can play a significant role in reducing pests in agro-ecosystems (Symondson et al. 2002), and the conservation of native assemblages of natural enemies has become an important component of integrated pest management (Barbosa 1998). Spiders are an abundant group of natural enemies in row crops including corn and soybeans (Young and Edwards 1990), and studies suggest that assemblages of spiders can effectively suppress pest populations (Riechert and Lockley 1984, Lang et al. 1999, Riechert 1999, Sunderland 1999). As a result, the effect of agricultural field practices on spider abundance and diversity, particularly wolf spiders (Araneae, Lycosidae), has been well-studied (Bishop and Riechert 1990, Balfour and Rypstra 1998, Marshall and Rypstra 1999, Rypstra et al. 1999, Marshall et al. 2002). To promote the conservation of spiders and other agriculturally important natural enemies, farmers have been encouraged to maintain uncultivated natural areas adjacent to or within crop systems (Thomas et al. 1992, Nentwig et al. 1998, Landis et al. 2000). Herbaceous or grassy riparian buffers may play a similarly important conservation function by providing complex habitat structure, favorable microclimate, and alternative food resources for generalist arthropod predators.

Emerging aquatic insects are also known to subsidize the diets of generalist predators residing in riparian buffers (Henschel et al. 1996, Power and Rainey 2000, Power et al. 2004, Paetzold et al. 2005). Parker and Power (1993), for example, reported that lycosid spiders dramatically responded to experimental increases in insect emergence within 24 hours. Stable isotope analyses of arthropods collected in riparian zones, particularly spiders and carabid beetles, confirmed that aquatic insects constitute a significant portion of their diet (Collier et al. 2002, Sanzone et al. 2003, Akamatsu et al. 2004, Briers et al. 2005). In addition, the timing of aquatic insect emergence with respect to the phenology of terrestrial prey plays a significant role in determining the contribution of aquatic insects to predator diets as well as predator distribution in the riparian zone (Kato et al. 2003). Thus, previous studies demonstrated that a terrestrial-aquatic linkage exists between emerged adult aquatic insects and terrestrial arthropod predators in desert, forest and alpine shore habitats where prey emerging from productive aquatic habitats subsidized the diets of generalist predators in less productive terrestrial habitats. Yet, no study to date has examined this linkage in an agricultural system where insects emerging from streams flowing through conservation buffers may subsidize invertebrate predators of agricultural importance when adjacent crop fields are less hospitable, particularly following harvest and over winter. Further, the activity and movement dynamics of ground-dwelling lycosid spiders towards and within riparian buffer habitats following field disturbance has not been well-studied (but see Buddle et al. 2004).

In Maryland, pro-active best management practices, namely the creation of riparian conservation buffers, have promoted diverse aquatic insect communities in agricultural headwater streams (Moore and Palmer 2005). Many of the aquatic insects found in these streams are known to emerge en masse at times of the year when terrestrial productivity in natural forest habitats and agricultural fields is reduced (Hershey and Lamberti 2001, Nakano and Murakami 2001), and further, tend to remain within 10-20 m of the stream channel following emergence (Petersen et al. 2004). Thus, the timing and distribution of emerged aquatic resources from streams with conservation buffers may result in an important trophic link between agricultural and stream ecosystems.

Here, I examine the potential for terrestrial-aquatic linkages in corn agro-ecosystems bordered by stream buffers in central Maryland, USA. I focused on the assemblage of wolf spiders (Araneae, Lycosidae), a group of common and highly mobile generalist predators in both agricultural fields and riparian zones. In this paper, I address the following questions:

1. What is the activity of wolf spiders in the riparian buffers compared to adjacent agricultural fields and how does it change seasonally?
2. What is the potential food supply for wolf spiders in riparian buffers and adjacent agricultural fields and how does food availability change seasonally?
3. Does the emergence of aquatic insects add to food availability in the riparian zone?
4. Do wolf spiders readily consume aquatic prey? What contribution does aquatic prey make to wolf spider diets?
5. Do wolf spiders actively move between the riparian buffer and an adjacent agricultural field?

Methods

Study sites

I conducted a field study at three farms in central Maryland, USA, from August 2003 – August 2004: Central Maryland Research and Education Center at Folly Quarter (***FQ***, Howard Co., 39°15’22.9” N, 76°55’38.6” W), Rodman Myers Farm (***RM***, Frederick Co., 39°39’44.7” N, 77°22’45.2” W), and Myers Windsor Farm (***MW***, Carroll Co., 39°32’57.0” N, 77°5’3.9” W). Each site has a first-order stream separated from an adjacent corn field by a treeless riparian buffer. All streams drained ≤ 1 km^2 watersheds that were dominated by agricultural land use. Buffers contained mixtures of grass and herbaceous vegetation including foxtails (*Setaria* P. Beauv.), reed canary grass (*Phalaris arundinacea* L.), rice cutgrass (*Leersia oryzoides* L.), sedge (*Carex* L.), knotweeds (*Polygonum* L.), goldenrod (*Solidago* L.), jewelweed (*Impatiens capensis* Meerb.), common milkweed (*Asclepias syriaca* L.), hemp dogbane (*Apocynum cannabinum* L.), nightshade (*Solanum* L.), and thistles (*Cirsium* Mill.), and were not actively managed by growers during the study period. Average buffer width varied among sites; the buffer at FQ (18.2 m) was wider than RM (3 m) and MW (5.8 m). In 2003, corn was harvested mid-September at MW. At FQ and RM corn was left to dry on the field, and was not harvested until mid-October and the first week of November, respectively. Growers at all sites used no-till best management practices following the autumn harvest, leaving corn residues on the field through the non-growing season. Corn was planted late-April through mid-May at all sites in spring 2004. Four transects were randomly established (but separated by at least 5 m) along a 60 m length of stream at each site and extended perpendicularly from the stream into the field (Figure 1).

Seasonal activity across habitats

Lycosid spiders

I measured the activity-abundance of lycosid spiders using pitfall traps at the three field sites. Pitfall traps were installed in two locations, 1 m from the stream in the riparian buffer (hereafter, Riparian) and 3.5 m from the buffer into the corn field (hereafter, Field), along the four transects at each site (Figure 1). Round plastic cups (9 cm diameter) were buried flush with the ground surface and were filled with ~ 3 cm of a dilute solution of dish soap to reduce surface tension and serve as a mild preservative. I used a 15 cm diameter plastic plate cover, elevated ~ 8 cm over the cups to exclude rain and vertebrates. Pitfall traps were set at each site for a 3-day period during six sampling intervals: 28 August - 11 September 2003, 29 September - 6 October 2003, 10 – 23 November 2003, 12 – 20 March 2004, 30 April – 15 May 2004 and 18 – 25 June 2004.

Following each sampling interval, contents of the pitfall traps were returned to the laboratory, rinsed through a 250 µm sieve and preserved in 70% ethanol. Occasionally, pitfall samples had to be discarded due to the incidental capture and death of rodents that may have served as an attractant for some arthropods. Lycosid spiders were classified as adults, juveniles, or spiderlings based on size and development of genitalia. Adults were identified to genus (Dondale 2005), and where possible, species using Kaston (1972) and Vogel (2004). Numbers generated from pitfall catches were reported as activity-abundance, or number captured over a 3-day period. For graphical and comparison purposes, activity-abundance was plotted at the mid-point of each sampling interval: 16 March, 8 May, 22 June, 6 September, 3 October and 17 November.

All statistical analyses were conducted using SAS v.9.1.3 (2006, SAS Institute Inc., Cary, NC, USA). For the analysis of adult lycosid activity-abundance, I used a generalized linear mixed model approach as recommended by Littell et al. (2006) for count data because they frequently violate the assumptions of standard linear models. Mean lycosid adult activity-abundance in each habitat per site per sampling period was calculated and the averages (weighted by number of traps) were analyzed with an ANOVA using the negative binomial distribution and log link (Proc GLIMMIX). This enabled the comparison of differences in mean activity-abundance of lycosid adults between habitats (riparian buffer vs. corn field) through time, blocking by field sites (FQ, RM, MW). Given the low counts for juveniles and individual genera, each trap was scored for the presence and absence of juveniles and the three most common genera. An ANOVA (the binomial distribution and logit link, Proc GLIMMIX) was used to compare the mean proportion of traps containing juveniles or each of the most common genera between habitats through time, again blocking by site.

Total species richness was compared between field and riparian buffers over the study period using a paired t-test (Proc TTEST). The Jaccard index of similarity between field and riparian buffers was calculated using the total pooled species richness from the four pitfall traps in each habitat at each site on each sampling date. To determine if spider assemblages in field and buffer habitats became more or less similar over time, I used a repeated measures ANOVA, blocking by site (Proc MIXED).

Terrestrial and aquatic prey

In addition to the lycosid spiders, the pitfall traps also captured many of their ground-dwelling terrestrial arthropod prey. The following orders of arthropods were enumerated as potential lycosid prey items (Lang et al. 1999, Nyffeler 1999, Toft and Wise 1999, Ishijima et al. 2006): Isopoda, Collembola, Thysanoptera, Homoptera, Hemiptera, Orthoptera, Diptera, and Lepidoptera. Prey numbers generated from pitfall catches were also reported as activity-abundance, the number captured over a 3-day period.

During the same 3-day terrestrial sampling periods described above, the emergence of aquatic insects from each stream was measured. One emergence trap (0.07 m^2 bottom opening, 0.7 mm mesh) was anchored to the stream bottom where each of the four transects intersected the stream (Figure 1). Contents of the traps were collected and preserved in 70% ethanol. Emerged insects were identified to family using Merritt & Cummins (1996) and body lengths (excluding antennae and cerci) were measured to the nearest 0.1 mm under a dissecting microscope (10X magnification). Biomass was then estimated using published length-dry mass equations for aquatic insects (Sabo et al. 2002). Emergence was reported as both dry biomass (mg m^{-2} day^{-1}) and abundance (total individuals during 3-day period).

Mean activity-abundance of terrestrial prey, weighted by trap effort and blocked by site, were compared between the field and riparian buffer habitats over the six sampling periods using mixed model repeated measures ANOVA (Proc MIXED).

Multiple means comparisons were accounted for using the Bonferroni adjustment. Similarly, the mean abundance and biomass of emerging aquatic insects were compared among the six sampling periods with repeated measures ANOVA, blocking by site. In addition, the relative proportions of major insect orders represented in emergence samples were examined at each site on each date.

Consumption of aquatic prey

Three common genera of lycosid spiders, *Pardosa*, *Hogna*, and *Rabidosa*, were evaluated for their ability to consume different live, adult aquatic insects: midges (Diptera: Chironomidae), caddisflies (Trichoptera: Hydropsychidae) and damselflies (Odonata: Calopterygidae, Coenagrionidae). The three spider genera were chosen because they represented a range of sizes (5 – 12 mm body length), and were locally available for collection at FQ in June 2005. Following collection, all spiders were starved in individual 9-cm-diameter Petri dishes with moist filter paper for 24 hours prior to the feeding trial. Feeding trials took place in a growth chamber with 16:8 light:dark cycle at 25°C, beginning at 12:30. Midges and caddisflies were live-collected with a light trap while damselflies were live-collected with sweep nets from the stream at FQ. One living adult prey item was added to each dish. Petri dishes were returned to the growth chamber and checked every hour for five hours, at which time prey were recorded as consumed or unconsumed. The number of replicates varied for each predator species and each prey item depending on limited availability in the field (Table 2). The number of insects consumed by *Pardosa* and *Rabidosa* was compared within each genus across prey species. The number of spiders that consumed aquatic insects in the feeding trials was compared across spider genera for both caddisflies and damselflies. Contingency tables were constructed for all comparisons and were analyzed with χ^2 tests (Proc FREQ). Fisher exact tests were used if some cells contained low values.

Stable isotope analysis

Samples of lycosid spiders and their potential aquatic food sources were collected at FQ for preliminary stable isotope analyses in March 2005. While the natural abundance of ^{13}C and ^{15}N have been successfully used in natural systems to calculate the contribution of aquatic insects to spider diets with linear mixing models (Collier et al. 2002, Sanzone et al. 2003, Akamatsu et al. 2004, Kato et al. 2004, Paetzold et al. 2005), the feasibility of using the natural abundance of carbon and nitrogen isotopes has not been assessed in agro-ecosystems.

Lycosid spiders were hand-collected in both the riparian buffer near the stream edge and in the corn field and identified to genus. Common aquatic insect larvae were collected with a D-net from random locations in the stream and identified to family. Late-instar aquatic insect larvae and freshly emerged adult aquatic insects, the most vulnerable to spider predation, are known to have similar isotopic signatures (Paetzold et al. 2005). Trichoptera (caddisflies) collected included the Limnephilidae, Hydropsychidae, Phryganeidae, and Philopotamidae. Ephemeroptera (mayflies) included Heptageniidae and Leptophlebiidae while Diptera (true flies) were composed of Chironomidae and Simuliidae. Odonata (damselflies) were represented by the Coenagrionidae and Calopterygidae. All spiders and aquatic insects were held in separate containers for 24 hours to allow for gut clearance and were then frozen. Samples were dried at 60°C for 48 hours, and then several individuals of each taxon were finely ground and combined into a composite sample for ^{13}C and ^{15}N analyses (1.0 – 2.9 mg dry mass).

Additionally, samples of terrestrial and aquatic primary producers were collected. Periphyton was sampled by scraping random rocks from the stream while benthic organic matter was collected with grab samples from the stream. Stems of the most common grass, *Phalaris arundinacea* L., were collected in the riparian buffer, and dried corn leaves were collected from residues left on the field from previous harvest. Samples were dried and similarly prepared for ^{13}C and ^{15}N stable isotope analysis (6.0 – 7.0 mg dry mass). Because terrestrial arthropod prey were particularly rare during the March sample collection, the δ^{13}C values of terrestrial prey from the riparian and corn field habitats would be inferred from primary producers, corrected for ~ 1‰ fractionation (Peterson and Fry 1987).

All samples were analyzed at the UC Berkeley Center for Stable Isotope Biogeochemistry using high-temperature direct combustion and continuous flow analysis. Results are reported in the following δ notation:

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = [(R_{sample}/R_{standard})-1] \times 1000$$

where R_{sample} = ^{13}C:^{12}C or ^{15}N:^{14}N in the sample and $R_{standard}$ = ^{13}C:^{12}C in Pee Dee belemnite limestone or ^{15}N:^{14}N in the atmosphere (Peterson and Fry 1987).

The δ^{13}C and δ^{15}N of the sampled food web components in this preliminary analysis were graphically examined to ensure the clear separation of primary producer δ^{13}C and δ^{15}N values, a necessary requirement for using a dual isotope (δ^{13}C and $\delta^{15}N$), three-source mixing model to calculate the contribution of aquatic insects to lycosid spider diets (Phillips 2001, Phillips and Gregg 2001).

Directional movement

To assess patterns of lycosid movement between the riparian buffer and corn field, a directional movement study was performed at Folly Quarter (FQ) from April - November 2005. For this study, I expanded the 2003-2004 study area to incorporate a 100 m length of stream. Ten pairs of pitfall traps, each separated by 10 m, were installed at the field-buffer margin (average distance from stream: 15.4 m) and ten pairs, again each separated by 10 m, in the buffer near the stream edge at the margin of wet and dry soils (average distance from stream: 3.7 m) . Each pair consisted of two aluminum flashing guides (height = 25 cm, total length = 1 m) that were angled in opposite directions (toward and away from the stream) and driven into the ground ~3 cm. At the center of each guide, I buried pitfall traps identical to those described in the previous field study to capture spiders walking in a particular direction (Figure 2). Pitfall traps in this study were set for a two-day period each month from April to November 2005. Aluminum guides were removed and pitfall traps covered when not in use. Lycosid adults, juveniles and spiderlings were identified as above. In 2005, corn was planted at FQ in mid-May and harvested in late October.

Paired t-tests were used to evaluate differences in direction of the number of adult lycosids captured at each habitat boundary for each month (Proc TTEST). In cases of non-normal distribution of paired differences, the non-parametric Wilcoxon signed rank test was used. In addition to all adult lycosids, paired t-tests were performed on the three most abundant taxa (*Pardosa, Pirata,* and *Hogna*) for each month. Pending difficulties in detecting directional movement, samples from each paired trap array were combined into a single sample, and lycosid activity-abundance in the interior riparian buffer was compared to the field edge through time, using repeated measures ANOVA (Proc MIXED). If significant habitat by time interactions were detected, buffer and field edge activity-abundance were compared during each month with planned contrasts.

Results

Seasonal activity across habitats

Lycosid spiders

Two-hundred-fourteen individual adult and juvenile lycosid spiders were captured over the six sampling dates at the three sites, representing six different genera and varying size classes (Table 1). Pitfall traps from the March and November sampling periods contained so few spiders (< 9% total catch) that they were dropped from statistical analyses. The mean activity abundance of lycosid adults did not differ significantly from May – October ($F_{3,15.38} = 1.14$, $p = 0.36$) nor by habitat ($F_{1,15.29} = 2.29$, $p = 0.15$), although there was a trend of greater mean activity abundance in the riparian buffer (mean ± SE: 2.1 ± 0.5) than field (mean ± SE: 1.2 ± 0.3) (Figure 3A). The proportion of pitfall traps containing juvenile lycosids varied significantly with both habitat ($F_{1,17.42} = 12.39$, $p = 0.003$) and time ($F_{3,17.11} = 4.72$, $p = 0.01$) (Figure 3B). Overall, a greater proportion of traps in the riparian buffer contained juveniles (mean ± SE: 0.49 ± 0.13) than in the field (mean ± SE: 0.14 ± 0.07). In addition, a greater proportion of traps contained juveniles later in the field season (September and October) than in the spring.

Pardosa, *Pirata*, and *Hogna* were the most common lycosid genera collected in the multi-site study, representing 95% of the total number of adults captured (Table 1). Across four sampling periods (May – October), a greater proportion of pitfall traps in the field habitat (mean ± SE: 0.48 ± 0.12) contained *Pardosa* than in the riparian buffer (mean ± SE: 0.17 ± 0.08) ($F_{1,14.37} = 4.30$, $p = 0.06$). The proportion of traps capturing *Hogna* from May – October did not differ significantly among habitats ($F_{1,16} = 1.24$, $p = 0.28$). However, from May – September, a greater proportion of traps in the riparian buffer (mean ± SE: 0.37 ± 0.30) captured *Pirata* compared to the field (mean ± SE: 0.05 ± 0.07) ($F_{1,10.18} = 13.60$, $p < 0.01$) (Figure 4).

Overall, total species richness in the field and riparian buffer did not differ significantly (paired $t = 1.39$, df = 2, $p = 0.30$). However, mean Jaccard similarity scores indicated that the assemblages of wolf spiders in field and riparian habitats, while overlapping, were not identical (range: 0.33 – 0.44) and did not vary temporally over the study period ($F_{3,6} = 0.08$, $p = 0.97$).

Terrestrial and aquatic prey

The activity-abundance of terrestrial prey items did not differ significantly between field and riparian buffer habitats ($F_{1,24} = 0.01$, $p = 0.91$) (Figure 5). A significant effect of time on the abundance of prey was detected ($F_{5,24} = 4.65$, $p < 0.01$); however, means comparisons adjusting for multiple comparisons with the Bonferroni correction ($\alpha = 0.003$) suggested that significant differences in abundance only occurred between the March sampling period, when the lowest activity-abundance was observed, and the May and September sampling periods, when the greatest activity-abundance was observed.

Across sites, neither the mean abundance nor mean biomass of emerged aquatic insects varied through time (*abundance*: $F_{5,9.25} = 1.44$, $p = 0.30$; *biomass*: $F_{5,9.19} = 1.28$, $p = 0.35$) (Figure 6). Interestingly, the taxonomic composition of aquatic insect emergence did vary among the sites through time (Figure 7). FQ was largely dominated by midges (Diptera: Chironomidae) throughout the entire study (range: 52 – 100%). However, when emergence biomass peaked at FQ in June, caddisflies (Trichoptera: Hydropsychidae) accounted for 48% of the biomass. Diptera (Chironomidae) dominated emergence biomass at MW throughout the entire year (range: 80-100%). At RM, several different taxa dominated emergence biomass at different times during the year. Stoneflies (Plecoptera: Capniidae, Nemouridae, Taeniopterygidae) were abundant in March and May (52% and 24 %, respectively). Caddisflies (Trichoptera: Hydropsychidae) represented the greatest proportion of emergence biomass in the late summer (68%) while mayflies (Ephemeroptera: Baetidae) represented a significant portion of biomass at RM in October (60%).

Consumption of aquatic prey

All predator genera tested consumed live aquatic prey (Table 2). All *Pardosa* consumed midges (Diptera: Chironomidae), but ate lower proportions of the other two prey: caddisflies (Trichoptera: Hydropsychidae) and damselflies (Odonata: Coenagrionidae) ($\chi^2 = 21.18$, df = 2, $p < 0.0001$). All *Rabidosa* consumed damselflies (Odonata: Calopterygidae), but consumed lower proportions of caddisflies (Fisher exact test, $p = 0.02$). *Rabidosa* and *Pardosa* did not statistically differ in the proportion of individuals that consumed hydropsychid caddisflies. (Fisher exact test, $p = 1.0$). However, the proportion of individuals that consumed damselflies did differ significantly among predators (Fisher exact test, $p < 0.001$) with greater proportions of *Rabidosa* (Fisher exact test, $p < 0.001$) and *Hogna* (Fisher exact test, $p = 0.04$) consuming odonates than *Pardosa*.

Stable isotope analysis

As expected, values of $\delta^{13}C$ for corn, a C_4 plant, clearly separated from stream periphyton and the C_3 riparian grass (Figure 8). However, the $\delta^{13}C$ signatures for riparian grass and periphyton could not be distinguished. Several samples of periphyton submitted for analyses did not contain enough carbon to accurately determine $\delta^{13}C$, and those samples that did have enough carbon were widely varying in $\delta^{13}C$. Values of $\delta^{15}N$ for periphyton and corn could not be measured due to nitrogen concentrations below detectable limits. Additionally, both grass and corn benthic organic matter were collected in the stream and had similar mean isotopic signatures to terrestrially collected samples of grass and corn. Thus, preliminary analyses indicated that calculating the contribution of terrestrial and aquatic prey to lycosid predator diets using the natural abundance of $\delta^{13}C$ and $\delta^{15}N$ and the three-source mixing model would be impossible in this system without the addition of a ^{15}N tracer (Sanzone et al. 2003).

Nonetheless, the isotopic similarity of lycosid spiders collected in the riparian and corn habitats to aquatic insects and primary producers in those habitats could be examined graphically. Riparian *Pardosa* and *Rabidosa* had $\delta^{13}C$ values closer to riparian grass, periphyton, and aquatic insects than to corn. The $\delta^{13}C$ and $\delta^{15}N$ signatures of the riparian lycosids were very similar to the Odonata larvae, known predators in the agricultural stream food web. *Pardosa* captured in the corn field likely consumed prey that fed on both corn and C_3 plants in the riparian buffer, given a $\delta^{13}C$ value more depleted than corn.

Directional movement

One-thousand-fifty-two spiders from six genera were captured over the eight sampling dates in the riparian buffer and field edge at FQ in 2005. As observed in the seasonal activity study, *Pardosa*, *Pirata*, and *Hogna* were the most abundant taxa, representing 90% of the total adult lycosids collected.

At the wet-dry soil boundary in the riparian buffer, there were no differences in the direction of capture of adult lycosids or the common genera in any month ($p > 0.05$). At the field-buffer boundary, there were differences in the direction of movement for *Pardosa* in September (Wilcoxon Signed Rank S = 17.5, $p = 0.04$), where significantly more *Pardosa* were captured moving from the corn field towards the buffer. However, no significant differences were detected for all adult lycosids combined or the other common genera in any month ($p > 0.05$).

Because the number of individuals within each genus collected in each habitat on each date was insufficient for some statistical analyses in the seasonal activity study, data from the paired traps used in the directional movement study were combined to assess seasonal generic patterns in activity-abundance in the interior riparian buffer and at the field edge at FQ. Considering all adult lycosid spiders combined, I detected a significant habitat by time interaction ($F_{7,91} = 7.70$, $p < 0.0001$). Activity-abundance of adults was significantly greater in the interior riparian buffer than at the field edge in both April and May ($p < 0.05$) (Figure 9A).

Analysis of juvenile lycosid spiders also revealed a significant habitat by time interaction ($F_{7,104} = 4.86$, $p < 0.0001$). Like adults, juveniles were more active in the interior riparian buffer than at the field edge in April ($p < 0.0001$); however, in September, juvenile activity-abundance was greater at the field edge ($p = 0.02$) (Figure 9B). Significant habitat by time interactions were also detected for the three most common genera, *Pardosa* ($F_{7,105} = 9.31$, $p < 0.0001$), *Pirata* ($F_{7,109} = 5.42$, $p < 0.0001$), and *Hogna* ($F_{7,109} = 4.72$, $p < 0.0001$). Patterns of activity-abundance differed greatly among these genera in the buffer and at the field edge through time (Figure 10). *Pardosa* was much more abundant in the buffer than at the field edge in April and May ($p < 0.0001$), but later became more abundant at the field edge, particularly in July and September ($p < 0.001$). While similarly low in abundance in both habitats in the spring and fall, *Pirata* was consistently more active in the interior buffer than the field edge June – September ($p < 0.01$). *Hogna* was more abundant at the field edge than the buffer in June, September, and October ($p < 0.001$), and did not differ in abundance from the buffer in the other months.

Discussion

Herbaceous and grassy riparian buffers may provide complex habitat structure, favorable microclimate, and alternative food resources for arthropod predators when adjacent agricultural fields are less hospitable, particularly following harvest and over winter. The major aims of this study were to evaluate the use of riparian conservation buffers as refugia for lycosid spiders, a common generalist predator in corn fields, and determine if emerging aquatic insects provide an important alternative prey resource to the spiders. An additional aim was to assess this potential for terrestrial-aquatic linkages in an agro-ecosystem in comparison to unmanaged systems where recent studies have well-established trophic links between terrestrial arthropod predators and emerging aquatic insects (Henschel et al. 1996, Power and Rainey 2000, Sanzone et al. 2003, Power et al. 2004, Paetzold et al. 2005).

Several approaches were used to address these aims. First, the activity-abundance of lycosid spiders in riparian and corn field habitats at multiple sites was examined through time in relation to the availability of terrestrial and aquatic prey. I expected to find higher activity-abundance of lycosid spiders in the riparian buffer following harvest in the autumn and prior to planting in the spring; these are times of the year when terrestrial prey availability was predicted to be low and aquatic prey availability to be high. Second, the consumption of aquatic insects by lycosid spiders was evaluated directly with feeding trials and indirectly by analysis of the natural abundance of ^{13}C and ^{15}N in field-collected lycosid spiders. I hypothesized that lycosid spiders would readily consume aquatic insects and that aquatic insects would comprise a significant portion of spider diets in the riparian buffer. Finally, directional pitfall traps were used to assess the movement of lycosid spiders between the riparian buffer and the corn field. I predicted that spiders would exit the corn field and enter the riparian buffer following autumn harvest and then move from the riparian buffer back towards the fields early in the summer when the corn crop began to grow.

Taken together, evidence from these studies suggest that only a weak terrestrial-aquatic linkage exists between streams and lycosid spiders in neighboring agricultural fields. While a trend of greater adult activity-abundance was observed in the riparian buffer compared to the corn field in the 2003-2004 seasonal activity study, I did not witness a dramatic increase in spider abundance in riparian buffers following corn harvest in the autumn. Additionally, across all sites, patterns of aquatic insect emergence mirrored seasonal patterns of abundance in terrestrial prey, and the abundance of ground-dwelling terrestrial prey varied little between riparian and corn field habitats. In the feeding trials, lycosid spiders did consume adult aquatic insects, but varied by genus in the consumption of different aquatic prey. Stable isotope analyses of lycosids captured in the riparian buffer and corn field in March suggested that spiders in both habitats had consumed prey that fed on plants in the riparian buffer or that had emerged from the stream. However, the inability to separate the signatures of in-stream and riparian primary producers using natural abundances of ^{13}C and ^{15}N precluded the calculation of the specific contribution of aquatic insects to wolf spider diets. Finally, I did not observe any significant patterns of directional movement in lycosid spiders trapped at the corn field edge or in the riparian buffer at any time of the field season.

Why were the expectations of a strong-terrestrial-aquatic linkage not born out in these studies? First, it is possible that the distribution and movement of lycosid spiders in corn agro-ecosystems are not affected by the presence of riparian buffers and emerging aquatic prey, and therefore, one must reject the original hypotheses outlined above. The no-till best management practices employed in the corn fields by growers at all three sites may have eliminated an important productivity gradient previously found in natural systems to drive the aggregation of spiders in more productive riparian habitats compared to less productive upland habitats (Sanzone et al. 2003, Power et al. 2004). To this end, similar abundances of terrestrial prey were observed in the riparian buffer and corn field throughout the year, and emerging aquatic insects were most abundant during the time when terrestrial prey were most abundant. Additionally, corn litter left on the field may have provided favorable habitat structure that promoted the habitat residency of lycosid spiders (Uetz 1991, Marshall and Rypstra 1999, Halaj et al. 2000, Marshall et al. 2000, Buddle and Rypstra 2003). However, it is also quite possible that the strength of terrestrial-aquatic linkages in agro-ecosystems is highly species-specific, reflecting each individual predator's habitat and prey preferences, behavior and seasonal phenology.

Examining patterns of activity-abundance for the three most common genera collected during the field studies may provide important insights regarding the use of riparian buffers and the potential for each to consume aquatic prey. In the seasonal activity study across sites (2003-2004), *Pardosa* was captured more frequently in the field habitat than in the riparian buffer. Data pooled from paired traps used in the directional movement study (2005) corroborated these findings of greater *Pardosa* abundance in the corn field in the summer, but also revealed that *Pardosa* was much more active in the interior riparian buffer in April and May, prior to the growth of the corn crop. While *Pardosa* has previously been reported to have large densities in crop fields (5-100 m^{-2}, Marshall and Rypstra 1999, Marshall et al. 2002), it is also a highly mobile habitat generalist (Marshall and Rypstra 1999) and is thought to have evolved in riparian areas frequently disturbed by flooding (Wissinger 1997, Marshall and Rypstra 1999). Thus, *Pardosa* likely spends some time in the riparian buffer, and, as suggested by the preliminary stable isotope analyses, may consume terrestrial or even aquatic prey there. However, if *Pardosa* do in fact consume aquatic prey, the feeding trials suggest that they are more likely to eat only very small prey items (e.g., chironomid midges, average length: 4.5 mm).

In contrast to *Pardosa*, *Pirata* was more frequently captured in riparian habitats than in agricultural fields during the seasonal activity study. This is consistent with previously observed preferences of *Pirata* for moist habitats (Graham et al. 2003, Hendrickx and Maelfait 2003, DeVito et al. 2004). Activity-abundance data from the directional movement study suggest that *Pirata* is most abundant in the interior riparian buffer throughout the summer. Interestingly, the abundance and biomass of emerging aquatic insects was found to be the greatest across sites during the summer. Thus, given a phenology overlapping the period of greatest aquatic prey abundance as well as proximity to streams, *Pirata* may exemplify a strong terrestrial-aquatic linkage.

Hogna, unlike either *Pardosa* or *Pirata*, showed no preference for either the riparian or field habitat in the seasonal activity study. Despite being considered a common inhabitant of agro-ecosystems (Marshall and Rypstra 1999), *Hogna* may have lower habitat tolerances than the co-occurring *Pardosa* and likely emigrates from agricultural fields to more suitable habitats to overwinter (Marshall and Rypstra 1999, Buddle and Rypstra 2003). Increased activity of *Hogna* was recorded at the field edge in the autumn during the movement study and may be indicative of emigration from the field, although monthly sampling of paired directional pitfall traps was unable to detect any net direction of movement. If *Hogna* indeed overwinters in riparian buffers, the potential for a terrestrial-aquatic linkage exists given the emergence of some aquatic insects during the winter and early spring (e.g., winter stoneflies (Plecoptera) captured in emergence traps at RM in March, Figure 7).

While the evidence for terrestrial-aquatic linkages between streams and neighboring agricultural fields may be weak and somewhat species dependent, results from this study do suggest that riparian buffers along adjacent streams have conservation and management value in agro-ecosystems. Riparian buffers next to agricultural fields did maintain a diverse assemblage (with respect to both taxa and size distribution) of lycosid spiders that overlapped the composition of wolf spiders in adjacent fields, and also harbored additional species and increased relative abundance of common species throughout the year. These spiders have the potential to enrich surrounding crop fields and contribute to the control of pest species. To this end, recent studies have suggested that increased richness of natural enemies can contribute to increased pest suppression (Cardinale et al. 2003, Snyder and Ives 2003, Snyder et al. 2006). The question remains, however, what specific role *riparian* conservation buffers play as compared to other types of conservation buffers not associated with streams. Future studies should directly compare natural enemy diversity, pest suppression, and the contribution of alternative prey resources to predator diets in agricultural fields with riparian buffers, fields with conservation strips not associated with streams, and fields without any alternative habitat to elucidate an answer to this question.

Tables

Table 1. Abundance of lycosid spiders (adult and juvenile) over six sampling periods, collected by pitfall traps placed in field and riparian buffer habitats at each site (FQ, MW, RM). Superscript ‘s’ indicates clutch(es) of spiderlings were collected with females.

		FQ		**MW**		**RM**	
	Average size (mm)	Field (n = 22)	Riparian (n = 19)	Field (n = 22)	Riparian (n = 23)	Field (n = 19)	Riparian (n = 24)
Adults							
Pardosa	4.9	25^{s}	23	10	2	7	7^{s}
Pirata	4.4	2	11	3^{s}	29^{s}	.	1
Hogna	14.3	2	6	4	7^{s}	1	9^{s}
Rabidosa	14.3	.	.	.	.	.	1^{s}
Allocosa	5.2	.	.	.	.	.	1
Schizocosa	6.6	.	.	.	1	.	2^{s}
Unknown		.	1	.	1	1	.
Juveniles		5	17	1	16	6	12
Total abundance		34	58	18	56	15	33
Total taxa		3	4	3	5	3	6

Table 2. Proportion of lycosid spiders consuming adult aquatic prey in feeding trials. Proportions with the same letter, within a column, are not significantly different at the $p < 0.05$ level. N indicates the total number of feeding trials conducted for each predator taxon with each prey type.

		Aquatic Prey		
Predator	**Predator Size (mm)**	**Chironomidae**	**Hydropsychidae**	**Odonata**
Pardosa	5.4	1.0 (n = 12)	0.29^a (n = 17)	0.10^a (n = 10)
Rabidosa	11.7		0.17^a (n = 6)	1.0^b (n = 6)
Hogna	12.1			0.75^b (n = 4)

Figure legends

Figure 1. Sampling design for seasonal activity study conducted 2003-2004 at three sites in Maryland: FQ, MW, RM. Dashed lines indicate randomly selected transects along 60 m length of stream at each site. Dark circles indicate pitfall traps in two habitats: corn field (n = 4 per site) and riparian buffer (n = 4 per site). Open triangles indicate in-stream emergence traps (n = 4 per site).

Figure 2. Sampling design for directional movement study conducted at FQ in 2005. Paired pitfall traps (dark circles) placed with aluminum flashing guides (dark Vs) in two habitats: field edge (n = 10 per date) and wet-dry soil boundary in riparian buffer (n = 10 per date). Note only two paired trap arrays per habitat are shown in figure.

Figure 3. Activity-abundance (mean ± SE) of adult lycosid spiders (A) and proportion (mean ± SE) of traps containing juvenile lycosids (B) in corn field (open circles) and riparian buffer (closed circles) during seasonal activity study across three sites in 2003-2004.

Figure 4. Proportion (mean ± SE) of pitfall traps containing the three most common lycosid spiders (*Pardosa*, *Pirata*, *Hogna*) in corn field (open bars) and riparian buffer (dark bars) during seasonal activity study across three sites and four dates† (May-October) in 2003-2004. * indicates difference between field and buffer at $p = 0.06$. ** indicates difference between field and buffer at $p < 0.01$.

† Model used to calculate proportion of *Pirata* in each habitat only included three dates (May – September).

Figure 5. Activity-abundance (mean ± SE) of terrestrial prey (includes Isopoda, Collembola, Thysanoptera, Homoptera, Hemiptera, Orthoptera, Diptera, and Lepidoptera) captured with pitfall traps in corn field (open circles) and riparian buffer (closed circles) during seasonal activity study across three sites in 2003-2004.

Figure 6. Abundance (mean ± SE), dark circles (left axis), and biomass (mean ± SE), open triangles (right axis), of aquatic insect emergence from three streams in 2003-2004 seasonal activity study.

Figure 7. Mean biomass of aquatic insect emergence at three field sites in 2003-2004, with contributions by major taxonomic orders.

Figure 8. Natural abundance of $\delta^{13}C$ and $\delta^{15}N$ (mean ± SE) from composite samples of primary producers, aquatic prey, and lycosid spiders collected at FQ. Primary producers are represented by circles and included periphyton (n = 2), benthic organic matter (BOM) from corn (n = 3) and grass (n = 2) collected in the stream (open circles), grass (n = 2) collected in the riparian buffer (grey circles) and corn leaves (n = 3) collected in the agricultural field (black circles). Aquatic insects (open squares) included the Ephemeroptera (n = 2), Diptera (n = 3), Trichoptera (n = 11), and Odonata (n = 3). Lycosids collected in the riparian buffer (grey triangles) included

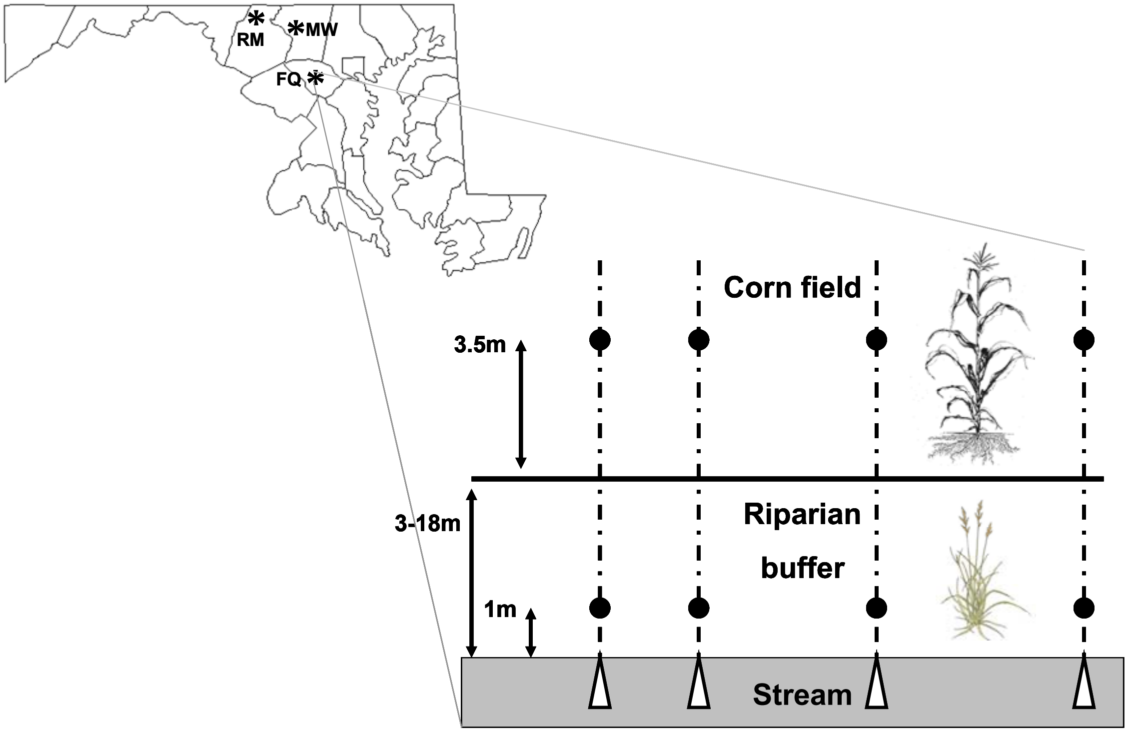
Pardosa (n = 4) and *Rabidosa* (n = 3). *Pardosa* (black triangle) was the only lycosid captured in the corn field (n = 3).

Figure 9. Activity-abundance (mean ± SE) of adult (A) and juvenile (B) lycosid spiders from combined, paired pitfall samples at the corn field edge (open circles) and interior riparian buffer (dark circles) at FQ in 2005.

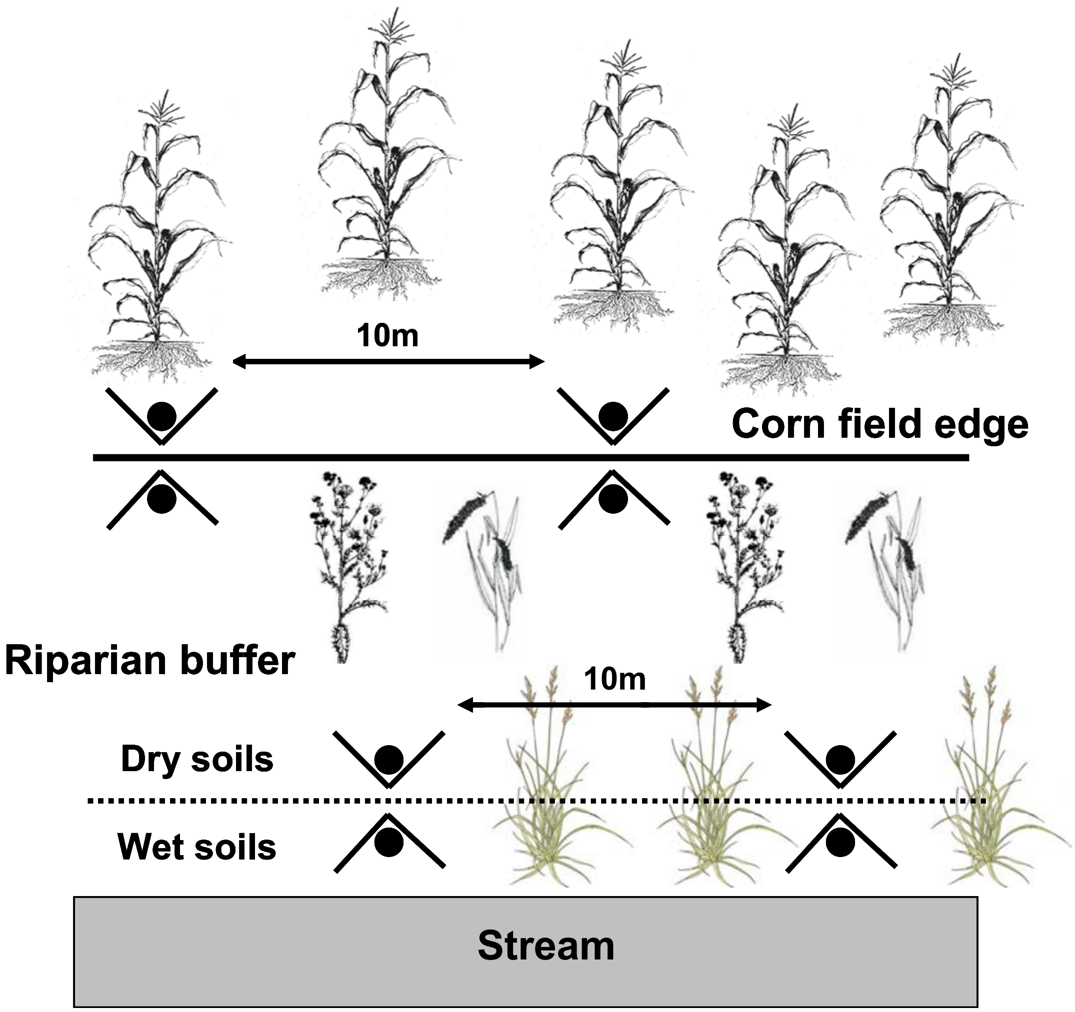
Figure 10. Adult activity-abundance (mean ± 95% CL) of three common genera of lycosid spiders (*Pardosa*, *Pirata*, *Hogna*) from combined, paired pitfall samples at the corn field edge (open circles) and interior riparian buffer (dark circles) at FQ in 2005.

Figures

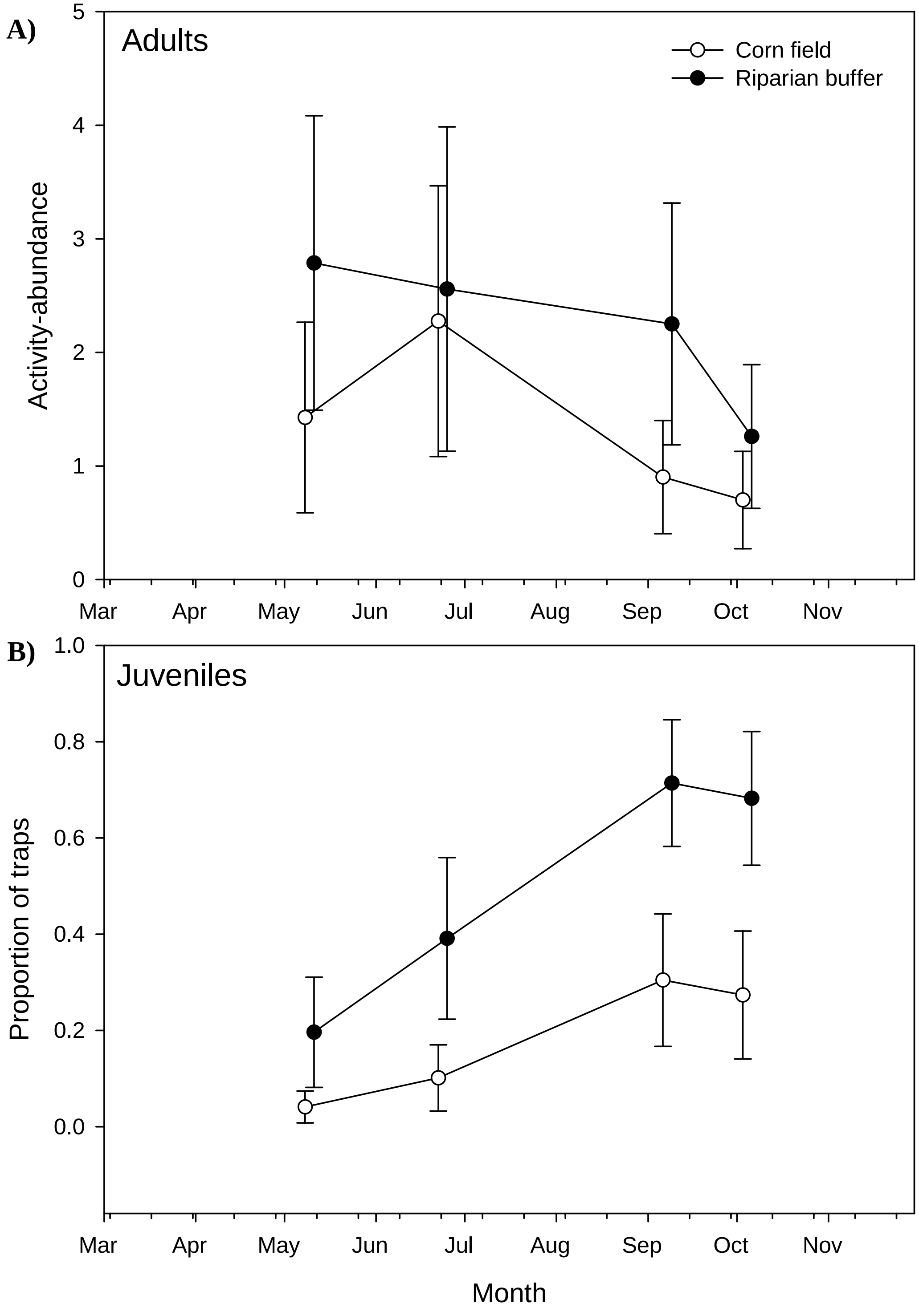
(Figure 1)



(Figure 2)

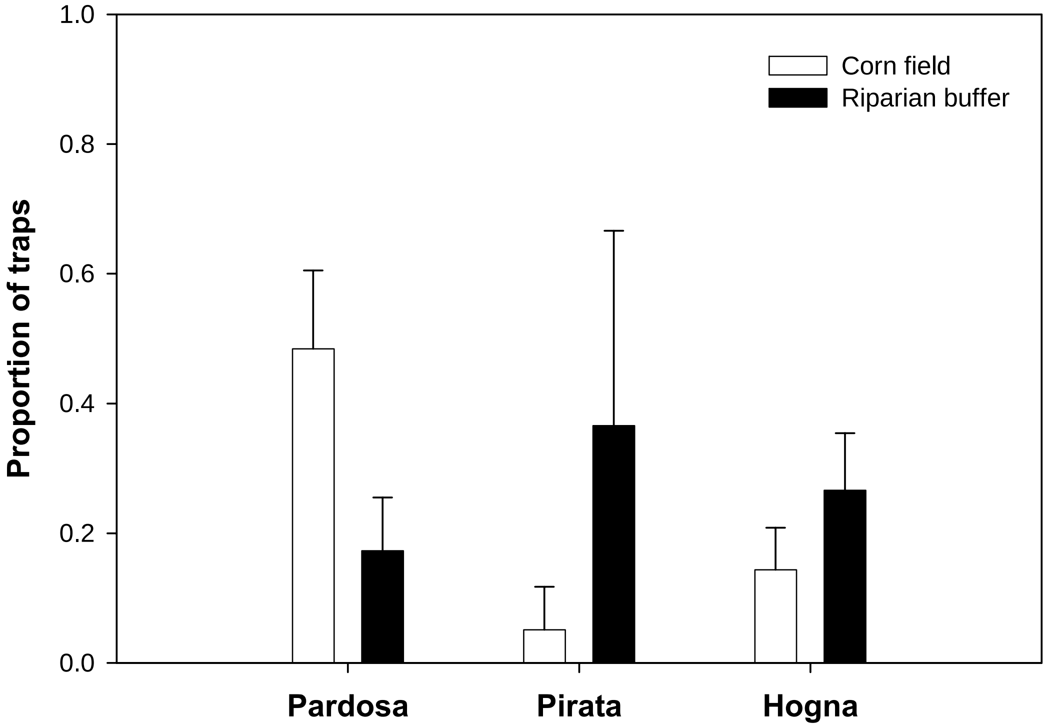

10m
Corn field edge
Riparian buffer
10m
Dry soils
Wet soils
Stream

(Figure 3)

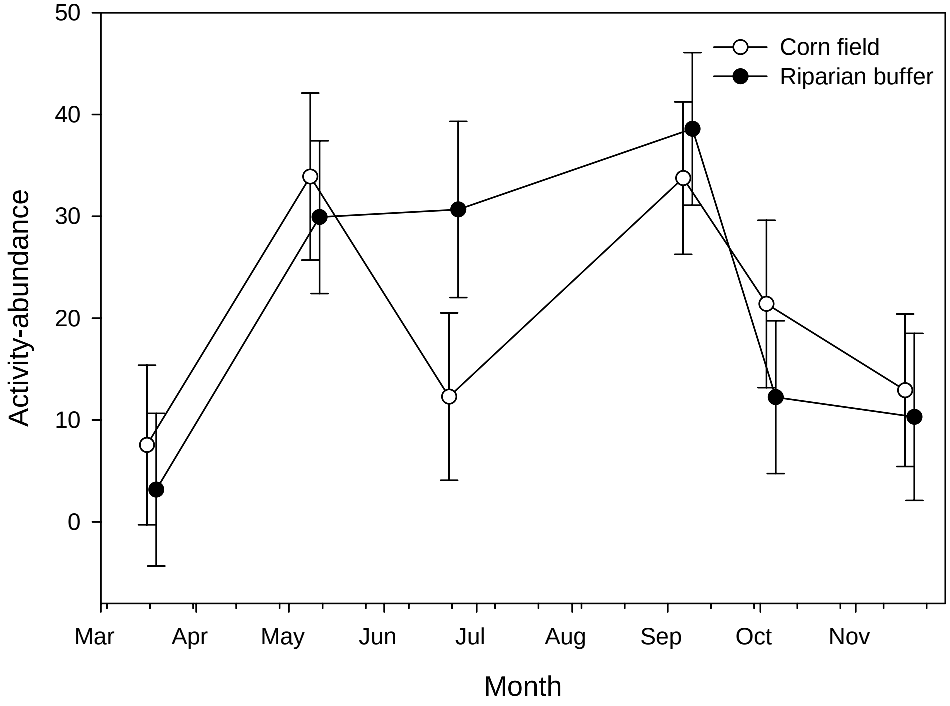


A)
Adults
Corn field
Riparian buffer
Activity-abundance
5
4
3
2
1
0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
B)
Juveniles
Proportion of traps
1.0
0.8
0.6
0.4
0.2
0.0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Month

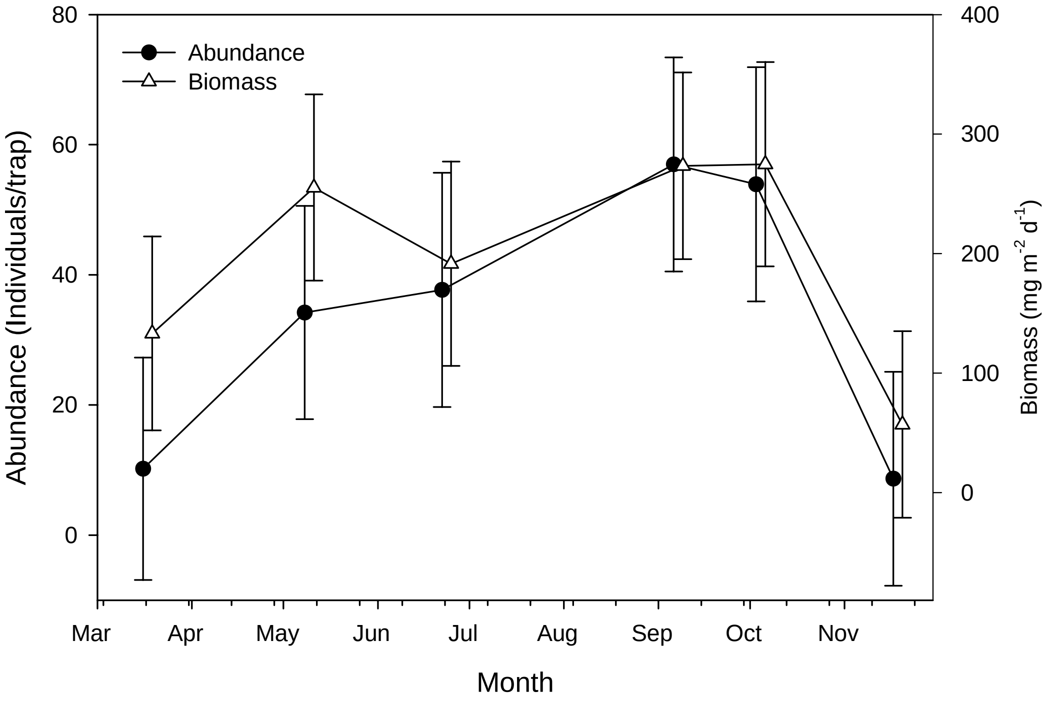
(Figure 4)


1.0
0.8
0.6
0.4
0.2
0.0
Proportion of traps
Corn field
Riparian buffer
Pardosa
Pirata
Hogna

(Figure 5)

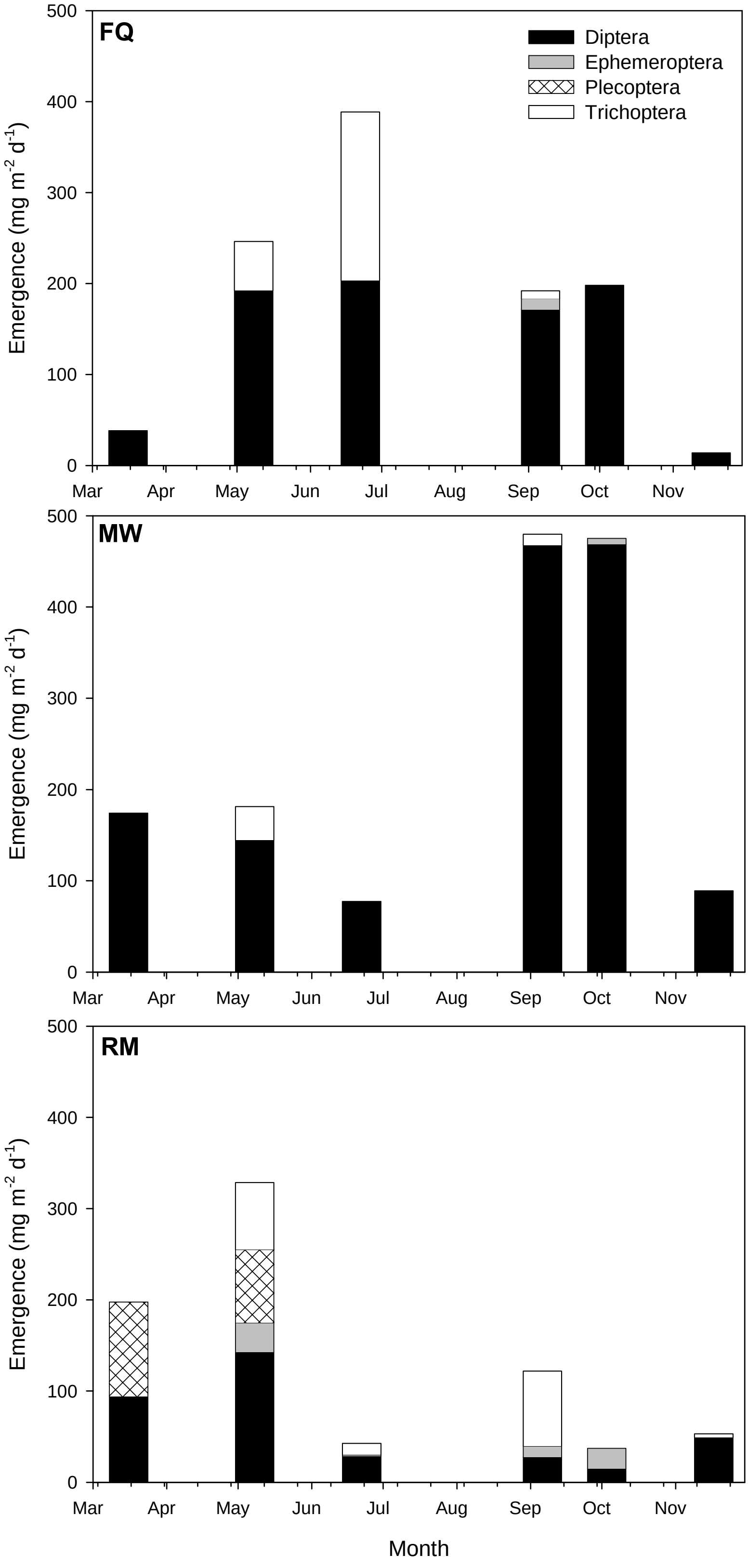

Corn field
Riparian buffer
Activity-abundance
50
40
30
20
10
0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Month

(Figure 6)

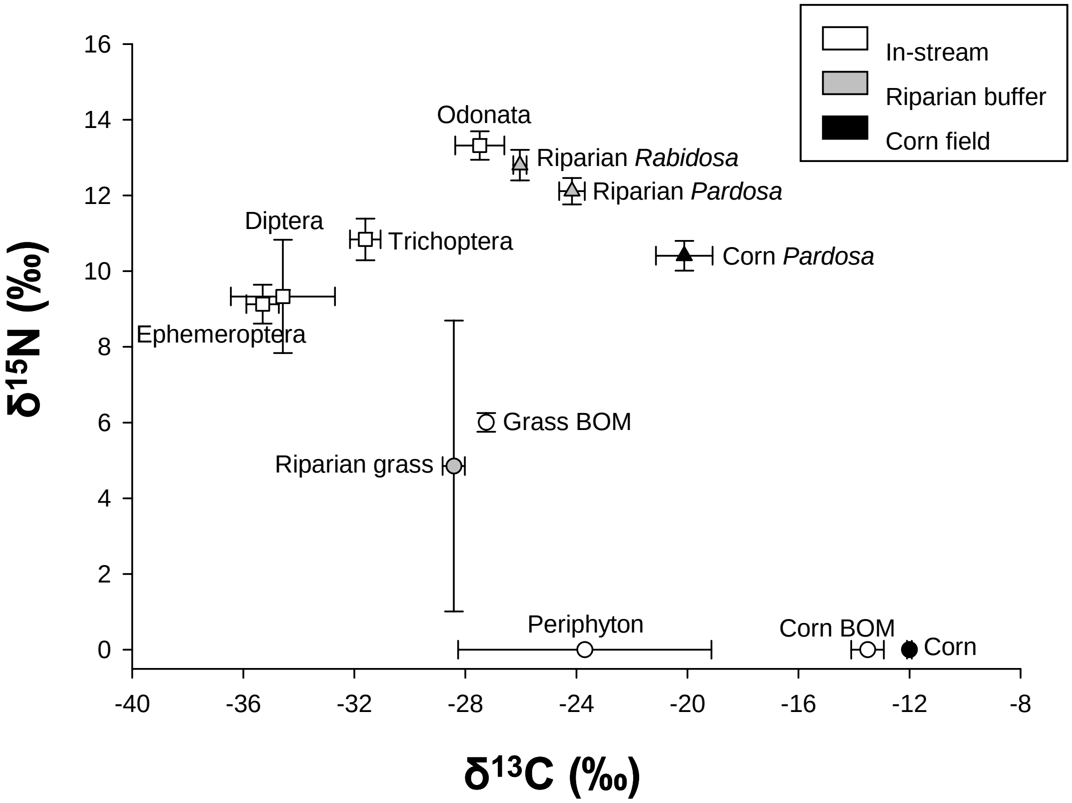


Abundance
Biomass
Abundance (Individuals/trap)
Biomass (mg m^{-2} d^{-1})
Month
80
60
40
20
0
400
300
200
100
0
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

(Figure 7)

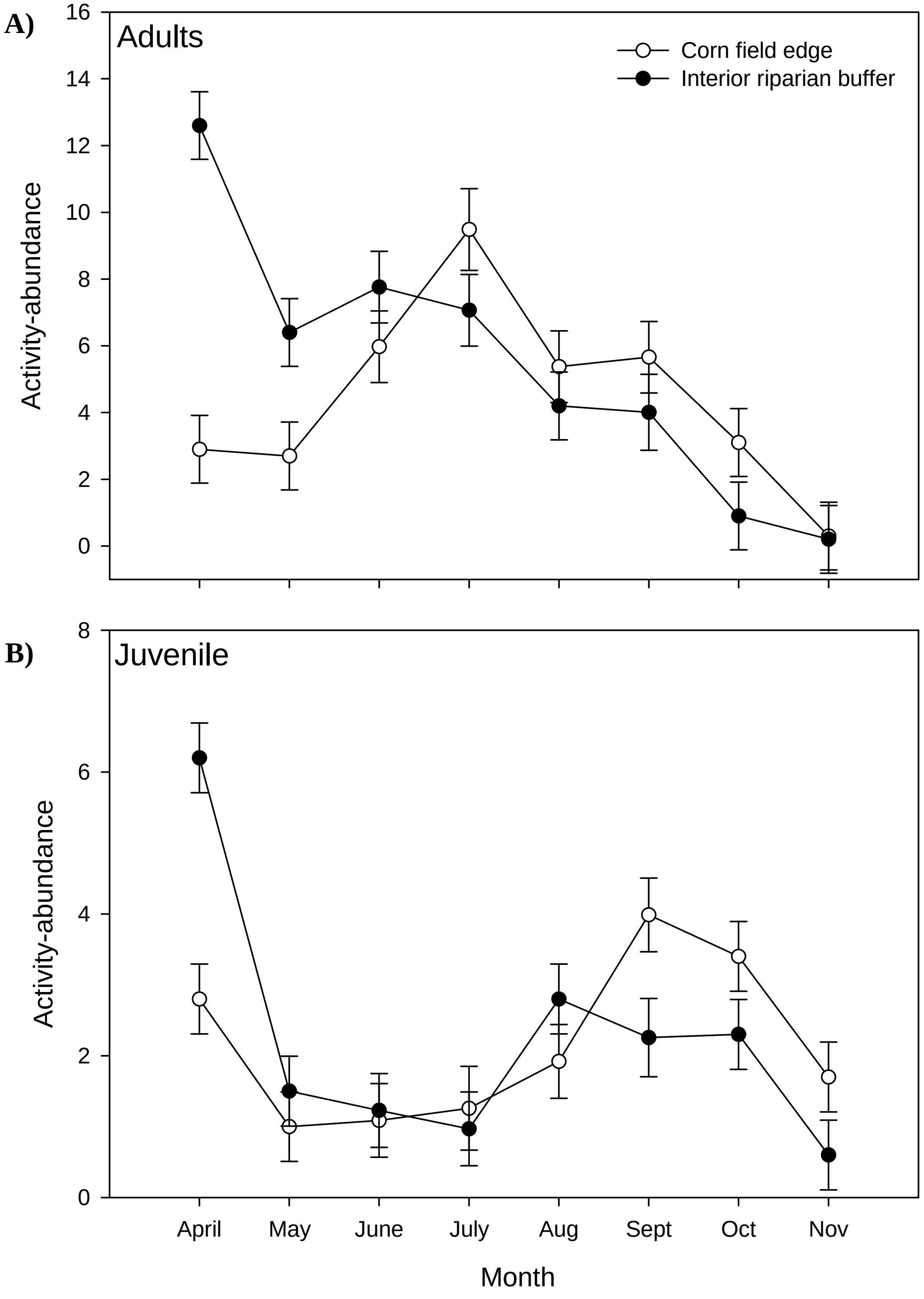

FQ
MW
RM
Diptera
Ephemeroptera
Plecoptera
Trichoptera
Emergence (mg m^{-2} d^{-1})
0
100
200
300
400
500
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Month

(Figure 8)

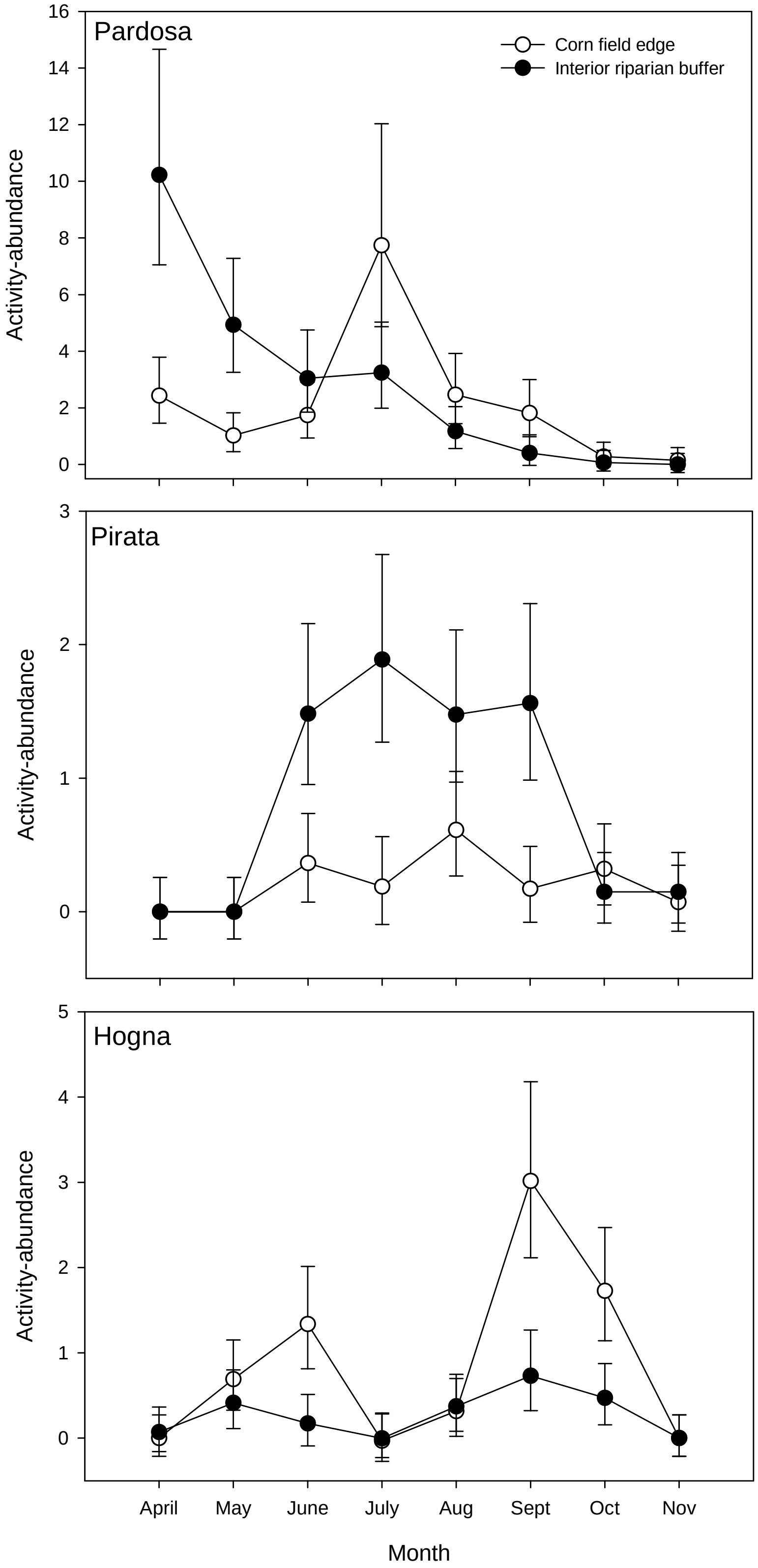


In-stream
Riparian buffer
Corn field
Odonata
Riparian *Rabidosa*
Riparian *Pardosa*
Diptera
Trichoptera
Corn *Pardosa*
Ephemeroptera
Grass BOM
Riparian grass
Periphyton
Corn BOM
Corn
16
14
12
10
8
6
4
2
0
-40
-36
-32
-28
-24
-20
-16
-12
-8
δ15N (‰)
δ13C (‰)

(Figure 9)


A)
Adults
Corn field edge
Interior riparian buffer
Activity-abundance
16
14
12
10
8
6
4
2
0
B)
Juvenile
Activity-abundance
8
6
4
2
0
April
May
June
July
Aug
Sept
Oct
Nov
Month

(Figure 10)



Pardosa
Corn field edge
Interior riparian buffer
Activity-abundance
16
14
12
10
8
6
4
2
0
Pirata
Activity-abundance
3
2
1
0
Hogna
Activity-abundance
5
4
3
2
1
0
April
May
June
July
Aug
Sept
Oct
Nov
Month

Conclusion

In this work, I examine the exchange of terrestrial and aquatic resource subsidies across the boundary of stream and riparian habitats and measure the effects of those subsidies on consumers and ecosystem processes in the recipient habitats. While previous work has focused largely on subsidy flux in natural ecosystems, I purposely examine cases in landscapes altered by agricultural and suburban development with the intent of informing conservation and restoration practices for impacted habitats and ecosystem services.

In two cases where I study the effects of terrestrial subsidies on stream consumers and ecosystem processes (Chapters I and II), I find strong evidence for terrestrial-aquatic linkages. Herbaceous vegetation and grasses provide a substantial allochthonous resource for treeless headwater streams that in turn supports a functionally diverse macroinvertebrate community. Periodical cicada detritus falling into forested suburban streams during the summer provides a pulse of terrestrial resources that is locally utilized and causes dramatic increases in whole-stream community respiration. In both cases, terrestrial subsidies provide a large quantity of high quality, allochthonous resources to stream ecosystems.

Interestingly, in the reciprocal exchange of aquatic subsidies to terrestrial predators (Chapter III), I find very weak evidence for a terrestrial-aquatic linkage. Wolf spiders are generally more abundant in the riparian buffers adjacent to crop fields, but show no specific seasonal shifts in abundance or net movement between field and buffer habitats as I had predicted would occur. Further, while I observe wolf spiders consuming adult aquatic insects in the lab, I could not resolve the specific contribution aquatic insects make to the diets of field-collected wolf spiders.

The results that I present here strongly suggest that the characteristics of the boundary habitat mediate the transfer of resource subsidies across the terrestrial-aquatic interface. For example, in Chapter I, the narrow study streams allow dense herbaceous vegetation and grasses growing along the edges to fall into and over the stream, providing a substantial detrital resource and blocking light to benthic primary producers. This results in a much different resource dynamic than has previously been described for agricultural streams (Delong and Brusven 1998). In Chapter II, I report that the disturbed site, with a much narrower riparian forest than the undisturbed intact site, actually receives greater inputs of cicada detritus, despite lower cicada emergence at the disturbed site. I suggest that the narrow buffer and the young trees planted nearby may provide a preferred chorusing and oviposition habitat for adult cicadas (White 1980, Rodenhouse et al. 1997, Yang 2006), resulting in increased cicada aggregation near the stream and potentially greater input of cicada detritus. In Chapter III, I seek an explanation for the weak terrestrial-aquatic linkage between spiders and emerging aquatic insects. One possibility is that the no-till best management practices employed on the corn fields by growers provides favorable habitat structure for spiders (Uetz 1991, Marshall and Rypstra 1999) and eliminates any potential productivity gradient at the riparian-field boundary that would drive spiders to aggregate in the buffers (Sanzone et al. 2003).

Further, I find that the effect of subsidy fluxes to recipient ecosystems appears to depend largely on the temporal context in which it occurs. For example, periodical cicada detritus, a resource available only once every 17 years, enters streams at a time of the year when other allochthonous inputs are typically low, and therefore provides a brief, but novel resource pulse that is readily used by stream heterotrophs. Similarly, the timing of cross-habitat subsidies may also be important for the transfer of aquatic resources to terrestrial consumers. Previous studies report a temporal asynchrony between aquatic insect emergence and terrestrial prey abundance that facilitates a terrestrial-aquatic linkage (Nakano and Murakami 2001, Kato et al. 2003). Perhaps emerging aquatic insects have little effect on the distribution of wolf spiders at the agricultural sites I study because the largest pulse of emergence from the streams occurs at the same time of the year as the greatest activity-abundance of terrestrial insects, rather than at alternate times when terrestrial prey abundance is low.

The results of Chapters I and III have important implications for the management and conservation of riparian buffer habitats adjacent to agricultural lands. While forested buffers are often preferred and a stream restoration target, herbaceous and grassy stream buffers are known to have value in agricultural landscapes as a best management practice to decrease erosion and reduce nutrient loads (Maryland Department of Agriculture 1996; Lyons *et al.* 2000; Wigington *et al.* 2003). Here, I provide evidence that the plants in these buffers may also provide high quality allochthonous resources that promote macroinvertebrate diversity in agricultural streams. While I offer weak support for a terrestrial-aquatic linkage between emerging aquatic insects and wolf spiders, I do show that riparian buffers next to agricultural fields maintain a diverse assemblage of lycosid spiders, including some genera not found in adjacent fields, and support a greater abundance of some common species throughout the year. These spiders have the potential to enrich surrounding crop fields and contribute to the control of pest species. Thus, riparian buffers composed of herbaceous and grassy vegetation have potential conservation and management value to both stream and agro-ecosystems.

The results of Chapter II have important implications given that human activities have accelerated ecological commerce, or the exchange of subsidies across habitats (Palumbi 2003). The frequency of unnatural resource subsidy input to ecosystems will increase as a result of the introduction of pests and pathogens and increases in nutrient subsidies from agriculture and urbanization (Riley and Jefferies 2004). If the whole-stream response to the irregular, but natural resource pulse provided by periodical cicada detritus is any indication, unnatural resource pulses will profoundly impact stream ecosystems.

The evidence that I present in this body of research suggests that terrestrial-aquatic linkages are important in human-altered ecosystems. The relative strength of those linkages, however, depends on a number of factors including the identities of the taxa involved, the direction of the subsidy flux, the nature of the land-water boundary, and the temporal context in which they occur.

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