RESPONSE OF AQUATIC BIOTA TO CHANGING LAND USE PATTERN IN STREAMS OF WEST GEORGIA, USA

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RESPONSE OF AQUATIC BIOTA TO CHANGING LAND USE PATTERN IN STREAMS OF WEST GEORGIA, USA

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RESPONSE OF AQUATIC BIOTA TO CHANGING LAND USE PATTERN IN STREAMS OF WEST GEORGIA, USA

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Brian Scott Helms, son of R. Gary Helms and Frances P. Helms, brother of Shannon N. Helms, husband of Kristen T. Helms and father of Isaac L. Helms, was born on February 27, 1973, in Gaston County, NC. He graduated from Ashbrook High School, Gastonia, NC in 1991. He then moved to Raleigh, NC, where he earned a Bachelor of Science in Biology and a Bachelor of Science in Zoology from NC State University in 1995. In 2000, he received a Master of Science in Biology from Appalachian State University, Boone, NC, under the guidance of Dr. Robert P. Creed. Following 2 years with the North Carolina Botanical Garden, he entered the Department of Biological Sciences under the guidance of Dr. Jack Feminella in 2002 and earned a Doctor of Philosophy in Biological Sciences in 2008.

DISSERTATION ABSTRACT

RESPONSE OF AQUATIC BIOTA TO CHANGING LAND USE PATTERN IN STREAMS OF WEST GEORGIA, USA

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Watershed land use change is one of the most pervasive influences facing streams in the southeastern United States. In particular, watershed urbanization has a potentially dramatic impact on stream biota. Through direct alteration of several interrelated instream processes including hydrology, geomorphology, and physicochemistry, land use change can indirectly influence stream biotic composition and quality. Starting in 2002, I examined aquatic biotic responses to changing watershed land use/cover (LU/LC) and subsequent abiotic alterations in the Lower Piedmont ecoregion north of Columbus, Georgia, USA, in 25 small streams (2 – 3rd order) whose watersheds (500 – 2500 ha) varied in their degree of urbanization, residential development, pasture, managed and unmanaged forest cover.

Benthic macroinvertebrates, as taxa richness and Shannon's diversity (H'), were negatively associated with increasing urban cover, peak stream discharge, and water temperature, and positively associated with increasing forest cover and dissolved oxygen (DO) levels. Further, macroinvertebrate biomass increased while seasonal variation decreased with increasing urban cover. Fish assemblages were largely explained by a combination of land use and landscape (stream hydrology, geomorphology) variables that vary seasonally, with stronger land use signals in the summer and a stronger fish response to landscape variables in the winter and spring. Fish assemblages shifted from cyprinid-based in forested (managed and unmanaged) and pasture watersheds to centrarchid-based in urban and suburban watersheds; this shift was correlated with increasing spate frequency, stream temperature and decreasing DO. Stable isotopes analyses revealed food webs in watersheds with increased LU/LC disturbance were significantly different than food webs in forested watersheds. Further, overall food chain length and mean trophic position decreased with increasing impervious surface. Specifically, food chain length increased with stream habitat quality whereas chain length and mean trophic position decreased with increasing maximum stream discharge and duration of high flows.

My results suggest that changing land use exerts multiple direct and indirect stressors on stream biota that vary depending on the biology of the organism or assemblage under consideration. Specifically, streams in urbanized watersheds are harsh environments that have less diverse assemblages dominated by few tolerant taxa, minimal seasonal variation, and simplified food webs.

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CHAPTER 1. Introduction to land use effects on stream biota.

1.1 INTRODUCTION

Biotic composition and quality of aquatic systems are strongly affected by watershed land use (Karr et al. 1985, Lenat and Crawford 1994, Weaver and Garman 1994, Wang et al. 2001). In the southeastern United States, silviculture and agriculture are common types of traditional land use, and disturbance from each type may exert its own unique pressures on receiving streams (Brown et al. 2005). However, one of the more pervasive and rapidly growing forms of land use change is the conversion of natural vegetation or agriculture to urban environments (urbanization). Urban land use has more than tripled in the United States since 1950 (8,065 mi^2 to 27,838 mi^2 in 1990,(Wang and Lyons 2003a). However, population density in these urbanized areas has actually decreased (6,121 to 3,411 people / mi^2, US Census Bureau 2001) because of the phenomenon of increasing lower-density, primarily residential, populations (urban sprawl). As a result of increased urban land use and associated urban sprawl, it is estimated that >60% of the world's population will live in urbanized areas by 2030 (US Census Bureau 2001).

The inevitable change in land use/land cover (LU/LC) associated with human population expansion has demonstrated, far-reaching effects on stream biotic integrity. In general, increased LU/LC influence aquatic organisms through interrelated impacts on water quality, hydrology, and habitat (Hirsch et al. 1990, Herlihy et al. 1998, Paul and Meyer 2001, Allan 2004, Walsh et al. 2005b). Effects of increased LU/LC disturbance on biota often are manifested as increased flood magnitude and frequency (Booth and Jackson 1997), altered streambed morphology and stability (Booth and Jackson 1997, Wang and Lyons 2003b) altered sediment and chemical inputs (Wernick et al. 1998, Allan 2004), and degraded riparian zones (Finkenbine et al. 2000, Groffman et al. 2003). Many studies have described the negative effects of LU/LC on stream benthic macroinvertebrates (Klein 1975, Kennen 1999) and, to a lesser degree, periphyton (Chessman et al. 1999, Sonneman et al. 2001) and fish (Weaver and Garman 1994, Wang et al. 2000). However, key aspects remain unclear about specific tolerance thresholds of stream communities to urbanization. The complex nature of streams has caused the specific mechanisms of LU/LC change, particularly urbanization, on biota and community interactions to be poorly understood (Paul and Meyer 2001). Further, most humans dwell in urbanized areas, so it is essential, both from ecological and socioeconomic viewpoints, to understand the associated impacts of changing land use on water quality and ecosystem services of surrounding streams (Groffman et al. 2003).

LU/LC exerts dramatic physical and chemical effects on stream ecosystems, but wholesale impairment may not be evident for years or decades following development (Fitzgerald et al. 1998, Harding et al. 1998). Effects often are episodic, becoming more pronounced seasonally or with increased precipitation, which thus requires continuous and expensive monitoring (Wang and Lyons 2003a). A relatively cost-effective means of evaluating stream integrity is to document responses biota, particularly macroinvertebrates and fish (Karr and Dudley 1981), which integrate dynamic physicochemical conditions and thus indicate stream condition (Karr et al. 1987, Barbour et al. 1999). Beyond its use in biomonitoring, understanding the response of biota to development in impaired streams is critical information necessary for the sustainable use of ecosystem services.

Benthic macroinvertebrates are particularly good indicators of localized stream conditions because they have limited migration patterns, have complex yet short life histories, and exhibit a broad range of environmental tolerance (Barbour et al. 1999). They are also a diverse group, filling the roles of stream predator, prey, herbivore, and detritivore (Allan 1995). Examination of fish in biological monitoring efforts also is useful, particularly in determining long-term effects (Karr et al. 1986) because fish are relatively long-lived. As a result of their varied life histories and tolerances, fish assemblages can reflect a broad range of environmental conditions. Further, assemblages often incorporate multiple trophic levels and, thus, integrate lower trophic level effects (Barbour et al. 1999).

As a result of the relatively extreme stream conditions associated with LU/LC change, particularly urbanization, the Harsh-Benign hypothesis (Peckarsky 1983, Menge and Sutherland 1987) of community regulation may apply to community interactions within these systems. This hypothesis posits that in relatively harsh environments, abiotic regulation of community structure exerts primary control, whereas in relatively benign systems, biotic control of community structure is most important (Menge and Sutherland 1987). Specifically, predation regulates prey populations when environmental conditions are benign enough to support a large predator assemblage. However, as environmental harshness increases, the effectiveness of predators decreases and competition between prey taxa increases. As harshness increases to high levels and causes physical or physiological stress to taxa, biological interactions decrease in importance, and abiotic factors (e.g., flow, temperature, pollution) regulate community structure (Peckarsky 1983).

One of the more dramatic effects of urbanization on streams is hydrologic alteration, which results in increasingly harsh physical conditions, including increased spate flows, sedimentation, and streambed scour (Paul and Meyer 2001, Wang and Lyons 2003b). Species respond differently to increasing environmental harshness in streams (Poff and Ward 1989, Poff and Allan 1995). As a result of their broad distribution among streams of various water quality, tolerant organisms may have different trophic positions and/or community impacts depending upon the particular stream they inhabit, which could lead to altered food webs in disturbed streams. Thus, strongly contrasting environmental harshness associated with different LU/LC could be an important driver of variations in and interactions among biota inhabiting such contrasting streams.

Many facets of LU/LC effects are known, but there are many aspects that remain elusive. The primary focus of my research was to investigate the role of land use change on stream biota in 1st- to 3rd-order streams across an urban–rural gradient. The primary objectives of this study were:

1. To determine the relative influence of watershed LU/LC vs. natural watershed attributes (size, discharge, etc.) on fish assemblage structure (Chapter 2);

2. To quantify the relative explanatory power of stream hydrology, physicochemistry, and habitat variables associated with LU/LC change on variation in fish assemblages (Chapter 3);
3. To investigate the relative seasonal influence of various LU/LC conditions on stream macroinvertebrate assemblages (Chapter 4);
4. To evaluate impacts of urbanization on a common species (redbreast sunfish ([*Lepomis auritus*]) by examining its feeding, growth, and trophic position (Chapter 5); and
5. To examine the role of watershed LU/LC and instream conditions on food chain length and structure of stream food webs

The overall goal of this research was to provide scientists and resource managers with basic and applied information regarding influence of changing LU/LC on aquatic biota which can enhance management of small watersheds in the face of anthropogenic change.

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CHAPTER 2. Detection of biotic responses to urbanization using fish assemblages from small streams of western Georgia, USA.

2.1 ABSTRACT

I examined relationships between stream fish assemblages and land use alteration associated with urbanization in 15 lower Piedmont watersheds, along an urbanization gradient north of Columbus, western Georgia. Based on land cover data from 2002 Landsat 7 TM imagery aerial photos, streams drained watersheds that were largely urban, developing (suburban), agricultural (pasture), managed pine forest, and unmanaged mixed-forest. I quantified fish seasonally from 3 run-pool segments in each stream, and used a variety of metrics as response variables in analyses of relationships between fish assemblage structure and land use and natural basin variation. In general, Georgia-Index of Biotic Integrity (GA-IBI) values, Bray-Curtis faunal similarity of streams to mean conditions within reference streams, and proportions of fish as lithophilic spawners decreased while fish with eroded fins, lesions, tumors decreased with increasing urbanization. Multiple regression indicated that assemblages were explained by a combination of land use and natural basin variables (basin size, average discharge, nearest distance to a larger downstream tributary [colonization source]), with land use variables being important predictors of summer assemblages and natural basin variables being more important in winter and spring assemblages. Non-metric multidimensional

scaling (NMDS) ordinations revealed strong separation between assemblages in urban watersheds and forested watersheds, whereas assemblages in agricultural and developing watersheds were intermediate between those in urban and forested watersheds. Our data suggest that fish are reliable indicators of anthropogenic disturbance at the landscape scale, at least seasonally, and may be used to forecast the magnitude of landscape-level changes in stream structure and function associated with the conversion of forests to urban/suburban land in the Southeast.

2.2 Introduction

Environmental quality and biotic composition of aquatic systems often are strongly affected by land use (Lenat and Crawford, 1994; Weaver and Garman, 1994; Wang et al., 2001). One of the more pervasive and rapidly growing forms of land use change is the conversion of natural forested or vegetated agricultural land to urban environments (urban sprawl, US Census Bureau, 2001; Wang and Lyons, 2003). Inevitable landscape alteration associated with human population expansion has revealed dramatic effects on water quality and aquatic biota (Benke et al., 1981; Hirsch, 1990; Limburg and Schmidt, 1990; Weaver and Garman, 1994). Fish are particularly useful in assessing long-term environmental impacts of urbanization because they integrate multiple trophic levels in aquatic communities, are relatively long-lived, and are easily sampled (Karr, 1987; Barbour et al., 1999). In this context, increasing environmental stress associated with watershed urbanization often may decrease overall fish richness, abundance, and diversity, and cause shifts in assemblages from intolerant to tolerant and/or introduced species (Klein, 1979; Marsh and Minckley, 1982; Onorato et al., 1998; Walters et al., 2003a).

Aquatic system response to urbanization often is linked to increased impervious surfaces within developing watersheds, which can alter stream water quality, quantity, and habitat availability (Hirsch, 1990; Herlihy et al., 1998; Paul and Meyer, 2001; Walsh et al., 2001). Such physicochemical alterations may manifest as increased flood magnitude and frequency (flashiness) and increased delivery of nutrients, metals, pesticides, and organic contaminants to receiving streams, all of which may degrade fish assemblages (Weaver and Garman, 1994; Lenat and Crawford, 1994; Wang et al., 2000; Paul and Meyer, 2001; Wang et al., 2003). A particularly pervasive impact of forest land conversion on fish is through increased sedimentation (Tebo, 1955; Berkman and Rabeni, 1987; Sutherland et al., 2002; Iwata et al., 2003). Sedimentation in streams resulting from agriculture and logging are well known (Tebo, 1953; Cordone and Kelly, 1961; Waters, 1995; Rier and King, 1996), and emerging research suggests sedimentation in urbanized watersheds can reduce habitat quality and cause shifts in fish feeding and reproductive guilds toward generalist species (Berkman and Rabeni, 1987; Schleiger, 2000; Walters et al., 2003a).

In high-gradient upland streams of northern Georgia, USA, a region with naturally high fish diversity and endemism, urbanization has been implicated in increased abundance of cosmopolitan species, or stream 'homogenization' (sensu Walters et al., 2003a). Fish assemblages in sandy, low-gradient streams within this same region are naturally less diverse and show comparatively lower endemism (Swift et al., 1986). Urbanization of lowland streams may, therefore, exhibit disparate influences on fishes than in upland systems. I quantified fish assemblage structure in these lowland streams along an urbanization gradient, to assess the degree to which assemblages reflected variation in land use from urbanization. Specifically, I examined 1) the relative influence of watershed land use versus natural basin attributes (primarily physical habitat measures) on fish assemblage structure, and 2) if assemblage shifts varied predictably with increasing land use change attributable to urbanization in study watersheds.

2.3 METHODS

2.3.1 Study Area

I studied tributaries of the middle Chattahoochee River, western Georgia, USA, occurring in the Southern Outer Piedmont ecoregion. The Piedmont biogeoclimatic province historically was developed for agriculture, although it now harbors many of the burgeoning metropolitan areas of the Southeastern US (Richmond, Raleigh/Durham, Greenville/Spartanburg, Atlanta), as well as extensive managed pine plantations. The west Georgia landscape and the area surrounding the city of Columbus is a notable example of this trend (Lockaby et al., 2005). Present-day development from Columbus is constrained by the Chattahoochee River to the west and a large military installation (Fort Benning) to the southeast, so most land conversion and urban expansion occurs mainly to the northeast.

I sampled fifteen 2nd - to 3rd-order streams in 15 watersheds (4–25 km^2) along an urbanization gradient stretching from the geologic fall line in the city of Columbus to an area 80 km northeast (Fig. 1). Study streams were typical of those in the lower Piedmont, consisting of sandy-bottom channels and a run-pool morphology with infrequent riffles (Mulholland and Lenat, 1992). Average pool depth was ~0.25m and channel width ~10 m. Watersheds ranged in land use/cover from intense urbanization (up to 50% urban cover) and active suburban development to heavily forested (up to 95% forest cover).

This relatively large range in landscape character allowed us to compare across geomorphically similar streams that differed primarily in watershed-level land use and associated variation in streamwater physicochemical conditions (Schoonover et al., 2008).

2.3.2 Landscape Classification

Initially, land use/cover was quantified in the study watersheds using 2002 Landsat 7 TM imagery (30-m resolution) and ArcView© software (Version 3.2a, Environmental Systems Research Institute, Inc., Redlands, California). I derived 4 primary land use categories (showing >30% of a given category) from this classification: % of the watershed occurring as urban (=% Urban), % of the watershed as coniferous forest (=% Conifer), % of the watershed as mixed coniferous-deciduous forest (=% Mixed), and % of the watershed as pasture (=% Pasture). I also classified 3 forested watersheds that contained active or recent development into a separate category (Developing). In addition to quantifying % Conifer and % Mixed I also combined these 2 classifications into a single forest category (=% Total Forest) for each watershed.

Following analysis of Landsat data, the amount of impervious surface in study watersheds was determined by manually digitizing 1-m resolution, 3-band aerial photographs (taken March 2003). I determined watershed boundaries, size, average slope, and nearest distance to a larger downstream tributary (used as a conservative measure of potential source habitat for fishes) from USGS 30-m resolution digital elevation models (DEMs) and ArcView.

2.3.3 Field sampling

I quantified fish seasonally (summer/fall, winter, spring) from July 2002 to September 2003 from 3 run and pool habitats per stream along a representative 100-m reach. I sampled fish in most habitats to depletion with block nets and backpack electroshocker (Smith-Root LR-24), and seining. I excluded juvenile fish (<20 mm total length, TL) from analyses because of inefficiency in their capture. I identified fish to species, measured TL, and then examined them for eroded fins, lesions, tumors, and overall health (% DELT, Schleiger 2000). Except for voucher specimens, I returned all fish to the stream near the point of capture. Three streams (SB2, MU3, HC) could not be sampled in Summer 2002 because of stream drying, and 1 stream (MU1) contained no fish in Winter 2002, so I excluded these streams from analyses.

I classified species into breeding and feeding guilds, and assigned them to intolerant, moderately intolerant, tolerant, or pioneer tolerance classes (S. L. Schleiger, Georgia Department of Natural Resources, personal communication, Table 2). I defined pioneers as those species that quickly reinvade a previously disturbed habitat (Smith 1979). I assigned fish to 5 breeding guilds (see Muncy et al., 1979; Berkeman and Rabeni 1987). Fish were first classified into complex or simple breeders, based on the degree to which species prepare spawning sites, defend nests, and show pre-spawning social behavior (Pflieger, 1975; Trautman, 1981). I further divided complex breeders into those species showing parental care (=P/C) and those that do not (= No P/C). I divided simple breeders into spawners requiring clean, gravel substrate (lithophilous spawners, = Lithophils) and those capable of spawning on sand, silt, or vegetation (generalist spawners, = Simple Spawners). I also calculated several community variables

(Table 2) including density, species richness, diversity (Shannon's *H'*), and relative abundance for each stream and season.

I used Bray-Curtis similarity index (Krebs 1999) to determine the pairwise similarity of fish assemblages at each stream based upon mean conditions from 4 reference watersheds (MK, CB, BC, MU3, Table 1). I considered these sites to be close to or at the reference condition, based on 1) a high proportion of their watersheds in forest and correspondingly low silviculture, agriculture, or urbanization, and 2) their generally high apparent stream biotic integrity and physical condition. I used tolerance values and breeding and feeding guilds in an Index of Biotic Integrity (IBI) developed for streams fishes in west-central Georgia (Schleiger, 2000).

I also measured stream discharge monthly over the sampling period using the velocity-area method (Gore, 1996) with a Marsh-McBirney flow meter (Schoonover et al., 2005). I used mean discharge along with basin size, average slope, and downstream distance to the next largest stream as measures of variation in hydrologic and geomorphologic conditions among study watersheds, and as a suite of natural basin variables to contrast with land use variables in statistical analyses.

2.3.4 Data Analyses

First, I used simple Pearson correlations (Zar 1999) to examine general relationships between fish variables and land use/natural basin variables. This procedure allowed us to assess general trends and identify potential multicollinearity among variables. Second, I used stepwise multiple regressions to develop season-specific models of relationships among fish and land use/natural basin variables (30-m resolution classification, Table 3) to assess the relative strength of land use vs. natural basin variables on fish variables. I used variance inflation factors (VIF) to reduce the number of environmental variables in multiple regressions and avoid multicollinearity (variable removed if VIF >10, Myers, 1990). Model selection was based on Mallow's C(p), R^2_{adj}, and parsimony (Myers, 1990). Third, in addition to multiple regressions applied to 30-m spatial data, I used simple linear regressions between % impervious surface in the watershed, quantified from the 1-m resolution spatial data, against fish variables. Impervious surface is considered a useful landscape metric in studies characterizing urbanization impacts on streams (McMahon and Cuffney, 2000; Walsh et al., 2004), so I considered this analysis potentially useful in describing additional variation between fish and land use variables. Finally, I used non-metric multidimensional scaling (NMDS) to describe overall variation in fish assemblages (using species abundance data) among sites and seasons. NMDS is an ordination technique that uses pairwise similarity or dissimilarity matrices to determine positions of sites in terms of species space (Hawkins et al., 1997; McCune and Grace, 2002). Sites nearest to or furthest from each other on the ordination are those displaying highest and lowest faunal similarity, respectively. I transformed proportional relative abundance data using arcsin-square root to satisfy assumptions of normality and homoscedasticity, and I excluded rare species (those in <10% of sites) for each season to reduce the influence of rare taxa on ordinations. This step resulted in a 42 x 20 site by species matrix on which I based ordinations using a Sorenson distance measure. I used SAS (version 8.2, SAS Institute Inc., Cary, North Carolina) for all correlation and regression analyses and PC-ORD (version 4, MjM Software Design, Glenden Beach, Oregon) for NMDS.

2.4 RESULTS

I collected 33 fish species (3772 individuals) from 7 families (Catastomidae, Centrarchidae, Cyprinidae, Ictaluridae, Percidae, Petromyzontidae, Poeciliidae) during the study. Centrarchidae and Cyprinidae were the most common families, composing 24 and 55% of total fish collected, respectively. Bandfin shiners (*Luxilus zonistius*), bluegill (*Lepomis macrochirus*), redbreast sunfish (*L. auritus*) and mosquitofish (*Gambusia affinis*) were the most abundant species. *Lepomis auritus* was the most frequently collected species, occurring in 90% of samples, *L. macrochirus* was the 2nd-most frequent (74% of samples), and the silverjaw minnow (*Notropis buccata*) the 3rd-most frequent fish in collections (62%).

The number of fish collected ranged from 2 to 284 per stream, richness from 2 to 16, *H*' from 0 to 2.24, and IBI score from 24 to 52 (Table 4). Insectivores (~82% of total assemblage) and complex breeders with parental care (P/C, ~34%) were the most abundant feeding and breeding guilds, respectively (Table 4). In general, IBI, Bray-Curtis similarity to mean reference condition, and % of the assemblage as lithophilic spawners were negatively correlated with % Urban, whereas % DELT and % of the assemblage as herbivores (primarily *Campostoma pauciradii*) were positively correlated with % Urban, and in turn negatively correlated with % Total Forest (Table 5). In particular, abundance of *N. buccata*, *L. zonistius*, *Nocomis leptocephalus*, *N. longirostris*, and *Semotilus atromaculatus* decreased with increasing % Urban. Proportion of the assemblage as tolerant species was positively correlated with % Pasture but was uncorrelated with % Urban (Table 5). The % of the assemblage as lithophilic spawners, IBI, and Bray-Curtis similarity to reference condition all were significantly correlated with % Conifer, % Mixed, and/or % Total Forest in study watersheds (Table 5).

As a result of multicollinearity determined by inspection of high VIF scores, I used only 5 independent variables in multiple regressions, including 2 land use variables (% Urban, % Pasture) and 3 natural basin variables (basin size, average discharge, nearest distance to a downstream source). I observed significant relationships between the above independent variables and 10 fish variables, although the strength of relationships varied seasonally (Table 6). Percent DELT and IBI were the only fish variables that were consistently explained by land use (vs natural basin) variables. The % DELT was explained by % Urban in all 3 seasons (summer: $R^2_{adj} = 0.755$, $p = 0.0002$; winter: $R^2_{adj} = 0.591$, $p = 0.0008$; spring: $R^2_{adj} = 0.582$, $p = 0.0006$), whereas IBI were explained by % Urban and % Pasture, but only in summer ($R^2_{adj} = 0.495$, $p = 0.0187$, Table 6).

In contrast, several fish variables were best explained by natural basin variables. *H'* was explained by basin size and average discharge ($R^2_{adj} = 0.342$, $p = 0.0321$), but only in winter. Proportion of the assemblage as cyprinid insectivores was explained by basin size and distance to a larger downstream source in summer ($R^2_{adj} = 0.433$, $p = 0.0314$), and by basin size and discharge in winter ($R^2_{adj} = 0.406$, $p = 0.0027$). Proportion of the assemblage as pioneer species and omnivores both were explained by the distance to a downstream source in some (but not all) seasons (Table 6). However, variation in most fish metrics was explained by a mixture of land use and natural basin variables. For example, richness and % tolerant species were explained by a combination of % Urban, % Pasture, and basin size ($R^2_{adj} = 0.510$ $p = 0.0335$; $R^2_{adj} = 0.660$ $p = 0.0082$, respectively) in summer. In winter, IBI and proportion of the assemblage as herbivores were explained by % Urban and basin size ($R^2_{adj} = 0.529$, $p = 0.0064$; $R^2_{adj} = 0.681$, $p = 0.0007$, respectively). In spring, % Urban, % Pasture, and basin size best explained IBI ($R^2_{adj} = 0.638$, $p = 0.0024$) and % Pasture and average discharge explained proportion of the assemblage as tolerant species ($R^2_{adj} = 0.341$, $p = 0.0324$, Table 6).

Use of finer scale (1-m resolution) % impervious surface data in simple regressions did little to improve relationships between and land use and fish assemblages (Table 6). I found significant relationships for only 3 fish variables: % DELT increased with increasing impervious surface, and IBI decreased with increasing impervious surface (all seasons), whereas % herbivores increased with increasing impervious surface (summer and winter, Table 6).

NMDS revealed 2 axes that together accounted for 65.9% of the total variation in the fish assemblage among sites and seasons (Fig. 2). Axes 1 and 2 accounted for 21.1 and 44.8% of the total variation, respectively (number of dimensions = 3, number of iterations = 162, final stress = 14.21%). Percent impervious surface ($R^2 = 0.34$, $p < 0.0001$) and distance from the study site to a larger downstream source ($R^2 = 0.20$, $p = 0.0033$) were both negatively related to Axis 1 (Table 7), whereas % Conifer ($R^2 = 0.43$, $p < 0.0001$) and % Total Forest ($R^2 = 0.40$, $p < 0.0001$) were positively related to Axis 2 (Table 7, Fig. 2). Streams in urban and developing watersheds tended to group to the left of the ordination, whereas streams draining watersheds with less urbanization, including managed (high % Conifer) and unmanaged (high % Mixed) streams, grouped to the right (Fig. 2). Streams within agricultural watersheds (high % Pasture) showed no clear grouping with respect to Axes 1 and 2 (Fig. 2).

Axis 1 of the NMDS ordination was defined largely by abundance of pioneer species, primarily *G. affinis* and *C. pauciradii*, and 2 *Lepomis* species (Table 8, Fig. 2). In contrast, Axis 2 was defined mostly by abundance of lithophilic spawners, particularly *N. leptocephalus* and *L. zonistius* (Table 8, Fig. 2). IBI and Bray-Curtis similarity values were positively associated with Axis 2 ($R^2 = 0.38$, $p < 0.001$; $R^2 = 0.36$, $p < 0.0001$, respectively, Table 7), whereas % DELT was negatively associated with this axis ($R^2 = 0.22$, $p = 0.0023$).

2.5 DISCUSSION

Our results provide correlative evidence that watershed urbanization and the concomitant reduction in forest cover may exert strong negative impacts on stream fish assemblages. These data corroborate earlier findings of stream fish studies in other urbanizing areas of the United States (e.g., Weaver and Garman, 1994; Wang et al., 2000; Walters et al., 2003a). In other studies, impacts of urbanization often manifest as decreased richness, diversity, sensitive species, and fish health as well as increased tolerant and introduced species (Roth et al., 1996; Wang et al. 2000). I observed many of these same patterns in west Georgia streams. Fish health (as indicated by the % DELT), the proportion of fish in environmentally sensitive breeding guilds (% lithophilic spawners), and measures of fish biotic integrity (IBI values, Bray-Curtis similarity scores) all generally declined with increasing watershed urbanization (Table 5). Proportions of tolerant fish species increased with increasing watershed pastureland, although, somewhat surprisingly, this variable was unassociated with watershed urbanization.

2.5.1 Seasonality of fish response

The purported mechanisms of declines in fish health and assemblage structure in urbanized streams often stem from altered physicochemical and hydrologic conditions (Booth and Jackson, 1997; Sutherland et al., 2002; Schoonover et al., 2005). I suspect alterations of the hydrograph (i.e., increased flashiness and attendant increases in bed shear stress) in urbanized and developing watersheds, and increased sedimentation in the pasture-dominated watersheds, are important drivers of fish assemblage structure in west Georgia streams. Several anticipated relationships were not observed, however, such as decreasing species richness and diversity with increasing urbanization. Although difficult to reconcile, it is tempting to suggest that this disparity results from relatively high abundance of cosmopolitan fish species in our study streams, possibly resulting from a combination of stable biogeography and an extended history of human landscape alteration in the region (Smith, 1981; Hilliard, 1984; Swift et al., 1986; Feminella, 2000).

I observed considerable seasonal variation in the importance of watershed land use versus natural basin variables on fish assemblages. Whereas 2 fish variables (% DELT, IBI) showed consistent relationships with land use in every season (Table 6), relationships between land use/natural basin attributes and virtually all other fish variables were inconsistent across seasons. Perhaps most indicative of urban impact was the strong, seasonally invariant relationship between % Urban and the % of fish with eroded fins, lesions, and tumors. Moreover, land use both as high % urban cover and % pasture was particularly important in terms of low IBI values in summer, a time when streams are at baseflow, and dissolved nutrients, pathogenic bacteria, and other contaminants may reach highest annual concentrations (Schoonover et al., 2005).

In contrast, the higher relative importance of natural basin variables on fish assemblages in winter and spring may result from a combination of a decreased influence of factors linked with urbanization (e.g., reduced chemical toxicity during times when discharge is high and streamwater concentrations are low and fish are metabolically less active), and an attendant increase in importance of hydrological or geomorpholgical factors that structure fish assemblages by physical means (e.g., high shear stress during peak discharge, availability of refugia). Precipitation and discharge is typically highest during winter and spring in our streams (B. Helms, *unpublished data*). Hence, naturally larger basins or those with altered hydrographs from substantial landscape change, such as in high urban watersheds, may show higher peak discharges and greater physical disturbance to fish and other biota (Shaw, 1988; Booth et al., 2002). Taken together, our data suggest that in addition to quantifying remote landscape features it is necessary to consider importance of local geomorphic factors that may influence the degree to which changes in landscape conditions can exert strong effects on stream biota (Process Domain Concept, *sensu* Montgomery, 1999; see also Walters et al., 2003b).

2.5.2 Impervious surface and fish response

Somewhat surprisingly, use of % impervious surface at a finer scale of resolution (i.e., 1-m, cf 30-m spatial data) did not improve relationships between urbanization and fish assemblage structure, as several variables were unassociated with this measure (Table 6). Watershed imperviousness has been considered a good indicator of urbanization and has been implicated as a main driver in urban stream degradation (Schueler, 1994; McMahon and Cuffney, 2000; Walsh, 2000; Paul and Meyer, 2001; Walsh et al., 2004). Degradation typically occurs at a low % impervious surface (10-

15%, Schueler, 1994; Wang et al., 2000), a level close to average imperviousness in our watersheds (~8%, Table 3). At least 2 explanations for this equivocal pattern exist. First, whereas I selected sites that spanned a wide range of imperviousness overall (0 to 37%), impervious surface in all but 3 watersheds (BU1, BU2, RC, Table 1) was <10%, including our 3 developing sites (SB1, SB2, SB4, Table1). Thus it is possible that generally low correspondence between fish variables and impervious surface in simple regression models may have resulted, at least in part, from a lack of intermediate levels of impervious surface watersheds in our data set. Developing watersheds were primarily selected based on active development, rather than proportion of impervious surface. Thus, from a spatial perspective and in terms of impervious surface and forest cover, developing watersheds appeared more like forested than urban watersheds. Second, recent studies suggest that total impervious surface may not reflect an accurate hydrologic connection between watershed imperviousness and actual runoff delivered to streams (Brabec et al., 2002; Walsh et al., 2005). If true for our watersheds, then imperviousness, while relatively simple to quantify from remotely sensed imagery, may be a less useful measure of the linkage between landscape alteration and stream structure and function. However, fish assemblages in developing watersheds, in general, were more similar to urban watersheds than forested watersheds (Fig. 2). Taken together, these data suggest that impervious surface, while a reliably persistent component of the urban environment, is not the sole force governing fish assemblages in these watersheds. Our multiple regression models suggested that fishes in these watersheds are responding not to a single landscape factor or driver, but rather a complex suite of anthropogenic, basin, stream, and seasonality influences.

2.5.3 Urbanization and assemblage structure

There was a strong shift in fish assemblage structure along our urbanization gradient, a result reported from other systems (Weaver and Garman, 1994; Walters et al., 2003a). Clear separation existed between assemblages in urban/developing streams and those from forested watersheds, which was largely evident by differences in proportions of centrarchid species (Fig. 2). Centrarchids in our streams, primarily including *Lepomis auritus, L. macrochirus, L. cyanellus*, and *Micropterus salmoides*, are generally tolerant species that often are numerical dominants in disturbed habitats (Karr, 1981; Weaver and Garman, 1994). Also locally abundant in our urban sites and curiously scarce in other streams was the weed shiner, *N. texanus*. This coastal plains minnow was rarely found outside of the urban streams, yet its low abundance in streams from forested watersheds likely resulted more from these watersheds being at the periphery of this species' range (Boschung and Mayden 2004). The bluefin stoneroller (*C. pauciradii*) also was abundant in urban streams. Species in *Campostoma* are herbivores as adults and can readily consume large turfs of filamentous algae (Power and Matthews, 1983). Thus, the predominance of *C. pauciradii* in urban sites may be a combination of its tolerance of physicochemical extremes and this species' capacity to consume abundant algae resulting from high NO_3–N and NH_4–N levels in these streams (Schoonover et al., 2005, B. Helms, *unpublished data*).

Abundance of lithophilic spawners was clearly related to urbanization, being prevalent in forested watersheds and comparatively scarce in urban watersheds. This pattern was largely driven by abundances of the bluehead chub (*N. leptocephalus*), bandfin shiner (*L. zonistius*), and the longnose minnow (*N. longirostris*). Other fish associated with the less-urbanized sites were the rough shiner (*N. baileyi*), creek chub (*S. atromaculatus*), and the filter-feeding Southern brook lamprey (*Ichthyomyzon gagei*). Some of these species patterns may reflect interspecific associations as well as differential environment tolerance. For example, during spawning male bluehead chubs create, maintain, and guard gravel-mound nests where females deposit eggs, and males tolerate nest associates such as bandfin shiners and rough shiners (Johnston and Birkhead, 1988). Bluehead chub and bandfin shiner abundances were highly correlated in our study ($r = 0.684$, $p < 0.0001$). It is unknown if nest association between bluehead chubs and bandfin shiners is obligatory or facultative (Johnston and Birkhead, 1988). If the association is facultative, then each species may respond to stresses of urbanization independently. However, if nest association between species is obligatory, then absence of bluehead chubs from urbanized streams will likely govern bandfin shiner abundance. Further, subtle changes in stream abiotic conditions (e.g. initial changes associated with urbanization) could alter the reproductive behavior of these fishes and increase the currently benign impact of introduced nest associates like *N. baileyi* on *L. zonistius* (Herrington and Popp 2004). Such indirect effects of urbanization on the dynamics of fish assemblages are largely unknown but may be potentially far-reaching.

In summary, our results suggest urban land use in general, but not solely in terms of the proportion of impervious surface, was a strong determinant of fish assemblage structure. Moreover, fish assemblages showing clear signs of deteriorating health were consistently observed in urban and developing streams, so urban land use appears to exert a stronger influence on fish assemblages than watersheds predominantly in agricultural or silvicultural land use. Our results also demonstrate that streams with relatively low levels of species endemism also can display dramatic shifts in assemblages in response to urbanization similar to systems with high endemism (Walters et al., 2003a). However, increases in the magnitude of urbanization are likely to increase dramatically in future (Cohen 2003), so to understand the responses of fish assemblages it may be necessary to investigate the complex interplay among several environmental factors including land use, seasonality, stream geomorphology and hydrology, and biotic interactions.

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Table 1. Characteristics of the 15 study watersheds. LU/LC refers to the dominant land use/land cover in the watershed based on GIS. A watershed was classified only if it contained >30% of a given land use category, except for Developing, which showed <30% urban cover but contained active residential development. UTM coordinates were taken at the sampling site furthest downstream. Trib. = tributary.

Site	Stream	Watershed size (km^2)	LU/LC	UTM North	UTM East
SB 1	Schley Creek	20.09	Developing	0685312	3608722
SB 2	Standing Boy Creek Trib.	6.34	Developing	0693082	3614122
SB 4	Standing Boy Creek	26.59	Developing	0696898	3612214
HC	House Creek Trib.	6.55	Coniferous	0678280	3630695
MU 2	Mulberry Creek Trib.	6.06	Coniferous	0709195	3621084
SC	Sand Creek	8.96	Coniferous	0680325	3635890
BC	Beech Creek	6.47	Mixed	0704322	3657675
MK	Flat Creek Trib.	6.63	Mixed	0703887	3668333
CB	Cline's Branch	8.97	Mixed	0681196	3623522
MU 3	Turntime Branch	10.44	Mixed	0701795	3619093
FS 1	Wildcat Creek	24.20	Pasture	0684280	3641319
MU1	Ossahatchie Creek Trib.	11.95	Pasture	0712764	3615524
BU 1	Lindsey Creek	25.47	Urban	0693619	3593874
BU 2	Cooper Creek	24.69	Urban	0695357	3596969
RC	Roaring Branch Creek	3.67	Urban	0691329	3602142

Table 2. Fish metrics quantified by stream and season in the 15 study watersheds. Complex breeders that lack parental care were simply classified "Complex". P/C = complex breeders showing parental care, No P/C = complex breeders showing no parental care. See text for definitions of breeding guilds and tolerance values.

Diversity/similarity	**Feeding guild**	**Breeding guild**	**Tolerance value**
Shannon's H'	Filter-feeder	Complex	Pioneer
Bray-Curtis similarity	Insectivore	Complex P/C	Tolerant
	Piscivore	Complex No P/C	Moderate
	Herbivore	Simple Spawners	Intolerant
	Omnivore	Simple Lithophils	
	Generalist		

Table 3. Initial land use and natural basin variables quantified in the 15 study watersheds. Asterisks indicate those variables used in final analyses.

Variable	**Mean**	**Range**
Land use		
Urban (%)*	11.1	0.1–48.9
Impervious surface (%)*	8.66	1.22–37.11
Pasture (%)*	24.6	4.0–52.7
Mixed Forest (%)	37.2	22.5–55.2
Conifer (%)	26.0	8.4–69.6
Total Forest (%)	63.2	30.9–94.8
Natural basin		
Average discharge (m^3/s)*	0.282	0.003–0.910
Basin size (ha)*	1352	366–2659
Average basin slope (%)	13.6	5.3–146.1
Average channel slope (%)	0.05	0.02–0.08
Distance to downstream source (km)*	2.9	0.2–10.0
Link magnitude (count)	4.3	1.0–12.0

Table 4. Summary fish data for the 15 study watersheds. Values are cumulative for the sites (seasons combined). IBI= GA Index of Biotic Integrity (see Schleiger 2000). % DELT = proportion of fish in the sample with eroded fins, lesions, or tumors. P/C = proportion of complex breeders showing parental care, No P/C = proportion of complex breeders showing no parental care. See text for further explanation of variables.

	Mean	Range
Assemblage variable		
Number collected	91.9	2–284
H'	1.47	0.17–2.24
Species richness	8.4	2.0–16.0
Bray-Curtis similarity	31.05	3–68
IBI	41.37	24–52
Tolerant species (%)	16.34	0–98.47
Pioneer species (%)	28.56	0–82.76
% DELT	6.61	0–85.7
Feeding guild variable		
Piscivore (%)	1.99	0–14
Herbivore (%)	5.53	0–50
Omnivore (%)	4.2	0–28
Insectivore (%)	81.85	49–100
Filter feeder (%)	2.71	0–44
Generalist feeder (%)	3.64	0–23
Breeding guild variable		
No P/C (%)	25.15	0–5.26
P/C (%)	34.11	0–96.95
Simple spawner (%)	17.02	0–100
Lithophilic spawner (%)	23.49	0–78.57

Table 5. Pearson product-moment correlation coefficients between selected fish variables and land use variables (based on 30-m resolution Landsat data, see text). % Herbivore = proportion of herbivorous species in the sample, % Simple spawner = proportion of species in the sample showing no complex spawning behavior, % Lithophils = proportion of species in the sample requiring clean, gravel substrate for spawning, %Tolerant = proportion of tolerant species in the sample, % DELT = proportion of fish in sample with eroded fins, lesions, or tumors in the sample, Bray-Curtis = stream faunal similarity to average reference condition, IBI= Georgia Index of Biotic Integrity (see Schleiger 2000). *p = 0.05, ** p = 0.01, *** p < 0.001. ns = nonsignificant.

Fish variable	**% Urban**	**% Pasture**	**% Conifer**	**% Mixed**	**% Total Forest**
% Herbivore	0.4804***	ns	ns	ns	–0.3136*
% Simple spawner	ns	ns	ns	ns	ns
% Lithophilic spawner	–0.4454**	ns	0.453**	ns	0.4829***
% Tolerant	ns	0.4238**	ns	ns	ns
% DELT	0.7222***	–0.3075*	–0.371*	–0.3405*	–0.5244***
Taxa richness	ns	ns	ns	ns	ns
H'	ns	ns	ns	ns	ns
Bray-Curtis similarity	–0.3795*	ns	0.3117*	0.3001*	0.4486**
IBI	–0.6012***	ns	0.4714**	0.3803**	0.6365***

Table 6. Seasonal multiple regression models for select fish metrics and simple linear regressions of fish metrics with 1-m resolution % impervious surface. % Herbivore =proportion of herbivorous species in the sample, % Omnivore =proportion of omnivorous species in the sample, % Cyprinid insectivore =proportion of insectivorous species in the family Cyprinidae, % Pioneer = proportion of pioneer species in the sample, % DELT = proportion of fish in sample with eroded fins, lesions, or tumors in the sample, Bray-Curtis = stream faunal similarity to reference stream, and IBI= Georgia Index of Biotic Integrity (see Schleiger 2000). Direction of relationships for simple regressions are denoted by (+) and (–) in the R^2 column when appropriate.

	Variables in multiple regression model			Impervious surface	
		R^2adj	p	R^2	p
Summer					
H'	----	----	----	----	----
Species richness	urban, pasture, basin size	0.4760	0.0432	----	----
Tolerant species	urban, pasture, basin size	0.672	0.0071	----	----
% Herbivore	pasture, source distance	0.461	0.0252	0.456 (+)	0.0160
% Omnivore	----	----	----	----	----
% cyprinid insectivore	basin size, source distance	0.433	0.0314	----	----
% Pioneer	source distance	0.340	0.0274	----	----
% DELT	Urban	0.755	0.0002	0.871 (+)	<0.0001
Bray-Curtis similarity	----	----	----	----	----
IBI	urban, pasture	0.495	0.0187	0.376 (–)	0.0341
Winter					
H’	basin size, discharge	0.342	0.0321	----	----
Species richness	----	----	----	----	----
Tolerant species	----	----	----	----	----
% Herbivore	urban, discharge	0.681	0.0007	0.636 (+)	0.0006
% Omnivore	----	----	----	----	----
%Cyprinid insectivore	basin size, discharge	0.4060	0.0027	----	----
% Pioneer	----	----	----	----	----
% DELT	urban	0.591	0.0008	0.733 (+)	<0.0001
Bray-Curtis similarity	----	----	----	----	----
IBI	urban, discharge	0.529	0.0064	0.414 (–)	0.0130
Spring					
H'	----	----	----	----	----
Species richness	----	----	----	----	----
Tolerant species	pasture, discharge	0.341	0.0324	----	----
% Herbivore	----	----	----	----	----
% Omnivore	source distance	0.8183	<0.0001	----	----
% Cyprinid insectivore	----	----	----	----	----
% Pioneer	source distance	----	----	----	----
% DELT	Urban	0.582	0.0006	0.720 (+)	<0.0001
Bray-Curtis similarity	pasture, discharge	0.398	0.0190	----	----
IBI	urban, pasture, basin size	0.6381	0.0024	0.369 (–)	0.0163

Table 7. Watershed and fish variables regressed against Axes 1 and 2 in non-metric multidimensional scaling (NMDS) space based on abundance of 20 most common fish species in the 15 study watersheds. Values are R^2 that were significant ($p < 0.05$).

	NMDS Axis 1	NMDS Axis 2
Watershed variables		
% Impervious surface		0.3375
% Pasture		
% Conifer		0.4305
% Total Forest		0.3975
Basin size		0.0963
Distance from source	0.2004	
Fish variables		
% Pioneer	0.4504	0.2288
% Omnivore	0.3218	
% Lithophilic Spawner		0.4956
% DELT		0.2145
Bray-Curtis similarity		0.3561
IBI		0.3829

Table 8. Pearson product-moment correlation coefficients and associated *p* values of fish species associations with Axes 1 and 2 of a non-metric multidimensional scaling (NMDS) ordination based on abundance of 20 most common fish species in the 15 study watersheds. Significant correlations and associated *p* values are shown in bold.

Species	**Species Code**	**NMDS Axis 1**	***p***	**NMDS Axis 2**	***p***
Ameirus natalis	A_NATA	0.211	0.1858	–0.175	0.2733
Campostoma pauciradii	C_PAUC	**–0.599**	**<0.0001**	0.196	0.2202
Ericymba buccata	E_BUCC	0.196	0.2190	–0.241	0.1283
Gambusia affinis	G_AFFI	**0.836**	**<0.0001**	0.093	0.5640
Hybopsis sp.	H_SPEC	–0.262	0.0979	0.293	0.0628
Ichthyomyzon gagei	I_GAGE	–0.180	0.2588	**–0.542**	**0.0003**
Lepomis auritus	L_AURI	**–0.470**	**0.0002**	**0.430**	**0.0052**
Lepomis cyanellus	L_CYAN	**–0.416**	**0.0069**	0.059	0.7157
Lepomis gulosus	L_GULO	0.153	0.3385	0.294	0.0624
Lepomis macrochirus	L_MACR	0.024	0.8785	**0.659**	**<0.0001**
Luxilus zonistius	L_ZONI	0.016	0.9187	**–0.820**	**<0.0001**
Micropterus salmoides	M_SALM	–0.200	0.2089	0.210	0.1886
Minytrema melanops	M_MELA	–0.100	0.5345	0.195	0.2228
Nocomis leptocephalus	N_LEPT	–0.227	0.1530	**–0.700**	**<0.0001**
Notropis baileyi	N_BAIL	–0.184	0.2482	**–0.319**	**0.0418**
Notropis longirostris	N_LONG	0.099	0.5389	**–0.508**	**0.0007**
Notropis texanus	N_TEXA	–0.203	0.2023	**0.390**	**0.0160**
Percina nigrofasciata	P_NIGF	–0.036	0.8216	–0.271	0.0865
Pomoxis nigromaculatus	P_NIGM	0.098	0.5425	0.371	0.1710
Semotilus atromaculatus	S_ATRO	–0.098	0.5404	**–0.543**	**0.0002**

Figure. 1. Map of the 15 study watersheds (shaded regions) in the middle Chattahoochee River Basin in Muscogee, Harris, Meriwether, and Troup counties, west Georgia.

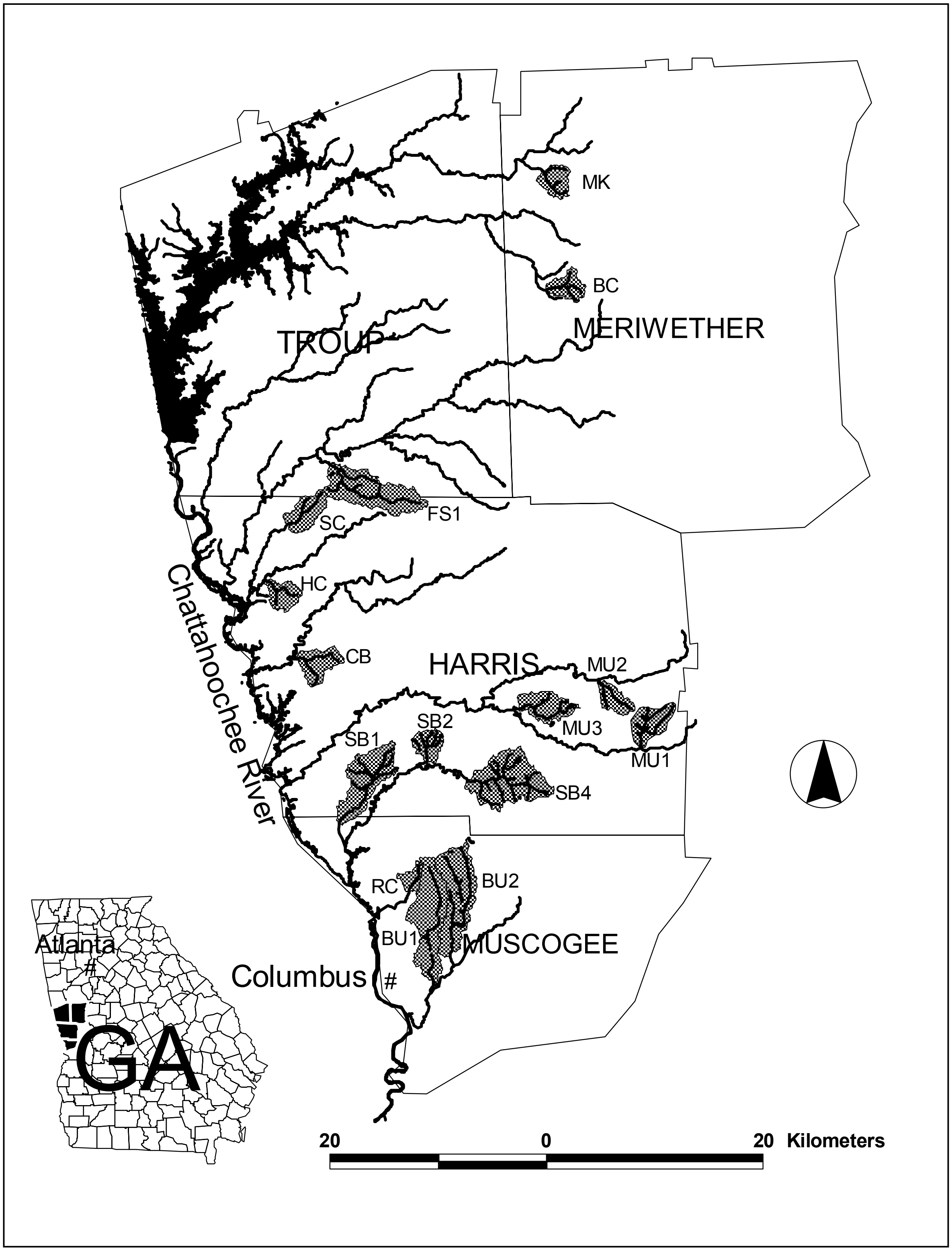
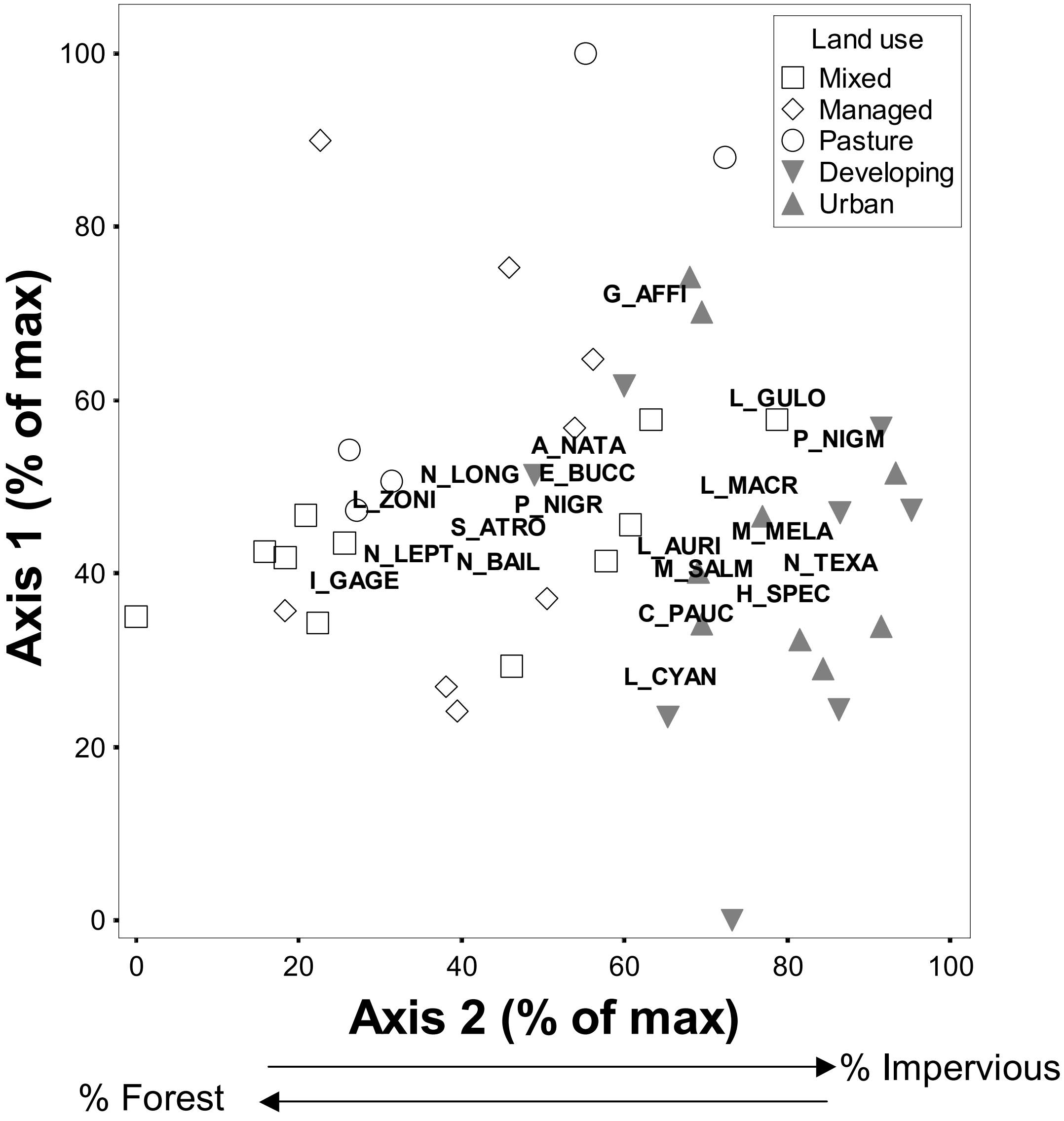


Figure 2. Non-metric multidimensional scaling (NMDS) ordination of study sites in fish species space. Axes are scaled proportionate to the longest axis (% of Max). Symbols are the 15 study streams in different seasons, and fish species are labeled according to abbreviations defined in Table 8. Land use classifications were based on the predominant land use in the watershed (>30% of a given land use category), except for "Developing" sites, which showed <30% urban cover but contained active residential development. Land use and natural basin variables significantly correlated with NMDS axes were the proportions of watershed impervious surface (=% Impervious Surface) and total forest cover (=% Forest Cover) on Axis 1, and nearest distance from the study site to a larger downstream tributary (=Distance to Source) on Axis 2. Arrows on x and y axes show direction of increasing values.



CHAPTER 3. Assessing influences of hydrology, physicochemistry, and habitat on stream fish assemblages across a changing landscape

3.1 ABSTRACT

I evaluated the indirect impact of land use/land cover on fish assemblages by examining relationships between stream hydrology, physicochemistry, and instream habitat and their association with fish responses over a 12-mo period of record (POR) in streams draining 18 watersheds of the Lower Piedmont of western Georgia, USA. Several important relationships between watershed land use and physicochemical, hydrological, and habitat parameters were observed, particularly increased frequency of spate flows and decreased dissolved oxygen with increasing impervious surface cover, increased habitat quality with forest cover, and increased suspended solids with increasing pasture cover. Fish assemblages however were largely explained by physicochemical and hydrological rather than habitat variables. Specifically, fish species diversity, richness, and biotic integrity were lower in streams that received high frequency of spate flows. Also, overall fish assemblage structure (as determined by non-metric multidimensional scaling) was best described by dissolved oxygen (DO), with low DO streams containing sunfish-based assemblages and higher DO streams containing minnow-based assemblages. Our results suggest that altered hydrological and physicochemical conditions, induced largely by impervious surface, may be a strong

driver of fish assemblage structure in these lowland streams. These analyses allow for a more mechanistic understanding of how land use ultimately affects these systems.

3.2 INTRODUCTION

Biotic patterns in stream communities often are attributable to the combined influences of broad-scale environmental factors, regional species pool, watershed-specific processes, and local conditions (Frissell *et al.*,1986; Poff, 1997; Fausch *et al.*, 2002). Human activities at the landscape level can affect these filters and thus have dramatic effects on stream community structure and function. In particular, watershed land use and/or land cover (LU/LC) can alter local conditions by directly affecting water physicochemistry, hydrology, and instream habitat, which, separately or in combination, in turn can influence biotic composition and ecological integrity (Lenat and Crawford, 1994; Clements, 2000; Paul and Meyer, 2001; Allan, 2004; Schoonover *et al.*, 2006).

Increased levels of agriculture and urbanization in watersheds can lead to several significant changes to many stream features. In general, agricultural and urbanized land has been implicated in increased streamwater pollutants, decreased riparian cover, elevated water temperatures, altered hydrology, increased storm flows and sedimentation, and overall reduced habitat quantity/quality (Paul and Meyer, 2001; Allan, 2004). All of these impacts have been shown to decrease biotic integrity, such as reducing species richness/diversity, increasing physiological stress, and causing assemblage shifts (Scott *et al.*, 1986; Schleiger, 2000; Walters *et al.*, 2003; Weaver and Garman, 1994; Helms *et al.*, 2005; Roy *et al.*, 2005a).

Of the multiple direct abiotic consequences watershed land use has on receiving streams, hydrological alteration is one of the more obvious and pervasive (Booth and

Jackson, 1997; Groffman *et al.*, 2003; Wang and Lyons, 2003; Walsh *et al.*, 2005). As a result of high levels of watershed imperviousness and connectedness, streams draining urban and urbanizing watersheds often display flashy hydrographs with multiple peak flows and reduced base flows (Ferguson and Suckling, 1990; Rose and Peters, 2001; Schoonover *et al.*, 2006). Storm flows often increase in magnitude and frequency in agricultural settings because of the use of drainage ditches, loss of wetlands, and soil compaction (Peterson and Kwak, 1999; Allan, 2004). Such hydrological alteration can have far-reaching effects on instream conditions. Increased peak flows can accelerate geomorphic changes in stream channels, leading to increased sedimentation, scour, and channelization, the combination of which may reduce biotic habitat quality and quantity (Wolman, 1967; Hammer, 1972; Bledsoe and Watson, 2001). In addition, stormwater runoff in urbanized watersheds often elevates chemical pollutants, including nutrients, metals, pesticides, and pharmaceuticals (Paul and Meyer, 2001; Kolpin *et al.*, 2002; Wang and Lyons, 2003), and water temperature. Changes in temperature may cause thermal pulses and altered thermal regimes in receiving waters, which can increase mortality of sensitive species and skew assemblages towards tolerant species (Galli, 1991; Wang *et al.*, 2000; Krause *et al.*, 2004).

Thus conceptually, watershed LU/LC can directly alter hydrological regimes which in turn lead to degradations in physicochemical and geomorphic conditions. Watershed LU/LC also can directly influence physicochemical (e.g. point-source pollution) and geomorphic conditions (e.g. livestock trampling). Altered hydrological regimes can then directly influence biota and/or indirectly through alterations in physicochemical and geomorphic conditions (Figure 1).

In a previous study, I described the relationships between urbanization and fish assemblage structure in streams of western Georgia, USA (Helms *et al*., 2005). There I reported that declines in biotic integrity and assemblage shifts were associated with watershed land use as well as broad physical/environmental features in high flow seasons. As a result, I suspected that differences in hydrographs across these watersheds were important in explaining fish assemblages. Our present study therefore was designed to investigate in more detail the association of land use and altered hydrology on stream fish assemblage structure in this area in a subsequent year. Specifically, I examined the direct relationships among 1) watershed land use and the physical instream factors hydrology, habitat, and water physicochemistry; and 2) these physical instream factors with fish assemblages. Our objective was to determine relative explanatory power of hydrology, physicochemistry, and habitat variables associated with LU/LC change on variation in fish assemblages.

3.3 STUDY AREA

I studied stream reaches from tributaries of the middle Chattahoochee River, western Georgia, USA, occurring in the Southern Outer Piedmont ecoregion (Griffith *et al*., 2001). Currently, conversion of pasture and forests to urbanized areas is occurring rapidly northeast of the city of Columbus, Muscogee County. Therefore, I sampled 2nd- to 3rd-order streams within 18 watersheds (4–25 km^2) along this urbanization gradient from the geologic fall line in the city of Columbus to an area 80 km northeast (Muscogee, Harris, Troup, and Meriwether counties, Figure 1). All study reaches were typical of the lower Piedmont, consisting of sandy-bottom channels with run-pool morphologies (Mulholland and Lenat, 1992). Watersheds ranged in land cover from intense urbanization and active suburban development to pasture to heavily forested areas. This relatively large range in landscape character allowed comparison across geomorphically similar streams that differed primarily in watershed-level LU/LC and associated variation in streamwater physicochemical conditions.

3.4 METHODS

3.4.1 Land cover analysis

I determined watershed boundaries and size from USGS 30-m resolution digital elevation models and ArcView 3.2a software (Environmental Research Systems Institute, Inc., Redwoods, Calfornia). True color (3-band) aerial photographs of study watersheds were taken in March 2003 during leaf-off to determine LU/LC. Impervious surface (IS) and water bodies were manually digitized and the remaining land cover was classified using a hybrid unsupervised/supervised classification scheme, a modification of the Anderson Classification Scheme (Myeong *et al*., 2001; Lockaby *et al*., 2005). Watersheds were ground-truthed to verify LU/LC classes, and the overall classification accuracy (all land covers combined) was 91% (see Lockaby *et al*., 2005 for method). I used % of each watershed as IS, pasture, and forest (deciduous + evergreen) for analyses. I also assigned each watershed to 1 of 4 broad LU/LC categories (Urban, Developing, Pasture, and Forest) to aid in describing any perceived differences among watersheds (Table 1). These categories were based on the dominant land cover in the watershed (% IS, pasture, and/or forest) from land cover analysis except for the Developing, which were predominantly forested but contained active or recent residential development.

3.4.2 Hydrology measures

I quantified continuous stream discharge (Q) from July 2003 to July 2004 using a Mini-Troll® pressure transducer data logger (In-Situ Inc., Ft. Collins, Colorado) housed in PVC pipe and installed near the outflow point of each watershed. I set data loggers to record a stage reading at 15-min intervals (0.01-m depth resolution) and then, by correlating these stage readings with discharge (either directly measured or calculated at various stages (Gordon *et al*., 2004)), I developed stage–Q rating curves for each watershed to estimate continuous Q (Schoonover *et al*., 2006). I characterized 5 separate elements of Q from each hydrograph (Table 2): 1) *Baseflow* (groundwater contribution), 2) *Predictability/Flashiness* (rate/amount of change in Q), 3) *Duration* (length of time associated with a particular high or low Q event), 4) *Magnitude* (amount of Q for a given interval), and 5) *Frequency* (number of occurrences of a given magnitude of Q) (Poff and Ward, 1989; Richter *et al*.,1996; Poff *et al*., 1997; McMahon *et al*., 2003).

I predicted baseflow for each watershed using a 5-d smoothed minima technique (Gustard, 1992; Schoonover *et al*., 2006), calculated by dividing the Q data into non-overlapping 5-d blocks and determining the minimum flow in each block. The minimum value in a given block was compared to the minimum values of the previous and subsequent 5-d blocks (Gustard, 1992). If the minimum value was less than these adjacent values, it was considered an estimate of baseflow for that period. Then, I used linear interpolation between each baseflow estimate to predict baseflow for each observed flow measure for the entire data set. I then developed a baseflow index measure of overland flow (BI) as:

$$\sum \text{predicted baseflow} / \sum \text{observed flow.}$$

BI values can range from 1, when 100% of observed Q was from baseflow (low overland contribution) to 0 when 0% of observed Q was from baseflow (high overland contribution, see Gustard *et al*., 1992; Schoonover *et al*., 2006). Ultimately, I calculated 29 hydrological variables considered important in describing stream biotic parameters (Richter *et al*., 1996; Poff *et al*., 1997; Roy *et al*., 2005a) for each watershed (Table 2).

3.4.3 Physicochemistry measures

I measured several physicochemical variables over the hydrological period of record (Table 3). Stream temperature was measured continuously with HOBO® Temp data loggers placed near the pressure transducers, DO and pH were measured seasonally in areas where fish were sampled while total dissolved solids (TDS) and total suspended solids (TSS) were determined monthly as detailed in Schoonover and Lockaby (2006).

3.4.4 Fish and habitat sampling

I sampled stream fish assemblages in June 2004 from 3 run and 3 pool habitats per stream along a representative 100-m reach. I sampled fish in each habitat to depletion with block nets, a backpack electroshocker (Smith-Root LR-24) and seines. I field-identified and measured total length (TL) of all fish captured and returned them near the point of collection, except for voucher specimens of each species, which were deposited in the Auburn University Museum Fish Collection.

I assigned species to feeding and breeding guilds (Muncy *et al*., 1979; Berkeman and Rabeni, 1987), as they have been shown by others to be reliable indicators of biotic integrity in Georgia piedmont streams (Schleiger, 2000; Helms *et al*., 2005). For feeding guilds, fish were classified as piscivores, insectivores, herbivores, omnivores, or filter feeders. For breeding guilds, I initially classified fish as complex or simple breeders, based on the degree to which species prepare spawning sites, defend nests, and show pre-spawning social behavior (Pflieger, 1975; Trautman, 1981). Complex breeders were then further classified into those species that show parental care (P/C) and those that do not (No P/C) while simple breeders divided into spawners requiring clean, gravel substrate (lithophilic spawners, = Lithophils) and those capable of spawning on sand, silt, or vegetation (generalist spawners, = Simple Spawners). I used these classifications to assess whether there were functional changes in assemblages associated with different stream conditions.

I calculated species richness and species diversity (Shannon's *H*') for each stream. Richness and *H*' are commonly used metrics for comparing fish assemblages; however, human disturbance may cause only nominal changes in *H*' or species richness but major changes in composition (Scott and Helfman, 2001; Walters *et al.*, 2005). Therefore, I also calculated a stream-specific Index of Biotic Integrity (IBI) modified for Georgia piedmont streams (Schleiger, 2000) and relative abundance for use in a non-metric multidimensional scaling (NMDS) ordination to describe overall fish variation among watersheds.

To assess available habitat quality/quantity, I used a comprehensive multimetric habitat assessment from the Georgia Environmental Protection Division designed for use in fish biomonitoring (GA DNR, 2005). This Habitat Index included visual estimates of available cover (number and frequency of habitats), substrate characterization (type and condition), pool morphology (shape and frequency), channel alteration (frequency of riprap, dredging, etc), channel sinuosity (run-to-bend ratio), sediment deposition (particle, point bar, and island size), flow status (degree to which channel is filled with water), bank condition (erosion potential and vegetation cover) and riparian condition (vegetation cover/quality) (GA DNR, 2005). This assessment involves taking the average of 3 individuals' summed scores (1-10 or 1-20, depending upon parameter) of the different habitat parameters to obtain an overall habitat quality value for the representative reach, with high average score indicating high habitat quality. I used the same 3 observers at all sites.

In addition to the GA DNR habitat assessment, I assessed stream habitat by estimating habitat volume (mean depth x width x length), benthic organic matter abundance (BOM), substrate particle sizes, and benthic shear stress (T_G) in each habitat unit at the time of fish sampling. I estimated BOM and substrate size by sampling transitional areas between the runs and pools where fish were sampled to standardize our efforts and avoid error associated with scour in the runs and deposition in the pools. I sampled BOM by determining the ash-free dry mass (AFDM) of 9 replicate 2.5 x 10 cm benthic cores. For substrate particle size, I collected 3 benthic samples per stream (near where BOM was sampled) using a 76.2-mm diameter PVC substrate core to a depth of 10 cm. I dried samples and separated particles into 5 size classes: gravel-cobble (>2mm), very coarse sand (1 – 2 mm), coarse to medium sand (0.25 – 1 mm), fine sand (0.1 – 0.25 mm), very fine sand (0.05 – 0.1mm), and silt/clay (< 0.05mm) to determine median substrate size by weight (USDA 1951). I estimated T_G close to where pressure transducers were located using

$$T_G = pgRS$$

where p is the density of water, g is gravitational acceleration, R is hydraulic radius, and S is energy slope (Gore, 1996).

3.4.5 Data analyses

I used simple Pearson correlations to examine relationships between environmental variables (hydrology, habitat, physicochemical) and LU/LC. All continuous variables were log-transformed and percent variables were arcsine-squareroot transformed as needed to meet assumptions of normality (Zar, 1998).

Second, I used non-metric multidimensional scaling (NMDS) to describe overall variation in fish assemblages among sites. NMDS is an ordination technique that handles data with many zeroes and nonnormal data (both common in species data) better than other ordination techniques such as Principal Components Analysis (PCA, McCune and Grace, 2002) but, unlike PCA, the order of the axes in the resultant ordination does not necessarily imply the order of greatest variation explained. I transformed proportional relative abundance data using arcsin-square root and excluded rare species (those in <10% of sites) to reduce the influence of rare taxa on ordinations. This step resulted in an 18 x 23 site–species matrix on which I based ordinations using a Sorenson distance measure (McCune and Grace, 2002). I correlated all environmental variables and fish assemblage variables to the resulting NMDS ordination to assess changes over the landscape.

Last, I used stepwise multiple regression analyses ($p = 0.05$ to enter and leave the model) to determine which environmental variables, directly or indirectly related to LU/LC, had the most explanatory power in regards to fish assemblages. To conform to the conceptual model in Figure 1, any hydrologic variable not related to some aspect of LU/LC was dropped from multiple regression as were any physicochemical or habitat variable not related to either LU/LC or the selected hydrologic variables. In order to avoid multicollinearity among predictors, all parameters in the final models had a variance inflation factor (VIF) < 10 (Myers 1990).

3.5 RESULTS

3.5.1 Stream hydrology

In general, the hydrographs of the urban and developing watersheds were flashier and less stable than hydrographs in other watersheds (Table 2). There was a strong relationship between urbanization and the frequency and predictability of hydrological events as evidenced by several parameters being positively correlated with IS, notably the measures 5XMed, 7XMed, 9XMed and N>99th and the variables Inc1h100 and Inc3h100 (Table 2). Median Q also was positively correlated and Inc1h5000 was negatively correlated with proportion of watershed as pasture. There was no significant relationship between any hydrological parameter and proportion of watershed as forest (Table 2). I therefore used these 8 hydrologic variables in subsequent multiple regressions since they showed significant relationships with some aspect of watershed LU/LC.

3.5.2 Physicochemistry and habitat

Physicochemical and habitat parameters were variable across the watersheds with all parameters associated with either watershed LU/LC and/or hydrology (Tables 3 & 4). In general, higher stream temperatures and lower DO levels were associated with increased watershed IS and spate flows (5xMed, 7xMed, and 9xMed, Tables 3 & 4). Mean and minimum DO levels were highly correlated with each other ($r = 0.884$, $p < 0.001$), and since mean DO was a continuous measure and minimum DO was a single measurement, I used mean DO for statistical analyses. Further, TDS was positively associated with IS cover and spate frequency measures, TSS was positively correlated with % pasture and the flashiness variable Inc1h5000, and pH was positively correlated with Inc1h100 and Inc3h100 (Table 3 & 4). Of the habitat variables considered, habitat volume and median substrate size were positively correlated with IS while OM and the Habitat Index were positively correlated with forest cover (Table 3). Substrate size was also positively correlated with spate frequency variables, tractive force increased with median discharge, and the Habitat Index increased with Inc1h5000. All physicochemical variables were correlated with either a hydrologic or LU/LC variable, therefore they were all included in multiple regressions analysis.

3.5.3 Fish assemblage structure

I collected 27 fish species (1152 individuals) in 7 families during the study, with Cyprinidae (minnows) and Centrarchidae (sunfishes) being the most common and abundant families (Table 5). Of the breeding and feeding guilds, proportion of lithophilic spawners declined with increasing IS ($r = -0.66$, $p < 0.01$) and increased with total forest cover ($r = 0.51$, $p < 0.05$) while proportion of insectivores increased with IS ($r = 0.57$, $p < 0.05$) and decreased with forest cover ($r = -0.51$, $p < 0.05$). Species richness ranged from 2 to 13 species, with highest measures in pasture and forested watersheds, and was negatively correlated with IS ($r = -0.66$, $p < 0.01$) (Table 6). *H'* ranged from 1.07 to 2.95, with the highest values in forested and pasture dominated watersheds, and was negatively correlated with IS ($r = –0.85$, $p < 0.01$) and positively correlated with forest cover ($r = 0.52$, $p = 0.03$), while proportion of sunfish increased with urban cover (Table 6). IBI ranged from 22 to 42, with highest values in pasture and forested watersheds; however, IBI was not significantly correlated with any land cover.

NMDS axes 1 and 3 ($NMDS_1$ and $NMDS_3$) were the two axes describing the most variation in fish assemblages among streams (48.7 and 22.8%, respectively; stress = 13.8, instability = 0.00001, iterations = 91; Figure 3). Streams in Urban and Developing watersheds generally grouped to the left of the ordination whereas streams from Forest and Pasture watersheds grouped mostly to the right (Figure 3). Number of fish collected, *H'*, proportion of lithophils, and IBI all were positively correlated with $NMDS_1$ while the proportion of sunfish, insectivores, and fish showing no parental care, were all negatively correlated with $NMDS_1$ (Figure 3). The proportion of the assemblage showing parental care was significantly correlated with $NMDS_3$. There were several environmental parameters associated with these shifts in fish assemblage structure across the landscape, including stream DO levels, water temperature, TDS, substrate size, frequency of spate flows, and habitat volume (Figure 3).

3.5.4 Influence of environmental variables

Multiple regression analyses revealed that hydrologic and physicochemical variables were good predictors of fish assemblages (Table 6). Models describing richness, diversity, and the IBI all contained measures of spate frequency (5xMed, 7xMed, and N>99). Stream water temperature was the best predictor of number of fish collected while temperature and 5xMed best described taxa richness (Table 6). TDS was also prominent in models as a strong predictor of diversity and % sunfish (Table 6). Interestingly, no habitat variables were included as parameters in any best models.

3.6 DISCUSSION

Environmental controls of stream fish assemblages are varied, often interactive, and frequently associated with landscape disturbance (Roth *et al.*, 1996, Matthews, 1998;

Lammert and Allan, 1999). Our results provide additional empirical evidence that the indirect effects of land use on the integrity of fish assemblages can occur through the alteration of instream environmental conditions, particularly alterations in hydrological and physicochemical conditions.

3.6.1 Hydrology and fish assemblages

Stream flow is often considered the master variable limiting aquatic biota by its effects on instream physicochemistry, geomorphology, and habitat diversity (Poff and Allan, 1995; Poff *et al*., 1997). In our study streams, hydrology appeared to have a strong effect on differences in fish assemblages among watersheds. Richness, *H*', and IBI all were lower in streams experiencing numerous high-magnitude flows, whereas more taxonomically rich and diverse assemblages were associated with streams experiencing fewer high-magnitude flows. Fish patterns were also strongly associated with the number of events that exceeded 5 , 7, and 9 times median flow, moderate events that, on average, were all less than 33% of bankfull Q in these watersheds. Small, frequent spates have been suggested to be more important than infrequent larger events in causing ecological impacts (Walsh *et al*., 2005). Moreover, baseflow index (BI) was a strong correlate of NMDS axis 1, suggesting that increases in overland flow events and associated spate frequency, and not necessarily alterations in the duration, predictability, or magnitude of flows, are strong hydrological drivers of fish assemblages in these watersheds. These findings support other studies on fish reporting increased proportions of habitat generalist species with increasing frequency of hydrological disturbance, and taken together, underscore the far-reaching effects of hydrology on stream ecological integrity (Resh *et al.*, 1988; Poff *et al.*, 1997; Freeman *et al.*, 2001; Roy *et al.*, 2005a). If true for other piedmont watersheds, then such frequency-based hydrological variables should be taken into consideration by resource managers to identify flow-related impacts to fish in developed/developing watersheds.

As shown by others, fish assemblages overall show lower diversity and biotic integrity in developing and highly urbanized watersheds compared with less-developed watersheds (Koel and Petarka, 2003; Walters *et al.*, 2003; Helms *et al.*, 2005; Roy *et al.*, 2005a). As determined from the NMDS ordination, this pattern appeared to correspond to the combined changes in stream hydrological and physicochemical conditions associated with increasing impervious surface and connectedness in the Urban and Developing watersheds. Interestingly, BI was not significantly correlated to any LU/LC variable, likely offset by the relatively high % Forest in the Developing streams, demonstrating the pervasive influence of even a small percentage of watershed urbanization. In a related study of these same sites (Schoonover *et al.*, 2006) measures of BI suggest that overland flow (vs. baseflow inputs) contributed up to 90% of Q reaching Urban streams and 65 to 90% of Q reaching Developing streams. High overland flow and associated spates are not only likely to contribute significant physical impacts on fishes (i.e., through downstream displacement of individuals, habitat alterations, etc.), but can also act to transport pollutants, elevate water temperatures and bacteria and nutrient concentrations from terrestrial sources and also resuspend materials in the stream bed (Casey and Farr, 1982; Paul and Meyer, 2001).

In our study streams TDS and temperature were generally elevated and DO decreased in urbanized systems and were associated with decreased fish diversity. Many other studies have also observed elevated TDS (or specific conductivity) with increased urban area / impervious surface (Dow and Zampella 2004) as well as with decreased biotic integrity (Walsh et al., 2001; Roy et al. 2003). However, TDS concentrations were not necessarily at biologically significant levels, as most aquatic systems with biota can withstand TDS levels up to 1000 mgL^{-1} (Boyd 2000). Therefore the strong association of TDS with urbanized/urbanizing watersheds suggests that it is a likely indicator of increased non-point pollution associated with efficient runoff, thus an "anthropogenic marker" in these streams.

Water temperature and DO are major regulators of fish distribution, growth, migration, and survival (Fry, 1947; Regeir *et al.*, 1990; Smale and Rabeni, 1995; Krause *et al.*, 2004), and levels of each of these parameters are important predictors of fish assemblages in streams of western Georgia. Warmwater sunfish species were ubiquitous in our study streams, but they were far more abundant in streams with higher water temperatures and lower DO than in streams without these stressors. This pattern suggests that elevated stream temperature and low DO, particularly in urban and developing streams with thermally enhanced overland flow and/or reduced riparian cover (Van Buren, 2000; Roy *et al.*, 2005b), may negatively affect presence or abundance of fishes in general. It seems unlikely though that elevated temperature directly affected fishes as the maximum water temperature I observed ($25.6^{O}C$) was well below most physiological thresholds and habitat requirements for most native fish of this region (Aho *et al.*, 1986; Brown, 1974; Krause *et al.*, 2004). However, besides causing mass fish kills (Gafny *et al.*, 2000), low DO may produce important sublethal effects, leading to habitat and behavioral shifts in populations and, ultimately, altered local assemblage structure

(Kramer,1987; Matthews, 1987;1998). Specifically, critical DO levels for similar fish assemblages in warm-water streams range 0.49 to 1.49 mgL^{-1} and strong effects of hypoxia on fish habitat use and species composition have been implicated when water DO minima fall below 4 to 5 mgL^{-1} (Smale and Rabeni, 1995). DO levels in our streams occasionally reached these lethal levels and frequently reached those reported levels that could influence species distribution over the period of record.

Altered land use can induce physical changes in stream channels, influencing the dynamics and spatial arrangement of channel features and instream habitat (Allan, 2004). Our analyses indicated that some instream fish habitat conditions were related to watershed LU/LC. However, habitat variables in general were weak predictors of fish assemblage structure. There was a relationship between assemblage structure and substrate size as evidenced by NMDS axis 1, with more tolerant assemblages being associated with streams with large substrate size. This habitat feature is likely the result of bed coarsening and flushing, and is common in urban and other hydrologically altered watersheds (Finkenbine *et al*., 2000; Walsh *et al*., 2005). However, considering the size range (0.5 – 1.8 cm), and that lithophilic spawners were negatively associated with substrate size, substrate composition was unlikely to be an important driver of assemblages in these streams. Taken together, our results suggest that hydrological regimes may influence instream habitat conditions in these watersheds, but local habitat *per se* is not a strong driver of the observed differences in fish assemblages (*cf*. Poff *et al*., 1997; Sutherland *et al*., 2002). It should be noted, however, that the weak link between fish assemblages and habitat variables, compared with hydrological and physicochemical measures, may reflect a disparity of 1) scale between our measures of habitat (100-m study reaches) and potential longitudinal movement of fish (>100 m), 2) sampling, given that I measured hydrology and physicochemistry multiple times (and, for some measures, continuously) over the study, and habitat variables were measured just once, and 3) the biotic composition of fishes in general in lower Piedmont watersheds of the Chattahoochee drainage, which have a natural predominance of widespread species (Hilliard, 1984; Swift *et al.,* 1986).

3.6.2 Conclusions

Our results suggest that LU/LC induced changes in hydrology and streamwater physicochemistry, particularly in urban/urbanizing watersheds, influence stream fish assemblages more so than alterations in physical habitat; however, there is undoubtedly high complexity in the functional interrelationships of environmental variables in these streams. Physicochemical conditions are closely linked to hydrology and land use, and teasing the relative importance of each is a daunting task. The use of multivariate analyses effectively allowed us to identify important correlates of fish assemblage structure that, as a result of the nature of the suburban landscape, were not strongly associated with measured LU/LC values (e.g., BI). However, many physicochemical conditions are correlated, so it may only be necessary to identify a single physicochemical or hydrological group of variables for certain management and/or restoration goals (e.g. spate frequency, temperature/DO). Further, in these lower Piedmont systems with a history of land use degradation, an assemblage-based response (such as the NMDS ordination) may be better suited to evaluating the impacts of human induced change than traditional metrics (e.g. *H'*) because of the high abundance of widely distributed species and relatively few endemics, often hindering useful comparisons to degraded systems.

Human population expansion and the inevitable landscape alteration caused by such growth have produced dramatic impacts on stream ecosystems. By attempting to identify the specific hydrological and physicochemical driver(s) of biotic composition resulting from these perturbations, I can better address management and/or restoration needs designed to protect or minimize changes in stream biotic integrity.

3.7 REFERENCES

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Table 1. Land cover and physical characters of study watersheds. **IS** = % impervious surface cover, **Pasture** = % pasture cover, and **Mixed Forest** = % managed and unmanaged forest cover, and **LU/LC** = dominant land use/land cover in watershed, and **Spate *f*** = spate frequency category assigned each watershed (see Results).

ID	Site	Stream	Watershed size (km^2)	IS	Pasture	Forest	LU/LC
1	SB1	Schley Creek	20.1	2	20	73	Developing
2	SB2	Standing Boy Creek Trib.	6.3	3	20	73	Developing
3	SB4	Standing Boy Creek	26.6	3	28	64	Developing
4	HC	House Creek Trib.	6.6	1	20	75	Forest
5	MU2	Mulberry Creek Trib.	6.1	1	9	82	Forest
6	SC	Sand Creek	9.0	1	21	74	Forest
7	BC	Beech Creek	6.5	2	13	81	Forest
8	BLN	Blanton Creek	3.6	1	19	76	Forest
9	MK	Flat Creek Trib.	6.6	2	20	74	Forest
10	MO	Cline's Branch	9.0	2	13	81	Forest
11	MU3	Turntime Branch	10.4	2	15	78	Forest
12	FS2	Wildcat Creek Trib.	14.5	3	36	59	Pasture
13	FS3	Wildcat Creek Trib.	3.0	3	34	62	Pasture
14	HC2	House Creek	14.1	2	44	52	Pasture
15	MU1	Ossahatchie Creek Trib.	12.0	4	37	53	Pasture
16	BU1	Lindsey Creek	25.5	40	23	34	Urban
17	BU2	Cooper Creek	24.7	25	25	46	Urban
18	RB	Roaring Branch	3.7	30	27	39	Urban

Table 2. List of hydrological variables used in analyses and their range of values, Pearson correlations to predominant land cover classes in the 18 watersheds, and loadings on Principal Components Analysis (PCA) axes. **IS** = proportion of impervious surface cover, **Forest** = proportion of forest (managed + unmanaged) cover, **Pasture** = proportion of pasture cover, **PCA1** and **PCA2** = Principal Components Analysis axes 1 and 2, respectively. * $p < 0.05$, ** $p < 0.01$.

Variable ID	Description	Range	IS	Forest	Pasture
Magnitude					
MedQ	Median discharge ($L\ s^{-1}$)	0.01 – 0.90			0.49*
MaxQ	Maximum discharge ($L\ s^{-1}$)	0.54 – 21.98			
MinQ	Minimum discharge ($L\ s^{-1}$)	0 – 0.38			
	Frequency (# times exceeded threshold)				
3xMed	# of times discharge exceeded 3x median flow	5 – 116			
5xMed	# of times discharge exceeded 5x median flow	1 – 70	0.50*		
7xMed	# of times discharge exceeded 7x median flow	1 – 64	0.56*		
9xMed	# of times discharge exceeded 9x median flow	0 – 58	0.58*		
>75th	# of times discharge exceeded 75th percentile	25 – 115			
>95th	# of times discharge exceeded 95th percentile	12 – 66			
>99th	# of times discharge exceeded 99th percentile	2 – 35	0.62**		
	Duration (# of hours spent above threshold)				
>3xMed_d	Hours discharge was >3x median flow	36.5 – 3026			
>5xMed_d	Hours discharge was >5x median flow	6 – 2518			
>7xMed_d	Hours discharge was >7x median flow	1.5 – 2412			
>9xMed_d	Hours discharge was >9x median flow	0 – 17			
Predictability and Flashiness					
C.V.	% Coefficient of Variation	42 – 402			
Inc1h100	# of events discharge increases by 100% within 1 hr	7 – 109	0.55*		
Inc1h1000	# of events discharge increases by 1000% within 1 hr	0 – 31			
Inc1h5000	# of events discharge increases by 5000% within 1 hr	0 – 17			-0.47*

Inc3h100	# of events discharge increases by 100% within 3 hr	11 – 122	0.53*
Inc3h1000	# of events discharge increases by 1000% within 3 hr	0 – 44	
Inc3h5000	# of events discharge increases by 5000% within 3 hr	0 – 19	
Dec1h100	# of events discharge decreases by 100% within 1 hr	0 – 67	
Dec1h1000	# of events discharge decreases by 1000% within 1 hr	0 – 28	
Dec1h5000	# of events discharge decreases by 5000% within 1 hr	0 – 12	
Dec3h100	# of events discharge decreases by 100% within 3 hr	1 – 92	
Dec3h1000	# of events discharge decreases by 1000% within 3 hr	0 – 36	
Dec3h5000	# of events discharge decreases by 5000% within 3 hr	0 – 18	
Baseflow (L s^{-1})			
Med_bf	Median baseflow (L s^{-1})	0.04 – 730	
BI	Baseflow index (∑ predicted baseflow/ ∑observed flow)	0.03 – 0.82	

Table 3. Physicochemical and habitat (environmental) variables used in analyses, the range of values, and their Pearson correlations to predominant land cover classes in the 18 watersheds. **IS** = proportion of impervious surface cover, **Forest** = proportion of forest cover (managed + unmanaged), **Pasture** = proportion of pasture cover. * $p < 0.05$, ** $p < 0.01$, $p < 0.001$***.

Variable ID	**Description**	**Range**	**IS**	**Forest**	**Pasture**
Temp	Median water temperature (^{o}C)	13.3 – 15.6	0.67**	-0.54*	
DO	Mean dissolved O_2 (mg L^{-1})	8.6 – 14.5	-0.50*		
minDO	Minimum dissolved O_2 (mg L^{-1})	0.2 – 8.3			
pH	Mean pH	5.7 – 6.9			
TDS	Mean total dissolved solids concentration (mg L^{-1})	19.9 – 58.6	0.58*		
TSS	Mean total suspended solids concentration (mg L^{-1})	2.1 – 8.1			0.54*
Volume	Mean depth x width x length of habitat sampled (m^3)	0.6 – 6.9	0.76***	-0.65**	
OM	Benthic organic matter (g)	0.3 – 1.2		0.47*	
Substrate	Median substrate size (cm)	0.5 – 1.8	0.52*		
Tg	Tractive force	2.7– 73.9			
Habitat Index	Habitat assessment index score	54.2 – 125.5		0.48*	

Table 4. Associations between select hydrologic variables and environmental variables. Values are Pearson correlation coefficients, and only those with a significant correlation are shown. * $p < 0.05$, ** $p < 0.01$, $p < 0.001$***.

	MedQ	5xMed	7xMed	9xMed	Inc1h100	Inc1h5000	Inc3h100
Temp		0.55*	0.66**	0.69**	0.48*		
DO		-0.59*	-0.69**	-0.72**			
pH					0.76***		0.73**
TDS		0.78***	0.84***	0.85***			
TSS						-0.69**	
Substrate		0.72**	0.74***	0.73**	0.53*		0.48*
Tg	0.52*						
Habitat Index						0.55*	

Table 5. Fish species collected and Pearson correlation coefficients to non-metric multidimensional scaling (NMDS) axes 1 and 3. Rare species excluded from NMDS analyses are denoted by dashes. Breeding guild abbreviations: S = Simple miscellaneous, L = Simple lithophil, Cpc = Complex with parental care, Cnc = Complex with no parental care. Feeding guild abbreviations: P = Predator, I = Insectivore, H = Herbivore, O = Omnivore, F = Filterer.

Family	**Species**	**Common name**	**Breed**	**Feed**	**NMDS$_1$**	**NMDS$_3$**
Catastomidae	*Erimyzon oblongus*	Creek chubsucker	S	I	0.38	0.18
	Hypentelium etowanum	Alabama hog sucker	L	I	0.12	0.22
	Minytrema melanops	Spotted sucker	L	I	-	-
Centrarchidae	*Lepomis auritus*	Redbreast sunfish	Cpc	I	-0.37	0.72
	L. cyanellus	Green sunfish	Cpc	I	-0.39	0.19
	L. gulosus	Warmouth	Cpc	P	-0.29	-0.34
	L. macrochirus	Bluegill	Cpc	I	-0.52	-0.55
	L. megalotis	Longear sunfish	Cpc	I	-0.39	-0.43
	L. miniatus	Redspotted sunfish	Cpc	I	0.06	0.22
	Micropterus salmoides	Largemouth bass	Cpc	P	-0.29	0.13
Cyprinidae	*Campostoma pauciradii*	Bluefin stoneroller	Cnc	H	0.04	0.06
	Luxilus zonistius	Bandfin shiner	L	I	0.81	0.24
	Nocomis leptocephalus	Bluehead chub	Cnc	O	0.82	0.17
	Notemigonus crysoleucas	Golden shiner	S	I	-0.35	-0.30
	Notropis baileyi	Rough shiner	L	I	0.65	-0.19
	N. buccatus	Silverjaw minnow	S	I	0.19	-0.37
	N. longirostris	Longnose shiner	L	L	0.48	-0.11
	N. texanus	Weed shiner	S	I	-0.43	-0.12
	Semotilus atromaculatus	Creek chub	Cnc	O	0.61	0.07
Ictaluridae	*Ameirus natalis*	Yellow bullhead	Cpc	O	-0.40	0.16
	A. nebulosus	Brown bullhead	Cpc	O	0.07	0.37
	Ictalurus punctatus	Channel catfish	Cpc	O	-	-
	Noturus leptocanthus	Speckled madtom	Cpc	I	-	-
Percidae	*Percina nigrofasciata*	Blackbanded darter	L	I	-0.17	-0.29
Petromyzontidae	*Ichthyomyzon gagei*	Brook lamprey	Cnc	F	0.38	0.37
Poeciliidae	*Gambusia affinis*	Western mosquitofish	Cnc	I	-0.43	0.14

Table 6 Fish metrics and their correlations watershed LU/LC and with best NMDS axes. Only significant correlations are shown. **IS** = proportion of impervious surface cover, **Forest** = proportion of forest cover, **Pasture** = proportion of pasture cover, **NMDS$_1$** and **NMDS$_2$** are NMDS axes 1 and 2, respectively. Fish metrics are as described in text. * p < 0.05, ** p < 0.01.

Metric		**IS**	**Forest**	**Pasture**	**NMDS$_1$**	**NMDS$_3$**
Breeding						
	Parent Care					0.78***
	No Parent Care				-0.61**	
	Simple Lithophilic	-0.66**	0.51*		0.87***	
Feeding						
	Piscivore					
	Insectivore	0.57*	-0.51*		-0.57*	
	Herbivore					
	Omnivore				0.61**	
	Filterer				0.50*	
Assemblage						
	Number				0.50*	
	Richness	-0.66**			0.46*	
	Diversity	-0.85***	0.52*		0.55*	
	% Sunfish	0.58*			0.75***	
	IBI				0.48*	

Table 7. Best multiple regression models for fish assemblage variables with standardized regression coefficients and R^2_{adj}. Fish metric definitions are as in text, Predictor definitions are as in Tables 2 and 3. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Metric	**Predictors**	**Standardized Estimate**	**R^2_{adj}**
N	Temp	-0.58	**0.29****
Richness	5xMed	-0.68	**0.43****
	Temp	-0.40	
Diversity	TDS	-0.54	**0.54*****
	N>99	-0.40	
%Sunfish	TDS	0.73	**0.48****
	MedQ	0.43	
IBI	7xMed	-0.52	**0.22***

Figure 1. Conceptual model of the potential causal relationships between land use/land cover, abiotic conditions, and biotic assemblages of streams.

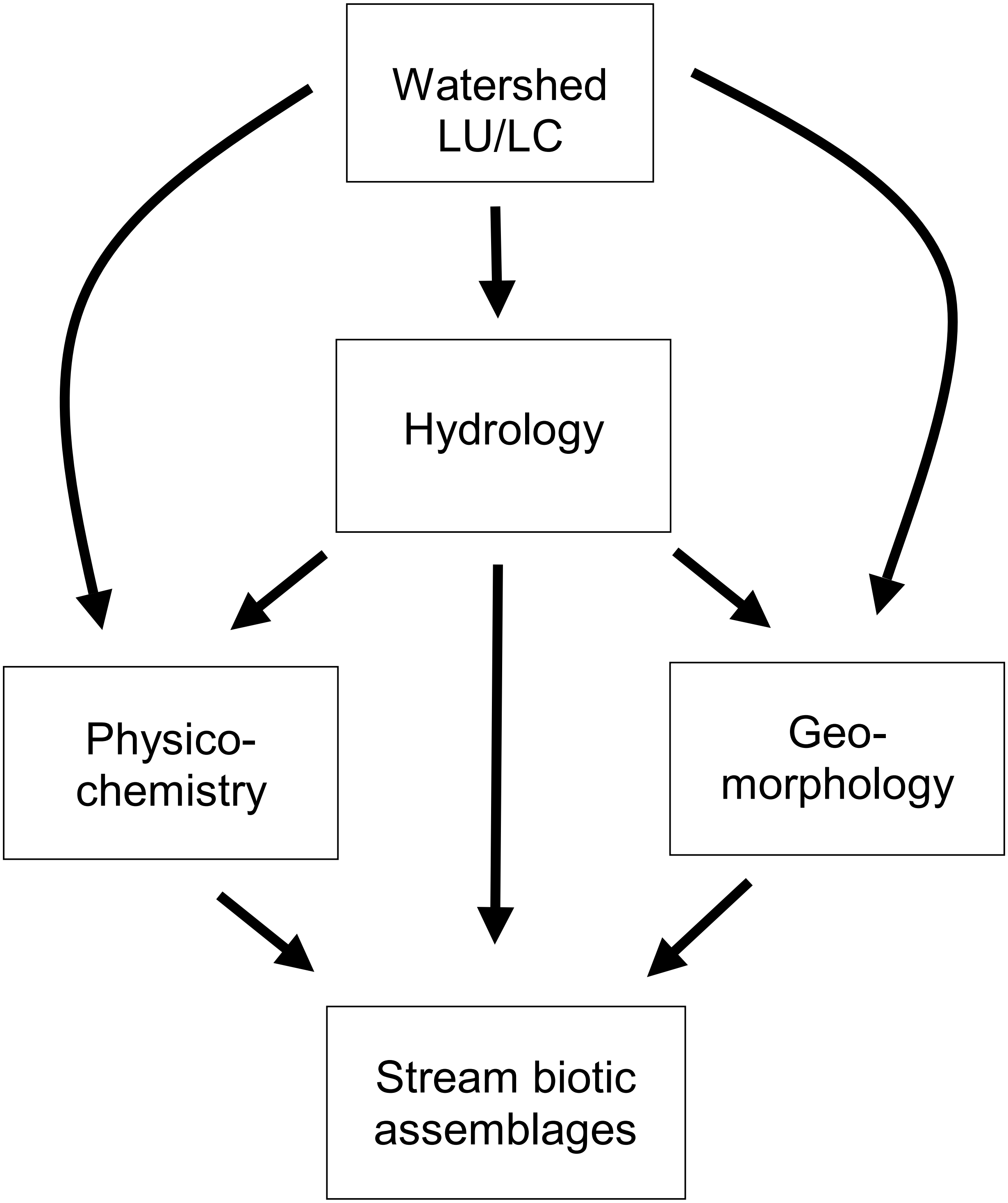


Figure 2. The study area included 18 small watersheds (shaded) of the Chattahoochee River basin in 4 counties in the Lower Southern Piedmont ecoregion. The city of

Columbus is located in western Muscogee County. County names are in capital letters. Numbers refer to watersheds and correspond to codes in Table 1.

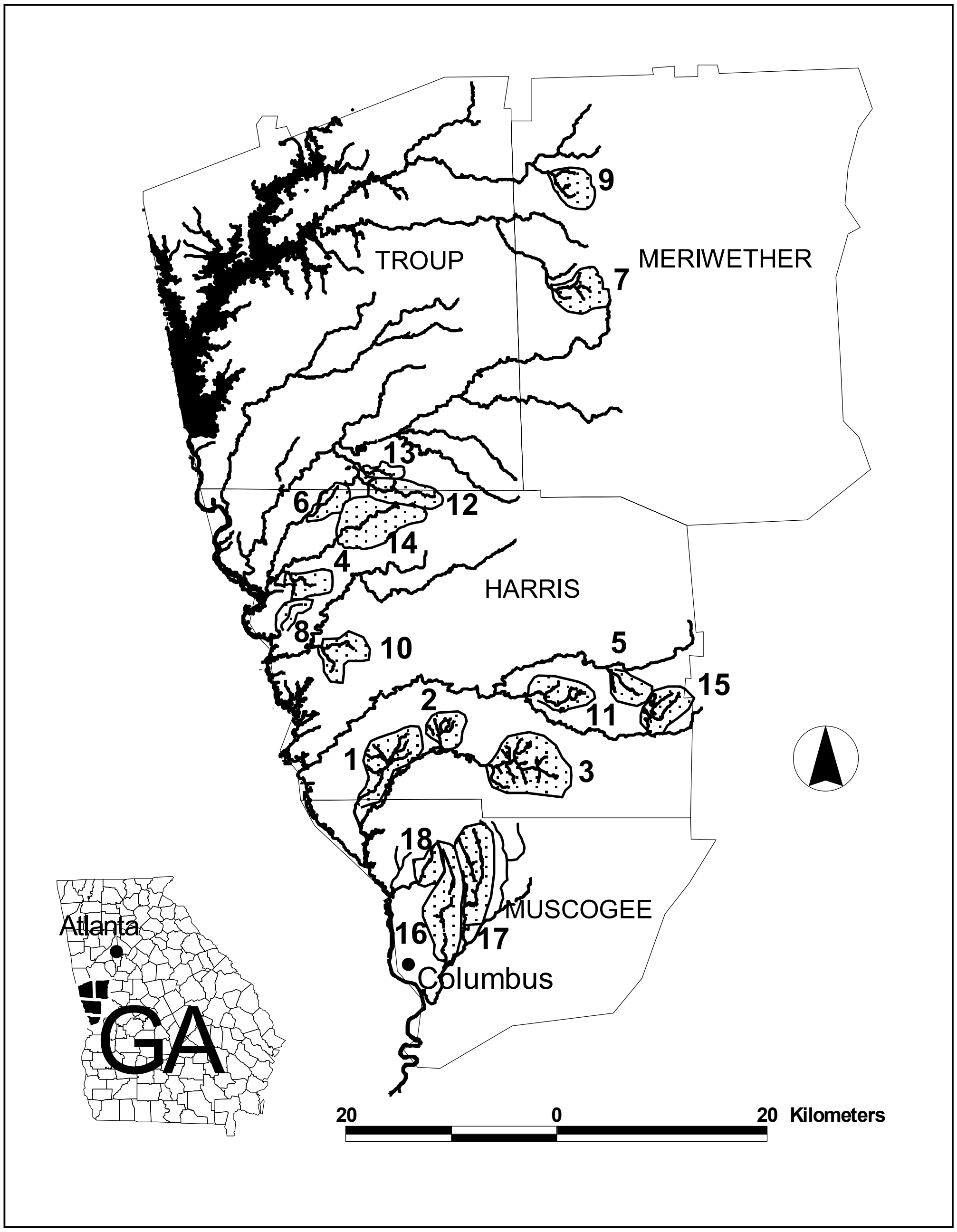
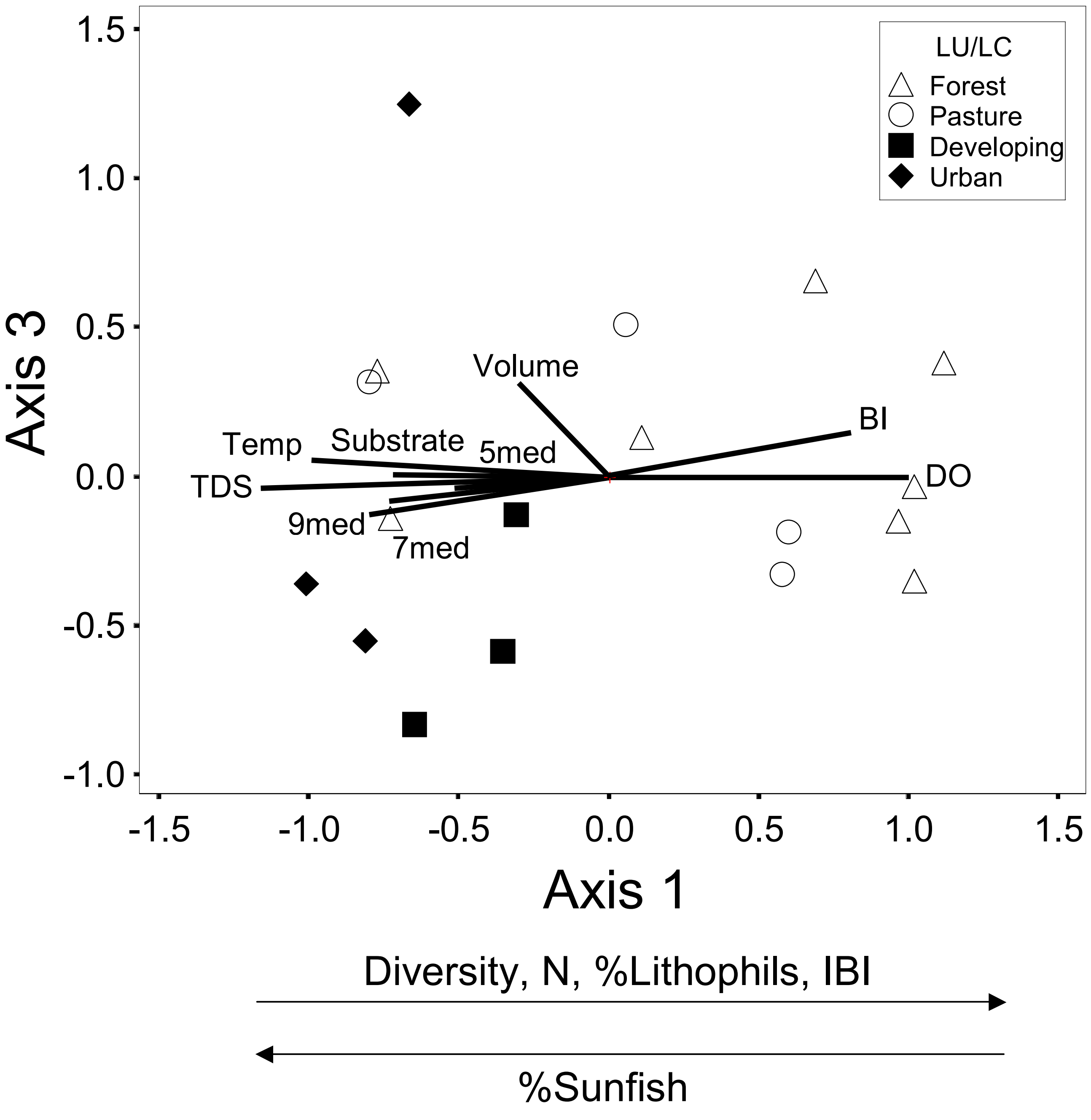


Figure 3. Non-metric multidimensional scaling ordination (NMDS) of sites in ordination space. Axes are scaled proportionate to the longest axis (% of max). Symbols are the 18 study sites coded by land use classifications as described in text with vectors that show

relative direction and strength of correlated environmental variables. Arrows on x and y axes show direction of correlated fish assemblage values. Axes 1 and 3 explain 57.1 and 25.3% of the total variation, respectively.



CHAPTER 4. Land use impacts on stream macroinvertebrate assemblages: temporal variability and the interplay of hydrology, physicochemistry, and geomorphology

4.1 ABSTRACT

I examined the influence of land use / land cover (LU/LC) on macroinvertebrate assemblages over a 12-mo period of record in streams draining 20 small watersheds in the Lower Piedmont of Georgia, USA. Specifically, I quantified seasonal relationships between LU/LC (as % impervious surface [IS], pasture, silviculture, and mixed forest) and several macroinvertebrate metrics as well as the relative influence of hydrology, physicochemistry, and geomorphology on annual values of macroinvertebrate metrics. There were seasonal differences in all macroinvertebrate metrics, but most revealed no seasonal interaction with LU/LC. High-IS watersheds generally had more biologically impaired streams (with degraded conditions generally appearing at ~10% IS) than watersheds containing intense pasture, silviculture, and suburban development, compared with forested reference watersheds. Several elements of hydrology, geomorphology, and physicochemistry were related to LU/LC, including measures of spate flow frequency, benthic habitat conditions, stream temperature, sulfate, nitrate, and fecal coliform levels, although only physicochemical and geomorphological variables were associated with macroinvertebrate variables. Nonmetric multidimensional scaling revealed that macroinvertebrate assemblages were associated with benthic detritus cover, dissolved oxygen levels, stream water temperature, and total dissolved solid concentration. Our

results suggest that the influence of LU/LC on aquatic biota remains invariant throughout the year and that macroinvertebrate assemblages are more directly influenced by changes in physicochemistry and benthic habitat conditions than by hydrological alterations associated with LU/LC in the watersheds of this region.

4.2 INTRODUCTION

Human activities are responsible for much of the alteration in land-use/land cover (LU/LC) worldwide, and rivers and streams are among the most affected ecosystems by these changes (Hammett 1992, Schnaiberg et al. 2002). LU/LC within a watershed can influence the overall quality of stream ecosystems by directly altering hydrology, physicochemical conditions, and geomorphology, which, in turn, determine biotic composition (Bormann et al. 1999, Peterson and Kwak 1999, Clements et al. 2000, Bledsoe and Watson 2001, Riis and Sand-Jensen 2001, Maloney et al. 2005). Ultimately, even slight changes in LU/LC can dramatically alter stream biotic integrity by increasing physiological stress of individuals, reducing population sizes, and causing alterations in species diversity and other measures of community structure (Lenat and Crawford 1994, Paul and Meyer 2001, Roy et al. 2003, Walters et al. 2003, Allan 2004, Maloney and Feminella 2006).

In the southeastern United States, silviculture, agriculture, and urbanization are common types of land use, and disturbance from each type may apply its own unique suite of pressures on receiving streams (Brown et al. 2005). Timber harvest and agricultural practices often degrade receiving waters through the alteration/removal of riparian and watershed vegetation, which can increase stream bank failure and sedimentation, nutrient and pesticide concentrations and loads, light levels, water temperature, and productivity (Allan 2004, Fortino et al. 2004). Disturbance from silviculture is generally not thought to be as damaging as row crop agriculture since post-harvest vegetation regrowth often approaches predisturbance levels, whereas it does not with row crop agriculture (Campbell and Doeg 1989, Fortino et al. 2004); however the impacts of both are often minimized with implementation of Best Management Practices (BMP) guidelines (Prud'homme and Greis 2002, Wang et al. 2002, Fortino et al. 2004).

Neither silviculture nor agriculture is as damaging to receiving waters as are the physical and chemical impacts from urbanization. The substantial influence of watershed urbanization on streams are often considered a direct result of, or mediated by, altered hydrologic regimes (Paul and Meyer 2001, Allan 2004). Increases in impervious surface runoff and stormwater conveyance can dramatically increase magnitude and frequency of storm flows, accelerating nutrient and pollutant transport, altering thermal and decomposition dynamics, eroding streambeds, and displacing organisms (Jones and Clark 1987, Walsh et al. 2001, Walters et al. 2003, Roy et al. 2005, Chadwick et al. 2006). The predictable biotic impacts from watershed disturbance has led to the identification of a generalized ecosystem distress syndrome (or specifically “urban stream syndrome” in urbanized watersheds (*sensu* (Meyer et al. 2005), which includes reduced biodiversity, altered productivity, and increased abundance of tolerant and exotic species (Rapport et al. 1985, Walsh et al. 2005b).

Effects of LU/LC on streams often are regional and episodic, varying geographically and seasonally, usually becoming more pronounced with increased precipitation and discharge (Weaver and Garman 1994, Helms et al. 2005, Walsh et al. 2005b). In addition, the shape of biotic response (e.g., linear, threshold, subsidy-stress) to LU/LC disturbance depends upon the species sensitivity and the stressor's mode of action (e.g. toxicity, sub-lethal stress), properties that also can vary spatially and temporally (Allan 2004). Further, specific mechanisms of LU/LC-associated impacts on aquatic systems have been elusive because of their interrelated nature (Paul and Meyer 2001, Allan 2004). A more comprehensive understanding of temporal and spatial influences of LU/LC on receiving waters at the regional scale is essential for effective monitoring, assessment, and management of aquatic resources in streams draining degraded watersheds. Our study was designed to further examine these LU/LC impacts on stream macroinvertebrates in the Southern Outer Piedmont of the US, and examine potential mechanisms associated with any observed biotic changes. Specifically, I quantified 1) the relative seasonal impact of various LU/LC conditions on stream macroinvertebrate assemblages, and 2) the relative influence of putative hydrological, chemical, and geomorphological stressors associated with LU/LC disturbance. This information will allow for a more time-integrated, mechanistic understanding of LU/LC impacts on stream biota in attempts to minimize anthropogenic impacts on freshwater systems.

4.3 METHODS

4.3.1 Study area

I studied stream reaches from tributaries of the middle Chattahoochee River, western Georgia, USA, occurring in the Southern Outer Piedmont ecoregion, 45b (Griffith et al. 2001). Conversion of pasture and forests to urbanized areas is occurring rapidly northeast of the city of Columbus, Muscogee County. Therefore, I sampled 2nd- to 3rd-order streams within 20 watersheds (4–25 km^2) along an urbanization gradient from the geologic fall line in the city of Columbus to an area 80 km northeast (Muscogee, Harris, Troup and Meriwether counties, Figure 1). Stream study reaches were ~100 m and typical of the lower Piedmont, consisting of sandy-bottom channels and run-pool morphologies. The relatively large range in landscape character in the region allowed comparison across geomorphically similar streams that differed primarily in watershed-level LU/LC and associated variation in streamwater physicochemical conditions.

4.3.2 Land cover / land use analysis

I determined watershed boundaries and size from US Geological Survey 30-m resolution digital elevation models and ArcView 3.2a software (Environmental Research Systems Institute, Inc., Redwoods, California). In March 2003, true-color 1-m resolution aerial photographs of the study watersheds were taken coinciding with leaf-off. Impervious surfaces (IS) were manually digitized and remaining land cover was classified using a hybrid unsupervised/supervised technique, resulting in a land cover classification similar to the Anderson Classification Scheme (Myeong et al. 2001). For each watershed I determined % IS, % pasture, % evergreen forest, and % deciduous forest for analyses. Detailed image processing methods for the study watersheds are presented elsewhere (Lockaby et al. 2005). I then inferred land use by grouping each watershed into the following categories based on predominant land cover and assumed influential land use assessed in the field: *Forest* (mixed evergreen/deciduous forests); *Silviculture* (heavily managed pine forests); *Pasture* (cattle grazing and/or forage production); *Developing* (forested but with current or recent residential development); and *Urban* (downtown Columbus) (Table 1).

4.3.3 Stream hydrology variables

I quantified stream discharge (Q) from June 2003 to June 2004 using a Mini-Troll® pressure-transducer data logger (In-Situ Inc., Ft. Collins, Colorado) installed in each study stream. Data loggers were set to measure water depth every 15 min (0.01-m depth resolution), and I then developed depth–Q rating curves to estimate continuous Q (Schoonover et al. 2006). I characterized 5 separate elements of Q from each watershed hydrograph: 1) *magnitude* (amount of Q for a given interval), 2) *frequency* (number of occurrences of a given magnitude of Q, 3) *duration* (length of time associated with a particular high or low Q event, 4) *predictability/flashiness* (coefficient of variation and rate of change of Q), and 5) *baseflow* (predicted baseflow contribution to Q and baseflow index, BI) (Richter et al. 1996, Poff et al. 1997, McMahon et al. 2003). I predicted baseflow for each watershed using a 5-d smoothed minima technique (Gustard et al. 1992) and calculated the BI as:

$$\sum \text{predicted baseflow} / \sum \text{observed flow}$$

where 1 = no overland contribution and 0 = complete overland contribution to observed flow (Gustard et al. 1992, Schoonover et al. 2006). Ultimately, I calculated 28 hydrologic variables considered important in determining aquatic biota (Richter et al. 1996, Poff et al. 1997) (Table 2).

4.3.4 Physicochemical variables

I measured several stream-specific physical and chemical variables thought to be important in determining biotic assemblages over the hydrological period of record (Table 3). I measured stream temperature continuously with HOBO® Temp data loggers placed near pressure transducers used for Q. Dissolved oxygen (DO) and streamwater pH were measured seasonally. In addition, I quantified several nutrient and sediment parameters, including total suspended solids (TSS), total dissolved solids (TDS), fecal coliform colonies (FC), total phosphorus (P), dissolved organic carbon (DOC), SO_4^{2-} and NO_3^- concentrations. I measured each of the above parameters by taking with streamwater grab samples collected monthly for each watershed (see methods in (Schoonover and Lockaby 2006).

4.3.5 Macroinvertebrates

I quantified benthic macroinvertebrates in 3 pools and 3 runs per stream reach during September (summer), February (winter), and April – May (spring) in 2003 – 2004 using a Surber sampler (250-µm mesh; 0.093 m^2 sampling area). I consolidated multiple Surber collections in each habitat (3 for pools, 4 for runs), resulting in a 0.27- and 0.36-m^2 sample from each pool and run, respectively (1.89 m^2 total area sampled for each study reach per stream and season). I elutriated excess sediment and preserved all samples with 95% EtOH in the field. In the laboratory, I removed all organisms >2mm with the unaided eye, and subsampled the remainder under a dissecting microscope (≥ 300 organisms, (Vinson and Hawkins 1996). I counted, measured length (nearest mm), and identified macroinvertebrates to the lowest possible taxonomic level (usually genus or morphospecies) using keys in (Merritt and Cummins 1996), (Wiggins 1996), and (Epler 2001) and also assigned macroinvertebrates to functional feeding, habit, and tolerance groups (Merritt and Cummins 1996).

I calculated several benthic macroinvertebrate metrics selected from standard US Environmental Protection Agency (USEPA) bioassessment protocols (Barbour et al. 1999) spanning 4 broad categories of metrics (Table 5): (1) *Taxonomic* metrics, which included the proportion and/or taxa count of particular taxonomic groups, such as Ephemeroptera, Plecoptera, Trichoptera, and other putatively sensitive groups; (2) *Functional* metrics, which included the proportion and/or taxa count of macroinvertebrates in various functional feeding groups (FFGs), habitat uses, and tolerance classes; (3) *Community* variables, which included diversity (as Shannon's *H'*), taxa richness, total invertebrate biomass using published length-mass relationships (Benke et al. 1999), and density; and (4) a single *Composite* variable, which was the Georgia Benthic Macroinvertebrate Index (GA-BMI, (GADNR 2007). The GA-BMI is an ecoregion-specific multimetric index designed for streams in Georgia, with 6 metrics calculated for the Southern Outer Piedmont, where scores ≥ 84 = very good, 56 – 83 = good, 32 – 55 = Fair, 17 -31 = Poor, and < 17 = Very Poor (GADNR 2007). For seasonal analyses, I used seasonal macroinvertebrate values from each watershed, whereas for annual analyses I averaged seasonal values to obtain one value per watershed.

I characterized stream microhabitat when macroinvertebrates were sampled by quantifying mean depth, width, current velocity (Marsh-McBirney model 2000 flow meter) and benthic substrate composition at each run and each pool habitat in each season (Table 4). Benthic substrate characterization consisted of estimating the % cover of clay, silt, sand, gravel, cobble, wood, detritus, and wood in 10% increments in each habitat sampled. All substrate estimates were done by a single observer (BSH) to reduce observational error. In addition to the measures taken seasonally, I quantified mean benthic organic matter (BOM), substrate size, and tractive force (shear stress, T_G (Gordon et al. 1992)) for each watershed once over the study. I estimated BOM and substrate size by sampling in transitional areas between runs and pools in all streams to minimize the influence of deposition and scour on our estimates. I quantified BOM by determining the ash-free dry mass (AFDM) of 9 replicate 2.5 x 10 cm benthic cores. For substrate particle size I collected 3 benthic samples per stream (near where BOM was sampled) using a 76.2-mm diameter PVC core inserted into the substrate to a depth of 10 cm. I dried samples and separated particles into 5 size classes: gravel-cobble (>2mm), very coarse sand (1 – 2 mm), coarse to medium sand (0.25 – 1 mm), fine sand (0.1 – 0.25 mm), very fine sand (0.05 – 0.1mm), and silt/clay (< 0.05mm) to determine median substrate size by mass. I estimated T_G close to where pressure transducers using the formula

$$T_G = pg\mathrm{RS}$$

where p is the density of water, g is gravitational acceleration, R is hydraulic radius, and S is slope of the energy line (Newbury 1996).

4.3.6 Statistical analyses

I used general linear models (GLMs) to describe broad differences in macroinvertebrate community and composition metrics among LU/LC categories, seasons, and potential LU/LC–season interactions. Following GLM, I assessed any differences between sites and seasons with Tukey HSD multiple comparison tests (Zar 1999). Two sites (FR and BR) were only sampled for macroinvertebrates once (Spring) and thus had no accompanying hydrographs; therefore, I excluded these watersheds from all subsequent multivariate analyses.

Simple Pearson correlation analyses were used to relate hydrologic, habitat, and chemical variables to LU/LC variables. I then conducted 3 separate Principal Component Analyses (PCA) to describe overall variation in hydrologic, physicochemical, and habitat conditions, respectively, in study watersheds. Annual values of all environmental variables for each particular group (hydrology = 28 variables, physicochemistry = 11, habitat = 12) were used in the respective PCA ordinations, resulting in 3 site – parameter matrices, upon which ordinations were constructed (18 x 28 hydrology, 18 x 11 physicochemistry, and 18 x 12 habitat). I transformed all variables as needed to meet assumptions of normality and based ordinations on the correlation cross-products matrix. The resulting ordinations were used to isolate groups of variables explaining a large proportion of the environmental variance, with first 2 PC axes from each ordination used as predictor variables in subsequent multiple regression analyses between community and composition macroinvertebrate variables.

I used nonmetric multidimensional scaling (NMDS) to describe overall variation in macroinvertebrate assemblages among sites. NMDS, an ordination technique that uses species data to create pairwise similarity matrices to determine positions of sites in species space, handles nonnormal data (e.g., with many zero counts) better than other ordination techniques (Hawkins et al. 1997, McCune and Grace 2002). NMDS ordinations were based upon annual presence/absence of macroinvertebrates, with rare taxa (those occurring in only 1 site) being excluded. This step resulted in an 18 x 113 site-species matrix on which ordinations were based using a Sorenson distance measure (McCune and Grace 2002). I then correlated environmental and macroinvertebrate responses to the 2 most explanatory axes of the NMDS.

I used simple regressions to determine the best LU/LC predictor for the community and composite macroinvertebrate metrics. Then, using the first 2 axes from each PCA as predictors and the composite/community metrics and the best NMDS axis as response variables, I used stepwise multiple regression ($p = 0.05$ to enter and leave the model) to determine the environmental parameter groups with the most explanatory power regarding annual values of macroinvertebrate metrics. Parameters in final models had a variance inflation factor (VIF) <10; thus, multicollinearity was avoided (Myers 1990).

I used SAS (version 8.2, SAS Institute Inc., Cary, North Carolina) for all correlation and regression analyses and PC-ORD (version 4, MjM Software Design, Glenden Beach, Oregon) for PCA and NMDS. For all analyses, $\alpha = 0.05$.

4.4 Results

4.4.1 Environmental variables and LU/LC

Many environmental variables showed strong associations with LU/LC. In general, spate flow frequency and overall flashiness increased with % IS, as evidenced by the positive relationships between IS and 5xMed, 7xMed, 9xMed, N>99, and Inc3h100 (Table 2). Also, substrate and habitat conditions differed across sites given contrasting LU/LC, with substrate size increasing and benthic detritus decreasing with % IS, benthic detritus increasing with % deciduous forest, and OM increasing with % evergreen forest (Table 3). Chemical conditions also were related to LU/LC. Temp, TDS, SO_4 and FC all increased with increasing IS and decreased with increasing deciduous cover (Table 4). Further, DO increased with % deciduous cover and decreased with % IS, whereas NO_3 was positively associated with % pasture and negatively associated with % evergreen forest (Table 4; see (Schoonover and Lockaby 2006, Schoonover et al. 2006) for details about hydrologic and chemical associations with LU/LC).

4.4.2 Macroinvertebrate assemblages

I collected a total of 148 unique taxa in 52 families, with Chironomidae (Diptera), Hydropsychidae (Trichoptera), Tubificidae (Haplotaxida) and Simuliidae (Diptera) being the 4 most common groups. Gatherers and Filterers generally were the most abundant FFGs, whereas Clingers and Scrapers were the least abundant (Table 5). Filterers had the highest single occurrence (64% of total abundance; BU2) whereas Shredders were virtually absent from several streams, primarily in winter and spring. Numerical dominance of FFGs varied by season, with Shredders and Filterers being dominant in summer, Gatherers in winter, and Filterers and Gatherers in spring (Table 5). Clingers, Filterers, Gatherers, and Predators occurred at all sites.

H' ranged from 0.79 to 2.90, taxa richness ranged from 14 to 64, biomass ranged from 1 to 759 g / m^2, and density ranged from 2504 to 68,429 individuals / m^2. GLM indicated strong seasonal and LU/LC differences in macroinvertebrate metrics. *H'* was highest in summer ($F_{2,55} = 3.47$, $p = 0.04$), richness ($F_{2,55} = 6.21$, $p = 0.0004$) and biomass ($F_{2,55} = 5.33$, $p = 0.006$) were highest in spring, and density ($F_{2,55} = 4.2$, $p = 0.022$) was highest in winter (Table 6, Fig. 2). GA-BMI ranged from 3 to 75 and was highest in summer ($F_{2,55} = 27.93$, $p < 0.001$) (Table 6, Fig. 2). Forest watersheds generally showed higher richness ($F_{4,55} = 24.96$, $p< 0.001$), *H'* ($F_{4,55} = 5.89$, $p = 0.001$), and GA-BMI ($F_{4,55} = 18.12$, $p < 0.001$) than Urban watersheds, with Silviculture, Pasture, and Developing watersheds generally being intermediate between Forest and Urban watersheds (Fig. 2). In contrast, mean biomass was higher ($F_{4,55} = 3.96$, $p = 0.011$) in Urban than Forest, Silviculture, and Pasture watersheds (Fig. 2).

Across seasons, the best LU/LC predictors of community and composite macroinvertebrate metrics were % deciduous forest and IS (Table 7). % deciduous cover best described seasonal averages for richness ($R^2 = 0.73$, $p < 0.0001$), *H'* ($R^2 = 0.42$, $p = 0.002$), and GA-BMI ($R^2 = 0.67$, $p < 0.0001$) whereas % IS best described seasonal means for biomass ($R^2 = 0.39$, $p = 0.003$). GA-BMI also was inversely related to IS, with metric scores decreasing as a curvilinear function of increased % IS (Fig. 3).

4.4.3 Multivariate relationships

In the hydrology PCA, the first 2 axes (H-PC_1 and H-PC_2) explained 69.8% of the variation (45.3 and 19.4%, respectively) among sites. In general, median discharge (MedQ), median baseflow (MedBF), and groundwater contribution to baseflow (BI) decreased whereas spate frequency (as 5xMed, 7xMed) and flashiness (as Inc1h1000, Inc3h1000, Inc3h5000, Dec1h100, Dec3h100) increased with H-PC_1 (Table 8). Maximum discharge (MaxQ) and spate frequency (as 3, 5, 7xMed) decreased whereas BI increased with H-PC_2.

For substrate/habitat PCA, the first 2 PCA axes (S-PC_1 and S-PC_2) explained 57.8% of the variation (35.1 and 22.7%, respectively). Substrate size decreased along S-PC_1, with proportion of sand and wood being positively correlated and proportion of gravel, cobble, and bedrock negatively so with S-PC_1 (Table 8). Substrate size increased whereas organic matter (OM) and proportion of detritus decreased along S-PC_2 (Table 8).

For the water chemistry PCA, axis 1 (C-PC_1) explained 50.1% and axis 2 (C-PC_2) explained 20.9% of the variation (71% total). Many chemical parameters loaded strongly on C-PC_1, with temperature, pH, TDS, SO_4, NH_4, DOC, and FC all decreasing and DO increasing along this axis. TSS and NH_4 increased and NO_3 decreased along C-PC_2 (Table 8).

NMDS axes 1 and 2 described the most variation in macroinvertebrate assemblages among streams (79.3 and 9.8%, respectively; stress = 13.4, instability = 0.00001, iterations = 66; Fig. 4). Streams of similar watershed LU/LC generally grouped together, although streams in Urban watersheds grouped far to the left of the other groups (Fig. 4); thus, I considered $NMDS_1$ to be a general urbanization axis, and used it as an invertebrate response variable in multiple regressions.

Based on NMDS ordination, Diptera and EPT richness and % scrapers were more associated with Forest and Developing watersheds whereas % tolerant taxa and % Oligochaetes were higher in Urban than other sites. Regarding composite and community metrics, GA-BMI, *H'*, and richness all were positively correlated with $NMDS_1$ and negatively so with $NMDS_2$ (Table 9). In addition, biomass was negatively correlated with $NMDS_1$ and density negatively so with $NMDS_2$ (Table 8). Last, spate flow frequency (5xMed, 7xMed, 9xMed), spate magnitude (N>99), substrate size, water temperature (MeanT, MaxT), DO, and SO_4 all were negatively associated with $NMDS_1$ (Table 9).

All multiple regression models based on the 1st and 2nd axes of the 3 PCAs for composite and community macroinvertebrates were significant, most with R^2_{adj} >0.75 (Table 7). Generally, water chemistry was the overall best predictor of composite and community macroinvertebrate responses, as evidenced by the presence and large standardized estimate of either C-PC_1 or C-PC_2 (or both) in all best multiple regression models (e.g., 11 of 15 significant factors were C-PC_1 or C-PC_2, Table 7). In contrast, hydrologic axes (i.e., H-PC_1 and H-PC_2) were entirely absent as predictors from all best models.

4.5 DISCUSSION

Environmental factors shaping benthic macroinvertebrate distributions in streams are numerous, often interactive, and frequently associated with landscape disturbance (Allan 2004). Like other studies, our results show that LU/LC is particularly influential on macroinvertebrate assemblage structure and its effects persist across different seasons. In our study, streams with any level of recent human watershed activity (as agriculture, silviculture, urban development) had generally fewer species, more tolerant taxa, and overall lower biotic integrity scores than those streams draining primarily mixed forest. These impacts undoubtedly occur via several pathways and mechanisms, but LU/LC-induced changes in stream physicochemical conditions appears to be paramount in influencing assemblage structure in these systems.

4.5.1 Relative impacts of different LU/LC

Urbanization has been identified as one of the most pervasive and damaging types of landscape disturbance on aquatic systems (Paul and Meyer 2001). Streams in our study within heavily urbanized watersheds had consistently lower biological integrity, and generally different macroinvertebrate assemblages altogether, than other watersheds, suggesting an alternative urban stable state or dynamic regime (Scheffer and Carpenter 2003). Urban sites were characterized by increased proportions of a suite of tolerant taxa (e.g. oligochaete worms, physid snails, *Corbicula*, hydropsychid caddisflies) and a concomitant low abundance of many otherwise common macroinvertebrates. This pattern is likely a function of increased spate flow frequencies, chemical concentrations, water temperature and decreased DO and benthic habitat observed in these streams, together considered part of the urban stream syndrome (Walsh et al. 2005b).

Overall, % IS or Deciduous were the best LU/LC predictors of macroinvertebrate metrics. IS cover in these watersheds spanned a broad range, yet most watersheds had <4% and were largely indistinguishable below this level. In contrast, deciduous cover across the study watersheds was much more even (8 – 38%) and, thus, could be considered the inverse of general human disturbance from silviculture, pasture, and/or urbanization. Therefore, macroinvertebrate responses best described by % IS (i.e., biomass and NMDS_1) ostensibly were driven by the small proportion of urban sites in our study, and likely best captured the degradation associated with this land use. Therefore, the differences between urban and non-urban sites likely account for most of the variation in macroinvertebrate assemblage structure and biomass. Richness, *H'*, and GA-BMI were best described inversely by % Deciduous, suggesting these metrics discerned variability associated with general, rather than urban, LU/LC disturbance. Interestingly, GA-BMI scores were better predicted by % deciduous forest, but they responded non-linearally to % IS. This pattern suggests a threshold of urban degradation ~10% watershed imperviousness, a level similar to what other studies have reported (Booth and Jackson 1997, Wang et al. 2000, Walsh et al. 2005b). Although these 2 land cover classes were largely complementary in urban watersheds, the fact some metrics were best predicted by deciduous forest cover and some by IS cover suggests nuances in metric sensitivities to the various conditions associated with different land covers.

Streams draining managed pine forests, agriculture, and residential development generally showed intermediate levels of impairment, with no discernable differences among them in richness, *H'*, or biotic integrity. It is generally considered that disturbance from timber harvest is less intense than that from agriculture (Fortino et al. 2004). It has also been suggested that although food web structure can change somewhat, overall stream biotic integrity may not be strongly affected by timber harvest in low-gradient streams of the southeastern US Piedmont (Goodman et al. 2006) similar to those of our study. Further, prior studies examining fish in these streams reveal similar assemblage structure and hydrology between the Urban and Developing watersheds (Helms et al. 2005, Schoonover et al. 2006). It was therefore surprising that silviculture, pasture, and developing watersheds were so similar to each other in their macroinvertebrate assemblages. However, the agriculture in these watersheds is primarily pasture, and the influence of pasture land use is often less than that of intensive cultivation (Strayer et al. 2003), which could explain unexpectedly high macroinvertebrate integrity in these watersheds. In addition, although all silviculture watersheds had intact riparian zones and operations ostensibly followed BMP guidelines, timber harvesting in 2 of these watersheds was a recent activity (within 2 years prior to sampling), which, could explain the lower than expected response. Last, although Developing and Urban streams have much flashier hydrographs than the Forest streams (Schoonover et al. 2006), the proportion of benthic detritus was similarly high in streams of Developing and Forest watersheds (as opposed to streams in Urban watersheds), emphasizing the important role of benthic habitat quality for macroinvertebrates (Roy et al. 2003).

4.5.2 Macroinvertebrate seasonality

Stream macroinvertebrate assemblages show dramatic seasonal variation in species presence/absence, richness, diversity, and calculated biotic indices (Minshall 1981, Rosillon 1985, Linke et al. 1999). There was no seasonal interaction with LU/LC in our study, although macroinvertebrate richness, *H'*, biomass, and density all were highest in spring than other seasons. The GA-BMI was highest overall in summer, as were %Shredders and %Scrapers, 2 components of this index. However, trends between LU/LC categories remain constant throughout the year and since there were no interactions between seasons and LU/LC category the metrics considered, these results suggest that these metrics are robust enough to use for relative comparative purposes year-round.

4.5.3 Potential assemblage drivers

As evidenced by the NMDS ordination, the most diverse and highest integrity assemblages were largely associated with streams containing relatively cool water, low SO_4^{-} and TDS, and high DO, benthic detritus, and current velocity. Further, multiple regressions suggest that water chemistry and, to a lesser degree, stream geomorphology, were the best predictors of macroinvertebrate assemblages. Interestingly, stream hydrology did not appear in any of the multiple regression models nor were hydrological variables one of the stronger correlates of $NMDS_1$; taken together, these results suggest that gross hydrologic changes associated with LU/LC alteration may not directly influence macroinvertebrates in these streams. This result is counter to other studies that have shown strong relationships between altered hydrology and aquatic biota, particularly those involving fishes (Freeman et al. 2001, Roy et al. 2005). As a result of their close association with the benthos, small size and short generation time, benthic macroinvertebrates may be more susceptible to the indirect effects of altered hydrology (e.g. reduced water and habitat quality from increased runoff and spate frequency) rather than direct effects (e.g. individual or egg displacement) that are often implicated in larger, more nektonic organisms like fish (Freeman et al. 2001).

As in our study streams, many studies have observed elevated TDS (or specific conductivity) with increased urban area / impervious surface (Zampella 1994, Dow and Zampella 2000) as well as with decreased biotic integrity (Walsh et al. 2001, Roy et al. 2003). However, TDS concentrations were not necessarily at biologically significant levels, as most aquatic systems with biota can withstand TDS levels up to 1000 mgL^{-1} (Boyd 2000). Therefore, strong association of TDS and other dissolved solids, such as SO_4^{-}, within urbanized watersheds suggest that TDS is likely a surrogate for increased non-point pollution associated with efficient runoff, thus anthropogenic markers in these streams.

Temperature and DO were 2 of the strongest correlates with macroinvertebrate assemblages. Temperature is one of the most important environmental variables regulating aquatic biota, affecting metabolic rates and feeding requirements as well as growth and development (Ward and Stanford 1982). Even small changes in temperature (1 – $5^{O}C$) can alter hatching, emergence, growth, and recruitment of aquatic organisms (Beacham and Murray 1990, Sweeney 1993). Associated with increasing water temperature is decreasing DO concentrations, and several studies have demonstrated elevated water temperature associated with increased biochemical oxygen demand (BOD) in streams, especially those draining urbanized watersheds (Sponseller et al. 2001, Walsh et al. 2001, Krause et al. 2004). This pattern frequently results from increased discharge, which may scour, widen and/or straighten channels, effectively causing decreased riparian shading and increased transport of thermally heated stormwater to the channel (Trimble 1997, Krause et al. 2004). In our study, more diverse benthic assemblages occurred in streams within predominately forested watersheds, even those with high levels of residential development, which showed on average cooler, more oxygenated water. In marked contrast, Oligochaetes and other tolerant organisms were strongly associated with streams containing higher temperature and lower DO. Mean temperatures across the sites showed a range of ~2.5^{O}C whereas mean DO showed a range of ~5.9 mgL^{-1}. These contrasting conditions collectively are well within the realm of biological significance as potential direct drivers of macroinvertebrate assemblages, possibly acting as life history constraints, influencing food resources, predators or all of these factors (Hynes 1970, Ward and Stanford 1982, Allan 1995).

4.5.4 Conclusion and Implications

Use of a categorical approach to investigate land use and a correlative approach to investigate land cover allowed us to quantify and compare putative impacts of watershed LU/LC change on stream benthic assemblages; our analyses suggested that impacts are far-reaching and that some level of biological impairment is accompanied with all the common LU/LC disturbances in this area. Intense urbanization appears to be the predominant land use influencing assemblages in these watersheds when considered together, and significantly more so than residential development, pasture, and silviculture land uses. And, although the interrelated influences of watershed disturbance are difficult to separate, macroinvertebrate responses in these systems were most strongly associated with alterations in water chemistry parameters and benthic habitat such that hydrologic alterations appeared to play an indirect role structuring benthic assemblages.

By attempting to identify specific environmental drivers of biotic composition resulting from LU/LC perturbations operating at watershed scales, I can better address management and/or restoration needs designed to protect or minimize changes in stream biotic integrity. Therefore, management and restoration efforts in disturbed systems, and particularly urban watersheds, should be directed at both the reach- and watershed-scale (Rabeni and Sowa 1996, Walsh et al. 2005a). Improved riparian and instream conditions, such as BMP implementation, riparian reconstruction, and habitat augmentations, are essential to increasing biotic integrity in disturbed streams, as has been shown in other studies (Gore et al. 1998, Northington and Hershey 2006, Yates et al. 2007). However, without addressing hydrological influences associated with human alterations it is unlikely that riparian or benthic habitat quality improvements will have significant long-term effects, particularly in urban systems (Gore et al. 2001, Walsh et al. 2005a) . Reducing overland flow and pollutant inputs in urbanized watersheds as a restoration approach has been shown to enhance instream restoration efforts (Charbonneau and Resh 1992). Thus, habitat and physicochemical conditions (ostensibly influenced by hydrological alterations) in disturbed watersheds will unlikely be influenced by reach-scale restoration efforts alone. As such, implementation of biologically realistic management strategies in human-influenced systems may rely upon a multi-scale and hierarchical approach to assessment and abatement.

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Table 1. Land cover and size of study watersheds. **IS** = % impervious surface cover, **Grass/Transistion** = % pasture cover, **Deciduous** = % deciduous forest cover, **Evergreen** = % evergreen forest cover, and **LU/LC** = dominant land use/land cover in watershed.

ID	Site	Stream	Watershed size (km^2)	IS	Grass/Transition	Deciduous	Evergreen	LU/LC
1	SB1	Schley Creek	20.1	1.88	20.38	35.14	38.35	Developing
2	SB2	Standing Boy Creek Trib.	6.3	3.41	20.00	35.52	37.04	Developing
3	SB4	Standing Boy Creek	26.6	3.33	27.70	22.81	40.98	Developing
4	HC	House Creek Trib.	6.6	1.33	19.57	26.76	47.78	Silviculture
5	MU2	Mulberry Creek Trib.	6.1	1.39	14.86	37.20	41.33	Silviculture
6	SC	Sand Creek	9.0	1.24	20.89	28.86	44.68	Silviculture
7	BC	Beech Creek	6.5	2.29	13.26	34.14	46.53	Forest
8	BLN	Blanton Creek	3.6	1.41	18.65	28.30	47.85	Forest
9	MK	Flat Creek Trib.	6.6	2.28	19.82	37.98	36.31	Forest
10	MO	Cline's Branch	9.0	1.53	13.04	33.07	48.19	Forest
11	MU3	Turntime Branch	10.4	1.39	36.77	24.24	29.24	Forest
12	FS2	Wildcat Creek Trib.	14.5	2.74	35.79	28.21	30.71	Pasture
13	FS3	Wildcat Creek Trib.	3.0	2.58	33.91	29.91	31.96	Pasture
14	HC2	House Creek	14.1	1.64	43.95	22.22	30.46	Pasture
15	MU1	Ossahatchie Creek Trib.	12.0	1.89	14.86	37.20	41.33	Pasture
16	BU1	Lindsey Creek	25.5	40.40	23.31	12.66	21.37	Urban
17	BU2	Cooper Creek	24.7	25.06	24.90	15.87	30.43	Urban
18	RB	Roaring Branch	3.7	30.30	27.11	11.07	28.36	Urban
19	BR	Brookstone Creek	4.7	19.15	33.84	15.66	31.07	Urban
20	FR	Flat Rock Creek	23.9	13.70	43.37	8.05	32.72	Urban

Table 2. List of hydrological variables used in analyses, their range of values, and significant Pearson correlations to percentage of watershed as impervious (**% IS**), pasture (**% P**), evergreen forest (**% EF**) and deciduous forest (**% DF**). * $p < 0.05$, ** $p < 0.01$.

Variable ID	Description	Range	% IS	% P	% EF	% DF
Magnitude						
MedQ	Median discharge (L s^{-1})	0.01 – 0.90		**0.49***		
MaxQ	Maximum discharge (L s^{-1})	0.54 – 21.98				
Frequency (# times exceeded threshold)						
3xMed	# of times discharge exceeded 3x median flow	5 – 116				
5xMed	# of times discharge exceeded 5x median flow	1 – 70	**0.50***			
7xMed	# of times discharge exceeded 7x median flow	1 – 64	**0.56***			
9xMed	# of times discharge exceeded 9x median flow	0 – 58	**0.58***			
>75th	# of times discharge exceeded 75th percentile	25 – 115				
>95th	# of times discharge exceeded 95th percentile	12 – 66				
>99th	# of times discharge exceeded 99th percentile	2 – 35	**0.62****			
Duration (# of hours spent above threshold)						
>3xMed_d	Hours discharge was >3x median flow	36.5 – 3026				
>5xMed_d	Hours discharge was >5x median flow	6 – 2518				
>7xMed_d	Hours discharge was >7x median flow	1.5 – 2412				
>9xMed_d	Hours discharge was >9x median flow	0 – 17				
Predictability and Flashiness						
C.V.	% Coefficient of Variation	42 – 402				
Inc1h100	# of events discharge increases by 100% in 1 hr	7 – 109	**0.55***			
Inc1h1000	# of events discharge increases by 1000% in 1 hr	0 – 31				
Inc1h5000	# of events discharge increases by 5000% in 1 hr	0 – 17		**- 0.47***		
Inc3h100	# of events discharge increases by 100% in 3 hr	11 – 122	**0.53***			

Inc3h1000	# of events discharge increases by 1000% in 3 hr	0 – 44
Inc3h5000	# of events discharge increases by 5000% in 3 hr	0 – 19
Dec1h100	# of events discharge decreases by 100% in 1 hr	0 – 67
Dec1h1000	# of events discharge decreases by 1000% in 1 hr	0 – 28
Dec1h5000	# of events discharge decreases by 5000% in 1 hr	0 – 12
Dec3h100	# of events discharge decreases by 100% in 3 hr	1 – 92
Dec3h1000	# of events discharge decreases by 1000% in 3 hr	0 – 36
Dec3h5000	# of events discharge decreases by 5000% in 3 hr	0 – 18
Baseflow		
MedBF	Median baseflow ($L\ s^{-1}$)	0.04 – 730
BI	Baseflow index (∑ predicted baseflow/ ∑observed flow)	0.03 – 0.82

Table 3. Physicochemical variables used in analyses, their range of values, and significant Pearson correlations to percentage of watershed as impervious (**% IS**), pasture (**% P**), evergreen forest (**% EF**) and deciduous forest (**% DF**). * $p < 0.05$, ** $p < 0.01$.

Variable	**Description**	**Range**	**% IS**	**% P**	**% EF**	**% DF**
Temp	Mean water temperature (^{o}C)	13.3 – 15.8	**0.83*** **			**- 0.66***
DO	Mean dissolved O_2 (mg L^{-1})	8.6 – 14.5	**- 0.50***			**0.68***
pH	Mean pH	5.7 – 6.9				
TSS	Mean total suspended solids concentration (mg L^{-1})	2.1 – 8.1		**0.54***		
TDS	Mean total dissolved solids concentration (mg L^{-1})	19.95 – 58.63	**0.58**			
NO_3^{-}	Mean monthly nitrate concentration (mg L^{-1})	0.14 – 4.45		**0.75*** **	**- 0.54***	
SO_4^{-}	Mean monthly sulphate concentration (mg L^{-1})	0.53 – 9.19	**0.82*** **			**- 0.48***
NH_4^{+}	Mean monthly ammonium concentration (mg L^{-1})	0 – 0.33				**- 0.69***
P	Mean total phosphate (mg L^{-1})	0.05 – 0.12				
DOC	Mean monthly dissolved organic carbon concentration (mg L^{-1})	1.59 – 8.55				
FC	Mean monthly fecal coliform colonies (# 100ml^{-1})	127 – 15847	**0.87*** **		**- 0.54***	**- 0. 54***

Table 4. Geomorphic variables used in analyses, their range of values, and significant Pearson correlations to percentage of watershed as impervious (**% IS**), pasture (**% P**), evergreen forest (**% EF**) and deciduous forest (**% DF**). * $p < 0.05$, ** $p < 0.01$.

Variable	**Description**	**Range**	**% IS**	**% P**	**% EF**	**% DF**
Flow	Mean current velocity at invertebrate sample ($m\ s^{-1}$)	0.07 – 0.38				
OM	Mean benthic organic matter (g)	0.3 – 1.2			**0.58***	
Substrate	Median substrate size (cm)	0.5 – 1.8	**0.52***			
Tg	Tractive force ($N\ m^{-2}$)	2.7– 73.9				
Clay	Proportion benthic clay	0 – 0.07				
Silt	Proportion benthic silt	0 – 0.18				
Sand	Proportion benthic sand	0.20 – 1.00	**- 0.44***			
Gravel	Proportion benthic gravel	0 – 0.52	**0.44**	**- 0.48***		
Cobble	Proportion benthic cobble	0 – 0.43				
Wood	Proportion benthic wood	0 – 0.22	**- 0.56***			
Detritus	Proportion benthic detritus	0 – 0.17	**- 0.55***			**0.67****
Bedrock	Proportion benthic bedrock	0 – 0.22	**0.45***		**- 0.44***	

Table 5. Mean seasonal and annual values for macroinvertebrate variables and their ranges over the study. Seasonal values for each stream were used for **Range** values and to acquire averages for **Summer, Winter,** and **Spring** values and total stream averages were used for **Annual** values.

Variable	Summer	Winter	Spring	Annual	Range
Composite					
GA-IBI	49.4	30.2	30.0	36.3	3 – 75
Community					
H'	2.1	1.9	2.1	2.0	0.8 – 2.9
Richness	34.1	33.3	38.8	35.5	14 – 64
Biomass (g / m^2)	16.5	26.9	43.5	32.9	6.9 – 101.6
Density (no. / m^2)	12510	21307	19998	15119	2504 - 68429
Functional					
%Shredders[§]	38.4	0	0	12.3	0 – 87.6
%Scrapers[§]	3.5	0.9	1.2	1.9	0 – 12.3
%Clingers	4.7	0.5	1.8	2.3	0 – 15.3
%Filterers	25.5	10.8	19.8	18.7	0.7 – 64.1
%Gatherers	17.5	20.6	18.0	18.7	0.3 – 41.6
%Predators	10.3	11.0	10.7	10.7	0.3 – 41.8
Swimmers[§]	1.4	0.9	1.7	1.3	0 – 3
%Tolerant	3.1	1.8	10.0	5.1	0 – 48.6
Taxonomic					
EPT	6.9	7.6	7.3	7.3	1 – 17
%Ephemeroptera	9.0	1.6	2.8	4.4	0 – 27.8
%Plecoptera[§]	0.3	8.9	1.5	3.5	0 – 32.8
%Trichoptera	15.6	1.0	7.2	7.9	0 – 55.8
Diptera	18.2	18.2	21.1	19.2	7 – 31
%Chironomidae	65.1	70.0	72.9	69.5	22.9 – 98.8
Coleoptera[§]	2.2	70.0	72.9	69.5	22.9 – 98.8
%Oligochaete[§]	2.1	8.8	10.0	7.1	0 – 67.6

[§] metrics used for Georgia Biotic Macroinvertebrate Index

Table 6. Results from General Linear Model testing the effects of land use/land cover (LU/LC) and season on macroinvertebrate metrics across the study watersheds. For LU/LC, $F_{4, 55}$, for Season, $F_{2, 55}$, and for LU/LC-season interactions (Interaction), $F_{6, 55}$. GA-BMI = Georgia Benthic Macroinvertebrate Index

Metric	**Source**	***F***	***p***
Richness	LU/LC	24.96	< 0.001
	Season	6.21	0.004
	Interaction	0.25	0.978
H’	LU/LC	5.89	0.001
	Season	3.47	0.04
	Interaction	0.42	0.902
Density	LU/LC	2.01	0.11
	Season	4.2	0.022
	Interaction	2.64	0.02
Biomass	LU/LC	3.96	0.011
	Season	5.33	0.006
	Interaction	1.06	0.497
GA-IBI	LU/LC	18.12	< 0.001
	Season	27.93	< 0.001
	Interaction	0.61	0.763

Table 7. Best models for **Composite** and **Community** macroinvertebrate responses. **LU/LC** column shows the best single land use / land cover predictor and **Multivariate** column shows the best model from multiple regressions with PCA axes as predictors, and. For the **Multivariate** column, C-PC$_1$ and C-PC$_2$ are physicochemical PCA axes 1 and 2, respectively, and S-PC$_1$ and S-PC$_2$ are substrate PCA axes 1 and 2, respectively while **LU/LC** classes are as defined in Table 1. GA-BMI = Georgia Benthic Macroinvertebrate Index and NMDS$_1$ = axis 1 from NMDS ordination . Models are based on mean annual data. All models are of the form y = ax + b. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Metric	**LU/LC**	**R^2**	**Multivariate**	**Standardized Estimate**	**R$^2_{adj}$**
Richness	Deciduous	**0.73*****	C-PC$_1$	0.77	**0.80*****
			C-PC$_2$	-0.48	
H'	Deciduous	**0.42****	C-PC$_1$	0.67	**0.78*****
			S-PC$_1$	-0.34	
			C-PC$_2$	-0.62	
Density	ns	–	S-PC$_1$	-0.42	**0.40*****
			C-PC$_2$	-0.56	
Biomass	IS	**0.39****	S-PC$_2$	-0.98	**0.25***
			C-PC$_1$	-0.83	
GA-BMI	Deciduous	**0.67*****	C-PC$_1$	0.74	**0.78*****
			C-PC$_2$	-0.52	
NMDS$_1$	IS	**0.77*****	C-PC$_1$	0.91	**0.83*****

Table 8. Loadings (eigenvalues) and associated axis correlations for 1st and 2nd axes of **Hydrologic**, **Geomorphic**, and **Chemical** PCA ordinations. Variable descriptions are as in Tables 1 – 3. *p < 0.05, **p < 0.01, ***p < 0.001.

	Loadings		**Correlations**	
	PC$_1$	**PC$_2$**	**PC$_1$**	**PC$_2$**
Hydrologic				
MedQ	-0.17	-0.01	-0.70**	
MaxQ	0.05	-0.23		-0.47*
3xMed	0.14	-0.32		-0.70**
5xMed	0.21	-0.24	0.67**	-0.66**
7xMed	0.22	-0.22	0.66**	-0.63**
Inc1h1000	0.23	0.13	0.72**	
Inc3h1000	0.24	0.11	0.78***	
Inc3h5000	0.24	0.16	0.63**	
Dec1h100	0.24	0.15	0.72**	
Dec3h100	0.22	0.05	0.73**	
MedBF	-0.22	0.07	-0.72**	
BI	-0.19	0.22	-0.67**	0.56*
Habitat				
OM	-0.16	-0.36		-0.57*
Substrate	-0.22	0.42	-0.47**	0.72**
Sand	0.47	0.11	0.93***	
Gravel	-0.3	0.26	-0.58*	
Cobble	-0.44	-0.12	-0.86***	
Wood	0.44	-0.24	0.86***	
Detritus	0.02	-0.5		-0.80***
Bedrock	-0.41	-0.03	-0.80***	
Chemical				
Temp	-0.37	0.11	-0.77***	
DO	0.38	-0.02	0.86***	
pH	-0.24	-0.10	-0.54*	
TSS	-0.06	0.48		0.75***
TDS	-0.41	-0.17	-0.94***	
NO_3	0.02	0.57		-0.87***
SO_4	-0.38	-0.21	-0.86***	
NH4	-0.12	0.49	-0.49*	0.59*
DOC	-0.38	-0.19	-0.79***	
FC	-0.30	0.26	-0.65**	

Table 9. Environmental variable and macroinvertebrate metric Pearson correlations with 1st and 2nd axes of nonmetric multidimensional scaling (NMDS) ordination. Only variables with significant correlations to NMDS Axis 1 or Axis 2 are shown.
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Hydrologic, Habitat, and Chemical variable defintions are as in Tables 2 – 4. ICI = Invertebrate Community Index and GA-BMI = Georgia Benthic Macroinvertebrate Index

Variable		$NMDS_1$	$NMDS_2$
Hydrologic			
	5xMed	-0.60**	
	7xMed	-0.73**	
	9xMed	-0.76***	
	Inc1h100	-0.55*	
	N>99	-0.56*	
	BI	0.56*	
Habitat			
	Flow	0.61**	
	Substrate	-0.68**	
	Detritus	0.55*	-0.54*
Chemical			
	Temp	-0.89***	
	DO	0.80***	
	TSS		0.53*
	TDS	-0.81***	
	SO4	-0.87***	
	NH4	-0.57*	0.62**
	DOC	-0.65**	
	FC	-0.71**	
Macroinvertebrate			
	Richness	0.82***	-0.83***
	H’	0.60**	-0.74***
	Density		-0.64**
	Biomass	-0.57*	
	GA-BMI	0.79***	-0.74***

Figure 1. The study area included 20 small watersheds (shaded sections) of the Chattahoochee River Basin in 4 counties in the Lower Southern Piedmont ecoregion of western Georgia, USA. Numbers refer to watersheds and correspond to Table 1. The city of Columbus is located in western Muscogee County. County names are in capital letters

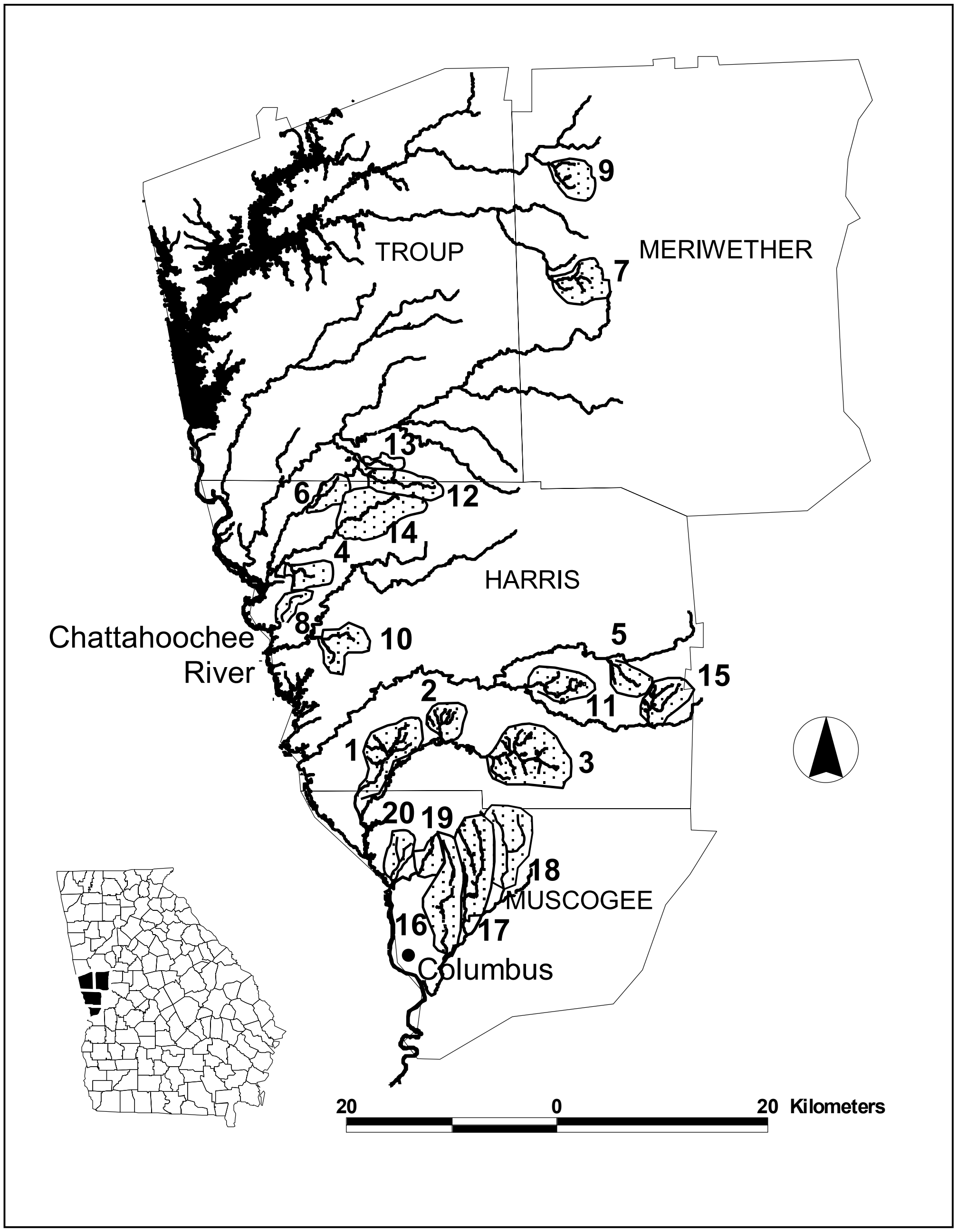

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Figure 2. Composite and community invertebrate metrics as a function of land use /land cover (LU/LC) category. Horizontal lines are based on annual site means, symbols are seasonal site means. Letters identify significant LU/LC category differences from annual General Linear Model.

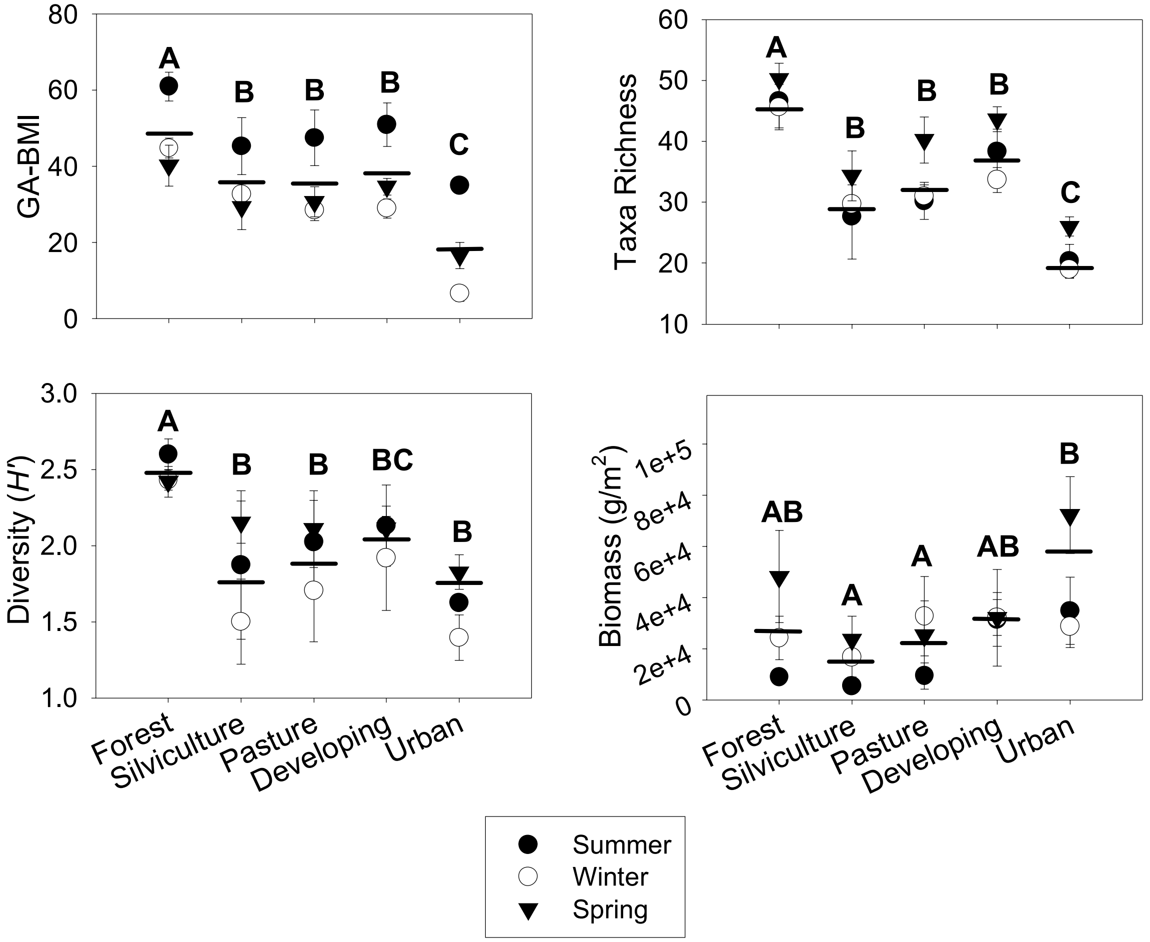


Figure 3. GA-BMI ($y = 11.658x^{-0.3104}$) as function of Impervious surface (IS), illustrating potential watershed IS threshold beyond which biotic integrity is compromised.

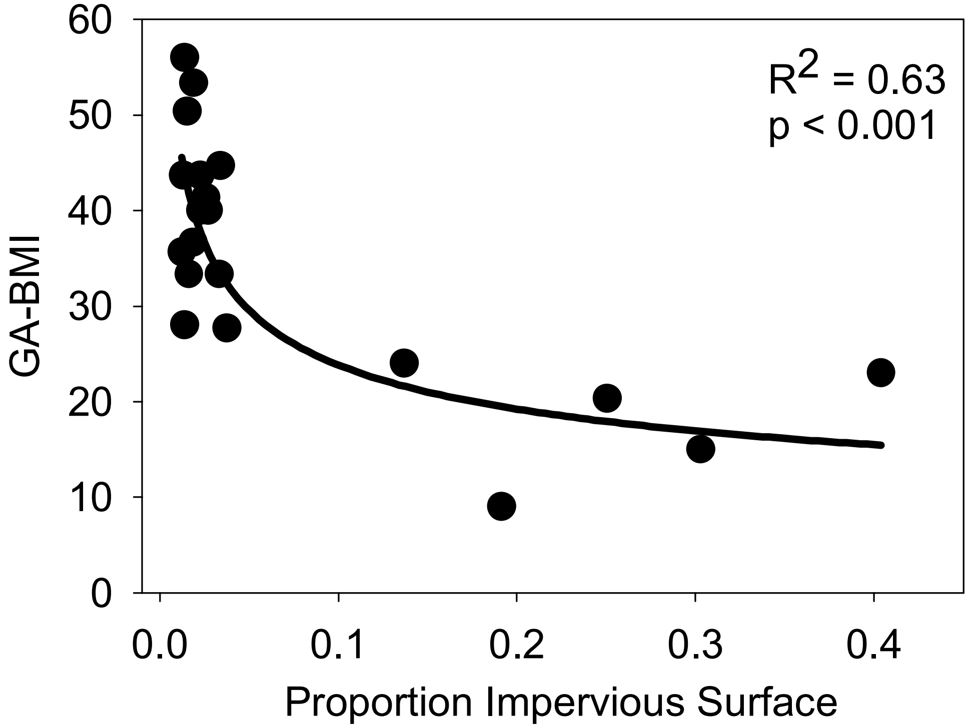
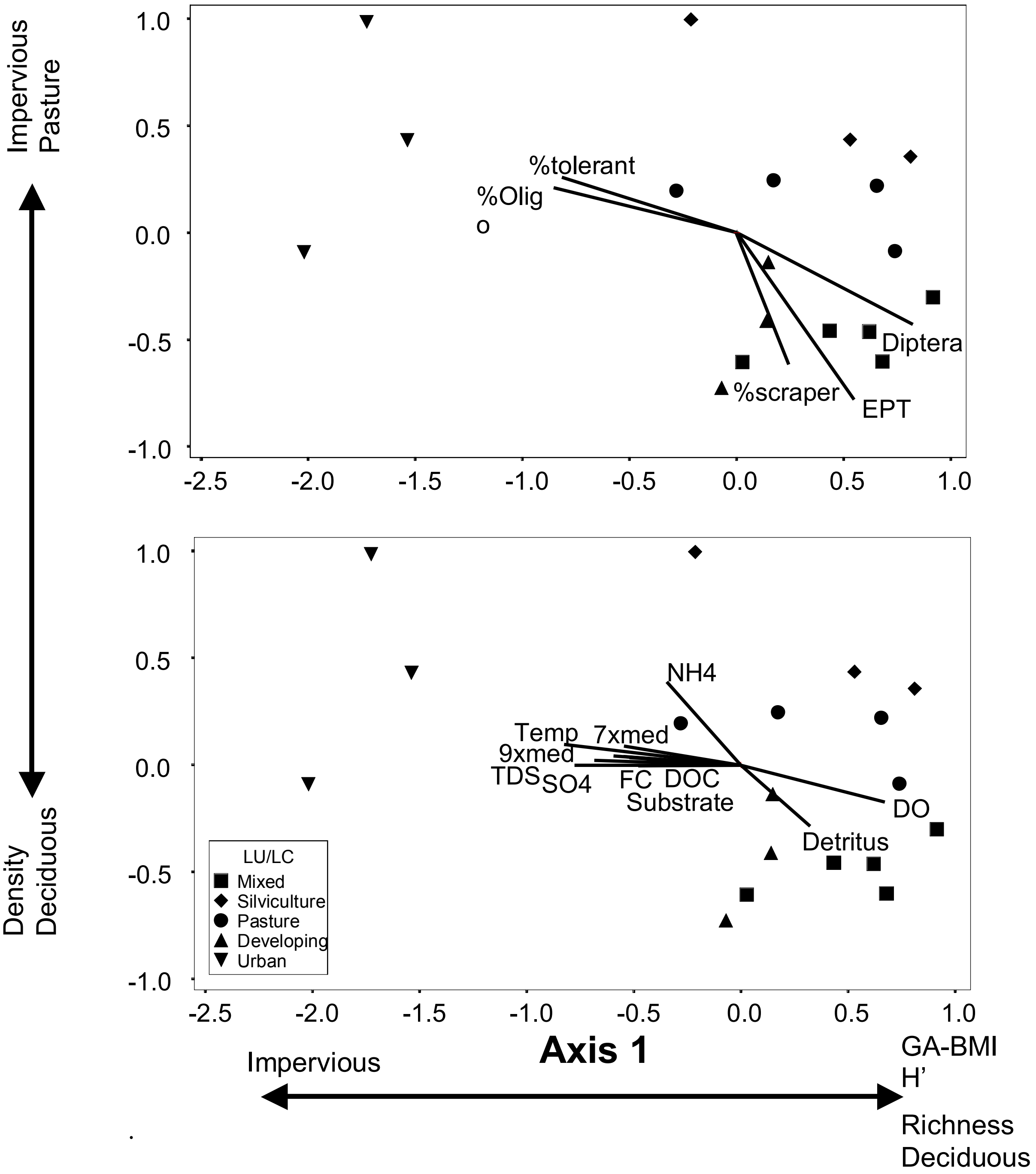


Figure 4. Nonmetric multidimensional scaling ordination (NMDS) of sites in species space. Symbols are study sites coded by land use classifications. Arrows on axes show direction of significant correlated LU/LC and macroinvertebrate community / composite metric scores and vectors show relative direction and strength of correlated values for A) macroinvertebrate functional feeding and taxonomic groups and B) environmental variables. Axes 1 and 2 explained 79.3 and 9.8% of the total variation, respectively. Stress = 7, Final instability = 0.00001, number iterations = 66.



CHAPTER 5. Land use effects and the influence of ecosystem size, resource availability, and disturbance on stream food webs.

5.1 ABSTRACT

Food webs in aquatic systems can be constrained by several factors including, but not limited to, ecosystem size, resource availability and disturbance. I evaluated the impact of these influences on stream food webs in watersheds that differed in their degree of land use / land cover (LU/LC) alteration in streams draining 12 watersheds (3 urban, 3 suburban, 3 pasture, 3 forest) of the Lower Piedmont of western Georgia, USA. Specifically, I quantified the relationships between LU/LC and several measures of ecosystem size, resource availability, and disturbance and how these environmental factors interact to explain mean trophic position (TP), food chain length (FCL), and food web structure using stable C and N isotope signatures ($\delta^{13}C$ and $\delta^{15}N$, respectively). $\delta^{13}C$ showed significant enrichment with increasing watershed impervious surface and significant depletion with increasing forest cover, suggesting a basal resource shift in food web structure and the potential for $\delta^{13}C$ as an indicator tool. Also, many of the environmental predictors were related to LU/LC, particularly average stream area (ecosystem size), chlorophyll *a* abundance (resource availability), spate flow frequency (disturbance) and water temperature (disturbance). Accordingly, FCL, which increased with taxa richness, showed strong negative associations with disturbance variables, but not ecosystem size or resource availability. Further, average food web architecture

revealed that terrestrial subsidies were an important resource in all food webs and that forest stream food webs had a high degree of feeding segregation with more overlap among feeding compartments in streams with higher LU/LC disturbance. Together, these results provide empirical evidence that LU/LC – induced disturbance can dramatically influence the length and overall architecture of stream food webs.

5.2 INTRODUCTION

The study of energy transfers among basal resources, producers, and consumers has long been a topic of ecological interest (Elton 1927, MacArthur 1955). From simple food chains to detailed energy transfer webs, the examination of food webs can provide inference on observed community structure as well as reveal patterns of resource use among organisms, including such interactions as herbivory, competition, and predation (Paine 1966, 1980, Carpenter et al. 1985, Power 1990, Navarrete et al. 2000). In addition to these familiar interactions, food web structure in freshwater systems can be influenced by myriad factors such as colonization potential, terrestrial subsidies, and gene flow, all of which operate at various spatial and temporal scales (Post 2002a, Woodward and Hildrew 2002). Recognizing the influence of such disparate drivers of freshwater food webs can help lead to a better understanding of the processes shaping these ecosystems.

Food chain length (FCL), the number of transfers of energy from the base to the top of a food web, is a fundamental characteristic of the structure and function of food webs (Elton 1927, Vander Zanden and Fetzer 2007). FCL influences foodweb dynamics and trophic interactions (Oksanen et al. 1981, Pace et al. 1999), modifies regulation of biogeochemical cycles (Wootton 1994, Schindler et al. 1997), and influences the bioaccumulation of contaminants (Kidd et al. 1995). Inherent in the examination of FCL is trophic position (TP), or the location of an organism in the food web (Post 2002a). In contrast to discrete trophic levels, TP is a continuous measure of the energy path to a consumer that incorporates omnivory and other complexities of natural systems (Levine 1980, Polis and Strong 1996, Vander Zanden and Rasmussen 1999). FCL can be considered the maximum TP in a system; thus both measures are integral in understanding ecological processes and food web dynamics of a community (Post 2002b).

FCL, and food webs in general, are determined by several interacting factors operating at different scales. First, the history of community organization, such as colonization history, membership, and biogeographical constraints can strongly influence food web structure, particularly in isolated or evolutionarily young systems (Post 2002a). When colonization constraints do not limit food web structure, resource availability and/or ecosystem size can exert influence. According to the Productive Space Hypothesis, FCL should increase as a function of both ecosystem size and resource availability (Schoener 1989), however, most evidence points more to effects of ecosystem size than resources; there has been less evidence that resource availability strongly influences FCL in aquatic systems (Spencer and Warren 1996, Vander Zanden et al. 1999, Post et al. 2000). Predator-prey interactions can also influence FCL by moderating species' abundances or by causing species absence and/or avoidance (Hildrew et al. 1984, McPeek 1990), particularly at low-intensity levels of disturbance (Peckarsky 1983). At higher-intensity disturbance, predation may become less important and competition between organisms increases, potentially influencing FCL (Peckarsky 1983, Menge and Sutherland 1987). In systems with frequent, extreme disturbance, FCL should shorten with the dynamical constraints of abiotic instability largely regulating community structure (Pimm and Lawton 1977, Peckarsky 1983, Menge and Sutherland 1987).

Human activities can also strongly influence FCL and the structure of aquatic food webs. Resource alteration through nutrient enrichment (sewage inputs, fertilizer runoff) is a significant factor affecting food web structure, often leading to increases in primary productivity of opportunistic producers and potentially causing changes in community structure (Carpenter et al. 1998, deBruyn et al. 2003, Tewfik et al. 2005). Species invasions and other anthropogenic alterations in species interactions such as predator removal have been shown to have dramatic effects on food webs by shortening FCL (Pauly et al. 1998, Rahel 2000). Further, changes in disturbance regimes, particularly hydrologic alterations, can result in unstable environments that exclude all but the most tolerant of organisms and contribute to species invasion, all of which can simplify food webs and potentially shorten FCL (Wootton et al. 1996, Nystrom and McIntosh 2003, Walsh et al. 2005b). However, extensive empirical evidence for the role of disturbance on FCL is lacking (Post 2002a)

In this study, I examined the role of human-induced disturbance in the form of watershed land use / land cover (LU/LC) change on FCL and structure of stream food webs. I used stable C and N isotope ratios (δ^{13}C and δ^{15}N, respectively) to provide time-integrated data regarding energy flow and feeding relationships of stream organisms in multiple watersheds with various levels of LU/LC disturbance. ^{13}C of many primary producers vary but the stable C isotope ratios (δ^{13}C, where δ = deviation from a standard) of consumers are similar to that of their food (DeNiro and Epstein 1978). However, the

N pools of animals are enriched with ^{15}N relative to their food and this enrichment is on average +3.4 ‰, i.e. 3.4 ‰ difference in trophic levels (Deniro and Epstein 1981, Minagawa and Wada 1984). Thus, the use of stable isotopes can be used to infer the continuous trophic position of organisms and, by avoiding the discreteness of trophic levels, may provide a more realistic picture of the feeding relationships by incorporating the influence of omnivory (Post 2002b).

The objectives of my study were to relate stream FCL to watershed LU/LC and instream conditions in an attempt to understand the potential impacts of resource availability, system size, and environmental stability on food web patterns associated with anthropogenic disturbance. Further, I constructed and compared generalized food webs among different types of LU/LC. I predicted that FCL would decrease with increased LU/LC disturbance and that food webs in forested watersheds (reference conditions) would be more complex with upper trophic levels more reliant upon instream prey resources than food webs from LU/LC disturbed watersheds.

5.3 METHODS

5.3.1 Study area

I studied stream reaches from tributaries of the Chattahoochee River in west Georgia, USA, in the Southern Outer Piedmont ecoregion (Figure 1). Twelve small watersheds that varied in their degree of urbanization and consequently stream physicochemical conditions were selected in and around the city of Columbus, Muscogee County (Table 1). Watersheds ranged in land cover from intense urbanization and active suburban development to pasture to heavily forested areas and streams draining these watersheds were 2nd to 3rd order. This large range in landscape character allowed comparison across geomorphically similar streams that differed primarily in watershed-level LU/LC and associated variation in streamwater physicochemical conditions.

I determined watershed boundaries and size from USGS 30-m resolution digital elevation models and ArcView 3.2a software (Environmental Research Systems Institute, Inc., Redwoods, Calfornia). True color (3-band) aerial photographs of study watersheds were taken during leaf-off in March 2003 to determine LU/LC. I also assigned each watershed to 1 of 4 broad LU/LC categories (Urban, Developing, Pasture, and Forest) to aid in developing LU/LC specific food webs (Table 1). These categories were based on the dominant land cover in the watershed (% IS, pasture, and/or forest) from land cover analysis except for Developing which was largely forested with current or recent residential development (See (Lockaby et al. 2005) for detailed land cover analyses methods).

5.3.2 Resource availability

All food web and environmental variables were collected from a 100 to 200 m representative stream reach in each watershed. To address potential differences among watersheds in resource availability, I determined mean macroinvertebrate biomass, algal biomass, and organic matter abundance. Macroinvertebrate biomass was determined by quantifying benthic macroinvertebrates in 3 pools and 3 runs per stream reach during September (summer), February (winter), and April – May (spring) in 2003 – 2004 using a Surber sampler (250-µm mesh; 0.093 m^2 sampling area). I consolidated multiple Surber collections in each habitat (3 for pools, 4 for runs), resulting in a 0.27- and 0.36-m^2 sample from each pool and run, respectively (1.89 m^2 total area sampled for each study reach per stream and season). I elutriated excess sediment and preserved all samples with

95% EtOH in the field. In the laboratory, I removed all organisms >2mm with the unaided eye, and subsampled the remainder under a dissecting microscope (≥ 300 organisms, (Vinson and Hawkins 1996). I counted, measured length (nearest mm), and identified macroinvertebrates to the lowest possible taxonomic level (usually genus or morphospecies) using keys in (Merritt and Cummins 1996), (Wiggins 1996) and estimated biomass using published lengh / mass equations (Benke et al. 1999).

To estimate benthic algal biomass, I removed the top layer of benthic sediment near where invertebrates were sampled with a shallow inverted 5 cm diameter (15 mL volume) petri dish and trowel (Barbour et al. 1999). Samples were kept on ice in the dark until processed for chlorophyll *a.* I extracted chlorophyll *a* from the sediment of each sample in 90% acetone and measured this extracted pigment fluorometrically (Turner TD-700, Turner Designs, Sunnyvale, CA). I averaged 3 petri dish samples for each of the 6 habitats (3 runs and 3 pools) and used these averaged habitat values to determine mean chlorophyll abundance.

I quantified benthic organic matter (OM) and substrate size by sampling transitional areas between runs and pools where organisms were sampled to standardize efforts and avoid error associated with scour in runs and deposition in pools. I sampled OM by determining the ash-free dry mass (AFDM) of 9 replicate 2.5 x 10 cm benthic cores.

5.3.3 Environmental stability

To assess potential differences among watersheds in environmental stability, I measured several physicochemical and hydrological variables that have been shown to be influential to aquatic taxa as well as computed a general habitat quality index in each stream. Stream temperature was measured continuously with HOBO® Temp data loggers from July 2003 – July 2004, whereas total dissolved solids (TDS) and total suspended solids (TSS) were determined monthly, as detailed in (Schoonover and Lockaby 2006). Continuous stream discharge (Q) was quantified from July 2003 to July 2004 using a Mini-Troll® pressure transducer data logger (In-Situ Inc., Ft. Collins, Colorado) installed near the outflow point of each watershed to determine relative hydrologic signatures of the 12 streams (Schoonover et al. 2006). I considered 2 parameters of the hydrographs reflecting general magnitude and frequency of spate flows, maximum discharge (MaxQ) and # times discharge exceeded 7 x median flow (7xMed). These parameters were shown to be important predictors of biota in previous studies (Chapter 2,3).

To assess available habitat quality/quantity, I used a comprehensive multimetric habitat assessment from the Georgia Environmental Protection Division designed for use in fish biomonitoring (GADNR 2007). This Habitat Index included visual estimates of available cover (number and frequency of habitats), substrate characterization (type and condition), pool morphology (shape and frequency), channel alteration (frequency of riprap, dredging, etc), channel sinuosity (run-to-bend ratio), sediment deposition (particle, point bar, island size), flow status (degree to which channel is filled with water), bank condition (erosion potential and vegetation cover) and riparian condition (vegetation cover/quality) (GADNR 2007). This assessment involves averaging 3 individuals' summed scores (1-10 or 1-20, depending on parameter) of the different habitat parameters to obtain an overall habitat quality value for the representative reach, with high average score indicating high habitat quality. The same 3 observers were used at all sites (BSH, KOM, RMM). All environmental data were correlated with watershed LU/LC and food web variables (see below).

5.3.4 System size

Along with watershed size, I also estimated mean available wetted area of the stream reach (i.e., mean stream size). This variable was the product of the mean width and the mean depth of the stream as measured 3 times a year from 2002 – 2004.

5.3.5 Field collections

Each stream reach was sampled for periphyton, invertebrates and vertebrates in spring 2006. Each stream had undergone exhaustive sampling in other studies (see Chapters 2 – 5), so the resident organisms present in each stream were well known and, thus, sampling proceeded until at least all common organisms were collected. All samples were replicated 3 to 5 times when possible and immediately put on ice in the field and later frozen until processed in the laboratory.

Periphyton was collected by removing the top layer of benthic sediment with a shallow inverted 5 cm diameter (15 ml volume) petri dish and trowel (Barbour et al. 1999). Samples were collected in transitional areas between runs and pools to balance the influences of scour and deposition. Organic matter, in the form of leaf detritus, was collected from leaf packs in depositional areas. Terrestrial invertebrate drift was collected using 4 drift nets ($0.09m^2$ sampling area, 250 µm mesh) set for 4h during daylight hours in each stream. Aquatic invertebrates and salamanders were collected with dip-nets (250 µm mesh) and fish were collected with seines and a backpack electroshocker (Smith-Root LR-24) from all available habitats in the reach. All aquatic macroinvertebrates were assigned to one of 7 functional feeding group (Merritt and

Cummins 1996) including collector/filterers (CF), collector/gatherers (CG), predators (PR), scrapers (SC), shredders (SH), and scavengers/crayfish (SV). Fish were assigned to one of four feeding guilds (Schleiger 2000), including herbivores (HBV), insectivores (ISV), omnivores (OMN), and piscivores (PSV).

5.3.6 Sample preparation and isotope analysis

In the laboratory, I removed, counted, measured length, and identified all macroinvertebrates (family level, subfamily for Chironomidae) from the dip net samples using standard keys (Merritt and Cummins 1996, Wiggins 1996, Epler 2001). For each fish specimen, I measured length and weight and then removed a skinned, boneless portion of dorsal muscle for analysis, whereas for salamanders, a portion of the tail was removed. After rinsing in distilled water, all foodweb samples were dried 48h at 60°C, ground to a fine powder with a mortar and pestle and then stored in clean scintillation vials. Subsamples for most samples were then weighed (nearest 10^{-5} g) and placed in 4 x 6 mm tin capsules for isotopic analysis. For some smaller macroinvertebrates, several whole individuals were prepared without grinding to achieve necessary weight limits for analysis.

All samples were analyzed for isotope ratios (^{13}C / ^{12}C and ^{15}N / ^{14}N) by gas isotope-ratio mass spectroscopy at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University, Flagstaff, AZ, USA. Isotope ratios are reported in parts per thousand (‰) relative to standards (Pee Dee Belemnite for C, atmospheric N for N), defined in delta notation as:

$$\delta^{13}C \text{ or } \delta^{15}N = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 10^3$$

where $R = {}^{13}C / {}^{12}C$ or ${}^{15}N / {}^{14}N$ (Craig 1957, Jepsen and Winemiller 2002).

5.3.7 Data analysis

For each watershed, I calculated mean C ($\mu\ \delta^{13}C$) and N ($\mu\ \delta^{15}N$) isotopic signature as well as mean TP and FCL. There is often considerable variation in $\delta^{15}N$ and $\delta^{13}C$ in basal resources among different aquatic systems, so it is generally necessary to baseline-correct $\delta^{15}N$ values to compare trophic position among systems (Cabana and Rasmussen 1996, Vander Zanden et al. 1997, Post 2002b). Therefore to determine trophic position (TP) for each organism, I used:

$$\lambda + (\delta^{15}N_{\text{sample}} - \delta^{15}N_{\text{base}}) / \Delta_n$$

and, similarly, to determine FCL, I used:

$$\lambda + (\delta^{15}N_{\text{top consumer}} - \delta^{15}N_{\text{base}}) / \Delta_n$$

where λ is the trophic position of the organism used to estimate $\delta^{15}N_{\text{base}}$, $\delta^{15}N_{\text{sample}}$ is the isotopic signature of an individual sample, $\delta^{15}N_{\text{top consumer}}$ is the isotopic signature of the top consumer, $\delta^{15}N_{\text{base}}$ is the isotopic signature of the baseline resource, and Δ_n is the trophic fractionation of N, generally considered 3.4‰ per trophic level (Post 2002b, Vander Zanden and Fetzer 2007). Detrital energy sources in aquatic systems, however, often show high temporal variation in $\delta^{15}N$ and $\delta^{13}C$ (France 1995c, a, Cabana and Rasmussen 1996, Post 2002b). Also, after evaluation of C:N biplots, it became apparent that most organisms were not using leaf detritus or algae as a primary C source (i.e. most were not situated directly above organic matter or algae in C:N space), but instead, a slightly less enriched source. Therefore, for the baseline resource I used an inferred averaged value for particulate organic matter (POM) based on the signatures of primary consumers (Post 2002b). These consumers included all macroinvertebrates known to be collectors in a given stream (*Corbicula*, *Cheumatopsyche*, Chironominae, etc.) and the isotopic signature of POM was estimated as

$$\delta^{13}C_{POM} = \delta^{13}C_b - 1‰ \text{ and}$$

$$\delta^{15}N_{POM} = \delta^{15}N_b - 3.4‰$$

where POM is particulate organic matter, b is collector and 1‰ and 3.4‰ are the mean trophic fractionation values for C and N, respectively (Post 2002b, Vander Zanden and Fetzer 2007). A POM value was generated for each CF and then averaged for an inferred, stream-specific POM value.

Stable C and N values, mean TP, and FCL were then correlated with LU/LC, resource, size and stability variables and regressed against total taxa richness. Using means for invertebrate functional feeding groups, fish feeding guilds, and salamanders for each stream, I constructed 4 functional food webs based on means for LU/LC (Forest, Pasture, Developing, and Urban). Only functional groups found in at least 2 of the 3 streams per category were included in the mean webs to minimize influence of local variation. Finally, pairwise comparisons between Forest and all other food webs (Forest vs. Pasture, Forest vs. Developing, Forest vs. Urban) were made by calculating the directional change of each consumer component in food web biplots and circular statistics were used to determine any significant differences in these changes (Schmidt et al. 2007). Directional change was measured as the length (r) and angle (μ) of difference between each corresponding functional group in trophic space ($\delta^{13}C - \delta^{15}N$) in a comparison 2 mean food webs. Rao's spacing test for circular uniformity (U) was used to determine whether each foodweb comparison departed nonrandomly from uniformity and showed evidence for a preferred direction (Batschelet 1981).

5.4 RESULTS

In total, 834 samples were collected for analysis, representing at least 54 different taxa, including 30 invertebrate families, 21 fish species, 1 salamander, 1 toad, and benthic algae taxa (Table 3). Aquatic taxa richness ranged from 8 – 30 across the watersheds and many watersheds were well represented with multiple taxa in each functional group (Table 4).

5.4.1 Trophic position and food chain length

Mean $\delta^{13}C$ values ranged from -31.043 to -23.190 ‰ whereas mean $\delta^{15}N$ values ranged from 5.141 to 8.842 ‰ (Table 5). Carbon values were strongly correlated with LU/LC, showing overall enrichment with increasing impervious surface and concomitant depletion with increasing watershed forest cover (Table 6). Somewhat surprisingly, $\delta^{15}N$ values were not significantly correlated to any LU/LC parameter. However, mean $\delta^{15}N$ significantly increased with watershed size and TSS concentration (Table 6).

TP ranged from 1.456 in the heavily urbanized BU1 to 2.356 in HC2, a pasture watershed. FCL ranged from 2.623 in BU2, an Urban watershed, to 4.338 in the heavily forested MO (Table 5). In all of the Urban and 2 of the 3 Developing watersheds, the top consumer was a sunfish (Family Centrarchidae, Table 5). In all but 1 of the other streams, the top consumer was a benthic-feeding fish (Table 5).

Mean TP and FCL decreased with increasing % impervious surface and FCL increased with % forest cover. Neither mean TP nor FCL were correlated with system size variables, however, both were strongly correlated to several resource and environmental variables (Table 6). Mean TP significantly decreased with increasing invertebrate biomass and chlorophyll *a* (Table 6), whereas both mean TP and FCL decreased with median stream temperature and TDS concentrations (Table 6). Spate frequency was also related significantly to mean TP and FCL, as both decreased with increasing frequency of spate flows, as measured by the variables 7xMed. Further FCL was significantly longer in streams with higher quality habitat, as evidenced by the significant positive correlation with the habitat index score (Table 6). Further, mean TP and FCL both significantly increased with increasing taxa richness (Figure 2).

5.4.2 Mean Food Webs

In general, streams draining urban watersheds showed slightly more variation within functional groups for δ^{13}C, and less so for δ^{15}N, than did the other LU/LC streams (Figure 3). However, within-group variation was relatively consistent as there was no significant difference between the different LU/LC types in terms of C or N isotopic variation of functional groups (Figure 4). The only functional group that was not found in all LU/LC categories was shredders (SH), which was absent from Urban streams. There also were several cases among Urban streams, and to a lesser extent in the Pasture and Developing streams, where a functional group was found in only 1 of the 3 replicate streams (Table 4).

Basal resources in the food webs were generally consistent among LU/LC categories, particularly OM (Figure 5). Derived POM was generally less C-enriched than OM, except for Urban streams, where it was more enriched. In all food webs, benthic algae were highly N-enriched, often at or above δ^{15}N signatures of secondary consumers (Figure 5).

Food webs seemed to show a distinct separation between vertebrates and invertebrates, and particularly so in the Developing web, with most fish being relatively

N-enriched and C-depleted as compared to invertebrates (Figure 5). Exceptions to this generalization were with terrestrial insects, which were relatively C-enriched, and with crayfish, which showed C- and often N-enrichment compared with other aquatic invertebrates (Figure 5). With few exceptions, most macroinvertebrate consumers were positioned over POM. Exceptions were the SH category in the Forest web (δ^{13}C enriched) and in the Developing web (δ^{13}C depleted) as well as the SC category in the Forest web (Figure 5).

The Urban food web, in general, was more C-enriched than the Forest and Developing food webs and significantly so for fish ($F_{3, 11} = 5.99$, $p = 0.019$; Figure 5). Based on their position in each web, OMN, ISV, and PSV fishes and salamanders appeared to be deriving their ultimate C from both terrestrial and aquatic resources. Piscivores and/or insectivores were consistently at the top of the food webs, except in the Pasture web, where HBV fish were particularly N-enriched. Also, with the exception for the Urban web, HBV fish were depleted in δ^{13}C compared with other fish feeding guilds (Figure 5).

The Forest foodweb biplot was significantly different from the Pasture, Developing, and Urban foodweb biplots in terms of shared components (Figure 6). There was a significant directional movement of shared taxa ($\mu = 74.7^{\circ}$, $r = 0.96$, Rao's U = 266.1, $p < 0.01$) in the Forest to Pasture comparison of foodweb biplots (Figure 6). There was also significant directional movement in the Forest to Developing foodweb biplot comparison ($\mu = 326.2^{\circ}$, $r = 0.71$, Rao's U = 176.2, $p < 0.05$). Finally, the Forest to Urban foodweb comparison also showed strong, significant directional movement ($\mu = 79^{\circ}$, $r = 0.99$, Rao's U = 283.1, $p < 0.01$).

5.5 DISCUSSION

The analysis of food webs with stable C and N isotopes allows ecologists to describe broad-scale energy flow in and trophic arrangement of systems in a time-integrated fashion (Peterson and Fry 1987). My study shows that stable isotope analysis of food webs can be used to examine the community-level impact of LU/LC on streams. Specifically, these results provide empirical evidence that disturbance associated with LU/LC, particularly urbanization, can have strong effects on the structure and function of stream food webs.

5.5.1 δ^{13}C and δ^{15}N differences among watersheds

Interestingly, there was no overall δ^{15}N-enrichment observed with increasing urbanization as has been observed in other studies of urban streams (McClelland et al. 1997, Steffey and Kilham 2004, Ulseth and Hershey 2005). However, there was considerable δ^{13}C enrichment associated with the loss of watershed forest cover / increase of urban cover as well as with stream size, as evidenced by the correlation analyses and the average food webs. Stable carbon isotope signatures often vary from system to system for various reasons (France 1995b, Finlay 2001), however systematic shifts over 12 systems as observed in my study suggest alterations in basal resources. Since stream size and loss of forest cover was correlated with C enrichment, it is possible that there was a shift in the importance of allochthonous litterfall in the smaller streams to autochthonous producers in the larger streams, particularly in the larger streams of the Urban and Pasture watersheds (Vannote et al. 1980, Rosenfeld and Roff 1992, Jones et al. 1998). Urban and Pasture watersheds in this area have been shown to have increased stream temperatures and levels of nutrients (Schoonover and Lockaby 2006), which could lead to increases in primary productivity, yet, we saw little evidence in our biplots for major differences in ultimate source of basal carbon. However, basal resources are notoriously variable (spatially and temporally) in terms of C and N isotopic signatures (France 1995b, Finlay 2001), so further sampling in other seasons would be necessary to fully address this shift in δ^{13}C among the streams.

I also observed δ^{13}C enrichment with increased % impervious surface cover. A likely explanation for this enrichment is fecal contamination in urbanized watersheds as a result of increased faulty sewage lines, combined sewer overflow inputs, and other sources of fecal contamination. In fact, near stream manhole covers were routinely displaced during heavy rain events in some of the urban watersheds in this study, allowing untreated sewage inputs directly to the stream (personal observation). Moreover, these urban watersheds have been shown to have elevated fecal coliform counts, particularly during storm events (Schoonover and Lockaby 2006). Further, human sewage particulate organic matter generally has a heavier C isotope ratio than stream POM (Spies et al. 1989); thus consumers using such a fecal-contaminated source of OM would be expected to show enriched δ^{13}C signatures. Therefore in these watersheds, as in some other studies, δ^{13}C of stream organisms can possibly serve as a time-integrated label for fecal contamination or urbanization in general and thus a potentially meaningful management tool (Spies et al. 1989, deBruyn and Rasmussen 2002).

5.5.2 Correlates of food chain length

Several interacting factors are thought to explain food chain length, including resource availability, system size, colonization history, and environmental stability

(Pimm 1982, Briand and Cohen 1987, Schoener 1989, Post 2002a). In addition, there is a growing literature integrating landscape influences on food web structure, emphasizing geology, hydrology, land use and habitat fragmentation on trophic interactions (Polis et al. 1997, Woodward and Hildrew 2002). Specifically, effects of land use disturbance on stream systems often are considered functions of increased flood magnitude and frequency (Booth and Jackson 1997), altered streambed morphology and stability (Booth and Jackson 1997, Wang and Lyons 2003b) altered sediment and chemical inputs (Wernick et al. 1998, Allan 2004), and degraded riparian zones (Finkenbine et al. 2000, Groffman et al. 2003). In my study, FCL decreased with increasing landscape disturbance, as reduced forest cover and elevated impervious surface cover. It should be noted, however, that these 2 sources of landscape disturbance, although correlated, are not entirely reciprocal. Except for the Urban streams, most watersheds had low % IS and were indistinguishable, so that FCL relationships with impervious surface largely reflect the influence of intense urbanization. In contrast, % forest cover was more evenly spread across study watersheds, with Urban watersheds having the lowest % cover, followed by Pasture, Developing, and Forest watersheds. Thus, the % Forest metric better reflects the entire spectrum of LU/LC disturbance in the watersheds than % IS or % pasture.

Interestingly, on a reach scale, FCL was not correlated with watershed size or resource availability; however, there were strong correlations with reach measures of disturbance. A similar trend was observed in relatively pristine Alaskan streams, where FCL was shorter where disturbance was greater (Parker and Huryn 2006). In my streams, FCL decreased with increasing average stream temperature, TDS concentrations, and spate flow frequency and increased with increasing instream habitat quality. There was also a strong relationship between FCL and taxa richness. These relationships suggest hydrologic alteration associated with LU/LC disturbance as a strong driver of food web structure in these streams.

Of the multiple landscape disturbances affecting streams, hydrological alteration is one of the more obvious and pervasive (Booth and Jackson, 1997; Groffman *et al*., 2003; Wang and Lyons, 2003; Walsh *et al*., 2005). As a result of high levels of watershed imperviousness and connectedness, streams draining urban and urbanizing watersheds often display flashy hydrographs with multiple peak flows and reduced base flows (Ferguson and Suckling, 1990; Rose and Peters, 2001; Schoonover *et al*., 2006). Stormflow magnitude and frequency often increase in agricultural settings because of the use of drainage ditches, loss of wetlands, and soil compaction (Peterson and Kwak, 1999; Allan, 2004). This effective transport of overland flow can have far-reaching implications on instream conditions, including elevated water contaminants and solutes, elevated water temperature, altered instream habitat, loss of species and alterations of assemblages; each of these stressors could have separately or in combination reduced FCL in study watersheds (Paul and Meyer 2001, Allan 2004).

5.5.3 Food chain length and web structure

My results in part support the model of dynamical constraints in that FCL was reduced in systems with higher disturbance (Pimm and Lawton 1977, Menge and Sutherland 1987). However, the model suggests that rare species high on the food chain are more likely to be lost from a disturbance event than the more abundant lower consumers, resulting in shorter food chains in disturbed environments (Jenkins et al. 1992, Thompson and Townsend 2005). In my study, there was not the general loss of the top consumer group, as insectivores and omnivores were consistently top consumer in all streams irrespective of disturbance intensity; however, there was a general loss of benthic-feeding fish in the more hydrologically disturbed streams. In addition, increased disturbance appeared to have a strong effect on organisms in the middle trophic positions, particularly shredding macroinvertebrates and crayfish, and to a lesser extent filtering macroinvertebrates, salamanders, and herbivorous fish. In fact, the longest and the shortest FCL in the study (MO and BU2, respectively) both contained *Lepomis* sunfish as the top consumer. This pattern of middle trophic position loss but maintenance of similar top consumers (at least functionally) across a disturbance gradient is partially contributable to the generalist behavior and broad diets of many top consumers in these streams. Many of the fish species in these streams are cosmopolitan (Swift et al. 1986) and thus are capable of inhabiting a wide array of conditions (Boschung and Mayden 2004); therefore, they should be somewhat resilient to compositional changes in food resources attributable to landscape differences in these streams. In summary, disturbance and environmental stability appears to reduce FCL in these streams by limiting the species of top predator, but not the entire functional group, as well as consumer membership in middle trophic positions.

Mean food web biplots revealed certain trends and trophic relationships that were not obvious with simple FCL examination. As noted in other systems, terrestrial inputs into these streams, particularly terrestrial invertebrate prey for fish, appears to play an important energetic role (Nakano et al. 1999, Baxter et al. 2005). Insectivorous and omnivorous fish in all streams, on average, were more $\delta^{13}C$ enriched than most of the aquatic invertebrates, and were more positioned over terrestrial invertebrates in biplot space, suggesting a heavy reliance on terrestrial prey. However, there were many differences among the different types of LU/LC food webs. In particular, mean biplots revealed a smaller spread of $\delta^{13}C$ and very little overlap of functional groups in the Forest than the other streams, stronger segregation between benthos and fish in the Developing and Pasture streams than in Forest and Urban streams, and an almost chain-like appearance of the food web in the Urban streams. Further, mean Forest foodwebs were significantly different than Pasture, Developing, and Urban foodwebs. The mean vector of change from Forest to Pasture and from Forest to Urban foodwebs revealed strong $\delta^{13}C$ enrichment, while the mean vector of change from Forest to Developing suggested slight $\delta^{15}N$ enrichment. Taken together, these suggest 1) a close association between fish, benthos, and terrestrial resources in the Forest watersheds and this association tends to break down with increased landscape disturbance as benthos become less important of a resource for fish (Baxter et al. 2005); 2) a higher degree of feeding (niche) compartmentation in the Forest streams and higher feeding (niche) overlap in the more disturbed systems (Death 2004); and 3) that Urban stream food webs are dramatically simplified and retain minimum function with fewer functional groups (Walsh et al. 2005b).

5.5.4 Conclusions

My results suggest that disturbance from watershed LU/LC can have a dramatic impact on food web architecture in southeastern streams subject to human influence. In these streams, $\delta^{13}C$ appears to be an indicator of general LU/LC disturbance. This has important implications for management, as many physicochemical impacts of LU/LC disturbance are episodic in nature and can occur at relatively low levels of landscape alteration (Allan et al. 1997, Barbour et al. 1999, Schoonover and Lockaby 2006). Thus a time integrated marker of anthropogenic disturbance can be a valuable identification and management tool.

FCL in these watersheds appears to be more determined by disturbance, particularly hydrologic alteration, than by ecosystem size or resource availability. Although the role of ecosystem size or resource availability should not be ruled out, especially given the temporal, interrelated nature of these influences (Post 2002a, Thompson and Townsend 2005), disturbance appears to be an overwhelming influence in these systems, particularly the Urban watersheds.

Human population expansion and the inevitable landscape alteration caused by such growth have produced dramatic impacts on stream ecosystems. By attempting to identify and address the specific drivers of biotic associations resulting from these perturbations, we can better address management and/or restoration needs designed to protect or minimize changes in stream biotic integrity.

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Table 1. Land cover and physical characters of study watersheds. **Watershed** is the watershed size, **Stream** = mean depth x width for the stream draining the watershed, %**IS** = % impervious surface cover, %**Pasture** = % pasture cover, and % **Forest** = % forest cover, and **LU/LC** = dominant land use/land cover in watershed.

ID	**Site**	**Stream**	**Watershed (km^2)**	**Stream (m^2)**	**% IS**	**% Pasture**	**% Forest**	**LU/LC**
1	SB1	Schley Creek	20.1	0.40	2	20	74	Developing
2	SB2	Standing Boy Creek Trib.	6.3	0.22	3	20	73	Developing
3	SB4	Standing Boy Creek	26.6	0.71	3	28	64	Developing
4	BLN	Blanton Creek	3.6	0.25	1	19	76	Forest
5	MO	Cline's Branch	9.0	0.37	2	13	81	Forest
6	MU3	Turntime Branch	10.4	0.58	2	15	78	Forest
7	FS2	Wildcat Creek Trib.	14.5	0.64	3	36	59	Pasture
8	FS3	Wildcat Creek Trib.	3.0	0.85	3	34	62	Pasture
9	HC2	House Creek	14.1	0.53	2	44	52	Pasture
10	BU1	Lindsey Creek	25.5	2.00	40	23	34	Urban
11	BU2	Cooper Creek	24.7	0.98	25	25	46	Urban
12	RB	Roaring Branch	3.7	0.68	30	27	39	Urban

Table 2. Resource, environmental, and size variables used in analyses, their range of values, and their Pearson correlations to predominant land cover classes in the 12 watersheds. %**IS** = proportion of impervious surface cover, %**Forest** = proportion of forest cover. There were no significant correlations between any variables and proportion of pasture cover in the watersheds. * $p < 0.05$, ** $p < 0.01$.

Variable ID	**Description**	**Range**	**% IS**	**% Forest**
Resource				
Invert Biomass	Mean macroinvertebrate biomass (g / m^2)	11.2 – 51.5		
Chlorophyll *a*	Mean periphyton biomass (g / m^2)	0.03 – 1.97	0.62*	
OM	Benthic organic matter (g)	0.3 – 1.2		
Habitat Index	Habitat assessment index score	54.2 – 125.5		0.48*
Environmental				
Temp	Median water temperature (^oC)	13.3 – 15.6	0.84**	-0.59*
TDS	Mean total dissolved solids concentration (mg L^{-1})	19.9 – 58.6	0.65*	
TSS	Mean total suspended solids concentration (mg L^{-1})	2.1 – 8.1		
MaxQ	Maximum discharge (L s^{-1})	0.54 – 21.98		
7xMed	# of times discharge exceeded 7x median flow	1 – 64	0.63*	
Size				
Watershed	Watershed size (km^2)	3.0 – 26.6		
Stream	Mean width x mean depth of stream (m^2)	0.34 – 1.20	0.67*	-0.77**

Table 3. Taxa collected for stable isotope analysis over the 12 watersheds. **Group** refers to broad functional grouping used in construction of food webs.

Taxon Name	Family	Order	Group
benthic algae	-	-	Basal/Terrestrial
organic matter	-	-	Basal/Terrestrial
ant	Formicidae	Hymenoptera	Basal/Terrestrial
Anchytarsus	Elmidae	Coleoptera	Invertebrate
Optioservus	Elmidae	Coleoptera	Invertebrate
Cyclopoida	-	Cyclopoida	Invertebrate
Cambarus latimanus	Cambaridae	Decapoda	Invertebrate
Procambarus versutus	Cambaridae	Decapoda	Invertebrate
Non -Tanypod chironomid	Chironomidae	Diptera	Invertebrate
Tanypod chironomid	Chironomidae	Diptera	Invertebrate
Tabanus	Tabanidae	Diptera	Invertebrate
Hexatoma	Tipulidae	Diptera	Invertebrate
Tipula	Tipulidae	Diptera	Invertebrate
Baetis	Baetidae	Ephemeroptera	Invertebrate
Ephemerella	Ephemerellidae	Ephemeroptera	Invertebrate
Hexagenia	Ephemeridae	Ephemeroptera	Invertebrate
Stenonema	Heptageniidae	Ephemeroptera	Invertebrate
Isonychia	Isonychiidae	Ephemeroptera	Invertebrate
Tricorythodes	Tricorythidae	Ephemeroptera	Invertebrate
Corydalus	Corydalidae	Megaloptera	Invertebrate
Boyeria	Aeshnidae	Odonata	Invertebrate
Calopteryx	Calopterygidae	Odonata	Invertebrate
Cordulegaster	Cordulegastridae	Odonata	Invertebrate
Macromia	Corduliidae	Odonata	Invertebrate
Gomphus	Gomphidae	Odonata	Invertebrate
Allocapnia	Capniidae	Plecoptera	Invertebrate
Acroneuria	Perlidae	Plecoptera	Invertebrate
Physella	Physidae	Pulmonata	Invertebrate
Cheumatopsyche	Hydropsychidae	Trichoptera	Invertebrate
Pycnopsyche	Limnephilidae	Trichoptera	Invertebrate
Lebertid mite	Lebertidae	Trombidiformes	Invertebrate
Corbicula fluminea	Corbiculidae	Veneroida	Invertebrate

Table 3. continued.

Taxon Name	**Family**	**Order**	**Group**
Bufo fowleri	Bufonidae	Anura	Vertebrate
Eurycea cirrigera	Plethodontidae	Caudata	Vertebrate
Hypentelium etowanum	Catastomidae	Cypriniformes	Vertebrate
Minytrema melanops	Catastomidae	Cypriniformes	Vertebrate
Campostoma pauciradii	Cyprinidae	Cypriniformes	Vertebrate
Luxilus zonistius	Cyprinidae	Cypriniformes	Vertebrate
Nocomis leptocephalus	Cyprinidae	Cypriniformes	Vertebrate
Notemigonus chrysoleucuas	Cyprinidae	Cypriniformes	Vertebrate
Notropis baileyi	Cyprinidae	Cypriniformes	Vertebrate
Notropis buccata	Cyprinidae	Cypriniformes	Vertebrate
Notropis longirostis	Cyprinidae	Cypriniformes	Vertebrate
Notropis texanus	Cyprinidae	Cypriniformes	Vertebrate
Semotilus atromaculatus	Cyprinidae	Cypriniformes	Vertebrate
Lepomis auritus	Centrarchidae	Perciformes	Vertebrate
Lepomis cyanellus	Centrarchidae	Perciformes	Vertebrate
Lepomis gulosus	Centrarchidae	Perciformes	Vertebrate
Lepomis macrochirus	Centrarchidae	Perciformes	Vertebrate
Micropterus salmoides	Centrarchidae	Perciformes	Vertebrate
Percina nigrofasciata	Percidae	Perciformes	Vertebrate
Ameiurus brunneus	Ictaluridae	Siluriformes	Vertebrate
Ameiurus natalis	Ictaluridae	Siluriformes	Vertebrate
Ameiurus nebulosus	Ictaluridae	Siluriformes	Vertebrate
Noturus sp.	Ictaluridae	Siluriformes	Vertebrate

Table 4. Number of different taxa collected from each Functional Group in each watershed. For invertebrates, CF = collector/fileters, CG = collector/gatherers, PA = parasites, PR = predators, SC = scrapers, SH = shredders, and SV = scavengers (crayfish). For vertebrates, HBV = herbivores, ISV = insectivores, OMN = omnivores, PSV = piscivores, SAL = salamander, TOAD = toad. Site codes are as in Table 1. Only invertebrates that could be identified to family-level were included.

SITE	LU/LC	CF	CG	PR	SC	SH	SV	HBV	ISV	OMN	PSV	SAL	TOAD	TOTAL
SB1	**Developing**	1	4	3	0	1	1	1	5	1	0	1	0	18
SB2	**Developing**	0	3	1	1	1	0	0	4	1	1	0	0	12
SB4	**Developing**	0	3	3	1	0	1	0	6	2	2	1	0	19
BLN	**Forest**	2	3	6	1	2	2	1	9	2	1	1	0	30
MO	**Forest**	1	4	6	1	1	1	1	7	3	1	1	0	25
MU3	**Forest**	2	3	4	1	0	1	0	5	3	2	0	0	21
FS2	**Pasture**	0	2	3	1	1	2	1	9	2	0	1	0	22
FS3	**Pasture**	1	3	3	1	0	2	1	4	3	0	1	0	19
HC2	**Pasture**	0	3	3	1	0	2	0	7	2	0	0	0	18
BU1	**Urban**	0	3	4	1	0	0	1	2	1	1	0	1	14
BU2	**Urban**	1	2	2	0	0	0	0	5	0	1	1	0	12
RB	**Urban**	2	2	2	1	0	0	0	1	0	0	0	0	8

Table 5. Stable isotope results for 12 watersheds. $\delta^{13}C$ and $\delta^{15}N$ values are site averages, **µTP** is mean trophic position, **FCL** is maximum trophic position (food chain length), **Top Consumer** is the organism with the maximum trophic position, and **FG** is the functional group of the top consumer (see Table 4 for abbreviation explanations)

Site	**µ $\delta^{13}C$ (‰)**	**µ $\delta^{15}N$ (‰)**	**µ TP**	**FCL**	**Top consumer**	**FG**
SB1	-31.043	5.232	1.645	3.024	*L. macrochirus*	ISV
SB2	-29.677	5.195	1.769	2.985	*L. auritus*	ISV
SB4	-29.348	8.655	1.9	2.97	*P. nigrofasciata*	ISV
BLN	-28.17	6.192	1.833	3.675	*P. nigrofasciata*	ISV
MO	-29.436	5.141	2.265	4.338	*L. macrochirus*	ISV
MU3	-29.262	6.912	1.815	3.253	*P. nigrofasciata*	ISV
FS2	-27.639	7.361	2.247	3.393	*M. melanops*	ISV
FS3	-28.61	6.895	1.726	2.934	*H. etowanum*	ISV
HC2	-27.116	6.616	2.356	3.525	*A. natalis*	OMN
BU1	-23.19	7.126	1.456	2.741	*L. auritus*	ISV
BU2	-26.538	8.842	1.676	2.623	*L. auritus*	ISV
RB	-28.195	4.233	1.373	3.015	*L. macrochirus*	ISV

Table 6. Significant correlation coefficients between stable isotope results and land cover, resource, environmental and system size. Variable definitions are as in Tables 1 – 2 * $p < 0.05$, ** $p < 0.01$.

Variable	**μ $\delta^{13}C$**	**μ $\delta^{15}N$**	**μ TP**	**FCL**
% IS	0.75**		-0.67*	-0.58*
% Pasture				
% Forest	-0.78**			0.58*
Invert Biomass			-0.60*	
Chlorophyll *a*			-0.68*	
Temp			-0.81**	-0.65*
TDS			-0.73**	-0.66*
TSS		0.70*		
7xMed			-0.71**	-0.63*
Habitat				0.75**
Watershed		0.65*		
Stream	0.76**			

Figure 1. The study area included 12 small watersheds (shaded sections) of the Chattahoochee River Basin in 4 counties in the Lower Southern Piedmont ecoregion of western Georgia, USA. Numbers refer to watersheds and correspond to Table 1. The city of Columbus is located in western Muscogee County. County names are in capital letters.

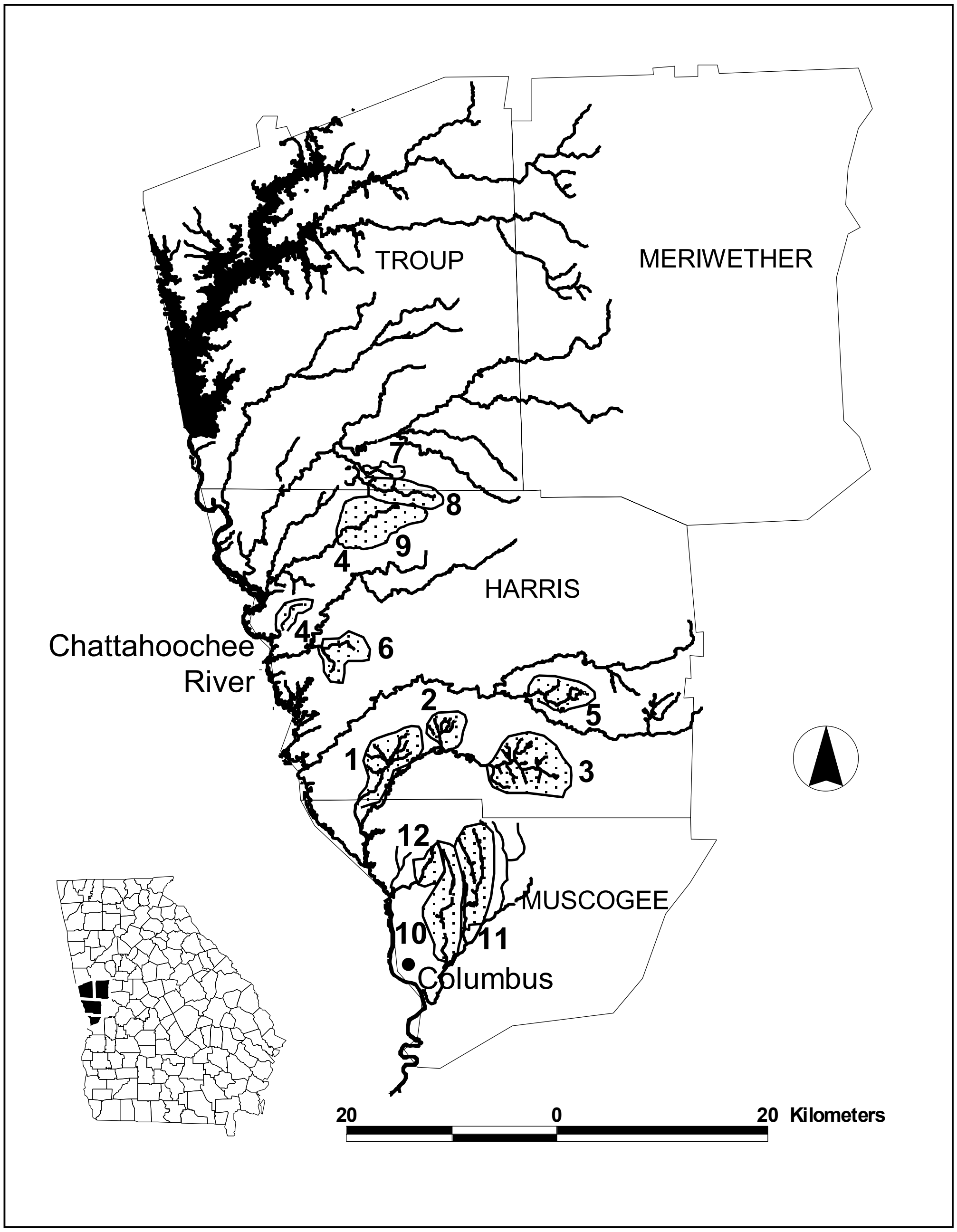


Figure 2. Relationship between mean trophic position and taxa richness and maximum food chain length and taxa richness in 12 streams.

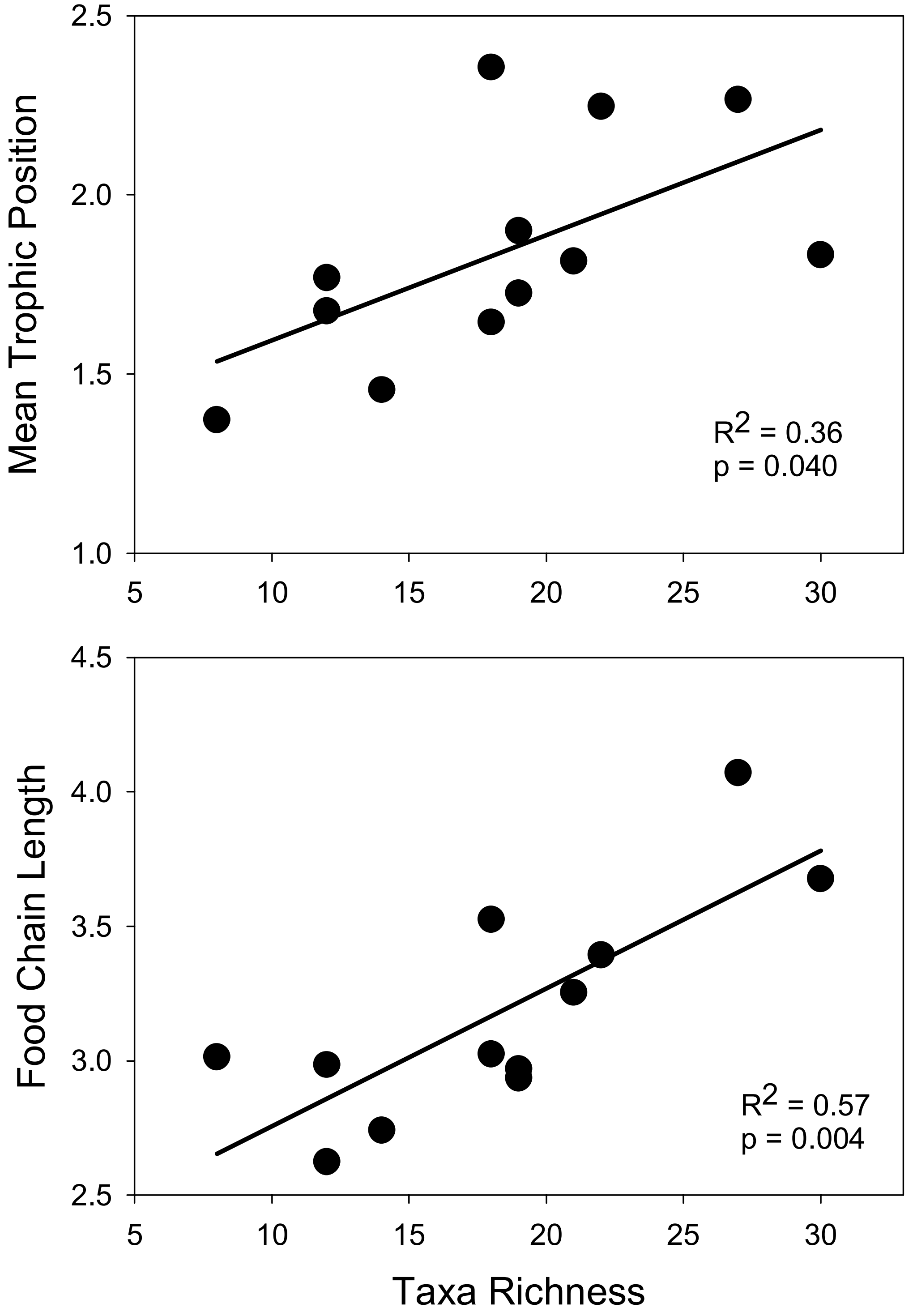


Figure 3. Standard errors of mean δ^{13}C and δ^{15}N functional group values for 4 land use types.

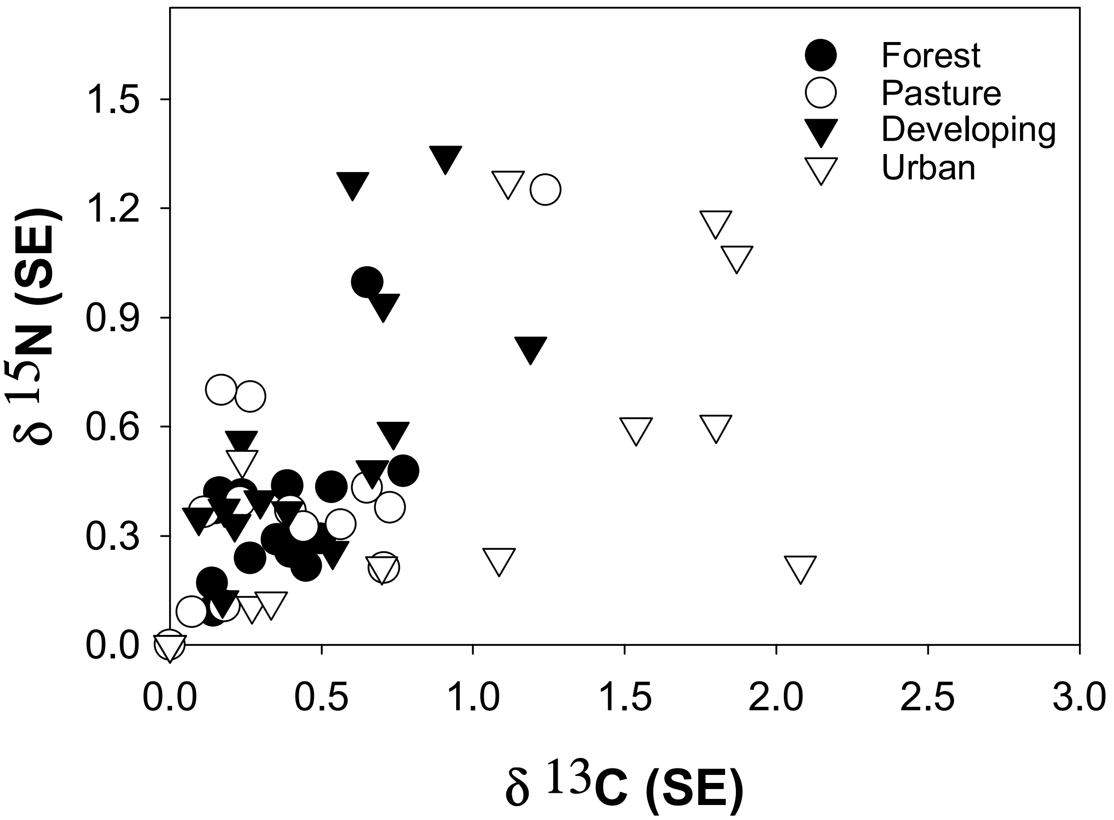


Figure 4. Mean standard deviations for averaged δ^{13}C and δ^{15}N values in each LU/LC category. There is no significant difference in the variation between categories.

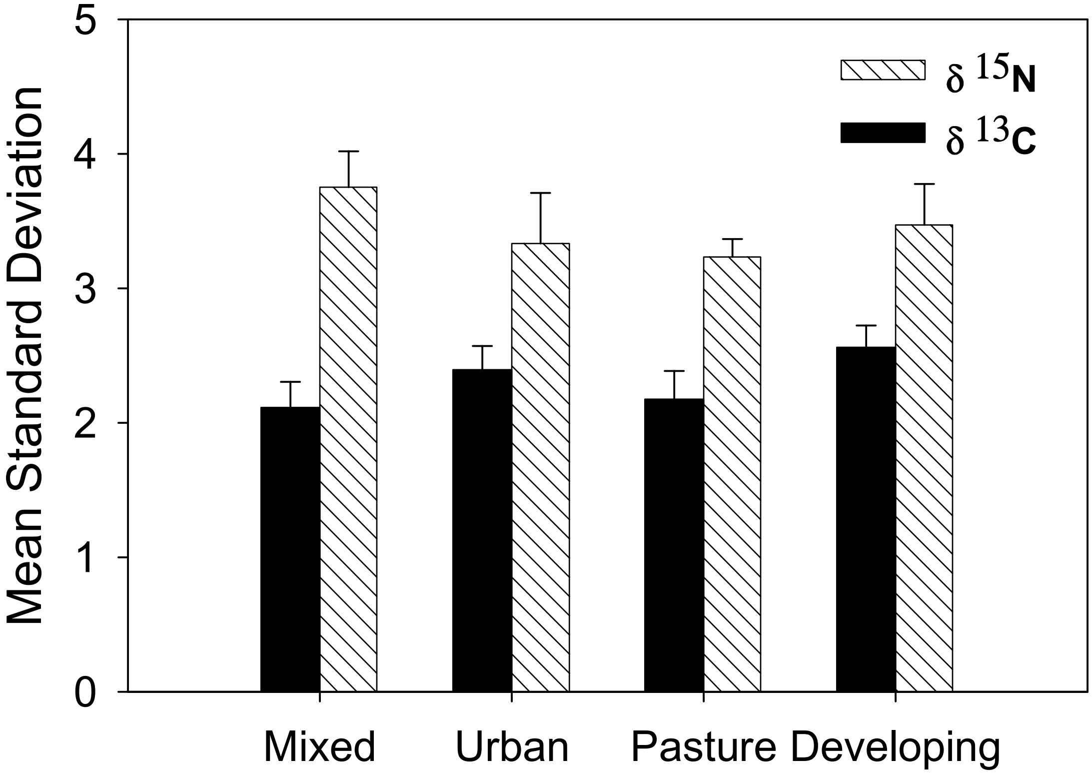


Figure 5. Biplots of average δ^{13}C and δ^{15}N (+ 1 SE) values for functional groups for 4 land use categories (3 streams per category). A given functional group had to be present in at least 2 of the 3 streams per category to be included. Dark grey values are vertebrates, light grey are invertebrates, and black values are basal / terrestrial resources. Error bars are present but obscured on some points.

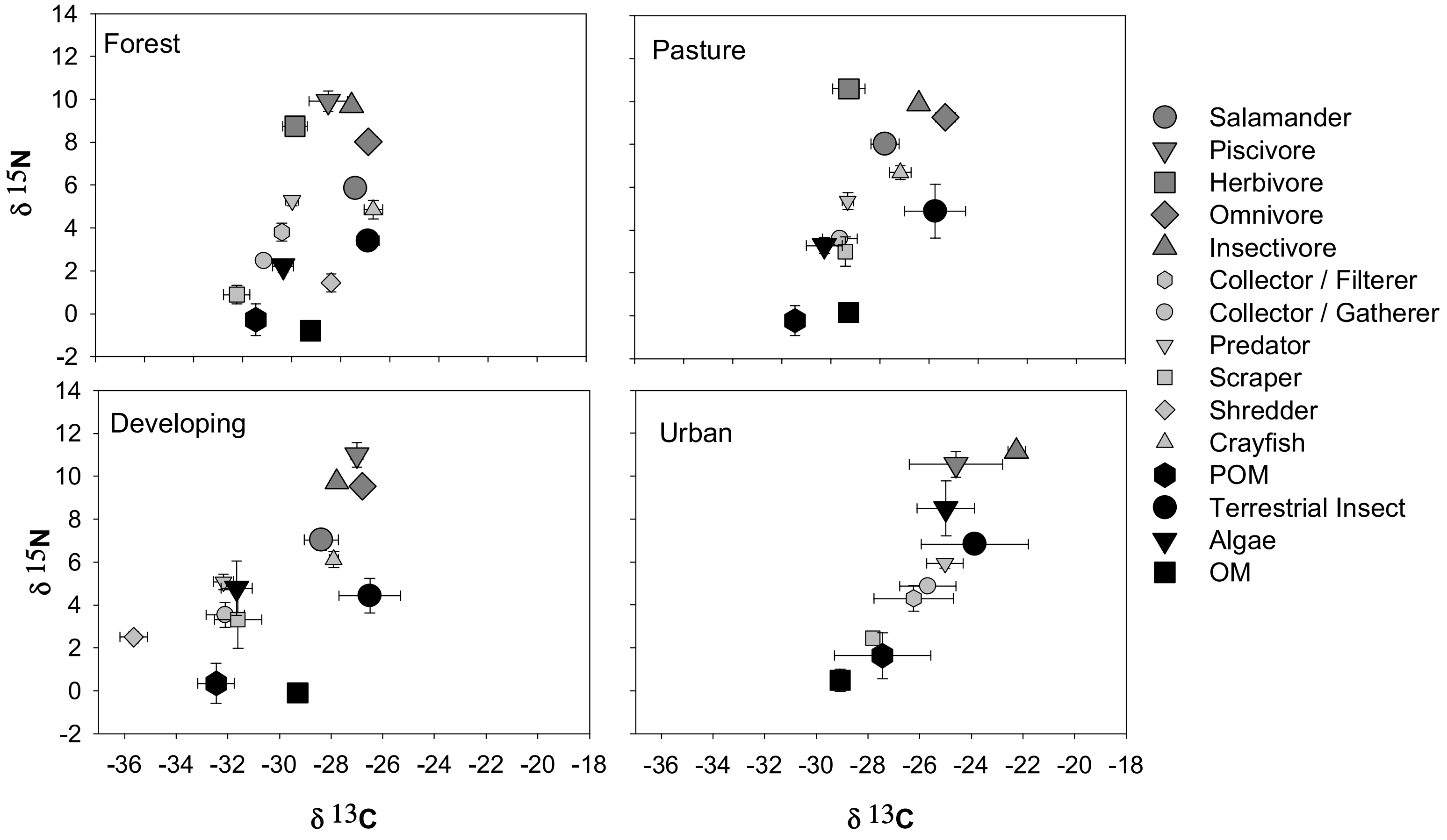
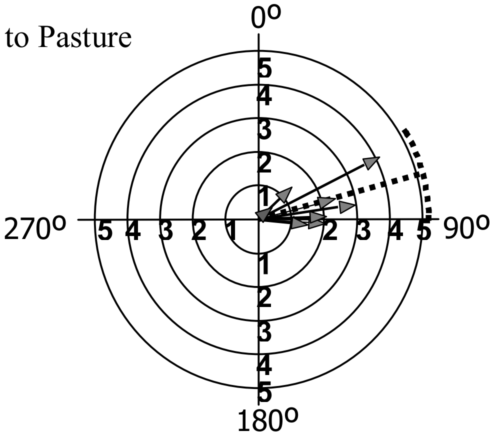
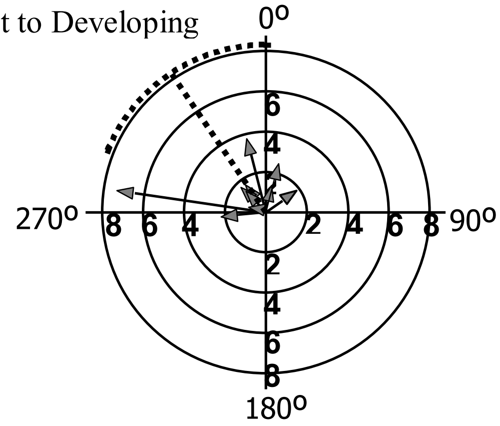


Figure 6. Arrow diagrams of direction and magnitude of change for consumer groups that correspond between compared food webs. Each diagram represents a comparison of 1 mean food web to another. The length of the arrows represent the magnitude of change for each group shared in both food webs, concentric circles correspond to the magnitude of change, dashed lines are the mean vector of change, and curved dashed lines are 95% confidence intervals of the vector of change.

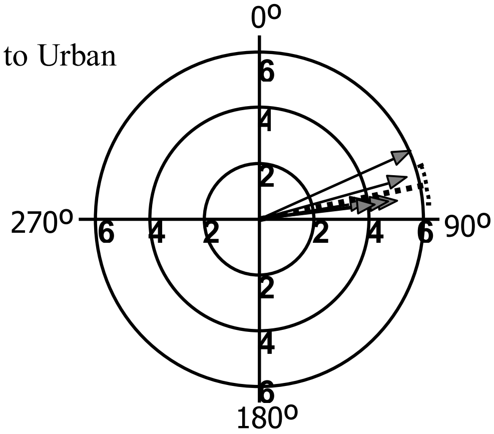
A. Forest to Pasture



B. Forest to Developing



C. Forest to Urban



APPENDIX. Watershed and biotic summaries for each watershed sampled during the studies. AFDM: Ash-free dry mass, Diversity: Shannon's *H'*, GA-BMI: Georgia Benthic Macroinvertebrate Index, GA-IBI: Georgia Index of Biotic Integrity

Watershed ID	BC		
Watershed Area	647 ha		
Tributary Name	Beech Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	703868	3657575
Seasons Sampled	6		
Total Macroinvertebrate Richness	145		
Total Fish Richness	15		

Parameter	Mean	Max	Min	SE
Algae				
AFDM (g / m^2)	0.45	0.04	1.08	0.25
Chlorophyll *a* (mg / m^2)	0.32	0.01	0.64	0.11
Macroinvertebrates				
Biomass (g / m^2)	9.72	0.42	20.59	2.48
Diversity (*H'*)	2.64	2.44	3.12	0.09
Richness	42.50	22.00	59.00	5.20
GA-BMI	53.33	32.00	80.00	7.22
Fish				
Diversity (*H'*)	1.30	1.03	1.57	0.10
Richness	9.00	6.00	11.00	0.84
GA-IBI	40.80	32.00	44.00	2.33

Watershed ID	BLN		
Watershed Area	364 ha		
Tributary Name	Blanton Creek		
Stream Order	1		
UTM Zone 16 Coordinates	16 N	677570	3625622
Seasons Sampled	3		
Total Macroinvertebrate Richness	92		
Total Fish Richness	18		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.02	0.02	0.02	0.00
Chlorophyll *a* (mg / m^2)	0.70	0.47	0.92	0.23
Macroinvertebrates				
Biomass (g / m^2)	31.43	9.82	62.04	12.85
Diversity (*H′*)	2.74	2.59	2.97	0.10
Richness	56.67	51.00	64.00	3.84
GA-BMI	56.00	41.00	75.00	10.02
Fish				
Diversity (*H′*)	2.09	1.94	2.21	0.08
Richness	12.33	11.00	14.00	0.88
GA-IBI	36.00	34.00	38.00	1.15

Watershed ID	BSB		
Watershed Area	697 ha		
Tributary Name	Blue Springs Branch		
Stream Order	1		
UTM Zone 16 Coordinates	16 N	690427	3621407
Seasons Sampled	3		
Total Macroinvertebrate Richness	90		
Total Fish Richness	16		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.82	0.05	1.56	0.44
Chlorophyll *a* (mg / m^2)	0.71	0.51	0.95	0.13
Macroinvertebrates				
Biomass (g / m^2)	15.95	3.20	23.57	5.24
Diversity (*H′*)	2.51	1.74	3.04	0.32
Richness	48.67	23.00	63.00	12.86
GA-BMI	53.67	46.00	58.00	3.84
Fish				
Diversity (*H′*)	1.95	1.87	2.04	0.05
Richness	10.67	9.00	12.00	0.88
GA-IBI	46.67	46.00	48.00	0.67

Watershed ID	BU1		
Watershed Area	2546 ha		
Tributary Name	Lindsey Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16N	693323	3592891
Seasons Sampled	6		
Total Macroinvertebrate Richness	70		
Total Fish Richness	12		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.58	0.00	1.49	0.36
Chlorophyll *a* (mg / m^2)	0.61	0.11	1.82	0.41
Macroinvertebrates				
Biomass (g / m^2)	40.58	13.70	113.14	13.96
Diversity (*H′*)	1.82	1.43	2.31	0.12
Richness	20.33	15.00	29.00	1.98
GA-BMI	28.67	10.00	43.00	4.70
Fish				
Diversity (*H′*)	1.17	0.23	1.69	0.26
Richness	5.40	2.00	8.00	0.98
GA-IBI	32.00	26.00	36.00	1.90

Watershed ID	BU2		
Watershed Area	2469 ha		
Tributary Name	Cooper Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	695222	3595956
Seasons Sampled	6		
Total Macroinvertebrate Richness	83		
Total Fish Richness	20		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.51	0.02	1.16	0.29
Chlorophyll *a* (mg / m^2)	0.41	0.05	0.93	0.18
Macroinvertebrates				
Biomass (g / m^2)	34.43	14.15	55.97	5.83
Diversity (*H′*)	1.72	1.24	2.37	0.15
Richness	23.50	19.00	30.00	1.67
GA-BMI	24.83	7.00	35.00	4.18
Fish				
Diversity (*H′*)	1.64	1.28	1.77	0.09
Richness	10.00	9.00	11.00	0.45
GA-IBI	36.40	32.00	40.00	1.83

Watershed ID	FPBW		
Watershed Area	489 ha		
Tributary Name	Five Points Branch		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	689255	3621326
Seasons Sampled	3		
Total Macroinvertebrate Richness	104		
Total Fish Richness	10		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.85	0.03	1.58	0.45
Chlorophyll *a* (mg / m^2)	0.81	0.47	1.00	0.17
Macroinvertebrates				
Biomass (g / m^2)	26.23	9.66	42.23	7.68
Diversity (*H′*)	2.34	1.76	3.04	0.31
Richness	57.67	29.00	74.00	14.38
GA-BMI	51.67	48.00	59.00	3.67
Fish				
Diversity (*H′*)	1.83	1.72	1.96	0.07
Richness	8.00	7.00	9.00	0.58
GA-IBI	44.67	44.00	46.00	0.67

Watershed ID	FR		
Watershed Area	2396 ha		
Tributary Name	Flat Rock		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	699161	3599824
Seasons Sampled	1		
Total Macroinvertebrate Richness	26		
Total Fish Richness	8		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	-	-	-	-
Chlorophyll *a* (mg / m^2)	-	-	-	-
Macroinvertebrates				
Biomass (g / m^2)	61.24	61.24	61.24	-
Diversity (*H′*)	2.20	2.20	2.20	-
Richness	26.00	26.00	26.00	-
GA-BMI	24.00	24.00	24.00	-
Fish				
Diversity (*H′*)	1.46	1.46	1.46	-
Richness	8.00	8.00	8.00	-
GA-IBI	38.00	38.00	38.00	-

Watershed ID	FS1		
Watershed Area	2420 ha		
Tributary Name	Wildcat Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	684091	3641414
Seasons Sampled	3		
Total Macroinvertebrate Richness	66		
Total Fish Richness	15		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	1.00	0.04	2.87	0.94
Chlorophyll *a* (mg / m^2)	0.38	0.03	0.88	0.25
Macroinvertebrates				
Biomass (g / m^2)	15.98	8.19	20.96	3.22
Diversity (*H′*)	2.20	1.57	2.78	0.29
Richness	37.00	24.00	46.00	6.66
GA-BMI	44.67	38.00	50.00	3.53
Fish				
Diversity (*H′*)	1.93	1.73	2.13	0.12
Richness	11.00	7.00	15.00	2.31
GA-IBI	45.33	42.00	48.00	1.76

Watershed ID	FS2		
Watershed Area	1449 ha		
Tributary Name	Wildcat Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	685946	3639085
Seasons Sampled	3		
Total Macroinvertebrate Richness	55		
Total Fish Richness	15		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.00	0.00	0.00	0.00
Chlorophyll *a* (mg / m^2)	0.01	0.01	0.01	0.00
Macroinvertebrates				
Biomass (g / m^2)	11.17	4.85	18.09	3.13
Diversity (*H'*)	1.93	1.40	2.61	0.29
Richness	33.67	31.00	35.00	1.33
GA-BMI	40.00	25.00	66.00	13.05
Fish				
Diversity (*H'*)	1.96	1.90	2.06	0.05
Richness	10.67	10.00	11.00	0.33
GA-IBI	37.33	34.00	42.00	2.40

Watershed ID	FS3		
Watershed Area	296 ha		
Tributary Name	Wildcat Creek		
Stream Order	1		
UTM Zone 16 Coordinates	16 N	685956	3640196
Seasons Sampled	3		
Total Macroinvertebrate Richness	66		
Total Fish Richness	16		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.62	0.04	1.20	0.58
Chlorophyll *a* (mg / m^2)	1.03	1.02	1.03	0.00
Macroinvertebrates				
Biomass (g / m^2)	41.14	24.45	65.65	10.22
Diversity (*H′*)	2.37	2.31	2.42	0.03
Richness	41.00	36.00	51.00	5.00
GA-BMI	41.33	36.00	52.00	5.33
Fish				
Diversity (*H′*)	2.00	1.87	2.08	0.06
Richness	11.00	10.00	12.00	0.58
GA-IBI	30.67	30.00	32.00	0.67

Watershed ID	FS5		
Watershed Area	1183 ha		
Tributary Name	Flat Shoals		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	707467	3652031
Seasons Sampled	3		
Total Macroinvertebrate Richness	84		
Total Fish Richness	9		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.96	0.03	2.73	0.89
Chlorophyll *a* (mg / m^2)	0.23	0.09	0.37	0.08
Macroinvertebrates				
Biomass (g / m^2)	8.95	7.30	10.61	0.96
Diversity (*H′*)	2.78	2.68	2.88	0.06
Richness	59.00	56.00	62.00	2.45
GA-BMI	31.50	22.00	41.00	7.76
Fish				
Diversity (*H′*)	1.17	0.80	1.41	0.19
Richness	4.33	3.00	6.00	0.88
GA-IBI	38.00	36.00	40.00	1.15

Watershed ID	FS6		
Watershed Area	922 ha		
Tributary Name	Flat Shoals		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	707446	3651910
Seasons Sampled	3		
Total Macroinvertebrate Richness	21		
Total Fish Richness	9		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.51	0.22	0.81	0.17
Chlorophyll *a* (mg / m^2)	0.23	0.06	0.48	0.13
Macroinvertebrates				
Biomass (g / m^2)	0.68	0.00	1.36	0.39
Diversity (*H′*)	0.84	0.00	1.68	0.48
Richness	10.50	1.00	20.00	7.76
GA-BMI	29.00	20.00	38.00	7.35
Fish				
Diversity (*H′*)	1.30	1.11	1.48	0.11
Richness	5.33	4.00	6.00	0.67
GA-IBI	33.33	30.00	36.00	1.76

Watershed ID	HC		
Watershed Area	655 ha		
Tributary Name	House Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	678141	3630775
Seasons Sampled	5		
Total Macroinvertebrate Richness	115		
Total Fish Richness	17		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.40	0.01	1.10	0.35
Chlorophyll *a* (mg / m^2)	0.08	0.04	0.10	0.02
Macroinvertebrates				
Biomass (g / m^2)	16.56	1.66	41.87	6.91
Diversity (*H′*)	2.11	1.13	2.70	0.24
Richness	35.20	30.00	41.00	1.85
GA-BMI	45.00	33.00	61.00	6.19
Fish				
Diversity (*H′*)	1.63	1.17	2.03	0.20
Richness	7.75	6.00	10.00	0.85
GA-IBI	37.50	28.00	48.00	4.27

Watershed ID	HC2		
Watershed Area	655 ha		
Tributary Name	House Creek		
Stream Order	3		
UTM Zone 16 Coordinates	16 N	683811	3634666
Seasons Sampled	3		
Total Macroinvertebrate Richness	52		
Total Fish Richness	17		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.01	0.00	0.02	0.01
Chlorophyll *a* (mg / m^2)	0.22	0.03	0.40	0.18
Macroinvertebrates				
Biomass (g / m^2)	6.96	1.38	15.83	3.66
Diversity (*H′*)	1.69	0.81	2.56	0.41
Richness	31.67	25.00	40.00	4.41
GA-BMI	33.33	23.00	39.00	5.17
Fish				
Diversity (*H′*)	1.94	1.79	2.01	0.08
Richness	12.33	12.00	13.00	0.33
GA-IBI	40.67	40.00	42.00	0.67

Watershed ID	MK		
Watershed Area	663 ha		
Tributary Name	McKoon Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	703701	3668559
Seasons Sampled	6		
Total Macroinvertebrate Richness	126		
Total Fish Richness	20		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.52	0.01	1.06	0.30
Chlorophyll *a* (mg / m^2)	0.13	0.02	0.33	0.07
Macroinvertebrates				
Biomass (g / m^2)	5.87	1.91	10.97	1.39
Diversity (*H′*)	2.46	2.11	2.60	0.08
Richness	37.83	28.00	44.00	2.46
GA-BMI	48.67	26.00	60.00	5.05
Fish				
Diversity (*H′*)	1.94	1.65	2.24	0.11
Richness	12.00	7.00	16.00	1.52
GA-IBI	42.00	30.00	52.00	4.60

Watershed ID	MO		
Watershed Area	897		
Tributary Name	Cline's Branch		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	680997	362509
Seasons Sampled	6		
Total Macroinvertebrate Richness	167		
Total Fish Richness	25		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.82	0.01	1.94	0.48
Chlorophyll *a* (mg / m^2)	0.31	0.16	0.57	0.09
Macroinvertebrates				
Biomass (g / m^2)	19.71	3.25	55.01	7.82
Diversity (*H′*)	2.48	2.06	2.95	0.12
Richness	47.83	40.00	57.00	2.94
GA-BMI	53.83	40.00	67.00	4.71
Fish				
Diversity (*H′*)	1.78	1.43	2.12	0.11
Richness	10.50	6.00	15.00	1.28
GA-IBI	38.33	28.00	46.00	2.85

Watershed ID	MU1		
Watershed Area	1178 ha		
Tributary Name	Ossahatchie Creek		
Stream Order	3		
UTM Zone 16 Coordinates	16 N	712939	3615237
Seasons Sampled	32		
Total Macroinvertebrate Richness	102		
Total Fish Richness	11		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.62	0.00	1.60	0.49
Chlorophyll *a* (mg / m^2)	0.11	0.00	0.25	0.07
Macroinvertebrates				
Biomass (g / m^2)	32.55	6.79	75.78	12.25
Diversity (*H′*)	2.02	1.45	2.37	0.13
Richness	28.00	22.00	35.00	1.86
GA-BMI	33.00	23.00	49.00	3.82
Fish				
Diversity (*H′*)	1.03	0.17	2.01	0.33
Richness	5.40	3.00	9.00	1.29
GA-IBI	30.33	26.00	36.00	1.58

Watershed ID	MU2		
Watershed Area	606 ha		
Tributary Name	Mulberry Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	708913	3621461
Seasons Sampled	5		
Total Macroinvertebrate Richness	90		
Total Fish Richness	14		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	0.49	0.06	1.33	0.42
Chlorophyll *a* (mg / m^2)	0.10	0.05	0.16	0.03
Macroinvertebrates				
Biomass (g / m^2)	5.08	0.88	15.97	2.16
Diversity (*H′*)	2.06	1.06	2.47	0.20
Richness	23.50	14.00	35.00	2.93
GA-BMI	31.83	18.00	42.00	3.22
Fish				
Diversity (*H′*)	1.65	1.38	1.96	0.10
Richness	6.80	5.00	10.00	0.97
GA-IBI	38.40	30.00	44.00	3.06

Watershed ID	MU3		
Watershed Area	1044 ha		
Tributary Name	Turntime Branch		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	701261	3618978
Seasons Sampled	5		
Total Macroinvertebrate Richness	124		
Total Fish Richness	19		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.39	0.02	1.14	0.37
Chlorophyll *a* (mg / m^2)	0.19	0.01	0.42	0.12
Macroinvertebrates				
Biomass (g / m^2)	32.40	7.27	111.39	16.41
Diversity (*H′*)	2.42	2.08	2.62	0.10
Richness	40.20	32.00	45.00	2.31
GA-BMI	50.20	40.00	58.00	3.46
Fish				
Diversity (*H′*)	1.81	1.47	2.08	0.13
Richness	9.75	8.00	12.00	0.85
GA-IBI	36.50	24.00	46.00	5.19

Watershed ID	RB		
Watershed Area	367 ha		
Tributary Name	Roaring Branch		
Stream Order	1		
UTM Zone 16 Coordinates	16 N	691357	3602110
Seasons Sampled	6		
Total Macroinvertebrate Richness	71		
Total Fish Richness	13		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.56	0.01	1.29	0.25
Chlorophyll *a* (mg / m^2)	0.39	0.07	0.65	0.10
Macroinvertebrates				
Biomass (g / m^2)	40.77	15.68	65.67	7.37
Diversity (*H′*)	1.86	1.25	2.47	0.15
Richness	20.00	15.00	30.00	2.22
GA-BMI	20.33	3.00	34.00	5.41
Fish				
Diversity (*H′*)	0.99	0.59	1.53	0.15
Richness	6.00	5.00	8.00	0.45
GA-IBI	27.67	22.00	36.00	2.65

Watershed ID	RC		
Watershed Area	471 ha		
Tributary Name	Rushing Creek		
Stream Order	1		
UTM Zone 16 Coordinates	16 N	688583	3600821
Seasons Sampled	1		
Total Macroinvertebrate Richness	23		
Total Fish Richness	8		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	-	-	-	-
Chlorophyll *a* (mg / m^2)	-	-	-	-
Macroinvertebrates				
Biomass (g / m^2)	101.55	101.55	101.55	-
Diversity (*H′*)	1.90	1.90	1.90	-
Richness	23.00	23.00	23.00	-
GA-BMI	9.00	9.00	9.00	-
Fish				
Diversity (*H′*)	1.47	1.47	1.47	-
Richness	8.00	8.00	8.00	-
GA-IBI	36.00	36.00	36.00	-

Watershed ID	SB1		
Watershed Area	2009 ha		
Tributary Name	Schley Creek		
Stream Order	3		
UTM Zone 16 Coordinates	16 N	685293	3608160
Seasons Sampled	6		
Total Macroinvertebrate Richness	131		
Total Fish Richness	15		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.53	0.01	1.97	0.48
Chlorophyll *a* (mg / m^2)	0.66	0.11	1.14	0.27
Macroinvertebrates				
Biomass (g / m^2)	13.37	1.33	38.81	5.26
Diversity (*H'*)	2.40	2.05	2.70	0.09
Richness	38.33	27.00	48.00	3.54
GA-BMI	41.17	27.00	51.00	3.98
Fish				
Diversity (*H'*)	1.48	1.04	1.76	0.11
Richness	6.83	3.00	12.00	1.22
GA-IBI	34.00	22.00	46.00	3.76

Watershed ID	SB2		
Watershed Area	634 ha		
Tributary Name	Standing Boy Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	692405	3613831
Seasons Sampled	6		
Total Macroinvertebrate Richness	114		
Total Fish Richness	12		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.42	0.02	1.40	0.33
Chlorophyll *a* (mg / m^2)	0.36	0.05	0.48	0.11
Macroinvertebrates				
Biomass (g / m^2)	17.01	1.40	36.87	4.96
Diversity (*H′*)	2.37	2.15	2.63	0.09
Richness	37.40	27.00	43.00	3.08
GA-BMI	46.00	34.00	61.00	4.71
Fish				
Diversity (*H′*)	1.01	0.49	1.65	0.24
Richness	6.00	3.00	9.00	1.47
GA-IBI	33.00	28.00	40.00	2.65

Watershed ID	SB4		
Watershed Area	2659 ha		
Tributary Name	Standing Boy Creek		
Stream Order	3		
UTM Zone 16 Coordinates	16 N	697366	3612240
Seasons Sampled	6		
Total Macroinvertebrate Richness	132		
Total Fish Richness	23		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	1.05	0.00	1.62	0.53
Chlorophyll *a* (mg / m^2)	0.22	0.19	0.24	0.02
Macroinvertebrates				
Biomass (g / m^2)	31.68	4.22	69.02	9.04
Diversity (*H′*)	1.88	1.26	2.33	0.16
Richness	36.33	30.00	44.00	2.63
GA-BMI	41.67	26.00	58.00	4.59
Fish				
Diversity (*H′*)	1.68	1.00	2.09	0.19
Richness	10.20	9.00	12.00	0.58
GA-IBI	40.00	32.00	50.00	3.52

Watershed ID	SC		
Watershed Area	896 ha		
Tributary Name	Sand Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	680233	3635938
Seasons Sampled	6		
Total Macroinvertebrate Richness	116		
Total Fish Richness	14		

Parameter	**Mean**	**Min**	**Max**	**SE**
Algae				
AFDM (g / m^2)	0.58	0.03	1.13	0.55
Chlorophyll *a* (mg / m^2)	0.27	0.06	0.48	0.21
Macroinvertebrates				
Biomass (g / m^2)	11.90	0.90	26.79	3.15
Diversity (*H′*)	1.73	1.21	2.39	0.16
Richness	33.83	26.00	40.00	2.29
GA-BMI	35.17	21.00	44.00	3.65
Fish				
Diversity (*H′*)	1.52	0.69	1.85	0.17
Richness	7.00	2.00	10.00	1.15
GA-IBI	37.33	28.00	44.00	2.67

Watershed ID	WC		
Watershed Area	2193 ha		
Tributary Name	Weracoba Creek		
Stream Order	2		
UTM Zone 16 Coordinates	16 N	691980	3590902
Seasons Sampled	3		
Total Macroinvertebrate Richness	47		
Total Fish Richness	10		

Parameter	Mean	Min	Max	SE
Algae				
AFDM (g / m^2)	2.41	2.41	2.41	0.00
Chlorophyll *a* (mg / m^2)	0.05	0.05	0.05	0.00
Macroinvertebrates				
Biomass (g / m^2)	20.13	1.33	53.06	13.49
Diversity (*H'*)	1.74	1.46	2.25	0.21
Richness	22.67	17.00	33.00	5.17
GA-BMI	17.33	15.00	20.00	1.45
Fish				
Diversity (*H'*)	1.76	1.58	2.04	0.14
Richness	7.33	6.00	9.00	0.88
GA-IBI	35.67	35.00	36.00	0.33