LAURA ERIN ENGLAND
Riparian Forest Cover at Multiple Scales: Influences on Instream Habitat, Aquatic
        Assemblages, and Food Webs in Headwater Streams
(Under the direction of AMY D. ROSEMOND)

Strong connectivity between terrestrial and aquatic ecosystems means that

landscape alterations have the potential to profoundly impact freshwaters. Effective

management of riparian buffers to minimize these impacts requires identification of

buffer attributes that most influence stream ecosystems. This research assessed instream

habitat conditions, aquatic assemblages, and food webs in a set of headwater streams

comprising a gradient in forest cover on multiple scales.   Network scale riparian buffer

width and continuity and watershed land cover were correlated with instream

physical/chemical variables that were strong predictors of macroinvertebrate and fish

assemblages. Results indicated that land cover ultimately influenced stream biota via

changes in habitat quality. Stable isotope analyses of food webs suggested that

reductions in forest cover on multiple scales led to a reduced dependence of headwater

food webs on terrestrial organic matter subsidies. Thus, continuous and wide riparian

forests along entire stream networks may be critical for sustaining stream ecosystems.

INDEX WORDS: terrestrial-aquatic linkages, deforestation, riparian buffers,

                 watershed land use, multiple scales, GIS, habitat alteration, biotic

                 integrity, macroinvertebrates, fishes, stable isotopes, terrestrial

                 subsidies, headwater streams, trout, southern Appalachians

RIPARIAN FOREST COVER AT MULTIPLE SCALES: INFLUENCES ON

INSTREAM HABITAT, AQUATIC ASSEMBLAGES, AND FOOD WEBS IN

HEADWATER STREAMS

by

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DEDICATION

In memory of Martha Kyler Cole England, whose passion for life and enduring belief in

me have been my inspiration.

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CHAPTER 1

INTRODUCTION

For decades, research in freshwater ecology has acknowledged the interaction between terrestrial and aquatic ecosystems, with specific focus on the many ways in which water bodies are influenced by their watersheds. Over 25 years ago, H.B.N. Hynes (1975) asserted that all aspects of stream ecosystems are influenced by stream valleys, and this concept is still driving research pursuits in stream ecology. In the southern Appalachians of the United States, stream valleys and watersheds were predominantly forested prior to the arrival of humans approximately 12,000 years ago (Yarnell 1998). Because stream biological communities in this region evolved in forested landscapes, forest cover is critical to the structure and function of southern Appalachian stream ecosystems (Jones et al. 1999).

Watershed deforestation and stream ecosystems

Watershed forest cover influences numerous physical, chemical, and biological dimensions of stream ecosystems. Forest cover is an important driver of watershed and stream hydrology (Dunne and Leopold 1978), and deforestation may result in altered stream baseflows and stormflows (Likens et al. 1970, Wright et al. 1990). Shifts in channel morphology and increased sediment yields often follow hydrologic alterations (Knighton 1998). Watershed forest cover also influences streamwater temperature through shading the stream surface and by maintaining cool soil and air temperatures in

both riparian and upland areas (Brosofske 1997). Furthermore, forest cover affects stream nutrient budgets in both temperate regions (Likens et al. 1970, Bolstad and Swank 1997) and tropical regions (Neill et al. 2001).

More recently, stream ecologists have documented a multitude of biological impacts that follow the physical and chemical alterations driven by watershed deforestation. Typically, biological communities (macroinvertebrates, fishes, and amphibians) undergo declines in diversity and abundance with increasing deforestation, but the opposite trends have also been documented (Allan 1995, Scott and Helfman 2001). Community composition changes occur as rare and sensitive species with narrow habitat requirements are replaced by more generalist species that can tolerate the disturbed habitat conditions in deforested watersheds (Morse et al. 1993, Morris and Corkum 1996, Scott and Helfman 2001).   In summary, deforestation at the watershed scale can have multiple impacts on stream ecosystems. Deforestation on more local scales, specifically in streamside or riparian zones, may be equally or more damaging to stream ecosystems (Sweeney 1992).

Riparian forests as stream buffers

Riparian forests have been defined in several different ways: as ecotones between aquatic ecosystems and upland terrestrial ecosystems, as distinct ecosystems that are delineated by the spatial extent of hydrologic influence from an adjacent water body, or more broadly as corridors with proximity to stream channels that are the setting for a number of terrestrial-aquatic linkages (Malanson 1993). In undisturbed landscapes,

riparian ecosystems are characterized by bi-directional interactions and mutual dependence of terrestrial and aquatic ecosystems (e.g. Nakano and Murakami 2001).

In the past twenty years, riparian forests have been studied intensively due to recognition of their capacity to "buffer" streams from watershed land use disturbances. "Riparian buffer" is a term often used interchangeably with riparian ecosystem. However, "buffer" emphasizes a unidirectional interaction and the role that riparian zones play in protecting aquatic ecosystems from the effects of disturbed landscapes. It should be acknowledged that this term de-emphasizes the significance of riparian forests as unique terrestrial habitats that are in turn dependent upon adjacent aquatic ecosystems (e.g. Sanzone et al. 2003).

It has been argued that riparian buffers are one of the single most important factors affecting the integrity of aquatic ecosystems today (Sweeney 1992). Research has shown that riparian buffers in agricultural watersheds are highly effective at retaining sediment and nutrients in runoff from upland disturbance (Lowrance et al 1997). In general, retention of sediment is a positive function of buffer width and a negative function of buffer hillslope (Wenger 1999). Longitudinal continuity of riparian buffers along stream corridors may also be required for effective sediment retention (Rabeni and Smale 1995). Sediment retention is an extremely important buffer function, considering the many detrimental ecological and economic effects of fine sediment in streams and rivers (Waters 1995).

Additional riparian influences on streams

In addition to buffering freshwater ecosystems from watershed land use disturbances, riparian forests have a number of functions that support aquatic ecosystems. Riparian forests help control thermal regimes, input terrestrial organic matter, and stabilize instream habitat. In headwater streams, riparian forests form a canopy over the stream channel, reducing insolation and greatly impacting streamwater temperature regimes. Riparian forests also impact stream thermal regimes by maintaining a thermal buffer of cool air and soil temperatures adjacent to streams (Brosofske et al. 1997). Consequently, streams with riparian forests are cooler and have less diel and seasonal fluctuation in temperature than pasture streams (Chen and Chen 1994, Sweeney 1992). Thermal functions of buffers are important because temperature affects water quality (e.g. dissolved oxygen concentrations), ecosystem functions (e.g. litter decomposition), and aquatic taxa that have narrow thermal tolerance ranges (Rutherford et al. 1997).

Conventional stream theory predicts that terrestrial subsidies, or allochthonous inputs, dominate the energy base of food webs in headwater streams where primary production is limited by shading (Vannote et al. 1980, Cummins et al. 1989). Allochthonous inputs are typically dominated by riparian leaf litter, but woody debris, fine particulate organic matter (FPOM), and dissolved organic matter (DOM) can also be substantial inputs (Webster et al 1999). Long-term exclusion of terrestrial detritus from a headwater stream in the southern Appalachians highlighted the importance of terrestrial subsidies in supporting diverse stream communities. Reduced production of multiple trophic levels that followed exclusion of detritus demonstrated food web dependence on allochthonous inputs (Wallace et al. 1997). Food web tracer studies using stable isotopes

have also documented the importance of terrestrial organic matter as a basal resource in undisturbed stream food webs (e.g. Bunn et al. 1989, Rosenfeld and Roff 1992). Further, stable isotope studies comparing forested stream reaches to pasture/grassland reaches have demonstrated shifts from food web dependence on allochthonous detritus to greater utilization of instream autochthonous production (e.g. Rounick et al. 1982, Hicks 1997). Thus, riparian subsidies of headwater food webs may be important to stream ecosystem structure and function.

Instream physical habitat is dynamic and governed by the interaction of riparian vegetation, geomorphology and hydrology (Maddock 1999). For example, Sweeney (1992) found that forested reaches of streams have significantly greater bankfull width, and thus greater benthic habitat than pasture reaches. Lammert and Allan (1999) showed that the percentage of streambed area covered by pool habitat was positively related to riparian forest cover. In addition, instream habitat diversity, important to maintaining diverse aquatic assemblages, may be influenced by the length of upstream riparian forest patches (Jones et al 1999).

Riparian buffer policy and project origin

These terrestrial-aquatic linkages, mediated by riparian forests, are vitally important to stream ecosystem integrity. The principal focus of riparian regulation on state and local levels has been setting minimum riparian buffer widths that will maintain buffer functions. However, despite an abundance of riparian research, including over 700 publications on the water quality functions of riparian buffers alone, the literature is often inadequate to inform specific buffer policy decisions (Correll 2000). In the southeastern

United States, most riparian research has focused on coastal plain watersheds where the land use is predominantly agriculture, whereas montane regions have been underrepresented (Correll 2000). The deficiency of knowledge regarding buffer function in montane settings became immediately relevant in the state of Georgia following a change in buffer regulations. In the spring of 2000, the Georgia State Legislature passed House Bill 1426, an amendment to the state's Erosion and Sedimentation Act of 1975 (Chapter 7 of Title 12 of the Official Code of Georgia Annotated). Among other changes, HB 1426 reduced the minimum allowable riparian buffer width on Georgia's trout streams from the previous 100 ft requirement to 50 ft. Given accelerating suburban development in the southern Appalachians and anticipated impacts on water quality in the region (Wear et al. 1998), this reduction in buffer requirements provoked great concern among aquatic scientists and stakeholders alike.

Following this policy change, Georgia Department of Natural Resources contracted with a team of University of Georgia researchers (James Kundell, Judy Meyer, Liz Kramer, Rhett Jackson, and Geoff Poole) to conduct the Trout Stream Buffer Study (hereafter Buffer Study), a study aimed at evaluating the effectiveness of 50 ft versus 100 ft riparian buffers in protecting trout streams. This thesis research developed alongside of work done by the Buffer Study. While the Buffer Study conducted work in 3rd and 4th order streams large enough to support trout, I was interested in headwaters within trout stream watersheds. Since headwater streams may be more tightly coupled to riparian and hillslope processes than their larger, downstream counterparts (Gomi et al. 2002), riparian buffer width and continuity may be especially critical in these small watersheds. Further,

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conditions in downstream trout habitat may be dependent on headwaters because of the intimate longitudinal linkage provided by downstream flow (Meyer and Wallace 2001).

Research Overview

　　This research was conducted under the general hypothesis that extent of riparian forest cover, in terms of buffer width and longitudinal continuity, plays a major role in shaping both the structure and function of headwater stream ecosystems. Unique contributions of this research to the study of stream response to changing land cover derive from the detailed spatial analysis of forest cover (lateral and longitudinal distribution rather than just % forest cover), the high resolution of spatial data, and the focus on a small number of sites with little variation in watershed area, elevation, and stream gradient. Chapter 2 examines the effects of reductions in riparian forest cover on instream physical/chemical habitat conditions and how these habitat alterations in turn affect the composition and integrity of macroinvertebrate and fish assemblages. Chapter 3 concerns flows of carbon and nitrogen in headwater stream food webs, focusing on how reductions in riparian forest cover influence the relative importance of allochthonous inputs versus instream autochthonous production in supporting headwater biota. An issue addressed throughout is the scale at which forest cover is most relevant to headwater streams. Finally, in the concluding chapter, I explore implications of this work for policy, conservation, and management of streams and riparian buffers.

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CHAPTER 2

INFLUENCES OF RIPARIAN DEFORESTATION ON HEADWATER STREAM

HABITAT AND AQUATIC ASSEMBLAGES: A MULTIPLE SCALE ASSESSMENT[1]

ABSTRACT

Riparian forest cover may be a key factor influencing headwater stream ecosystems, yet the impact of partial riparian deforestation on streams is largely unknown. We assessed instream physical/chemical habitat conditions and macroinvertebrate and fish assemblages in southern Appalachian headwater streams that comprised a gradient in riparian deforestation on multiple scales, but had relatively high watershed forest cover (83 – 96 %). Rigorous site selection resulted in a set of just seven sites, but conferred the advantage of minimal intersite variation in potential confounding factors such as watershed area, elevation and stream gradient. Riparian forest cover measures, obtained from analysis of high resolution aerial images, described the spatial distribution of forest cover in both the lateral (buffer width) and longitudinal (buffer continuity) dimensions. We related variation in physical/chemical variables to riparian forest cover at local (100 m reach) and stream network (entire stream length) scales, as well as to watershed land cover. Measures of watershed and network scale riparian forest cover (width and continuity) were correlated with numerous instream physical/chemical factors. Three physical/chemical variables that were highly correlated with riparian and watershed land cover (substrate diameter variation, coarse particulate organic matter and percentage of fine sediment in riffles) were also highly predictive of characteristics of fish and macroinvertebrate assemblages. Large variations in macroinvertebrate taxa richness and fish species richness were observed over relatively moderate variation in mean riparian buffer width (34-96 ft) and watershed impervious surface cover (0.6-2.8%). Indirect ordination of macroinvertebrate assemblages and correlations with the resulting axis also suggested a prominent role of network scale riparian forest cover and streambed substrate

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heterogeneity in structuring biotic assemblages. These results indicate that riparian

buffer width and continuity, as well as well as watershed land cover, ultimately affect

stream biota via influence on stream habitat quality. This research supports the

importance of maintaining continuous and wide riparian buffers, as well as low amounts

of impervious cover, throughout headwater stream networks to maintain integrity of fish

and macroinvertebrate assemblages.

Introduction

Terrestrial-aquatic interactions that link adjacent riparian and stream ecosystems have

been a central focus of lotic ecology research for several decades (e.g. Hynes 1975, Karr

and Schlosser 1978, Cummins et al. 1989, Gregory et al. 1991, Nakano et al. 1999,

Jacobsen and Bojsen 2002). The strong connectivity that exists between terrestrial and

aquatic ecosystems means that anthropogenic alterations of landscapes will unavoidably

affect stream and river systems. Land cover modifications on multiple scales have

proven detrimental to water quality, instream habitat, and aquatic assemblages (Roth et

al. 1996, Wang et al. 1997, Jones et al. 1999, Scott and Helfman 2001, Scott et al. 2002,

Sutherland et al. 2002, Roy et al. 2003). Unfortunately, watershed land use disturbance is

inevitable because of needs of societal and economic systems. Consequently, riparian

forest buffer regulations have become a primary policy tool for the prevent degradation

of valuable freshwater ecosystems under anthropogenic land cover alterations such as

urbanization, agriculture and silviculture that are pervasive on present landscapes

(Castelle et al. 1994, Wenger 1999).

Riparian forests are essential to the protection of streams due to their capacity to

buffer streams from upland disturbance by retaining non-point source pollution

(Peterjohn and Correll 1984, Lowrance et al. 1985) and controlling thermal regimes (Sweeney 1992, Chen and Chen 1993). Further, riparian forests support stream ecosystems by subsidizing stream food webs with leaf litter and terrestrial insects (Cummins et al. 1989, Edwards and Huryn 1996, Nakano et al. 1999, Wallace et al. 1999). Riparian forests also help maintain instream habitat through large woody debris inputs (Bilby and Likens 1980, Smock et al. 1989) and bank habitat stabilization (Beeson and Doyle 1995). Effective riparian management to provide these buffer functions requires identification of riparian buffer attributes (e.g. scale, width, continuity) that most influence instream conditions.

Riparian buffer regulation in the United States has focused primarily on buffer width, but research has provided some evidence that other aspects such as length and continuity of buffers may be important (Barton et al. 1985, Jones et al. 1999). Assessing the effects of riparian land cover has often been included as a secondary objective in studies of watershed land cover impacts on streams. However, the resolution of images typically used to generate watershed land cover data (e.g. 30 m resolution Landsat TM images, Sponseller and Benfield 2001) may not be fine enough for accurate analyses of land cover in narrow riparian corridors, which are wide relative to resolution of these images. Still, such studies have revealed relationships between riparian buffer forest cover and instream conditions that warrant further study (Richards et al. 1996, Roth et al. 1996, Scott et al. 2002, Roy et al. 2003, Sponseller and Benfield 2001).

Spatial distribution of riparian forest cover within a buffer may also affect terrestrial-aquatic linkages. A central principle of landscape ecology is that interactions between biotic and abiotic components of landscapes are spatially mediated, i.e.

controlled by spatial proximity and structure (Forman 1995, Malanson 1993). Hence, a 50 % forested riparian buffer may function very differently if that forest cover is directly adjacent to the stream and longitudinally continuous as opposed to concentrated in more upland areas of the buffer and with discontinuities that create buffer gaps. The importance of longitudinal extent of riparian forest cover was highlighted in a study of 3rd-5th order streams, which showed that benthic fine sediment and integrity of fish assemblages were related to a gradient in the length of deforested areas above a stream reach (Jones et al. 1999). Scott et al. (2002) demonstrated the importance of riparian forest cover along the entire mainstem length (headwater tributaries excluded) of a stream in predicting physicochemical conditions.

Headwater streams are particularly important in river networks since they constitute the majority of stream miles, offer habitat that supports unique aquatic assemblages, and are important sites of organic matter retention and processing (Leopold et al. 1964, Minshall et al. 1983, Meyer and Wallace 2001, Gomi et al. 2002). In addition, headwater streams may be more tightly coupled to riparian and hillslope processes than their larger, downstream counterparts (Gomi et al. 2002). Consequently, it is important to address the role of riparian forest cover in small watersheds in terms of both forest extent and spatial distribution relative to streams. This study focused on headwater streams in the southern Appalachian mountains of the southeastern U.S., a region that is experiencing rapid population growth and development pressure (Wear et al. 1998). We determined how variation in riparian forest width and continuity influenced habitat conditions in headwater streams, and how habitat was in turn related to aquatic assemblages.

Poff's (1997) conceptual model of hierarchical habitat filters provides a useful framework for considering this multi-scaled question. This model asserts that local aquatic assemblages are subsets of the regional species pool, constrained by habitat filters that exist on hierarchical scales ranging from watershed context to instream microhabitat factors (Frissell et al. 1986, Poff 1997). Identifying trans-scale linkages (sensu Poole 2002) among these hierarchical habitat filters may enable the prediction of how aquatic assemblages will respond to landscape alterations such as riparian deforestation. We obtained riparian forest cover data using high resolution aerial images and developed multiscaled riparian metrics that described lateral (buffer width) and longitudinal (buffer continuity) distribution of riparian forest cover. We determined which forest cover metrics were correlated with physical/chemical factors including aspects of water quality, benthic habitat and allochthonous resources. Multiple regression models and indirect ordination analyses were used to identify which of these habitat variables best explained variation in macroinvertebrate and fish assemblages.

Methods

Our study sites comprised gradients in riparian deforestation on local (100 m reach) and network (entire stream length upstream of study site) scales within watersheds with moderately low deforestation (3.7 – 17.5 % of watershed area under anthropogenic land cover types). We focused on a set of physical/chemical factors that have been established by previous work as being susceptible to change under deforestation disturbance including water chemistry (e.g. Bolstad and Swank 1997), thermal regime (e.g. Barton et al. 1985, LeBlanc et al. 1997), streambed substrate characteristics (e.g. Waters 1995),

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distribution of streambed habitat types (Lammert and Allan 1999), habitat heterogeneity (e.g. Jones et al. 1999), geomorphic stability (e.g. Trimble 1997), and availability of allochthonous organic matter (e.g. Webster et al. 1990). We assessed biotic response by calculating assemblages metrics that were selected based on previous demonstration of susceptibility to land use disturbance including abundance, taxa richness, tolerance, and trophic metrics (Roth et al. 1996, Richards et al. 1996, Harding et al. 1998, Scott and Helfman 2001, Roy et al. 2003, Sutherland et al. 2002).

Land Use Assessment

The study streams were located in the Upper Chattahoochee River basin in the Blue Ridge province of Georgia, USA, the southernmost extent of the Appalachian Highands (Appendix A, Figure 2.1). Rigorous site selection resulted in a set of just seven sites (Figure 2.1), but conferred the advantage of minimal intersite variation in potential confounding factors. Among study streams there were narrow ranges in watershed area (1.9 – 7.2 km^2), mean width (1.2 – 3.6 m) elevation (430 - 530 m), and gradient (0.6 – 1.6 %). High-resolution (1-2 m, National Aerial Photography Program, USGS) color-infrared aerial photographs of study watersheds (March 1999) were digitized, georeferenced and rectified for analysis using ERDAS Imagine® 8.4 (ERDAS®, Atlanta, GA, USA). Watershed boundaries were delineated and land cover types in study watersheds were classified, resulting in a thematic raster layer that allowed determination of percentages of each land cover type (forest, impervious, and agricultural cover). Building density and stream/riparian road crossings within watersheds were counted manually from images.

Riparian land cover was determined from thematic raster layers by delineating

100 ft buffers (imperial units are typically used for buffer regulations in the U.S., Castelle

1994) around study streams throughout the entire stream network above study reaches.

All gaps in forest cover within the 100 ft buffer were digitally measured (Figure 2.2) and

these data were used to calculate several riparian forest cover metrics (see Table 2.1).

Continuity of stream canopy cover and riparian buffers was calculated as the % stream

length with a buffer wider than 0 ft and 100 ft, respectively. Mean buffer width (MBW)

was calculated for multiple scales: (100 m local reach, 1000 m of network above study

site, and entire stream network above study site) using the following weighted-average

formula:

$$\text{MBW} = \frac{\Sigma\ L_{BG} * W_{BG} + \ 100 * (L_{TS} * 2\ -\ \Sigma L_{BG})}{L_{TS} * 2} \qquad\qquad \text{(Eq. 1)}$$

$$L_{BG} = \text{length of buffer gap}$$

$$W_{BG} = \text{buffer width at gap}$$

$$L_{TS} = \text{total stream length}$$

Since the southern Appalachian forests have a long history of anthropogenic

disturbance, (Yarnell 1998), we did a very basic assessment of historic land cover by

visually examining aerial photos from 1938. While all watersheds were predominantly

forested in the uplands in 1938, there was considerable variation in forest cover in the

stream valleys due to agricultural clearings. A valley deforestation index value (1 – 4,

increasing with deforestation) was assigned for each study stream, taking into account the

longitudinal extent of deforestation along stream valleys, width of deforested patches and downstream proximity of valley deforestation to study reaches.

Characterization of Instream Physical/Chemical Habitat Conditions

Temperature data loggers (HOBOs, Onset Corp.®) were deployed in study streams in April 2001. HOBOs were programmed to measure water temperature at 30 minute intervals, and were downloaded monthly until September 2002. Raw temperature data were imported into a database that was used to calculate temperature metrics (maxima, minima, diel variation, and seasonal variation measures). Spatial variation in temperature and dissolved oxygen (DO) was assessed with a YSI® DO meter in September 1999 by sampling 50 points along a zig-zag survey within the 50 m sample reach.

Baseflow streamwater grab samples were collected in August 2001. Samples were filtered streamside (Gelman® A/E 0.45 μm glass fiber filters), transported on ice, and analyzed for concentrations of NO_3–N, NH_4–N and PO_4-P using an Alpkem colorimeter by the Analytical Chemistry Lab of the University of Georgia Institute of Ecology. Grab samples were also analyzed for specific conductivity using a conductivity meter (Orion Research Inc.®). Turbidity was sampled monthly at baseflow from May 2001 – April 2002 using a Hach® turbidometer, and spatial variation in turbidity was assessed in October 2001 by sampling 15 randomly chosen points within the sample reach.

Stream bed substrate was characterized in several ways. Pebble count surveys (n = 100, Wolman 1954) were used to determine median particle diameter (D_{50}) and assess substrate heterogeneity by calculating a coefficient of variation for substrate diameter. Riffle sediment cores were taken from 3 riffles per site and were dried, sieved and

weighed to determine particle size distributions. Embeddedness of riffles with fine sediment was assessed visually (1-4, representing 25 % increments of low to high embeddedness) using a clear-bottomed viewbox.

We assessed the distribution of streambed habitat types by measuring each habitat element (riffles, pools, and runs) within the 50 m sample reach and calculating the fraction of stream bed area in each habitat type. Habitat heterogeneity was assessed by calculating coefficients of variation for baseflow depth and velocity measurements taken at 50 random sample points with a velocity meter (Marsh-McBirney Inc.® Flo-mate). Benthic coarse particulate organic matter (CPOM) was quantified in the fall (November 2000) and the following spring (May 2001). A 1-m^2 plot, assembled from PVC pipe and divided into four quadrants, was used to survey CPOM coverage of the streambed. Percent coverage by CPOM for each of the four quadrants was visually estimated to the nearest 10 % at 30 1-m^2 plots in the study reach. At alternating survey plots, CPOM within the plot was collected, oven dried at 40 °C and weighed to determine dry mass of CPOM per m^2 of streambed. A habitat-weighted measure of CPOM was calculated as a sum of habitat-specific CPOM standing crop (g/m^2, average of fall and spring) weighted by the percent of stream bed area in each habitat type (i.e. pool, riffle, or run). All large woody debris (LWD = > 10 cm diameter, > 1 m length) within the study reach was counted and measured (length and diameter) in November 2000.

Several metrics were used to evaluate geomorphic stability. Relative bed stability at baseflow was calculated from mean velocity and D_{50} as in Jowett (1989). Stream retentiveness was approximated as the fraction of fall CPOM remaining in the spring. Counts of bank erosion (both fluvial and mass wasting) for both right and left banks were

made for the entire 50 m sample reach. Finally, a bank instability index, modified from

Simon and Downs (1995), was determined from width: depth ratio, bank vegetation, bank

material and bank morphology.

Characterization of Biotic Assemblages

Macroinvertebrates were sampled in April 2000 following a multihabitat sampling

approach outlined in the U.S. EPA Rapid Bioassessment Protocol for Streams and

Wadeable Rivers (Barbour et al. 1999). This protocol involved d-net kicks and sweeps in

riffles, pools and banks and yielded one composite sample per site. Specimens were

separated from organic matter and preserved in 70 % ethanol. Invertebrates were

identified to genus (with the exception of chironomids) and given a functional feeding

group (FFG) designation using Merritt and Cummins (1996). Because sampling methods

were not spatially quantitative, densities of taxa (number per m^2) could not be

determined. However, sampling effort (number of kicks and sweeps) was equivalent

across sites, so we compared abundances (number) of taxa and FFGs across sites.

Several assemblage metrics were then calculated based on taxa abundance data (metrics

in Table 2.2, taxa list in Table 5).

Fish assemblages were sampled in August 2000 by quantitatively sampling all

habitat within a 50 m sample reach (20 x stream width on average) via electroshocking.

Stunned individuals were collected with dipnets and a seine net, identified to species,

counted (excluding young of the year), and released. An additional 50 m reach was

shocked exclusively to search for additional species. Shock time and area sampled (from

habitat distribution measurements above) for the quantitative reach were used to

normalize catch data by effort. Individuals were classified as native or introduced, highland endemic or widely distributed, and by trophic guild (Mayden 1987, Warren et al. 2000). Related metrics were then calculated (see Table 2.2 for metrics, Table 6 for species list).

Data Analysis

The above methods generated a large data set of over 100 variables describing forest cover and land use, physical/chemical conditions (subdivided into categories: temperature, chemistry, sediment/substrate, allochthonous resources, mesohabitat scale and geomorphic variables), and biotic assemblages (Appendix B). Assumptions of normality were tested for all variables using Shapiro-Wilks tests and non-normal variables were transformed (Sokal and Rohlf 1995); percentage variables were arcsin-squareroot transformed and network scale mean buffer width was cosine transformed. To reduce the number of statistical tests performed and thereby reduce the chance of type I error (Rice 1989), steps were taken to compress the variable set into a smaller subset that was then used in inferential analyses. A correlation matrix was used to reduce the number of variables in each physical/chemical habitat category by eliminating autocorrelated variables (correlations with $p < 0.05$) within each category. Choices between autocorrelated variables were made in favor of measures that were more parsimonious, quantitatively rigorous, or common in the literature. Data reduction resulted in a subset of 20 physical/chemical variables that were then used in inferential analyses (Table 2.2). Linear regression analysis was then used to identify relationships between forest cover and these selected physical/chemical variables.

In analyses of biotic assemblages, we evaluated the relative predictive capacity of land cover versus physical/chemical variables. We used simple linear regression to determine whether land cover was related directly to macroinvertebrate or fish assemblage metrics. In addition, the extent to which macroinvertebrate and fish assemblage metrics were related to physical/chemical variables was assessed using stepwise multiple regression. To avoid multicollinearity among explanatory variables, a correlation matrix of the 20 physical/chemical factors was used to select a final subset of six non-correlated explanatory variables that were entered into multiple regression models (noted in Table 2). We then made bivariate plots of the physical/chemical variables that were the best single predictors of macroinvertebrate and fish assemblage metrics (based on partial R^2 values). We also plotted these physical/chemical variables against the land cover variables with which they were most highly correlated to identify potential breakpoints or ranges in land cover variables that were related to physical/chemical variables most important to aquatic assemblages.

While multiple regression was used to build predictive models, it is a reductionist approach in that it only allows evaluation of one aspect of aquatic assemblages (i.e. one metric) at a time. Multivariate ordination, a more holistic approach that is not meant for predictive capability, was used to ascertain which environmental factors were responsible for structural differences in entire assemblages among sites by looking at all taxa simultaneously. Multivariate analyses of macroinvertebrate and fish assemblages were completed using PC-ORD for Windows version 4.14 (McCune and Mefford 1999). Taxa abundance matrices (log (x + 1) transformed) were analyzed using non-metric multidimensional scaling (NMS), an indirect ordination technique that is capable of

handling typically non-normal abundance data and is recommended as the most generally

effective for ecological community data (McCune and Grace 2002). We used NMS with

Sorenson (Bray-Curtis) as the distance measure to position stream sites in taxa space, and

resulting axes were evaluated for significance using Monte Carlo tests of stress reduction

(McCune and Grace 2002). Finally, we regressed all potential aquatic assemblage

metrics, forest cover and physical/chemical variables against significant NMS axes to

identify the factors that accounted for positioning of sites along ordination axes.

Results

Watershed and Riparian Forest Cover

Analysis of aerial images showed that riparian forest cover varied among sites from

approximately 50 % to 100 % depending on the spatial scale of analysis, though all sites

were predominantly forested at the watershed scale (83 – 96 %). The order of sites from

least to most forested differed depending on scale of analysis (Table 2.1). For example,

Site 7 had the second highest local buffer width, but the lowest network scale buffer

width. This scale-dependent variation in forest cover allowed us to address the question

of the relative importance of various scales of forest cover (see Table 2.1). For all study

streams, watershed forest cover (%) was within 15 % of the forest cover within a 100 ft

riparian buffer (%, network scale). For most sites, watershed and riparian forest cover

values were within 5 % of each other with slightly higher forest cover in watersheds than

in riparian buffers.

Instream Physical/Chemical Habitat Conditions vs. Forest Cover and Land Use

Physical/chemical conditions and aquatic assemblages varied considerably among stream sites (Table 2.2). In simple linear regression analyses, most physical/chemical variables analyzed were related to at least one measure of forest cover or land use (Table 2.3). Only one physical/chemical variable was related to local scale riparian land cover. Temperature variables were negatively related to forest cover on network and watershed scales, indicating that decreased riparian and watershed forest cover resulted in warmer stream temperatures with greater annual temperature variation. In addition, daily variation in temperature increased with increased stream/riparian road crossings. (Table 2.3).

Sediment characteristics were related to riparian and watershed forest cover. Positive relationships were observed between percentage of coarse substrate and canopy cover (local scale) whereas substrate diameter variation was positively related to network riparian forest cover. Variables indicating degraded streambed sediment characteristics (e.g., riffle fine sediment) were related to increased impervious cover or building density in the watershed. Mesohabitat variables were related to land cover at the watershed and network riparian scale. The strongest of these relationships was between variation in streamwater velocity and the number of road crossings along the entire length of stream (i.e., network scale). Interestingly, our categorization of historic deforestation (VALDEF38) was related to three variables describing stream geomorphology. Higher historic valley deforestation was associated with higher bank erosion and instability.

Benthic CPOM standing crop increased with riparian forest cover on the network scale as well as watershed scale forest cover (Table 2.3). LWD standing crop was not

related to any of the forest cover variables in analyses using all seven study streams. However, the least forested stream (7) had among the highest LWD standing crops of the streams studied. Nearly all of the wood in this stream comes from mass wasting of banks and bank trees; we have documented several new fallen bank trees during the course of the study (L. England, unpub. data). We suggest that a different mechanism (bank instability) was operating to explain the LWD standing crop at stream 7 compared to other sites, so we removed stream 7 from analyses. LWD at the remaining six stream sites was positively related to watershed forest cover. Chemistry variables and turbidity were not significantly related to measures of forest cover or land use.

Aquatic Assemblages vs. Physical/Chemical Conditions and Forest Cover
Variation in nearly all aquatic assemblage metrics (except NCBI and fish catch/m^2) was explained by at least one physical/chemical variable (adjusted R^2 values ranging from 0.59 – 0.95, Table 2.4). CPOM standing crop entered four regression models, and was the primary predictor in each model (highest partial R^2). Measures of both macroinvertebrate and fish community integrity increased with CPOM. Maximum depth also entered four regression models, but had low partial R^2 values. Substrate diameter variation was one of the primary predictors of macroinvertebrate assemblage metrics. Macroinvertebrate taxa richness, sensitive taxa abundance, and B-IBI all increased with substrate diameter variation. Total abundance of macroinvertebrates and abundance of sensitive taxa declined with increasing bank erosion. Percentage fine particles in riffles was an important explanatory variable in fish models; fish species richness and benthic invertivore abundance decreased with increasing riffle fine sediment.

Three physical/chemical factors, substrate diameter variation, CPOM standing crop, and riffle fine sediment, explained the greatest proportions of variance in macroinvertebrate and fish assemblage metrics (Figure 2.3 a, b, and c). These factors were also highly correlated with land cover at network and watershed scales (Fig 2.3 d, e, and f). Macroinvertebrate taxa richness and integrity (as measured by B-IBI) were reduced to half their values over a decline in substrate diameter variation from 1.75 to 1 (Fig 2.3 a). This range in substrate variation was associated with reductions in buffer width from approximately 100 to 50 ft (Figure 2.3 d). Macroinvertebrate shredder and fish abundance (catch/shock time) showed nearly 3-fold reductions as CPOM decreased from 100 to 20 g/m^2 (Figure 2.3 b). These standing crops were associated a range of 90 % to 50 % of stream length having wider than 100 ft forested buffers (Figure 2.3 e). Similarly, fish species richness declined from 9 to 3 with percentage of fine particles in riffles from 10 % to 30 % (Fig 2.3 c). This range in fine sediment was associated with increases in watershed impervious cover from approximately 0.5 to 3 % (Figure 2.3 f).

Proportion of highland endemics in fish assemblages was not a useful metric because only one species, *Cottus bairdi*, could be considered a highland endemic (and only tentatively because the species is relatively widespread). Forest cover was not useful in directly predicting aquatic assemblage metrics. Only one significant relationship resulted from these analyses; macroinvertebrate shredder abundance was positively related to MBW1000 (p = 0.03, R^2 = 0.64).

Ordination Analyses of Aquatic Assemblages

As assessed by Monte Carlo tests, no significant axis was found in NMS ordination of the

fish species abundance matrix, perhaps due to the low number of species making up the

input species abundance matrix for these small headwater streams (13 species total,

maximum of 9 and minimum of 2 at individual sites). In contrast, NMS ordination of the

macroinvertebrate taxa abundance matrix yielded one significant axis (Monte Carlo test p

= 0.03, final stress = 10.2) that represented 89.8 % of variance in macroinvertebrate

assemblages across sites. Moving in a positive direction along the NMS axis (Figure

2.4), macroinvertebrate assemblages increased in total taxa and EPT richness and also

increased in abundance of EPT taxa, coleopterans, and shredders. B-IBI was positively

related to the axis. Moving in a negative direction along the NMS axis, tolerance of the

macroinvertebrate assemblages, as measured by NCBI, increased and the assemblages

shift to higher dominance by dipterans. Riparian forest cover at the network scale

(MBW1000, MBW, CONTIN-CC) was positively related to the NMS axis (Figure 2.4).

Substrate diameter variation also had a strong positive relationship with the axis.   No

measure of local riparian cover or watershed forest cover or land use was related to the

ordination axis (p > 0.1).

Discussion

Relative Importance of Watershed and Riparian Land Cover Variation

The concept of hierarchical habitat filters is useful for understanding how multiple

environmental factors, from landscape scale down to microhabitat scale, interact to

determine the composition of local biotic assemblages (Poff 1997, Angermeier and

Winston 1998). Our results demonstrate the important role of forest cover on several scales in structuring instream physical/chemical habitat conditions that in turn constrained aquatic assemblages. Watershed and network scale forest cover were far better than local scale forest cover at predicting physical/chemical factors that were important to aquatic assemblages. Aspects of water quality, benthic habitat, and allochthonous resources were related to network scale riparian forest cover. Watershed scale measures of suburban land use (% impervious cover and building density) were stronger predictors of some substrate variables and mesohabitat scale variables, while historic valley deforestation best predicted geomorphic stability metrics. Our results indicated that riparian buffer continuity, not just buffer width, was an important driver of instream conditions. Continuity of canopy cover and continuity of buffers (> 100 ft) were highly correlated with stream thermal regimes and terrestrial organic matter resources, respectively. Furthermore, both measures of continuity were related to substrate diameter variation.

One limitation in this study is that the gradient for some land cover variables used in analyses was not continuous. Stream site 7 was much less forested than other sites on some scales, and as a result some of the relationships observed between land cover and physical/chemical conditions were driven by this site. A better test of these relationships would examine a larger number of study sites that comprise a smoother gradient in forest cover on all scales. However, the group of streams we studied included every stream from the set of possible streams in the Upper Chattahoochee basin that met selection criteria designed to control for potential confounding factors (e.g. watershed area, stream gradient, and elevation). Rigorous site selection that minimized intersite variation in

potential confounding factors may explain our detection of strong relationships with just seven stream sites.

Since Hunsaker and Levine (1995) posed the question of the relative importance of watershed versus riparian land cover in predicting instream physical/chemical habitat condition and biotic integrity, a number of studies have concluded that the watershed scale is dominant (Richards et al. 1996, Roth et al. 1996, Allan et al. 1997, Wang et al. 1997, Harding et al. 1998, Sutherland et al. 2002). In contrast, we found that network scale riparian land cover was at least as good as watershed land cover (and far better than local reach land cover) at predicting physical/chemical factors that were most important to aquatic assemblages. A similar finding was reported by Lammert and Allan (1999). Differing results with respect to the importance of riparian land cover may be due to differences in study designs. All of the studies cited above, excluding ours, used images with 30-m or coarser resolution (compared to 1-2 m resolution for this study) to generate riparian land cover data. This spatial resolution may not be sufficient to generate accurate land cover data for measured buffers (30 m to 100 m wide), since accurate spatial pattern analysis requires resolution that is appropriate to the features being measured (O'Neill et al. 1996). Therefore, conclusions that watershed land cover is more important than riparian land cover should be interpreted with caution.

Another potential explanation for weak relationships between network scale riparian cover and instream condition in other studies is that typical riparian assessments (% forest cover in a set-width buffer) describe only the quantity of forest cover within a buffer. Riparian metrics in this study (e.g. CONTIN-CC, CONTIN-BW) contain information about how forest cover is distributed both laterally and longitudinally along

streams, which is potentially important to buffer function. Therefore, these types of

riparian measures may be more likely to reveal existing relationships between riparian

forest cover and instream conditions. For example, we found that continuity of canopy

cover along entire stream networks (CONTIN-CC) was the best land cover predictor of

some physical/chemical factors.

Physical/Chemical Habitat Conditions Important to Biota

Numerous studies have reported instream habitat alteration as a consequence of

deforestation. Conversion of forested land to anthropogenic uses has been associated

with increased water temperatures, but riparian forest cover may dampen the temperature

effects of upland deforestation (Chen and Chen 1994, Rowe and Taylor 1994, LeBlanc et

al. 1997). Maximum water temperature metrics in this study were most strongly related

to continuity of stream canopy cover, suggesting that gaps in forested buffer impact

stream thermal regimes. In a wide range of stream sizes in the southern Appalachians,

Scott et al. (2002) found that mainstem riparian forest cover (%) had the strongest

influence among other factors in a predictive model of mean summer temperatures.

While most studies have focused on summer temperature regimes (Chen and Chen 1994),

we found that winter minimum temperatures and annual variation also increased with

reductions in riparian forest cover. Summer daily variation in temperature in our study

increased with the number of stream-road crossings, perhaps due to associated buffer

gaps and heat released from insolated asphalt (Trombulak and Frissell 2000). Our results

suggest that continuous riparian forest cover throughout stream networks may be

necessary for riparian buffers to effectively maintain natural stream thermal regimes.

Standing crop of CPOM in our study declined with reductions in forest cover at network and watershed scales. While local deforestation may disrupt input of leaf litter to a stream, forest disturbance on large scales has been shown to increase transport of CPOM as a result of altered hydrology (Webster et al. 1990). Thus, the large scale of the forest cover-CPOM relationship we observed suggests that riparian influence on retention and transport, rather than on inputs of CPOM, is likely the dominant mechanism of this relationship. A similar scale relationship was documented for riparian forest cover influence on suspended CPOM in a prairie river (Johnson and Covich 1997). Reductions in CPOM are of concern because of strong coupling that exists between production of aquatic biota and terrestrial organic matter resources in headwater streams (Wallace et al. 1999). Experimental additions of litter have demonstrated that macroinvertebrate shredder populations can be food-limited even under natural rates of terrestrial litter input (Richardson 1991). In addition, experimental litter reductions (Rowe and Richardson 2001) and exclusions (Wallace et al. 1999) have demonstrated macroinvertebrate behavioral responses (i.e. drifting) and multiple trophic level population responses, respectively. In our study, shredder abundance and macroinvertebrate integrity metrics declined with decreasing CPOM standing crop. CPOM was also one of the strongest predictors of fish assemblage metrics in our study. Similarly, variation in CPOM was the strongest predictor of fish assemblage changes following deforestation in headwaters of the Amazon (Bojsen and Barriga 2002). Thus, continuous and wide corridors of riparian forest cover throughout stream networks may be necessary to maintain standing crops of CPOM that will support native headwater assemblages.

Substrate diameter variation (hereafter substrate heterogeneity) was related to network scale riparian forest cover and its importance to biotic integrity was supported by both multiple regression models and ordination of assemblage data. Evidence from other studies suggests that substrate heterogeneity has an important influence on the structure of macroinvertebrate assemblages (Minshall and Robinson 1998, Beisel et al. 2000, Palmer et al. 2000). In a study of urbanizing watersheds, Roy et al. (2003) found that variability in substrate phi (a transformation of substrate diameter) was positively related to forest cover (%) in a 100 m buffer and was a good predictor of macroinvertebrate community integrity. Substrate heterogeneity has also been shown to be important in mediating stream ecosystem functions like primary production of benthic biofilms (Cardinale et al. 2002) and relationships across trophic levels such as algal-grazer interactions (Poff and NelsonBaker 1997). Thus, homogenization of streambed habitat following riparian deforestation may result in reduced biotic integrity and functional changes in streams.

Although fine sediment in riffles was not related to riparian forest cover in our study, fine sediment increased with watershed impervious cover, an indicator of suburban land use. This relationship is surprising given the low and narrow range of impervious cover (~ 0.5 – 3 %) in our study watersheds. Other studies have reported thresholds of 10 % impervious cover for instream degradation (Booth and Jackson 1997), but thresholds in montane settings may be lower. This relationship also suggests that the source of increased fine sediment in our study may have been channel (rather than upland) erosion, since sedimentation in urbanizing watersheds is often dominated by channel erosion due to the hydrologic alterations that accompany impervious cover (Trimble 1997,

Trombulak and Frissell 2000). While substrate characteristics in other studies have been related to stream gradient, sediment and substrate variables measured in our study were not related to stream gradient. This was perhaps due to the intentionally narrow range in gradient, suggesting that site selection to avoid potential confounding from factors such as stream gradient was effective. The impacts of fine sediment on aquatic assemblages have been well documented and include reductions in total abundance and diversity of fishes and macroinvertebrates and loss of sensitive taxa such as EPT taxa and fish that are benthic feeders or spawners (Morse et al. 1993, Waters 1995, Angradi 1999, Jones et al. 1999, Sutherland et al. 2002). In this study, riffle fine sediment was the strongest negative predictor of fish community integrity, with particular susceptibility among the benthic invertivore trophic guild.

Roles of Land Cover and Instream Factors in Determining Aquatic Assemblages
An additional scale comparison that is often made is the relative strength of land cover versus instream habitat conditions in predicting aquatic assemblage structure. We found that land cover measures were poor predictors of aquatic assemblages compared to instream physical/chemical conditions. Others have also found that landscape patterns are less important than physical/chemical habitat conditions in explaining variation in macroinvertebrate and fish assemblages (Lammert and Allan 1999, Roy et al. 2003). Perhaps this result is attributable to the fact that stream biota do not interact directly with landscapes but do interact directly with instream habitat. Still, landscape patterns were important to aquatic assemblages because physical/chemical habitat conditions that varied as a function of land cover could in turn be used to predict aquatic assemblage

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metrics. This suggests that instream physical/chemical habitat factors functioned as intermediaries in translating the effects of changes in land cover to changes in aquatic assemblages and biotic integrity. Other studies have involved watersheds with much higher percentages of anthropogenic land uses compared to the highly forested watersheds examined in this study. However, scale-transcending impacts of land cover on instream biota via habitat changes similar to those observed in our study (watershed area 1.8 - 7.2 km^2, non-forest cover: 3.7 – 17.5 %) have been demonstrated in wider ranges of watershed area (12-150 km^2) and land use intensity (non-forest cover: 13 – 81 %, Lammert and Allan 1999, Roy et al. 2003).

Effects of Historical and Current Land Use

Legacies of historic land use disturbance persist in stream channels today (Harding et al. 1998, Scott et al. 2002). In our study, bank erosion and instability were not related to current land cover patterns; in fact the most forested stream also had the greatest bank erosion. However, this apparent contradiction was explained by historical land use. Valley deforestation in 1938 was positively related to both bank erosion and bank instability. Bank erosion in several study streams was dominated by mass wasting or slumping of banks rather than fluvial erosion. This may be evidence that these streams are downcutting through sediments that aggraded on the floodplain (Leigh 1994, Knighton 1998) during intensive agricultural use of these valleys in the first half of the 20th century. Bank erosion was negatively related to macroinvertebrate community integrity, supporting Harding et al.'s (1998) assertion that historic land use may be a strong predictor of current biotic integrity in streams.

We observed increases in temperature and reductions in substrate heterogeneity and allochthonous resources with reductions in riparian forest cover in southern Appalachian headwater streams. These changes correspond to Scott and Helfman's (2001) definition of habitat homogenization for small, high elevation streams, which they identify as a functional transformation to a stream context more typical of lower elevations. Though our study watersheds were relatively high in forest cover (83 - 96 %), less than 20 % watershed deforestation in the southern Appalachians has been associated with water quality degradation (Bolstad and Swank 1997) and declines in sensitive fishes such as benthic crevice spawners and gravel spawners, reproductive guilds that include many of the imperilled species in the southern Appalachians (Sutherland et al. 2002). Montane regions may suffer greater declines in stream integrity at low levels of deforestation because steep hillslopes amplify the effects of hydrologic alterations associated with deforestation. Therefore, it may be especially critical to protect continuous and wide corridors of riparian forest cover along entire stream networks in this region. Such riparian protection, along with watershed management, will help maintain instream habitat conditions that support the unique native communities of the southern Appalachian headwaters, and protect downstream systems that depend on the health of these headwater streams.

Acknowledgements

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Table 2.1. Forest cover and land use metrics for streams studied in the Upper Chattahoochee River basin, Georgia, USA, April 2000 - September 2002. Metrics are divided into categories by spatial scale. Stream sites were given identification numbers by watershed forest cover (most to least = 1 - 7).

Forest cover and land use	Abbreviation	Stream						
		1	2	3	4	5	6	7
Watershed scale								
Forest cover (%)	FWS	96.3	94.3	91.2	90.6	89.8	88.4	82.5
Impervious cover (%)	IMWS	1.5	0.6	2.5	2.9	2.4	2.8	1.8
Density of buildings in watershed (#/km^2)	BDGDENS	33.3	24.7	40.0	26.8	18.7	33.3	22.4
Network riparian scale								
Mean buffer width (ft): network	MBW	96.5	91.5	85.8	92.5	87.9	83.6	56.8
Mean buffer width (ft): 1000 m of network	MBW1000	95.2	71.6	80.8	92.8	81.5	75.1	33.7
Continuity of canopy cover (%)	CONTIN-CC	100.0	97.6	96.4	100.0	95.0	95.3	63.2
Continuity of a buffer > 100 ft (%)	CONTIN-BW	92.5	86.2	79.1	84.5	81.2	77.5	52.3
Stream/riparian road crossings (#)	RDXINGS	3	4	3	0	11	13	7
Local riparian scale (100 m reach)								
Mean buffer width (ft): local	MBW100	84.5	92.5	71.0	100.0	94.2	91.6	97.4
Canopy cover (%): local	CANOPY	81.4	85.3	87.7	81.9	77.2	85.5	88.7
Historic land cover								
1938 Valley deforestation index	VALDEF38	4	2	3	4	1	3	3
Stream physical characteristics								
Watershed area (km^2)		3.90	2.67	1.85	1.94	7.17	3.21	2.37
Stream network length (km)		4.31	7.39	4.68	2.02	14.93	10.39	3.13
Elevation of study reach (m)		499	517	533	482	431	465	432
Gradient of study reach (m/m)		0.006	0.015	0.016	0.014	0.015	0.013	0.013

Table 2.2. Subset of physical/chemical and biotic assemblage variables used in statistical analyses. Explanatory variables used in multiple regression analyses of assemblage metrics are noted by a §. To achieve normality, percentage variables were arcsin-squareroot transformed. Bank stability index modified from Simon and Downs (1995), NCBI from Lenat (1993), and B-IBI modified from Kerans and Karr (1994).

Abbreviation	Description	Min	Mean	Max
Temperature				
Max daily max §	Maximum daily maximum (C)	20.6	22.3	25.2
Max 7-day max	Maximum 7-day moving average maximum (C)	19.5	20.8	22.7
Mean daily min	Mean daily minimum (C)	13	13.5	14.2
Annual variation	Maximum daily mean - minimum daily mean (C)	14.5	17.2	19.6
Daily variation	Summer mean daily variation (C)	1.5	1.9	2.5
Chemistry				
Total N	Total nitrogen (mg L^{-1})	0.04	0.155	0.269
SC	Specific conductivity ($\mu s\ cm^{-1}$)	17.8	21.2	24.6
Sediment & Substrate				
Turbidity	Baseflow turbidity (NTU)	4.2	6.6	11.1
% fines §	Fraction of riffle substrate < 2 mm (%)	10.1	20.3	30.7
% pebbles	Fraction of riffle substrate 16-32 mm (%)	5.4	19	28
% coarse	Fraction of riffle substrate > 64 mm (%)	14	36.6	56
Embeddedness	Riffle embeddedness index (1-4)	1.5	1.9	2.1
Substrate diameter variation §	Substrate diameter (mm) coefficient of variation	0.76	1.35	1.7
Mesohabitat & Geomorphic variables				
Max depth §	Maximum water depth (cm)	22.5	35.9	51
Depth variation	Water depth coefficient of variation	0.43	0.57	0.82
Velocity variation	Water velocity coefficient of variation	0.67	0.84	1.08
Bank instability	Bank instability index (1-4)	1.3	1.7	1.9
Bank erosion §	Counts of bank erosion observed	0	5.9	11
Allochthonous organic matter				
CPOM §	Standing crop of coarse particulate organic matter (g/m^2)	23	77.7	105.6
LWD	Large woody debris surface area in 50 m sample reach	0	2.1	5.9
Macroinvertebrate communities				
Total abundance	Total number of individuals found in equivalent sample	77	200.4	277
Taxa richness	Number of taxa	12	26	34
EPT richness	Number of EPT taxa	4	13.1	18
Shredder abundance	Number of shredder individuals caught	4	13	20
Sensitive taxa abundance	Number of sensitive individuals caught	5	36.7	75
NCBI	North Carolina Biotic Index ($\uparrow$ with disturbance)	4.09	4.81	5.57
B-IBI	Benthic Index of Biotic Integrity ($\downarrow$ with disturbance)	26.9	51.9	66.7
Fish communities				
Catch/shock time	Number of individuals caught per unit shock time	0.07	0.141	0.218
Catch/m^2 sampled	Number of individuals caught per m^2 sampled	0.07	0.14	0.22
Species richness	Number of species	2	5.6	9
Native abundance	Number of native individuals caught	59	148.3	270
Benthic invertivore abundance	Number of benthic invertivore individuals caught	0	39.7	79

Table 2.3. Most significant bivariate relationships between forest cover/ land use and subset of physical/chemical variables. Scale of each relationship is classified as local (100 m reach), network, or watershed; variable abbreviations as in Table 1. R^2 is reported for significant regression models (* = p < 0.05, ** = p < 0.01, and *** = p < 0.001). Direction of relationship is indicated by +/-.

Physical/chemical habitat	Forest cover/land use	Scale	R^2
Temperature			
Max 7-day max	- CONTIN-CC	network	0.66*
	- MBW1000	network	0.57*
Max daily max	- CONTIN-CC	network	0.85**
	- MBW1000	network	0.68*
	- CONTIN-BW	network	0.63*
	- FWS	watershed	0.59*
Mean daily min	- MBW1000	network	0.57*
Annual variation	- CONTIN-CC	network	0.59*
Daily variation	+ RDXINGS	network	0.68*
Chemistry			
Total N	none		
Conductivity	none		
Sediment/Substrate			
Turbidity	none		
% fines	+ IMWS	watershed	0.88**
% pebbles	+ BDGDENS	watershed	0.65*
% coarse	+ CANOPY	local	0.58*
Riffle embeddedness	none		
Substrate diameter variation	+ MBW1000	network	0.66*
	+ CONTIN-CC	network	0.63*
	+ CONTIN-BW	network	0.57*
Mesohabitat/Geomorphic variables			
Max depth	- BDGDENS	watershed	0.64*
	- VALDEF38	network	0.60*
Depth variation	- IMWS	watershed	0.83**
Velocity variation	+ RDXINGS	network	0.86**
Bank instability	+ VALDEF38	network	0.85**
	+ BDGDENS	watershed	0.65*
Bank erosion	+ VALDEF38	network	0.73*
Allochthonous organic matter			
CPOM	+ CONTIN-BW	network	0.58*
	+ FWS	watershed	0.46*
LWD †	+ FWS	watershed	0.76*

† Only six sites used in this analyses, see Results for rationale

Table 2.4. Significant multiple regression models showing biotic assemblage metric relationships with subset of six physical/chemical variables.   Explanatory variables used in analyses and abbreviations as in Table 1. Model significance is noted by $* = p < 0.05$, $** = p < 0.01$, and $*** = p < 0.001$). NCBI and fish catch/m^2 are excluded from table because there were no significant models for these metrics. B-IBI is expected to decrease with disturbance (Kerans and Karr 1994).

	Explanatory variables	Partial R^2	Adjusted R^2
Macroinvertebrates			
Total abundance	- Bank erosion	0.55	0.92**
	- Max depth	0.40	
Taxa richness	+ Substrate diameter variation	0.83	0.95**
	+ Max depth	0.14	
EPT richness	+ CPOM	0.59	0.59*
Shredder abundance	+ CPOM	0.63	0.86*
	- Max depth	0.17	
	- % fines	0.13	
Sensitive taxa abundance	- Bank erosion	0.57	0.67**
	+ Substrate diameter variation	0.21	
B-IBI	+ Substrate diameter variation	0.72	0.72*
Fish			
Catch/shock time	+ CPOM	0.67	0.73*
	+ Max depth	0.15	
Species richness	- % fines	0.68	0.68*
Native abundance	+ CPOM	0.62	0.62*
Benthic invertivore abundance	- % fines	0.51	0.95***
	- Max daily max temperature	0.47	

Table 2.5. Macroinvertebrate taxa list for study streams.

Order	Family	Genus	Order	Family	Genus
Anisoptera	Aeschnidae	*Boyeria*	Ephmeroptera	Heptageniidae	*Stenonema*
Anisoptera	Cordulegastridae	*Cordulegaster*	Ephmeroptera	Isonychiidae	*Isonychia*
Anisoptera	Gomphidae	*Dromogomphus*	Hemiptera	Hebridae	*Lipogomphus*
Anisoptera	Gomphidae	*Erpetogomphus*	Hemiptera	Saldidae	*Salda*
Anisoptera	Gomphidae	*Gomphus*	Hemiptera	Veliidae	*Rhagovelia*
Anisoptera	Gomphidae	*Hagenius*	Megaloptera	Corydalidae	*Corydalus*
Coleoptera	Elmidae	*Dubiraphia*	Megaloptera	Corydalidae	*Nigronia*
Coleoptera	Elmidae	*Macronychus*	Plecoptera	Chloroperlidae	*Utaperla*
Coleoptera	Elmidae	*Macronychus*	Plecoptera	Perlidae	*Acroneuria*
Coleoptera	Elmidae	*Microcylloepus*	Plecoptera	Perlidae	*Agnetina*
Coleoptera	Elmidae	*Optioservus*	Plecoptera	Perlidae	*Claassenia*
Coleoptera	Elmidae	*Promoresia*	Plecoptera	Perlidae	*Eccoptura*
Coleoptera	Gyrinidae	*Dineutus*	Plecoptera	Perlidae	*Neoperla*
Coleoptera	Psephenidae	*Ectopria*	Plecoptera	Perlidae	*Perlesta*
Coleoptera	Psephenidae	*Psephenus*	Plecoptera	Perlodidae	*Isoperla*
Diptera	Ceratopogonidae	*Forcipamyia*	Plecoptera	Perlodidae	*Remenus*
Diptera	Chironomidae	*aggregated*	Plecoptera	Pteronarcyidae	*Pteronarcys*
Diptera	Dixidae	*Dixa*	Trichoptera	Brachycentridae	*Brachycentrus*
Diptera	Simulidae	*Simulium*	Trichoptera	Hydropsychidae	*Ceratopsyche*
Diptera	Tanyderidae	*Protoplasa*	Trichoptera	Hydropsychidae	*Cheumatopsyche*
Diptera	Tipulidae	*Antocha*	Trichoptera	Hydropsychidae	*Hydropsyche*
Diptera	Tipulidae	*Brachyprema*	Trichoptera	Lepidostomatidae	*Lepidostoma*
Diptera	Tipulidae	*Dicranota*	Trichoptera	Leptoceridae	*Oecetis*
Diptera	Tipulidae	*Prionocera*	Trichoptera	Limnephilidae	*Pychnopsyche*
Diptera	Tipulidae	*Tipula*	Trichoptera	Philopotamidae	*Dolophilodes*
Ephmeroptera	Ephemerellidae	*Drunella*	Trichoptera	Polycentropodidae	*Cyrnellus*
Ephmeroptera	Ephemerellidae	*Ephemerella*	Trichoptera	Polycentropodidae	*Paranyctiophylax*
Ephmeroptera	Ephemerellidae	*Eurylophella*	Trichoptera	Polycentropodidae	*Polycentropus*
Ephmeroptera	Ephemerellidae	*Serratella*	Trichoptera	Rhyacophilidae	*Rhyacophila*
Ephmeroptera	Heptageniidae	*Cinygmula*	Zygoptera	Calopterygidae	*Calopteryx*
Ephmeroptera	Heptageniidae	*Epeorus*			

Table 2.6. Fish species list including endemic and native status as well as trophic guild designations. H = herbivore, BI = benthic invertivore, DI = drift invertivore, GI = generalized invertivore, DE = detritivore, C= carnivore/piscivore.

| Family	Species	Common name	Highland endemic (HE) Widely distributed (WD)	Native (N) Introduced (I)	Trophic Guild
Catostomidae	*Hypentelium etowanum*	Alabama hogsucker	WD	N	BI
Catostomidae	*Minytrema melanops*	Spotted sucker	WD	N	DE
Centrarchidae	*Lepomis cyanellus*	Green sunfish	WD	I	GI
Centrarchidae	*Lepomis macrochirus*	Bluegill	WD	N	GI
Centrarchidae	*Micropterus salmoides*	Largemouth bass	WD	N	C
Cottidae	*Cottus bairdi*	Mottled sculpin	HE	N	BI
Cyprinidae	*Campostoma pauciradii*	Bluefin stoneroller	WD	N	H
Cyprinidae	*Luxilus zonistius*	Bandfin shiner	WD	N	DI
Cyprinidae	*Nocomis leptocephalus*	Bluehead chub	WD	N	C
Cyprinidae	*Notropis lutipinnis*	Yellowfin shiner	WD	N	DI
Cyprinidae	*Semotilus atromaculatus*	Creek chub	WD	N	C
Percidae	*Percina nigrofasciata*	Blackbanded darter	WD	N	BI
Salmonidae	*Oncorhynchus mykiss*	Rainbow trout	WD	I	DI
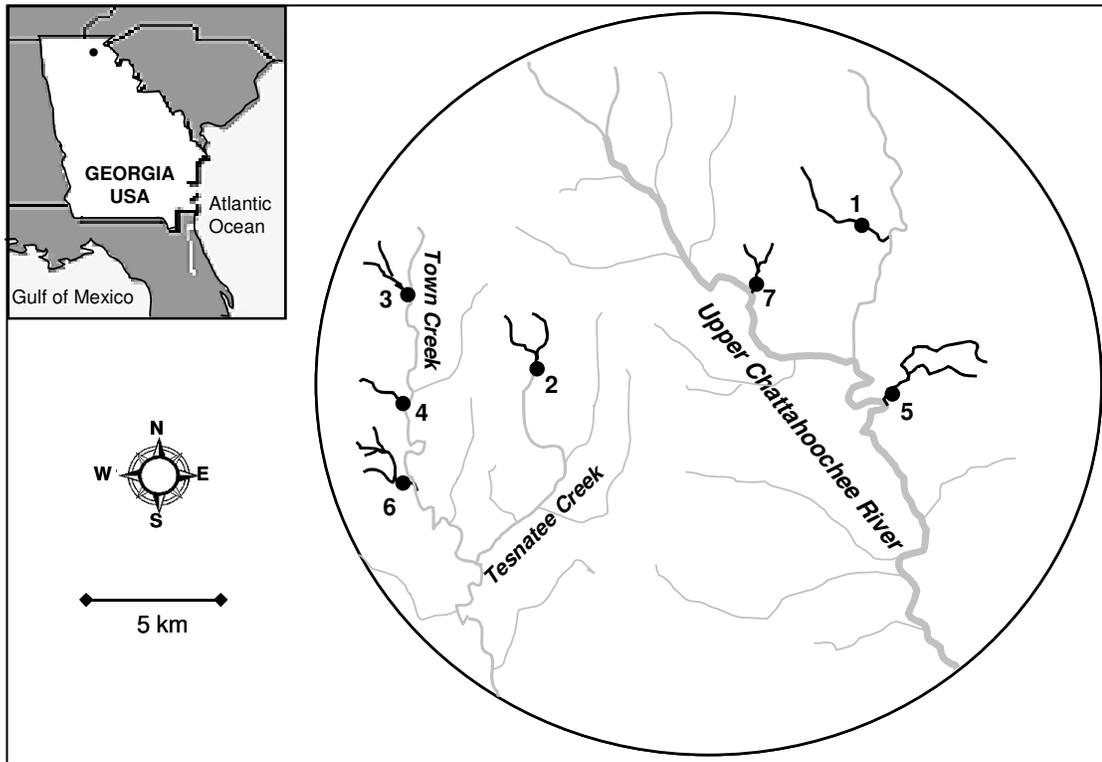
Figure 2.1. Map of study stream locations (1-7 in order from most to least forested watersheds) in the Upper Chattahoochee River basin, Georgia, USA. Town Creek flows into Tesnatee Creek, which flows into the Chestatee River and eventually into the Upper Chattahoochee River. All study sites are within the Blue Ridge physiographic province at the southernmost extent of the southern Appalachians. See Appendix A for names and GPS coordinates of sites.
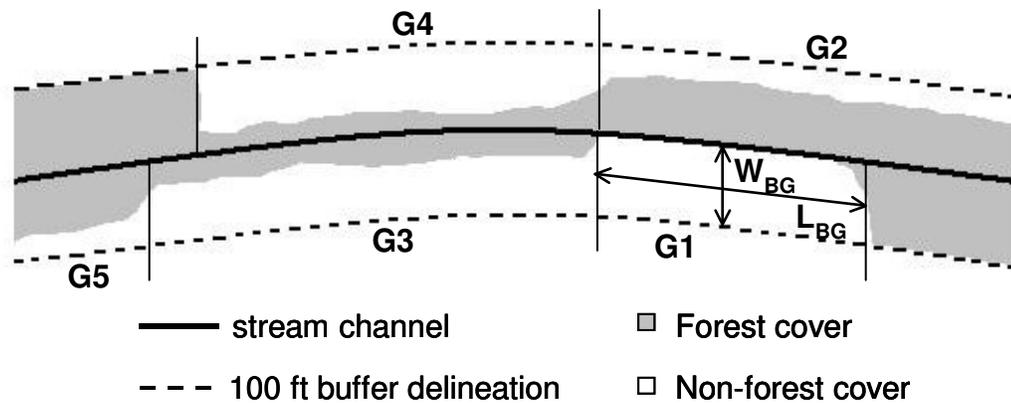
Figure 2.2. Schematic illustrating how buffer gap measurements were made along a hypothetical stream reach. Areas within the 100 ft buffer delineation without forest cover were considered buffer gaps, shown as white areas. The two sides of each stream were analyzed separately as forest cover often varied considerably from one side to the other. For each gap (here G1-G5), a gap width (W_{BG}) and length (L_{BG}) were measured. Gaps along the entire stream network above the sample reach were measured and these data were used to calculate riparian forest cover width and continuity metrics at multiple scales.
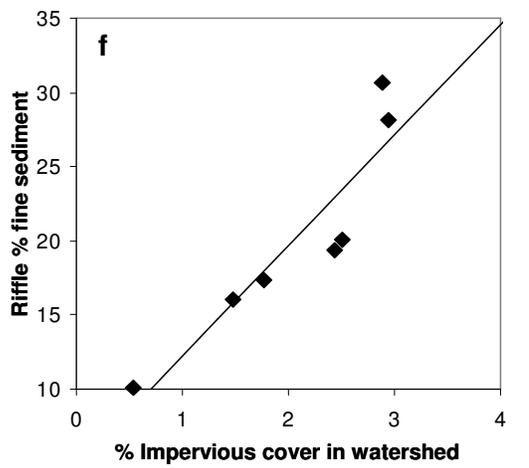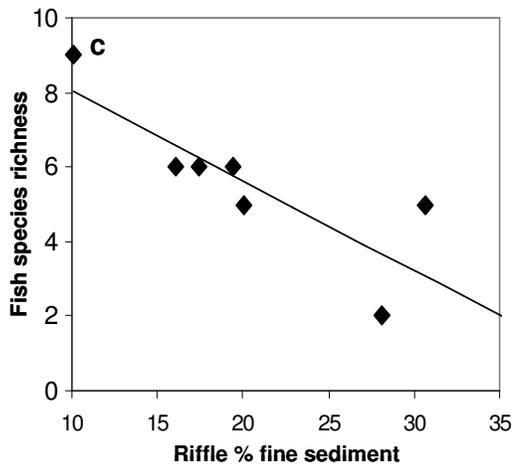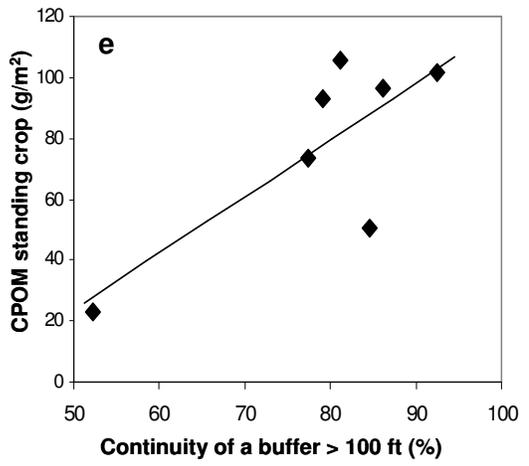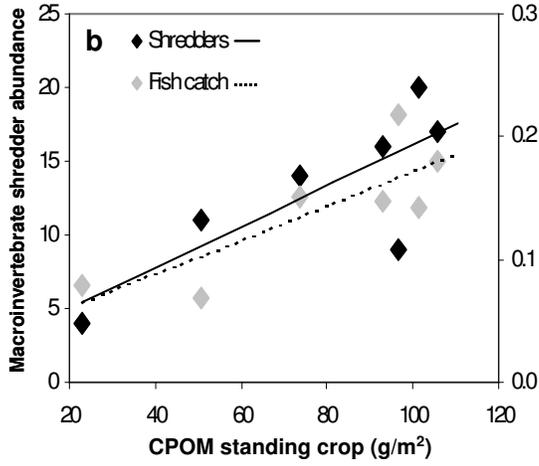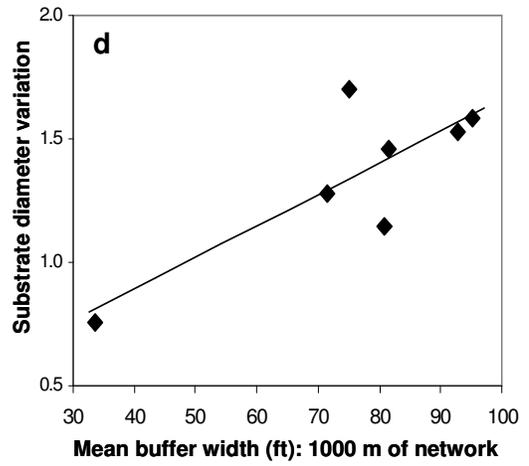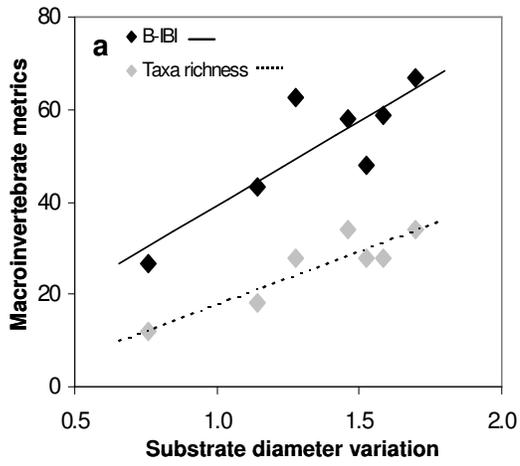
Figure 2.3. Bivariate plots of physical/chemical variables that were the best predictors of macroinvertebrate and fish assemblages: substrate diameter variation, CPOM standing crop, and percentage fine sediment in riffles (Fig 2.4 a, b, and c, see Table 2.4 for p and R^2 values). These physical/chemical variables were also highly correlated to land cover variables; plots 2.3 d, e, and f show the relationship between each physical/chemical variable and the strongest land cover predictor (see Table 3 for p and R^2 values).
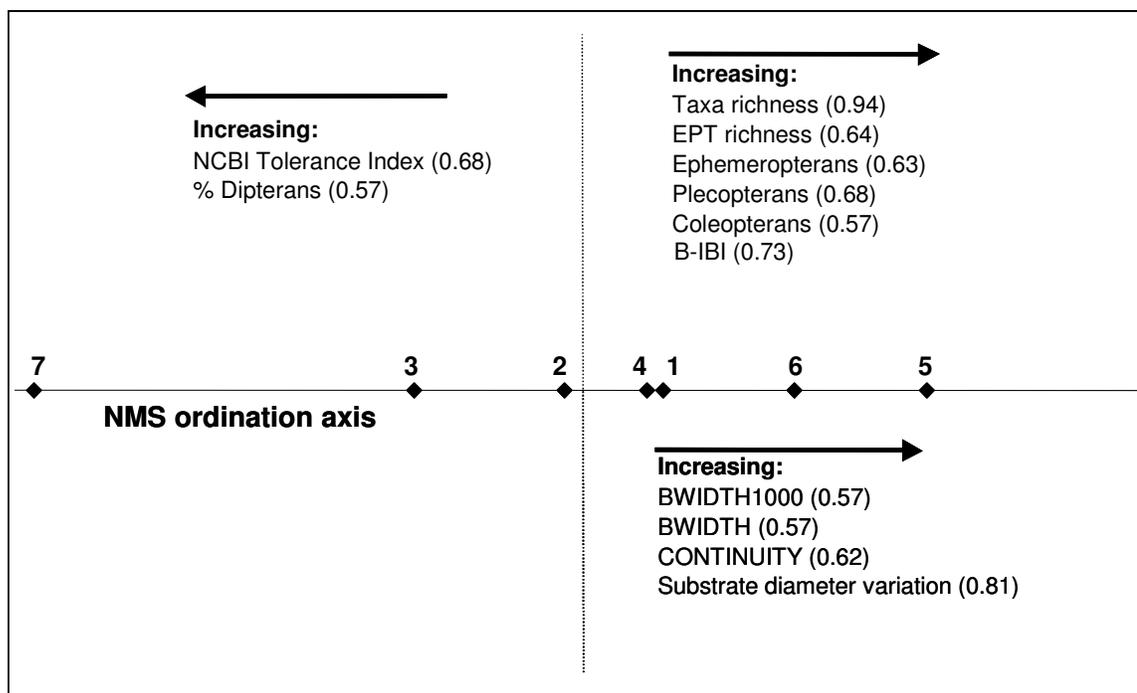
Figure 2.4. Non-metric multidimensional scaling (NMS) ordination results for macroinvertebrate taxa abundances (log (x +1) transformed). Monte Carlo tests resulted in selection of just one significant axis (shown horizontally) that represented 89.8 % of variation among sites in macroinvertebrate assemblages. Significant regressions with NMS axis are noted (assemblage metrics above axis, physical/chemical and forest cover variables below axis). R^2 for regressions is reported in parentheses. Point labels are site identification numbers (1 – 7) from Table 1.

CHAPTER 3

RIPARIAN DEFORESTATION ALTERS THE ENERGY BASE OF HEADWATER

STREAM FOOD WEBS [1]

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SUMMARY

1. We conducted an assessment of deforestation impacts on the energy base of headwater food webs in seven headwater streams in the Upper Chattahoochee basin, GA, U.S.A. We measured terrestrial organic matter standing crop and determined consumer (crayfish and insectivorous fish) dependence on terrestrial vs. aquatic energy sources via gut content and stable isotope analysis.

2. Standing crop of coarse particulate organic matter (CPOM) declined with deforestation at large scales (i.e. watershed deforestation and riparian deforestation at the entire stream network-scale). Terrestrial plant matter, the dominant component of crayfish guts, declined in guts with reductions in CPOM standing crop and deforestation.

3. Crayfish and insectivorous fish $\delta^{13}C$ became relatively enriched with deforestation, indicating isotopic divergence from CPOM, the most ^{13}C-depleted basal resource, with reductions in watershed and entire network-scale riparian forest cover. Crayfish $\delta^{13}C$ also diverged from CPOM $\delta^{13}C$ with decreasing CPOM standing crop.

4. A concentration-dependent, dual isotope mixing model was used to calculate the relative dependence of crayfish and fish on terrestrial vs. aquatic basal resources. Results suggested that both were important basal resources. Consumer dependence on CPOM was positively related to the most local riparian forest cover variable, reach canopy cover.

5. Our data suggest the importance of forest cover at several scales, and that relatively low levels of riparian deforestation along headwater streams can lead to reductions in stream food web dependence on terrestrial subsidies.

Introduction

Streamside, or riparian forests influence physical, chemical, and biological dimensions of streams and mediate a number of terrestrial-aquatic linkages (Karr & Schlosser 1978, Gregory et al. 1991, Sweeney 1992). Strong connectivity between adjacent terrestrial and aquatic ecosystems can result in reciprocal subsidies (*sensu* Nakano & Murakami 2001). In headwater streams, aquatic insect emergence may be the primary stream-to-forest subsidy, while forest-to-stream fluxes include nutrients, dissolved and fine particulate organic carbon, coarse detritus and debris, and terrestrial arthropods (Polis et. al 1997). These allochthonous resources can potentially have great impacts on the productivity of receiving systems (Polis & Hurd 1996, Nakano *et al.* 1999, Wallace *et al.* 1999), but are donor-controlled (Polis *et al.* 1997) and consequently may depend on the condition of the donor system. The dominant role of terrestrial detritus subsidies in the food web base of forested headwater streams was highlighted by a long-term leaf litter exclusion experiment in the Appalachian mountains of the southeastern U.S. Exclusion of riparian inputs in this study resulted in lower productivity of both primary and higher order consumers, indicating system dependence on terrestrial subsidies (Wallace *et al.* 1999).

The River Continuum Concept (RCC, Vannote *et al.* 1980) asserts that there is a longitudinal gradient in terrestrial subsidies of aquatic food webs in river networks. Headwater food webs are largely supported by inputs of allochthonous detritus that become less important as autochthonous production increases downstream. This prediction is based on relatively higher canopy cover in headwaters, that results in increased allochthonous detrital inputs/m^2 of streambed (Webster *et al.* 1990) and

decreased autochthonous production through light limitation (Minshall et. al 1983, Feminella *et al.* 1989) compared to downstream reaches. While some of the RCC's longitudinal linkage predictions have been supported for river systems in relatively undisturbed catchments (e.g. Rosi-Marshall & Wallace 2002), these are rare in today's landscapes. The question of how anthropogenic alteration of watersheds and riparian landscapes affects the energy base continuum within river systems remains essentially unanswered. Further, though the impacts of watershed clearcuts (Webster *et al.* 1990) and exclusion of all detrital inputs have been studied (Wallace et. al 1999), it is unclear how gradients in landscape alteration affect the magnitude of allochthonous inputs to streams, and how potential gradients in allochthonous resource availability impact stream food webs.

Stable isotopes (mainly of C and N) have been employed extensively as food web tracers (Rounick & Winterbourne 1986, Peterson & Fry 1987) and have been useful in establishing the relative importance of terrestrial versus aquatic energy sources in supporting stream food webs in systems where these basal resources have distinct isotope signatures (Rounick *et al.* 1982, Rosenfeld & Roff 1992, Finlay 2001). However, most research in this area has focused on undisturbed lotic systems (Bunn *et al.* 1989, Rosenfeld & Roff 1992, Hamilton *et al.* 1992, Thorp et. al 1998, Finlay 2001, Lewis et. al 2001) or comparisons of forest versus pasture, grassland, or clear cut streams (Rounick *et al.* 1982, Hicks 1997, Parkyn *et al.* 2001). To our knowledge, no published isotope studies have assessed effects of gradients in deforestation on the relative importance of terrestrial versus aquatic resources in the energy base of stream food webs.

On current landscapes, riparian forests are commonly narrow, discontinuous

corridors of vegetation along streams ("buffers") embedded within watershed matrices of

anthropogenic land use patches and forested patches in various stages of recovery from

both anthropogenic and natural disturbance (Malanson 1993, Yarnell 1998). Ecologists

are just beginning to examine the effects of such disturbance on food web structure and

dynamics (Power & Dietrich 2002). The focus of this research was to assess how

gradients in watershed and riparian deforestation affected (a) the availability of terrestrial

organic matter in headwater streams and (b) the dependence of headwater stream food

webs on terrestrial energy sources using gut content and stable isotope analyses. We

determined relationships between forest cover, standing crop of allochthonous detritus

and isotopic signatures of top consumers. Study streams encompassed a relatively

narrow range in riparian forest cover within watersheds that were predominantly forested;

thus our results are indicative of the impacts of relatively subtle forest cover changes.

We assessed forest cover at multiple scales, from local reach up to watershed, to

determine the scale(s) of deforestation impacts on headwater food webs.

Methods

Land Use Assessment

Seven study streams (Fig. 3.1) were selected from the Upper Chattahoochee River Basin,

GA, USA based on a suite of criteria including watershed area, elevation, gradient, and

access; summary characteristics for streams are shown in Table 3.1. High resolution (1-2

m, National Aerial Photography Program, USGS) color-infrared aerial photographs of

study watersheds (March 1999) were digitized, georeferenced and rectified for analysis

using ERDAS Imagine® 8.4 (ERDAS®, Atlanta, GA, USA), an image processing software package. Watershed boundaries were delineated and land cover types in study watersheds were classified with the supervised classification procedure described in the ERDAS Imagine® Tour Guides™ (1999). Classification resulted in a thematic raster layer that allowed determination of percentages of each land cover type, including forest cover, impervious cover, and agricultural cover.

To assess riparian land cover, 100 ft buffers (buffer laws in the U.S. are typically written using imperial units) were delineated around study streams throughout the entire upstream networks and land cover within the buffers was determined from the land cover raster layers. All gaps in forest cover within the 100 ft buffer were digitally measured (Fig. 3.2) and these data were used to calculate several riparian forest cover metrics (see Table 3.1). Continuity of stream canopy cover and riparian buffers was calculated as the % stream length with a buffer wider than 0 ft and 100 ft, respectively. Mean buffer width (MBW) was calculated for multiple scales: (100 m local reach, 1000 m of network above study site, and entire stream network above study site) using the following weighted-average formula:

$$\text{MBW} = \frac{\Sigma L_{BG} * W_{BG} + 100 * (L_{TS} * 2 - \Sigma L_{BG})}{L_{TS} * 2} \qquad \text{(Eq. 1)}$$

L_{BG} = length of buffer gap

W_{BG} = buffer width at gap

L_{TS} = total stream length

Stream canopy cover was determined for each study reach by averaging spherical densiometer measurements at five points along each reach.

Availability of Allochthonous Materials

Benthic coarse particulate organic matter (CPOM) was quantified in the fall (Nov. 2000) and the following spring (May 2001). A 1-m^2 plot, assembled from PVC pipe and divided into four quadrants, was used to survey CPOM coverage of the streambed. Percent coverage by CPOM for each of the four quadrants was visually estimated to the nearest 10 % at 30 1-m^2 plots in each stream. At every other survey plot (n = 15/stream), CPOM within the plot was collected, oven dried at 40 °C and weighed to determine dry mass of CPOM per m^2 of streambed. A sum of habitat-specific CPOM standing crop (g/m^2) weighted by the percentage of streambed area in each habitat type (i.e. pool, riffle, or run) was calculated for fall and overall (fall/spring average). Standing crop of large woody debris (LWD = > 10 cm diameter, > 1 m length) was assessed once in November 2000. All LWD within the sample reach was measured (diameter and length) in order to estimate surface area of LWD habitat.

Natural Abundance Stable Isotopes and Food Web Energy Base

To assess the relative importance of aquatic vs. terrestrial energy sources to consumers in these headwater streams, we determined carbon and nitrogen isotope signatures for basal food web resources of terrestrial and aquatic origin and top consumers (crayfish and insectivorous fish). All food web components were sampled for isotopic analyses in October and November 2001. Three replicates of allochthonous (CPOM) and autochthonous (epilithic biofilm) basal resources as well as seston were sampled from each study stream. CPOM was collected from natural leaf accumulations in study streams and oven dried at 40 °C. For seston, we collected and filtered 4 – 5 L of stream

water and the resulting filters were oven dried at 40 °C. Epilithon was sampled by taking

epilithic scrapings of median-sized cobbles from similar flow velocity environments in

all study streams to minimize isotopic variation due to flow (Finlay *et al.* 1999).

We attempted to isolate algae from other epilithon components using a density-

gradient centrifugation technique that relies on differential densities of epilithic biofilm

components (Hamilton & Lewis 1992). However, due to low algal biomass and a high

proportion of diatoms (which have a high density relative to other algae) in these heavily

shaded streams, effective algal isolation (evaluated by microscopic examination) with

this technique was achieved for just two samples, hereafter "pure algae" samples.

Therefore, we considered Finlay's (2001) alternative approach of using herbivores as an

isotopic proxy for algae, which has been successful in getting strong (nearly 1:1)

relationships between isolated epilithic algal $\delta^{13}C$ and herbivore $\delta^{13}C$ across a wide range

in stream size (Finlay 2001). We sampled the predominant herbivore in our streams,

heptageniid mayflies (S*tenonema* spp.), for isotope analysis and also conducted gut

analysis to evaluate their potential as an algal proxy (see *Gut Content Analysis* below).

For each study stream, 3 riffles were sampled and 5-10 individuals for each of three size

classes (0-5 mm, 5-10 mm, and 10-15 mm) were collected. Individuals within a size

class were combined, their guts were removed, and remaining tissue was oven dried at 40

°C.

In sampling consumers for isotope analyses, we focused on top trophic levels

since they are isotopic integrators of lower trophic levels. We sampled crayfish

(*Cambarus* sp.), which are omnivores that feed on terrestrial detritus and aquatic insects,

often in varying proportions with age (Momot *et al.* 1978, Huryn & Wallace 1987,

Whitledge & Rabeni 1997, Parkyn *et al.* 2001) and insectivorous fishes. We collected the six most common species of insectivorous fishes (Alabama hog sucker *Hypentelium etowanum*, bandfin shiner *Luxilus zonistius*, blackbanded darter *Percina nigrofasciata*, bluehead chub *Nocomis leptocephalus*, mottled sculpin *Cottus bairdi*, and yellowfin shiner *Notropis lutipinnis*), but not all species were present at all study sites. Insectivorous fish (5 individuals for each species present) and crayfish (6-10 individuals, total carapace length measured) were collected from study streams via electroshocking. All specimens were returned to the laboratory on ice. In the laboratory, tail muscle tissue (crayfish) and caudal-peduncle muscle tissue (fish) was removed for isotope analysis and oven-dried at 40 °C.

All dried samples were ground, weighed, and analyzed using a Finnigan Delta C mass spectrometer linked with a Carlo Erba 1500 CHN analyzer. Standard methods for reporting isotopic composition were followed (DeNiro & Epstein 1978, Rounick & Winterbourne 1986).

Gut Content Analysis

Since crayfish feed directly on terrestrial leaf litter (unlike the insectivorous fish sampled), we analyzed crayfish gut contents to test whether crayfish diet varied with riparian deforestation. Crayfish collected for isotope analyses were also used for gut content analyses in which we measured the relative proportion (by area, using microscopy) of different classes of food particles found in crayfish guts. Crayfish guts were dissected, and gut content slides were prepared following standard protocol (Cummins 1973, Hall *et al.* 2000). Slides were viewed at 100x magnification using an

Olympus BX40 phase-contrast compound microscope, and digital images of 20-30

randomly chosen microscope fields per slide were taken with a video camera. Image

analysis software, Image-Pro® Plus 3.0.1 (Media Cybernetics, Silver Spring, MD, USA),

was then used to analyze digital images by identifying and digitally measuring the area of

50 food particles per slide, as is standard for this type of diet analysis (Cummins 1973,

Hall *et al.* 2000). Particles were classified as plant matter (leaf and wood material),

diatoms, filamentous algae, animal material (invertebrates), or amorphous detritus (no

cellular structure), and the percentage of area contributed by each of these classes was

calculated for individual crayfish.

Previous work has shown that *Stenonema* larvae may derive large portions of their

carbon from bacteria (Edwards & Meyer 1990, Hall & Meyer 1998). Thus, to evaluate

the potential use of *Stenonema* herbivores as an isotopic proxy for algae, we analyzed

Stenonema gut contents to determine how much of their assimilated carbon could

potentially be attributed to algae. *Stenonema* individuals (5-10) from 3 riffles were

sampled in each study stream and preserved in formalin. Guts for individuals from the

same riffle were combined onto one slide for analysis following the above methods, but

these slides were viewed under 400x magnification. Food particles were classified as

diatoms, filamentous algae, or amorphous detritus, and assimilation efficiency corrections

from the secondary production literature were applied as follows: 10 % for amorphous

detritus and 30 % for diatoms and filamentous algae (Benke &Wallace 1980, Hall *et al.*

2000).

Data Analysis and Mixing Models

Assumptions of normality were tested using Shapiro-Wilks tests, and non-normal data were transformed prior to statistical analysis (percentage variables were arcsin-squareroot transformed and network mean buffer width was cosine transformed) (Sokal & Rohlf 1995). Regression analysis was used to identify relationships between forest cover and CPOM standing crop, LWD standing crop, and gut contents of crayfish and *Stenonema*. Crayfish gut data were also analyzed for relationships with total carapace length to test for diet changes with age that have been previously shown (e.g. Whitledge & Rabeni 1997, Parkyn *et al.* 2001).

Analysis of variance (ANOVA) coupled with Ryan's Q and a Kramer correction for unequal sample size, was used to determine differences among basal resources in isotopic composition. Ryan's Q is a stepwise multiple comparisons test most strongly recommended in a review of unplanned multiple comparison tests (Day & Quinn 1989). Multiple analysis of variance (MANOVA) was used to determine whether basal resources differed in bivariate (i.e. dual isotope, C and N) space. The approach taken for analyses of isotopic data with forest cover was two-fold: regression and a mixing model. First, regression was used to determine if $\delta^{13}C$ of top consumers were related to changes in forest cover. Because CPOM was the most ^{13}C depleted (i.e. most negative) food web component, trends of consumer $\delta^{13}C$ enrichment (increasing $\delta^{13}C$) indicated divergence from terrestrial detritus signatures, whereas depletion (decreasing $\delta^{13}C$) indicated movement towards terrestrial detritus signatures. Regression was also used to determine if trophic position of omnivorous crayfish, assessed by crayfish $\delta^{15}N$, varied with CPOM

availability and forest cover. To test for effects of anthropogenic sources of N, which are typically ^{15}N enriched relative to atmospheric and soil nitrogen (Mayer *et al.* 2002), we used regression to determine if $\delta^{15}N$ of food web components varied with streamwater N concentrations or anthropogenic land uses (agricultural and impervious land cover in watersheds).

Second, we used a concentration-dependent, dual isotope (C and N) mixing model developed by Phillips & Koch (2002), which calculates the relative importance of food sources in a consumer's diet while accounting for differences in C and N content of food sources. Most published models assume that the proportions of C and N a consumer obtains from a food source are identical, but when food sources differ substantially in C and N content (e.g. leaf litter vs. algae) this assumption is not valid (Phillips & Koch 2002). We used this mixing model to compare the importance of terrestrial (CPOM) versus aquatic (algae, represented by "adjusted epilithon" isotope data, see Results for rationale) basal resources in supporting crayfish and insectivorous fishes. Trophic fractionation corrections were based on the product of trophic level (1.6 for crayfish determined from corrected gut analysis results, and 2 for fish) and fractionation values (0.4 ‰ $\delta^{13}C$ and 3.4 ‰ $\delta^{15}N$, Post 2002). CPOM C and N content values for each stream came from elemental composition analysis that is coupled with isotope analysis. For algae, we used an N content of 4 % (Pandian & Marian 1986) and then calculated C content (26.5 %) using the Redfield ratio of 106 C: 16 N (Wetzel 2001). Regression was then used to determine whether forest cover on multiple scales could explain variation in consumer dependence on CPOM (mixing model results). All statistical tests were performed using SAS[®] 8.02 (SAS Institute, Cary, NC).

Results

Watershed and Riparian Forest Cover

Study watersheds were predominantly forested (83 – 96 %), while agricultural and

impervious cover made up much smaller percentages (Table 3.1). The sites comprised a

gradient in riparian forest cover that varied with the scale of analysis; that is the ranking

of streams from most to least forested depended on scale. Network-scale riparian buffer

variables (MBW, CONTIN-CC, and CONTIN-BW) were correlated with % forest in the

watershed, unlike the more local scale buffer variables (canopy cover, MBW100), which

varied independently of watershed forest cover. For all study streams, watershed %

forest cover was within 15 % of the % forest cover within a 100 ft riparian buffer (stream

network scale). For most sites, watershed and riparian forest cover values were within 5

% of each other with greater forest cover in watersheds than in riparian buffers.

Availability of Allochthonous Materials vs. Forest cover

Habitat-weighted CPOM standing crop was positively related to both watershed and

network-scale riparian forest cover (Table 3.2). Over a narrow range in watershed

deforestation, from 96 to 83 % forest, fall CPOM standing crop declined from nearly 200

g/m^2 to about 25 g/m^2 (Fig 3.3). CPOM standing crop was also related to MBW and

other network-scale riparian variables, but was not related to local scale riparian variables

(Table 3.2). Spring CPOM standing crop was not related to measures of forest cover

(p>0.05). LWD standing crop was not related to any of the forest cover variables.

However, the least forested stream (7) had among the highest LWD standing crop of

71

streams studies. This stream has highly unstable banks and nearly all of the wood in it comes from mass wasting of banks and bank trees. We suggest that a different mechanism (bank instability) was operating to explain the LWD standing crop at stream 7 compared to other sites, so we removed stream 7 from analyses. LWD surface area (total m^2 for 50 m reach) at the remaining six stream sites was positively related to watershed forest cover (Table 3.2).

Gut contents vs. Forest cover

Plant matter (leaf and woody material) was the predominant component of crayfish guts at all sites followed by animal matter and amorphous detritus (Table 3.4); both diatoms and filamentous algae were rarely found and made up less than 1% of crayfish gut contents at each site. Plant matter in crayfish guts was positively related to fall CPOM standing crop (Fig 3.4), but not to overall CPOM standing crop ($p > 0.05$), perhaps because crayfish were collected in the fall. Increases in plant matter consumption came at the expense of animal matter consumption, which declined with CPOM standing crop ($p < 0.01$, $R^2 = 0.12$), but consumption of amorphous detritus did not vary with CPOM standing crop ($p > 0.05$). Crayfish gut content % plant matter also was positively related to watershed forest cover and network-scale riparian forest cover variables (Table 3.2), suggesting increased consumption of CPOM by crayfish with increasing CPOM availability and forest cover at large scales. Crayfish gut contents were not related to carapace length ($p > 0.05$, $n = 62$, length range: 1.2 – 3.9 cm), indicating no significant feeding shifts with age.

Stenonema gut content % algae (mostly diatoms but some filamentous algae)

ranged from 23.9 – 58.4 % and averaged 36.1 ± 3.4 % while amorphous detritus averaged

63.9 ± 3.4 % (mean ± S.E.) in study streams. Algae (%) in *Stenonema* guts was

negatively related to canopy cover but not to any other riparian forest cover variables

(Table 3.2). By applying assimilation efficiency corrections (10 %: amorphous detritus

and 30 %: diatoms and filamentous algae, Benke and Wallace 1980), we determined that

algae contributed 62.8 % while amorphous detritus contributed 37.2 % of organic matter

assimilated by *Stenonema* in study streams. Based on these percentages, we concluded

that *Stenonema* in these streams were not likely to be accurate isotopic proxies for algae,

but rather represent what consumers assimilate from epilithon.

Stable Isotopes vs. Forest cover

Terrestrial CPOM was the most δ^{13}C depleted of all basal resources sampled (Table 3.3).

Basal resource type was a significant effect in ANOVA (blocked by stream) for both

δ^{13}C ($p< 0.0001$, df = 2, F = 96.47) and δ^{15}N ($p< 0.0001$, df = 2, F = 53.2), while stream

was not significant for either ($p>0.05$). Ryan's Q multiple comparisons test separated

each basal resource (CPOM, epilithon, and seston) as an isotopically distinct group for

both C and N isotopes. In addition, MANOVA, used to determine if basal resources

differed in dual isotope (C and N) bivariate space, showed a significant effect of basal

resource type (Wilk's Lambda statistic $p <0.0001$). Though algal isolation by density

gradient centrifugation was not consistent for all samples, effective isolation was

achieved for two samples. These two "pure algae" samples were several ‰ enriched in

^{13}C relative to CPOM (Table 3.3); therefore although epilithon values (determined from

Stenonema) were only slightly enriched relative to CPOM, we inferred that instream primary production resources were generally more ^{13}C enriched than CPOM in these streams. Seston δ^{13}C was most similar to the "pure algal" samples (Table 3.3), suggesting a large algal component in seston.

Generally, crayfish and insectivorous fish δ^{13}C were negatively related to forest cover indicating more positive signatures (divergence from CPOM) with less forest cover. Crayfish δ^{13}C was negatively related to CPOM standing crop, watershed forest cover, and network-scale riparian forest cover (Fig. 3.5 and Table 3.2), indicating divergence of crayfish δ^{13}C from CPOM δ^{13}C with reductions in CPOM and forest cover at large scales. Local scale riparian variables were not predictive of short-term (gut contents) or long-term (δ^{13}C) measures of crayfish diets.

Isotope signatures of the six sampled species of insectivorous fishes were combined into one consumer category as there were no significant differences in isotope signatures among species (ANOVA, $p > 0.05$). Similar to crayfish, insectivorous fish δ^{13}C showed significant negative relationships with watershed forest cover (Fig. 3.5) and two of the network-scale riparian forest cover variables (Table 3.2), indicating ^{13}C enrichment and thus divergence from terrestrial δ^{13}C with reductions in forest cover at large scales. Unlike crayfish, fish δ^{13}C was negatively related to canopy cover (Table 3.2), suggesting isotopic divergence of fish from terrestrial carbon sources with local riparian deforestation. In general, relationships between consumer δ^{13}C and forest cover had relatively low R^2 values.

Consumer Nitrogen Isotopes

Insectivorous fish δ^{15}N (9.91 ± 0.16 ‰, mean ±1 S.E.) was consistently several ‰

higher than crayfish (6.83 ± 0.23 ‰, mean ±1 S.E.), indicating a higher trophic position

for insectivorous fish than crayfish. Crayfish δ^{15}N was negatively related to fall CPOM

standing crop (p < 0.01, R^2 = 0.10), indicating enrichment in crayfish δ^{15}N with

reductions in CPOM availability. Enrichment in crayfish δ^{15}N signifies higher trophic

position, perhaps due to greater reliance on aquatic insect prey with reductions in CPOM

availability. Crayfish δ^{15}N was not related to measures of forest cover (p > 0.05).

However, δ^{15}N in food webs in this study may have been influenced by anthropogenic

nitrogen sources, as epilithon δ^{15}N and crayfish δ^{15}N were both positively related to

stream water total nitrogen ($NO_3^--N + NH_4^+-N$) concentrations (Fig 3.6). In addition,

crayfish δ^{15}N (p = 0.001, R^2 = 0.15) and fish δ^{15}N (p = 0.002, R^2 = 0.09) were positively

related to watershed impervious cover, and index of suburban land use, but not to

agricultural cover (p > 0.05).

Terrestrial Dependence: Mixing Model Results

Since epilithon isotope signatures (inferred from herbivore signatures) were quite

different from pure algae signatures (Table 3.3) and since herbivore guts were dominated

by amorphous detritus rather than algae (table 3.4), we did not use herbivores as an algal

proxy in mixing model calculations. Instead, we used "adjusted epilithon" signatures as

an algal proxy; the differences between the 2 pure algae samples and respective epilithon

signatures (Δ 2.43 δ^{13}C, Δ 1.43 δ^{15}N) were used as correction factors to adjust the

epilithon data for all sites. Isotope data for adjusted epilithon, CPOM, and consumers

were entered into the mixing model, which showed that both terrestrial and aquatic basal

food web resources were important in these headwater streams (Table 3.4). Crayfish and

fish showed similar dependence on terrestrial CPOM ranging from 44 – 76 % (crayfish)

and 41 – 70 % (fish) with an average of approximately 60 % for both consumer groups.

Of the several combinations of non-autocorrelated forest cover variables tested in

multiple regression analyses, the only variables that were significant predictors of

consumer dependence on CPOM were the two most local scale riparian variables: canopy

cover and 100 m reach mean buffer width. A multiple regression model using these two

factors explained 88 % of the variation in crayfish dependence on CPOM (Fig. 3.7A),

while canopy cover, the only significant explanatory variable for insectivorous fish

dependence on CPOM, explained 57 % of the variation (Fig. 3.7B).

Discussion

Our data suggest that riparian deforestation, even over a narrow range, decreases the

terrestrial support of headwater stream food webs. Two lines of evidence from our data

support this conclusion. First, deforestation was associated with ^{13}C enrichment of top

consumers, indicating isotopic divergence of consumers from terrestrial carbon with

deforestation (regression results). Second, dependence of consumers on terrestrial

CPOM decreased with local riparian deforestation (mixing model results). Relationships

between consumer δ^{13}C and forest cover were relatively weak (low R^2 values), but it is

notable that relationships spanned a wide range in scales of analyses from landscape

patterns to isotope patterns (which are ultimately controlled by molecular level

processes). Further, because of the detail in forest cover and food web characteristics obtained, we were limited in the number of sites feasible to study (n = 7).

The consumer ^{13}C enrichment (and divergence from CPOM δ^{13}C) we observed with increasing watershed and riparian deforestation could be explained by changing patterns of basal resource consumption in food webs. This mechanism relies on changes in the availability of basal resources with deforestation, which was documented for benthic CPOM. Standing crop of benthic CPOM was not related to local riparian variables, but declined with watershed and network-scale riparian deforestation. Consumption patterns within food webs may have shifted to higher dependence on basal resources that are ^{13}C enriched relative to CPOM (e.g. epilithon, pure algae, and seston) with reductions in CPOM and forest cover on large scales. In these same streams, we have documented a decline in the abundance of macroinvertebrate shredders with reductions in CPOM standing crop (England *et al.*, in prep.), a community shift that may have contributed to reductions in food web dependence on CPOM with deforestation at the network scale. A similar large scale relationship with riparian forest cover was demonstrated for suspended CPOM in a large river (Johnson & Covich 1997). The large spatial scale of the deforestation-benthic CPOM relationship in this study suggests that the dominant mechanism may be the larger-scale processes of transport and retention, not local CPOM inputs. Our data suggest that any effect of local riparian forest cover on CPOM inputs was obscured by larger scale forest cover effects.

Retention of organic materials is generally highest in headwater portions of river systems (Meyer & Wallace 2001, Gomi *et al.* 2002), and is controlled in large part by hydrology (Gurtz *et al.* 1988). Watershed deforestation, and resulting hydrologic

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alterations, can lead to greater particulate organic matter transport and lower retention

capacity in streams (Likens et. al 1970, Webster *et al.* 1990). Large woody debris is also

important to organic matter retention, especially in headwater streams (Bilby 1981,

Webster *et al.* 1994, Hedman *et al.* 1996). LWD standing crop in this study declined

with watershed deforestation; thus reductions in LWD retention of CPOM may be

partially responsible for the decline in CPOM standing crop with watershed deforestation.

In contrast with consumer $\delta^{13}C$, consumer dependence on CPOM (mixing model

results) was related only to the most local riparian variables, particularly canopy cover.

These results appear to be contradictory in terms of which scale of forest cover was

driving food web changes. We suggest that it is not a contradiction but rather that

different forest cover scales (large versus local) influenced different food web pathways

(heterotrophic vs. autotrophic pathways). Our data suggest that large scale forest cover

influenced food webs through the heterotrophic pathway through control of detrital

standing crops. We suggest that local canopy cover influenced food webs through the

autotrophic pathway. Canopy cover did not significantly influence standing crop of

allochthonous materials, but was inversely related to the proportion of algae in

Stenonema guts. This result suggests an increasing proportion of algae in epilithon with

decreasing canopy cover.

Consumer dependence on instream primary production (approximately 40 %) was

high considering that conventional stream theory predicts dominance by terrestrial

detrital support in headwaters with high canopy cover. A number of recently published

stable isotope analyses of aquatic food webs also report a larger than expected

contribution of autochthonous production to higher trophic levels based on the relative

magnitude of algal standing crop (Rosenfeld & Roff 1992, France 1995, Bunn *et al.*

1997, Thorp et. al 1998, Bunn *et al.* 1999, Lewis et. al 2001, McCutchan & Lewis 2002,

Thorp & Delong 2002).   Thus, even in systems where carbon budgets are dominated by

allochthonous materials such as headwater streams (Fisher & Likens 1973) and large

floodplain rivers (Lewis *et al.* 2001), autochthonous production may be important due to

higher nutritional quality and assimilation efficiencies (Cummins 1974, Rosenfeld &

Roff 1992).

Enrichment in ^{13}C for several food web components (algae, herbivores, collectors,

and fish) has been demonstrated with increasing watershed area (Finlay 2001), which is

one measure of position within the continuum of river systems. In general, increasing

watershed area is associated with reduced terrestrial inputs per unit area of stream bed

(Vannote *et al.* 1980) and increased algal productivity, which may lead to enriched algal

communities (Finlay 2001). Due to the intentionally narrow range in watershed area, we

did not find strong relationships between ^{13}C and watershed area. However, our results

suggest that deforestation may result in food webs that function more like downstream

reaches (i.e. larger watershed area). Specifically, CPOM standing crop and reliance of

food webs on terrestrial subsides declined while consumer δ^{13}C enrichment and diverged

from CPOM δ^{13}C with increasing deforestation. These findings bear out a prediction

made by the authors of the RCC who suggested that human impacts may alter the degree

of autotrophy or heterotrophy of a stream and may potentially result in longitudinal shifts

in the river continuum (Vannote *et al.* 1980). Borrowing from a term common in

ecological competition literature ("apparent competition", Bonsall & Hassell 1997)

"apparent continuum shifts" may be described as changes in stream ecosystem structure

that cause a stream reach to appear like more upstream or downstream positions in the river continuum. Apparent continuum shifts with deforestation have been previously shown for stream community structure such as the replacement of endemic highland fish species with lower elevation cosmopolitan fish species in the southern Appalachians (Scott & Helfman 2001). Our study showed apparent continuum shifts in stream food web energy base with reductions in riparian forest cover.

The ^{15}N enrichment observed in epilithon and crayfish with increasing streamwater N concentration and suburban land use suggests that there may be anthropogenic sources of nitrogen being incorporated into these stream food webs. Streamwater nitrate ^{15}N enrichment in urban and agricultural catchments has been attributed to several anthropogenic N sources that are ^{15}N enriched relative to atmospheric and soil nitrogen, including human sewage, manure, and fertilizer (Mayer *et al.* 2002). These ^{15}N – N concentration relationships may have introduced complications into the use of a mixing model with isotope data. However, it is unlikely to have caused substantial error because the mixing model calculates importance of basal resources based not on the absolute isotope values of consumers, but instead on the differences between basal resources and consumer isotope values in each individual stream. Also, streamwater N concentration was not related to the regression analysis factors (canopy cover, MBW100, and % dependence on CPOM, $p > 0.05$), so N concentration was probably not confounding in this analysis.

One limitation of this study was the small number of study sites and the narrow range of riparian and watershed forest cover examined; future work should address a wider range in deforestation. Nevertheless, the findings of this research suggest the

importance of forest cover at multiple scales ranging from local canopy cover to watershed forest cover. Multiple-scale analyses are becoming more prevalent in stream research due to the recognition that processes governing stream and riparian structure and function may be hierarchically arranged (Allan & Johnson 1997, Johnson & Covich 1997, Poole 2002). For example, Johnson & Covich (1997) propose that the mechanisms governing distribution of suspended detritus vary by scale. Unfortunately, one deficiency in many multiple-scale analyses is the lack of resolution in spatial data needed to make comparisons of the relative importance of local versus large scales. Many studies on the impacts of land cover on lotic systems acquire their land cover data from satellite images (Landsat TM) that have a spatial resolution of 30 meters (e.g. Sponseller & Benfield 2001). The percent error associated with assessing local riparian land cover is much greater than the percent error associated with assessing watershed land cover using such coarse resolution images. In other words, with a given spatial resolution, land cover classification error is inversely proportional to the area of land being analyzed, making it difficult to compare the predictive ability of land cover across different scales. Consequently, one strength of this study is the high resolution of spatial data (1-2 m), which is more appropriate for comparing the strength of relationships between land use and instream responses across multiple spatial scales. We recommend that future studies linking riparian land use with stream ecosystems be careful to select spatial data with resolution appropriate to the scale(s) of questions pursued.

Previous work has highlighted the importance of riparian subsidies in maintaining productivity of headwater streams draining forested catchments (Wallace *et al.* 1999). Our study provides evidence that a narrow range in headwater riparian deforestation can

lead to reduced dependence of headwater food webs on subsidies of terrestrial food resources. With reductions in riparian forest cover, headwater food webs may function more like higher order, downstream reaches where there is naturally less canopy cover and greater autochthonous production. Headwater streams, which make up nearly 75 % of stream miles in the United States (Leopold *et al.* 1964), play vital roles within the continuum, and are tightly linked in several ways to downstream systems (Webster *et al.* 1999, Meyer & Wallace 2001, Gomi et. al 2002). It is unknown how altered headwater food webs may affect downstream linkages and potentially fragment the river continuum. Further, our data suggest that watershed forest cover is also important for its role in governing availability and retention of allochthonous resources in headwater streams. Therefore, protection of both riparian and watershed forest cover, not just narrow riparian buffers, may be warranted in order to preserve terrestrial-aquatic linkages that are important in supporting native headwater stream food webs and their role within the continuum of river systems.

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Table 3.1. Summary characteristics for streams studied in the Upper Chattahoochee River basin, Georgia, USA, April 2000 - September 2002. Includes physical characteristics and results of land cover classification of study watersheds and riparian buffers. Streams are ordered left to right by watershed % forest cover.

Land use and summary characteristics	Abbreviation	Stream						
		1	2	3	4	5	6	7
Watershed								
% Forest	FWS	96.3	94.3	91.2	90.6	89.8	88.4	82.5
% Agriculture	AGWS	2.2	5.1	6.3	6.5	7.8	8.8	15.7
% Impervious	IMWS	1.5	0.6	2.5	2.9	2.4	2.8	1.8
Mean buffer width (ft)								
100 m reach	MBW100	84.5	92.5	71.0	100.0	94.2	91.6	97.4
1000 m reach	MBW1000	95.2	71.6	80.8	92.8	81.5	75.1	33.7
Entire network	MBW	96.5	91.5	85.8	92.5	87.9	83.6	56.8
Continuity of (%)								
Canopy cover	CONTIN-CC	100.0	97.6	96.4	100.0	95.0	95.3	63.2
Buffer > 100 ft	CONTIN-BW	92.5	86.2	79.1	84.5	81.2	77.5	52.3
Summary characteristics								
Mean width (m)		3.6	2.1	1.5	1.2	4.7	2.0	2.2
Mean depth (m)		0.12	0.12	0.10	0.11	0.19	0.13	0.11
Gradient (m/m)		0.006	0.015	0.016	0.014	0.015	0.013	0.013
Elevation (m)		499	517	533	482	431	465	432
Substrate D_{50} (mm)		29	39	30	13	120	20	43
Watershed area (km^2)		3.90	2.67	1.85	1.94	7.17	3.21	2.37
Canopy cover (%)		81.4	85.3	87.7	81.9	77.2	85.5	88.7
Total N (mg/L)		0.043	0.252	0.135	0.269	0.133	0.144	0.107

Table 3.2. Results of simple linear regression analyses. Direction of effect for relationships is noted by (+) or (-) followed by the coefficient of determination, R^2. Significant p-values are indicated by asterisk (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$), and non-significant results are indicated by ns. Percent variables were arcsin-squareroot transformed and network mean buffer width was cosine transformed to meet assumptions of normality for regression analyses. Only 6 sites were used for LWD analyses; see Results for rationale. Negative relationships between consumer $\delta^{13}C$ and land use variables indicate isotopic divergence from terrestrial CPOM $\delta^{13}C$ with increasing watershed or riparian deforestation, whereas positive relationships indicate movement towards terrestrial CPOM $\delta^{13}C$ with deforestation.

	Local scale riparian variables			Stream network-scale riparian variables			Watershed
Dependent variables	Canopy	Mean buffer width: stream length			Continuity of		Scale
	Cover	100m	1000 m	Network	Canopy	Buffer > 100 ft	% Forest
Allochthonous resources							
Habitat-weighted CPOM							
Overall	ns	ns	ns	(+) 0.21 ***	(+) 0.46 *	(+) 0.58 *	(+) 0.46 *
Fall	ns	ns	ns	(+) 0.38 ***	ns	ns	(+) 0.60 *
LWD surface area	ns	ns	ns	ns	ns	ns	(+) 0.76 *
Gut contents							
Crayfish guts							
% Plant matter	ns	ns	(+) 0.06 *	(+) 0.09 *	(+) 0.06 *	(+) 0.11 **	(+) 0.16 **
Stenonema guts							
% Algae	(-) 0.21 *	ns	ns	ns	ns	ns	ns
Consumer $\delta^{13}C$							
Crayfish	ns	ns	ns	(-) 0.23 *	(-) 0.09 *	(-) 0.09 *	(-) 0.15 **
Insectivorous fish	(-) 0.07 *	ns	ns	(-) 0.15 ***	(-) 0.05 *	ns	(-) 0.08 **

Table 3.3. Stable carbon (A) and nitrogen (B) isotope signatures of basal resources (site mean ± 1 S.E.). Epilithon was inferred from *Stenonema* signatures corrected for trophic fractionation. "Pure algae" are two samples for which algal isolation was successful using density gradient centrifugation. Using ANOVA blocked by stream, we determined that basal resource type (not including pure algae because of inadequate sample size) was a significant effect for $\delta^{13}C$ (p < 0.0001, df = 2, F = 96.5) and $\delta^{15}N$ (p < 0.0001, df = 2, F = 53.2). Ryan's Q multiple comparisons test showed that these three basal resources were isotopically distinct from each other for both C and N isotopes (a, b, c, denotes groupings from this test). FWS = % forest in watershed, ND= no data due to analytical error.

A) $\delta^{13}C$

			Basal Resource $\delta^{13}C$		
Stream	FWS	CPOM	Epilithon	Seston	Pure Algae
1	96.3	-29.17 ± 0.15	-27.13 ± 0.79	-22.88 ± 0.87	-24.19
2	93.6	-27.84 ± 0.07	-28.76 ± 0.26	-24.60 ± 0.55	
3	91.3	-27.23 ± 0.10	-27.55 ± 0.30	-23.24 ± 0.47	
4	90.7	-28.33 ± 0.29	-27.04 ± 0.28	-23.15 ± 0.38	
5	88.8	-29.25 ± 0.16	-26.65 ± 0.22	-25.95 ± 0.19	-24.73
6	88.1	-28.75 ± 0.30	-28.43 ± 0.33	-23.93 ± 0.43	
7	82.6	-29.52 ± 0.28	-29.82 ± 0.27	-21.76 ± 1.17	
Mean		-28.57 ± 0.19	-27.84 ± 0.23	-23.64 ± 0.25	-24.46
		a	b	c	

B) $\delta^{15}N$

			Basal Resource $\delta^{15}N$		
Stream	FWS	CPOM	Epilithon*	Seston	Pure Algae
1	96.3	-1.47 ± 0.10	1.89 ± 0.16	6.23 ± 3.74	2.71
2	93.6	-1.01 ± 0.42	3.90 ± 0.28	ND	
3	91.3	-0.47 ± 0.68	2.01 ± 0.33	7.48 ± 1.29	
4	90.7	1.30 ± 0.56	6.54 ± 0.53	6.35 ± 2.24	
5	88.8	-0.67 ± 0.62	4.24 ± 0.09	ND	6.27
6	88.1	-2.60 ± 0.62	3.04 ± 0.25	7.40 ± 2.97	
7	82.6	-0.63 ± 0.35	1.41 ± 0.10	5.25 ± 1.82	
Mean		-0.79 ± 0.29	3.25 ± 0.28	6.54 ± 0.99	4.49
		a	b	c	

Table 3.4. Trophic analyses for top consumers based on gut contents and dual isotope mixing model calculations. Diatoms and filamentous algae were found in some crayfish guts, but made up less than 1% by area at each site. Seston was used as an isotopic proxy for algae because isotopic similarity with two pure algae samples suggested a large algal content. Streams are ordered by watershed % forest cover (FWS).

		Gut Content Analysis			Mixing Model Results			
		Crayfish			Crayfish		Insectivorous fish	
		% Plant	% Animal	% Amorphous	% dependence on		% dependence on	
Stream	FWS	matter	matter	detritus	CPOM	algae	CPOM	algae
1	96.3	74.2	15.4	10.4	43.8	56.2	41.7	58.3
2	93.6	76.4	14.8	8.8	47.9	52.1	43.3	56.7
3	91.3	81.3	11.4	7.3	45.8	54.2	30.6	69.4
4	90.7	39.1	26.0	34.5	55.3	44.7	33.8	66.2
5	88.8	62.2	6.0	30.5	46.2	53.8	32.5	67.5
6	88.1	51.1	38.9	10.0	61.9	38.1	40.1	59.9
7	82.6	44.4	32.8	22.7	55.3	44.7	36.0	64.0
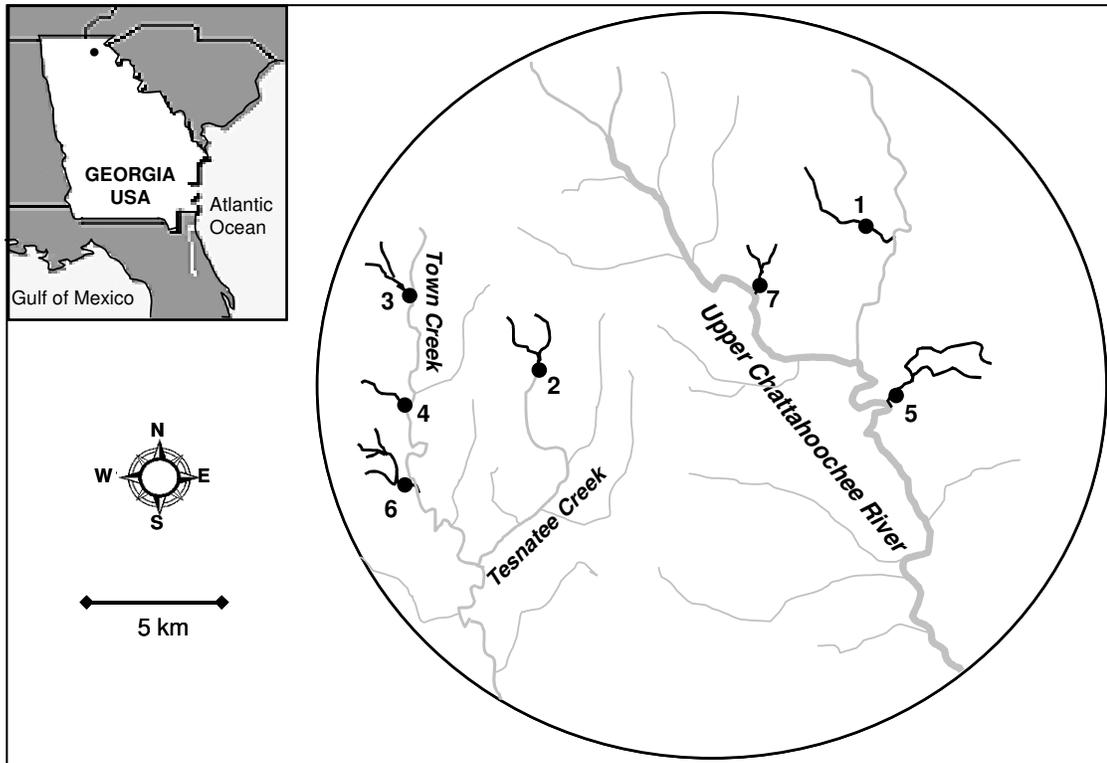
Figure 3.1. Map of study stream locations (1-7 in order from most to least forested watersheds) in the Upper Chattahoochee River basin, Georgia, USA. Town Creek flows into Tesnatee Creek, which flows into the Chestatee River and eventually into the Upper Chattahoochee River. All study sites are within the Blue Ridge physiographic province at the southernmost extent of the southern Appalachians. See Appendix A for names and GPS coordinates of sites.
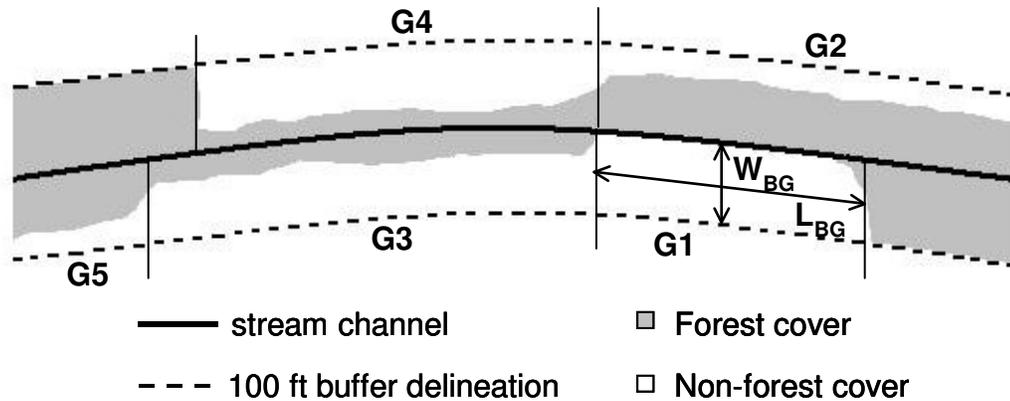
Figure 3.2. Schematic illustrating how buffer gap measurements were made along a hypothetical stream reach. Areas within the 100 ft buffer delineation without forest cover were considered buffer gaps, shown as white areas. The two sides of each stream were analyzed separately as forest cover often varied considerably from one side to the other. For each gap (here G1-G5), a gap width (W_{BG}) and length (L_{BG}) were measured. Gaps along the entire stream network above the sample reach were measured and these data were used to calculate riparian forest cover width and continuity metrics at multiple scales
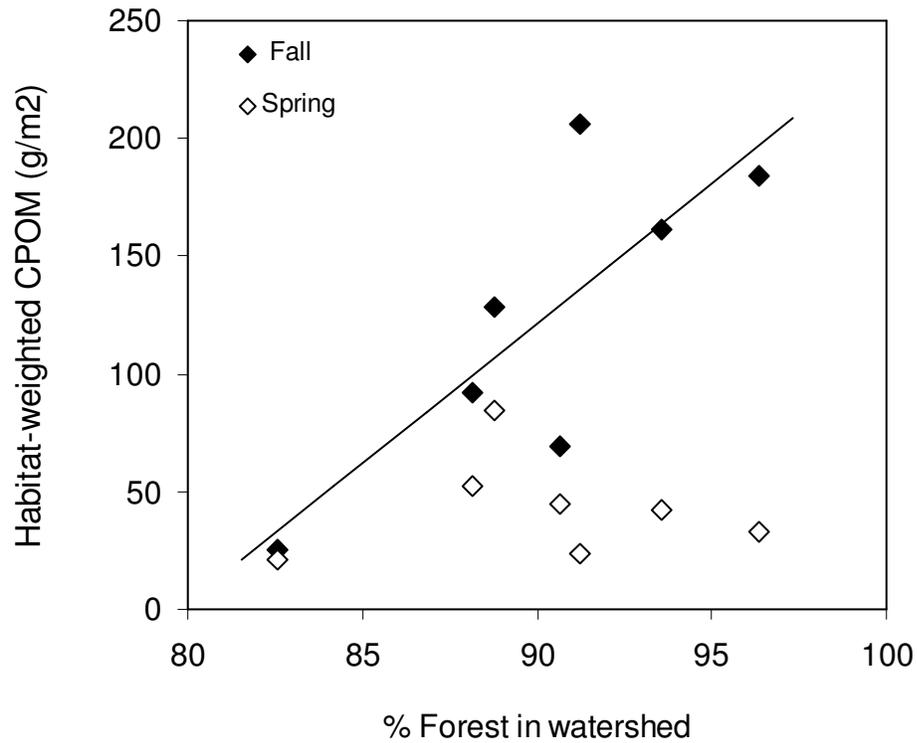
Figure 3.3. Linear regression analyses showed that fall CPOM standing crop was positively related to watershed forest cover ($p < 0.05$, $R^2 = 0.60$) while spring CPOM standing crop was not. CPOM standing crop variables are sums of habitat-specific CPOM standing crop weighted by the % stream bed area in each habitat type (pool/riffle/run). Percentage variables are graphed untransformed for ease in visual interpretation, but statistics apply to arcsin-squareroot transformed data.

Figure 3.4. Results of linear regression analyses for crayfish gut contents showing that as CPOM availability increased, crayfish consumed more plant matter ($p < 0.0001$, $R^2 = 0.28$). Error bars are ± 1 standard error and line indicates significant regression. Percentage variables are graphed untransformed for ease in visual interpretation, but statistics apply to arcsin-squareroot transformed data.
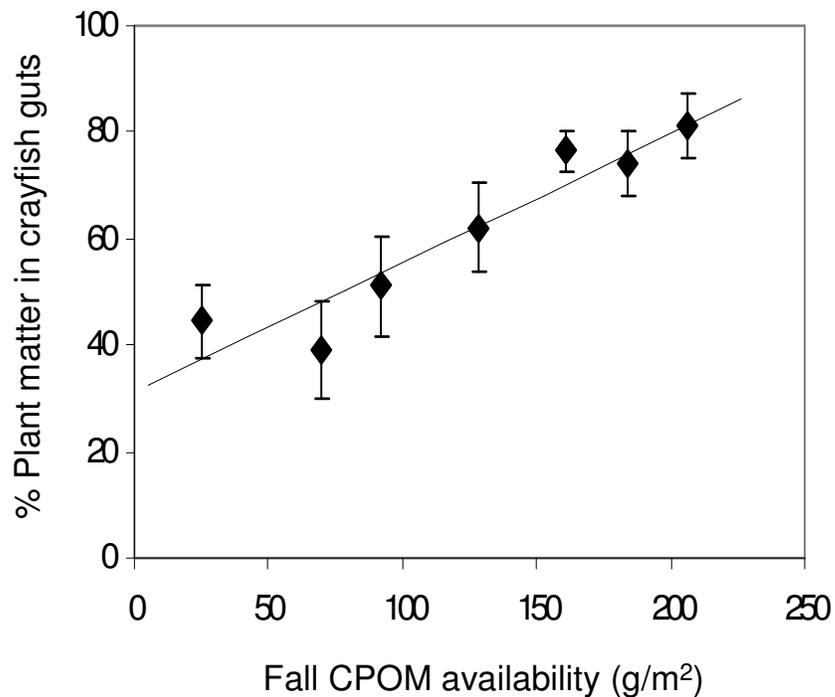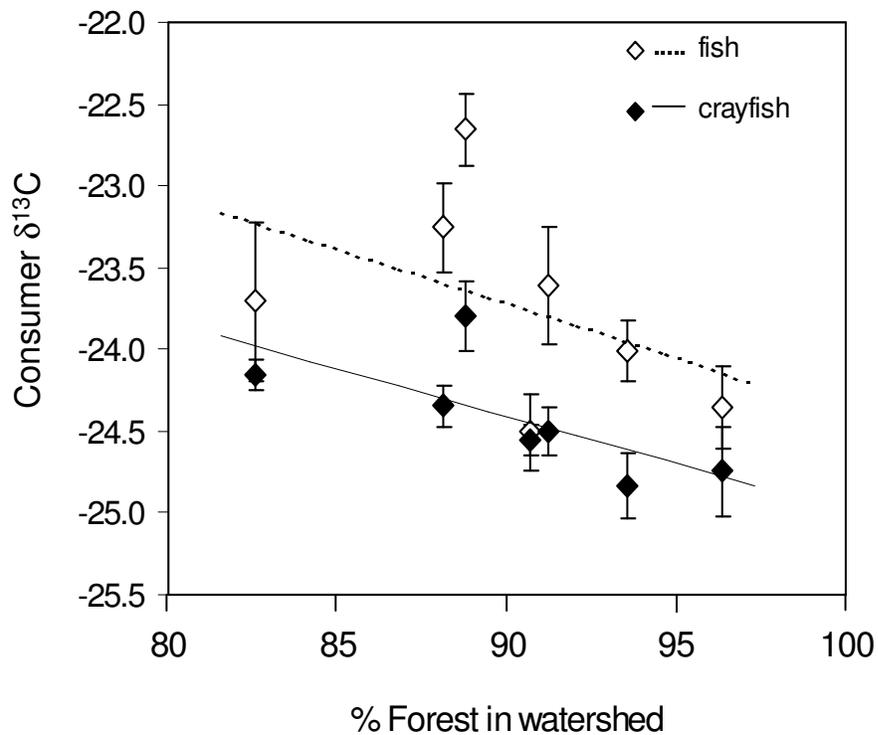
Figure 3.5. Consumer $\delta^{13}C$ signatures showed significant depletion with increasing

watershed forest cover. Examined in terms of increasing deforestation, consumer $\delta^{13}C$

showed enrichment. This indicates consumer divergence from $\delta^{13}C$ of terrestrial CPOM,

the most depleted food web component (mean CPOM $\delta^{13}C$ = -28.57) with deforestation.

Consumer $\delta^{13}C$ also showed enrichment with network scale riparian forest cover (Table

3.2). Error bars are ± 1 standard error and lines indicate significant regressions (crayfish:

$p < 0.01$, $R^2 = 0.15$, fish: $p < 0.01$, $R^2 = 0.0.08$).
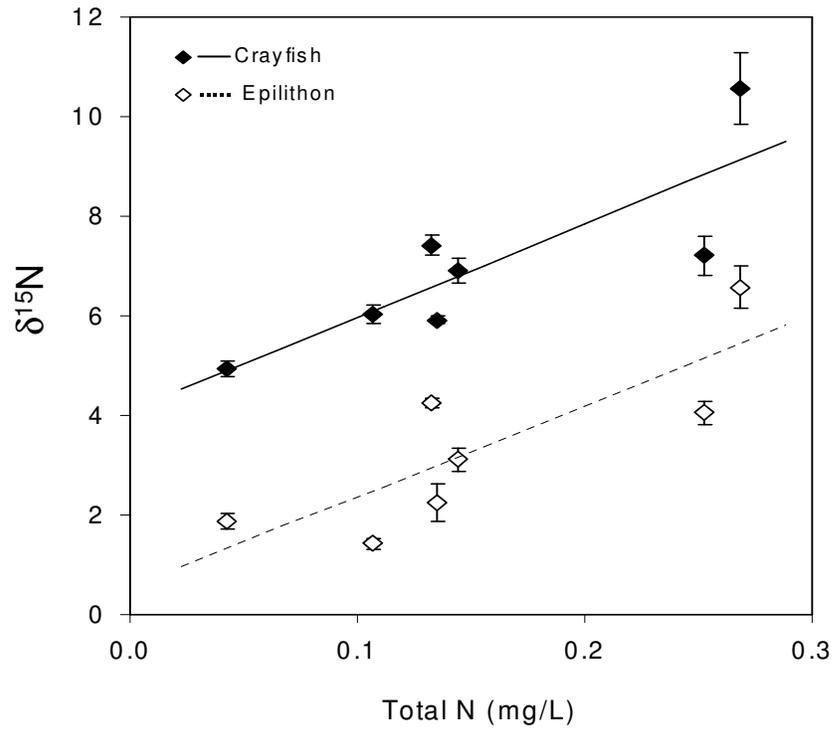
Figure 3.6. Crayfish and epilithon $\delta^{15}N$ showed significant enrichment with increasing

streamwater total nitrogen ($NO_3^--N + NH_4-N$). Epilithon $\delta^{15}N$ was determined by

correcting herbivore (*Stenonema* spp.) $\delta^{15}N$ for trophic fractionation. Error bars are ± 1

standard error and lines indicate significant regressions (crayfish: $p < 0.05$, $R^2 = 0.61$,

Stenonema: $p = < 0.05$, $R^2 = 0.63$).
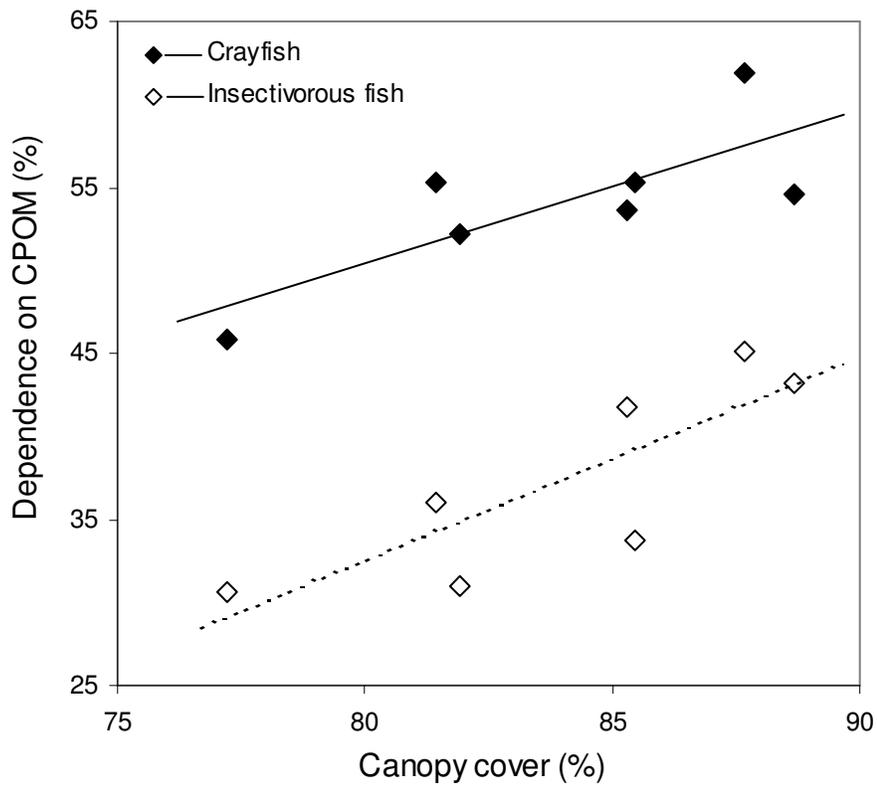
Figure 3.7. Dependence of consumers on CPOM as a basal resource as a function of local riparian canopy cover. Both top consumer categories showed decreasing dependence on terrestrial organic matter with declines in canopy cover (crayfish: p = 0.04, $R^2 = 0.59$, fish: p = 0.02, $R^2 = 0.69$). Dependence on CPOM was calculated using a mixing model. Percentage variables are graphed untransformed here for ease in visual interpretation, but statistics apply to arcsin-squareroot transformed data.

CHAPTER 4

SUMMARY AND CONCLUSIONS

Summary

The strong connectivity that exists between terrestrial and aquatic ecosystems
means that anthropogenic alterations of landscapes will unavoidably affect stream and
river systems. Land cover modifications on multiple scales have proven detrimental to
water quality, instream habitat, and aquatic assemblages (Roth et al. 1996, Wang et al.
1997, Jones et al. 1999, Scott and Helfman 2001, Scott et al. 2002, Sutherland et al. 2002,
Roy et al. 2003). Unfortunately, watershed land use disturbance is almost certainly
inevitable because of needs of societal and economic systems. However, freshwater
ecosystems are also vital to societies and economies because of the millions of dollars in
ecosystem services they provide to society each year (Wilson and Carpenter 1999).
Consequently, protection and management of riparian landscapes is critical to prevent
degradation of valuable freshwater ecosystems.

Effective riparian management requires identification of riparian buffer attributes
(e.g. scale, width, continuity) that most influence instream conditions relevant to aquatic
life. Poff's (1997) conceptual model of hierarchically scaled habitat filters provided a
useful framework for considering this multi-scaled question. Network scale riparian
forest cover explained significant amounts of variation in several instream
physical/chemical variables. Streams with wider, more continuous riparian forest cover

had cooler temperatures, less diel and annual temperature fluctuation, greater substrate heterogeneity, and higher availability of terrestrial organic matter (mostly leaf litter).

Streams with greater substrate heterogeneity and more abundant leaf litter in turn supported greater biotic integrity. Macroinvertebrates assemblages associated with these habitat conditions were higher in overall diversity and diversity of sensitive EPT taxa (mayflies, stoneflies and caddisflies) and scored better on biotic integrity indices. Fishes, especially native species, were more abundant in streams with abundant leaf litter. These relationships, along with ordination results, suggest that network scale riparian forest cover was a prominent factor shaping physical/chemical habitat conditions that were most relevant to stream biota. Watershed impervious cover was also influential through a positive relationship with percentage fine sediment in riffles, which in turn had negative impacts on fish species richness and the abundance of benthic feeding fishes. Historical land use also proved relevant, as 1938 valley deforestation better explained bank erosion than current land cover patterns, and abundance of both macroinvertebrates and fishes declined with bank erosion.

Food web dynamics, examined using stable isotopes techniques, were also related to riparian forest cover. Carbon isotope signatures of top consumers, crayfish and insectivorous fish, diverged from signatures of terrestrial leaf litter with increasing riparian deforestation at the network scale. This divergence suggests a diminishing reliance of top consumers on leaf litter as a basal food web resource with increasing riparian deforestation. Analysis of crayfish gut contents showed that these omnivores fed less on leaf litter with the reductions in availability of leaf litter that accompanied network scale riparian deforestation. The relative dependence of crayfish and fish on

terrestrial vs. aquatic basal resources, calculated using an isotope mixing model, showed that both leaf litter and algae were important basal resources. However, consumer dependence on leaf litter decreased with reductions in local riparian forest cover. These results suggest the importance of forest cover at several scales, and that headwater riparian deforestation may lead to reduced dependence on terrestrial subsidies.

In summary, continuous and wide (> 100 ft) corridors of riparian forest cover throughout stream networks may be necessary for lateral connectivity of terrestrial-aquatic linkages that are important in supporting food webs and biotic integrity in headwater communities. Furthermore, protection of wide and continuous buffers also promotes conservation of riparian forests as terrestrial ecosystems. This is a valuable goal in itself, given that riparian corridors are among the most diverse, complex, and threatened of all terrestrial ecosystems (Naiman et al. 1993).

Conservation Implications: 50 vs. 100 ft buffers on Georgia Trout Streams

While establishing the importance of riparian forest cover may be relatively straightforward, riparian buffer policy and management decisions are rather complicated since they must balance ecological values with societal and economic values. In the case of buffer policy on Georgia trout streams, ecological stakes are quite high since Georgia is within a regional hotspot for freshwater biodiversity (Lydeard and Mayden 1995). Further, societal valuation of high quality streams in this region is tremendous because of their ability to support recreational trout fisheries. Local economies have developed around this resource; businesses supplying fishing gear and guides, inns and cabins, restaurants and other tourism supporting businesses are all dependent upon the continued

existence of trout fisheries. In Georgia, the total economic impact of all freshwater angling is estimated to be over one billion dollars annually, including expenditures, wages/salaries for associated jobs, and state taxes (USFWS 1996). Given that over 30% of the more than 30 million freshwater anglers in the U.S. fish for inland trout (Boyle et al. 1996), the economic impact of trout stream resources to the economy of Georgia cannot be ignored.

As far as many in Georgia are concerned, trout stream buffer policy ultimately comes down to a balance between two economic values: development versus trout fisheries. Riparian buffer width on trout streams must maximize protection of trout fisheries while minimizing limitation of development. It follows that the critical question is, what is the minimum buffer width that will still support trout fisheries? Prior to 2000, 100 ft buffers were required on Georgia trout streams, but a 2000 amendment to the state's Erosion and Sedimentation Control Act reduced buffer width requirements to 50 ft. Questions regarding the protective capacities of 50 ft vs. 100 ft buffers prompted this project and other research.

Georgia has three trout species, the native brook trout (*Salvelinus fontinalis*) the introduced brown trout (*Salmo trutta*) of European origin and the most abundant introduced rainbow trout (*Oncorhynchus mykiss*) of western U.S. origin (Epifanio 2000). Since trout are a coldwater fishery, water temperature is the primary habitat factor determining the capacity of a given stream to support trout (Barton et al. 1985, Kundell et al. 2001). Availability of drifting macroinvertebrate prey, sedimentation, water depth and cover may be important secondary habitat constraints (Eaglin and Hubert 1993, Habera and Strange 1993).

In 1996, 28 states reported that "thermal stress" was a threat to naturally reproducing trout populations (Epifanio 2000). In a study of trout streams in southern Ontario, Barton et al. (1985) found that 22 ℃ (trimean weekly maximum temperature) was a threshold discriminating streams that could support trout from those that could not. Similar results were found in Georgia in an assessment of trout biomass (rainbow and brown trout) and maximum water temperatures in 30 primary trout streams, or streams thought to support naturalized trout populations as opposed to stocked secondary trout streams (Kundell et al. 2001). This study established that a maximum 7-day average maximum (M7DAM) temperature above 21 ℃ does not support trout, 19 – 21 ℃ is marginal habitat (suitable for stocked trout but does not support trout reproduction), and below 19 ℃ supports both stocked trout and naturalized trout reproduction. Further, % forest cover in a 30 m riparian buffer (for entire upstream network) was a strong predictor of maximum water temperatures along with basin area and elevation (Kundell et al. 2001).

Since buffer policy typically regulates buffer width, not % forest cover, I analyzed maximum temperatures against buffer width metrics from my stream sites and used temperature thresholds established by Kundell et al. (2001) to identify buffer widths associated with trout habitat categories (supporting <19 ℃, marginal 19-21 ℃, and not supporting > 21 ℃). Buffer width metrics were significantly related to M7DAM water temperatures (Figure 4.1). Based on the regression equations, the M7DAM temperature associated with a mean buffer width of 50 ft is over 22 ℃, regardless of longitudinal scale of buffer metric (1000 m or entire stream). This suggests that 50 ft buffers are inadequate to provide thermal habitat conditions that support trout. Further, a mean

buffer width of 100 ft is associated with M7DAM temperatures above 19 ºC, so 100 ft buffers may only provide marginal trout habitat with little native reproduction.

Regression equations between M7DAM and mean buffer width were used to predict buffer width ranges that correspond to the three trout habitat categories (Fig. 4.2). This model predicts that a minimum of 80 ft buffers would be necessary to provide marginal trout habitat. Mean buffer width necessary to provide "supporting" trout habitat is most likely greater than 100 ft, but cannot be predicted with confidence because it is outside the range of the regression model's prediction capabilities. Since elevation and basin area have a strong influence on temperature (Kundell et al. 2001), this model only applies to streams with similar elevation (430-530 m) and basin area (1-8 km^2) to streams studied herein. However, these predictions of buffer width requirements may be on the conservative side since most trout streams have larger basin areas, and thus are likely to be warmer given the same buffer width as the small streams used to generate this model.

The deleterious effects of buffer gaps along stream networks is demonstrated in Fig 4.3. Even with 90 % stream length with a forested buffer of some width (i.e. < 10 % length with buffer gaps), the regression model in Fig 4.3a. predicts M7DAM temperatures higher than the 21 C threshold for trout habitat. Although the relationship in Fig. 4.3a is to some extent driven by one point, the trend is still apparent, though not significant, when looking at the remaining six streams (Fig. 4.3b). Buffer gaps on just a small percentage of the stream network were associated with temperatures that are considered marginal or not supporting trout habitat. This result suggests the critical importance of strict requirements for granting buffer variances to prevent the creation of buffer gaps.

To evaluate 50 ft buffers in terms of native biota, Table 4.1 provides a brief comparison of the stream sites with mean buffer widths of approximately 50 ft and 100 ft. Substrate diameter variation was twice as high in the 100 ft buffer site compared to the 50 ft buffer site. Availability of leaf litter (CPOM) associated with a 100 ft buffer was nearly five times higher than with a 50 ft buffer. This reduction may be severe enough to limit detritus based headwater food webs. Overall biotic integrity in the 50 ft buffer site was much lower than the 100 ft buffer site. Macroinvertebrate abundance, especially of abundance of sensitive taxa, was much lower in the 50 ft buffer site. Reductions in macroinvertebrates in the headwaters of trout watersheds could potentially affect the abundance of prey items drifting into downstream trout habitat. Diversity of macroinvertebrates in the 100 ft buffer site was twice that of the 50 ft site. Fish metrics, with the exception of species diversity, show similar patterns. The 50 ft buffer site had less than one third of the native fish abundance and a fraction of the benthic invertivore abundance seen in the 100 ft buffer site.

Thus, regardless of whether trout fisheries or native assemblages are the primary concern, 50 ft buffers are unlikely to be protective of instream biota in these headwater Appalachian streams. The former buffer requirement of 100 ft would provide better trout habitat, but still may not be sufficient to support strong naturalized or "wild trout" fisheries. Nevertheless, public demand for wild trout fishing opportunities is high; angler opinion surveys report that the majority of anglers support management for wild trout populations (Habera and Strange 1993). In summary, the cumulative impact of riparian deforestation on many such headwaters streams in trout watersheds may result in warming of downstream trout habitat above thermal tolerances for naturalized and even

stocked trout. Therefore, protection of wide riparian buffers along entire stream networks in trout watersheds is essential to protect this economically important fishery and the unique native stream communities in the southern Appalachians.

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Table 4.1. Comparison of stream sites with network scale mean buffer widths of approximately 50 ft and 100 ft. Substrate diameter variation has no units because it was calculated as a coefficient of variation. Macroinvertebrate and fish abundance and richness metrics are number of individuals and number of taxa, respectively, collected with an equivalent sample effort.

	MBW	
	56.8 ft	96.5 ft
Physical/Chemical Habitat		
Max 7-day max temperature (ºC)	22.7	19.6
Substrate diameter variation	0.76	1.59
CPOM (g/m^2)	23	101.5
Embeddedness index (1-4)	2.0	1.5
Macroinvertebrate assemblages		
Total abundance	77	142
Taxa richness	12	28
Shredder abundance	4	20
Sensitive taxa abundance	5	34
Fish assemblages		
Catch/shock time (number/sec)	0.08	0.14
Species richness	6	6
Native abundance	59	173
Benthic invertivore abundance	1	79
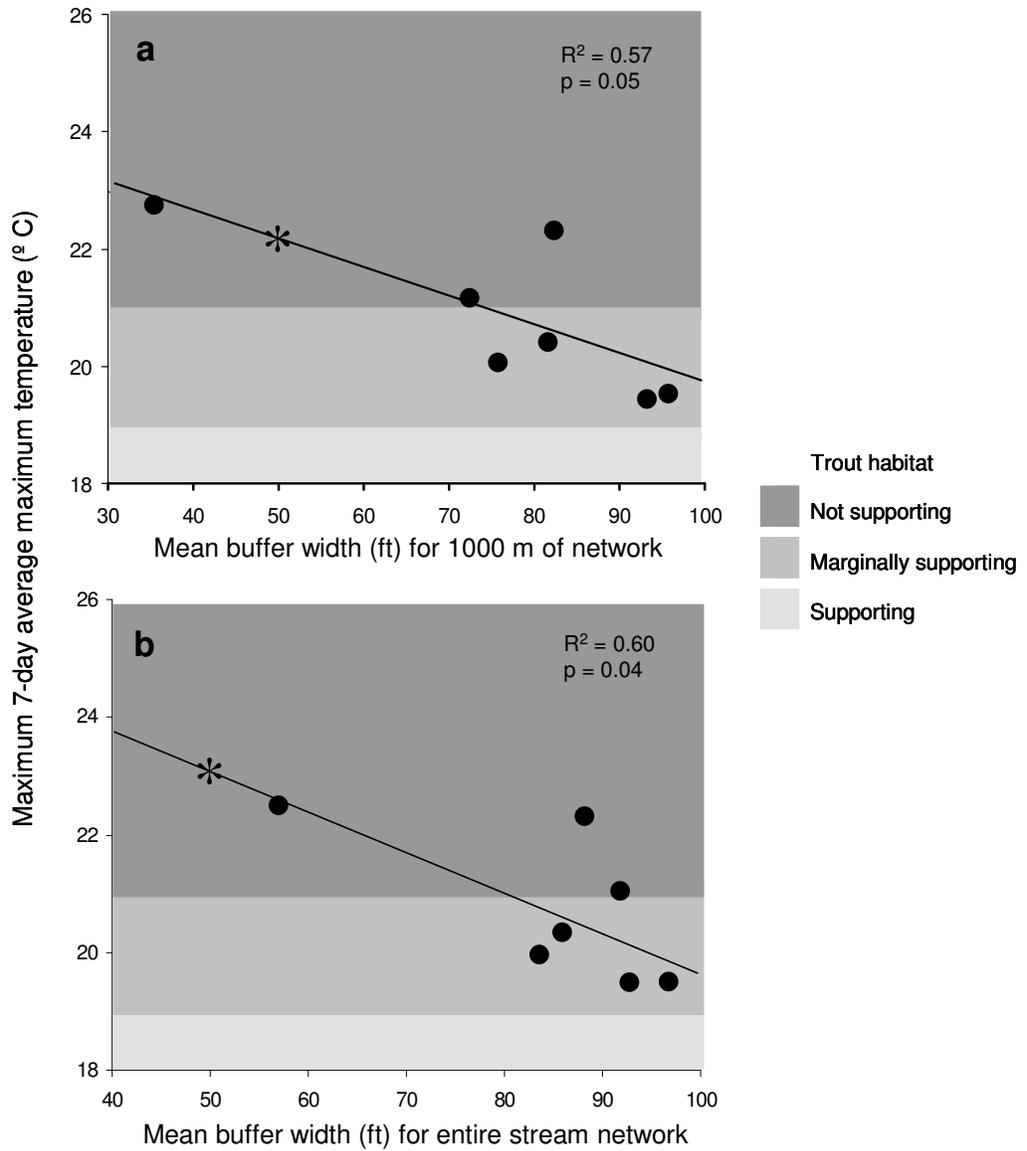
Figure 4.1. Relationships between maximum water temperatures and mean buffer width

for 1000 m of network (a) and entire stream network (b). Trout temperature thresholds

(Kundell et. al. 2001) are noted by grayscale. Asterisks note maximum temperature

predicted by regression equations for 50 ft buffers.
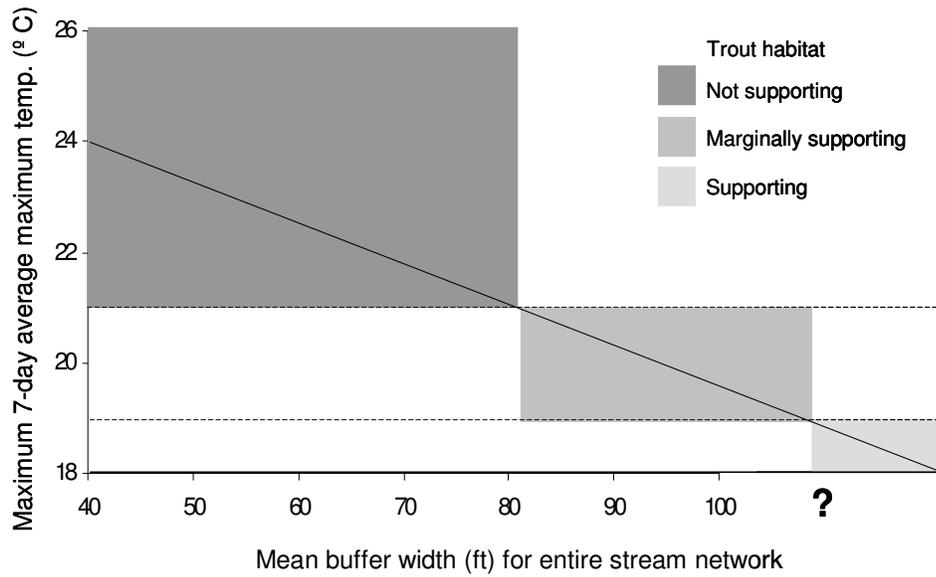
Figure 4.2. Prediction of buffer width ranges that will provide maximum temperatures corresponding to trout habitat categories based on regression relationship in Fig. 4.2. Mean buffer width necessary to provide "supporting" trout habitat is greater than 100 ft, but cannot be predicted with confidence because it is outside the range of the regression model's prediction capability.
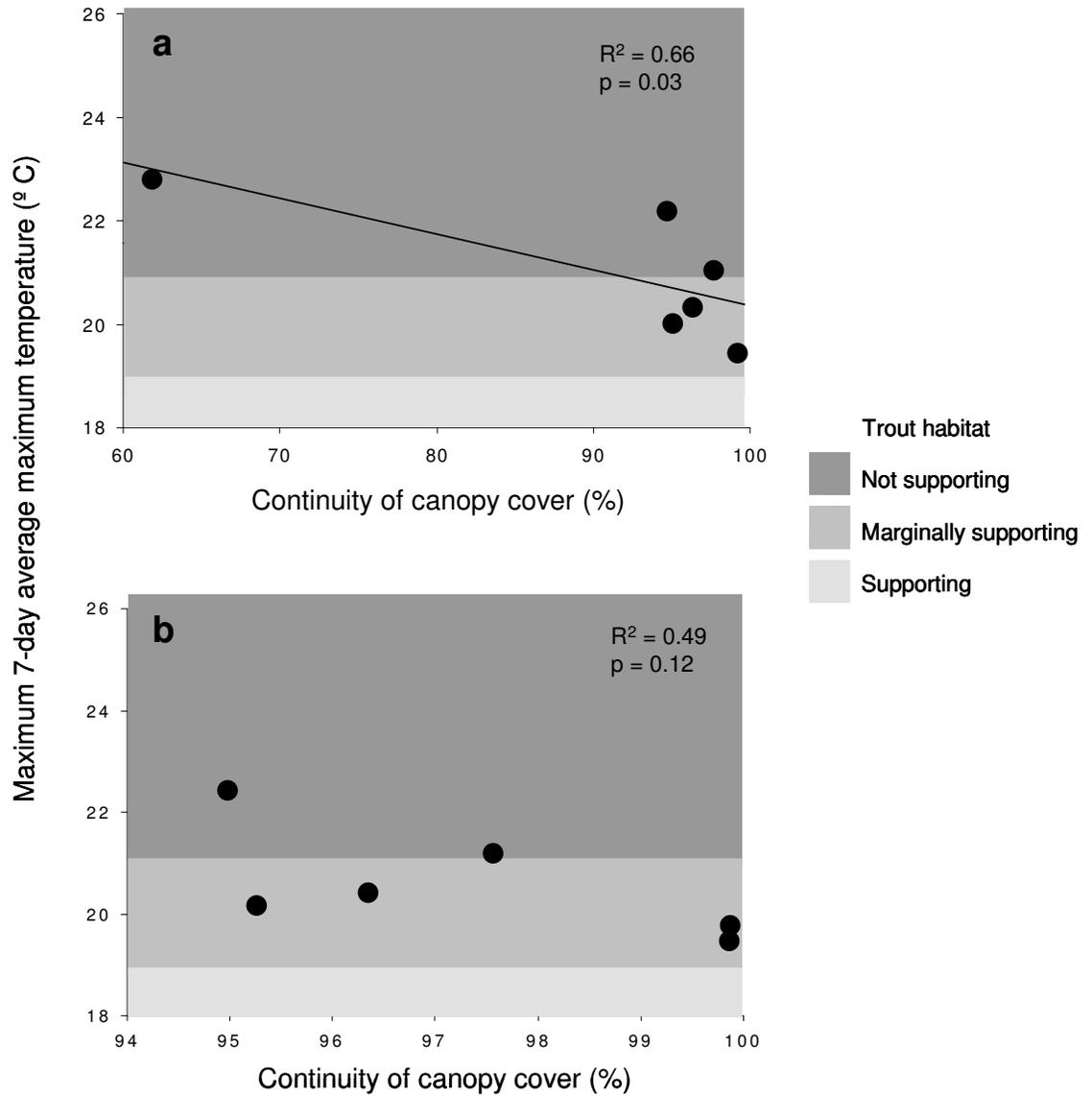
Figure 4.3. Relationships between maximum water temperatures and length of stream with a forested riparian buffer of some width (a). Bottom graph (b) shows the same relationship just for the six streams with greater than 90 % of stream length with forested buffer/canopy cover. Though the trend is not significant without inclusion of the seventh stream, it is visually clear. Trout temperature thresholds (Kundell et. al. 2001) are noted by grayscale.

APPENDICES

Appendix A. Names and coordinates of study stream sites.

Site ID	Stream Name	Site GPS Coordinates
1	York Creek	N 34' 43.441 min, W 83' 40.934 min
2	Cathey Creek	N 34' 39.345 min, W 83' 47.990 min
3	Town Creek tributary	N 34' 40.276 min, W 83' 51.270 min
4	Town Creek tributary	N 34' 38.496 min, W 83' 51.592 min
5	Maudin Mill Creek	N 34' 40.064 min, W 83' 38.875 min
6	Town Creek tributary	N 34' 36.803 min, W 83' 51.376 min
7	Bell's Creek	N 34' 41.958 min, W 83' 42.700 min

Appendix B. Descriptions of all variables measured and calculated for study streams.

Variable Category	Abbreviation	Units	Variable description (units)
Temperature †	M7DMAX01	°C	2001 maximum 7-day moving average maximum
	M7DMAX02	°C	2002 maximum 7-day moving average maximum
	ADMAX	°C	Mean daily maximum temperature
	ADMIN	°C	Mean daily minimum temperature
	MAT	°C	Mean annual temperature (April 2001-April 2002)
	OMT	°C	Overall mean temperature (April 2001 - September 2002)
	MDVAR	°C	Mean daily variation (mean of daily max - daily min)
	S01DVAR	°C	Summer 2001 mean daily variation (June-September)
	S02DVAR	°C	Summer 2002 mean daily variation (June-September)
	WDVAR	°C	Winter mean daily variation (December -March)
	MAXDMAX	°C	Maximum daily maximum
	MINDMIN	°C	Minimum daily minimum
	SVAR	°C	Seasonal variation (max daily max - min daily min)
	SMVAR	°C	Seasonal mean variation (max daily mean - min daily mean)
Chemistry	NO3N	mg/L	Nitrate-nitrogen concentration
	NH4N	mg/L	Ammonium-nitrogen concentration
	TOTALN	mg/L	Total nitrogen concentration (NO3-N + NH4-N)
	PO4P	mg/L	Phosphate-phosphorus concentration
	SPCOND	μS/cm	Specific conductivity
	DOAVG	mg/L	Mean dissolved oxygen (across 50 sample locations)
	DOMIN	mg/L	Minimum dissolved oxygen (across 50 sample locations)
Sediment	TURBAVG	NTU	Average turbidity (across 12 dates)
	TURBMAX	NTU	Maximum turbidity (across 12 dates)
	TURBCOVtime	na	Coefficient of variation in time (across 12 dates)
	TURBCOVspace	na	Coefficient of variation in space (across 15 locations)
	FINESGM2	g/m^2	Fine sediment / area of stream bed in g/m2 (average of 3 cores)
	EMBEDRIF	na	Riffle embeddedness (average of 30 observations)
	EMBEDRUN	na	Run embeddedness (average of 30 observations)
Substrate	CRCOARSE	%	Sediment core fraction of substrate > 64 mm diameter
	CR3264	%	Sediment core fraction of substrate 32-64 mm diameter
	CR1632	%	Sediment core fraction of substrate 16-32 mm diameter
	CRC816	%	Sediment core fraction of substrate 8-16 mm diameter
	CR48	%	Sediment core fraction of substrate 4-8 mm diameter
	CR24	%	Sediment core fraction of substrate 2-4 mm diameter
	CRFINE	%	Sediment core fraction of substrate < 2 mm diameter
	CTBDRK	%	Pebble count fraction of bedrock
	CTBLDR	%	Pebble count fraction of boulder
	CTCBBL	%	Pebble count fraction of cobble

	CTPBBL	%	Pebble count fraction of pebble
	CTGRVL	%	Pebble count fraction of gravel
	CTFINE	%	Pebble count fraction of fine sediment
	D_{16}	mm	Diameter of particle in 16th percentile
	D_{50}	mm	Median particle diameter
	D_{84}	mm	Diameter of particle in 84th percentile
Mesohabitat	PCPOOL	%	Percent of streambed in pool habitat
	PCRIFFLE	%	Percent of streambed in riffle habitat
	PCRUN	%	Percent of streambed in run habitat
	PCRIFRUN	%	Percent of streambed in riffle/run habitat
	DEPTHAVG	cm	Mean water depth (across 50 measurements)
	DEPTHMAX	cm	Maximum water depth (across 50 measurements)
	DEPTHCOV	na	Coefficient of variation for water depth (across 50 measurements)
	VELAVG	m/s	Mean baseflow water velocity (across 50 measurements)
	VELMAX	m/s	Maximum baseflow water velocity (across 50 measurements)
	VELCOV	na	Coefficient of variation for water velocity (across 50 measurements)
Geomorphic Stability	W:D	m/m	Width : depth ratio
	BANKANGLE	°	Bank angle (average of 5 measurements)
	PVEGBANK	%	Bank vegetation coverage
	TERSN	#	Total bank erosion observations (fluvial + mass wasting)
	LMWERSN	m	Length of bank mass wasting erosion in reach
	BANKMTRL	na	Bank material score (10 observations)
	BANKINSTAB	na	Bank instability index (10 observations, Simon and Downs 1995)
	$RBSD_{50}$	na	Relative bed stability at baseflow based on D_{50}
	$RBSD_{16}$	na	Relative bed stability at baseflow based on D_{16}
	GRADIENT	m/m	Stream gradient for 100 m reach
Allochthonous Resources	HABWTGM2	g/m^2	Habitat-weighted CPOM standing crop
	FHABWTGM2	g/m^2	Fall habitat-weighted CPOM standing crop
	SHABWTGM3	g/m^2	Spring habitat-weighted CPOM standing crop
	RTNTNCPOM	g/m^2	Retention of CPOM (fall - spring standing crop)
	LWDCT	#	Large woody debris count in 50 m reach
	LWDSA	m^2	Large woody debris surface area in 50 m reach
Visual Assessment	EPARBP	na	EPA Rapid Bioassessment Protocol
	SVAP	na	Stream Visual Assessment Protocol
Macroinvertebrate Assemblages	TOTAB	#	Total abundance
	TOTFAM	#	Total number of families
	TOTGEN	#	Total number of genera
	EPTTAXA	#	Number of EPT taxa
	EPTABUND	#	EPT abundance
	CHIRABUND	#	Chironomid abundance

	CFABUND	#	Collector-filterer abundance
	CGABUND	#	Collector-gatherer abundance
	PRABUND	#	Predator abundance
	SCABUND	#	Scraper abundance
	SHABUND	#	Shredder abundance
	SENABUND	#	Sensitive taxa abundance
	RBPTOL	na	RBP tolerance index
	BIBI	na	Modified Benthic Index of Biotic Integrity (Kerans and Karr 1994)
	NCBI	na	North Carolina Biotic Index (Lenat 1993)
Fish Assemblages	CUE	#/s	Catch per shock time
	NM2	#/m^2	Density of catch
	SPECIES	#	Species richness
	HENDABUND	#	Highland endemic abundance
	NATABUND	#	Native abundance
	BIABUND	#	Benthic invertivore abundance
	DIABUND	#	Drift invertivore abundance
	GIABUND	#	General invertivore abundance
	HABUND	#	Herbivore abundance
	CABUND	#	Carnivore abundance
Forest Cover and Land Use	WSAREA	km^2	Watershed area
	CANOPY	%	Local canopy cover
	MBW100	ft	Mean buffer width for 100 m reach
	MBW1000	ft	Mean buffer width for 1000 m of network
	MBW	ft	Mean buffer width for entire stream length
	CONTIN-CC	%	Continuity of canopy cover = % of stream length with buffer > 0
	CONTIN50	%	Continuity of 100 ft buffer = % of stream length with buffer > 50
	CONTIN-BW	%	Continuity of 100 ft buffer = % of stream length with buffer > 100
	F50BUFF	%	Forest cover in 50 ft buffer
	F100BUFF	%	Forest cover in 100 ft buffer
	FWS	%	Forest cover in watershed
	IMWS	%	Impervious cover in watershed
	AGWS	%	Agricultural cover in watershed
	VALDEF38	na	1938 Valley deforestation index (from 1938 aerial photos)
	RDDENS	km/km^2	Road density = length of roads per watershed area
	BDGDENS	#/km^2	Building density = buildings per watershed area
	RDXINGS	#	Road crossings in stream network

† Unless otherwise noted, temperature metrics calculated using all data collected from April 2001 - September 2002