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**ASSESSMENT OF THE EFFECTS OF LAND USE CHANGES ON
LOWER ST. JOHNS RIVER BASIN WATERSHED DETRITAL
INPUT**

FINAL REPORT



Final Report

Assessment of the Effects of Land Use Changes on Lower St. Johns River Basin Watershed Detrital Input

Submitted to

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1. General Introduction

Introduction 1.1

The research described in this report provides a basis for a predictive understanding of how historical changes in land use have affected the role of terrestrial leaf litter in aquatic food webs of the Lower St. Johns River Basin (LSJRB). Like much of the eastern United State, development of this watershed has resulted in large quantitative and qualitative changes to riparian plant communities. These changes, in concert with increases in nutrient loading, are likely to have had a great effect on the structure and function of aquatic food webs due to the close relationship between terrestrial leaf detritus and invertebrate communities of forested headwater streams.

The energy base for streams with forested watersheds is largely tree leaves that enter their channels during the autumn (Fisher & Likens 1973; Wallace, Eggert & Meyer 1997). A specific functional feeding group of macroinvertebrates—the “shredders”—process whole tree leaves to small organic particles through their feeding activities (Cummins & Merritt 1996). The palatability and food quality of different species and sources of leaf litter varies dramatically (Sweeney 1993), so streams receiving different types of litter, rather than different quantities, may show different levels of shredder production and community structure. Regardless of the species of litter, aquatic fungal colonization typically improves food quality for shredders (Suberkropp 1992). Aquatic fungi can assimilate carbon directly from leaf tissues but are able to obtain other nutrients (phosphorus, nitrogen) from the water column (Suberkropp & Chauvet 1995). Consequently, factors affecting water chemistry will also influence the rate of fungal colonization and thus palatability and nutrition of leaf detritus for shredders. The interaction between shredders and fungi is further complicated by the fact that different specific fungal species have different effects on shredder growth rates (Arsuffi & Suberkropp 1986).

In summary, the community attributes of riparian vegetation, aquatic fungi and shredders interact to structure stream food-webs. Changes in land use, such as those that have occurred in LSJRB, will affect these attributes in numerous ways and, in turn, may have large effects on the structure and function of stream ecosystems.

1.2 Field Design

The study streams selected represented a gradient of urban-rural land-use from the lowest to highest intensity of urban land-cover. Twenty catchments with streams will similar discharge, catchment area, geomorphology were selected with help from SJWMD personnel. Four catchments with similar channel forms and representing the breadth of the urban-rural gradient were designated as locations for intensive study (“focus” catchments). See the following chapter for more detailed information.

1.3 Goals

The specific information developed by our research has been based on a number of integrated tasks. As such we have:

- Quantified impervious surface areas for 18 catchments representing an urban-rural land-use gradient in the LSJRB
- Measured rates of break down for major riparian plant species in 18 streams representing an urban-rural land-use gradient in the LSJRB
- Quantified community attributes for invertebrates associated with leaf detritus in these streams
- Quantified the palatability and nutrition of major riparian plant species for a widespread gastropod
- Developed coarse organic matter budgets for 4 streams representing an urban-rural land-use gradient
- Quantified community attributes for invertebrates in 10 streams
- Assessed the suitability for stable isotope analysis (N) for quantifying the spatial scale of land-use effects on downstream communities
- Assessed the suitability of stable isotope analysis (C, N) for quantifying the relative importance of autochthonous and allochthonous organic matter for consumer production in these streams

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2. Comparison of Methods for Delineating Catchment Impervious Surface Area Using Multispectral DOQQs in the St. John's River Drainage Basin, Florida, U.S.A

2.1 Introduction

Rates of urbanization have been increasing consistently for many decades, but only fairly recently has research been conducted that examines the effects of this change in land use on stream ecosystems. Findings in this area are nearly universal, showing that urban expansion is a major degradative factor in the physical, biological, and chemical health of aquatic systems (Paul and Meyer 2001). Of the many measurements of urbanization, impervious surface has shown particular promise in being a predictor of the effects of urbanization on the biological communities (Arnold and Gibbons 1996, Gillies et al. 2003). Several recent studies have shown that, in at least some regions, there is a threshold relationship between the percent total impervious surface area (PTIA) within a stream's catchment and the biological richness of that stream (Arnold and Gibbons 1996, Morse et al. 2003, Ourso and Frenzel 2003, Wang et al. 2003).

In order to determine the most efficient and most accurate method to delineate PTIA, we performed a Normalized Difference Vegetation Index (NDVI), supervised and unsupervised classifications, and a principle components analysis (PCA) on one study catchment in our research area and then compared these derived PTIA values to manually derived ground truth data. The purpose of this work was to 1) determine which of the four methods resulted in the most accurate estimates of PTIA and 2) which of the four methods was the most efficient in terms of effort spent conducting the analysis.

2.2 Study area and data sets

2.2.1 Study area

The overall study area consists of twenty catchments (0.09-9.38 km²) that feed first- and second-order tributary streams in the Lower St. John's River Basin (LSJRB), Florida, USA. The LSJRB flows through the center of a large, rapidly growing metropolitan area (Jacksonville) and provides many ecological and economic services to the respective animal and human communities that live in association with it. The St. John's and its associated tributaries have also been grossly underrepresented in the literature and there is a paucity of sufficient baseline data that could be used to measure the urbanization impacts. For the purposes of comparing the PTIA delineation methods, we selected one study catchment to analyze intensively with each method.

2.2.2 Digital Orthophoto Quarterquads

The St. John's River Water Management District (SJRWMD) provided the images and catchment shape files that were used to derive impervious surface for this analysis. The images used for the analysis consisted of one color-infrared and one true-color Digital Orthophoto Quarterquad (DOQQ) which were taken with a Leica ADS40 Airborne Digital Sensor on December 15, 2003 (Fig. 1). The DOQQ's were taken at an altitude of 20,000 feet and resulted in a ground resolution of one meter (SJRWMD 2004). Unlike traditional DOQQs, the ADS40 uses a pushbroom scanner to create a digital image and as a result, no traditional film products are created in the initial image production (Leica Geosystems 2002). The sensor collected 12 bit image data that then

had to be converted into the standard 8 bit which resulted in a loss of color range from 4096 colors to 256 colors. Despite this loss of color, the 12-bit image data enabled differentiation of shadowed and bright objects through tonal enhancement prior to the reduction to 8-bit data (SJRWMD 2004). In addition and also unlike traditional DOQQs, the ADS40 produced true multispectral images yielding 3 different bands for the color-infrared image: Green (535-585 nm), Red (610-660 nm), and Near Infrared (835-885 nm) and for the true color image: Blue (430-490 nm), Green (535-585 nm), Red (610-660 nm) (Leica Geosystems 2002).



Figure 1. a) True color and b) color-infrared DOQQs

2.3 Methods

2.3.1 Catchment Delineation

In order to ease data analysis and reduce processing time, the catchment shape was delineated from the color infrared and the true color infrared DOQQs using ERDAS Imagine 8.7. A shape file for the catchment was overlain on the DOQQ image and was selected as an area of interest (AOI). The AOI was then converted to a subset image for use with further analyses (Fig. 2).

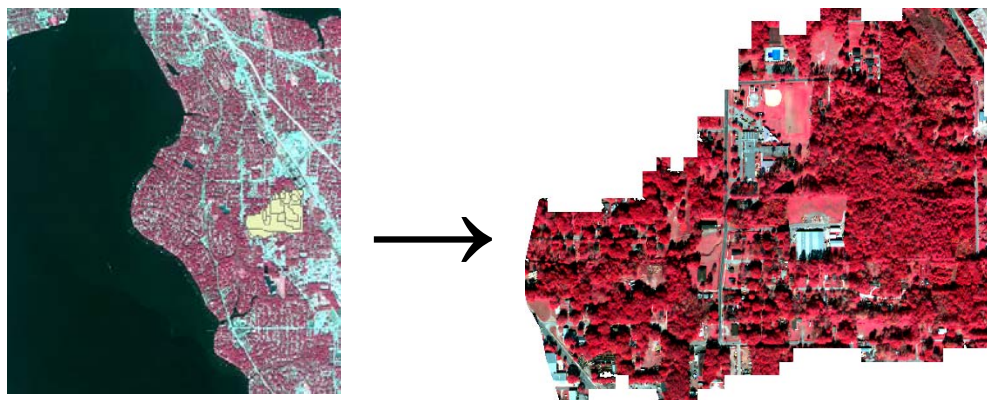


Figure 2. Delineation of study catchment from color-infrared DOQQ.

2.3.2 Normalized Difference Vegetation Index (NDVI)

Using the Spatial Modeler function in ERDAS Imagine 8.7, we performed an NDVI on the color-infrared delineated catchment for the study catchment 13. The NDVI equation is as follows:

$$\frac{(\rho_2 - \rho_1)}{(\rho_2 + \rho_1)}$$

Where: ρ_1 and ρ_2 = the brightness values of the Red and NIR bands respectively.

The results of the NDVI were then stretched along a 256 pixel grayscale within the model and assigned brightness values between 0-255 with 0 representing the lowest NDVI value and 255 the highest (Figure 3a). We then used the Raster Attribute Editor to manually determine the threshold pixel brightness values separating the three desired land cover classes (Water, Impervious Surface, and Vegetated Land) and assigned them the colors blue, red, and green respectively (Fig. 3b).

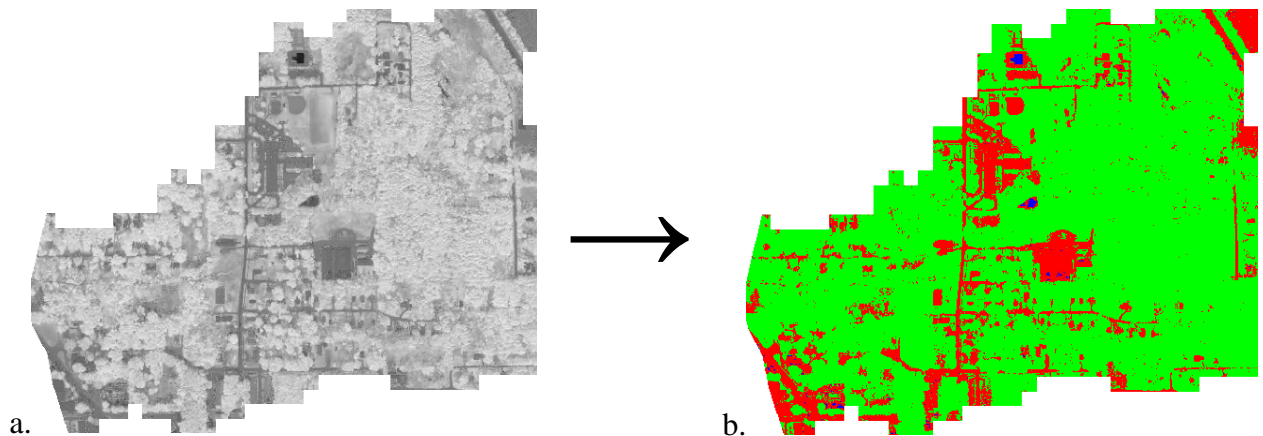


Figure 3. a) DET 13 NDVI image stretched along the grayscale from 0-255; b) NDVI land cover classification: blue = water, red = impervious surface, green = vegetated land.

Next, we used ArcMap 8.3 to reclassify the 256 color classes in the NDVI image into 3 land-cover classes (Water, Impervious Surface, and Vegetated Land) and overlaid a raster file of the catchment onto the NDVI image. We then performed a simple map algebra addition function that resulted in a new study catchment image that incorporated the above land cover classes. With the resultant image, we were able to calculate the estimated PTIA for the NDVI image.

2.3.3 Supervised Classification

Upon examination of the NDVI image, it became apparent that any substantial bare ground could cause problems in the analysis as it would nearly always be classified as impervious (e.g. see the baseball field in the upper center of Figs 2 and 3). As a result, we attempted to add a Bare Ground land-cover class to the original three land cover classes for the supervised classification. We selected twenty training sites for vegetated land and impervious surface, ten for bare ground and three for water.

The disparity in number of training sites was unavoidable due to the extremely small number of areas of water and bare ground within the image. With the training sites identified and combined, we then performed a minimum distance supervised classification. Once the classification was complete, we opened the image in ArcMap 8.3 and determined the PTIA value from the attributes table. In addition, we repeated the procedure for classifications that contained no water and no water or bare ground (see Results for rationale).

2.3.4 Unsupervised Classification

For the unsupervised classification, we started with 50 classes, initialized from statistics with a maximum of 20 iterations and a convergence threshold of 0.950. Upon completion of the classification, we used the mean scatter plot to identify what each class represented and combined those classes that were the same. Finally, we used the Raster Attribute Editor to assign class names and colors to the image. For the unsupervised classification, we only used two classes: Impervious Surface and Vegetated Land, as the addition of other classes caused large errors in classification (see Results).

2.3.5 Principle Components Analysis (PCA)

We ran a PCA analysis in ERDAS Imagine 8.7 selecting for three components to be derived from the three bands. The Eigenvector and Eigenvalues were then used to determine which PCA represented which band and what surface they were most associated with.

2.3.6 Ground Truthing

To compare the utility of the above methods, we manually delineated impervious surfaces using ArcView 3.3 on the true and color-infrared DOQQs. We first divided the true color catchment into 27 100m² polygons and then manually delineated all impervious surfaces within each polygon (Fig. 4). The location of each polygon was chosen to try and represent the full spectrum of impervious surface values in the image. We then compared the same polygons for each of the methods listed above and was able to determine their accuracy versus the control (i.e. the manually delineated polygon) (Fig. 5).

2.3.7 Statistical Analysis

As all method results satisfied normality requirements, the PTIA values for the test polygons were compared to the manually derived values using two sample t-tests with assumed equal variances and a significance level of $\alpha=0.05$. Additionally, linear regression was performed between the three methods and the manual delineation to determine which method resulted in the most accurate results overall.

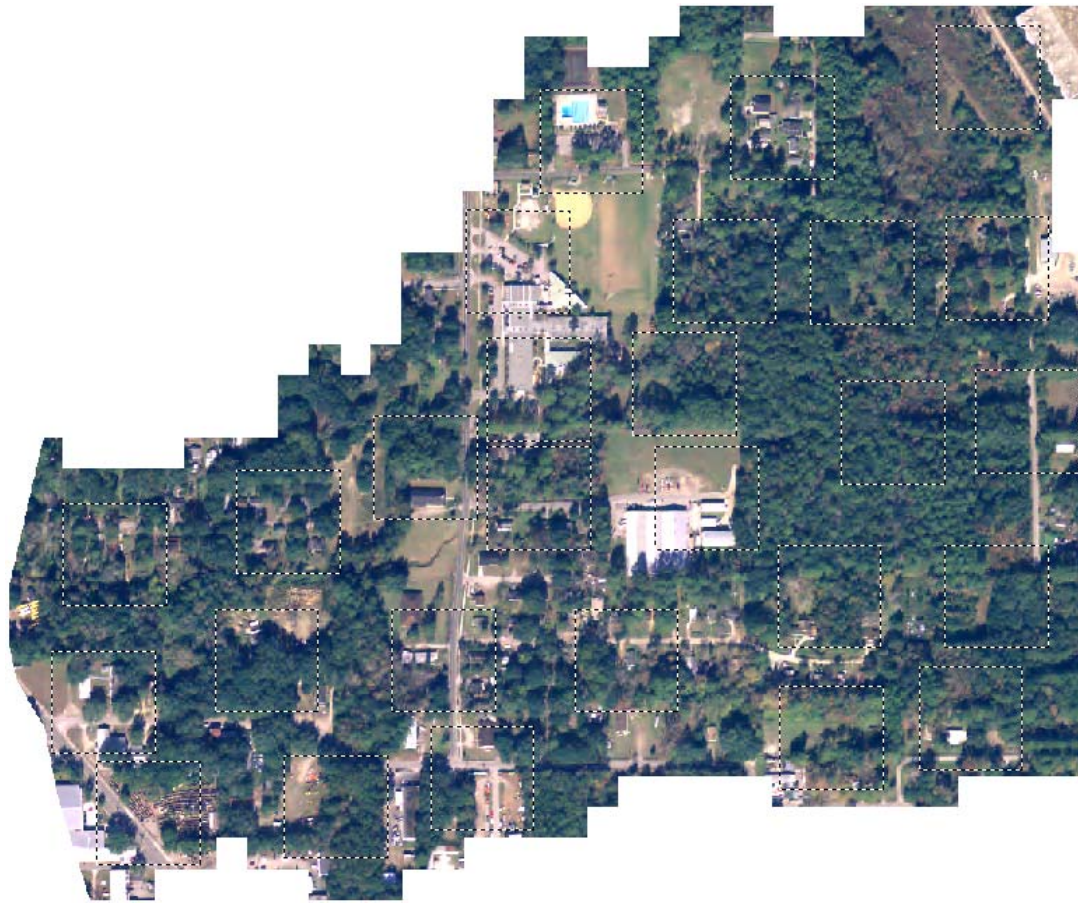


Figure 4. Selection of 27 100m² test polygons across the entire true color catchment DOQQ.

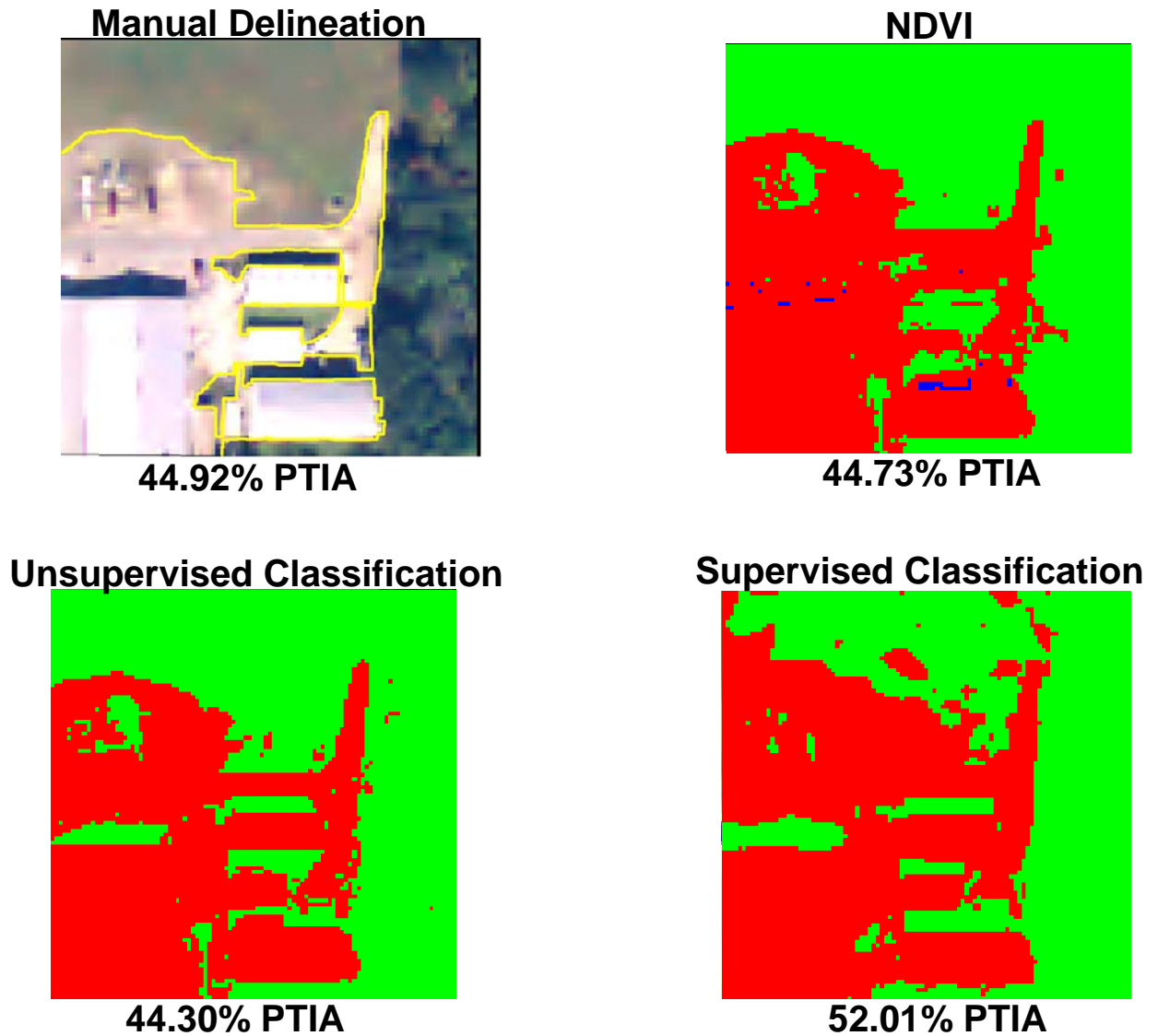


Figure 5. Comparison of manually delineated PTIA values with the NDVI, Supervised, and Unsupervised classification derived values for the same test polygon.

2.4 Results

Absolute PTIA values for all methods are displayed in Table 1.

2.4.1 Normalized Difference Vegetation Index

The NDVI yielded a total catchment PTIA of 16.73% and appeared initially to be a good representation of the ground features. The PTIA values for the test polygons also appeared to match up quite well (Table 1). In addition, the NDVI seemed to be unaffected by shadowing which did cause problems for the other classification methods.

Table 1. Test polygon PTIA values for the manual delineation, NDVI, Unsupervised, and Supervised classifications

TEST POLY	PTIA (m ²)			
	TRUE	NDVI	Unsupervised	Supervised
1	1141.23	1864.00	1555.00	1487.00
2	2838.61	2427.00	1793.00	1482.00
3	3176.14	3143.00	3566.00	4670.00
4	5433.32	5856.00	5834.00	7398.00
5	259.37	295.00	244.00	79.00
6	1258.31	1340.00	1383.00	2104.00
7	878.23	756.00	654.00	1024.00
8	0.00	120.00	20.00	5.00
9	4672.02	4652.00	4607.00	5409.00
10	1553.76	1825.00	1080.00	689.00
11	1527.58	1722.00	1351.00	1521.00
12	864.30	1263.00	862.00	705.00
13	1209.45	1081.00	683.00	559.00
14	3360.84	3536.00	3079.00	3897.00
15	5804.31	5071.00	4267.00	3401.00
16	227.63	1482.00	684.00	1324.00
17	3110.05	3490.00	2773.00	2616.00
18	2138.84	1612.00	1227.00	1237.00
19	671.75	526.00	474.00	714.00
20	260.32	315.00	128.00	156.00
21	746.56	735.00	651.00	793.00
22	647.59	930.00	730.00	1332.00
23	3267.78	4047.00	3491.00	4074.00
24	1616.47	1598.00	1102.00	1861.00
25	0.00	92.00	37.00	9.00
26	3802.00	3892.00	3684.00	3146.00
27	0.00	58.00	34.00	353.00

2.4.2 Supervised Classification

The first supervised classification yielded a total PTIA of 15.47% which alone seems to be a reasonable number. There were, however, major problems with the Water ground-cover class which was given as 13.8% of the catchment when in actuality it made up less than 1% of the total catchment (Fig. 6a). This was deemed to be an effect of shadowing and mostly reduced numbers in the Vegetated Land class. As a result of this error however, a second supervised classification was run with the Water class removed, this seemed to be justified because, as stated above, water included less than 1% of the total area within the catchment. This second classification yielded a total PTIA of 15.62%. However, upon inspection of this image, it appeared that while the bare

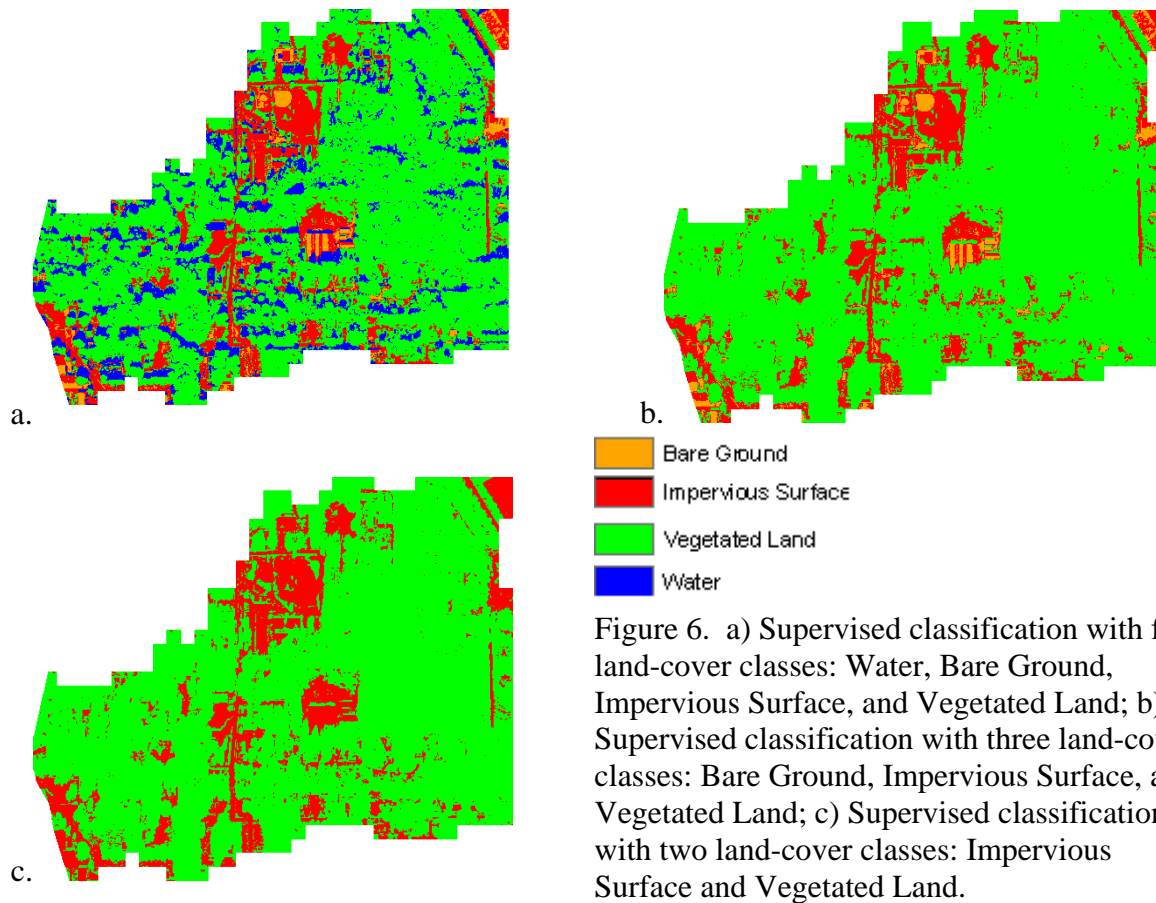


Figure 6. a) Supervised classification with four land-cover classes: Water, Bare Ground, Impervious Surface, and Vegetated Land; b) Supervised classification with three land-cover classes: Bare Ground, Impervious Surface, and Vegetated Land; c) Supervised classification with two land-cover classes: Impervious Surface and Vegetated Land.

ground classification did correctly classify the baseball field, it also included many buildings that should have fallen into the Impervious Surface class (Fig 6b). As a result, a third and final classification was deemed appropriate and was run with only two classes: Impervious Surface and Vegetated Land (Fig. 6c). This final classification yielded a PTIA of 18.00%

2.4.3 Unsupervised Classification

The unsupervised classification also had problems with shadowing similar to what occurred in the supervised classification (images not shown). Ultimately, the final classification included two classes: Impervious Surface and Vegetated Land and yielded a total PTIA of 14.18% (Fig. 7).

2.4.4 Principle Components Analysis

The PCA analysis was partially successful. The first principle component explained 91.3% of the variance in the image and the second component explained 8.1% for a total of 99.4% of the variation explained in the first two principle components (Table 2). The Eigenvectors for PCA-1 (Table 2) also indicate that it is most correlated with Band 1-NIR (i.e. vegetation) and upon examination, the gray-scale image for PCA-1 does indeed appear to be the best image to observe vegetation (Fig. 8b). The Eigenvectors for PCA-2 appear to be the most

correlated with Band 2-Red (Table 2) and upon examination, the gray-scale image for PCA-2 does appear to show the sharpest delineations of impervious surface as would be expected.

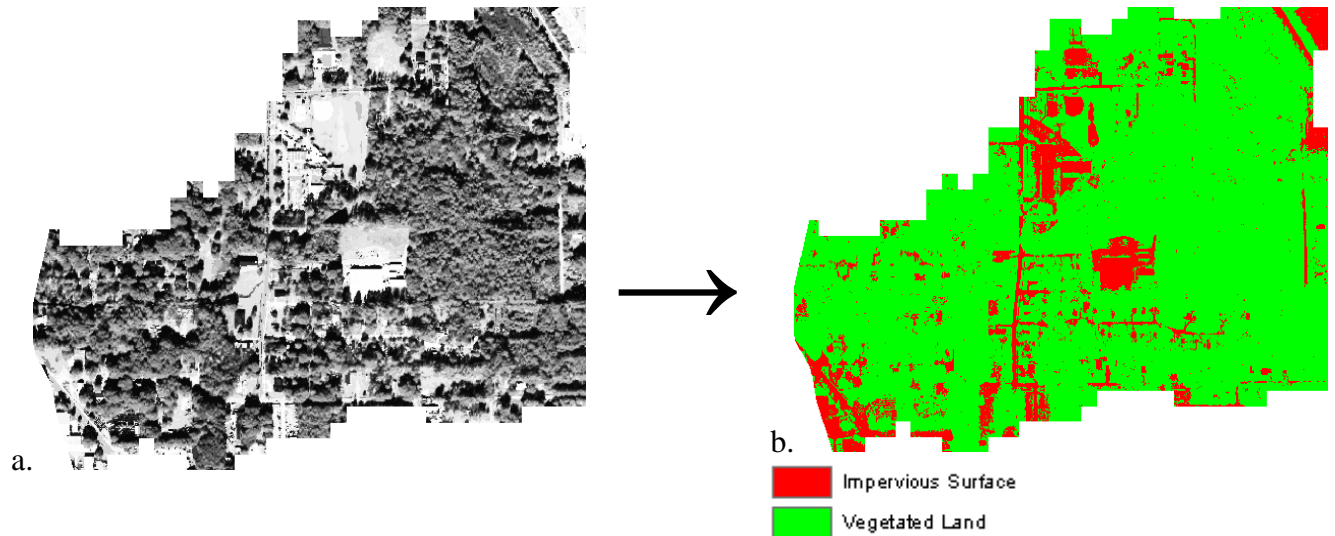


Figure 7. a) Gray-scale unsupervised classification resultant image; b) Unsupervised image reclassified into two classes: Impervious Surface and Vegetated Land

Unfortunately, we were unable to calculate actual factor loadings from the PCA analysis as the Eigenvalues that were produced were at least an order of magnitude larger than would be expected and gave factor loadings greater than 1, an impossibility by definition (Jensen 2005). One possible explanation for this contradictory result may be that the original data was produced in 12-bit format and was later reduced to 8-bit. This result may be an artifact of that process (L. Han personal communication).

Table 2. Eigenvalues and factor loadings for the study catchment principle components analysis

	Component p		
	1	2	3
Eigenvalues, λ_p			
Eigenvalue, λ_p	11057.14	976.14	67.86
Difference	10081.00	908.28	--
Total Variance	12101.15		
Percentage of Variance			
Percentage	91.37	8.06	0.56
Cumulative	91.37	99.43	100
Eigenvectors, (a_{kp})			
band _{k} 1	0.66	-0.72	-0.18
2	0.49	0.60	-0.62
3	0.56	0.31	0.75

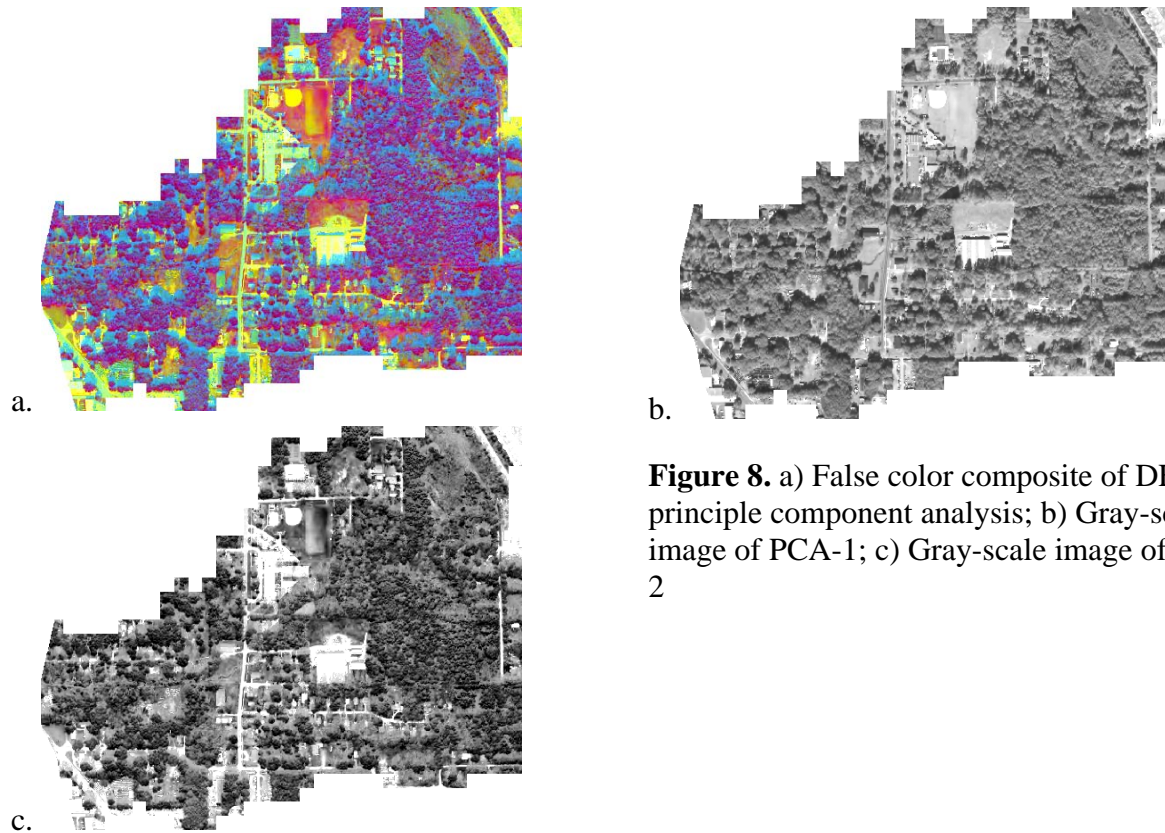


Figure 8. a) False color composite of DET 13 principle component analysis; b) Gray-scale image of PCA-1; c) Gray-scale image of PCA-2

2.4.6 Statistical Analysis

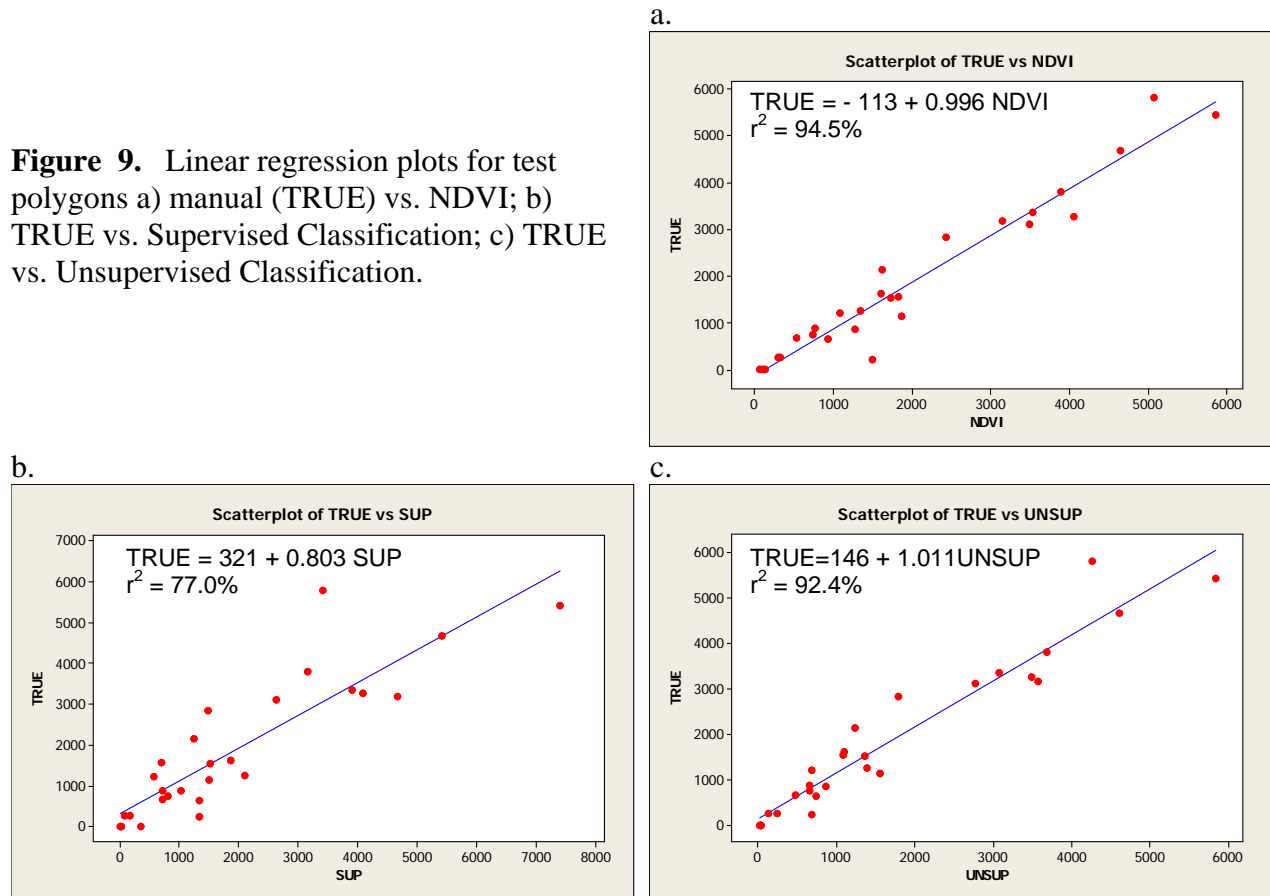
Two-sample t-tests on the test polygons between the manually delineated PTIA values for NDVI ($p=0.80$), Supervised Classification ($p = 0.90$), and Unsupervised Classification ($p=0.71$) showed that there was no statistical difference between the automated methods and the manual method at the $\alpha = 0.05$ significance level. Two-sample t-tests on the test polygons between all automated sampling methods also showed no statistical differences in method results.

Figure 9 shows the linear regression plots for each automated method versus the manual delineation method for the test polygons. As can be seen the r^2 value for the NDVI is the highest at 94.5% followed by the unsupervised classification ($r^2 = 92.4\%$) and then the supervised classification ($r^2 = 77.0\%$). All of these results would be deemed acceptable or very close to acceptable.

2.5 Discussion and Conclusion

All three of the classification methods, NDVI, supervised classification, and unsupervised classification yielded results that would be acceptable for the purposes of this study. The principle components analysis also did appear to quite accurately express the amount of impervious surface, particularly with PCA-1, but complete analysis of this method was confounded, as previously mentioned, by the high Eigenvalues

Figure 9. Linear regression plots for test polygons a) manual (TRUE) vs. NDVI; b) TRUE vs. Supervised Classification; c) TRUE vs. Unsupervised Classification.



In addressing the first objective of the study, there was no statistical difference between any of the classification methods. However, it would appear that the NDVI method yielded the best results. In addition, shadows within the image presented a problem for both supervised and unsupervised classifications and were often classified as water. This was solved by simply removing the ground-cover class Water. The removal of the Water ground-cover class for the study catchment was not a problem, because water constituted a very small area. However, this could be problematic for other catchments in the overall study with large amounts of water. In contrast, the NDVI was not significantly affected by the presence of shadows and was able to delineate shaded vegetated and impervious areas from the small amount of water that was present in the catchment. Taking this into account, it would appear that the NDVI did result in the highest accuracy among all the methods.

The second objective was to determine which method was the most efficient in terms of amount of effort required to conduct the analysis. All of the methods tested were close to an order of magnitude faster than the traditional manual delineation of PTIA. This fact should not be understated as even the worst automated method may have utility in its efficiency. That being said, the NDVI was noticeably faster than the other three methods as it is a “canned” index that can be easily plugged into the Spatial Modeler and run in less than thirty minutes. The other methods all required several additional steps that added to their processing time.

The NDVI has been used extensively in remote sensing studies (Jensen 2005) since its development by Rouse et al. (1974). Various published, remote sensing studies have used the NDVI as a means to classify and identify both vegetated areas (Gao and Li 2000), impervious surfaces (Goetz et al. 2003, Sawaya et al. 2003) within a study area and a handful have used these results to find a correlation to biological communities (Gillies et al. 2003) as is the goal in our study. In agreement with our study, Sawaya et al. (2003) also found that the NDVI was potentially the best technique to delineate impervious surfaces in a study in which they used multispectral IKONOS data with a similarly high-resolution to that of our DOQQ's. The NDVI has even been incorporated into more complex indices such as the Normalized Difference Built-up Index (NDBI) that can provide even more detailed analysis of urban areas (Zha et al. 2003).

In using the NDVI, and also the unsupervised and supervised classifications as shown in our results, it must be noted that there are certain terrain features such as bare ground or senescent vegetation that can confound and reduce the accuracy of relying solely on the NDVI or these other methods for determination of impervious surface. However, these factors are minimal in our study location.

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3. Urbanization regulates stream ecosystem function via changes to flow regimes, invertebrate richness, and water chemistry (submitted to *Ecological Applications*-revision requested)

3.1 Introduction

Conversion of land use from rural to urban can affect stream ecosystems via multiple pathways, including altered hydrology, water chemistry, channel geomorphology, and trophic resources (Paul and Meyer 2001). Hydrologic changes include increased total runoff, shorter duration and higher volume peak runoff, and altered baseflows (Gordon et al. 1992, Arnolds and Gibbons 1996, Booth and Jackson 1997, Paul and Meyer 2001). Water chemistry is widely acknowledged to be degraded in urbanized streams by both point and non-point sources of contaminants and nutrients (Porcella and Sorenson 1980, Paul and Meyer 2001, Pitt 1995, Hatt et al. 2004). Urbanized streams are routinely widened and incised due to both altered hydrology and management (Booth 1990, Paul and Meyer 2001). Urban development is likely to result in changes to riparian vegetation which can dramatically alter trophic dynamics (Fisher and Likens 1973, Wallace et. al 1997, Naiman et al. 2005). Clearly, effects of catchment urbanization on stream ecosystems can arise from a myriad of interrelated sources. However, catchment impervious cover has been shown to be a powerful proxy indicator for factors mentioned above (Klein 1979, Schueler 1994, Morse et al. 2003).

Several studies have shown increases in percent total impervious area (PTIA) within catchments results in changes in stream biotic conditions (May et al. 1997, Walsh et al. 2001, Stephenuck et al. 2002, Morse et al. 2003, Ourso & Frenzel 2003). These studies typically find decreases in macroinvertebrate diversity, particularly for sensitive taxa (*sensu* Hilsenhoff 1977) in the orders Ephemeroptera, Plecoptera, and Trichoptera. In addition, relative declines in biomass of sensitive taxa occur, while biomass of tolerant taxa increases (e.g., Chironomidae and Oligochaeta) (Paul & Meyer 2001). Much work has been done to show structural responses to changes in land use (e.g., Benke et al. 1981, Roy et al. 2003, Freeman and Schorr 2004); fewer studies have examined responses in functional measures (Bunn et al. 1999, Sponseller and Benfield 2001, Hurn et al. 2002).

Leaf litter processing, a measure of ecosystem function, has been suggested as a measure to assess anthropogenic impacts to stream ecosystems (Gessner and Chauvet 2002). Physical abrasion, aquatic fungi, bacteria, and shredder organisms all influence litter breakdown rates (Cummins et al. 1973, Suberkropp and Klug 1976, Anderson and Sedel 1979, Webster and Benfield 1986). Therefore, litter processing is controlled by multiple factors (e.g., hydrology, water chemistry) that can be altered during urbanization (Paul and Meyer 2001). The studies that have specifically addressed the effects of urbanization on litter processing have reported both increased rates (Collier and Winterbourne 1986, Paul 1999) as well as no change (Sponseller and Benfield 2001, Huryn et al. 2002).

The goal of this study was to examine the influence of catchment urbanization on ecosystem function in headwater tributaries to the St. Johns River in the vicinity of Jacksonville, Florida. We were particularly interested in how increases in PTIA along a land-use gradient affected the physical, chemical, and biological conditions of these tributaries. Specifically, we wanted to understand how both biotic factors (e.g., invertebrate richness and biomass) and abiotic factors (e.g., land use, flow regimes, and water chemistry) work together to regulate stream detritus processing.

3.2 Methods

3.2.1 Study sites and water chemistry

Eighteen streams along an urban-rural land-use gradient in the greater Jacksonville, Florida area were the focus of this study (Fig. 1). Catchment boundaries and estimates of land cover were provided by the St. John's River Water Management District (SJRWMD; <http://sjr.state.fl.us/programs/data.html>, Fig. 1). We assessed PTIA with a normalized difference vegetation index (NDVI) that was processed with ERDAS Imagine 8.7 (Leica Geosystems GIS and Mapping LLC., Atlanta, Ga). This was accomplished using multispectral digital orthophoto quarterquads (DOQQ) taken with a Leica ADS40 Airborne Digital Sensor (Leica Geosystems, Atlanta, GA, USA) between December 2003 and March 2004. The DOQQ's were taken at an altitude of 6100 m which resulted in a ground resolution of one meter (SJRWMD 2004). The NDVI is a common remote sensing index that measures the relationship between spectral reflectance of surfaces in the infrared and red wavelengths. The index allowed for the classification of DOQQ pixels into three land-cover classes: vegetated, non-vegetated, and submersed by water. All non-vegetated cover was assumed to be impervious which likely resulted in a minor overestimation of PTIA due to the inclusion of exposed, unvegetated soils. We believe that this overestimation is minor given that these catchments have minimal agriculture land cover (i.e., fallow fields). Quantification of the proportion of each surface cover type was done using GIS (ESRI(R) ArcMap(TM) 8.3, ESRI Inc., Redlands, CA).

A one hundred-meter stream reach was selected in each catchment. All streams had sandy substrata. Four lacked a riparian canopy and were dominated by aquatic macrophytes, particularly *Hydrilla verticillata*.

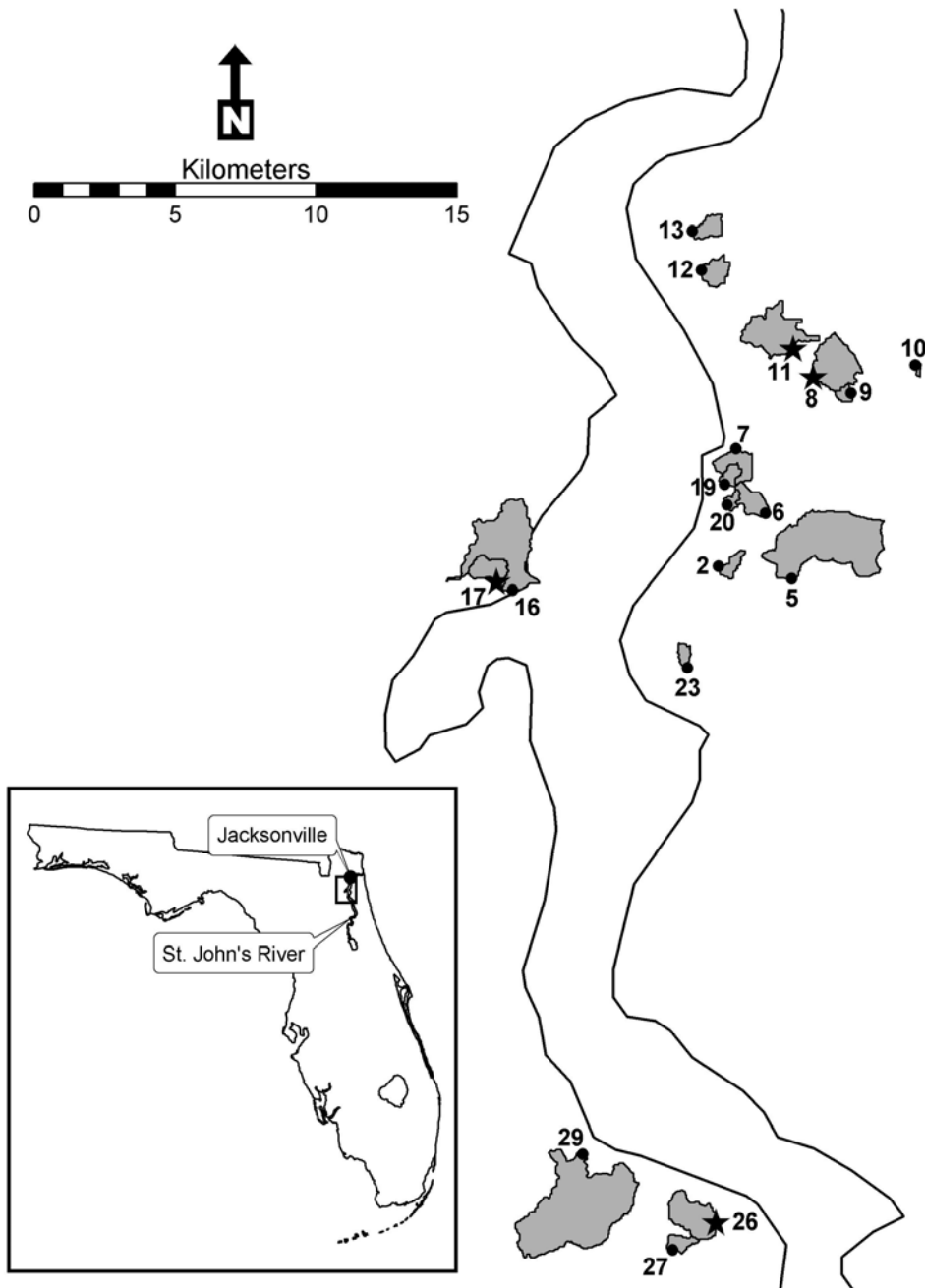


Figure 1. The Lower St. John's River, Florida and locations of the 18 study streams. Stars denote streams where fungal biomass was reported.

Reaches with a riparian canopy were dominated by red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and water oak (*Quercus nigra*). Because of the low channel gradients, stream habitats were composed of runs with occasional coarse woody snags.

Monthly water samples were analyzed for alkalinity (ALK), biological oxygen demand (BOD), chlorophyll a (Chla), conductivity (CON), dissolved oxygen (DO), dissolved organic carbon (DOC), ammonium (NH₄), nitrate (NO₃), total kjeldahl nitrogen (TKN), pH, dissolved phosphate (PO₄), total dissolved phosphorus (TP), total dissolved solids (TDS), total suspended solids (TSS), volatile suspended solids (VSS), and a suite of metals (Al, Cd, Cu, Fe, Mg, Mn, Ni, Pb, Zn). Water was filtered on site and all samples were analyzed within 24 hours of collection. Water temperature, conductivity, and dissolved oxygen data were collected using handheld YSI meters. Both the St. Johns River Water Management District laboratory and contracted laboratories were used for analysis of the array of water quality constituents. All analyses were performed using U.S. EPA and Florida Department of Environmental Protection approved methods (40 CFR 100-149, APHA 1998). Water temperature was measured continuously using temperature data loggers (Thermochron iButton, Maxim/Dallas, Sunnyvale, Ca). Current velocities, water depth, and cross-sectional area were measured monthly in each stream and used to calculate discharge (Q).

3.2.2 Litter bag methods

Newly abscised red maple and sweetgum leaves were collected and air dried. Approximately 4 g (\pm 0.1 g) of red maple leaves or 5 g (\pm 0.1 g) of sweetgum leaves were placed in each litter bag (35 x 15cm with 5-mm polypropylene mesh). Leaves were moistened before being placed in the bags to prevent fragmentation. In each stream, 5 metal fence posts (~120 cm long) were driven into the stream at ~10 meter intervals. Four litter bags of each leaf species were grouped together and secured to fence posts using cable ties. Bags were deployed immediately after peak of red maple leaf abscission in mid December 2003 (5 bags per litter species), and retrieved on 4 subsequent dates (2 weeks, 4 weeks, 8 weeks, 12 weeks following deployment). On each date, bags were removed from the streams, placed in individual plastic bags, and immediately returned to the laboratory on ice.

3.2.3 Laboratory methods

Contents of each litter bag were poured into a plastic basin containing water. Whole leaves and fragments were removed by hand. The material remaining in the plastic basin (i.e., macroinvertebrates and inorganics) was washed through a 250 μ m sieve and placed in whirlpak bags with ~70% ethanol. Leaf discs were cut from whole leaves from 4 streams (high, moderate, and low PTIA; see “Fungal biomass”, below) and placed in scintillation vials containing 5 ml of methanol. All remaining leaf material was dried to constant mass in a forced-air oven (60°C) and weighed to determine mass loss. A subsample (1–3 g) of this material was used to determine ash content. Ash-free dry mass (AFDM) remaining was then calculated from these measurements.

3.2.4 Fungal biomass

Fungal biomass was assessed in 4 streams (1 high, 2 moderate, and 1 low PTIA) for both leaf species using ergosterol concentrations. Ergosterol was extracted from leaf discs by refluxing in alkaline methanol and then quantified by comparing absorbance at 282 nm after separation by HPLC (Shimadzu) with standard ergosterol concentrations (Newell et al. 1988,

Weyers and Suberkropp 1996). These data were converted to fungal biomass assuming 5.5 μg ergosterol per mg mycelial dry mass (Gessner and Chauvet 1993).

3.2.5 Macroinvertebrates

Macroinvertebrate richness and biomass was analyzed for litter bags collected when fungal biomass peaked (see above). Material in 70% ethanol was washed through a 500- μm sieve and animals retained were identified to the lowest practical taxonomic level, and their length measured to the nearest 1 mm. Individual and total biomass was estimated using taxon-specific, length mass relationships (Benke et al. 1999). Taxa were also categorized into groups based on feeding strategies. The groups included taxa that primarily consumed either fine particulate organic matter (collector/gatherers), coarse particulate organic matter (shredders), or other animals (predators). Collector/gatherer and shredder feeding groups were further subdivided. Collector/gatherers were split into filtering and non-filtering taxa, while shredders were split into snails and all other taxa.

3.2.6 Analysis

Differences in leaf loss and fungal biomass among streams were assessed using the general linear model with reach as the main factor and time as a covariate (SAS Institute, 1989, SAS/STAT user's guide, version 6, 4th edition, Cary, North Carolina). An *a posteriori* test (Tukey test, Zar 1996) was used to assess differences among sites for fungal biomass. Differences in macroinvertebrate total richness and biomass and feeding group richness and biomass were assessed with one-way ANOVA for both leaf species (Zar 1996). Processing rates for both leaf species were estimated by fitting exponential decay curves to leaf mass vs. time (k_d with units of d^{-1}) or leaf mass vs. degree days (k_{dd} with units of dd^{-1}). Relationships between PTIA, macroinvertebrate biomass, and processing rates were determined using regression analysis (Zar 1996). Selected land-use, physical, chemical, and biological variables were analyzed with principle components analysis (PCA; Manly 1986). All variables were normalized prior to analysis. The first 6 principal components were used in stepwise regressions as predictors of litter processing rates (k_{dd}).

3.3 Results

3.3.1 Land use and water quality

Catchment size ranged from ~10 to 1000 ha (Table 1). Average discharge ranged from ~0 to 130 L s^{-1} however, most streams had discharges $< 35 \text{ L s}^{-1}$ (Table 2). Land use varied considerably among catchments, particularly for forest and urban cover (Table 1). Sites with high forest cover had low levels of urban development. Wetland cover varied from 0 to 30%, but was not related to other cover types. PTIA ranged from 0 to 66% (Table 1). All sites had circumneutral pH and similar alkalinity and conductivity (Table 2). Nutrients (e.g., N and P) varied among sites, but tended to be low for sites with low PTIA (Table 2). Concentration of metals were also variable, but tended to be highest for sites with the highest PTIA (Table 2).

Table 1. Summary of the distribution of percent land use, percent total impervious area (PTIA) and catchment area (ha) for the 18 study catchments.

site	agriculture	barren	rangeland	forests	urban	wetlands	PTIA	catchment area
2	0	4	0	0	88	3	51	41.81
5	0	2	6	6	73	8	26	686.72
6	0	2	0	8	85	1	28	81.87
7	0	1	0	3	95	0	26	94.03
8	0	9	2	17	64	3	46	231.30
9	0	5	0	0	95	0	66	25.71
10	0	0	0	0	65	30	43	9.48
11	0	13	1	13	60	9	35	261.57
12	0	1	0	4	89	3	24	76.07
13	0	1	0	1	85	13	17	63.65
16	0	7	1	7	74	9	32	453.85
17	0	1	0	6	83	9	29	91.04
19	0	1	0	4	94	1	8	39.16
20	0	6	0	20	73	1	19	24.33
23	0	0	0	5	87	1	21	29.80
26	0	0	0	82	0	18	0	188.47
27	0	0	0	91	0	9	0	46.60
29	24	4	11	36	12	13	17	937.56

Table 2. Selected physical and chemical conditions in the 18 tributaries on the St. Johns River, Florida. Alk=alkalinity reported in mg L⁻¹, Con=conductivity reported in umhos cm⁻¹, DOC=dissolved organic carbon reported in mg L⁻¹, Nutrients are reported in mg L⁻¹, Q=discharge reported in L s⁻¹, metal are reported in µg l⁻¹.

site	Alk	Con	DOC	pH	NH ₄	NO _x	PO ₄	Q
2	128	345	11.17	7.0	0.0280	0.0792	0.0081	0.57
5	77	288	5.60	7.7	0.0133	0.0311	0.0096	39.79
6	39	238	7.31	6.8	0.2483	0.1197	0.0067	4.24
7	39	394	7.59	6.6	0.1605	0.1511	0.0043	4.95
8	132	417	8.25	7.2	0.0719	0.1597	0.0145	28.15
9	100	368	5.68	6.7	0.0000	0.0479	0.0111	7.55
10	88	381	11.02	7.0	0.1095	0.1547	0.0459	33.13
11	128	383	7.98	7.4	0.0746	0.0601	0.0088	29.03
12	78	383	8.98	7.1	0.0976	0.2819	0.0382	10.06
13	71	386	9.46	6.9	0.2058	0.6918	0.0064	9.81
16	132	354	11.41	7.7	0.0994	0.0808	0.0472	118.61
17	148	380	8.00	7.6	0.0546	0.1016	0.0736	13.89
19	23	368	6.09	6.6	0.2002	0.1061	0.0048	10.51
20	82	312	7.10	7.3	0.0725	0.1478	0.0060	123.78
23	88	290	8.21	7.3	0.1077	0.0658	0.0056	2.52
26	111	359	56.89	6.9	0.0147	0.0119	0.0043	4.04
27	42	317	33.64	6.7	0.0154	0.0138	0.0050	0.00
29	15	254	19.66	7.0	0.1320	0.0612	0.0807	0.86

Table 2 cont.

site	Al	Cd	Fe	Mg	Mn	Ni	Pb	Zn
2	90.02	0.16	935	5340	27.09	2.25	0.96	9.04
5	274.09	0.18	866	8240	14.06	1.75	0.53	3.67
6	230.55	0.25	1643	4560	22.02	1.66	0.42	6.14
7	215.27	0.54	3650	12540	36.03	2.40	0.68	6.35
8	107.62	0.63	3913	10090	76.67	2.64	0.92	6.32
9	66.73	0.19	1899	9170	45.13	2.55	0.04	12.34
10	301.99	0.12	564	9850	81.43	1.74	1.09	23.26
11	429.91	0.18	1306	6850	26.37	2.49	0.56	3.71
12	160.68	0.19	696	10760	42.88	2.56	1.67	13.71
13	38.12	0.26	1028	8720	48.88	2.88	0.79	13.86
16	41.22	0.07	410	9560	35.27	2.38	0.59	4.83
17	54.39	0.12	233	8880	20.75	1.77	0.69	5.52
19	81.12	0.38	4497	9270	41.66	2.16	0.56	10.82
20	47.11	0.23	1001	7020	18.38	1.63	0.19	5.94
23	44.91	0.30	2126	4230	41.13	2.21	0.31	4.50
26	373.85	0.22	2358	4500	69.75	4.06	0.70	5.36
27	494.60	0.59	3669	3050	69.15	4.71	1.45	58.48
29	271.55	0.30	4264	6630	32.86	2.64	1.34	14.82

3.3.2 Litter processing and fungal biomass

Litter loss differed significantly among all streams for both red maple ($F_{18, 617} = 82.9$, $p < 0.001$) and sweetgum ($F_{18, 565}$, $p < 0.001$). Litter processing rates (k_d) ranged from 0.010 to 0.046 d^{-1} for red maple and 0.006 to 0.018 d^{-1} for sweetgum. Processing rates based on degree-days (k_{dd}), ranged from 0.0008 to 0.0033 dd^{-1} for red maple and 0.0004 to 0.0013 dd^{-1} for sweetgum.

Fungal biomass differed among streams for both leaf species (red maple: $F_{4, 33} = 3.05$, $p = 0.031$; sweetgum: $F_{4, 33} = 7.21$, $p = 0.003$) and peaked after 24 days (red maple: ~30-90 mg mycelial dry mass g AFDM leaf mass⁻¹; sweetgum: ~10-40 mg mycelial dry mass per g AFDM leaf mass⁻¹; Fig. 2). Based on *a posteriori* tests, the low PTIA stream (site 26) differed from the high PTIA stream (site 17) for red maple and the low (site 26) and a moderate PTIA stream (site 8) differed from the high PTIA stream (site 17) for sweetgum.

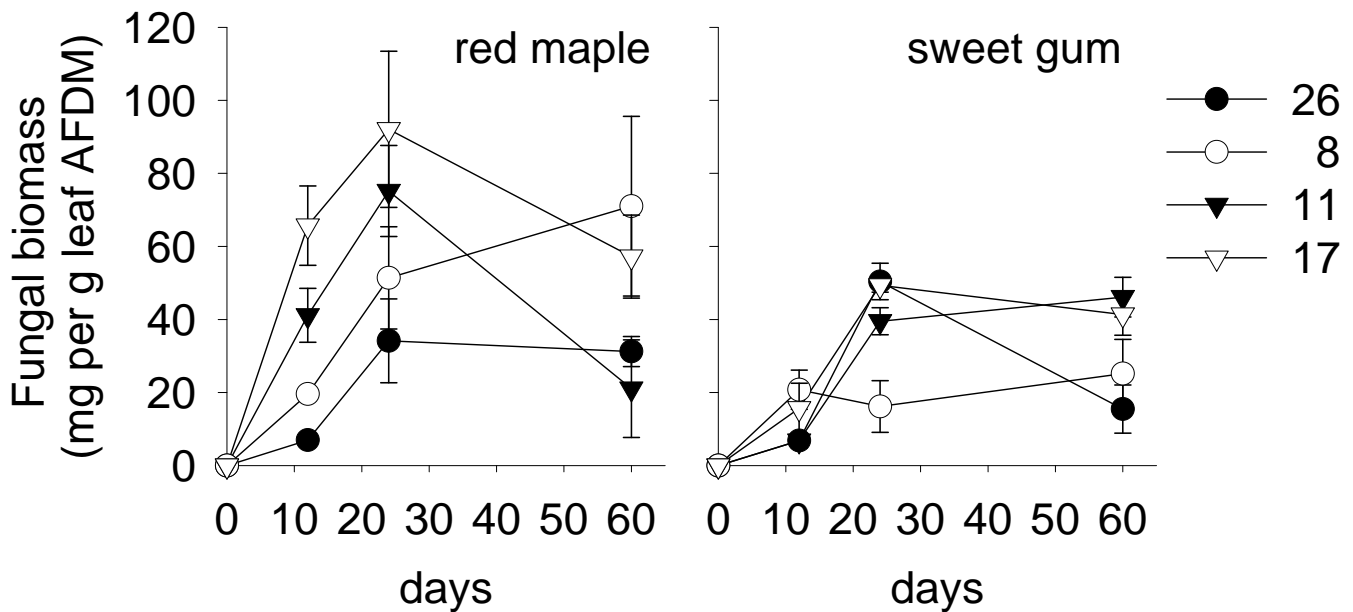


Figure 2. Fungal biomass from 4 streams (calculated from ergosterol concentrations) for red maple and sweet gum leaves. Error bars are ± 1 SE. 26=low PTIA, 8=moderate PTIA, 11=moderate PTIA with *H. verticillata*, 17=high PTIA.

3.3.3 Macroinvertebrates

The total number of taxa identified from each site ranged from 9–20 for red maple and 7–21 for sweetgum (Table 3). Total taxa richness varied significantly among sites for both leaf species (red maple: $F_{17, 65} = 6.63$, $p < 0.0001$; sweetgum $F_{17, 66} = 3.63$, $p < 0.0001$). For taxa richness by feeding groups, there were also significant differences for both leaf species (collector-gatherer (CG): $F_{red\ maple} = 3.26$, $p = 0.0003$, $F_{sweetgum} = 2.64$, $p = 0.0026$; filterer (FL): $F_{red\ maple} = 2.05$, $p = 0.0204$, $F_{sweetgum} = 3.50$, $p < 0.001$; predator (PR): $F_{red\ maple} = 3.86$, $p < 0.0001$, $F_{sweetgum} = 2.90$, $p = 0.0001$; snails (S): $F_{red\ maple} = 18.06$, $p < 0.0001$, $F_{sweetgum} = 7.26$, $p = 0.0001$; all other shredder (SH): $F_{red\ maple} = 3.69$, $p = 0.0001$, $F_{sweetgum} = 2.99$, $p = 0.0007$). The taxonomic composition of both types of litter bags (e.g., red maple or sweetgum) were similar (Tables 3, 4).

CG were mainly Orthocladinae, Tanytarsini, and Oligochaeta. FL were dominated by *Corbicula fluminea*. PR most commonly found were Turbellaria, zygopteran odonates, and Hirudinea. Snails included several taxa from Physidae, Ancyliidae, and Hydrobiidae (Table 4).

Total macroinvertebrate biomass varied significantly among sites for both leaf species (red maple: $F_{17, 65} = 3.26, p = 0.0003$; sweetgum $F_{17, 66} = 4.43, p < 0.0001$). Average biomass per site ranged from 17 to 354 mg bag⁻¹ for red maple and 15 to 399 mg bag⁻¹ for sweetgum (Table 3). Biomass by feeding groups showed several significant differences for both leaf species (CG: $F_{\text{red maple}} = 3.88, p < 0.0001, F_{\text{sweetgum}} = 3.27, p = 0.0026$; FL: $F_{\text{red maple}} = 2.05, p = 0.0202$; PR: $F_{\text{red maple}} = 2.12, p = 0.016$; S: $F_{\text{red maple}} = 9.53, p < 0.0001, F_{\text{sweetgum}} = 9.11, p = 0.0001$). Shredder biomass, excluding snails, was not different among streams for either leaf species ($F_{\text{red maple}} = 1.01, p = 0.4609, F_{\text{sweetgum}} = 1.65, p = 0.0762$). Filterer and predator biomass was also similar among sites for sweetgum leaves ($F_{\text{FL}} = 31.06, p = 0.4076; F_{\text{PR}} = 0.84, p = 0.6401$). At all sites consumers of coarse detritus (i.e., shredders and snails) accounted for 8-95% of the average biomass for red maple and 0-92% for sweetgum. In 11 of the 18 streams, these taxa, which were typically crustaceans (Asellidae, Hyalellidae, or Cambaridae) or gastropods (Hydrobiidae or Physidae; Table 4), had the highest average biomass.

Table 3. Macroinvertebrate biomass (mg bag⁻¹) and richness. CG=collector-gatherer, FL=filterer, PR=predator, S=snail, SH=shredders excluding snails. Biomass appears above richness for each site. Values in parentheses are 1 SE.

A. red maple						
site	Total	CG	FL	PR	S	SH
2	113.2 (97.7)	6.2 (2.6)	0.1 (0.1)	4.8 (4.2)	1.1 (0.7)	101.0 (99.8)
	12	5	2	3	1	1
5	98.4 (10.8)	23.9 (12.1)	0.0	29.2 (3.8)	23.6 (5.2)	21.7 (4.6)
	20	6	3	5	5	1
6	156.2 (35.0)	135.6 (42.2)	0.6 (0.6)	1.6 (0.6)	0.0	18.4 (13.9)
	10	4	1	3	0	2
7	65.0 (29.3)	44.6 (30.8)	0.0	0.6 (0.3)	3.2 (2.9)	16.6 (4.0)
	10	3	1	2	3	1
8	49.2 (6.9)	13.0 (4.3)	0.1 (0.0)	5.5 (2.4)	1.3 (1.1)	29.3 (7.9)
	13	5	2	3	2	1
9	165.8 (79.9)	1.8 (1.8)	0.5 (0.5)	34.9 (28.8)	69.8 (61.2)	58.8 (29.6)
	12	2	2	3	3	2
10	75.9 (23.1)	2.0 (0.6)	27.6 (18.0)	5.8 (2.0)	7.1 (2.1)	33.3 (8.4)
	15	3	4	4	2	2
11	118.7 (66.8)	7.6 (3.3)	0.0	5.6 (2.4)	4.4 (1.6)	101.2 (65.0)
	14	4	1	3	3	3
12	30.1 (3.7)	17.8 (6.3)	0.6 (0.5)	6.6 (4.5)	4.8 (1.9)	0.2 (0.2)
	12	4	1	4	2	1
13	51.2 (15.9)	15.2 (12.8)	0.0	11.2 (5.9)	20.7 (8.4)	4.2 (4.0)
	12	3	1	4	3	1
16	354.1 (89.0)	14.9 (9.8)	3.7 (1.7)	16.0 (3.5)	297.7 (84.5)	21.8 (11.9)
	16	4	1	4	6	1

17	311.6 (135.8)	279.8 (145.9)	0.2 (0.2)	8.3 (4.3)	0.2 (0.1)	23.0 (19.6)
	13	4	2	5	1	1
19	22.8 (5.8)	10.5 (6.4)	0.0	1.0 (0.5)	0.8 (0.6)	10.4 (3.6)
	9	3	2	2	1	1
20	103.6 (53.6)	80.8 (66.9)	3.2 (2.1)	17.1 (15.0)	2.4 (0.2)	0.1 (0.1)
	15	6	3	3	2	1
23	50.8 (14.2)	29.3 (9.5)	1.4 (1.2)	6.5 (2.7)	13.6 (7.1)	0.0
	14	6	3	2	3	0
26	20.3 (10.8)	10.0 (4.2)	0.1 (0.1)	0.4 (0.3)	1.1 (0.5)	8.8 (7.0)
	11	5	2	1	1	2
27	86.8 (30.6)	81.6 (30.3)	0.1 (0.0)	0.0	0.0	5.1 (3.2)
	10	5	2	0	0	3
29	16.9 (8.9)	10.9 (5.3)	0.1 (0.0)	3.6 (1.7)	2.1 (2.1)	0.1 (0.1)
	15	5	3	4	2	1

B. sweetgum

site	Total	CG	FL	PR	S	SH
2	16.0 (6.9)	11.2 (6.4)	0.2 (0.2)	1.5 (0.9)	0.4 (0.2)	2.7 (1.6)
	9	3	2	2	1	1
5	78.2 (26.3)	12.9 (4.5)	0.1 (0.0)	23.2 (17.8)	26.6 (10.2)	15.5 (6.7)
	21	9	2	3	6	1
6	255.5 (137.0)	251.6 (137.5)	0.1 (0.0)	1.0 (0.4)	0.0	2.8 (1.4)
	8	2	2	3	0	1
7	71.8 (12.8)	11.4 (8.6)	0.0	15.7 (12.5)	0.9 (0.9)	43.7 (11.7)
	12	4	1	3	2	2
8	60.9 (16.8)	17.4 (8.3)	0.0	4.9 (1.8)	7.3 (6.0)	31.3 (15.4)
	11	4	1	3	2	1
9	74.1 (29.3)	1.1 (0.8)	0.0	6.1 (6.0)	6.6 (3.6)	60.2 (27.0)
	7	2	0	1	2	2
10	92.8 (44.2)	8.5 (3.4)	30.9 (28.1)	9.1 (3.8)	24.8 (14.7)	19.5 (5.4)
	15	4	3	3	4	1
11	42.2 (16.7)	4.4 (1.8)	0.0	12.1 (3.2)	1.0 (0.5)	24.7 (14.5)
	12	5	0	2	1	4
12	19.1(2.9)	12.9 (3.3)	1.0 (0.5)	3.4 (1.7)	1.8 (1.3)	0.1 (0.1)
	14	5	1	5	2	1
13	72.4 (44.8)	1.0 (0.1)	0.0	15.5 (8.5)	55.7 (48.8)	0.3 (0.2)
	11	2	0	3	4	2
16	398.8 (111.4)	3.9 (2.8)	6.5 (6.0)	12.6 (7.6)	362.7 (105.3)	13.1 (4.2)
	20	3	1	6	8	2
17	59.8 (19.0)	45.8 (19.0)	0.1 (0.0)	12.7 (9.3)	1.0 (0.5)	0.4 (0.4)
	12	5	1	3	2	1
19	58.0 (30.3)	18.7 (16.5)	0.0	3.8 (3.3)	0.8 (0.4)	34.6 (24.3)
	13	4	2	4	2	1
20	76.3 (12.9)	38.0 (16.4)	0.5 (0.3)	15.1 (5.2)	5.4 (4.3)	17.2 (17.0)

	15	5	2	3	3	2
23	40.5 (5.4)	25.0 (8.9)	0.1 (0.1)	7.5 (1.7)	7.8 (5.3)	0.0
	11	5	2	2	2	0
26	39.1 (16.5)	23.7 (11.6)	0.5 (0.5)	0.4 (0.4)	0.1 (0.1)	14.4 (5.5)
	9	3	2	1	1	2
27	51.1 (23.2)	29.7 (13.7)	0.0	1.0 (1.0)	0.0 (0.0)	20.4 (19.6)
	11	5	1	3	0	2
29	14.8 (3.3)	10.3 (2.6)	0.1 (0.1)	3.3 (1.5)	0.9 (0.8)	0.2 (0.2)
	12	5	2	3	1	1

Table 4. Taxa that comprise greater than 5% of average litter bag biomass. FFG= functional feeding group, CG=collector-gatherer, FL=filterer, PR=predator, S=scrapper-snail, SH=shredder

site	red maple			sweetgum		
	FFG	taxa	% biomass	FFG	taxa	% biomass
2	SH	<i>Procambarus</i>	95	CG	Oligochaeta	26
				CG	Orthoclaadiinae	21
				SH	<i>Hyaella</i>	18
				CG	Tanytarsini	8
				PR	Tanypodinae	6
				FL	<i>Corbicula</i>	5
5	SH	<i>Caecidotea</i>	22	PR	<i>Enallagma</i>	33
				S	Hydrobiidae A	19
				SH	<i>Hyaella</i>	10
				PR	<i>Argia</i>	9
				S	Hydrobiidae B	8
				PR	Hirudinea	7
				CG	Tanytarsini	7
				PR	<i>Enallagma</i>	5
6	CG	Oligochaeta	75	CG	Oligochaeta	98
				SH	<i>Tipula</i>	16
				SH	<i>Hyaella</i>	6
7	SH	<i>Hyaella</i>	30	PR	<i>Belostoma</i>	44
				CG	Chironomini	24
				CG	Oligochaeta	19
				S	<i>Hebetancylus</i>	13
				CG	Orthoclaadiinae	7
8	SH	<i>Gammarus</i>	60	SH	<i>Gammarus</i>	48

	PR	<i>Argia</i>	15	S	<i>Haitia</i>	16
	PR	Tanypodinae	5	PR	<i>Erpobdella punctata</i>	11
	S	<i>Haitia</i>	5	CG	Orthocladiinae	4
9	S	Viviparus	51	SH	Procambarus	55
	PR	<i>Macrobodella diterta</i>	24	PR	<i>Placobdella ornata</i>	15
	SH	<i>Hyaella</i>	10	SH	<i>Hyaella</i>	13
	SH	<i>Procambarus</i>	7	S	<i>Hebetancylus</i>	5
10	FL	<i>Corbicula</i>	42	S	<i>Pomacea</i>	40
	SH	<i>Hyaella</i>	30	FL	<i>Corbicula</i>	21
	S	<i>Haitia</i>	10	S	<i>Planorbella</i>	17
	S	<i>Hebetancylus</i>	6	SH	<i>Hyaella</i>	10
11	SH	<i>Procambarus</i>	81	SH	<i>Procambarus</i>	66
	PR	<i>Argia</i>	5	PR	<i>Argia</i>	13
				SH	<i>Hyaella</i>	11
12	PR	<i>Macrobodella diterta</i>	43	S	Hydrobiidae B	27
	S	<i>Haitia</i>	12	PR	<i>Argia</i>	16
	S	Hydrobiidae A	8	PR	<i>Gloiobdella elongate</i>	12
	S	Hydrobiidae S	8	PR	<i>Probezzia</i>	8
	PR	<i>Gloiobdella elongate</i>	6	CG	Orthocladiinae	7
	CG	Orthocladiinae	5	FL	<i>Corbicula</i>	5
	CG	Chironomini	5	PR	Tanypodinae	5
				CG	Tanytarsini	5
13	CG	Diamesini	45	S	<i>Melanoides</i>	82
	SH	<i>Hyaella</i>	14	PR	<i>Argia</i>	11
	PR	<i>Argia</i>	10			
	S	<i>Haitia</i>	10			
	S	<i>Pseudosuccinea</i>	10			
16	S	Hydrobiidae A	38	S	Hydrobiidae A	43
	S	Hydrobiidae B	24	S	Hydrobiidae S	28
	S	Hydrobiidae S	14	S	Hydrobiidae B	7
	CG	Oligochaeta	7			
	SH	<i>Caecidotea</i>	5			
17	CG	Oligochaeta	84	PR	<i>Tabanus</i>	61
	SH	<i>Hyaella</i>	8	CG	Tanytarsini	13
				CG	Orthocladiinae	6
				PR	Tanypodinae	5

19	SH	<i>Hyaella</i>	44	CG	Oligochaeta	65
	CG	Orthoclaadiinae	24	SH	<i>Hyaella</i>	25
	S	<i>Laevapex diaphanous</i>	14			
	CG	Chironomini	5			
20	PR	Argia	37	SH	Procambarus	43
	CG	Tanytarsini	20	CG	Tanytarsini	13
	CG	Orthoclaadiinae	20	PR	<i>Macrobdella diterta</i>	13
	PR	Tanypodinae	11	PR	Tanypodinae	6
	FL	Cheumatopsyche	5	S	<i>Haitia</i>	5
				PR	<i>Enallagma</i>	5
23	S	<i>Haitia</i>	45	S	<i>Haitia</i>	28
	CG	Tanytarsini	26	CG	Tanytarsini	25
	PR	Tanypodinae	9	PR	Tanypodinae	19
	CG	Orthoclaadiinae	7	CG	Orthoclaadiinae	10
	S	<i>Micromenetus</i>	5	PR	Turbellaria	8
			S	<i>Micromenetus</i>	7	
26	SH	<i>Caecidotea</i>	61	SH	<i>Caecidotea</i>	58
	CG	Chironomini	11	CG	Chironomini	17
	CG	Oligochaeta	6	CG	Oligochaeta	7
	S	<i>Micromenetus</i>	6	FL	<i>Corbicula</i>	6
			PR	<i>Enallagma</i>	5	
27	CG	Orthoclaadiinae	44	SH	<i>Caecidotea</i>	65
	CG	Chironomini	28	SH	<i>Hyaella</i>	10
	SH	<i>Caecidotea</i>	16	CG	Chironomini	9
	CG	Oligochaeta	7	PR	<i>Tabanus</i>	7
			CG	Oligochaeta	5	
29	S	<i>Haitia</i>	43	PR	<i>Hetaerina</i>	40
	CG	Tanytarsini	11	CG	Tanytarsini	14
	PR	Tanypodinae	11	S	<i>Micromenetus</i>	10
	CG	Orthoclaadiinae	9	CG	Orthoclaadiinae	8
	CG	Oligochaeta	6	PR	Tanypodinae	8
	PR	<i>Probezzia</i>	6	CG	Chironomini	5

3.3.4 Relationships of PTIA, macroinvertebrates, and litter processing

Red maple and sweetgum litter processing rates showed similar patterns to differences in PTIA (Fig. 3). Processing rates tended to be low at both high and low levels and peaked at ~30-40% PTIA. The highest levels of average invertebrate biomass (Fig. 4A) and taxa richness (Fig. 4B) also corresponded to ~30% PTIA. Although the range of sweetgum processing rates were small when compared to that of red maple, average macroinvertebrate biomass and taxa richness

was quite similar (Table 3, Figs. 4A, B). We also found that processing rates for both litter species were positively related to average macroinvertebrate biomass (r^2 red maple = 0.49, r^2 sweetgum = 0.10) and taxa richness (r^2 red maple = 0.43, r^2 sweetgum = 0.25; Fig. 5). These relationships were mainly driven by snails (Tables 3, 4).

For red maple, the first 2 PCA axes were selected using stepwise regression and the resulting model of processing explained 71% of the variance among sites (Table 5). The first PCA axis selected in this model explained ~30% of the variance for the selected land-use, physical, chemical, and biological variables and 44% of the variance in processing rates (Table 5). Organic carbon, metals, and the proportion of forest land cover loaded negatively and discharge, conductivity, Mg, alkalinity, snail richness, pH, and urban and PTIA loaded positively (Table 6, Fig. 6). The second PCA axis explained ~13% of the variance for the selected, land-use, physical, chemical, and biological variables and 27% of the variance in processing rates among sites (Table 5). This axis had drainage area, total and snail taxa richness, snail biomass, nutrients, pH, discharge, and Mg load negatively, while urban land cover, PTIA, Fe, Cd, and suspended solids loaded positively (Table 6, Fig. 6).

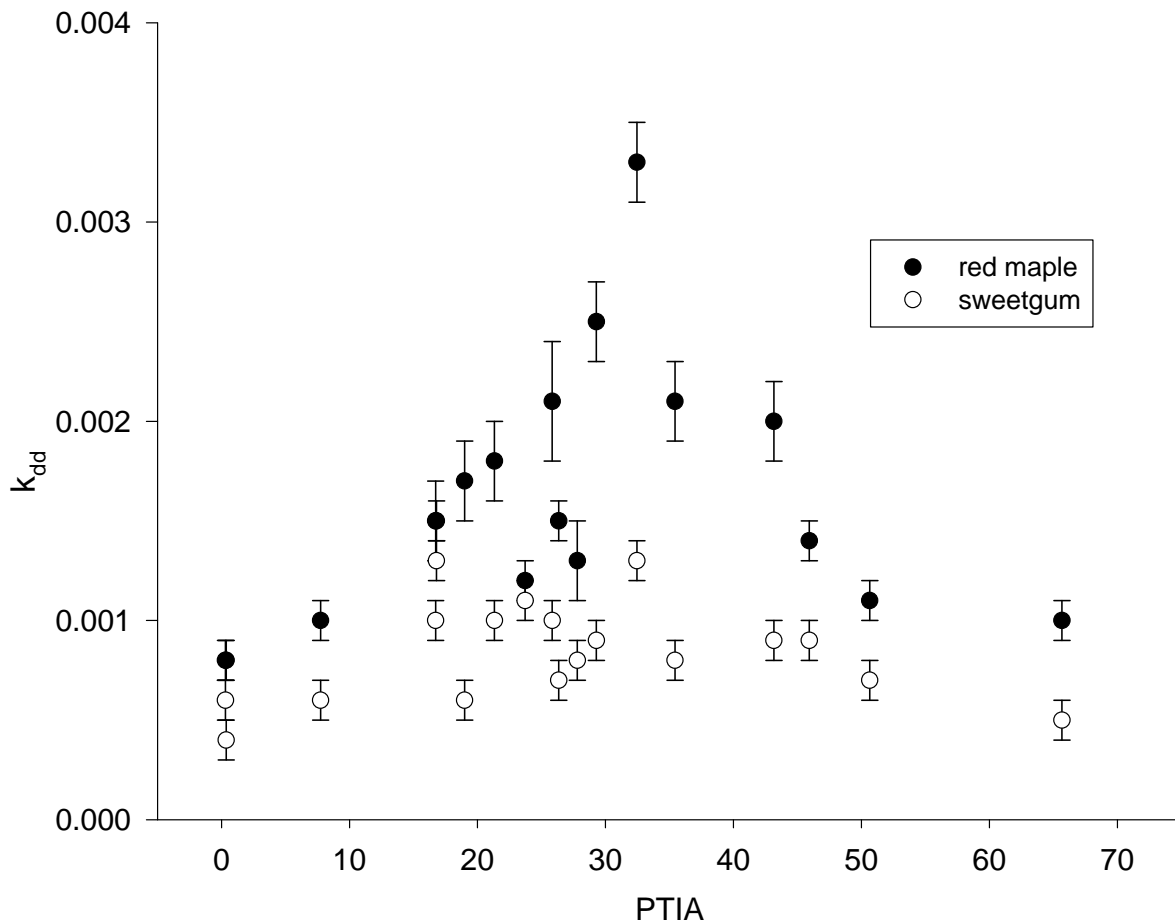


Figure 3. Litter processing rates using degree days (k_{dd} , $>0^{\circ}$ C) for red maple and sweetgum leaves versus PTIA. Error bars are ± 1 SE.

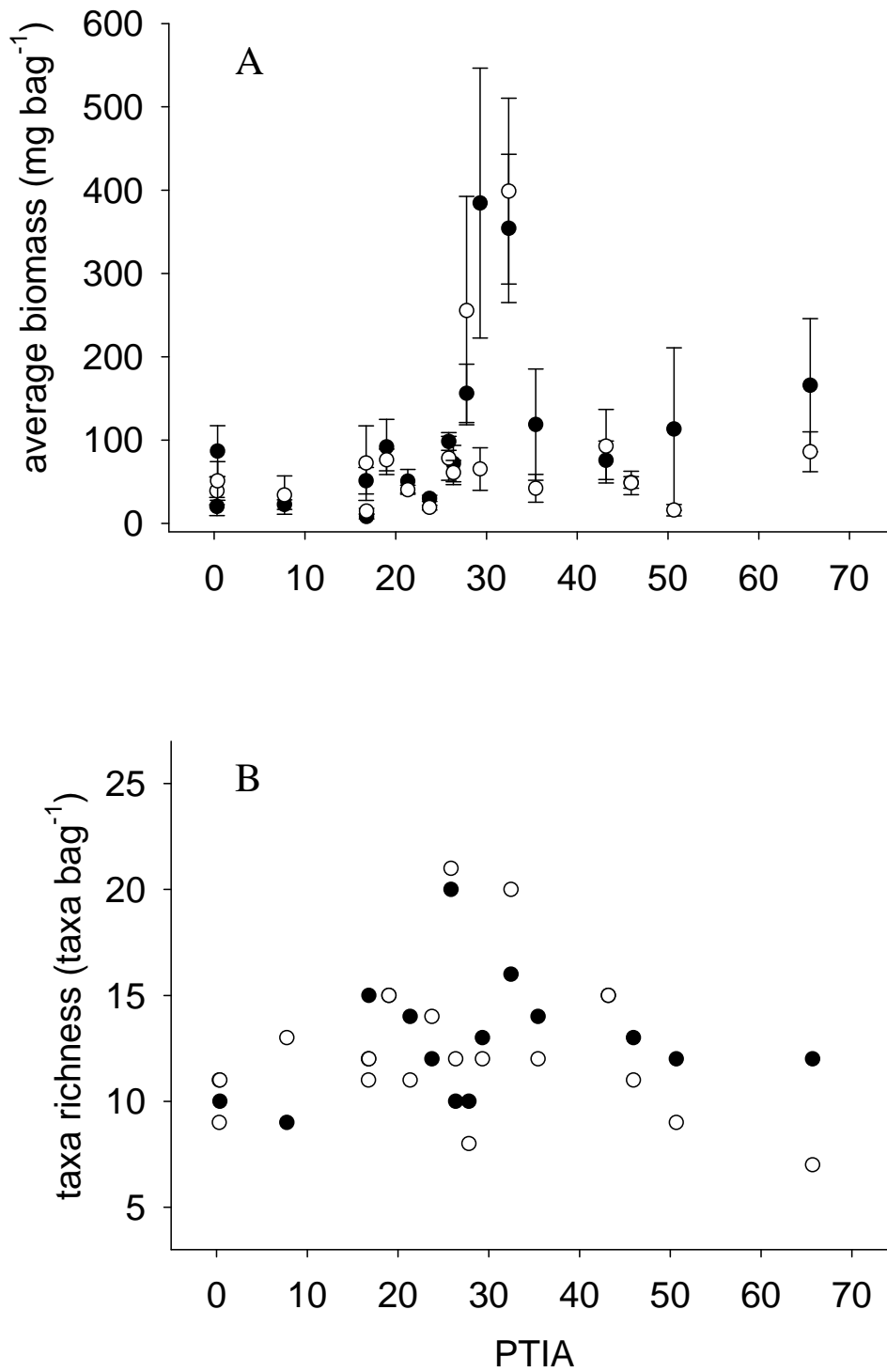
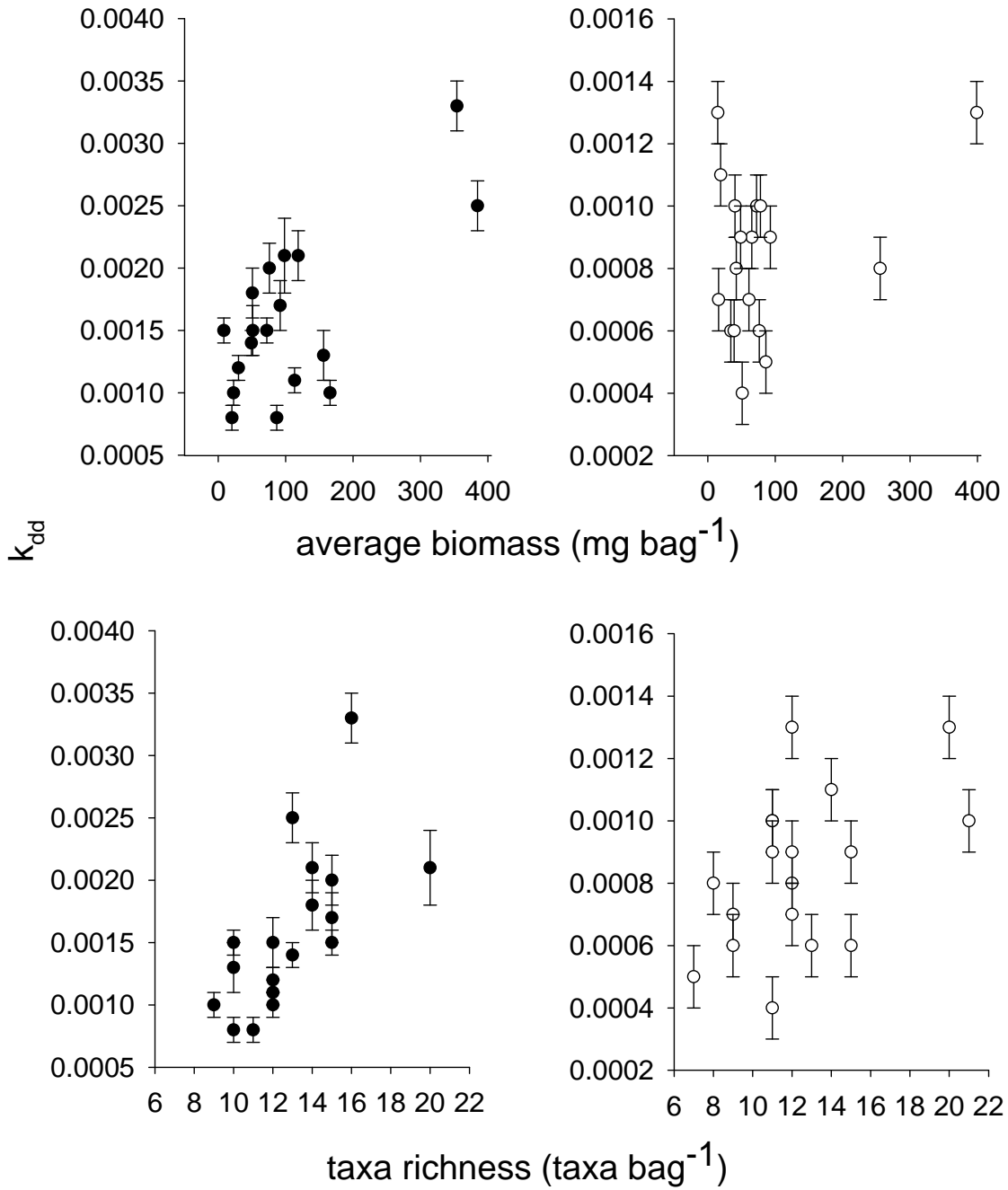


Figure 4. A) average macroinvertebrate biomass (mg bag⁻¹), and B) total taxa richness versus PTIA. Error bars are ± 1 SE.

Figure 5. Litter processing rates using degree days (k_{dd} , >0 C) versus average macroinvertebrate biomass (mg bag^{-1}) and total taxa richness (taxa bag^{-1}). Error bars are ± 1 SE. Red maple results are shown with filled circles; sweetgum results are shown with empty circles.



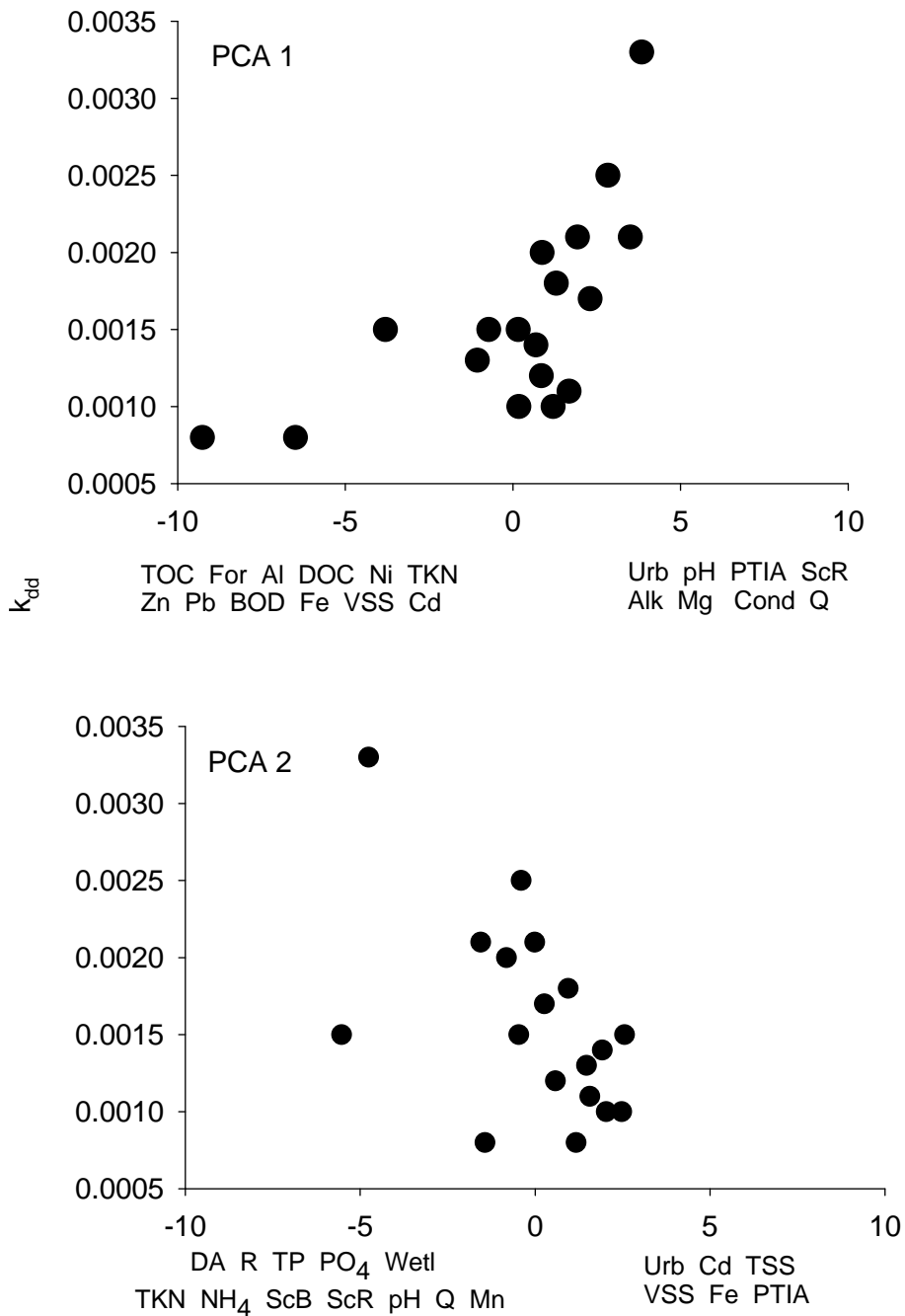


Figure 6. Relationships between the PCA axes selected using stepwise regression and red maple processing rates using degree day (k_{dd} , > 0 C). Labels on each X-axis indicate the influential variables in the PCA. Variable are listed in order of their importance. See the text for abbreviation meanings.

Table 5. Results from the principle component analysis and the stepwise regression. PCA-var=% of variance described in each PCA axis, p-r²=partial r², m-r²=model r².

	component	PCA results eigenvalue	PCA-var	p-r ²	stepwise regression results m-r ²	F	<i>p</i>
red maple	1	10.9	29.4	0.44	0.44	12.6	0.003
	2	4.8	13.0	0.27	0.71	14.3	0.002
sweetgum	2	4.9	13.1	0.37	0.37	9.24	0.008
	1	10.6	28.7	0.22	0.59	8.00	0.010
	3	4.6	12.3	0.14	0.72	6.92	0.020

Table 6. Eigenvectors associated with variables that were significantly correlated with litter processing rates. PCA axes were selected using stepwise regression. Land-cover variable: DA=drainage area, PTIA=% total impervious area, Urb=% urban land cover, For=% forest cover, Wetl=% wetland cover; Physical variable: Q=average discharge; Biological variable: R=total richness, SR=snail richness, SB=snail biomass, Chl-a=chlorophyll a; Chemical variables: TOC=total organic carbon, DOC=dissolved organic carbon, TDS=total dissolved solids, BOD=bio oxygen demand, VSS=volatile suspended solids, Alk=alkalinity, Cond=conductivity, Nutrients=TKN, TP (total P), PO₄, NH₄, Metals=Al, Ni, Zn Pb, Fe, Mg, Mn, Cd.

red maple PCA1		PCA2		sweetgum PCA2		PCA1		PCA3	
TOC	(-0.2659)	DA	(-0.3529)	SB	(-0.3003)	TOC	(-0.2670)	TDS	(-0.3629)
For	(-0.2654)	R	(-0.3440)	DA	(-0.2540)	For	(-0.2664)	Cond	(-0.2676)
Al	(-0.2600)	TP	(-0.3215)	Wetl	(-0.2529)	Al	(-0.2649)	Chl-a	(-0.2553)
DOC	(-0.2519)	PO ₄	(-0.3143)	SR	(-0.2481)	DOC	(-0.2535)	NO ₃	(-0.2030)
Ni	(-0.2472)	Wetl	(-0.2409)	R	(-0.2461)	Ni	(-0.2485)	Ni	(-0.1862)
TKN	(-0.2262)	TKN	(-0.2331)	TKN	(-0.2315)	TKN	(-0.2271)	Alk	(-0.1789)
Zn	(-0.2161)	NH ₄	(-0.2283)	TP	(-0.2294)	Zn	(-0.2141)	NH ₄	(0.2526)
Pb	(-0.1983)	SB	(-0.2155)	PO ₄	(-0.2193)	Pb	(-0.1976)	DA	(0.2618)
BOD	(-0.1964)	SR	(-0.2074)	Mn	(-0.1984)	VSS	(-0.1970)	TP	(0.2991)
Fe	(-0.1894)	pH	(-0.1753)	Q	(-0.1941)	BOD	(-0.1958)	PO ₄	(0.3038)
VSS	(-0.1881)	Q	(-0.1663)	NH ₄	(-0.1807)	Fe	(-0.1920)		
Cd	(-0.1622)	Mn	(-0.1107)	B	(-0.1772)	Cd	(-0.1598)		
Q	(0.1429)	PTIA	(0.1052)	pH	(-0.1432)	Cond	(0.1503)		
Cond	(0.1456)	Fe	(0.1172)	PTIA	(0.1427)	Q	(0.1531)		
Mg	(0.1518)	VSS	(0.1275)	VSS	(0.1653)	Mg	(0.1591)		
Alk	(0.1764)	TSS	(0.1743)	Cd	(0.1729)	R	(0.1700)		
SR	(0.1772)	Cd	(0.1906)	Urb	(0.1954)	PTIA	(0.1719)		
PTIA	(0.1788)	Urb	(0.2087)	TSS	(0.2339)	Alk	(0.1754)		
pH	(0.2143)					SR	(0.2010)		
Urb	(0.2406)					pH	(0.2155)		
						Urb	(0.2424)		

The model selected using stepwise regression for sweetgum litter processing contained the first 3 PCA axes and explained 72% of the variance (Table 5). The first PCA axis selected for this model explained ~13% of the variance for the selected land-use, physical, chemical, and biological variables and 37% of the variance in processing rates (Table 5). Measurements of taxa richness and biomass, nutrients, pH, discharge and % wetland cover loaded negatively on this axis (Table 6, Fig. 7), while PTIA, urban land use, Cd, and suspended solids loaded positively (Table 6, Fig. 7).

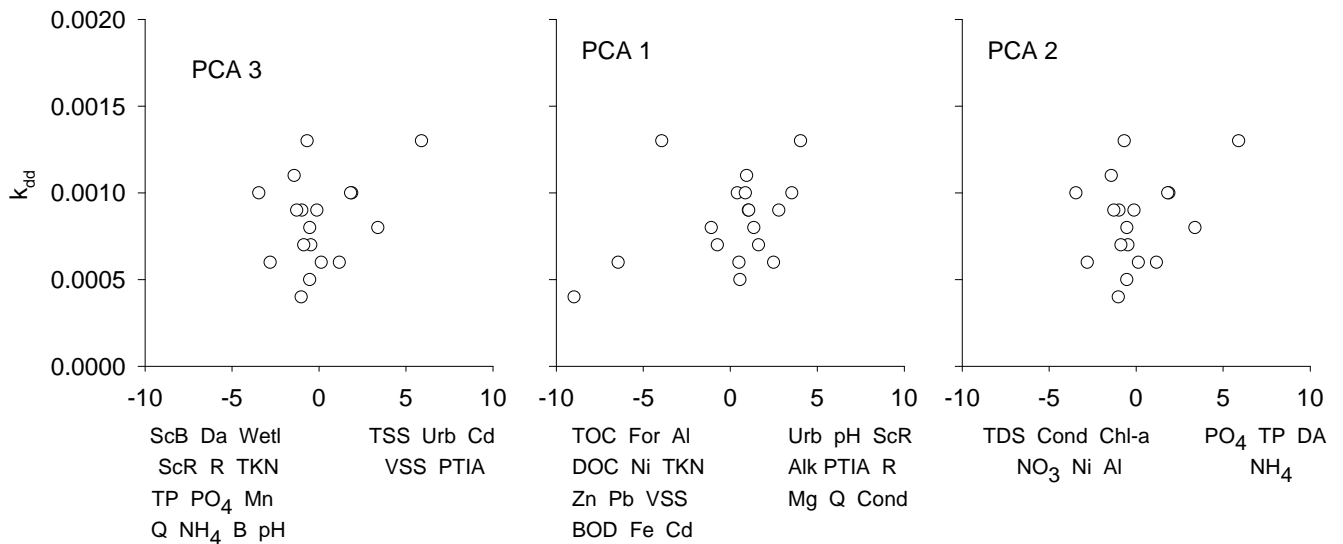


Figure 7. Relationships between the PCA axes selected using stepwise regression and sweetgum processing rates using degree days (k_{dd} , > 0 C). Labels on each X-axis indicate the influential variables in the PCA. Variable are listed in order of their importance. See the text for abbreviation meanings.

The second PCA axis explained ~29% of the variance for the selected land-use, physical, chemical, and biological variables and 22% of the variance in litter processing rates among sites (Table 5). This axis was very similar to the first axis selected in the red maple processing model. Total taxa richness, however, was found to be a more important variable for sweetgum (Table 6, Fig. 7). The third PCA axis explained 12% of the variance for the selected land-use, physical, chemical, and biological variables and 14% of the variance for sweetgum processing. This axis loaded negatively for total dissolved solids, conductivity, chlorophyll a, nitrate, Ni, and alkalinity and loaded positively for ammonium, drainage area, total phosphorus, and phosphate (Table 6, Fig. 7).

3.4 Discussion

Litter processing rates for red maple (0.010 to 0.046 d^{-1}) from most streams in our study were within the range of values that have been previously reported (Webster and Benfield 1986). Rates recorded for several streams appear to be the highest rates, however, on record (Webster

and Benfield 1986). Sweetgum rates (0.006 to 0.018 d⁻¹) were also similar to other reported values (0.033 d⁻¹, Short et al. 1984; 0.003 to 0.0110 d⁻¹, Rader et al. 1993). Although we saw similar patterns of processing for the two leaf species when compared with PTIA (Fig. 3), the muted response of sweetgum is likely due to intrinsic properties of these leaves. For example, Rader et al. (1993) found that current velocity, a correlate of mechanical abrasion, was unimportant in the breakdown in sweetgum. In our study, however, the sites with the greatest rates of processing were also the sites with the highest discharge (Table 1) and highest current velocities. For red maple, these sites had high rates of processing suggesting a strong influence of current velocity, which has been found previously in other urban-stream litter processing studies (Collier and Winterbourn 1986, Paul and Meyer 2001).

Stream flow conditions varied considerably among our sites (average discharge ranged from 0 to 125 L s⁻¹). The sites with the lowest levels of PTIA (e.g., Sites 26, 27, and 19) tended to have low discharge and current velocities, and in some streams flow ceased completely, resulting in dry stream channels (sites 26 and 27) or standing water with no flow (sites 13 and 19). Streams with the highest PTIA had discharges that were greater than streams with the lowest PTIA, but all had similar litter processing rates. Streams with moderate PTIA, however, had the greatest discharges and the fastest litter processing rates. The different flow regimes among the streams likely influenced macroinvertebrate community structure and other factors (e.g., measures of dissolved carbon, metals) found to be important in our PCA regressions, many of which directly and indirectly affect litter processing. Unlike streams in other urbanized areas, it appears that urbanization in the lower St Johns catchment may result in an increase in baseflow (Klein 1979, Barringer et al. 1994). We suspect that small streams in Northeast Florida with natural land-cover are intermittent, while similar sized stream in urbanized areas are perennial. We speculate that such a conversion in flow regime may be attributed to pumping of groundwater for irrigation combined with reduced evapotranspiration due to high levels of PTIA.

3.4.1 Invertebrates

The role that macroinvertebrates play in processing stream detritus is well known. Further, the response of macroinvertebrate communities to urbanization has also been widely reported (Paul and Meyer 2001, Huryn et al. 2002, Morse et al. 2003, Roy et al 2003, Gray 2004, Woodcock and Huryn 2004). Unlike previous studies, however, there was a conspicuous lack of arthropod shredders in headwater tributaries of the lower St Johns River (Table 4). This is not surprising given the sandy substrata and naturally species-poor communities that occur in these southeastern Coastal Plain streams (Smock et al. 1985, Rader et al. 1994). Arthropod shredders tended to be dominant only at forested, non-urban sites (Table 4). Sites where arthropod shredders were not prevalent tended to be dominated by snails (Tables 3, 4). These animals are often classified as browsers of periphyton, but they also can be effective shredders of living plant material and coarse detritus (Brown 1991, Lombardo et al. 2002). With the exception of streams with highly urbanized catchments and/or with dense populations of *Hydrilla*, the study streams were highly shaded due to closed canopies. This finding suggests that periphyton was limited and that snails were probably feeding primarily on detritus. Further, PCA axes that showed high loadings for either snail richness, biomass or both were selected in the stepwise model of litter processing (Tables 5, 6). The eigenvectors associated with snails were never among the highest (Table 6), but these parameters were always significantly correlated with rate of leaf litter loss. Snail richness and, to a lesser extent, snail biomass were some of the primary biotic variables explaining variation in litter processing among these sites.

We also found positive association between processing rates and average invertebrate biomass and total richness (Fig. 5). Both invertebrate biomass and richness were highest at intermediate PTIA and were not significantly correlated with each other ($p > 0.05$ for both leaf species). These results are similar to other litter processing studies that have shown that biomass and richness are key factors that influence rates of litter processing (Jonsson and Malmquist 2000, Huryn et al. 2002, Covich et al. 2004). For streams affected by urban influences, however, Huryn et al. (2002) caution that macroinvertebrate effects may only be apparent and more closely related to the other factors that vary with changes in PTIA. For headwater tributaries of the lower St Johns River, differences in flow regimes (i.e., intermittent or perennial flows) likely explain differences in both biomass and richness. Decreased biomass and richness associated with the highest levels of PTIA are likely driven by degraded environmental quality. Whether this difference in macroinvertebrate community structure is directly related to patterns of litter processing is unknown. Despite the mechanisms that cause changes in biomass and richness, our data support the concept that **both** biomass and richness can independently be important regulators of stream ecosystem function.

3.4.2 PCA

The processes involved in the breakdown of leaf litter in streams include leaching, microbial activity, fragmentation by macroinvertebrates, and mechanical abrasion. In studies that have shown an effect of urbanization on litter processing, mechanical abrasion associated with increased stream flow has been used to explain increased processing rates (see above, Collier and Winterbourne 1986, Paul and Meyer 2001). However, other changes associated with urbanization have the potential to both slow (e.g. metals, other toxins) and speed (e.g. increased nutrients) rates of processing (i.e., compensatory effects; sensu Gessner and Chauvet 2002). Our results clearly demonstrate the potential for such compensatory effects to be occurring among tributaries of the lower St Johns, because maximum processing rates occurred in streams draining catchments with intermediate levels PTIA (Fig. 3). Trying to tease apart the relations between litter processing and land-use, physical, chemical, and biological variables is difficult because of the strong correlations among the entire suite of variables. These correlations necessitated the use of data reduction techniques (e.g., PCA) and stepwise multiple regression.

Direct measures of land use were associated with the PCA axes that explained most of the variation in processing rates. These variables included percent urban land cover, PTIA, % forest, and % wetland cover. Percent wetland cover, however, is likely linked to management practices within catchments (i.e., retention ponds). Retention ponds may serve as nutrient and metal sinks and/or as buffers to changes in stream flow.

Other chemical measures that were relevant to the PCA analysis and the models of litter processing included nutrients and metals. The metal selected for these PCA axes loaded negatively, and increases in metals have been associated with decreased rates of litter processing in past studies (Maltby and Booth 1991, Woodcock and Huryn 2005). Elevated nutrients (e.g., N and P) are associated with faster rates of processing (Suberkropp and Chauvet 1995, Suberkropp 1998). We found that measures of both N and P were associated with the second and third axes, where loadings suggested that changes in both types of nutrients play an important role in litter processing across all sites.

3.4.3 Conclusions

Our results show that landscape-scale factors (PTIA) can be used to predict the influence of urbanization on ecosystem function (litter processing) in headwater streams. We used composite measures of land-use, physical, chemical, and biological variables to derive robust regression models describing landscape-level patterns of litter processing rates. We also showed that both biomass and richness of invertebrates are both positively correlated with litter processing rates. These results indicate that even though there are difficulties in identifying the independent effects of the myriad factors affecting streams in rapidly urbanizing catchments, the integration of these factors through the process of urbanization results in predictable changes in stream ecosystem function. With specific regard to litter processing, our results suggest that the effects of urbanization on stream discharge, biomass and richness of snails, and nutrients and metal concentrations are together primary determinants of litter processing rates in headwater streams of the southeastern Coastal Plain.

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4. Effects of land use on coarse organic matter and macroinvertebrates in small tributaries of the Lower St. Johns River (to be submitted to *The Journal of the North American Benthological Society*)

4.1 Introduction

In forested, headwater streams a dominant trophic resource for macroinvertebrates is coarse particulate organic matter (CPOM) supplied via terrestrial inputs (Webster and Meyer 1997, Webster et al 1999). Many studies of CPOM dynamics have outlined the biological, chemical and physical processes that regulate input, storage, and transport within stream ecosystems (Fisher and Likens 1973, Fisher 1977, Hynes 1975, Cummins et al. 1983, Vannote et al. 1980, Webster and Benfield 1986, Wallace et al. 1995, Webster and Meyer 1997, Webster et al. 1999). These processes include movement of material to stream channels, processing, consumption, storage, and downstream transport (Fisher and Likens 1973, Anderson and Sedell 1979, Cummins et al. 1983, Speaker et al. 1984, Webster and Benfield 1986, Webster and Meyer 1997 and references within, Webster et al. 1999). Further, direct dependence on CPOM by biotic communities has been well demonstrated (Wallace et al. 1997, 1999). Therefore, quantifying detrital dynamics provides insight into stream ecosystem structure and function (Webster and Meyer 1997, Chadwick and Huryn 2005, Lepori et al. 2005) and, as such, can be a useful indicator of impairment when coupled with other biological measurements of ecosystem health (e.g., macroinvertebrate community structure and function, rates of litter decomposition).

Land use change, including urbanization, is potentially the greatest threat to headwater catchments due to their ubiquity within landscapes and their size (Meyer and Wallace 2001). Urbanization has been shown to affect streams by altering hydrology, channel geomorphology, and riparian conditions (Booth 1990, Gordon et al. 1992, Paul and Meyer 2001, Hatt et al. 2004, Naiman et al. 2005). Changes in catchment hydrology due to urbanization can affect both inputs and storage of CPOM. Higher peak flows associated with urbanization can result in scouring of stream bank and increase inputs. Increased export can also occur with elevated discharge. Further, higher peak flow can increase tractive forces that can compromise retentive structures like snags (i.e. Bilby 1981, Boulton and Lake 1992). The type and degree of storage within a stream channel is attributable to both riparian conditions and channel geomorphology (Bilby 1981, Maridet et al. 1995, Wallace et al. 1995, Angradi 1996, Lamberti and Gregory 1996). Streams in urbanized catchments have channels that are both widened and incised due to both

altered hydrology and management (Booth 1990, Paul and Meyer 2001) which can result in decreased CPOM storage. Development along riparian areas result in changes to riparian vegetation which can dramatically alter both types and quantities of CPOM inputs (Naiman et al. 2005).

Numerous studies have found that there are predictable responses in the structure of stream invertebrate communities with increased urbanization (Paul and Meyer 2001; Table 1). In particular, decreases in diversity, abundance and biomass, particularly for Ephemeroptera and Trichoptera, are found along urban-rural gradients. Numerous mechanisms behind these effects have been hypothesized including increased toxicity due to point and NPS pollutants, loss of habitat due to sedimentation, changes in temperature, increased organic and inorganic nutrients, increased pesticides, reduced food quality, increased bed mobility and hydrological changes (Paul and Meyer 2001). However, studies that examine the response of both CPOM and invertebrate structure to urbanization are rare (Roy et al. 2003).

Prior to widespread development in the Lower St. Johns River Basin (LSJRB), the landscape was dominated by hardwood swamps, pine flatwoods, and upland forests. Development has resulted in increases in impervious surfaces and a likely decrease in the amount of CPOM inputs into streams. Percent total impervious area (PTIA) has been shown to be a powerful proxy indicator for the changes that occur because of urbanization (Klein 1979, Schueler 1994, Morse et al. 2003). The goal of this study was to examine how differing levels of PTIA and urban development affect CPOM input, storage and export in low order tributaries of the St. Johns River. Further, we seek to understand how changes in PTIA and CPOM dynamics affect resident macroinvertebrate communities.

TABLE 1. Review of literature relating percentage of total catchment impervious surface area (PTIA) to responses in stream biotic and abiotic variables.

Reference	Location	PTIA Threshold	Threshold Response
Klein (1979)	MD	10%	Decreased macroinvertebrate diversity
Jones & Clark (1987)	VA	15-25% ^a	Decreased macroinvertebrate diversity, increased relative abundance of tolerant taxa
Shaver (1995)	DE	8-15%	Decline in insect diversity
Schueler & Galli (1995)	MD	10-12%	Decline in insect diversity
Maxted (1996)	DE	10-15%	Loss of sensitive insect taxa, shift to tolerant insect taxa
Horner et al. (1997)	WA	1-6%	Decrease in insect IBI
May et al. (1997)	WA	5-10%	Decreased macroinvertebrate B-IBI
Yoder (1999)	OH	8%	Decrease in insect diversity
Stephenuck et al. (2002)	WI	8-12%	Increase in Hilsenhoff Family Biotic Index

Morse et al. (2003)	ME	6%	Decreased total insect and EPT taxonomic richness
Ourso & Frenzel (2003)	AK	1.2-3.4%	Decreased total taxa richness, increased Hilsenhoff FBI
Wang & Kanehl (2003)	WI, MN	7%	Decrease in EPT abundance, EPT taxa, filterers, and scrapers, increase in Hilsenhoff Family Biotic Index
Walsh et al. (2004)	Melbourne, Australia	9.6%	Loss of threatened amphipod <i>Austrogammarus australis</i>

4.2 Study Site

Eighteen first- and second-order streams representing a gradient of urban-rural land-use and PTIA in the LSJRB are the focus of this study (Fig. 1, Table 2). Each stream drained catchments in the LSJRB and were located in the vicinity of Jacksonville, Florida. The riparian vegetation at each stream was composed of red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and water oak (*Quercus nigra*). Four sites lacked a significant canopy cover and macrophytes (e.g., *Hydrilla verticillata*, *Myriophyllum sp.*, and *Alternanthera philoxeroides*) occurred in dense stands. One hundred-meter stream reaches were selected in each catchment. All streams had sandy substate, low channel gradients, and habitats composed of runs with occasional coarse woody snags.

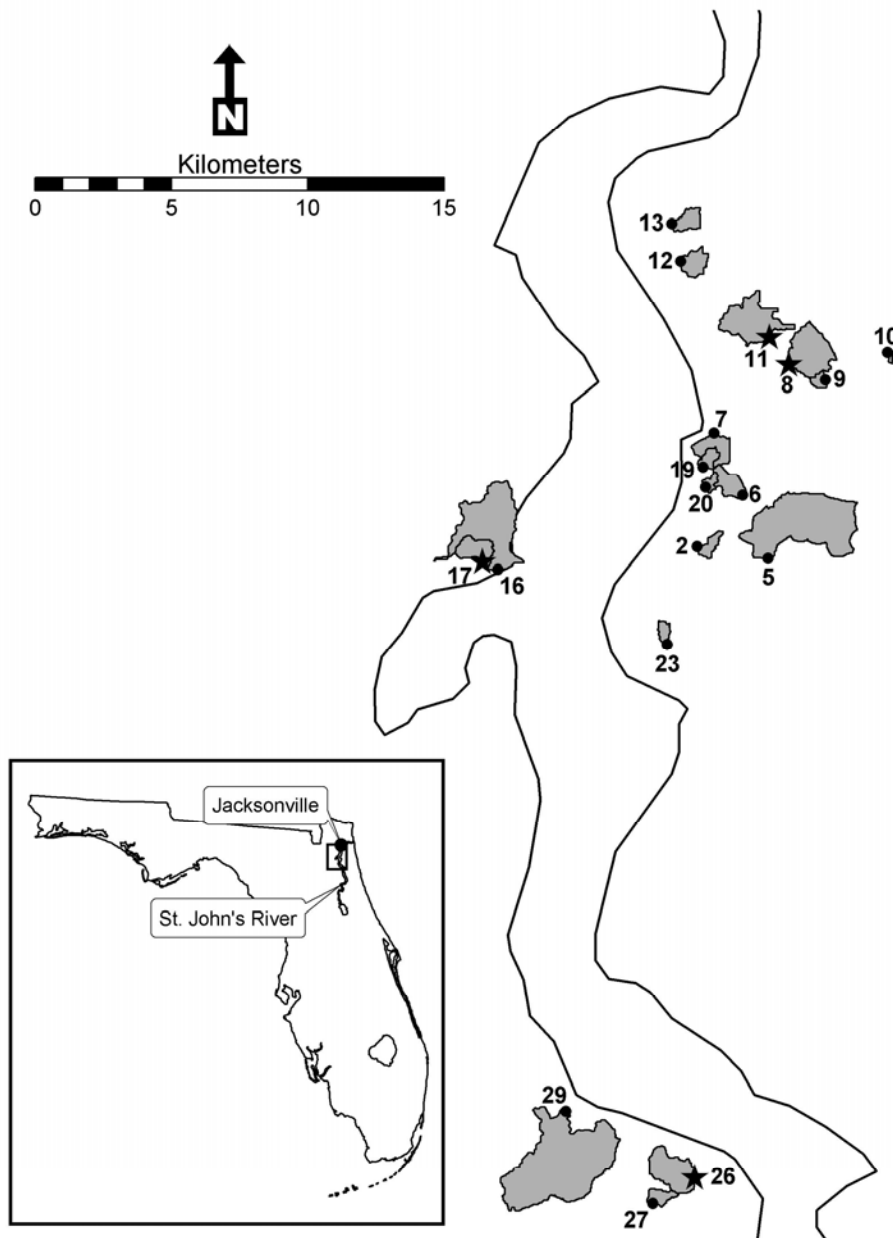


Figure 1. The Lower St. John's River, Florida and locations of the 18 study streams. Stars denote streams where CPOM inputs were measured.

Table 2. Summary of the distribution of percent total impervious area (**PTIA**), catchment area (**CA** in hectares), discharge (**Q** in $L s^{-1}$) for the 18 study catchments. Impervious surface cover was quantified using a normalized difference vegetation index derived from multispectral digital orthophoto quarterquads (see Chapters 2 & 3).

site	PTIA	CA	Q
2	51	42	1
5	26	687	40
6	28	82	4
7	26	94	5
8	46	231	28
9	66	26	8
10	43	10	33
11	35	262	29
12	24	76	10
13	17	64	10
16	32	454	119
17	29	91	14
19	8	39	11
20	19	24	124
23	21	30	3
26	0	189	4
27	0	47	0
29	17	938	1

4.3 Methods

4.3.1 CPOM Retention

Retention of CPOM was measured using leaf analogs (8 cm edged, equilateral triangles cut from blue tarp). Five hundred, individually labeled leaf analogs were released into each stream reach in September 2003. After 1 month, we surveyed each 100 meter reach and recorded distance moved from release point. Percent recovery and distance traveled for the 50th percentile were calculated for each stream. The relationship of both % recovery and distance traveled were then related to PTIA using linear regression.

4.3.2 CPOM Input

Ten vertical traps (0.25 m²) located directly over the streambed and ten lateral traps located adjacent to the streambed (0.5 m long x 0.2 m high x 0.3 m deep) were placed randomly along each 4 streams (8, 11, 17, and 26) to collect CPOM inputs. Traps were set in October 2003 and emptied monthly until October 2004. All material was sorted into CPOM types (pine needles, maple leaves, sweetgum leaves, oak leaves, other leaves, seeds/cones, woody debris, and other material), dried to constant mass (60° C), and then weighed. A portion from each sample was ashed (550° C) and weighed to calculate ash free dry mass (AFDM). Because lateral traps only sampled input from one side of each stream, AFDM was doubled to estimate total

lateral inputs. Average monthly input for each stream was calculated from 1,000 estimates generated by resampling with replacement. Total annual input was then calculated by summing across monthly estimates to create 1,000 estimates for each stream. Statistical comparisons between streams for vertical and lateral inputs were made by comparing 90% confidence intervals. Non-overlapping confidence intervals indicated a significant difference. Control of type II error was achieved by designating an α level of 0.10 prior to this study. Differences in the proportion of average annual input for each CPOM type were assessed using χ^2 tests. Comparisons were made both among streams by vertical and lateral inputs and between vertical and lateral input in each stream.

4.3.3 CPOM Storage and Macroinvertebrates

Benthic samples were collected approximately monthly in 4 streams (8, 11, 17, 26) and quarterly from 6 additional streams (2, 10, 12, 13, 20, 27). Samples were collected using a petite ponar grab (0.023 m²). At each stream, 5 randomly selected locations were selected prior to the sampling trip. At each location, 3 grabs were taken (right lateral, middle, and left lateral) and combined into one sample. The grabs were emptied into a 4 gallon bucket. All coarse material was removed by hand to a whirlpak bag. The remaining fines are sieved through a 250 μ m sieve and then washed into the whirlpak bag. All samples were preserved in the field with ~5% formaldehyde. In the lab, collected material was sieved into five fractions (2 cm, 2 mm, 1 mm, 500 μ m, and 250 μ m). The coarse fraction (> 2 cm) is split into the major litter types. All remaining fractions were sorted under magnification and all invertebrates were removed. All CPOM was processed in the same manner as inputs. Invertebrates removed from the sample were identified to the most practical taxonomic level, measured to the nearest mm, and enumerated.

4.4 Preliminary Results

4.4.1 CPOM Retention

After 1 month, analog recovery ranged 0-100% with 12 streams having recoveries >20% (Fig. 2a). In most of the sites, analogs were typically retained along the stream channel margins. In sites with open canopies, analogs tended to be retained on macrophytes. No attempt was made to look for analogs buried in stream sediments (e.g., sand), so we cannot assume that the unrecovered analogs were exported from the study reaches. Of the analogs that were recovered in each stream, the 50th percentile for distance traveled ranged from 0-88 meters with 7 streams having movement greater than 50 meters (Fig. 2b).

Recovery of analogs was negatively associated with PTIA ($r^2=0.29$), however it is likely that this relationship was driven by the high recovery associated with site with the lowest PTIA. The relationship between movement and PTIA was positive ($r^2=0.15$), but again this relation appears to be driven by the sites with the lowest PTIA. Comparisons between both analog recovery and movement to discharge show that sites with the lowest discharges had the highest rates of recovery and least movement (Fig. 2b,c).

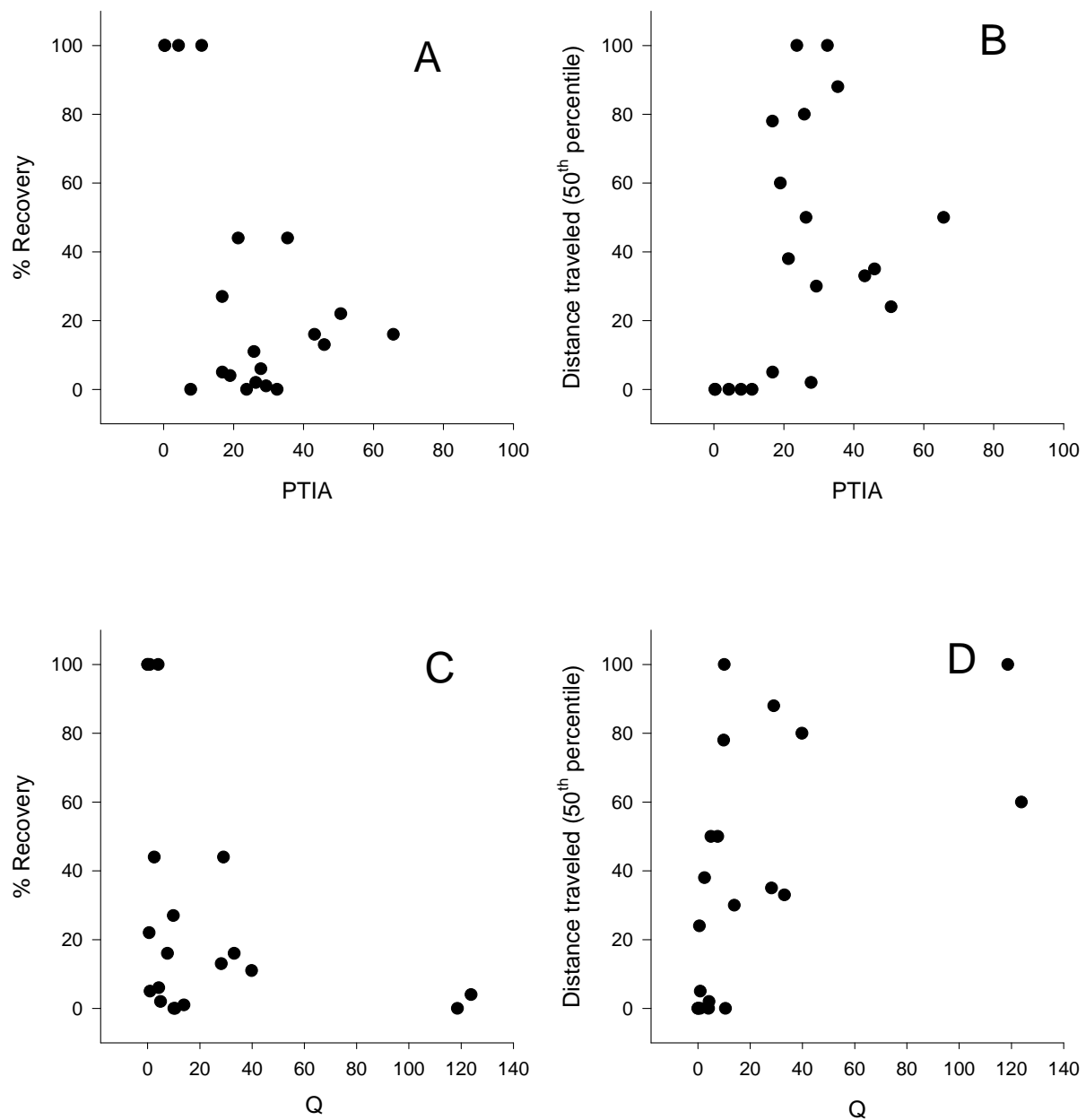


Figure 2. Results from the leaf analog releases: A) PTIA vs. % recovery, B) PTIA vs. 50th percentile distance traveled, C) discharge vs. % recovery, D) discharge vs. 50th percentile distance traveled. Q= average discharge ($L s^{-1}$).

4.4.2 CPOM Inputs

CPOM inputs ranged from ~ 600 to ~ 1000 $g AFDM m^{-2}$ (Fig. 3). Based on non-overlapping confidence intervals, the stream that lack a riparian canopy (11) had significantly lower input than the other 3 streams. At all streams, most CPOM entering the channel was via vertical inputs. Accordingly, lateral inputs comprised $< 10\%$ of total input. Monthly vertical inputs ranged from ~ 10 to ~ 150 $g AFDM m^{-2}$, were highly variable and showed little seasonal pattern (Fig. 4). Monthly lateral inputs ranged from < 1 to ~ 20 $g AFDM m^{-2}$. Unlike vertical

inputs, lateral inputs tended to follow seasonal patterns with the lowest levels of input occurring in summer. Stream 11 had the lowest inputs, likely due to the lack of a developed riparian canopy. This pattern appears particularly pronounced in autumn during leaf abscission. The average contribution of CPOM types (e.g., wood, leaves, needles, etc.) varied significant among streams for both vertical ($\chi^2_{21}=197$; $p < 0.001$) and lateral input ($\chi^2_{21}=177$; $p < 0.001$; Fig. 5). Difference between the distribution of inputs by CPOM type for each stream did not vary between lateral or vertical input, except for stream 11 ($\chi^2_7=17.0$; $p=0.03$; $p < 0.001$). In stream 11 there appears to be much high lateral inputs of wood rather than vertical inputs of wood.

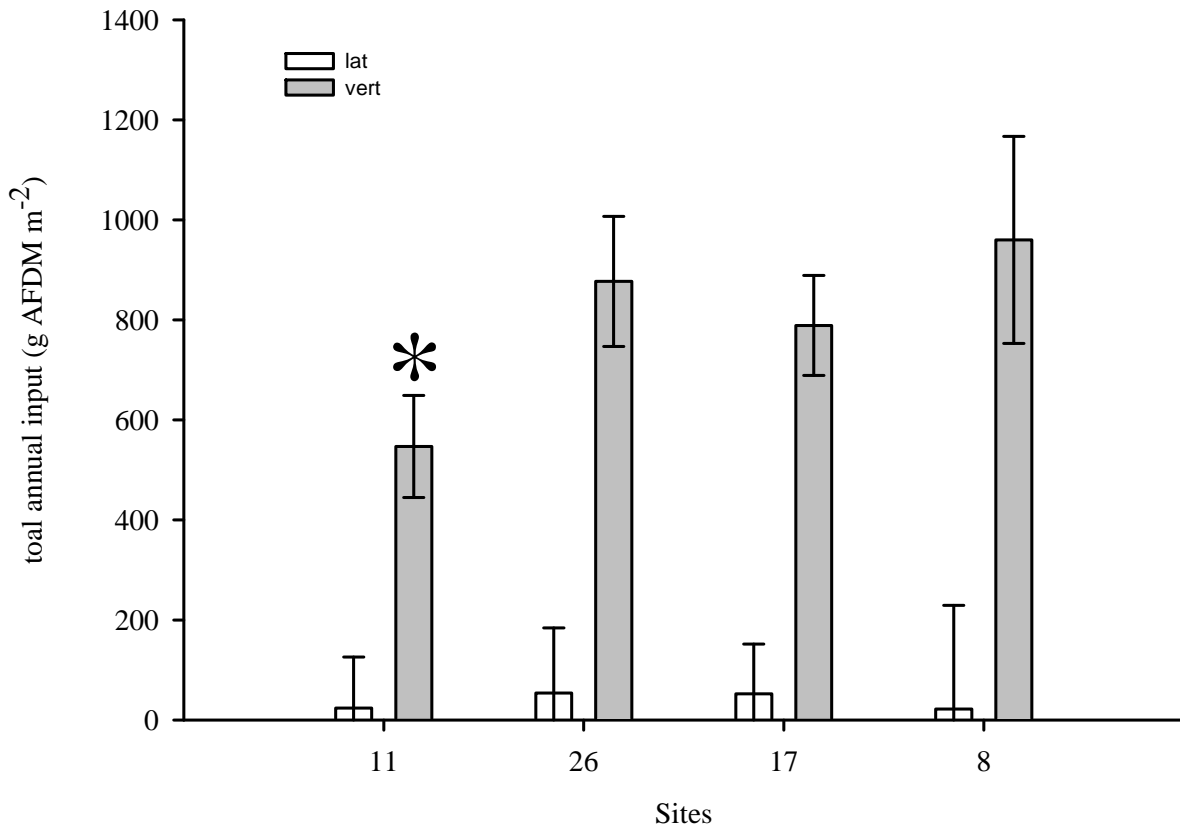


Figure 3. Total annual inputs of coarse particulate organic matter collected from lateral (lat) and vertical (vert) traps. Ten traps in each stream were set in October 2003 and emptied monthly until October 2004. Stream 11 had lower annual inputs of CPOM based on non-overlapping 90% confidence intervals.

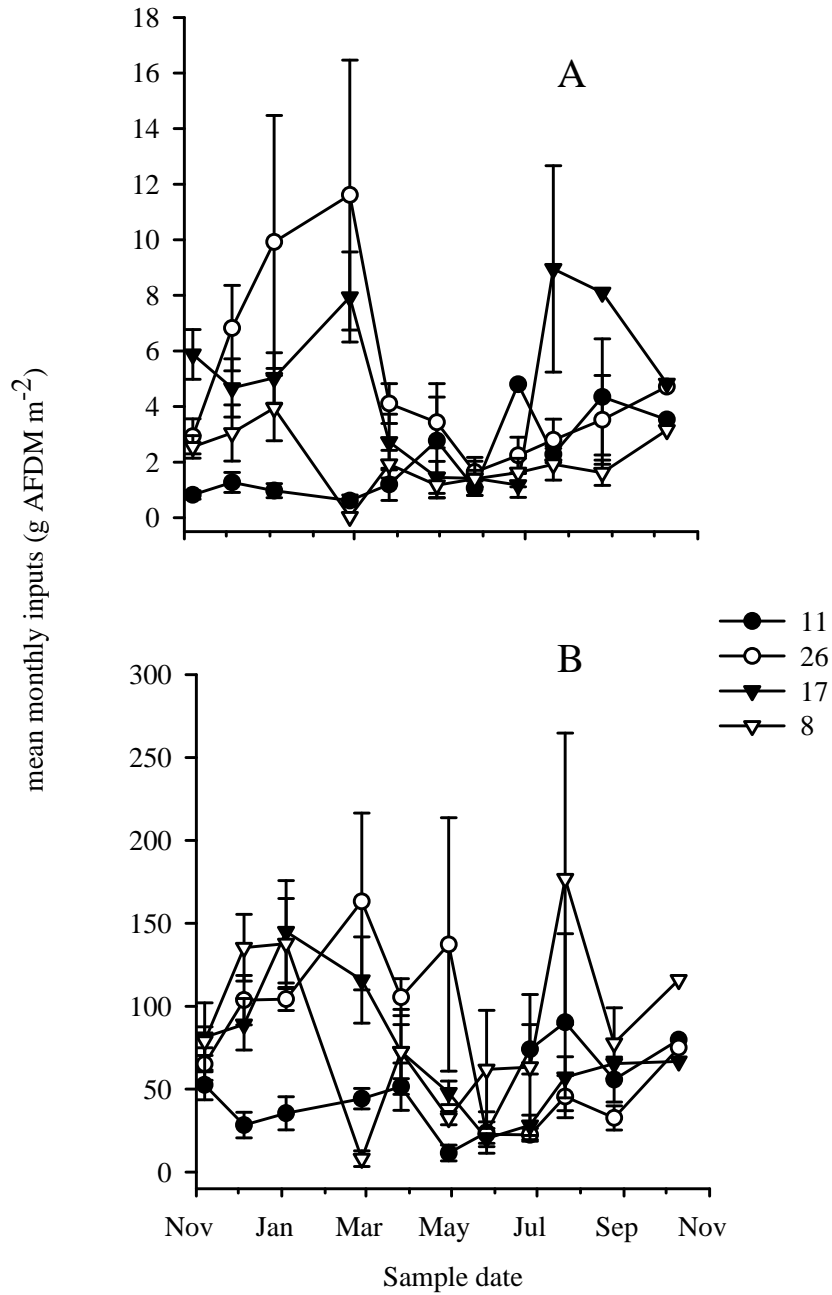


Figure 4. Mean monthly inputs of coarse particulate organic matter collected from lateral (A) and vertical (B) traps. Ten traps in each stream were set in October 2003 and emptied monthly until October 2004. Error bars are 1 SE.

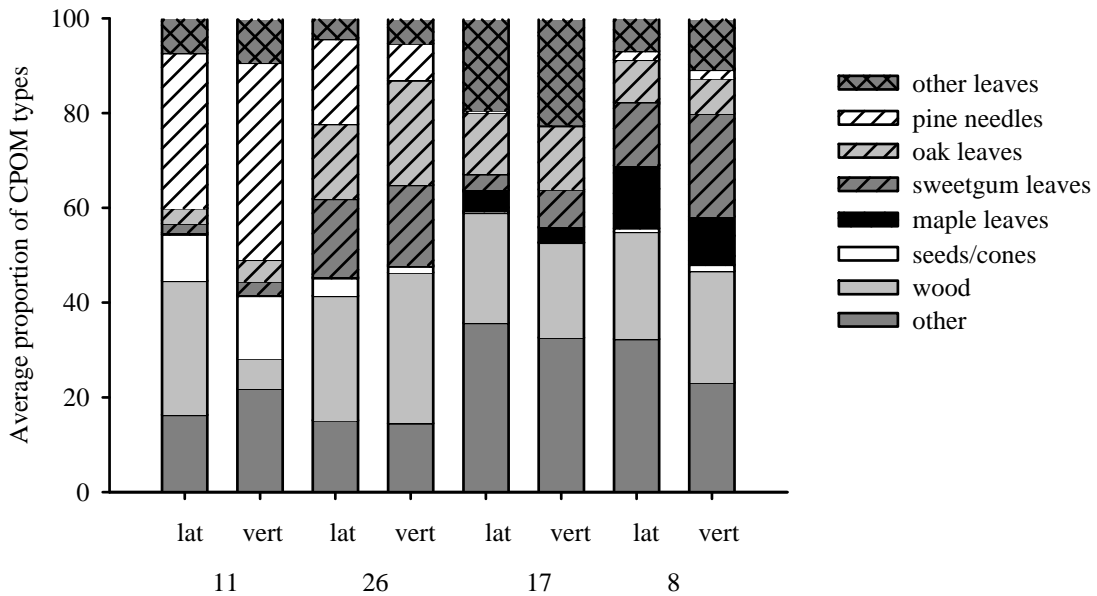
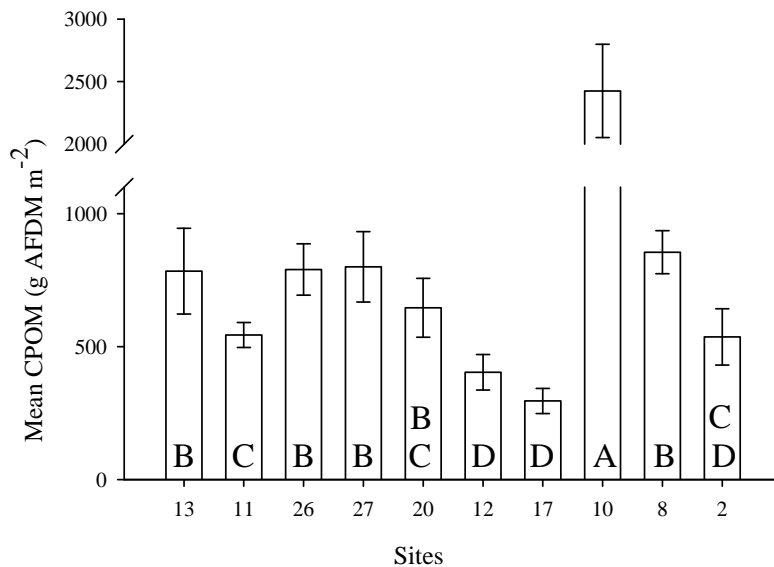


Figure 5. Mean annual contribution (proportion of total mean) of coarse particulate organic matter types collected from lateral (lat) and vertical (vert) traps.

4.4.3 CPOM Storage

CPOM storage ranged from ~400 to ~2500 g AFDM m⁻² (Fig. 6). Based on non-overlapping confidence intervals, stream could be classified into 4 groups. The grouping of streams based on mean standing stock was not related to PTIA or canopy cover. The site with the highest POM standing stock had an intact riparian canopy that was dominated by softwoods. The streams with the lowest CPOM standing stocks tended to have moderate levels of PTIA.

Figure 6. Mean CPOM standing stock. Sites are arranged from lowest to highest PTIA with the 2 stream that lacked riparian canopies appearing first (e.g., 13 and 11 with 11 having greater PTIA). Letters in each bar represent groupings based on non-overlapping 90% confidence intervals.



Monthly CPOM standing stocks ranged from ~50 to ~3000 g AFDM m⁻² and showed little seasonal pattern (Fig. 7). The sites that lacked a riparian canopy cover showed peak CPOM standing stocks in summer, and this is associated with macrophyte production, particularly *Hydrilla verticellata*.

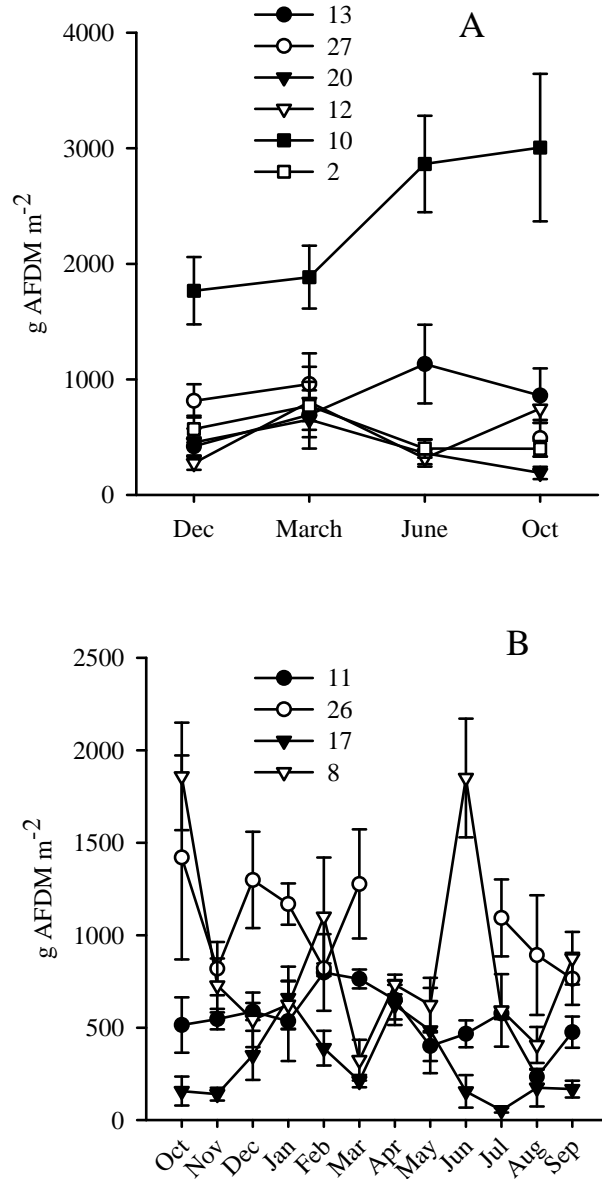


Figure 7. Mean monthly standing stocks of coarse particulate organic matter from quarterly (A) and monthly (B) samples streams. Error bars are 1 SE.

The average contribution of CPOM types (e.g., wood, leaves, needles, *Hydrilla*, etc.) varied among streams (Fig. 8). Miscellaneous organic matter (i.e., *other*-material that passed the 2mm sieve) was the dominate type found in each stream and comprised ~40 to 80% of all material collected. Wood was the second most common type and

comprised ~10 to 40% of CPOM. In the stream that lack riparian canopy, *H. verticillata* contributed ~20%.

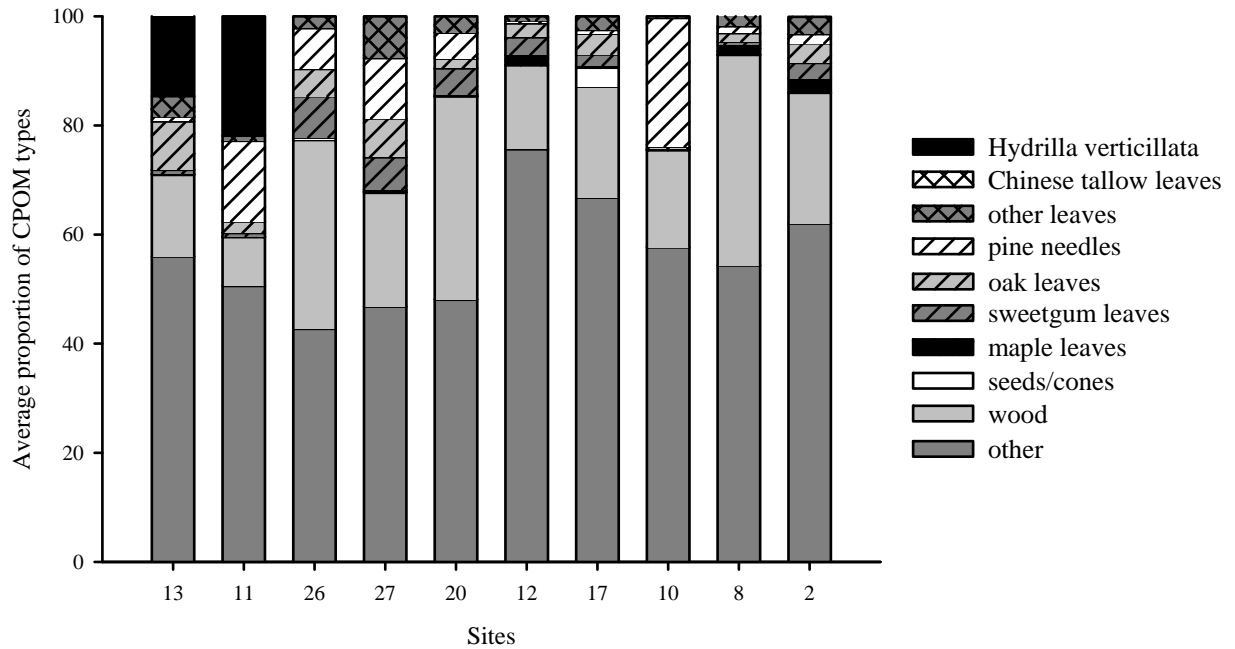


Figure 8. Mean annual contribution (proportion of total mean) of coarse particulate organic matter.

4.4.4 Macroinvertebrates

Macroinvertebrate richness ranged from 22 to 56 taxa (Table 3). Larval chironomids, Oligochaeta, leeches, and *Corbicula* were the most common taxa found among all streams. Mean abundance ranged from ~3500 to 17000 individuals m^{-2} (Fig. 9) Mean biomass ranged from < 5 to ~150 g dry mass (DM) m^{-2} (Fig. 10). Both abundance and biomass tended to be higher for stream that contained *H. verticillata*. Comparison of richness and abundance to PTIA showed no patterns (Fig. 11). However, the relationship between invertebrate biomass and PTIA was similar to the pattern found with litter decomposition (Fig. 11; see above). There were also no clear overall patterns found for the relationship between CPOM standing stock and invertebrate biomass (Fig. 12). Further investigation into these patterns is warranted.

Table 3. Taxonomic Composition (1=present and 0=absent).

Taxa	13	11	26	27	20	12	17	10	8	2
Amphipoda	0	0	1	1	0	0	0	0	0	0
<i>Anax</i>	1	0	0	0	0	0	0	0	0	0
<i>Anchytarsus</i>	0	0	0	0	0	1	0	0	0	0
Ancylidae	1	1	1	0	1	1	0	1	0	1
<i>Ancyronyx</i>	0	0	0	0	1	0	0	0	0	0
<i>Aphylla</i>	0	1	0	0	0	0	0	0	1	0
<i>Argia</i>	1	1	0	0	1	1	1	0	1	1
<i>Belastoma</i>	1	0	1	0	0	0	0	0	0	0
<i>Bittacomorpha</i>	0	0	0	1	0	0	0	0	0	0
<i>Boyeria</i>	0	0	1	0	0	0	0	0	0	0
<i>Caecidotea</i>	1	0	1	1	1	0	0	0	0	0
<i>Caenis</i>	0	1	0	0	0	1	0	0	0	0
<i>Calopteyx</i>	0	0	0	0	0	0	1	0	0	0
Cambaridae	1	1	1	1	0	0	1	0	1	1
<i>Campeloma</i>	0	0	0	0	0	1	0	0	0	0
Ceratapogonidae	1	0	0	1	1	1	0	1	0	1
<i>Chaoborus</i>	0	0	1	0	0	0	0	0	0	0
<i>Cheumatopsyche</i>	1	0	0	0	1	1	1	0	1	0
Chironomidae	1	1	1	1	1	1	1	1	1	1
<i>Chrysops</i>	0	0	1	1	1	0	0	0	0	0
Coenagrionidae	1	0	1	0	1	0	0	0	0	0
Copepoda	1	1	1	1	1	1	1	1	1	1
<i>Corbicula</i>	1	1	1	1	1	1	1	1	1	1
Corduliinae	1	0	0	0	0	0	0	0	0	0
<i>Desserobdella picta</i>	0	0	0	0	0	0	0	0	1	0
Dolichopodidae	0	0	1	1	1	0	0	0	0	0
<i>Dubiraphia</i>	0	0	1	0	0	0	0	1	1	0
Dytiscidae	0	0	1	1	0	1	0	0	0	0
Elmidae	0	0	0	0	1	0	0	0	0	0
Empididae	1	0	0	0	0	1	0	0	0	0
<i>Enallagma</i>	1	1	0	1	0	0	1	0	1	0
<i>Eropobdella</i>	0	1	1	0	0	0	0	0	1	0
<i>Erythemis</i>	1	0	0	0	0	0	0	0	0	0
<i>Erythrodiplax</i>	0	0	0	0	0	0	1	0	1	0
<i>Ferrissia</i>	1	0	0	0	0	0	0	0	1	1
<i>Gammarus</i>	0	0	0	1	0	0	1	0	1	0
Gastropoda	1	1	0	0	1	1	0	0	0	0
<i>Gliobdella elongata</i>	1	0	0	0	1	1	0	1	1	1
<i>Gomphus</i>	0	0	0	0	0	0	0	0	1	0
<i>Gynacantha</i>	0	0	1	0	0	0	0	0	0	0
<i>Haemopsis septagon</i>	0	0	0	0	0	1	0	0	0	0
<i>Haitia</i>	1	0	0	0	1	1	1	0	1	1

<i>Hebetancylus</i>	1	0	1	0	0	0	1	0	1	1
<i>Helisoma anceps</i>	0	1	0	0	0	0	0	0	1	0
<i>Helobdella fusca</i>	1	0	0	0	1	1	1	1	1	1
<i>Helobdella stagnalis</i>	1	1	1	0	1	1	1	1	1	1
<i>Helobdella triserialis</i>	1	1	0	0	1	1	1	1	1	0
<i>Hemerodromia</i>	0	0	0	0	0	0	0	0	1	0
<i>Hexatoma</i>	0	0	0	1	0	0	1	0	0	0
Hirudinea	1	0	0	0	1	1	0	1	0	0
Homoptera	0	0	0	0	0	1	0	0	0	0
<i>Hyaella</i>	0	1	0	0	1	1	0	1	1	1
<i>Hydaticus</i>	0	0	0	1	0	0	0	0	0	0
<i>Hydroporus</i>	0	0	0	0	0	1	1	0	0	1
<i>Ischnura</i>	1	0	0	1	0	0	0	0	0	0
Isotomidae	0	0	0	0	0	0	1	0	1	0
<i>Laevapex</i>	1	0	0	0	0	0	0	0	0	0
<i>Lestes</i>	1	0	0	1	0	0	0	0	0	0
<i>Libellula</i>	1	1	1	1	0	0	0	0	0	1
Libellulidae	1	0	0	1	1	1	0	0	0	0
<i>Lioporeus</i>	0	0	1	0	0	0	0	0	0	0
<i>Lipogomphus</i>	1	0	0	0	1	0	0	0	0	0
<i>Macrobdella</i>	0	0	0	0	0	0	1	0	0	0
<i>Macromia</i>	0	1	0	0	0	0	0	0	1	0
<i>Melanoides</i>	1	0	0	0	0	0	0	0	1	1
<i>Micromenetus</i>	1	0	1	0	1	1	1	0	0	1
<i>Microvelia</i>	0	0	0	1	0	0	0	0	0	0
<i>Molophilus</i>	0	0	0	1	0	0	0	0	0	0
<i>Mooreobdella</i>	1	1	0	0	0	1	0	1	0	0
Muscidae	1	0	0	1	0	0	0	0	0	1
<i>Musculium</i>	0	0	0	0	0	0	0	1	0	0
<i>Myzobdella</i>	1	0	0	0	0	1	1	1	1	0
<i>Nehalennia</i>	1	0	0	0	0	0	0	0	0	0
<i>Nemotelus</i>	1	0	0	1	0	1	0	1	0	1
<i>Neoporus</i>	0	0	1	0	0	0	0	0	0	0
<i>Neurocordulia</i>	1	0	0	0	0	0	0	0	0	0
Oligochaeta	1	1	1	1	1	1	1	1	1	1
<i>Orthemis</i>	1	0	0	0	0	0	0	0	0	0
Ostrococha	1	1	1	1	1	1	1	1	1	1
<i>Pachydiplax</i>	1	0	1	0	0	0	0	0	1	0
<i>Palpomyia</i>	0	0	1	0	0	0	0	0	0	0
<i>Parapoynx</i>	0	1	0	0	0	0	0	0	0	0
Pelecorhynchidae	1	0	0	1	0	0	0	0	0	0
<i>Peltodytes</i>	1	1	0	0	0	0	0	0	1	1
<i>Perethemis</i>	1	0	0	0	0	0	0	0	0	0
Phoridae	0	0	0	0	0	1	0	0	1	1
<i>Placobdella</i>	1	0	0	0	0	0	0	0	0	0
<i>Planorbella</i>	1	1	0	0	0	1	1	1	1	0

<i>Planorbella scalaris</i>	1	0	0	0	0	0	1	0	1	0
<i>Plathemis</i>	1	0	0	0	0	0	0	0	0	0
<i>Plathemislydia</i>	1	0	0	0	0	0	0	0	0	0
<i>Pomacea</i>	0	0	0	0	0	0	1	1	0	0
<i>Probezzia</i>	0	0	0	0	0	0	1	0	1	0
<i>Progomphus</i>	0	0	0	0	0	0	0	0	1	0
<i>Pseudolimnophila</i>	0	0	1	0	1	0	0	0	0	0
Pyrilidae	1	0	0	0	0	0	0	0	0	0
<i>Rhantus</i>	0	0	1	0	0	0	0	0	0	0
<i>Scirtes</i>	0	0	1	1	1	0	0	0	0	0
Sminthuridae	0	0	1	0	0	0	1	0	0	0
<i>Somatochlora</i>	0	1	0	0	0	0	0	0	0	0
<i>Sphaerium</i>	0	0	0	0	0	0	1	1	1	1
<i>Stenelmis</i>	0	0	0	1	1	1	0	0	1	1
Tabanidae	0	0	1	0	0	0	0	0	0	0
Tanypodinae	1	0	0	1	1	1	1	1	1	1
<i>Telebasis</i>	1	0	0	0	0	0	0	0	0	0
<i>Tipula</i>	1	0	0	0	1	1	1	0	1	0

Total Taxa	56	24	32	28	32	36	32	22	42	27

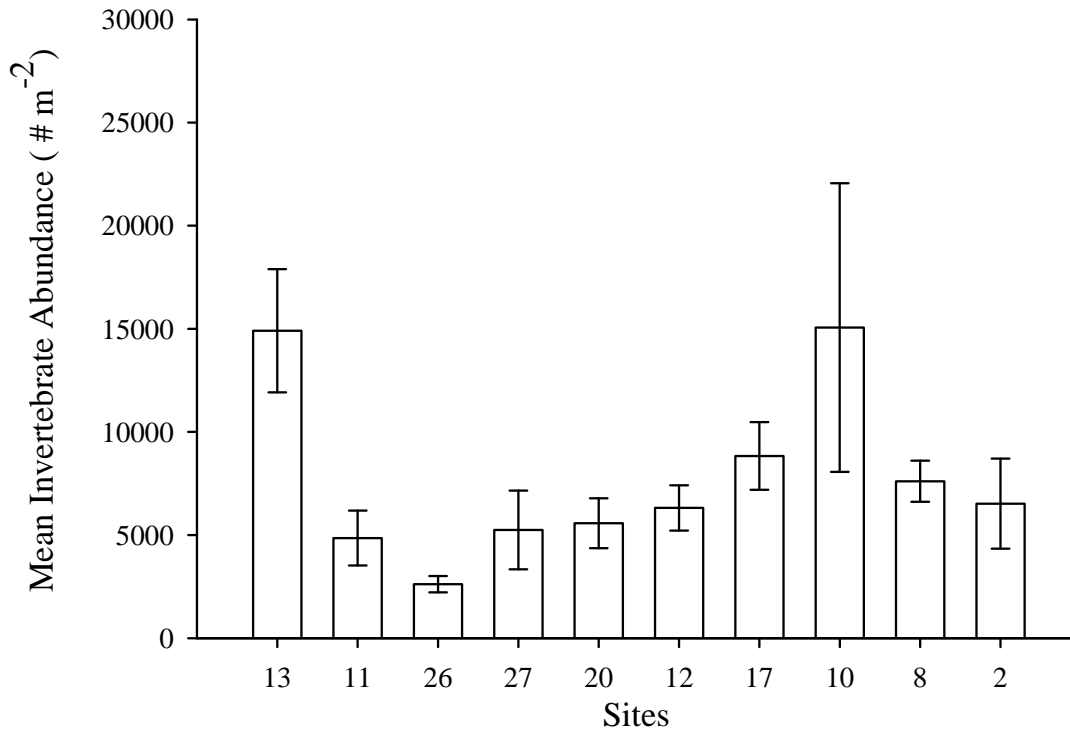


Figure 9. Mean annual invertebrate abundance. Error bars are 1 SE.

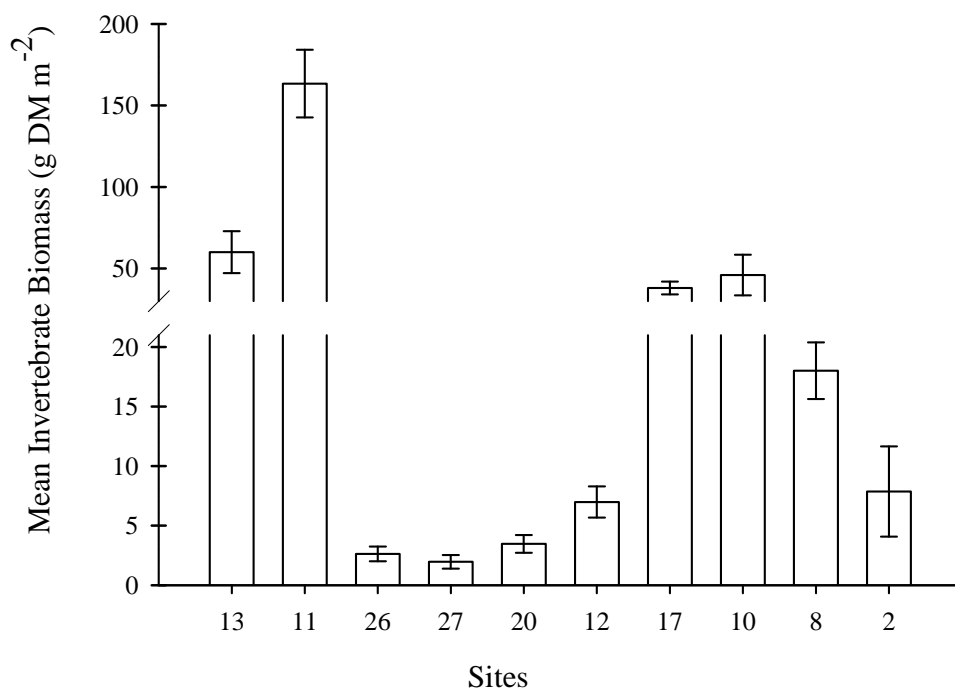


Figure 10. Mean annual invertebrate biomass. DM=dry mass. Error bars are 1 SE.

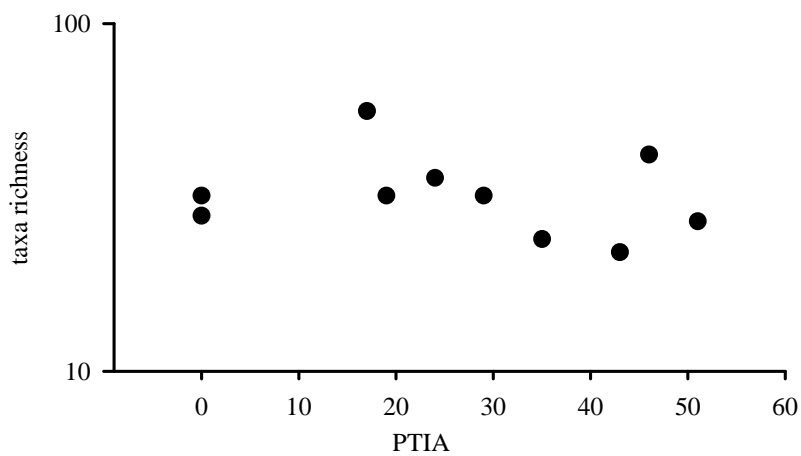
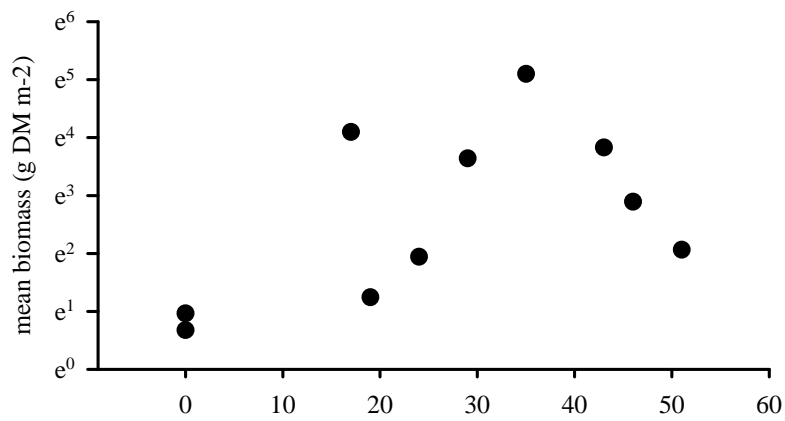
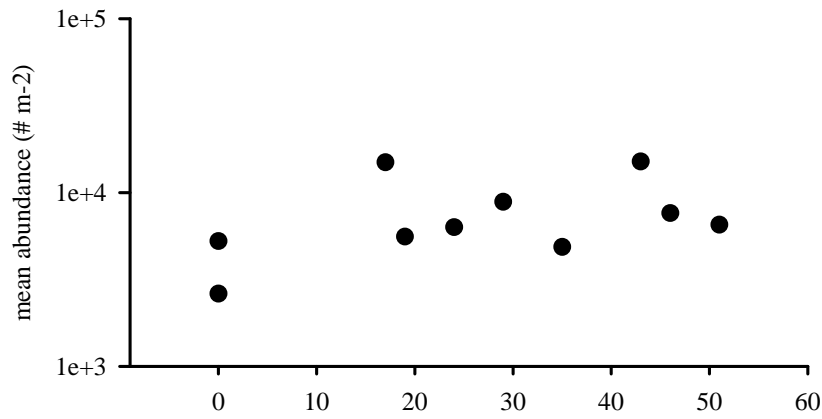


Figure 11.
 Relationship of PTIA
 to invertebrate
 abundance, biomass,
 and richness.
 DM=dry mass

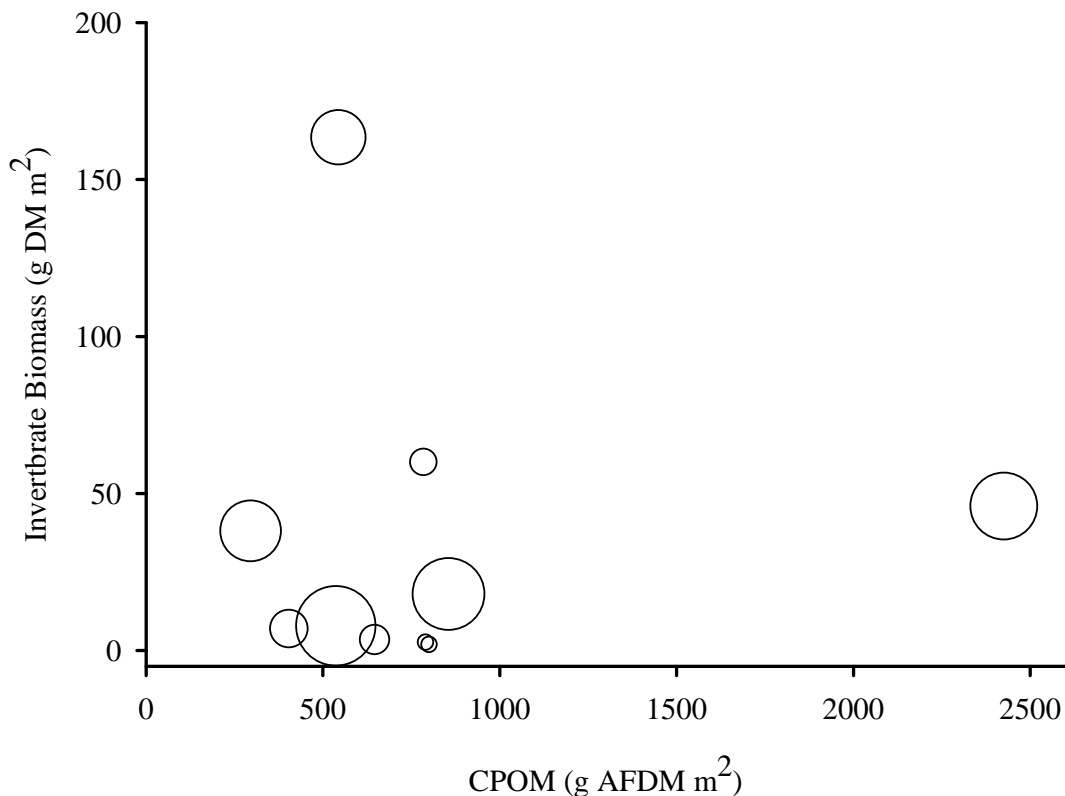


Figure 12. Relationship between CPOM standing stock and invertebrate biomass. The size of each circle is proportional to PTIA with the largest circles having the greatest PTIA. AFDM=ash free dry mass, DM=dry mass

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5. Effects of detrital food source on growth of a physid snail

(undergraduate mentored project conducted by Rachel S. Hicklen; to be submitted to the Journal of Molluscan Studies)

5.1 Introduction

Physid snails (Pulmonata: Physidae) are widespread in freshwater habitats throughout the holarctic (Burch 1989, Taylor 2003) and are generally considered to feed on periphyton (Brown 1991, Lombardo and Cooke 2002, Heard and Buchanan 2004). However, several studies have shown that they also consume living plant material and detritus (Lombardo and Cooke 2002, Taylor 2003). In streams where multiple food sources are available, snails may preferentially feed on resources based on palatability or accessibility. It is likely that snail feeding influences food availability and when preferable items (e.g., periphyton) are lacking less desirable food sources can be consumed (e.g., detritus)

In Florida, USA, six species of physid snails occur in low-order tributaries of the St. Johns River (Thompson, 1999), of which *Haitia pomilia* (Conrad) has been found to be abundant (M.A. Chadwick, unpublished data). The food sources available in the streams where *H. pomilia* has been collected vary dramatically due to the presence of a closed or open canopy. Streams with closed canopies are tree lined with red maple (*Acer rubrum* (Lamark)), sweet gum (*Liquidambar styraciflua* (Linnaeus)) and water oak (*Quercus nigra* (Linnaeus)). Streams with an open canopy (due to urbanization and stream channel modifications) have macrophytes, particularly the invasive *Hydrilla verticillata* (L.F.) Royle. *H. verticillata* was introduced from Asia to North America in the 1960's and its role as a potential food source is not well known (Higgins and Hann 1995, Langeland 1996). The goal of this study was to assess how differences in putative detrital food sources affect *H. pomilia* growth. Due to their ubiquitous distribution, understanding how snails respond to changes in the availability of different food sources may yield important insights into the ecosystem function of organic matter processing.

5.2 Methods

In June 2004, *H. pomilia* were collected from small tributaries of the St. Johns River in the vicinity of Jacksonville, Florida and transported to the Experimental Mesocosm Facility at the University of Alabama. Snails were kept in temperature controlled recirculation tanks (800 L, 5 m length, 0.4 m width, 18°C) and provided food sources including live *H. verticillata* and detritus composed of air-dried red maple, sweet gum, and water oak leaves and *H. verticillata*. In October 2004, feeding/growth experiments were initiated. Forty plastic Petri dishes were prepared with 1 of 4 treatments (*H. verticillata*, red maple, sweet gum, or water oak detritus). In order to homogenize the detritus, air-dried material of each source was conditioned in the mesocosm stream for 2 weeks, re-dried and then ground with a Wiley mill (#40 sieve). In each dish, 25 ml of distilled water and 75 mg of fine particulate organic matter (FPOM) were added. Snails were randomly selected from the mesocosm (total shell length ~3-6 mm), photographed (RT SE digital camera, Diagnostic Instruments, Inc., 6540 Burroughs Street, Sterling Heights, MI 48314), and then randomly assigned to a food source treatment. The treatments were then placed in a randomly blocked arrangement in an 18°C incubator. The experiment was conducted in an incubator to eliminate light and the potential for periphyton growth. Digital pictures of each snail were then retaken 18 days later. Shell lengths were measured directly from each picture using image analysis software (SPOT, Diagnostic Instruments, Inc., 6540 Burroughs Street, Sterling Heights, MI 48314). We developed a predictive model to estimate snail ash free dry mass from shell length (Table 1). Snail instantaneous growth rates (g) were calculated as $g = \ln(W_{\text{final}}/W_{\text{initial}})/\Delta t$, where W is snail mass (mg) and t is time (d). After 18 days, snails were removed from the dishes and all remaining material was dried and weighed. The remaining material was a mix of dissolved organic carbon, unconsumed FPOM and snail feces, but this measurement was used as a proxy for food consumption. One-way ANOVA was used to assess differences among treatment for both snail growth rates and food consumption.

5.3 Results and Discussion

Survival rates for snails among treatments ranged from 70-100%. Snail instantaneous growth varied significantly among treatments (Table 2a) with the *H. verticillata* treatment having much higher growth rates than the other 3 treatments (Fig. 1). Food consumption also varied significantly among the treatments (Table 2b) with the least amount of organic matter being found in the *H. verticillata* treatment (Fig. 2).

Table 1. Length-mass relationship for *Haitia pomilia*. A power function was used to estimate ash free dry mass from length (mass=a length^b), where a and b are constants. N=number of snails, % ash (shell) is the ash content for entire animals, SE=standard error, range=size of snails in mm..

a	SE	b	SE	r ²	n	range	% ash (shell)	SE
0.053	0.020	2.556	0.188	0.94	19	2.1-8.8	69.4	2.2

Table 2. Results from one way ANOVA: A) snail growth, B) food consumption. The food sources included detritus from: *H. verticillata*, red maple, water oak, and sweet gum

	Source	SS	df	MSE	F	P
A.	Food Source	0.002	3	0.001	5.863	0.003
B.	Food Source	0.001	3	0.0004	8.31	<0.001

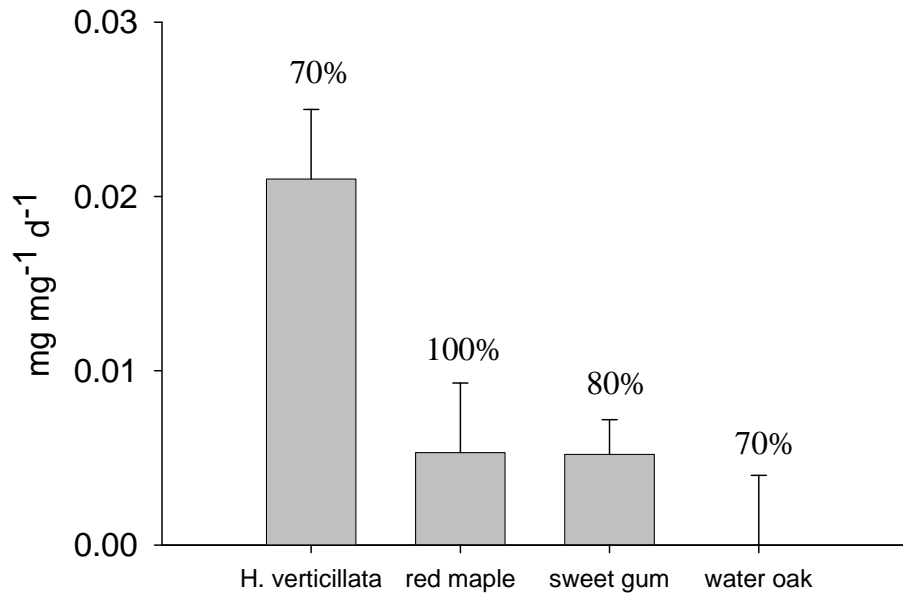


Figure 1. Experimentally derived snail growth rates. Snails in the *H. verticillata* treatment grew significantly faster than snails in the other treatments. Survival rates appear above each bar. Error bars are 1 SE.

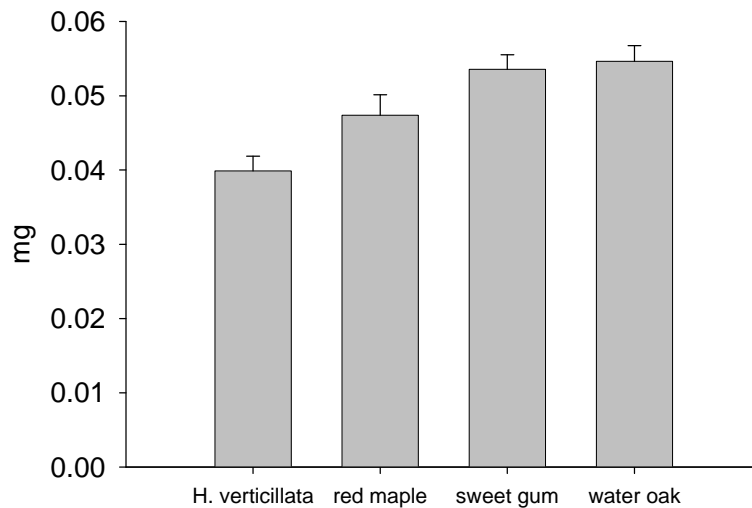


Figure 2. Estimated food consumption by snails (as dry mass of material remaining in the microenvironments). Error bars are 1 SE.

There are multiple plausible explanations for increased growth and consumption for snails placed in the *H. verticillata* treatments. Potentially, the consumption and successful assimilation of detrital remnants of *H. verticillata* is due to the plant's soft leaves (Battle and Mihuc 2000). The other treatments (i.e., deciduous leaves) were likely tougher and as such less palatable. This, however, may not be relevant because the food was ground. Finally, it is also possible that the snails were not assimilating *H. verticillata* itself, but rather the microbial community associated with the leaf surfaces. The large surface area of *H. verticillata* (Battle and Mihuc. 2000), relative to the other treatments, would be conducive to generating higher microbial biomass per gram leaf material while the material was conditioning. Leaves and leaf remnants with higher microbial activity are preferred by detritivores largely due to the fact that the microbes can provide more nutrition than the leaves themselves. All of these factors may account for the *H. verticillata* detritus consumption and growth rates shown for by *H. pomili*, a snail known to thrive on periphyton.

Growth rates on the other FPOM detrital sources were all much lower than the *H. verticillata* treatment (Table 2a, Fig. 1). Inferred food consumption was similar between the red maple, sweet gum, and water oak treatments, but less than consumption found in the *H. verticillata* treatment (Table 2b, Fig 2). This shows that the greater growth rates noted for snails feeding on *H. verticillata* were not due to food shortages in the other treatments. Rather, the treatments based on deciduous leaves appear to be either not palatable or nutritionally poor food sources for these snails. Regardless, this study has shown that *H. pomili* can survive and grow on *H. verticillata* FPOM. Further, because of the spread of the invasive *H. verticillata*, this work shows that snails could likely be an

important consumer in ecosystems where *H. verticillata* is playing an increasingly influential role.

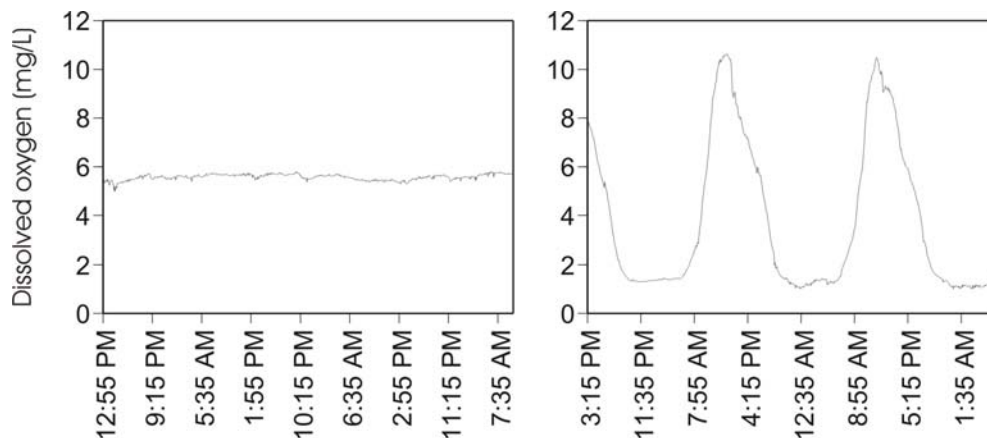
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6. Preliminary study of the metabolism of headwater tributaries of the lower St. Johns River

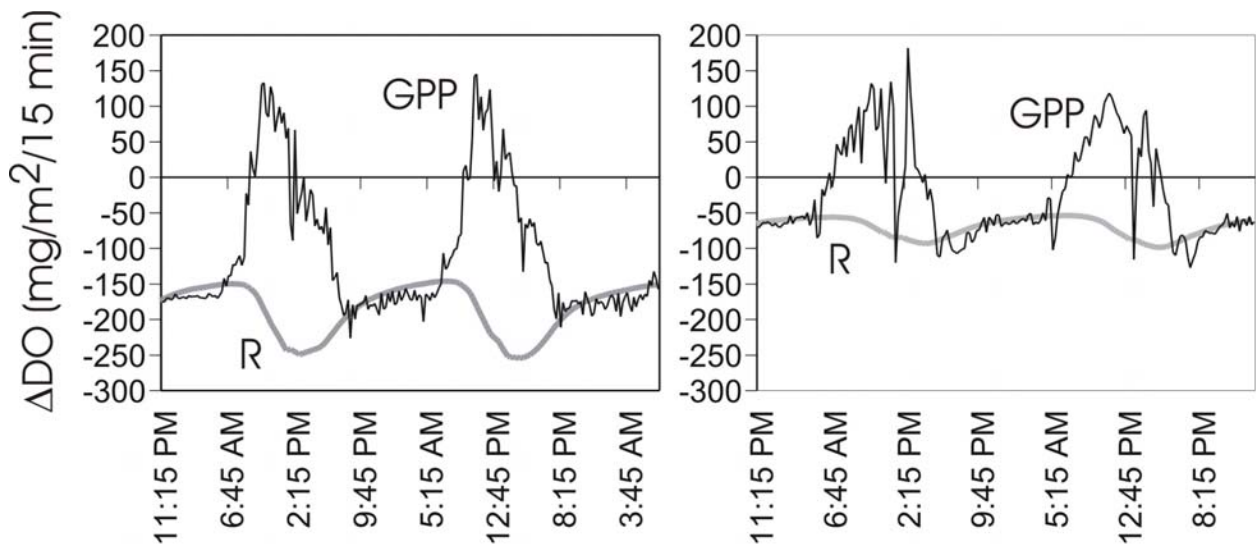
6.1 Preliminary results

Diel oxygen concentrations were measured at 5 minute intervals over a 48 hour period (23-26 May) in four headwater tributaries of the LSJRB. Two tributaries had forested riparian zones with canopies that fully shaded the stream channel; two had open canopies and their channels contained lush populations of macrophytes, the invasive plant *Hydrilla verticillata* in particular. The patterns of changing oxygen concentrations were dramatic, with concentrations being relatively constant in the shaded streams (e.g., 65-66% saturation; below, left panel) and showing wide diel fluctuations in the *H. verticillata* streams (e.g., range of 15% saturation during night to 122% during day; below, right panel).



The diel oxygen curves for the *H. verticillata* streams were analyzed using the night-time respiration method (Owens 1974; Young & Huryn 1996) to estimate gross primary production (GPP, $\text{mg O}_2 \text{ m}^{-2} \text{ 15 min}^{-1}$) and community respiration (R, $\text{mg O}_2 \text{ m}^{-2} \text{ 15 min}^{-1}$). A similar approach could not be used for the analysis of oxygen concentration data for the shaded streams due to low apparent levels of primary production, as indicated by the lack of diel fluctuation in dissolved oxygen concentrations (above left).

GPP for site 13 (below left) was $5.8 \text{ g AFDM m}^{-2} \text{ d}^{-1}$ and R was $11.7 \text{ g AFDM m}^{-2} \text{ d}^{-1}$. GPP for site 5 (below right) was $3.3 \text{ g AFDM m}^{-2} \text{ d}^{-1}$ and R was $4.6 \text{ g AFDM m}^{-2} \text{ d}^{-1}$. Although these streams were autotrophic for short periods during the afternoon, when photosynthetic rates were maximized, the streams were nevertheless highly heterotrophic when considered over the entire daily cycle. For example, respiration in site 13 over a 24 hour cycle required $11.7 \text{ g AFDM m}^{-2}$ while the total amount of organic matter produced by photosynthesis was only 49% of this demand. Presumably the greater levels of metabolism for site 13 are related to greater stores of organic matter that form the sediments of this channel. The lack of balance between GPP and R both streams indicates that their communities require sources of organic matter from outside their channels (e.g., particulate or dissolved organic matter) to support their metabolic activity.



The removal of forest vegetation from the riparian zone of headwater tributaries of the LSJRB facilitates the establishment of aquatic macrophytes, particularly the invasive species *H. verticillata*. This has large effects on the habitat structure and ecosystem processes of these streams. Although the effects of *H. verticillata* on ecosystem processes will be manifold, there are two that are of particular concern. First, relatively constant concentrations of dissolved oxygen are changed to widely fluctuating concentrations, which become catastrophically low during early morning (e.g., 15% saturation) to extreme supersaturation during afternoon. The effects of such dramatic fluctuations of DO on a fauna that is adapted to the relatively constant day-to-day conditions of the originally forested streams have probably been severe. Second, the source of organic carbon to the streams is shifted from a predominantly terrestrial origin (riparian leaf litter and dissolved organic carbon) to net production by *H. verticillata*,

which of course primarily aquatic in origin. The shift of particulate carbon sources from terrestrially derived organic matter to living *H. verticillata* tissues and detritus is expected to have large effects of consumer production due to differences in food quality. The tissues of living freshwater macrophytes are usually used by only a small subset of stream consumers, but these may have large effects on macrophyte populations (Newman 1991). Little is known about the fate of detritus produced from macrophyte litter. Given the potentially large quantities produced in *H. verticillata* streams, this carbon source may form an important subsidy to consumer production.

6.2 Literature cited

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7. Preliminary study of the use of natural-abundance stable C and N isotopes

7.1 Preliminary results

The relative abundance of different nitrogen isotopes in organic matter can be used as an indicator of the strength and distance of upstream-downstream linkages of anthropogenic sources of nutrients with stream food webs (Huryn et al. 2002). Major anthropogenic sources affecting basal-nitrogen stable-isotope ratios in aquatic ecosystems include sewage and fertilizers (McClelland et al. 1997). These sources may have large effects on the $^{15}\text{N}:^{14}\text{N}$ ratio of the labile forms of nitrogen which are transported to the food webs of adjacent streams with groundwater and eventually incorporated into consumer biomass. Changes in $^{15}\text{N}:^{14}\text{N}$ ratios have been used to show linkages between anthropogenic sources and consumer communities elsewhere (McClelland et al. 1997; Hicks 1997; Huryn et al. 2002).

To assess the feasibility of the natural abundance stable C and N isotope approach we sampled 4 streams (11, 26, 17, and 8) with differing levels of percent total impervious area (PTIA) in early March 2005. One stream (11) lacked a riparian canopy and *Hydrilla verticillata* was abundant in the stream channel. At each site we collected three replicate samples of putative food sources (riparian leaf litter, seston, stream conditioned detritus and *H. verticillata*) and numerically dominant invertebrates (Amphipoda, Ancylidae, *Caenis*, Cambaridae, Chironomidae, *Corbicula*, Hydropsychidae, Physidae, Planorbidae, Unionidae, Zygoptera). After collection all material was placed in scintillation vials with stream water for 24 h (to allow animals to evacuate feces),

removed from the vials, and then dried to constant mass. Samples were then analyzed at the Colorado Plateau Stable Isotope Laboratory. All $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values appear in Table 1 and Figure 1.

Table 1. Average $\delta^{13}\text{C}\%$ and $\delta^{15}\text{N}\%$ values for putative food sources and consumers from 5 March 2005. Stream 11 (PTIA =35) has an open canopy and was dominated by *H. verticillata*. Streams 26, 17, and 8 are forested and have PTIA of 0, 29, and 46, respectively. sd=standard error.

Stream	fraction	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ -sd	$\delta^{15}\text{N}$	$\delta^{15}\text{N}$ -sd
11	Amphipoda	-30.6	0.58	2.2	0.56
26	Amphipoda	-30.9	2.17	1.7	0.47
8	Amphipoda	-28.8	0.81	6.4	0.38
17	Ancylidae	-28.8	0.44	6.5	0.34
8	Ancylidae	-30.0	0.23	8.6	0.18
11	<i>Caenis</i>	-31.9	0.40	2.8	0.22
17	<i>Caenis</i>	-31.6	1.02	6.9	0.33
11	Cambaridae	-29.2	0.90	6.1	1.09
17	Cambaridae	-29.2	0.85	8.1	0.18
26	Cambaridae	-31.2	1.18	4.9	0.50
8	Chironimidae	-30.6	0.29	7.9	0.98
17	Chironomidae	-30.2	1.48	7.9	0.40
26	Chironomidae	-34.2	0.87	4.1	0.28
11	<i>Corbicula</i>	-31.4	0.27	6.5	0.12
17	<i>Corbicula</i>	-26.8	0.11	5.7	0.12
8	<i>Corbicula</i>	-26.8	0.05	5.7	0.01
8	Hydropsychidae	-35.2	0.80	6.8	0.79
17	Physidae	-31.1	3.45	6.4	1.02
8	Physidae	-31.7	0.35	8.4	2.01
11	Planorbidae	-31.9	1.00	2.9	0.28
11	Unionidae	-31.5	0.30	5.7	1.54
11	Zygoptera	-30.8	0.56	5.3	0.11
17	Zygoptera	-28.7	0.20	8.3	0.48
8	Zygoptera	-33.4	0.92	8.6	0.49
11	<i>Hydrilla</i>	-32.6	1.06	4.7	0.79
11	detritus	-28.3	0.61	0.9	0.55
17	detritus	-30.1	0.50	0.4	0.24
26	detritus	-28.6	1.19	-0.7	0.12
8	detritus	-29.9	0.57	1.5	1.27
17	oak leaves	-29.9	0.78	-0.1	0.32
26	oak leaves	-30.0	0.15	-0.8	0.25
8	oak leaves	-29.8	0.27	-0.7	0.46
17	maple leaves	-32.7	0.44	0.1	0.51

8	maple leaves	-30.4	0.29	-0.4	0.29
11	seston	-32.0	0.87	5.8	0.35
17	seston	-25.5	0.41	4.7	0.34
26	seston	-28.6	0.66	2.9	0.30
8	seston	-22.5	0.17	4.4	0.24
17	sweetgum leaves	-29.0	0.55	-0.2	0.72
8	sweetgum leaves	-29.9	0.62	-1.1	0.63

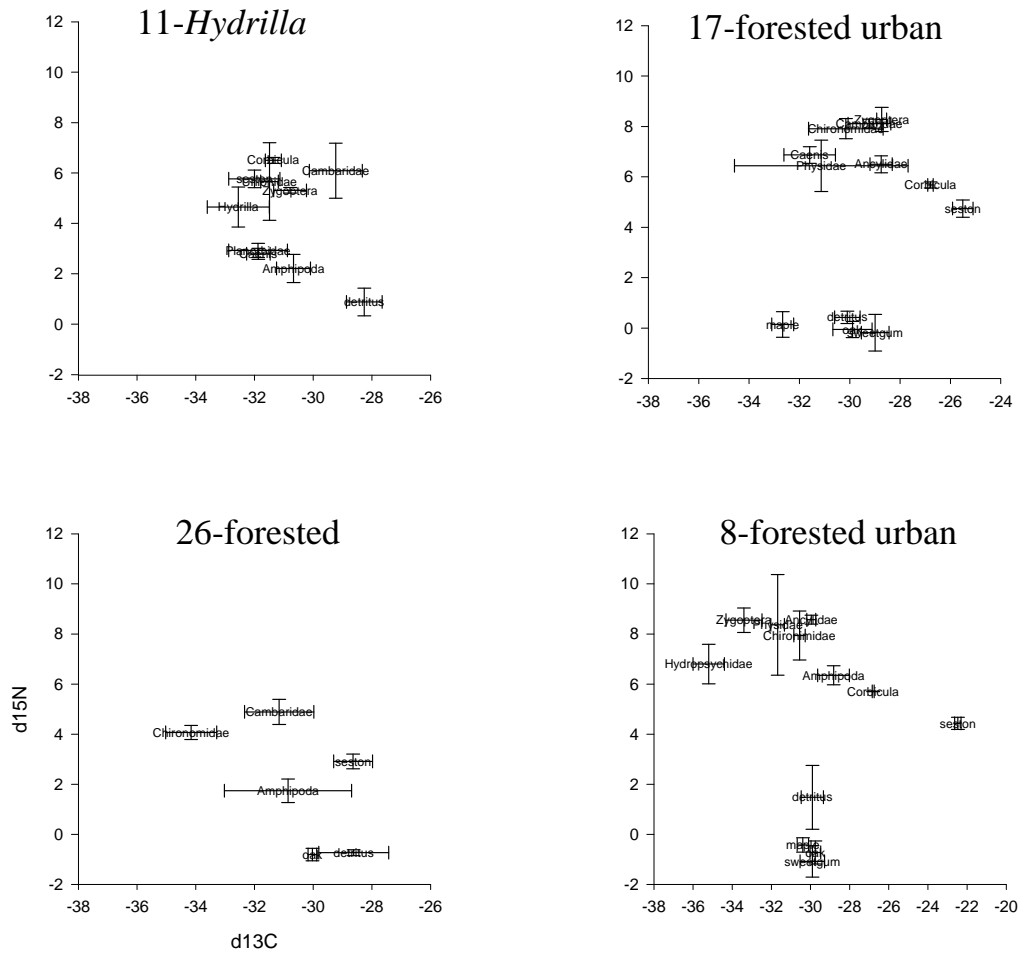


Figure 1. Average $\delta^{13}\text{C}$ ‰ and $\delta^{15}\text{N}$ ‰ values for putative food sources and consumers from 5 March 2005.

Mean $\delta^{13}\text{C}$ values among putative food sources were similar between streams for riparian leaf litter and stream conditioned detritus (-29.0 to -32.7‰ for riparian leaf litter, -28.3 to -30.1‰ for detritus). Seston $\delta^{13}\text{C}$ values varied more than other food sources and ranged from -22.5 to -32.0‰ with the most ^{13}C enrichment occurring at the *H. verticillata* site. *H. verticillata* mean $\delta^{13}\text{C}$ was -32.6‰.

Mean $\delta^{15}\text{N}$ values for putative food sources ranged from 5.7 to 3.0‰ for seston and *H. verticillata*. Riparian leaf litter and stream conditioned detritus had $\delta^{15}\text{N}$ values ranging from 1.5 to -1.5‰. For putative food sources in the forested sites (26, 17, and 8), it appears that $\delta^{13}\text{C}$ values decrease and $\delta^{15}\text{N}$ values increase with increasing PTIA.

Mean $\delta^{13}\text{C}$ values for consumers ranged from -26.4 to -33.4‰, while $\delta^{15}\text{N}$ values ranged from 8.6 to 1.7‰. Pattern in consumer signatures among all sites were less pronounced for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values which suggest that all food resources were not sampled. For $\delta^{15}\text{N}$ among streams, however, values tended to increase with PTIA.

These preliminary results suggest that ecosystem responses to urbanization is subtly reflected in natural abundance C and N isotopes. However, a few patterns can be seen and warrant further investigation. First, it appears that trophic resource other than the ones sampled must be available and play an important role in both forest and open canopy stream foodwebs. Second, seston does not appear to be an overly utilized food resource in the forest streams, but could be important in the *H. verticillata* stream. Third, it appear that management of the stream channel (e.g., riparian clearing) may be more important than catchment-scale changes in land use in determining food web structure. Given all of these factors, the use of isotopic tracers in these stream systems may provide further resolution for the foodweb structure and ecosystem responses to changes in land use.

7.2 Literature Cited

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8. Future Work

The work conducted in the first two years has allowed for a greater understanding of detrital dynamics of headwater tributaries of the St. Johns River. However, several areas still need to be addressed. First, the role that *Hydrilla verticillata* plays in regulating detrital inputs, trophic structure, and downstream effects along an urban-rural gradient is poorly understood. Second, only preliminary information on the importance of allochthonous vs. autochthonous carbon inputs to these streams has been generated. Finally, most downstream effects and stream-river interactions have not been addressed. The research for the third and fourth year of funding will seek to further understand the importance of catchment-scale land use changes on the structure and function of these stream ecosystems.

8.1 New research associated with original tasks

The research that will be conducted during the third and fourth year of this project will provide further information required for an understanding of the changes that have occurred to stream ecosystems in the lower St. Johns River basin due to land-use modifications. The specific information developed by this research will again be based on the original basic tasks.

Task 1: “Quantify detrital inputs along an urban-rural gradient”

- Quantify the extent to which *Hydrilla verticillata* and other associated macrophytes are found in headwater tributaries
- Measure standing stock biomass of *Hydrilla verticillata* and other associated macrophytes
- Measure rates of litter breakdown for red maple in freshwater-tidal reaches of 10 streams representing an urban-rural land-use gradient

Task 2: “Trophic changes along an urban-rural gradient”

- Measure whole stream metabolism in 6 stream reaches (3 with *Hydrilla* and 3 without) along a gradient of impervious surface cover
- Assess the relative importance of autochthonous vs. allochthonous organic matter for stream food webs using stable isotope analysis

Task 3: “Downstream effects”

- Quantify upstream/downstream linkages between headwater tributaries and the St. Johns River with bidirectional sampling of drift in freshwater-tidal reaches of 4 streams representing an urban-rural land-use gradient
- Quantify the community attributes for invertebrates associated with freshwater-tidal reaches of 4 streams representing an urban-rural land-use gradient
- Measure nutrient uptake, retention, and cycling through the ecosystem under ambient nutrient concentrations to determine upstream/downstream linkages between headwater tributaries and the St. Johns River and to assess whether tributaries act as nutrient sources or sinks