

Biotic and abiotic responses to rural development and legacy agriculture by southern Appalachian streams

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Abstract

Streams are integrative systems spanning multiple spatial and temporal scales. Stream researchers, land-use managers, and policy decision makers must consider the downstream displacement of streams when approaching questions about stream ecosystems. The study of how anthropogenic land-use influences streams demands an ecosystem perspective, and this dissertation is an example of applying large scale analyses of stream reach responses, and linking the activity of humans in the landscape to stream structure and function. I investigate whether rural development and agriculture land-cover types influence abiotic and biotic stream responses. I establish a method for considering land-cover as an independent variable at multiple scales throughout a streams' watershed using hydraulic modeling. The travel time required for water to drain from the watershed to a stream reach provided a continuous index to delimit watershed sub portions along a spatial continuum. Within travel time zones (TTZs), I consider land-use at increasingly larger scales relative to a stream reach within which biotic responses are typically measured. By partitioning land-cover in TTZs, I was able to determine the spatial scale at which land-cover was most likely to influence in-stream responses. I quantified a suite of physical and biotic responses typical to the aquatic ecology literature, and found that streams did not respond much to rural development. Rural development influenced suspended and depositional sediments, and likely altered watershed hydrology though I was unable to find significant evidence supporting a hydrologic effect. Subtle differences in assemblages suggest that differences in sediment dynamics influenced macroinvertebrates and fish. Using the Land Cover Cascade (LCC) design, I link the influence of land-cover to biotic responses through a suite of multivariate models, focusing on sediment dynamics in an attempt to capture the subtle influence of hydrology and sediment dynamics. My dissertation provides future researchers with improved methods for considering land-cover as an independent variable, as well as introduces multivariate models that link land-cover to sediment dynamics and biota. My dissertation will assist future research projects in identifying specific mechanisms associated with stream responses to disturbance.

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Dedication

This dissertation is dedicated to my wife, Shauna, for providing the foundation upon which our lives are built and within which my personal achievements are rooted. Without her, I truly would not have been able to balance my personal and professional lives. I also dedicate this to our children, whose mere presence has enhanced every facet of my life, and who demanded that I maintain the healthy balance necessary for academe. Shauna, Ella, and Eva give meaning to everything I do, and my dissertation is only one example.

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Chapter 1: Introduction. Stream responses to anthropogenic land-cover change

*But now, says the Once-ler,
Now that you're here,
the word of the Lorax seems perfectly clear.
UNLESS someone like you
cares a whole awful lot,
nothing is going to get better.
It's not.
– Theodor Seuss Geisel in The Lorax.*

Stream ecosystems

Stream ecosystems are influenced by the landscapes through which they flow, and reflect the interaction of precipitation with landscape surfaces, soil interstices, and groundwater aquifers. Water passing through a stream reach has been exposed to, and potentially influenced by, watershed features ranging from soil nitrifying bacteria, landscape land-cover, to groundwater chemistry. Stream ecologists have recognized the multi-dimensional nature of streams and that streams interact with the terrestrial environment beyond their channels. The river continuum concept (Vannote et al. 1980) established the longitudinal nature of stream transport. Hynes (1983) and others have recognized the hyporheic zone as defining the vertical interaction of stream water and the semi-aquatic and terrestrial environments. Ward (1989) added that streams are necessarily temporal and can vary within daily, annual, and geologic periods. Contemporary stream research must address streams with respect to longitudinal, lateral, vertical, and temporal dimensions.

Given that stream ecosystems are complex, multivariate systems that span broad temporal and spatial scales, it becomes necessary to establish an ecologically relevant boundary within which research efforts can be focused. Stream watersheds provide realistic boundaries of influence that are defined by stream reaches where stream elements are measured. Ridge tops defining drainage areas within watersheds designate the zone of influence pertinent to stream reaches and the elements measured therein. Much of stream research has examined stream responses at the reach or local scale and has considered that responses are influenced by interactions occurring between stream reaches and watershed boundaries. Watersheds provide a

suitable framework for stream study because they span multiple spatial scales, include longitudinal, lateral, and vertical dimensions and evoke short and long-term time scales ranging from seconds to eons. Stream research that is focused within watersheds, therefore, assumes an ecosystem perspective whereby researchers must consider multiple interacting variables functioning along a broad spatial continuum.

The ecosystem perspective, however, complicates stream research due to the expansive spatial scales, variable resource-use interests, and multiple interacting variables that researchers and land-managers must consider (Carpenter and Kitchell 1988). In-stream variables are often defined at the local, habitat, or patch scales (i.e., within reaches), whereas watershed scale investigations require a landscape perspective. Stream responses can be affected at scales much larger than those on which researchers or managers often focus. Human influence to streams often occurs at the watershed scale, through land-use changes including agriculture or urbanization, which occupy a large percentage of a watershed's area. However, stream responses to anthropogenic activity are often not observable at the large scale, rather, landscape influence is often studied by scientists or land-managers at the reach scale. Ecosystem services, such as the provisions of drinking water or recreation, are observable somewhere within the spatial continuum between stream reaches and landscapes. Therefore, study of anthropogenic disturbance to streams requires an approach that spans multiple spatial scales.

Consideration of ecosystem scale disturbance requires a holistic consideration of the stream and terrestrial environment (i.e., the watershed ecosystem). Anthropogenic activity, current knowledge of interactions among key ecosystem elements, and an understanding of socioeconomic goals are necessary to fully address anthropogenic disturbance to streams. Relationships among stream responses and watershed-scale phenomena including human activity, stream ecosystem responses, and ecosystem services are summarized in Figure 1. My dissertation focuses on interactions among anthropogenic land-cover change, physical stream elements, and fish and macroinvertebrate community responses.

Anthropogenic land-cover change

Streams in the southeastern United States have been influenced by human activity since pre-European settlement (SAMAB 1996, Wear and Bolstad 1998). However, most significant influences have been associated with post-European human manipulation of landscapes (i.e.,

watershed land-use) to supply consumptive services including timber harvest, agriculture, and urban infrastructure. Humans have recently become concerned with how consumptive uses have influenced stream structure and function.

In the eastern United States, deciduous forest has historically occupied much of the landscape. Trees were initially harvested for direct use and to clear land for other uses, including agriculture and urbanization. Deforestation influence to streams has been well documented, and patterns of stream response to deforestation are predictable (Vesterby and Krupa 2001). Removal of watershed rooted vegetation decreases soil stability and induces erosion. In-stream sedimentation dynamics are altered by anthropogenic land-use, and often sedimentation has been described as the most significant human disturbance to streams (Trimble and Crosson 2000). Erosional sediments alter in-stream habitat, reduce hyporheic exchange, and decrease stream interstices, especially when deforestation is followed by agricultural activity.

Streamside agriculture has long influenced streams in the eastern United States (Ramankutty et al. 2002). Most streams in the eastern deciduous forest have been influenced by a combination of deforestation and agriculture. Agriculture activity essentially perpetuates in-stream erosion by continually disturbing watershed soils. Continual row-crop culture and livestock grazing prevent the succession of near-stream vegetation rendering near-stream soils susceptible to erosion. Row-crop agriculture also delivers excess nutrients and harmful chemicals associated with fertilizer and pesticide application. Agriculture influences streams through continual sedimentation and nutrient enrichment.

Urbanization and urban sprawl are landscape activities that also influence streams. Roads, houses, and parking lots decrease the watershed area available to natural processes. Soil infiltration, nutrient transformations, groundwater recharge, and other processes are interrupted by impervious surface cover (ISC), which effectively decreases the portion of a watershed where these processes can occur. Watershed hydraulic dynamics are often drastically altered by urbanization as compared to other land uses (Finkenbine et al. 2000). Streams influenced by urban activity experience higher peak flows, more frequent flooding, and greater irregularity in flow patterns. Urban streams are also susceptible to drying and flooding extremes (Paul and Meyer 2001).

The transformation of landscapes for rural development is an increasingly common form of anthropogenic landscape disturbance (Kent et al. 2000). The decrease of small-scale

agriculture supplies formerly unavailable land for other uses including rural development. Rural development brings roads, buildings, and sewage infrastructure to areas previously disturbed by soil tilling, fertilizer application, and livestock grazing. Rural development is similar to urban sprawl, but is unique because it often occurs in formerly agricultural land. Streams influenced by rural development may continue to reflect the influence of agriculture (i.e., legacy effects sensu Harding et al. 1998). My dissertation addresses the potential influence of rural development on watershed ecosystems.

Dissertation goals

I investigated whether rural development influences abiotic and biotic elements in streams that have been impaired by historical agriculture. This investigation addressed several objectives. My first objective was to determine the extent to which rural development influenced streams and is presented in Chapter 3. Because rural development often involves the transformation of formerly agricultural areas, I specifically investigated whether rural development influenced responses in southeastern U.S. streams that had been historically influenced by agriculture.

My second objective was to develop an ecologically meaningful method for subdividing watersheds into smaller units in which to quantify land-cover and is presented in chapter two. Researchers have long recognized that stream reach-scale responses are differentially influenced by not only the type of land-cover but also the location and proximity of land-cover relative to the stream reach in which responses are quantified. Most of the progress has suggested various methods for subdividing watersheds by distance from stream reach. For example, riparian corridors (~30-m) have been used to define a watershed sub portion proximal to streams and more likely to influence stream responses. Often researchers quantify land-cover in riparian corridors and whole watersheds and use these to spatial extremes to examine the differential probability for influence by land-cover within each area. Sponseller and Benfield (2001) used 30-m riparian corridor sections, located at various distances upstream of sample reaches, to assess the longitudinal displacement of land-cover influence to streams. More recently, King et al. (2005) summarized and expanded contemporary techniques for assessing land-cover at continuous spatial scales using riparian corridors and concentric circles to subdivide research watersheds. These types of studies have supported the idea that land-cover likely influences

streams along both longitudinal and lateral vectors and that the degree of influence potential by land-cover is likely highest in an area extending upstream and outward of sample reaches.

My third objective was to link the abiotic and biotic responses I measured to land-cover and is presented in Chapter 4. Contemporary research often suggests that land-cover influences erosion, and that in-stream sediments influence biota. However, no study I am aware of has successfully linked land-cover, abiotic ecosystem components, and biota, although several recent studies have attempted to do so (see King et al. 2005). Because my investigation spanned spatial scales from stream interstices or individual invertebrates to large watersheds, I suspected I would be able to link responses to land-cover in watershed sub portions at various scales. One of my most important dissertation goals was to develop and test models that summarize relationships between land-cover, sediments, and biotic responses. Using structural equation modeling, I identify patterns among spatial scale, land-cover, and individual stream responses (e.g., fish diversity) that will influence future stream ecosystem research.

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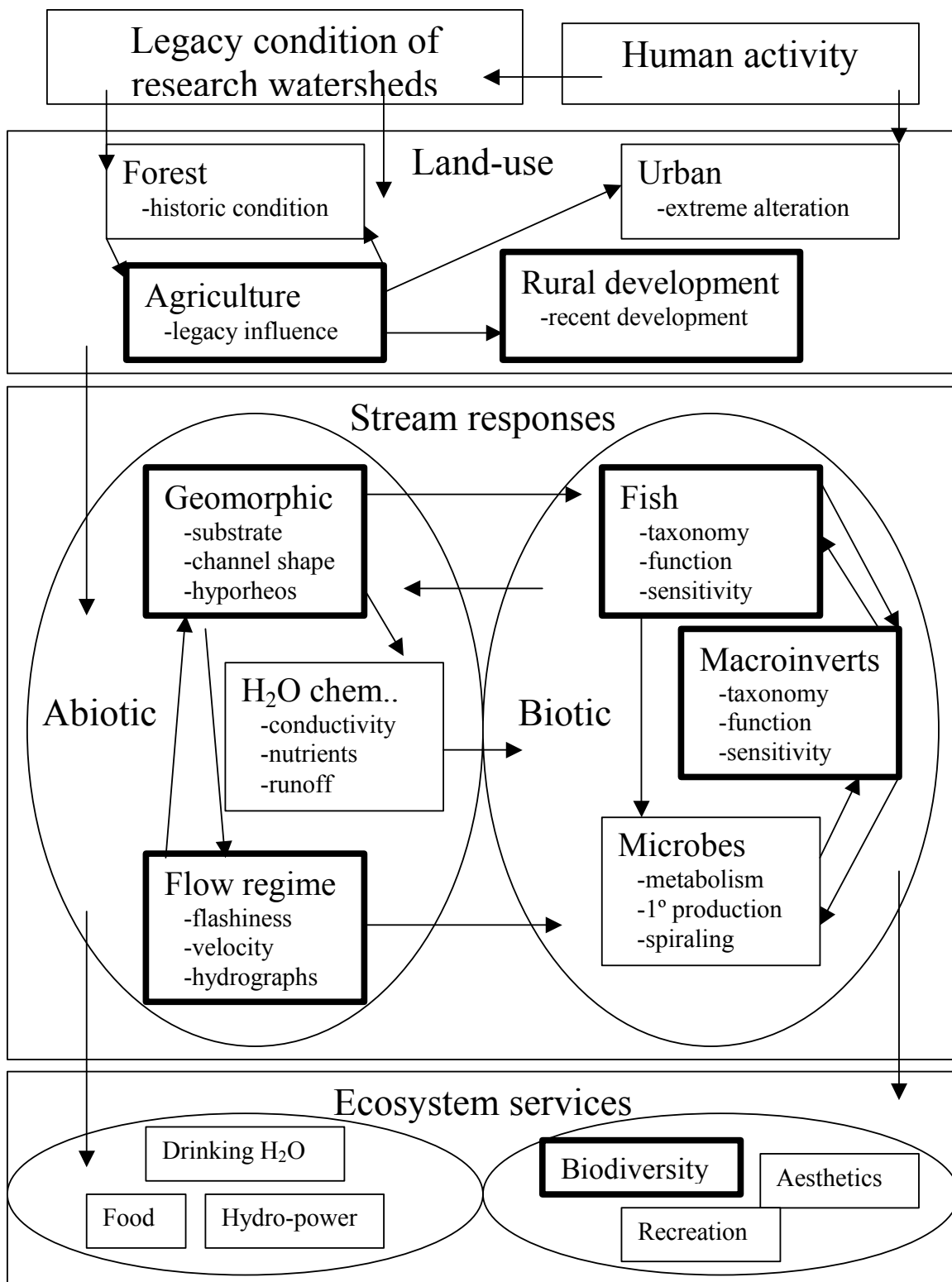


Figure 1.1. Links among human influence, stream ecosystem components, and ecosystem services. Bold boxes indicate elements measured in this study.

Chapter 2: Defining spatially explicit riparian zones using watershed hydrology

Abstract

Riparian zones have been identified as areas where the terrestrial landscape can disproportionately influence streams. However, defining riparian zones is complicated for several reasons. Near-stream areas represent dynamic spatial gradients, or zones, characterized by varying topography, geology, land-cover, and the degree of terrestrial – aquatic interaction. Many studies have considered these influence zones to be discrete watershed sub-portions (e.g., 100-m riparian corridors), whereas I consider zones of influence to be composed of multiple watershed sub-portions along the spatial continuum between near-stream areas and the watershed boundary. I describe a method for identifying zones of influence using watershed hydrologic patterns to delimit zones along a near-stream continuum between a downstream point (e.g., sample reach) and the watershed boundary. Using hydrologic modeling equations and GIS, travel time zones for ten streams were identified by watershed topography, surface roughness, and rainfall intensity. Travel time was calculated for every 30 X 30-m cell in each watershed, providing spatially explicit estimates of watershed hydrology and enabling us to calculate the travel time required for rainfall in any watershed cell to reach the watershed terminus, or stream reach. Mean watershed travel time varied from 45 to 264 minutes among ten watersheds. Shorter duration travel times (i.e., 30 – 60 minutes) described smaller areas than longer duration travel times (i.e., 210 – 300 minutes). Travel time zones were wider and shorter than traditional riparian corridors and described areas more ecologically relevant to stream reaches. I used correlation to assess the ‘best’ zone to use when defining disturbance type land cover influence on common biotic responses. Macroinvertebrate shredder and midge density were related to heavy and light urban land-cover defined within travel time zones between 90 and 240-min. Benthic invertivores and nest-associate fishes were also correlated to urban land-cover delimited by zones. Travel time zones were better (i.e., higher correlation coefficient and r^2) at detecting biotic responses than 100-m riparian buffers. This method provided a framework for analyzing landscape condition in continuous riparian zones that allowed comparison of ecologically relevant land-cover with response variables at multiple spatial scales.

Introduction

Streams are influenced by upstream factors associated with landscape condition (Wiens 2002). Studies of landscape - stream interactions are important for natural resource conservation, insightful land management, and understanding ecosystem structure and function. Researchers have often considered aspects of landscape condition (e.g., land-cover) to be influential determinants of physical, chemical, and biotic stream responses (Roth et al. 1996, Trimble and Crosson 2000). Multiple lines of evidence suggest that streams are affected by landscape condition (e.g., anthropogenic disturbance) and that stream responses are directly related to the type, intensity, and location of landscape disturbance factors (Gupta 1995, Gomi et al. 2002, Woessner 2000, Montgomery and MacDonald 2002). Most research has suggested that riparian zones are key areas that mediate the effects of landscape disturbance to streams (Friedman et al. 1996, Croke et al. 1999, Paringit and Nadaoka 2003).

Riparian zones are critical ecosystem components located at the terrestrial – aquatic interface (Decamps et. al 1988, NRC 2002, Moore and Richardson 2003). A wealth of evidence suggests that this near-stream environment mediates disturbance to stream ecosystems and that riparian zones are disproportionately sensitive to anthropogenic disturbance (Karr and Schlosser 1978, Decamps et. al 1988, Gregory et. al 1991, FIWG 1998, Naiman et. al 2001, Molnar et al. 2002). However, appropriate spatial boundaries that define riparian zones are not well understood. Consequently, there are multiple ways to describe riparian zones with respect to both the landscape and streams (Postel et. al 1996, Stanford 1998, COS 1999). Most define riparian zones as areas of terrestrial – aquatic interaction but disagree as to where to place boundaries. Researchers, land-managers, and ultimately, policy decision-makers often define riparian zones by criteria such as distinctive vegetation, periodic flood boundaries, or topographic features (NRC 2002). Many contemporary studies have defined riparian areas as uniform-width (e.g. 100-m buffer) corridors (e.g. Harding et al. 1998, Sponseller and Benfield 2001, Boothroyd et. al 2004, Lee et. al 2004). Most longitudinal analyses of streams, however, have indicated that lateral inputs become more important moving downstream, which suggests a non-uniform width of the riparian zone (e.g., Vannote et. al 1980, Montgomery 1999, Molnar et al. 2002). At minimum, riparian boundaries should vary with stream size and across physiographic provinces.

Researchers have demonstrated the need to consider multiple spatial scales when investigating stream responses to landscape disturbance (Smart et al. 2001, Wiens 2002, Townsend et al. 2003, King et al. 2005). Recent investigations have used exploratory methods to define riparian zones along spatial continua to allow comparison of stream responses with landscape condition at several spatial scales (Basnyat et al. 1999, Smart et al. 2001, Sponseller and Benfield 2001, Apan et al. 2002, Reed and Carpenter 2002, Townsend et al. 2003, Hyatt et al. 2004, Lee et al. 2004, King et al. 2005). These studies differ in how they consider spatial scale, but all aim to quantify near-stream areas that are spatially and ecologically relevant riparian zones and to use these zones as areas to focus their description of landscape condition. Given that riparian zone boundaries differ among systems, a standard definition should be a set of dynamic criteria used to define riparian zones in individual systems. This would allow for objective comparison among and between streams of various types. At present, the lack of a standard riparian definition limits our ability to associate landscape condition with detrimental stream responses, inhibits unified research across disciplines and lengthens the time required to make ecologically beneficial decisions (Steiner et al. 1998).

Here I present a method for delimiting multiple riparian zones of varying size around stream channels using surface hydrologic characteristics. King et al. (2005) suggested that hydrological connectivity should be considered when sub-dividing watersheds for land-cover analysis. Hydrologic features are useful because water, via the hydrologic cycle, unites streams with terrestrial landscapes (Gordon et al. 2004, McKergow et al. 2004). Riparian zones defined by hydrologic pathways include gradients from wet (i.e., streams) to dry (i.e., upland terrestrial) areas. Hydrologic patterns can be quantified and used to identify and describe spatially continuous, ecologically relevant riparian zones. In this chapter, I summarize watershed hydrology using estimates of watershed travel time, or the average time required for rainwater resulting from a uniform watershed rainfall to travel between any specified portion of the landscape and a typical stream reach.

The first objective of this study was to use travel time estimates to define continuous watershed sub-portions, or zones, along the spatial continuum from near-stream to the whole watershed. I used travel time to delimit ecologically different and spatially explicit watershed sub-portions or riparian zones. My second objective was to use travel time zones (TTZs) to describe land-cover characteristics in watershed sub-portions. I predicted that land-cover would

differ with the TTZ in which land-cover was delimited and provide a way to consider land use at multiple spatial scales. My third objective was to use TTZs to determine the appropriate spatial scale of land-cover that influenced each biotic response. I predicted that some responses would be related to (i.e., stronger correlation) to land-cover at larger spatial scales (i.e., longer duration TTZs) whereas other responses would be related to land-cover at smaller (i.e., more proximal, shorter duration TTZs) spatial scales. To address objective three, I compared land-cover described in multiple travel time zones to abiotic and biotic responses to determine the appropriate zone, and spatial scale, relevant to each response.

Methods

Conceptual approach

I used hydrologic dynamics as criteria to define spatially explicit riparian zones in disturbed watersheds because hydrologic dynamics address interactions between water, terrestrial areas, and stream channels and can be defined along a spatial continuum (Gupta 1995, Friedman et al. 1996, Walling 1998, Croke et al. 1999, Gomi et al. 2002, McKergow et al. 2004, Melesse and Graham 2004, Vidon and Hill 2004). I predicted that hydrologic estimates would describe watershed sub-portions resembling the zone described in Figure 2.1. Watershed hydrology results from rainfall flowing toward stream channels along lateral and longitudinal vectors. Hydrologic patterns define the watershed area where surface terrestrial – aquatic interaction are likely to occur (Fig. 2.1; Ward 1989, Smock et al. 1992) and describe a continuum of terrestrial – aquatic interaction. Areas within the riparian continuum that are closer to streams should reflect a higher degree of terrestrial – aquatic coupling than less proximal, more terrestrial areas. Near-stream areas are zones of influence and are more likely to introduce eroded soils or other artifacts of disturbance to stream channels during a typical rainfall than are less proximal areas.

I used travel time thresholds to delimit watershed sub-portions that were organized by the maximum travel time occurring in an area. Thus, TTZs were identified by the relative amount of terrestrial – aquatic interaction as defined by common travel times. Watershed sub-portions with similar travel time estimates could therefore be grouped into a TTZ. In this study, watershed sub-portions were composed of 30 X 30-m cells designated by GIS software. My models calculated the time required for uniform rainfall in a cell to travel to the nearest stream channel based on modeled landscape parameters including gradient, surface roughness, and proximity to

a stream reach or watershed outlet. Travel time zones represented the grouping of cells similar in the travel time required for rainfall to reach a stream channel. For example, a 60-min travel time zone would include all watershed cells where rainfall reached a stream channel within 60 minutes. Similarly, 60-min TTZs would be characterized as having a smaller area, being generally closer to a stream reach or watershed outlet, and having less terrestrial – aquatic interaction than a 120-min travel time zone. However, 120-min TTZs would include the 60-min TTZs and all other shorter-duration TTZs. Increasing the duration of a TTZ, therefore, involved adding new cells to the next-smaller TTZ. Potential riparian areas were thus defined by a continuum of short to long duration travel times with short duration travel times representing local, near-stream watershed spatial scales and longer duration travel times representing successively larger watershed areas.

Research watersheds

Travel time estimates were calculated for each 30 X 30-m cell (900-m²) in ten example watersheds (Table 2.1). I focused on watersheds disturbed by agriculture, averaging $23 \pm 5.6\%$ ($\bar{x} \pm SE$; range: 16 – 36%) row-crop agriculture. Watersheds were located in the Blue Ridge physiographic province of the southern Appalachians near Asheville, NC. Watersheds were similar size, ranging from approximately 900 – 3500 hectares ($\bar{x} = 1898$ ha), contained similar stream networks (7 – 28 km) featuring streams of 3rd – 4th order at the watershed outlet, occurred at approximately 2000 m elevation, and shared similar soil characteristics. The ten watersheds were considered comparable replicates and used to examine the variation in watershed areas prescribed by TTZs, 100-m corridors, and whole watersheds.

Hydrologic Equations and GIS

Stream networks were delineated and stream slope estimated using ESRI® ARCGIS® version 8.2, the spatial analyst extension, and 30-m digital elevation models obtained via the USGS seamless data distribution website*. Flow direction, accumulation, stream networks and watershed boundaries were delineated in ARCGIS® using the hydrology extension. Streams were truncated at flow accumulations of 250 cells to define the boundary between ephemeral and perennial flow and included only perennial flow (Saunders 2000). Land-cover estimates were obtained from National Land Cover Database (NLCD) and used to calculate surface roughness (EPA 2000; Homer et. al 2002). Twenty-seven NLCD land-cover categories present in study

*<http://www.seamless.usgs.gov/>

watersheds were collapsed into seven general groups due to limited availability of roughness coefficients (n) for specific land-cover types (Table 2.1). Because accurate estimates of n are not known for many land-cover types, I estimated n for unknown categories by extrapolating between known n values for intermediate land-cover types.

I used HEC-HMS equations developed by the US Army Corps of Engineers to quantify surface water velocity resulting from an average rainfall (assuming uniform rainfall in every watershed cell; USACE 2000). While HEC-HMS equations were developed to estimate overland flow velocity, I use travel time estimates as proxy measures of relative travel time to weight watershed sub-portions. These are standard equations commonly used to calculate water velocity resulting from storms of various intensities. Three types of flow were included in the analyses: Sheet flow (sf), concentrated flow (cf), and channel flow (ch). Sheet flow occurred along steep gradients, over impervious surfaces, or in ephemeral drainages changing to concentrated flow after 100-m (USACE 2000). Concentrated flow occurred throughout most of a watershed prior to water reaching a stream channel. Channel flow resulted from water entering stream channels. The following HEC-HMS equations were used to estimate these parameters (USACE 2000):

$$\begin{aligned}\text{sf travel time} &= \frac{0.42 (n * L)^{0.8}}{L(m) * P^{0.5} * S^{0.4}} \\ \text{cf travel time} &= 1 / (\text{sqrt}(S) * 295.2) \\ \text{ch travel time} &= n / 60\text{-min} * R^{2/3} * S^{1/2}\end{aligned}$$

where n was Manning's roughness coefficient for each land-cover type (sensu Zelinski and Quackenbush 1999; Table 2.1), L was the distance from stream channel (m), P was the rainfall estimate modeled (0.5-in for this study, assumed to be equivalent for each watershed cell), S was the slope over which water traveled and R was the estimated hydraulic radius of the stream channel. Constants were derived from HEC-HMS equations.

Travel time was calculated using the Spatial Analyst[®] raster calculator and produced spatially explicit GIS grids comprised of 900-m² cells with values defined as the travel time required for water to flow between that spatial location and the watershed outlet point. Velocity estimates (m min⁻¹) were reciprocated (min m⁻¹) as the time required for surface water to travel

one meter to allow consideration of the relative time required for a parcel of water to reach the watershed terminus, rather than the velocity of that water parcel. This rate was calculated for every watershed cell (30 X 30-m), estimating the time required for rain falling into that cell to reach a stream channel and ultimately the watershed outlet. Flow paths were determined by elevation differences estimated from digital elevation models (DEM). Therefore, each cell along a flow path would have a unique travel time estimate depending on the characteristics of accumulating cells along that flow path. The total distance of a cell (m) to the watershed outlet, as defined by the flow path, was equivalent to a travel time estimate (min) for that cell. Finally, watershed sub-portions were defined by common travel time values, or thresholds, producing zones characterized by similar travel time characteristics and thus a similar degree of terrestrial – aquatic interaction. For example, a 30 – 60-min TTZ described the watershed sub-portion where flow required between 30 and 60-min to reach the outlet.

Land-cover and biotic responses

I used TTZs to assess variability in land-cover estimates in seven NLCD land-use categories (Table 2.1), and compared percent land-cover among TTZs, 100-m corridors, and whole watersheds using analysis of variance. I used estimates of fish and macroinvertebrate diversity as potential responses to land-cover to explore potential differences in biotic responses with land-cover as delimited by TTZs (i.e., spatial influence). Quantitative (Surber, 500 μ m mesh) samples were collected in April 2001 and I calculated macroinvertebrate taxa richness (total number of taxa collected), density (number of individuals collected divided by sample area), and Simpson's diversity index ($D = (n/N)^2$, where n = density of taxa n , and N = total density of all taxa combined). Further, I quantified total macroinvertebrate density and the density of macroinvertebrates by functional feeding group (FFG; Merritt and Cummins 1996; Table 2.4). Fish taxa richness was calculated from quantitative fish samples collected during August 2002 by single-pass backpack electrofishing of 1 to 10-m stream reaches included within a 100-m sample reach. Other fish metrics, including density by trophic and reproductive guilds, were used to examine potential differences in fish assemblages with respect to taxonomy and links between reproductive and feeding behavior linked to habitat availability (Table 2.2). Trophic and reproductive habits were assigned according to literature available on individual species dietary constituents and reproductive habitat preference (Jenkins and Burkhead 1994, Etnier and Starnes 1993). When macroinvertebrate or fish taxonomic information was not

available, expert opinion was applied to place individual taxa into the most appropriate functional group or guild.

To address the influence of spatial scale as estimated by TTZs on the relationship between land-cover and biotic responses, I compared the degree of relatedness (e.g., correlation) between each TTZs for every biotic response measured using Pearson correlation (SigmaStat v. 3.0, SPSS, Inc). I compared the correlation coefficient (r value) and correlation direction (i.e., positive or negative) against each TTZ to determine the ‘best’ TTZ indicated for a particular biotic response, as indicated by the strongest significant correlation. Through these analyses I identified the most relevant spatial scale at which land-cover had the greatest potential to influences a biotic response. Land-cover proportions were arcsine-root-transformed, and Simpson’s index was log-transformed to meet normality assumptions necessary for linear regression (Zar 1999).

Results

Mean watershed travel time varied from 45 to 264 minutes (Table 2.3). Maximum travel time in any watershed ($n = 10$) varied from 257 to 1,973 min (Table 2.3). Within this range of whole watershed travel times, I was able to define TTZs by ten travel time thresholds; 30, 60, 90, 120, 150, 180, 210, 240, 270, and 300 minutes (Fig. 2.2). The smallest and largest TTZs, defined by 30-min (0.5-hr) and 300-min (5-hr) travel time, respectively, represented realistic endpoints for observed storms in the Asheville, NC vicinity (C.L. Burcher, personal observation).

Travel time zones

The spatial extent of a TTZ increased with travel time (i.e., longer duration TTZs covered successively larger watershed portions and included all smaller TTZs; e.g., Fig. 2.2). These patterns show that TTZs describe a continuous watershed sub-portion originating at the watershed outlet and becoming successively larger in area with increased travel time (Fig. 2.3). Each successively larger TTZ included the areas circumscribed by all shorter-duration TTZs (e.g., a 60-min TTZ would be within a 120 minute TTZ). I assumed that watershed areas remained wet, and thus, connected, through the duration of modeled rainfall.

Short-duration (30 to 60-min) TTZs encompassed, on average, less than 20 percent of watershed area (Table 2.3) and included areas lateral to stream channels but did not describe upstream areas to the same degree as longer-duration TTZs. Intermediate-duration (90 to 180

minute) TTZ coverage ranged from 37 to 68 percent watershed area (Table 2.4). Long-duration TTZs (210 - 300 minute) included 74 to 90 percent of watershed area on average, approaching the area defined by the whole watershed (Table 2.3). Long-duration TTZs covered watershed areas both farther upstream of and farther laterally to the watershed outlet compared to short-duration TTZs. One-hundred-meter riparian corridors occupied 3 to 4 % watershed area ($\bar{x} \pm SE = 4.0 \pm 0.0 \%$) although they included the watershed portion extending to the extreme headwaters but described a lateral area only 50-m on either side of stream channels. Variation (standard error) among sites ranged from 4 to 11 percent for TTZs, whereas 100-m riparian corridors and whole-watersheds exhibited low variation ($SE = 0.0 \%$; Table 2.3).

Areal coverage by TTZs differed from 100-m corridor coverage (Fig. 2.3). Travel time zones described much wider areas than 100-m corridors. Sixty minute and larger TTZs described a larger watershed sub-portion than 100-m corridors in all watersheds. Travel time zones also increased downstream with travel time duration, typically converging on 100-m corridors beyond 300-min. In general, 100-m corridors were much narrower and much longer than TTZs and delimited a smaller area than TTZs except for 100-min TTZs in four watersheds that delimited 1 to 3 % watershed area.

Land-cover and TTZs

Agriculture, forest, and barren land-cover proportions varied significantly when described at different spatial scales (i.e., using different TTZs; Table 2.4). Agriculture and forest proportions in short-duration TTZs (i.e., 30 to 90-min) were similar to agriculture and forest proportion delimited by 100-m corridors but significantly different from the proportion delimited by intermediate to long duration TTZs (120 to 300-min) and whole watersheds. Although not a disturbance-type land-cover, the proportion of barren areas also differed significantly with zone whereby 30-min TTZ and 100-m corridor (i.e., small scale) land-cover estimates were different from barren land-cover delimited by 60 to 300-min TTZs or whole watersheds (i.e., large scale). Land-cover proportions in other categories (i.e., open water, light and heavy urban, and riparian vegetation) did not differ significantly by zone.

Biotic responses; selecting the appropriate TTZ

Correlations between disturbance type land-cover in each TTZ (agriculture, light urban, heavy urban) and biotic responses were used to select the most appropriate, or most predictive, TTZ for a given biotic response. I used Pearson product moments (SigmaStat v. 3.0, SPSS Inc.)

to estimate the magnitude and direction of relationships between each biotic response and disturbance type land-cover within 30 to 300-min TTZs. Light and heavy urban land-cover types were significantly related to several macroinvertebrate and fish responses. Shredder density was positively correlated to both light and heavy urban land-cover (Fig. 2.4A,B) and midge density was positively correlated to light urban land-cover (Fig. 2.4C). Light urban land-cover was most predictive when prescribed within a 150-min TTZ and heavy urban land-cover was most predictive when prescribed within a 90-min TTZ (Fig. 2.4). The seven other macroinvertebrate metrics were not significantly correlated to land-cover as described by TTZs, 100-m corridors, or whole watersheds. Two of thirteen fish metrics were significantly correlated to disturbance type land-cover within TTZs. Nest associate density was most strongly predicted (negative relationship) by light urban land-cover within 240-min TTZs and benthic invertivore density (positive relationship) by heavy urban land-cover within 120-min TTZs (Fig. 2.5A,B). Other fish metrics were not significantly correlated to disturbance type land-cover, and no biotic responses were significantly correlated to agriculture.

The predictive value of strongly correlated TTZs was further assessed using linear regression of the most significant correlated TTZ – biotic response relationships. Light urban land-cover in 150-min TTZs significantly predicted midge density (Fig. 2.6A) and shredder density (Fig. 2.6B). Shredder density was also strongly predicted by heavy urban land-cover within 90-min TTZs (Fig. 2.6C). Similarly, fish nest associate density was strongly predicted by light urban land-cover within 240-min TTZs (Fig. 2.7A) and benthic invertivore density by heavy urban land-cover within 120-min TTZs (Fig. 2.7B). Significant biotic responses were best predicted by disturbance type land-cover prescribed in intermediate to long duration (i.e., 90 to 240) TTZs.

TTZs vs. 100-m riparian buffers

I assessed the relative value of TTZs compared to traditional 100-m buffer zones using the significant relationships above. TTZs always out performed 100-m corridors as interpreted by consistently higher correlation and regression coefficients (Table 2.5). Relationships between heavy urban land-cover to shredders and light urban land-cover to nest associates were not significant when land-cover was delimited by riparian corridors. Though highly correlated, land-cover prescribed within TTZs predicted biotic responses better than 100-m riparian corridors.

Discussion

Travel time zones

Spatially explicit travel time estimates provided a useful method to define continuous watershed sub-portions resembling my hypothesized zones of influence (Fig. 2.1). Travel times increased moving away from streams and provided an objective method to weight watershed sub-portions with respect to potential influence of landscape features on streams. Stream ecologists have long recognized the lateral and longitudinal nature of streams, that streams are influenced by material transport, and that researchers should consider lateral, longitudinal, and vertical dimensions (*sensu* Vannote et al. 1980, Ward 1989, Smock et al. 1992), and recent studies of land-cover influence on streams have explored inverse distance weighting (IDW) and other weighting schemes to account for potential changes to landscape influence with distance from streams (King et al. 2005). Weighting techniques, however, are not based on ecologically meaningful criteria but instead define the linear distance from a landscape area to a stream reach. Travel time zones reflect the lateral and longitudinal movement of water through the terrestrial environment to stream channels. These results provided a quantitative method to assess how landscape influence may be translated downstream-of and lateral-to a terrestrial location. Continuous riparian zones allow for considering lateral and longitudinal interactions with respect to sample locations. TTZs provide an appropriate method to evaluate the influence of scale relative to the types of responses measured.

Areal variation among zones was highest for short-duration TTZs (i.e., near-stream zones) compared to zones occupying larger portions of watersheds. While this is a subtle difference, it could suggest that near-stream areas are more likely to vary in size or travel time duration than less-proximal watershed areas. This observation agrees with the variable source concept that suggests near-stream areas disproportionately influence stream channels (Hewlett and Hibbert 1967). Similarly, variation in intermediate TTZs suggests that watershed areas between ridge tops and stream valleys are most likely to vary with respect to the type of land-cover present.

Biotic responses

As I predicted, biota were influenced by disturbance land-cover at some spatial scales (i.e., within some TTZs) but not others. Researchers have addressed the differential effects of spatial scale on biotic responses associated with land-cover spatial distribution (Harding et al.

1998, Sponseller and Benfield 2001, King et al. 2005), although I am not aware of other studies that used hydrology or other ecologically meaningful criteria to establish spatial gradients. Here, TTZs were successful in showing differential effects of land-cover at various spatial scales. Additionally, differences in biotic responses to land-cover at varying spatial scales suggests that studies relying solely on whole watershed or corridors to delimit land-cover may miss potentially meaningful relationships. For example, shredder density in my study streams was influenced by heavy urban land-cover within 90-min TTZs, but not by heavy urban land-cover prescribed by 100-m buffers. Had I used traditional methods, I would not have observed the potential influence of urban land-cover to shredder density.

Heavy and light urban land-cover types delimited by 90 to 240-min TTZs were most significantly related to the biotic responses we measured, whereas agriculture was not. Agriculture has been inferred as a likely influence on many of the biotic responses we measured, but neither TTZs nor traditional methods of land-cover suggested that agriculture was related to biotic responses in the streams we studied. Although agricultural land-cover dominated watersheds, our results suggest that urban land-cover types may be more influential to biota in these streams. Several researchers have suggested that urban land-cover types are more detrimental to streams than agriculture, and it is likely that we observed a similar phenomenon (Paul and Meyer 2001). Streams in the southern Appalachians have likely been influenced by agriculture for hundreds of years, and biotic assemblages may reflect acclimation to conditions induced by agriculture (Harding et al. 1998). Urban development in the study area is recent compared to agriculture, and we may have observed the response of assemblages to ‘unfamiliar’ disturbance influence.

Urban land-cover was positively correlated with both shredder and midge density. Shredders are organisms relying largely on allochthonous input of food associated with autumnal leaf fall in the eastern United States. *Tipula* (Diptera) and *Frenesia* (Trichoptera) dominated developing streams but were absent from agricultural streams. Increased shredder density with urban land use suggests that riparian vegetation is recovering in urban streams compared to agricultural areas. This is possible because agricultural streams typically contain denuded riparian areas, bare banks, and minimal allochthonous input, whereas urban systems do not necessarily feature denuded stream banks. However, we also observed increases to midge density associated with urban land-cover. Typically, midges are considered tolerant to pollution

and often are associated with impairment. That midges and shredders both increased with urban land use may therefore be contradictory. We did not, however, attempt to identify midges past family, which may be causing confusion in the interpretation of these results.

Urban land-cover also influenced fish assemblages. Benthic invertivore density increased with urban land-cover and nest associate density was negatively correlated to urban land-cover. Benthic invertivores typically have down-turned, or subterminal, mouths and may be associated with feeding on benthic invertebrates (Jenkins and Burkhead 1994). The increase of benthic invertivores suggests that prey items (i.e., macroinvertebrates) associated with benthic areas were readily available. Correlation of benthic invertivores with urban land-cover may suggest that conditions in the benthos were improved over streams influenced by agriculture. However, nest associate fishes tended to decrease in abundance with urban land-cover. Nest associates prefer to spawn in association with nest-building fish species including stonerollers and creek chubs. It is possible that altered watershed hydrology often associated with urban land-cover may reduce the success of the nest building and nest associate spawning strategies. Alterations to fish assemblages associated with urban land use suggests that rocky habitats and substrate conditions are influenced by urban land-cover, and that these changes may be influencing fish feeding and reproductive habits. Moreover, altered stream conditions likely favor fishes adapted to or able to acclimate to, substrate condition.

Ultimately, macroinvertebrate midge and shredder density and fish benthic invertivore and nest associate density were most related to urban land-cover described by intermediate to long-duration TTZs (i.e., 90 to 240-min). This is an indication that urban land cover at moderate to large spatial scales (i.e., including near stream and middle watershed areas, but not areas closer to the watershed boundary or farther away from stream reaches) is disproportionately influential to assemblages compared to other land-cover types or either near stream or large-scale urban land-cover. Despite the relatively small contribution of urban land-cover and the dominance of agriculture in watersheds (Table 2.1), biota appeared to be influenced only by urban land-cover. This suggests that urban land-cover induces a disproportionate influence on biota compared to agriculture, and that a large spatial scale (i.e., larger than 100-m corridors provide) should be considered when investigating assemblages potentially influenced by urban land use.

Selecting the appropriate TTZ

Variation in the proportion of land-cover delimited by TTZs suggested an effect of spatial scale. Peaks in response curves generated by correlations between biotic responses and TTZs indicated that urban land-cover defined between 90 and 240-min were most predictive and potentially highly influential on biota. Correlation analysis can be used in conjunction with TTZs to determine the appropriate area to consider when making management decisions. Many investigations, public projects, and management efforts need to assign the relevant sub-watershed area that is critical to respective criteria. For example stream management for Total Maximum Daily Loads (TMDLs) requires knowledge about the origin of sediments in order to successfully manage sediment delivery to streams. Using TTZs together with in-stream sediment sampling managers can focus efforts on land-cover types or other sub watershed criteria significantly related to sediment concentration. Travel time zones provide an ecologically relevant technique for subdividing watersheds along a spatial continuum and determining which of the subdivisions is most related to the management parameter of interest.

Further consideration

While travel time estimates appeared to provide insight regarding the relationship between land-cover and spatial scale for these watersheds, whether the selected equation parameters would be appropriate for other watersheds is unknown. It is difficult to validate spatially explicit models considering the inconsistent nature of rainfall and difficulties of empirically testing watershed hydrology. Potential error in travel time estimates depends on the accuracy of appropriate equation parameters and the nature of watershed hydro-dynamics. Several aspects of the selected equation terms merit future exploration to address questions of accuracy. For example, Manning's roughness coefficients have not been verified for land-cover types. Our estimates of n were based on available data, although the actual resistance supplied by each land-cover type is not well understood. I addressed potential circularity in using land-cover to estimate n , and deriving land-cover zones using travel time using linear regression. If n estimates disproportionately affected travel time estimates, travel times should have increased with forest cover and decreased with agriculture because forest cover was assigned a much higher n value relative to agriculture. Higher n values, theoretically, could have increased travel times due to increased surface roughness impeding water flow. Had travel time estimates been unrealistically long (e.g., 10,000 minutes), and could have been attributed to n values, I would

have reconsidered the n estimates used. Instead, I found that maximum travel time was positively associated with higher forest cover and negatively associated with higher agriculture in whole-watersheds. I considered this evidence that equations were not circular with respect to land-cover and n estimates. Similarly, this suggested that equations were not influenced greatly by n .

Other parameters that could create error include the digital elevation model (DEM) derived hydrology calculated in GIS. Several researchers have demonstrated errors associated with locating stream networks with DEMs, especially in low-gradient areas (Wang and Yin, 1997, Yin and Wang 1999, Moglen and Beighley 2002). Digital elevation model derived slope estimates also may not reflect true hillslope orientation and stream channel locations may differ subtly from actual locations. Similarly, the resolution of DEMs and land-cover data was 30-m (30 X 30-m cells). As a result, stream channels and hydrologic vectors were estimated to be much larger than they were. These potential problems may over or under estimate travel time calculations. Equations were selected to summarize watershed features believed to be important in these systems. Using travel time to define the extent of riparian zones worked well in disturbed 3rd – 4th order southern Appalachian streams. Whether larger watersheds, low-gradient streams or groundwater-dominated systems could be similarly analyzed is unknown. Researchers working in other streams should include the features important in those areas in equations.

Conclusion

Investigations of stream reach-scale responses to landscape condition could benefit from a spatially explicit consideration of the landscape (King et al. 2005). Here I present a conceptual approach that can be used across geographic, geologic, and elevation gradients. Using TTZs to define zones of influence is an accurate and appropriate method for use in disturbed watersheds with increased hydrologic activity. Future research can now consider stream responses to landscape condition defined at multiple spatial scales within continuous riparian zones. I suggest that research comparing in-stream responses to landscape condition should consider using travel time or similar spatially continuous hydrologic estimates to define land-cover as an independent variable for comparison with stream responses. This is one of the first studies suggesting the use of continuous spatial zones to define zones of influence. Further research will help modify equations to change the important parameters, reduce the necessary GIS estimates or the

associated error, improve estimates of roughness coefficients, and potentially validate travel time estimates to determine accuracy.

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Table 2.1. Stream/watershed characteristics for ten study streams, land-cover proportions calculated as the proportion of 30 X 30-m cells occupied by each category in the whole watershed, and Manning's roughness coefficients for seven categories.*

| Stream / watershed | WS Code | WS Area (ha) | Total Stream Length (km) | WS land cover proportion (%) | | | | | | |
|--------------------------------------|---------|--------------|--------------------------|------------------------------|-------|-------|------|------|-----|-----|
| | | | | OW | LU | HU | BA | RV | AG | FO |
| Avery Creek | AVE | 1743 | 12 | 0.2 | 1.1 | 0.2 | 0.9 | 1.2 | 21 | 75 |
| Brush Creek | BRS | 891 | 7 | 0.2 | 1.0 | 0.3 | 1.0 | 1.0 | 22 | 74 |
| Hooper's Creek | HDS | 3552 | 28 | 0.2 | 1.0 | 0.2 | 0.7 | 0.8 | 22 | 75 |
| Merril's Cove Creek | MCC | 1445 | 8 | 0.4 | 4.7 | 0.3 | 0.2 | 1.0 | 16 | 78 |
| Robinson Creek | ROB | 1349 | 9 | 0.2 | 21.7 | 2.1 | 0.2 | 1.1 | 18 | 56 |
| East Fork Bull Creek | EFB | 1601 | 14 | 0.0 | 0.0 | 0.1 | 0.7 | 0.3 | 19 | 80 |
| Gabriel's Creek | GAB | 2015 | 15 | 0.0 | 2.6 | 1.6 | 1.9 | 1.4 | 36 | 57 |
| Middle Fork Creek | MFD | 2049 | 15 | 0.3 | 0.0 | 0.4 | 2.4 | 1.7 | 75 | 20 |
| Paint Creek | PNT | 1286 | 16 | 0.0 | 0.0 | 0.1 | 0.8 | 0.4 | 22 | 77 |
| West Fork Bull Creek | WFB | 3049 | 23 | 0.0 | 0.0 | 0.1 | 1.6 | 0.5 | 22 | 76 |
| Manning's roughness coefficients (n) | | | | 0.00001 | 0.005 | 0.005 | 0.03 | 0.05 | 0.1 | 0.8 |

* WS = whole watershed; OW = open water; LU = light urban; HU = heavy urban; BA = barren; RV = riparian vegetation; AG = agriculture; FO = forest.

Table 2.2. Macroinvertebrate and fish response metrics estimated from biotic samples. FFG = functional feeding group.

| Biota | Metric class | Metric |
|-------------------|--------------|------------------------------|
| Macroinvertebrate | Taxonomic | Taxa richness |
| | | Total density |
| | | Midge density |
| | | Simpson's diversity index |
| | FFG | Shredder density |
| | | Scraper density |
| | | Collector gatherer density |
| | | Predator density |
| | | Collector filterer density |
| | | |
| Fish | Taxonomic | Taxa richness |
| | | Total density |
| | Distribution | Cosmopolitan species density |
| | | Endemic species density |
| | FFG | Herbivore density |
| | | Benthic invertivore density |
| | | General invertivore density |
| | | Drift invertivore density |
| | | Detritivore density |
| | Reproductive | Nest builder density |
| | | Nest associate density |
| | | Nest guarder density |
| | | Broadcast spawner density |

Table 2.3. Mean and maximum travel time statistics and watershed sub-portion (%) occupied by travel time zones, 100-m riparian corridors, and whole watersheds for ten research watersheds.*

| Stream | Maximum travel time (min) | Mean travel time (min; ± 1 SE) | Watershed area (%) occupied by a given zone | | | | | | | | | | | |
|--------|---------------------------|------------------------------------|---|-------|-------|-------|-------|-------|-------|-------|-------|-------|----------------|-----------------|
| | | | Travel time (min) | | | | | | | | | | 100-m corridor | Whole watershed |
| | | | 30 | 60 | 90 | 120 | 150 | 180 | 210 | 240 | 270 | 300 | | |
| AVE | 391 | 109(47) | 4 | 14 | 34 | 64 | 80 | 91 | 98 | 100 | 100 | 100 | 4 | 100 |
| BRS | 598 | 264(67) | 2 | 3 | 4 | 5 | 6 | 7 | 10 | 21 | 51 | 74 | 4 | 100 |
| HDS | 896 | 224(95) | 1 | 4 | 10 | 18 | 25 | 31 | 40 | 52 | 64 | 76 | 4 | 100 |
| MCC | 486 | 182(74) | 1 | 5 | 12 | 22 | 33 | 47 | 62 | 77 | 87 | 94 | 4 | 100 |
| ROB | 425 | 113(58) | 5 | 18 | 40 | 58 | 80 | 86 | 93 | 98 | 99 | 100 | 3 | 100 |
| EFB | 459 | 117(49) | 4 | 13 | 29 | 53 | 75 | 89 | 96 | 96 | 100 | 100 | 4 | 100 |
| GAB | 1021 | 261(129) | 3 | 7 | 11 | 15 | 21 | 31 | 41 | 46 | 50 | 56 | 4 | 100 |
| MFD | 1973 | 45(70) | 41 | 41 | 89 | 95 | 99 | 99 | 99 | 99 | 99 | 99 | 4 | 100 |
| PNT | 274 | 69(48) | 25 | 35 | 68 | 85 | 94 | 98 | 99 | 100 | 100 | 100 | 4 | 100 |
| WFB | 257 | 76(35) | 8 | 34 | 69 | 87 | 97 | 100 | 100 | 100 | 100 | 100 | 4 | 100 |
| | | | 9 | 17 | 37 | 50 | 61 | 68 | 74 | 79 | 85 | 90 | 4 | 100 |
| | | Mean (\pm SE) | \pm | \pm | \pm | \pm | \pm | \pm | \pm | \pm | \pm | \pm | \pm | \pm |
| | | | 4 | 4 | 9 | 11 | 11 | 11 | 10 | 9 | 7 | 5 | 0 | 0.0 |

* Site codes are the same as table 2.1

Table 2.4. Mean land-cover proportions (% \pm 1 SE) for ten watersheds within ten TTZs, 100-m corridors, and whole watersheds.*

| Land Cover | Travel time (min) | | | | | | | | | | 100-m corridor | Whole watershed |
|------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| | 30 | 60 | 90 | 120 | 150 | 180 | 210 | 240 | 270 | 300 | | |
| OW | 1.5 \pm 1.1 | 0.7 \pm 0.4 | 0.5 \pm 0.3 | 0.3 \pm 0.2 | 0.2 \pm 0.1 | 0.2 \pm 0.1 | 0.2 \pm 0.1 | 0.2 \pm 0.0 | 0.2 \pm 0.0 | 0.2 \pm 0.0 | 1.0 \pm 0.3 | 0.1 \pm 0.0 |
| LU | 6.3 \pm 3.1 | 6.7 \pm 3.9 | 6.1 \pm 3.9 | 5.1 \pm 3.4 | 5.1 \pm 3.5 | 4.0 \pm 2.5 | 3.8 \pm 2.3 | 3.7 \pm 2.1 | 3.5 \pm 2.1 | 3.4 \pm 2.1 | 3.8 \pm 2.5 | 3.2 \pm 2.1 |
| HU | 1.5 \pm 0.6 | 1.0 \pm 0.4 | 0.8 \pm 0.4 | 0.8 \pm 0.3 | 0.6 \pm 0.3 | 0.7 \pm 0.3 | 0.8 \pm 0.3 | 0.7 \pm 0.3 | 0.6 \pm 0.3 | 0.6 \pm 0.3 | 0.8 \pm 0.3 | 0.5 \pm 0.2 |
| BA* | 3.4 ^B \pm 0.8 | 2.5 ^A \pm 0.6 | 2.2 ^A \pm 0.6 | 1.9 ^A \pm 0.3 | 2.0 ^A \pm 0.3 | 1.9 ^A \pm 0.8 | 1.8 ^A \pm 0.7 | 1.4 ^A \pm 0.4 | 1.1 ^A \pm 0.3 | 1.0 ^A \pm 0.2 | 3.7 ^B \pm 1.0 | 0.9 ^A \pm 0.2 |
| RV | 1.2 \pm 0.3 | 1.2 \pm 0.3 | 1.3 \pm 0.3 | 1.1 \pm 0.2 | 1.1 \pm 0.2 | 1.0 \pm 0.2 | 1.0 \pm 0.2 | 1.0 \pm 0.2 | 1.0 \pm 0.2 | 0.9 \pm 0.2 | 0.1 \pm 0.0 | 0.8 \pm 0.1 |
| AG* | 47.3 ^B \pm 5.6 | 42.1 ^B \pm 4.3 | 39.2 ^B \pm 3.6 | 35.0 ^A \pm 3.7 | 32.4 ^A \pm 4.3 | 31.0 ^A \pm 4.5 | 30.2 ^A \pm 4.6 | 28.7 ^A \pm 4.1 | 25.9 ^A \pm 2.8 | 24.7 ^A \pm 2.7 | 47.5 ^B \pm 4.8 | 22.6 ^A \pm 1.8 |
| FO* | 38.8 ^B \pm 4.7 | 45.7 ^B \pm 5.5 | 50.0 ^B \pm 5.0 | 55.7 ^A \pm 5.2 | 58.6 ^A \pm 5.6 | 61.2 ^A \pm 5.5 | 62.6 ^A \pm 5.6 | 64.3 ^A \pm 4.9 | 67.7 ^A \pm 3.7 | 69.1 ^A \pm 3.6 | 43.1 ^B \pm 5.0 | 71.8 ^A \pm 2.7 |

* TTZ = travel time zone, OW = open water, LU = light urban, HU = heavy urban, BA = barren, RV = riparian vegetation, AG = agriculture, FO = forest. Land-cover categories exhibiting significantly different proportions in at least one zone (ANOVA, Holm-Sidak post-hoc test) are indicated with asterisks (*) and superscript letters.

Table 2.5. Comparison of TTZs with 100-m riparian corridors for biotic responses significantly related to disturbance type land-cover prescribed within TTZs. Sample size in most cases $n = 10$ except for LU 240 vs. BI ($n = 5$) and 100-m buffer ($n = 9$). HU = heavy urban, LU = light urban, TTZ = travel time zone, NA = nest associate, BI = benthic invertivore, ns = not significant.

| Biota | Biotic metric | Land-cover type and TTZ | TTZ | | 100-m buffer | |
|-------------------|------------------|-------------------------|-----------------------------------|----------------------------------|----------------------------------|----------------------------------|
| | | | correlation | regression | correlation | regression |
| Macroinvertebrate | | | | | | |
| Fish | Shredder density | HU 90 | p=0.006 r ² =0.887 | p<0.001 r ² =0.787 | ns | ns |
| | Shredder density | LU 150 | p=0.003 r ² =0.900 | p<0.001 r ² =0.810 | p=0.003 r ² =0.859 | p=0.003 r ² =0.738 |
| | Midge density | LU 150 | p=0.006 r ² =0.797 | p=0.006 r ² =0.635 | p=0.018 r ² =0.759 | p=0.018 r ² =0.577 |
| | NA density | LU 240 | p=0.015 r ² =-0.945 | p=0.015 r ² =0.893 | ns | ns |
| | BI density | HU 120 | p=0.007 r ² =0.784 | p=0.007 r ² =0.615 | p=0.037 r ² =0.663 | p=0.037 r ² =0.440 |
| | | | | | | |

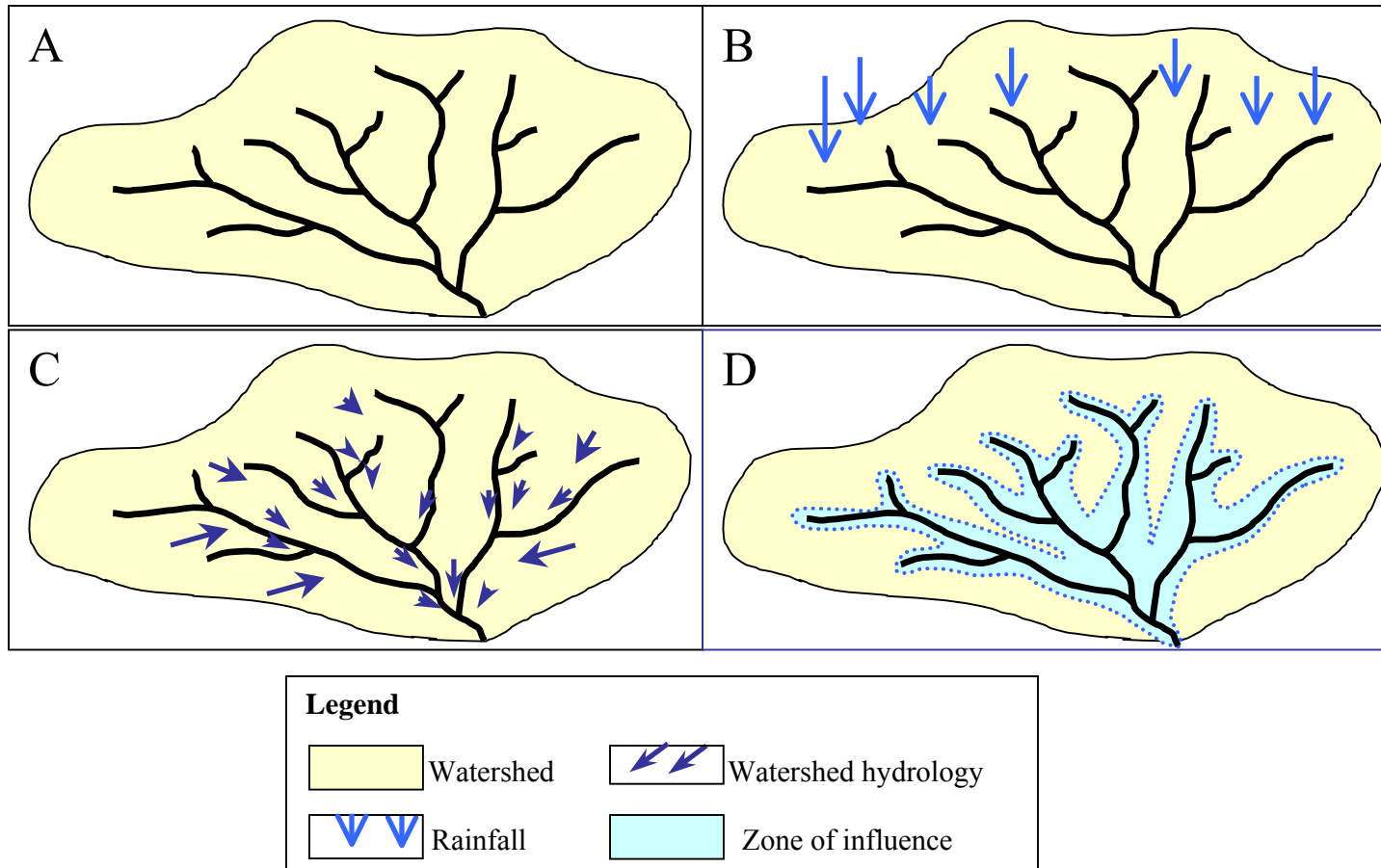


Figure 2.1. Theoretical zone of influence defined by a portion of the hydrologic cycle. Near-stream rainfall travels along flow vectors to stream channels and ultimately to the watershed outlet or stream reach where response variables are measured. Panel A shows a typical stream network and the watershed boundary defined by the outlet. Panel B shows a simulated, uniform rainfall over the entire watershed. Panel C shows the flow vectors resulting from rain. Panel D shows an example watershed sub-portion defined by the location and intensity of hydrologic activity.

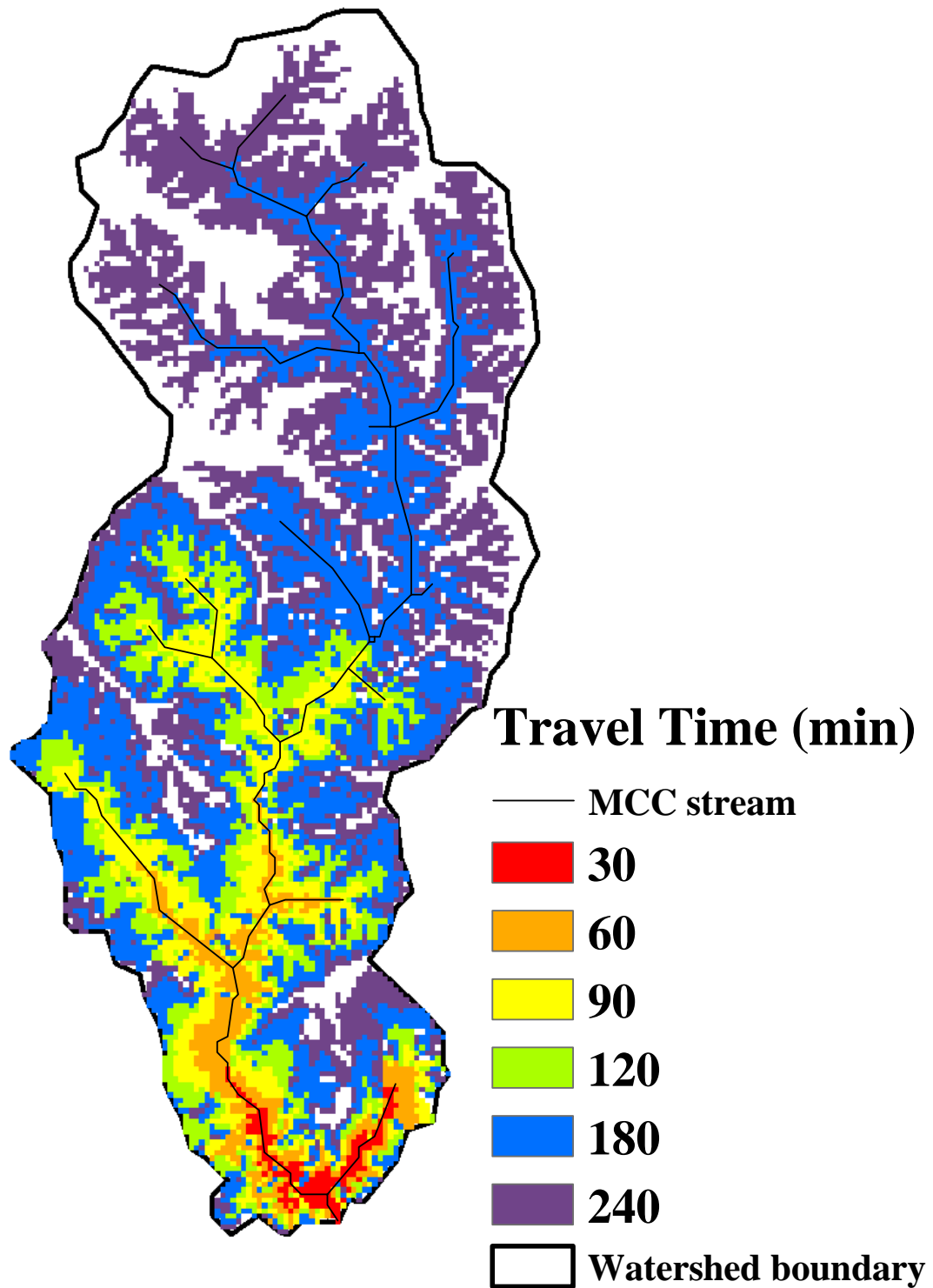


Figure 2.2. Example watershed (MCC) showing six travel time zones. White portion of watershed indicates areas where travel time was greater than 240 minutes.

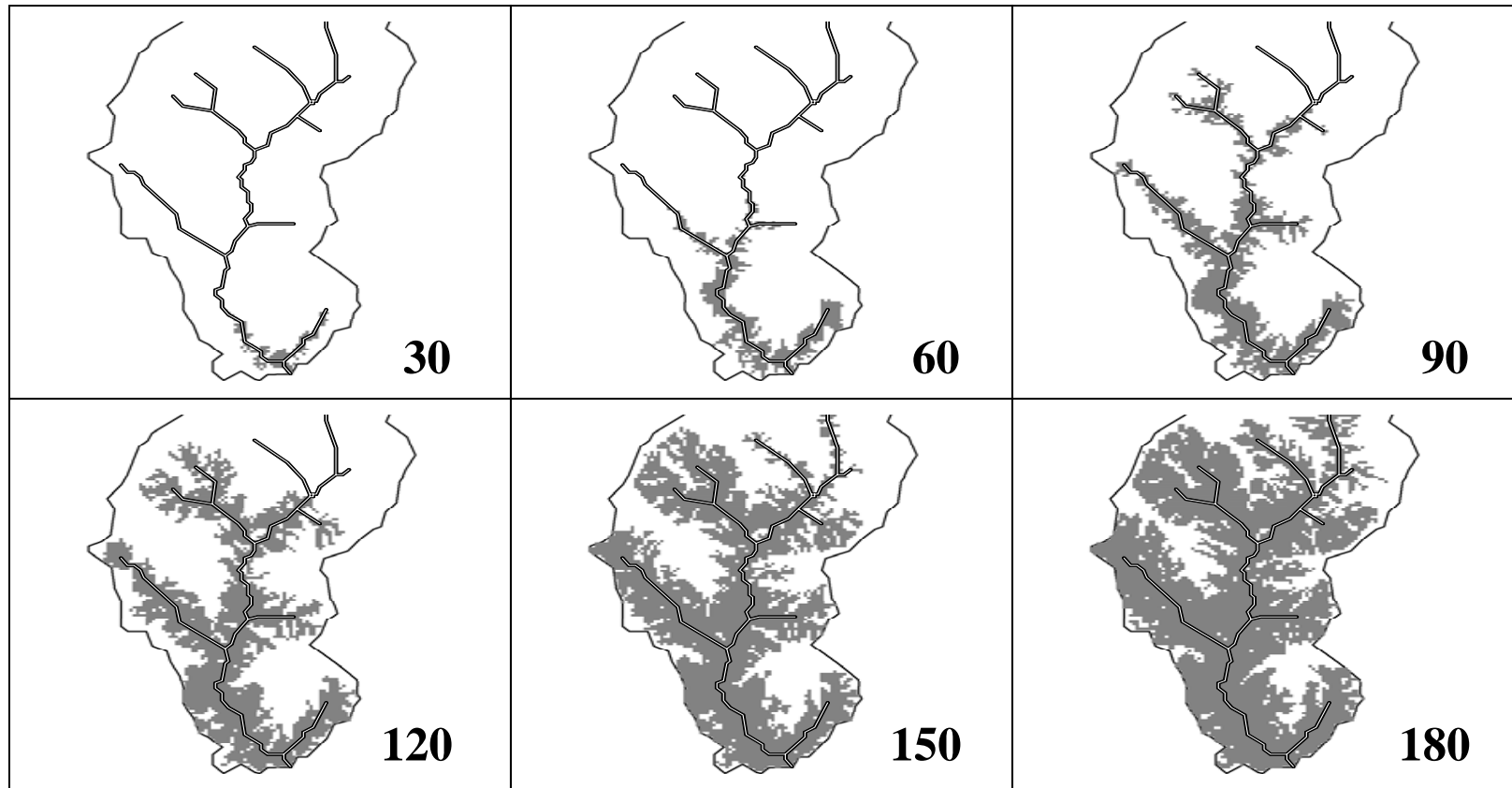


Figure 2.3. Visual comparison of 100-m riparian zones (dark shading) with 30, 60, 90, 120, 150, and 180 min travel time zones (gray shading) in lower MCC watershed.

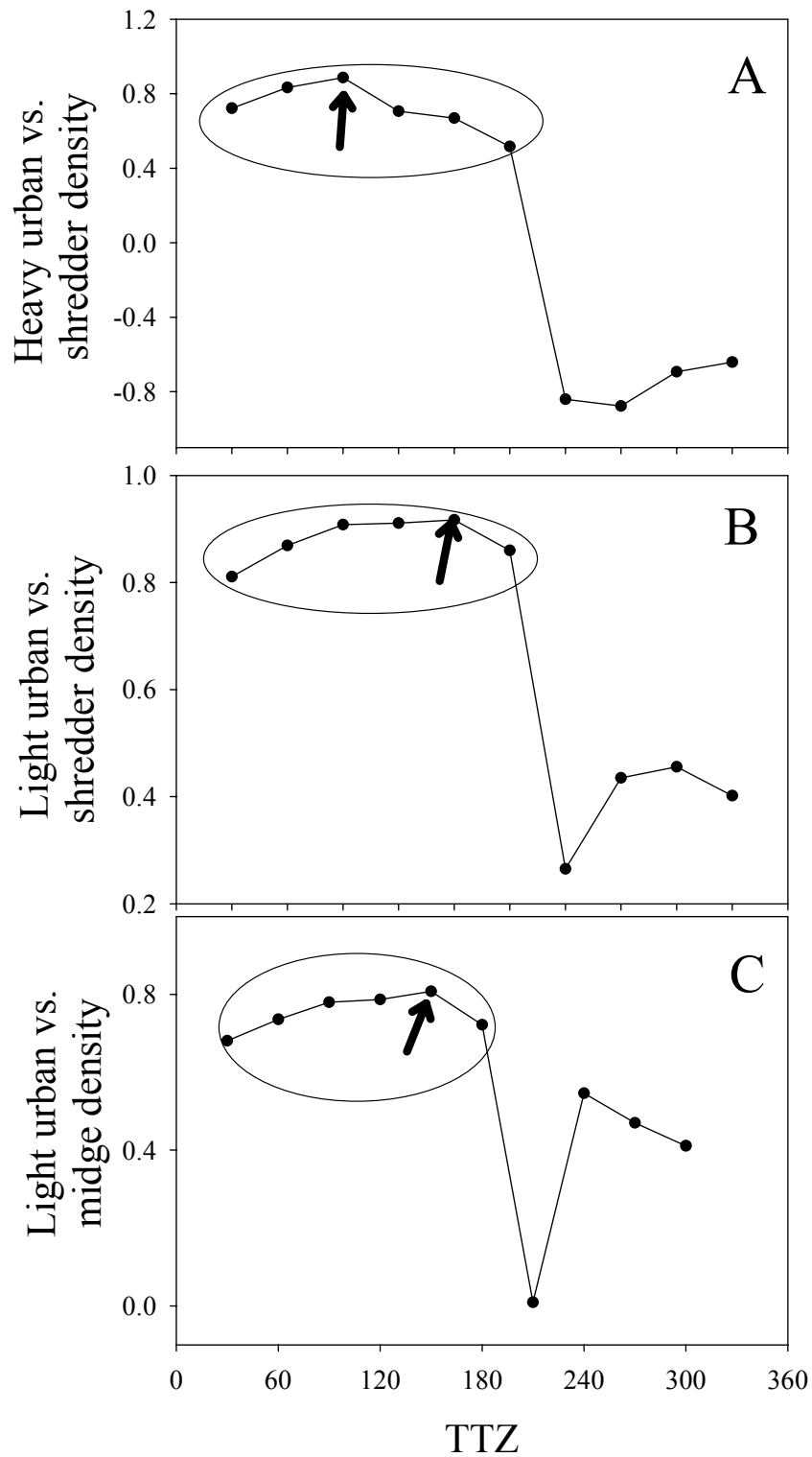


Figure 2.4. Correlation between TTZs (travel time zones) and shredder (panels A, B) and midge (panel C) density. Ovals indicate significant correlations and arrows indicate strongest correlation between TTZ and biotic response. Sign on y-axis indicates direction of correlation.

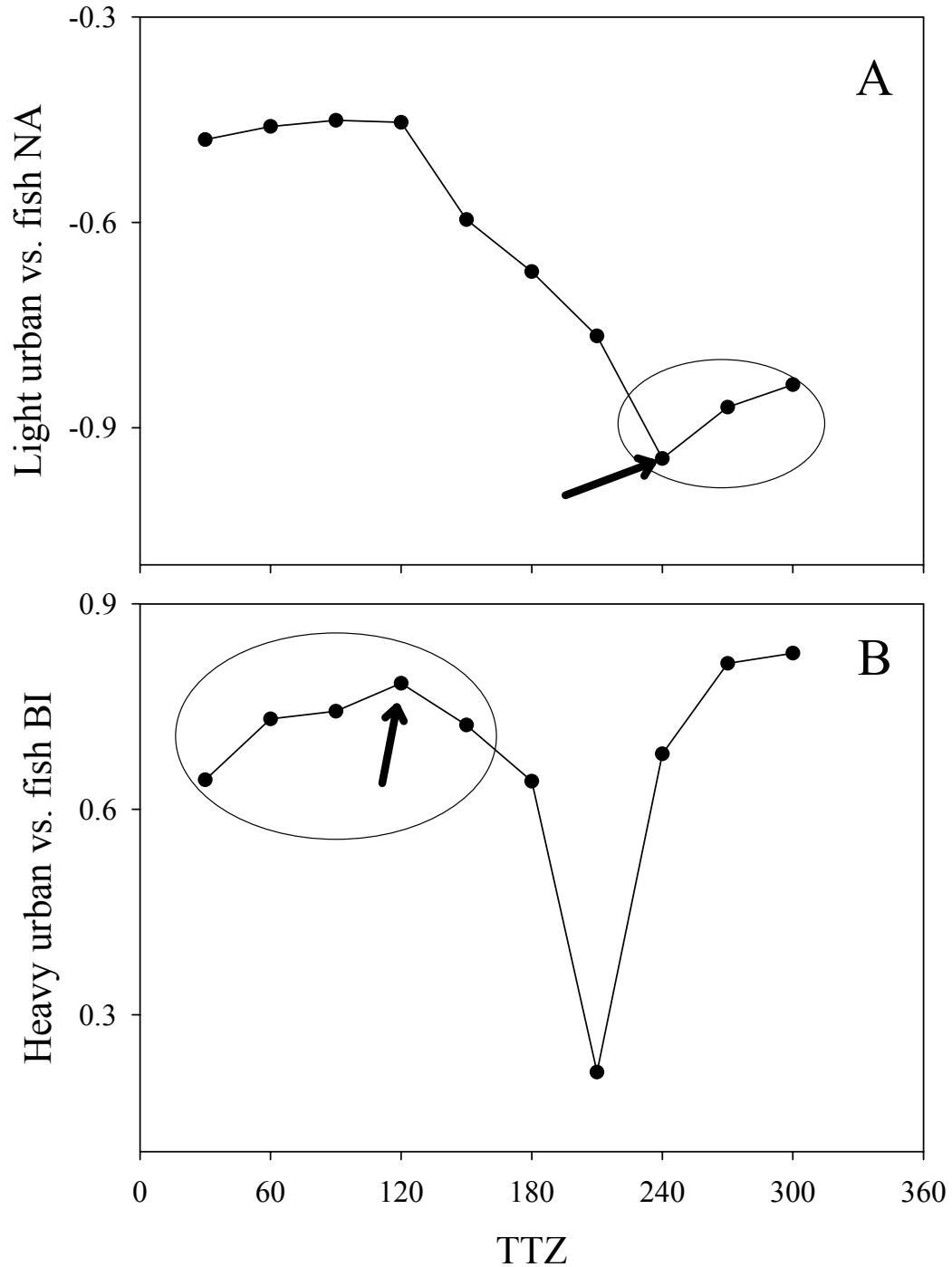


Figure 2.5. Correlation between TTZs (travel time zones) and fish NA (nest associate density, panel A) and fish BI (benthic invertivore density, panel B). Ovals indicate significant correlations and arrows indicate strongest correlation between TTZ and biotic response. Sign on y-axis indicates direction of correlation.

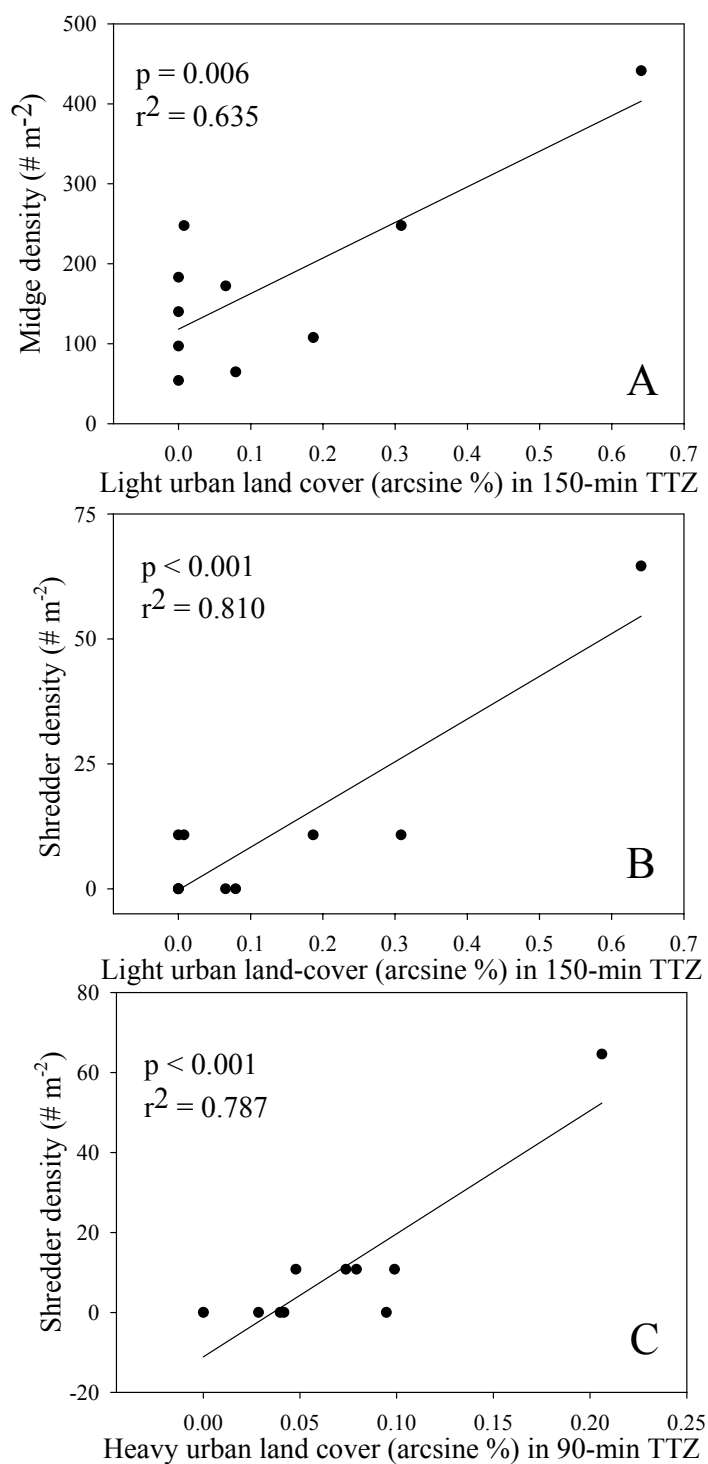


Figure 2.6. Linear regression showing relationships between most highly correlated TTZ and midge density (panel A) and shredder density (panels B,C). TTZ = travel time zone.

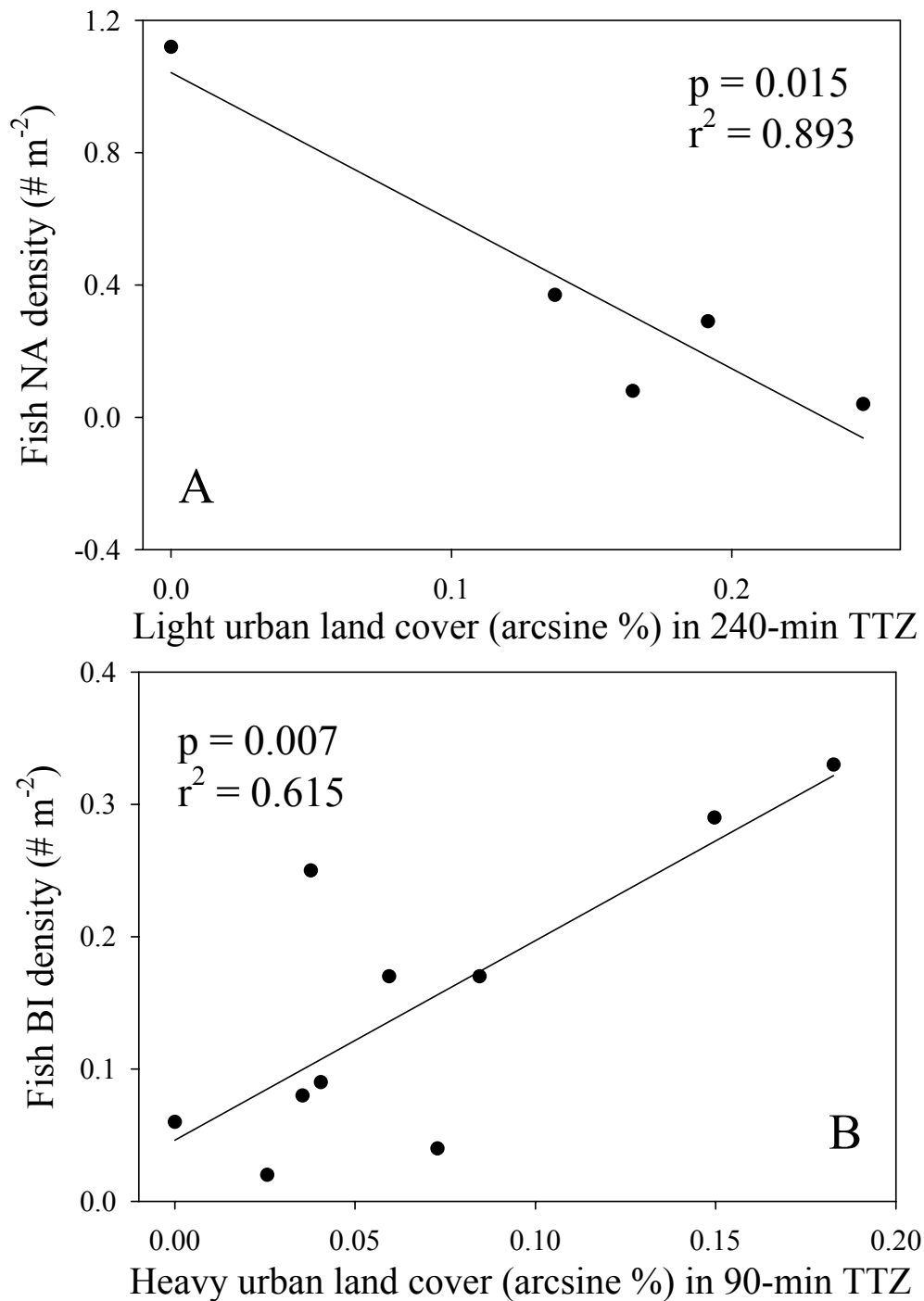


Figure 2.7. Linear regression showing relationships between most highly correlated TTZ and NA density (panel A) and BI density (panel B). NA = nest associate, BI = benthic invertivore, TTZ = travel time zone. $n = 5$ panel A, $n = 10$ panel B.

Chapter 3: Stream physical and biotic responses to rural development in historically agricultural watersheds

Abstract

I investigated whether rural development differentially influenced the physical and biotic characteristics of historically agricultural streams. I quantified physical and biotic elements in ten 3rd – 4th streams that drained historically agricultural watersheds located near Asheville, NC in the southern Appalachians. Five watersheds contained recent rural development in areas proximal to streams and five watersheds were not currently undergoing rural development. Five hydrologic, ten geomorphic, six erosional, three depositional (i.e. substrate), thirteen fish, and eight macroinvertebrate variables were estimated in the study streams. A total of 46 elements were compared using t-tests and MANOVA to detect differential influence of rural development and agricultural land-uses. Differences in land-cover influence were also assessed using ordination to detect subtle differences in taxonomic composition and abundance. Storm flow total suspended solid concentration (TSS) and substrate inorganic matter content were significantly lower in streams influenced by rural development. This suggests that watershed hydrology, sediment delivery, and sediment composition might be important factors influencing biota in streams draining agriculture versus rural development. Fish taxa richness and the density of non-guarding fishes were significantly higher in rural development sites versus agriculture sites. Though no significant differences in other fish or macroinvertebrate metrics were detected, ordination of sites by fish and macroinvertebrate species abundance separated stream types by land-use and suggested that biotic assemblages in developing streams were distinct from those in agricultural streams and that some taxa may have been influenced by rural development. My results suggest that assemblages were likely influenced by altered sediment dynamics associated with rural development. Streams did not appear to be further impaired by rural development, although assemblages were structurally different with stream type. I conclude that the influence of rural development to historically agricultural southern Appalachian streams is subtle but biotic assemblages in each stream type were different.

Introduction

Anthropogenic disturbance of the landscape is known to influence physical and biotic elements of stream ecosystems. Influences of agricultural and urban activities, including nutrient enrichment, tilling, animal grazing, chemical contamination, and building of human infrastructure, have been studied intensively for the last thirty years (Heimlich and Anderson 2001, Paul and Meyer 2001). This research has identified how streams respond to anthropogenic disturbance with respect to hydrologic (e.g., Poff and Allan 1995, Jones et al. 2000), geomorphic (e.g., Rhoads and Cahill 1999, Stanley et al. 2002), sediment (Trimble 1997), and biotic (e.g., Harding et al. 1998, Wang et al. 2001, Sutherland et al. 2002) elements. Agriculture is known to alter stream hydrology and geomorphology, reduce taxonomic diversity, and alter biotic structure and function (Harding et al. 1998, Cuffney et al. 2000). Urban development has also been shown to influence local hydrologic, geomorphic, and biotic stream elements (Wear et al. 1998, Paul and Meyer 2001). Both land-use types are known to impair physical and biotic stream elements.

Individually, agriculture and urban development induce characteristic physical responses in streams that can impair biota. Both disturbance types induce changes to hydrology and geomorphology (Heimlich and Anderson 2001). Both can enhance erosion due to the removal of rooted riparian vegetation (Neller 1988, Trimble 1997). In agricultural systems, erosional dynamics alter the concentration of in-stream suspended sediments, especially during storms. Removal of watershed vegetation also alters hydrologic activity in agricultural watersheds, which often results in higher maximum flows and more dynamic sediment movement (Bhaduri et al. 2000, Swank et al. 2001). Increased impervious surface cover (ISC) exacerbates overland flow hydrology in urban systems, where overland flow often dominates stream hydrographs (Jennings and Jarnagin 2002). Agricultural chemicals, including fertilizers and pesticides, introduced to streams through runoff also result in biotic impairment.

Rural development is an increasingly common phenomenon of recent interest to scientists, managers, and policy makers because it is a different form of urbanization that may differ in its influence. Rural development occurs in metropolitan or urban areas associated with urban sprawl, and includes the building of roads, parking lots, and housing developments. Unlike urbanization, rural development is typically characterized as conserving a greater degree of green space than true urban development (McDonnell and Pickett 1990, Heimlich and Anderson 2001). I define rural development as being similar to low-intensity urbanization but

occurring in association with smaller cities (i.e., population < 250,000) that sprawl into surrounding rural areas. Rural development could therefore induce a similar, but less severe, influence as urban development.

The combination of agricultural and rural development disturbances to streams is an increasingly common scenario associated with urban sprawl (Meyer and Turner 1992, Hunter 2000). The United Nations predicts that 85 - 90 percent of projected world population growth between 2000 and 2030 will occur as urban sprawl (United Nations 1999). The coupling of increased housing needs due to urban sprawl with the availability of formerly agricultural lands leads to rural development for housing developments and urban structures (Ramankutty et al. 2002). The decline of small-scale agriculture due to competition with agribusiness has increased the availability of agricultural lands to developers (Heimlich and Anderson 2001). In the southeastern US, rural development likely differs from urban development in the intensity and scope of the influence these disturbances have on the landscape.

I asked whether rural development altered physical and biotic characteristics of streams historically impaired by agriculture. Studies of stream responses to urban land-cover suggest that watershed hydrology can change dramatically relative to forested or un-urbanized systems (Paul and Meyer 2001). I predicted that rural development might induce a similar effect, but at a lower intensity. I expected rural development to induce flashier hydrographs and greater variation in hydrologic activity. I also expected that geomorphology and erosion dynamics would respond to increasing rural development relative to agricultural streams. I predicted that developing streams would become more channelized (i.e., have deeper and narrower stream channels) and potentially carry higher suspended sediment loads associated with erosion. I expected substrata in developing streams to have a smaller mean size and contain a higher amount of fine sediments relative to agricultural streams. I expected fish and macroinvertebrate assemblages to differ with rural development in response to altered hydrology and erosion. I predicted that biota sensitive to altered hydrology or sedimentation would be less abundant, or absent from developing streams. Fish and macroinvertebrate assemblages were predicted to show lower taxa richness and density, higher cosmopolitan fishes relative to endemics, and lower diversity of trophic (fish and macroinvertebrates) and reproductive (fish) strategies. I hypothesized that if rural development induced a measurable effect then streams would contain

different assemblages reflecting adaptation or acclimation of taxa to altered hydrology and sediment dynamics.

Methods

Research watersheds

Streams in the southern Appalachians have been affected by agriculture since pre-European settlement (SAMAB 1996). Several researchers investigating legacy effects of land-cover in this area have documented this history and the condition of local streams (Harding et al. 1998, Wear and Bolstad 1998). In western North Carolina, rural development is occurring as the city of Asheville sprawls into the surrounding, historically agricultural landscape.

I identified potential study areas in 3rd – 4th order streams draining watersheds featuring agriculture and rural development. I verified the presence of agricultural and development activity in watersheds near Asheville, visiting potential streams to observe watershed land-cover (i.e., the presence of agriculture and rural development). I quantified land-cover using the 1993 USGS national land-cover database (NLCD), combining NLCD land-use categories to agriculture, urban, forest, and other (USGS MRLC, draft, 2002; Homer et al. 2002). More recent data were unavailable for the study area preventing quantifying more recent land-cover. However, 1993 data largely verified visual estimates and provided approximations of land-cover in the study area (Table 3.1).

Suitable development sites needed to have been influenced by legacy agriculture and recent rural development located near an appropriately sized stream. These criteria proved difficult to meet, largely because rural development was spatially patchy and often did not occur in a portion of a watershed proximal to an appropriate-size stream. Often, rural development was located either too far from a stream or in an area not known to have been influenced by legacy agriculture. The five suitable watersheds meeting the criteria for rural development were compared to five similar streams (with respect to geologic, edaphic, and elevational characteristics) in the region that did not feature new developing areas (i.e., watersheds were mostly agricultural; Figure 3.1). I was able to identify five streams in the French Broad River basin that were historically impaired by agriculture but were currently (since at least 2000, ~2001) being developed to rural dwellings. Study watersheds ranged from 987 to 3552 ha (\bar{x} = 1908 ± 257 ha; Table 3.1).

In addition to land-cover constraints, watersheds were selected for similar geology, soil composition, stream network development, drainage area, and gradient using GIS. Every effort was made to ensure that the major difference among ten streams was the presence or absence of rural development proximal to stream channels. Controlling for these effects allowed us to attribute differences, with strong likelihood, to land-cover effects. To determine whether streams in historically agricultural watersheds were affected by rural development, I measured stream elements that have been shown to respond to agriculture and/or urbanization. Elements were quantified within 3rd – 4th order 100-m stream reaches defining the downstream watershed terminus.

Physical elements

Hydrologic features

Stream stage height was identified using a TopCon[®] laser survey unit to establish a permanent zero height of baseflow (0-cm). Discharge was measured and stage height recorded approximately monthly for 32 months at various flows. Rating curves estimating the relationship between stage height and discharge were developed to estimate discharge beyond the measurable range. Baseflow discharge (stage = 0-cm), storm flow discharge (stage = 50-cm), and the slope of the discharge / stage rating curve (an indication of flashiness) were estimated from these data. The difference in magnitude between baseflow and storm flow (Qdiff) was used as a measure of flashiness or how quickly streamflow responded to precipitation.

Watershed travel time for rainfall was estimated using Hydrologic Engineering Center – Hydrologic Modeling System (HEC-HMS) equations (See Chapter 2, this dissertation; USACE 2000). Estimates of surface roughness, hillslope gradient, and proximity to stream channels were used to calculate the time required for rainfall to travel between the terrestrial environment and the watershed outlet. We expected surface hydrology to be important to these streams affected by ISC and travel time estimates were used to quantify differences in land-cover factors (i.e., presence or absence of rural development). Mean and maximum travel times were calculated for each watershed and compared by land-use type.

Geomorphic features

Three channel cross-sections were measured (TopCon[®]) along each 100-m reach periodically in 2002 and 2003 to estimate changes to channel morphology. Eleven metrics were derived from these cross-sections (Montgomery and MacDonald 2002). Bank height, the

elevation difference between maximum thalweg depth and floodplain height, was calculated for each stream bank and averaged as a measure of channel deepening or incision magnitude. Bank incision ratio, the proportionate angles between maximum thalweg depth and floodplain height, was calculated for each bank. Both bank height and incision ratio were measured once during each sample year and the difference was calculated to estimate stream channel movement between sample dates.

I also calculated average baseflow width and depth and the mean width / depth ratio for each stream reach. Hydrologic and geomorphic information was used to calculate the Froude ($Fr = V / \sqrt{g \cdot D}$) number, where V is the mean water velocity (m s^{-1}), D is the mean baseflow depth (m), and g is the gravitational constant (m s^{-2} ; from Gordon et al. 2004).

Erosional features

Ten erosional metrics were estimated by measuring both suspended sediment concentration and bedload composition. Suspended sediments were collected using rising-limb sediment samplers (Braatz 1961) that collected stream sediment / water samples on the rising-limb of storm hydrographs. Bottles were collected after streams returned to baseflow and analyzed for total-suspended solids (TSS) and percent fine particulate organic matter (FPOM) using the ash-free-dry-mass (AFDM) method (Eaton et al. 1995). Ash-free-dry-mass was used to estimate the proportion of inorganic and organic content by filtering a known volume of stream water, drying and ashing the filtered sample, and calculating the dry and ash weights. The weight per volume of ashed material was used to approximate the concentration of inorganic sediments, and the difference between ash weight and dry weight to approximate the organic content. Similarly, bedload samples were collected using 50-cm long, 12-cm diameter PVC tubes buried within channels in the stream substrate. These containers passively collected bedload during intervals ranging from 0.5 to 1 month. Bedload samples were stored in 12 l containers, from which a subsample of fine benthic organic matter (FBOM; $0.45\text{-}\mu\text{m} < \text{FBOM} < 1\text{-mm}$) was removed from a slurry to estimate organic and inorganic matter content of bedload by the AFDM method. The remaining bedload sample was then dried and sieved to calculate D_{50} and percent fine substrates ($< 0.5\text{-mm}$).

Depositional features

Benthic substrate characteristics were estimated from three samples collected once at a riffle-pool interface downstream of a typical riffle in each stream. Samples were collected with a

spade, placed into a bucket, air dried, and dry sieved. This method only effectively sampled substrate smaller than 10-cm and likely underestimated the contribution of fine substrates because some material was lost during collection (Bunte and Abt 2001). However, I assumed the loss of fine substrate (e.g., sand) associated with the sample method would be similar among all streams. Similar to bedload sampling, wet substrate samples were slurried to collect a subsample for AFDM to estimate organic matter content in fine sediments.

Biotic assemblages

Fishes were sampled during August in 2002 and 2003 using single pass backpack electrofishing along 100-m stream reaches. Reaches were subdivided into 1 to 10-m sections using natural breaks in habitat units as boundaries between sub-units. A block seine (5-mm mesh) was established at the downstream end of each sub-unit and electrofishing helped herd fishes into the seine. Fishes were collected and identified to species after each sub-unit was sampled and returned downstream. Density was estimated as the number of individuals collected per stream area sampled (100-m X average stream width; # m⁻²). No differences were detected in density or species composition between the annual samples and only 2002 data were considered in further analyses.

Fishes were assigned to distributional, reproductive, and trophic guilds based on available information for each species. Distribution status reflects historic occurrence of a species within and across drainages (Scott and Helfman 2001). Cosmopolitan species are widely distributed through a drainage and span stream order and habitat gradients. Endemic species are localized, are often only found in a small portion of a drainage often in a very localized area. Endemic fishes have been associated with highland areas, or higher gradient, lower-order streams (Scott and Helfman 2001). Scott and Helfman (2001) showed that two distinct fish assemblages often occur in southern Appalachian streams reflecting high or low endemism.

Fishes were assigned to reproductive guilds based on recorded spawning habits of each species. Fishes vary in their mode of reproduction and can build nests, guard eggs, or simply broadcast eggs across the benthos. We placed each species encountered into 1 of 5 reproductive guilds (Jenkins and Burkhead 1994, Etnier and Starnes 1993). Nest builders (NB) are fishes that build and guard nests and included centrarchids and the fantail darter. Nest associates (NA) are fishes that often spawn in association with pebble mounds organized by another species and included Whitetail shiner, Warpaint shiner, and Central stoneroller minnows. Burying non-

guarders (NG) are fishes that hide eggs in substrate without further parental care and included species from several families. Broadcast spawners included species that spread eggs and milt over an area of substrate without burying or providing parental care and included Blacknose dace and White suckers.

Fish feeding habits were also used to categorize species by feeding strategy based on recorded knowledge of each species (Jenkins and Burkhead 1994, Etnier and guild 1993). Herbivores feed primarily on living plant material, algae, and detritus and included Bluegill, Redbreast sunfish, Whitetail shiner and Blacknose dace. Invertivores eat insects and crustaceans and were subdivided by the portion of the water column in which prey items are typically taken. Benthic invertivores pick prey items from substrata and often have specialized subterminal mouths designed for bottom feeding and included the Northern hogsucker. Drift invertivores lie-and-wait for drifting prey to be delivered to them, and included Warpaint and Saffron shiners. General invertivores are species known to collect prey items from multiple locations within a stream and included Creek chub, Central stoneroller, Rock bass, and Rainbow trout. Last, detritivores are species known to feed primarily on detritus and associated small organisms sifted from decaying organic matter and included White sucker and Mountain brook lamprey.

Macroinvertebrates were collected during late April 2003 using twenty quantitative (Surber, 500 μm mesh, 0.09 m^2 , 1.8 m^2 total area sampled per 100-m reach). Density ($\# \text{m}^{-2}$) was estimated from individual samples and average density by taxa calculated for each stream. Macroinvertebrates were preserved in 80% ethanol and identified to the lowest possible taxonomic level (typically genus). Taxa were placed into functional feeding groups (FFG) based on the classification by Merrit and Cummins (1996) or expert opinion for macroinvertebrates in southern Appalachian streams. Functional feeding groups included collector-filterers and collector-gatherers known to remove particulate matter from the water column, shredders that feed on decaying leaves, scrapers that have specialized mouthparts for removing algae from rock surfaces, and predators that consume other animals. I did not consider ontogenetic changes in feeding habits associated with early instars and assumed that individuals of a species could be classified into a single FFG.

Statistics

In total I measured or estimated five hydrologic, ten geomorphic, six erosional, three depositional (i.e., substrate) elements, thirteen fish, and eight macroinvertebrate metrics in each

stream (forty-six variables total). To detect differences attributable to rural development, each of the sample means were compared using simple t-tests between five agriculture and five rural development streams. Bonferroni adjustment was not necessary because the dependent variable was different for each comparison (e.g., baseflow discharge, particle size, macroinvertebrate taxa richness). I also used multivariate analysis of variance (MANOVA) to detect differences associated with organizational levels (e.g., hydrology). This technique allowed consideration of collinearity among intra-elemental variables (e.g., rating curve slope, mean travel time, etc.) that were present within each variable category. MANOVA was used because the technique can detect the influence of land-cover type on hydrology, geomorphology, erosional dynamics, substrate composition, biotic metrics, or some combination.

I predicted that rural development might induce a similar but less intense influence to streams than might urban development. To detect small differences in abiotic and biotic responses that might not be apparent with t-tests, I used Detrended Correspondence Analysis (DCA) to project sites in the space determined by abiotic or biotic characteristics (PCOrd v. 3.18, MJM software, Oregon, USA). DCA considers sites and taxa, projecting each into the space determined by weighted averages of taxa and site scores (Eigenvalues) along one or more axes.

Results

Physical responses

Hydrology

Hydrologic responses were not shown to be significantly different between stream type with either t-tests or MANOVA (Table 3.2). Mean baseflow discharge was $40 \pm 10 \text{ L s}^{-1}$ in developing streams and $36 \pm 6 \text{ L s}^{-1}$ in agricultural streams. Mean storm flow discharge (stream flow occurring at stage = 50 cm) estimated from rating curves was $1208 \pm 238 \text{ L s}^{-1}$ in developing streams, and $2163 \pm 1098 \text{ L s}^{-1}$ in agricultural streams. Rating curve slope averaged 0.9 ± 0.1 in streams draining both land use types. Mean watershed travel time was $178 \pm 30 \text{ min}$ in developing streams, and $113 \pm 39 \text{ min}$ in agricultural streams. Mean maximum travel time varied from $559 \pm 91 \text{ min}$ and $797 \pm 325 \text{ min}$ in developing and agricultural streams, respectively.

The difference between baseflow and storm flow (Qdiff) averaged $1167 \pm 240 \text{ L s}^{-1}$ in developing streams, and $2123 \pm 1094 \text{ L s}^{-1}$ in agricultural streams. This difference represents a discharge increase of 1 to 2 orders of magnitude for streams that averaged 40 L s^{-1} during typical

baseflow condition. Generally, all study streams appeared extremely flashy (C.L. Burcher, personal observation), which was supported by USGS stream gauges located on the mainstem Ivy River and near the confluence of Cane Creek on the mainstem French Broad River^{*}. I did not detect a difference in flashiness with stream type. Although I did not quantify flood recurrence interval, and have no historic record documenting floods in these streams, I observed several storms during the study period that would be considered catastrophic (i.e., streams breached 100 yr floodplain stage multiple times during a single year), and stormflow recorded by nearby USGS gauges during this period (March and April 2002 and 2003) were exceptionally high. Stream channels had likely been previously influenced by such flows, and further geomorphic changes would probably be induced only by extremely catastrophic flows beyond those observed during the study (Paul and Meyer 2001).

Ordination (DCA) of sites by hydrologic variables indicated that Paint and Middle Fork Creeks were outliers, separate from other streams and that these sites may be different with respect to the combined influence of the hydrologic variables I measured (Table 3.2).

Geomorphology

No significant geomorphic differences were detected between stream types using t-test or MANOVA (Table 3.3). Bank height and incision ratio varied little between two sample years, averaging 1.3 ± 0.0 m in year one for both stream types and 1.3 ± 0.0 m (dev) and 1.4 ± 0.1 m (ag) in year two. Bank height changed little between sample years and was 0.1 ± 0.0 m in developing streams and 0.2 ± 0.1 m in agricultural streams. Similarly, bank incision ratio averaged 33 % in developing streams during both years and averaged 30 % (year 1) and 34 % (year 2) in agricultural streams. Incision ratio changed an average of 2 ± 1 % in developing streams and an average of 5 ± 3 % in agricultural streams between sample years. Mean baseflow width was 3.7 ± 0.6 m in developing streams and 4.5 ± 0.3 m in agricultural streams. Mean baseflow depth was 0.14 ± 0.02 m in developing streams and 0.19 ± 0.02 m in agricultural streams. Mean width to depth ratio was 32 ± 9 in developing streams and 26 ± 4 in agricultural streams. The average Froude number was 0.14 ± 0.02 and 0.11 ± 0.02 in developing and agricultural streams, respectively, indicating that all streams were well below the threshold of critical flow.

^{*} <http://waterdata.usgs.gov/nwis/rt>

When sites were arranged in geomorphic space, DCA ordination indicated that Robinson Creek (developing) and Brush Creek (agriculture) were separate from other streams but that no land-cover influence was apparent. Separation of these two sites was related to the width / depth ratios. This could be due to Robinson Creek being exceptionally wide and shallow, whereas Brush Creek was narrow and deep (Table 3.3). Other sites clustered together intermediate to Brush and Robinson creeks, and no land-cover influence was apparent.

Erosional sediment

Storm flow TSS concentrations were estimated from TSS rating curves (relating discharge to TSS concentration) generated for four developing and two agriculture sites (Table 3.4). Storm flow TSS was not estimated for other streams due to lack of storm TSS samples. Storm flow TSS concentration differed significantly between land-cover types (t-tests $p < 0.001$), averaging $0.20 \pm 0.10 \text{ g l}^{-1}$ in developing streams and $1.4 \pm 0.0 \text{ g l}^{-1}$ in agricultural streams (Fig. 3.2A). However, percent organic matter (\bar{x} dev = $12 \pm 3 \%$; \bar{x} ag = $24 \pm 11 \%$) of suspended solids did not differ between stream types (Table 3.4).

Bedload characteristics were also similar between stream types and showed no significant land-cover effect (Table 3.4). Bedload D_{50} averaged $2.9 \pm 0.4 \text{ mm}$ in developing streams and $2.2 \pm 0.9 \text{ mm}$ in agricultural streams. Bedload mean percent fines averaged $32 \pm 4 \%$ in developing streams and $36 \pm 2 \%$ in agricultural streams. Bedload % organic matter was similar in each stream type and averaged $17 \pm 1 \%$ in developing stream and $13 \pm 1 \%$ in agricultural streams.

Ordination of erosional metrics indicated that East and West Fork Bull Creeks (agriculture) and Brush Creek (developing) were separate from a group of the seven other streams. However, this separation was likely influenced by zero values and reduced sample size associated with sampler loss or inadequate replication of erosional characteristics (Table 3.4). No land-cover influence associated with geomorphic attributes was apparent with DCA.

Depositional substrate

Depositional metrics were similar in streams draining different land-use types. However, substrate organic matter content (FBOM) was significantly higher in developing sites ($p < 0.05$), averaging $6.8 \pm 0.3 \%$ (vs. $5.8 \pm 0.2 \%$ in agricultural sites; Fig. 3.2B). Substrate D_{50} was similar, averaging $14.7 \pm 3.5 \text{ mm}$ in developing sites and 17.0 ± 3.1 in developing sites (Table 3.5). Percent fine substrate was also similar among stream types, averaging $13.7 \pm 4.4 \%$ in

developing sites and 14.2 ± 4.3 % in agricultural sites. Ordination of sites by substrate attributes did not indicate grouping structure or a land-use effect.

Biotic assemblages

Fifteen fish species were collected from streams and Robinson Creek (developing site) contained the highest taxa richness in any single stream (11 species, Table 3.6). Developing streams were dominated by Creek chub and Central stoneroller whereas Blacknose dace and Fantail darter were dominant in agricultural streams. Whitetail shiner and rainbow trout were absent from developing stream whereas agricultural streams did not contain Mottled sculpin, Mountain brook lamprey, Rock bass, Saffron shiners, or Redbreast sunfish. Fish taxa richness was significantly ($p = 0.017$) higher in developing sites, averaging 9 ± 0.9 taxa as opposed to agricultural stream fish taxa richness, which averaged 6 ± 0.6 taxa (Fig. 3.3A). Non-guarding fish density was also significantly ($p = 0.007$) higher in developing streams (Fig. 3.3B). In general, fish assemblage metrics were similar among streams draining the two stream types. Average total fish density was not different between stream types, and averaged 0.9 ± 0.2 in developing streams and 1.3 ± 0.3 in agricultural streams (Table 3.7). No other differences were detected in fish assemblages between stream types using t-tests. However, cosmopolitan fishes numerically dominated in both stream types. Stream trophic structure was dominated by herbivores and reproductive structure by either non-guarders (Fig. 3.3B) or nest associates (Table 3.7).

Despite general lack of significant differences between stream types suggested by inferential statistics, ordination of sites in fish species space suggested that assemblages differed with stream type. The arrangement of sites by species composition using DCA suggested separation of sites based on fish taxa and further explained the variation behind this separation as being a result of distinct assemblage composition in each stream type (Fig. 3.4). Axis 1 represented a gradient of species density and was largely driven by species absent in one land-use type (e.g., Redbreast sunfish present only in developing streams). Little variation existed in axis 2 (Eigenvalue 0.04): axis 1 having a much higher Eigenvalue (0.5). This suggests that most of the variation in assemblage structure can be explained by the occurrence and relative density of each taxa. Further, DCA distinguished between stream types based on fish assemblage structure. Detrended correspondence analysis suggested that developing stream assemblages were dominated by cyprinids including Warpaint shiners, Blacknose dace, Saffron shiners,

Central stonerollers, centrarchids including Bluegill, Redbreast sunfish, and Rock bass, and Mountain brook lamprey (Fig. 3.4). Separation of agricultural streams by ordination was largely driven by assemblages in these streams being dominated by Northern hogsuckers, Fantail darters, and Whitetail shiners.

Macroinvertebrate assemblages in developing streams were dominated by dipterans and largely by chironomids (Table 3.8). Agricultural streams also contained high midge density, but were dominated by ephemeropterans of the genera *Ephemerella*, *Stenonema*, and *Epeorus* (Table 3.8). Nine taxa co-occurred in both stream types, most notably Chironomidae, pleurocerid snails, ephemereid mayflies, *Psephenus* and *Stenelmis* beetles, tipulid flies, and hydropsychid caddisflies. Despite these similarities streams contained many taxa that only occurred in one stream type.

None of the macroinvertebrate metrics I estimated differed significantly between stream types (Table 3.9). Mean taxa richness was 11 ± 2 for all streams. Average total macroinvertebrate density was 700 ± 199 in developing streams and 654 ± 202 in agricultural streams. Midges comprised between 19 (agriculture) and 33 (developing) % of invertebrates by density (dev $\bar{x} = 230 \pm 57 \text{ m}^{-2}$; ag $\bar{x} = 121 \pm 35 \text{ m}^{-2}$). Shredders were nearly absent from agricultural streams ($\bar{x} = 2 \pm 2 \text{ m}^{-2}$) but averaged $19 \pm 11 \text{ m}^{-2}$ in developing streams. Macroinvertebrate assemblages in both stream types were dominated scraper or collector-gathering genera. Scrapers (dev $\bar{x} = 205 \pm 60 \text{ m}^{-2}$; ag $\bar{x} = 151 \pm 82 \text{ m}^{-2}$) comprised 29 % of developing stream and 23% of agricultural stream assemblages. Collector gatherers (dev $\bar{x} = 138 \pm 59 \text{ m}^{-2}$; ag $\bar{x} = 245 \pm 89 \text{ m}^{-2}$) comprised 20 and 37% of developing and agricultural streams assemblages, respectively. The average density of collector-filters was $60 \pm 22 \text{ m}^{-2}$ in developing streams and $121 \pm 25 \text{ m}^{-2}$ in agricultural streams, and did not differ significantly between the two land-uses. Predators comprised 7% of assemblages in developing streams ($\bar{x} = 47 \pm 17 \text{ m}^{-2}$) and only 2% in agricultural streams ($\bar{x} = 15 \pm 8 \text{ m}^{-2}$).

Detrended correspondence analysis by macroinvertebrate taxa indicated near separation of streams by stream type (Fig. 3.5). The distribution of sites along axis 1 (Eigenvalue 0.48) indicated two distinct macroinvertebrate groups that were separated by taxa present in only one stream type. Axes 2 and 3 did not add explanatory value to axis 1 and were not interpreted.

Discussion

Physical responses

Total suspended solid concentration was significantly lower ($p < 0.001$) in streams influenced by rural development than streams draining predominantly agricultural land-use (Figure 2A). Although I initially expected TSS to increase with rural development, I attribute this difference to altered overland flow and channel hydrology in developing streams. Finkenbine et al. (2000) suggested that initially, urbanizing watersheds contribute more suspended sediments associated with construction to streamflow, but during the second phase of urbanization, suspended sediment loads decrease relative to pre-disturbance conditions. Lower TSS concentration in developing streams could be because study streams were no longer receiving sediments associated with the initial phases of construction. However, this would imply that some hydrologic element interacted with sediments, and I did not detect an effect of rural development on the hydrologic elements quantified in these study streams. It is possible that some unmeasured hydrologic effect could have been influencing TSS in the streams I studied, for example, streambed shear stress (Krishnappan 2004) or terrestrial erosion. Surface runoff in agricultural areas may have been more erosional, delivering more suspended material to river channels compared to runoff associated with rural development. Similarly, it is possible that runoff in developed areas was exposed to a smaller volume of soil than agricultural runoff. This is a plausible explanation because rural development features more impervious surface cover, which has been shown to reduce the erosional potential of land surfaces (Jennings and Jarnagin 2002). Many researchers have attributed lower suspended particulates to increased impervious surface cover (Booth 1990, Crosbie and Chow-Frasier 1999). Similarly, in-stream sediment re-suspension is known to contribute to total suspended solid concentration, and it is uncertain whether higher TSS was due to near-stream erosion, in-stream re-suspension, or bank failure (Owens and Walling 2002). It is likely that developing streams carried a reduced suspended sediment load as a result of lower watershed terrestrial erosion due to the combination of more ISC, and lower in-stream particulate re-suspension.

Substrate organic matter standing stocks (% FBOM) were significantly higher in streams influenced by rural development (Fig. 2B). This suggests that the inorganic matter (IM) proportion of substrata was lower with rural development, and is of particular interest considering that total suspended solids were also lower in developing streams. Coupling TSS

and IM information suggests that agricultural streams were both more erosional in the terrestrial environment (as indicated by higher TSS), and hydrologically more disturbing to the substrate. Conversely, streams draining rural development had lower suspended sediments, yet FBOM concentrations were higher relative to agricultural streams. It is possible that retention mechanisms differed with land-cover type, though I did not quantify these features (Wang et al. 2001). Ultimately, these observations suggest that hydrology was different in the presence of rural development, yet I did not observe differences in the hydrologic elements I measured. However, the lack of significant differences in hydrologic elements may have been a result of high variance associated with these measures, and the difficulties in quantifying them (see Table 2). It is possible that my measurement of hydrology was inadequate to capture differences in hydrologic dynamics associated with land-use types. Hydrologic elements are notoriously difficult to quantify due to the stochastic nature of storms (Wondzell and Swanson 1999, Lake 2000), variability between high-flow periods (Resh et al 1988), and long-term hydrologic patterns (Richter et al. 1992).

Biotic responses

Ordination of streams by density of fish and macroinvertebrate taxa suggested that distinct assemblages were present in each stream type (Figs. 3.4, 3.5). In each scenario, sites separated (or nearly so) into two groups representing developing or agricultural streams. Ordination clearly indicated unique assemblages with land-use type, and I attribute this separation to altered hydrology and sediment dynamics. Alternatively, the nested condition of sites within parent watersheds (e.g., agricultural sites all drain into Ivy Creek, developing sites all located near Cane Creek) could explain differences in taxonomic composition. However, mainstem streams were located in close proximity (~25 km), were joined by the French Broad River, and would likely not inhibit fish movement between drainages. Similarly, watersheds were within 25 km of each other and limited macroinvertebrate dispersal could not explain the differences in macroinvertebrate assemblage composition we observed. If we assume the likelihood of a taxa being present was similar for each stream type, the presence of rural development near streams is a strong explanation of observed taxonomic differences.

Fish assemblages

Combination of ordination information and reproductive ecology of taxa helps explain differences in fish assemblage structure with stream type. Developing streams contained

Redbreast, Bluegill, and Rock bass sunfishes whereas centrarchids were absent from agricultural streams. Mottled sculpin was absent from agricultural streams, but occurred in 4 of 5 developing streams. Higher density of non-guarding fishes in developing streams likely resulted from the ability of centrarchids and sculpin to clean substrata for nests or tolerance to the hydrologic regime present in developing streams. Higher inorganic sediments associated with agricultural substrata could explain the reduced representation of nest builders in these streams. Nest associates that were largely comprised of Central stoneroller and Whitetail shiner (Cyprinidae) dominated agricultural streams. These two species typically spawn in association with aggregate nest builders (e.g., Creek chub) but can spawn successfully in the absence of nests (Jenkins and Burkhead 1994). The only nest-builders encountered in agricultural streams were Bluegill and the percid Fantail darter and I assumed that cyprinid nest associates were spawning via alternative methods in agricultural streams (Etneir and Starnes 1996).

Fish distribution status also helps explain site separation with ordination. Three fish species endemic to highland streams, Warpaint and Saffron shiners and Mottled sculpin, were collected in this study. Only Warpaint shiners were collected in agricultural streams, and the reduced representation of endemic species could reflect higher relative ability of diverse habitat and trophic resources in developing streams. Sculpin rely on benthic interstices for feeding and reproduction and their absence from agricultural streams could be related to the increased inorganic sedimentation we observed with agriculture. Higher density of endemic species generally reflects improved conditions in developing as compared to agricultural streams. Endemic species typically represent more facultative resource use and are associated with streams that offer broad trophic and habitat resources (Scott and Helfman 2001)

Macroinvertebrate assemblages

Although total density of macroinvertebrates was similar in the two stream types, taxonomic composition and trophic structure suggested that differences were present for which statistics could not account. Some variation in ordination patterns of macroinvertebrate taxa can also be explained by trophic habits. Though not significantly different, trophic structure (i.e., functional feeding group composition) in developing streams was largely composed of leaf shredding and algae scraping taxa (73% of non-midge taxa), whereas collector-gatherers and collector filterers (69% of non-midge taxa) dominated agricultural streams. I attribute increases to scraper density in developing streams to the reduction of inorganic matter associated with

substrata. Scrapers depend on benthic algae, and scouring or filling associated with fine inorganics may have decreased the suitability of substrata for algal production (Sutherland et al. 2002, Matthaei et al. 2003). Developing stream banks were often vegetated to some degree, whereas agricultural streams were nearly always denuded. Higher collector-filterer density in agricultural streams is largely attributable to hydropsychid caddisflies that are known to filter particulate organic matter from the water column using silk nets located on rock surfaces. Collector-gatherers rely on motility to locate and collect organic matter and were largely comprised of *Ephemerella* and *Epeorus* in agricultural streams. In contrast, hydropsychid caddisflies and *Ephemerella* were much less abundant in developing streams and *Epeorus* was absent.

Influence of land-use

Rural development in historically agricultural landscapes appeared to have minimal affect on the physical and biotic elements I measured in this study. However, some differences suggest a relationship between assemblage structure, sediment dynamics, and watershed hydrology. Fish assemblages influenced by rural development were comprised of more endemic species, more centrarchids, Mottled sculpin and were characterized by fishes that were non-guarders. Invertebrate assemblages influenced by rural development included taxa that feed largely on algae and leaves, whereas invertebrate assemblages in agricultural streams more likely depended on transported detritus. Rural development appeared to improve conditions relative to agriculture with respect to biodiversity.

The relationship between land-use and stream impairment (abiotic and biotic) can be summarized graphically through time (Fig. 3.6). Pre-European agriculture most certainly increased impairment to southern Appalachian streams that were previously forested. Researchers have hypothesized that reforestation of agricultural areas may improve stream conditions and reduce impairment (Harding et al. 1998, McTammany 2004). Three possible scenarios exist with respect to the future trajectory of impairment associated with rural development in formerly agricultural areas: 1) conditions worsen and impairment increases, 2) conditions change little and improvement continues on the same trajectory; and 3) conditions improve and the reduction to impairment accelerates. My results suggest that scenario 3 may apply whereby rural development contributes to reduced impairment associated with lower sediment input to southern Appalachian streams.

Conclusions

If we assume that these streams were similar enough in most respects excepting the presence or absence of rural development then these data suggest two conclusions. First, rural development did not appear to significantly alter the stream ecosystems I studied. This could be because there had been insufficient time for the streams to respond to this disturbance. The watershed development I investigated was fairly recent, and it is possible that the full impact of these changes has yet to be realized by the stream elements I measured. Second, if the full impact of rural development had been realized, it appears that rural development subtly improved conditions for biota.

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Table 3.1. Stream names, site codes, watershed area, stream length, and land-cover estimates for ten study streams. Dev = developing sites; Ag = historically agricultural sites not featuring rural development. Land-cover estimates for whole watersheds, and classified according to MRLC categories. 'Other' land-cover category included open water, wetland vegetation, and barren areas.

| Stream | Stream code | Land-cover category | Watershed area (Ha) | Stream length (km) | Land cover (%) | | | |
|-----------------------|-------------|---------------------|---------------------|--------------------|----------------|-------------|-------|-------|
| | | | | | Forest | Agriculture | Urban | Other |
| Avery Creek | AVE | Dev | 1744 | 12 | 75 | 21 | 1 | 2 |
| Brush Creek | BRS | Dev | 987 | 8 | 74 | 22 | 1 | 2 |
| Hooper's Creek | HDS | Dev | 3552 | 28 | 75 | 22 | 1 | 2 |
| Merril's Cove Creek | MCC | Dev | 1349 | 9 | 78 | 16 | 5 | 2 |
| Robinson Creek | ROB | Dev | 1445 | 8 | 56 | 18 | 24 | 2 |
| East Fork bull Creek | EFB | Ag | 2050 | 15 | 80 | 19 | 0 | 1 |
| Gabriel's Creek | GAB | Ag | 1601 | 14 | 57 | 36 | 4 | 3 |
| Middle Fork Creek | MFD | Ag | 3049 | 23 | 20 | 75 | 0 | 4 |
| Paint Creek | PNT | Ag | 1286 | 16 | 77 | 22 | 0 | 1 |
| West Fork Bull Creek | WFB | Ag | 2015 | 15 | 76 | 22 | 0 | 2 |
| Mean(± 1 SE) Dev | | | 1815(509) | 13(4) | 72(0) | 20(1) | 7(1) | 2(0) |
| Mean(± 1 SE) Ag | | | 1703(327) | 14(2) | 62(12) | 35(12) | 1(1) | 2(1) |

Table 3.2. Summary of mean hydrologic responses measured in ten study streams. Site codes from table 3.1. Qdiff = difference between baseflow and storm flow discharge estimates.

| Stream | Rating curve slope | Baseflow discharge (L s^{-1}) | Storm flow discharge (L s^{-1}) | Qdiff (L s^{-1}) | Mean travel time (min) | Maximum travel time (min) |
|-----------------------|--------------------------|---|---|-----------------------------|---------------------------|------------------------------|
| AVE | 1.0 | 40 | 1925 | 1885 | 109 | 392 |
| BRS | 0.5 | 67 | 507 | 440 | 264 | 598 |
| HDS | 0.8 | 57 | 1467 | 1410 | 224 | 896 |
| MCC | 1.0 | 23 | 1185 | 1161 | 183 | 486 |
| ROB | 1.1 | 15 | 955 | 941 | 113 | 425 |
| EFB | 0.9 | 19 | 621 | 602 | 117 | 459 |
| GAB | 1.0 | 42 | 1960 | 1919 | 261 | 1021 |
| MFD | 0.8 | 52 | 990 | 939 | 45 | 1973 |
| PNT | 0.8 | 34 | 788 | 754 | 69 | 274 |
| WFB | 1.2 | 52 | 6454 | 6403 | 76 | 257 |
| Mean(± 1 SE) Dev | 0.9(0.1) | 40(10) | 1208(238) | 1167(240) | 178(30) | 559(91) |
| Mean(± 1 SE) Ag | 0.9(0.1) | 39(6) | 2163(1098) | 2123(1094) | 113(39) | 797(325) |

Table 3.3. Summary of mean geomorphic responses measured in ten study streams. Site codes from table 3.1.

| Stream | Mean bank height (m) | | Mean incision ratio (%) | | Bank height change (m) | Incision ratio change (%) | Mean baseflow width (m) | Mean baseflow depth (m) | Width / depth ratio | Froude number |
|--------------------------|-------------------------|----------|----------------------------|--------|---------------------------------|------------------------------------|----------------------------------|-------------------------------|---------------------------|------------------|
| | Year 2 | Year 1 | Year 1 | Year 2 | | | | | | |
| AVE | 1.4 | 1.2 | 26 | 23 | 0.2 | 3 | 4.2 | 0.15 | 29 | 0.11 |
| BRS | 1.4 | 1.3 | 33 | 34 | 0.1 | 1 | 1.7 | 0.19 | 9 | 0.14 |
| HDS | 1.3 | 1.4 | 42 | 46 | 0.1 | 4 | 4.9 | 0.13 | 38 | 0.22 |
| MCC | 1.3 | 1.3 | 33 | 33 | 0 | 1 | 3.1 | 0.16 | 19 | 0.09 |
| ROB | 1.2 | 1.2 | 29 | 30 | 0 | 1 | 5.0 | 0.08 | 63 | 0.14 |
| EFB | 1.8 | 1.8 | 35 | 33 | 0 | 1 | 4.3 | 0.2 | 23 | 0.15 |
| GAB | 1.1 | 1.2 | 21 | 22 | 0.1 | 1 | 4.8 | 0.13 | 37 | 0.16 |
| MFD | 1.2 | 1.1 | 30 | 28 | 0.1 | 3 | 4.6 | 0.2 | 23 | 0.07 |
| PNT | 1.0 | 1.4 | 31 | 47 | 0.4 | 16 | 3.5 | 0.25 | 14 | 0.09 |
| WFB | 1.6 | 1.3 | 35 | 30 | 0.2 | 5 | 5.2 | 0.17 | 31 | 0.06 |
| Mean(± 1 SE) Dev | 1.3(0.0) | 1.3(0.0) | 33(3) | 33(4) | 0.1(0.0) | 2(1) | 3.7(0.6) | 0.14(0.02) | 32(9) | 0.14(0.02) |
| Mean(± 1 SE) Ag | 1.3(0.2) | 1.4(0.1) | 30(3) | 32(4) | 0.2(0.1) | 5(3) | 4.5(0.3) | 0.19(0.02) | 26(4) | 0.11(0.02) |

Table 3.4. Summary of mean (± 1 SE) erosional responses measured in ten study streams. Site codes from table 3.1. TSS = total suspended solids. Dashes denote parameters not estimated. Storm flow discharge occurred at stage = 50 cm. Asterisks (*) denote significant differences between means (t-test, $\alpha < 0.05$).

| Stream | *Mean storm flow TSS (g l ⁻¹) | Mean storm flow TSS organic matter (%) | Mean storm flow TSS inorganic matter (%) | Bedload D ₅₀ (mm) | Bedload fine substrate (%) | Bedload organic matter (%) |
|--------------------------|---|---|---|---------------------------------|-------------------------------|----------------------------------|
| AVE | 0.02 | 19 | 81 | 1.9 | 37 | 20 |
| BRS | 0.39 | 7 | 93 | - | - | - |
| HDS | 0.26 | 10 | 90 | 4.4 | 20 | 15 |
| MCC | - | - | - | 1.1 | 41 | 18 |
| ROB | 0.11 | 13 | 87 | 4.1 | 29 | 15 |
| EFB | - | - | - | - | - | - |
| GAB | 1.36 | 13 | 87 | 3.1 | 33 | 14 |
| MFD | - | - | - | 1.4 | 41 | 11 |
| PNT | - | - | - | - | 35 | 15 |
| WFB | 1.49 | 35 | 65 | - | - | - |
| Mean(± 1 SE) Dev | *0.20(0.10) | 12(3) | 87 (3) | 2.9(0.4) | 32(4) | 17(1) |
| Mean(± 1 SE) Ag | *1.43(0.00) | 24(11) | 76 (11) | 2.2(0.9) | 36(2) | 13(1) |

Table 3.5. Summary of depositional responses measured in ten study streams. Values are site means. Site codes from table 3.1. Asterisks (*) denote significant differences between means (t-test, $\alpha < 0.05$).

| Stream | Substrate D ₅₀ (mm) | Substrate organic matter (FBOM; %)* | Substrate fines (%) |
|-----------------------|--------------------------------|--|---------------------|
| AVE | 22.1 | 6.3 | 3.8 |
| BRS | 4.6 | 6.9 | 21.6 |
| HDS | 11.3 | 6.0 | 17.0 |
| MCC | 12.3 | 6.8 | 23.4 |
| ROB | 23.3 | 7.7 | 2.8 |
| EFB | 23.4 | 5.4 | 4.4 |
| GAB | 21.3 | 6.5 | 5.7 |
| MFD | 12.8 | 6.2 | 18.8 |
| PNT | 6.7 | 5.3 | 27.4 |
| WFB | 20.7 | 5.5 | 14.8 |
| Mean(± 1 SE) Dev | 14.7(3.5) | *6.8(0.3) | 13.7(4.4) |
| Mean(± 1 SE) Ag | 17(3.1) | *5.8(0.2) | 14.2(4.3) |

Table 3.6. Fish species collected, mean density by stream type, and guild assignment categories. Distribution status: c = cosmopolitan or widely distributed, e = endemic to local drainages. Reproductive guild: 1 = nest builder, guarder; 2 = nest associate, 3 = burying non-guarder, 4 = broadcast spawner. Trophic guild: 1 = herbivore, 2 = benthic invertivore, 3 = general invertivore, 4 = drift invertivore, 5 = detritivore.

| Species common name | Mean (SE) density (# m ⁻²) developing | Mean (SE) density (# m ⁻²) agricultural | Distribution status | Reproductive guild | Trophic guild |
|------------------------|--|--|------------------------|-----------------------|------------------|
| Creek chub | 0.288(0.05) | 0.04(0.02) | c | 3 | 3 |
| Blacknose dace | 0.17(0.04) | 0.22(0.05) | c | 4 | 1 |
| Northern hogsucker | 0.03(0.01) | 0.08(0.02) | c | 3 | 2 |
| Bluegill sunfish | 0.08(0.03) | 0.002(0.002) | c | 1 | 1 |
| Central stoneroller | 0.10(0.07) | 0.74(0.31) | c | 2 | 3 |
| Warpaint shiner | 0.06(0.05) | 0.03(0.02) | e | 2 | 4 |
| White sucker | 0.02(0.00) | 0.01(0.01) | c | 4 | 5 |
| Mottled sculpin | 0.06(0.03) | 0 | e | 1 | 2 |
| Fantail darter | 0.03(0.01) | 0.22(0.08) | n | 1 | 2 |
| Mountain brook lamprey | 0.02(0.00) | 0 | c | 3 | 5 |
| Rock bass | 0.002(0.002) | 0 | c | 1 | 3 |
| Saffron shiner | 0.03(0.02) | 0 | e | 3 | 4 |
| Redbreast sunfish | 0.002(0.002) | 0 | c | 1 | 1 |
| Whitetail shiner | 0 | 0.004(0.004) | n | 2 | 1 |
| Rainbow trout | 0 | 0.002(0.002) | n | 3 | 3 |

Table 3.7 Summary of fish assemblage responses. Values are site density estimates (# m⁻²) except TR (taxa richness) is number of fish species found at a site. Site codes from table 3.1. Asterisks (*) and letters denote significant effect of land-cover at alpha < 0.05. Cos = cosmopolitan; End = endemic; Herb = herbivore; BI = benthic insectivore; GI = general insectivore; DI = drift insectivore; Det = detritivore; NB = nest builder; NA = nest associate; NG = non-guarder; BC = broadcast spawner.

| Stream | Taxonomic | | Distributional | | Herb | Trophic | | | Det | NB | Reproductive | | |
|--------------------|-----------|---------|----------------|-------|-------|---------|-------|-------|-------|-------|--------------|-------|-------|
| | TR* | Density | Cos | End | | BI | GI | DI | | | NA | NG* | BC |
| AVE | 10 | 0.9 | 0.6 | 0.3 | 0.3 | 0.2 | 0.2 | 0.2 | 0.1 | 0.2 | 0.3 | 0.2 | 0.2 |
| BRS | 9 | 0.7 | 1.2 | 0.1 | 0.2 | 0.1 | 0.3 | 0.0 | 0.0 | 0.1 | 0.1 | 0.3 | 0.1 |
| HDS | 10 | 1.3 | 0.9 | 0.2 | 0.4 | 0.2 | 0.2 | 0.2 | 0.1 | 0.1 | 0.4 | 0.5 | 0.4 |
| MCC | 6 | 0.5 | 0.4 | 0.0 | 0.1 | 0.3 | 0.5 | 0.0 | 0.0 | 0.1 | 0.0 | 0.3 | 0.1 |
| ROB | 11 | 1.2 | 0.6 | 0.1 | 0.3 | 0.0 | 0.7 | 0.1 | 0.1 | 0.5 | 0.0 | 0.5 | 0.2 |
| EFB | 5 | 0.6 | 1.3 | 0.1 | 0.3 | 0.1 | 1.8 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.3 |
| GAB | 4 | 2.3 | 0.9 | 0.1 | 0.4 | 0.3 | 0.6 | 0.1 | 0.0 | 0.0 | 1.8 | 0.1 | 0.4 |
| MFD | 7 | 1.1 | 2.3 | 0 | 0.1 | 0.1 | 0.2 | 0.2 | 0.0 | 0.2 | 0.6 | 0.2 | 0.1 |
| PNT | 7 | 1.9 | 0.4 | 0 | 0.1 | 0.0 | 0.2 | 0.0 | 0.2 | 0.5 | 1.1 | 0.2 | 0.1 |
| WFB | 7 | 0.9 | 0.7 | 0 | 0.3 | 0.3 | 0.0 | 0.0 | 0.0 | 0.2 | 0.3 | 0.1 | 0.3 |
| Mean(±1 SE) Dev | 9* | 0.9 | 0.7 | 0.2 | 0.3 | 0.2 | 0.4 | 0.1 | 0.0 | 0.2 | 0.2 | 0.4* | 0.2 |
| | (0.9) | (0.2) | (0.1) | (0.1) | (0.1) | (0.1) | (0.1) | (0.1) | (0.0) | (0.1) | (0.1) | (0.1) | (0.1) |
| Mean(±1 SE) Ag | 6* | 1.3 | 1.1 | 0.1 | 0.2 | 0.1 | 0.6 | 0.1 | 0.0 | 0.2 | 0.8 | 0.1* | 0.2 |
| | (0.6) | (0.3) | (0.3) | (0.0) | (0.1) | (0.1) | (0.3) | (0.0) | (0.1) | (0.1) | (0.3) | (0.0) | (0.1) |

Table 3.8. List of macroinvertebrate taxa collected in developing and agricultural streams. Bold taxa indicated taxa common to both stream types. Density estimates are number of individuals m⁻² averaged among sites by land-cover category (n=5). Chironomids were not identified beyond family and nematodes were only identified to order. FFG = functional feeding group, P = predator, CF = collector filterer, CG = collector gatherer, SH = shredder, SC = scraper.

| Rural Development | | | | | Agriculture | | | | |
|----------------------|-----------------------|-----------------------|-----------|--------------|----------------------|-----------------------|-----------------------|-----------|--------------|
| Order | Family | Genera | FFG | Mean Density | Order | Family | Genera | FFG | Mean Density |
| Diptera | Chironomidae | - | - | 228 | Ephemeroptera | Baetidae | Paracloeodes | SC | 32 |
| Diptera | Empididae | Tabanus | P | 11 | Ephemeroptera | Baetidae | Dipheter | SC | 22 |
| Diptera | Simuliidae | Prosimulium | CF | 11 | Ephemeroptera | Ephemerellidae | Ephemerella | CG | 153 |
| Diptera | Tipulidae | Antocha | CG | 50 | Ephemeroptera | Heptageniidae | Stenonema | SC | 113 |
| Diptera | Tipulidae | Hexatoma | P | 27 | Ephemeroptera | Heptageniidae | Epeorus | CG | 129 |
| Diptera | Tipulidae | Tipula | SH | 27 | Trichoptera | Clossosomatidae | Glossosoma | SC | 16 |
| Coleoptera | Elmidae | ElmidAdult | | 11 | Trichoptera | Hydropsychidae | Hydropsyche | CF | 46 |
| Coleoptera | Elmidae | Oulimnus | SC | 24 | Trichoptera | Hydropsychidae | Cheumatopsyche | CF | 65 |
| Coleoptera | Elmidae | Stenelmis | SC | 61 | Trichoptera | Hydropsychidae | Potomyia | CF | 97 |
| Coleoptera | Psephenidae | Psephenus | SC | 86 | Trichoptera | Hydropsychidae | Arctopsyche | CF | 75 |
| Trichoptera | Hydropsychidae | Cheumatopsyche | CF | 41 | Trichoptera | Hydropsychidae | Diplectrona | CF | 22 |
| Trichoptera | Limnephilidae | Frenesia | SH | 22 | Trichoptera | Hydropsychidae | Parapsyche | CF | 11 |
| Trichoptera | Goeridae | Goera | SC | 11 | Trichoptera | Hydroptilidae | Leucotricia | SC | 11 |
| Trichoptera | Hydropsychidae | Hydropsyche | CF | 32 | Trichoptera | Leptoceridae | Setodes | CG | 11 |
| Trichoptera | Brachycentridae | Micrasema | SH | 11 | Diptera | Blephariceridae | Blepharicera | SC | 32 |
| Trichoptera | Uenoidae | Neophylax | SC | 140 | Diptera | Chironomidae | - | - | 116 |
| Gastropoda | Pleuroceridae | Pleurocera | SC | 111 | Diptera | Tipulidae | Antocha | CG | 60 |
| Lumbriculida | Lumbriculidae | Lumbriculus | CG | 108 | Diptera | Tipulidae | Hexatoma | P | 22 |
| Odonata | Aeshnidae | Boyeria | P | 11 | Coleoptera | Elmidae | Stenelmis | SC | 61 |
| Odonata | Cordulegasteridae | Cordulegaster | P | 11 | Coleoptera | Psephenidae | Psephenus | SC | 38 |
| Odonata | Gomphidae | Lanthus | P | 38 | Coleoptera | Ptilodactylidae | Anchytarsus | SH | 11 |
| Odonata | Gomphidae | Ophiogomphus | P | 22 | Plecoptera | Chloroperlidae | Utaperla | P | 11 |
| Plecoptera | Capniidae | Allocapnia | SH | 11 | Plecoptera | Perlidae | Neoperla | P | 11 |
| Plecoptera | Chloroperlidae | Alloperla | P | 11 | Plecoptera | Perlidae | Perlesta | P | 11 |
| Plecoptera | Chloroperlidae | Hastaperla | P | 11 | Nematoda | - | - | CG | 22 |
| Plecoptera | Perlidae | Acroneuria | P | 11 | Gastropoda | Pleuroceridae | Pleurocera | SC | 16 |
| Ephemeroptera | Ephemerellidae | Ephemerella | CG | 36 | Decapoda | Cambaridae | Cambarus | CF | 11 |
| Ephemeroptera | Ephemeridae | Ephemera | CG | 11 | Hydracarina | | | PR | 11 |
| Unionidea | Corbiculidae | Corbicula | CF | 27 | Unionidea | Corbiculidae | Corbicula | CF | 11 |

Table 3.9. Summary of macroinvertebrate assemblage responses. Values are site density estimates (# m⁻²) except TR (taxa richness) is number of fish species found at a site. Site codes from table 3.1. SH = shredder; SC = scraper; CG = collector-gatherer; CF = collector-filterer; P = predator.

| Stream | TR | Taxonomic | | SH | Functional Feeding Group | | | P |
|--------------------|-------|-----------|---------|--------|--------------------------|---------|---------|--------|
| | | Density | Midge | | SC | CG | CF | |
| AVE | 14 | 883 | 183 | 11 | 248 | 291 | 54 | 97 |
| BRS | 8 | 452 | 172 | 0 | 161 | 75 | 22 | 22 |
| HDS | 5 | 161 | 108 | 11 | 11 | 22 | 11 | 0 |
| MCC | 13 | 667 | 248 | 11 | 226 | 32 | 86 | 65 |
| ROB | 13 | 1335 | 441 | 65 | 377 | 269 | 129 | 54 |
| EFB | 15 | 1421 | 248 | 11 | 474 | 538 | 108 | 43 |
| GAB | 5 | 635 | 65 | 0 | 43 | 366 | 161 | 0 |
| MFD | 13 | 420 | 54 | 0 | 108 | 129 | 129 | 0 |
| PNT | 11 | 258 | 97 | 0 | 32 | 75 | 32 | 22 |
| WFB | 10 | 538 | 140 | 0 | 97 | 118 | 0.1 | 11 |
| Mean(±1 SE) Dev | 11(2) | 700(199) | 230(57) | 19(11) | 205(60) | 138(59) | 60(22) | 47(17) |
| Mean(±1 SE) Ag | 11(2) | 654(202) | 121(35) | 2(2) | 151(82) | 245(89) | 121(25) | 15(8) |

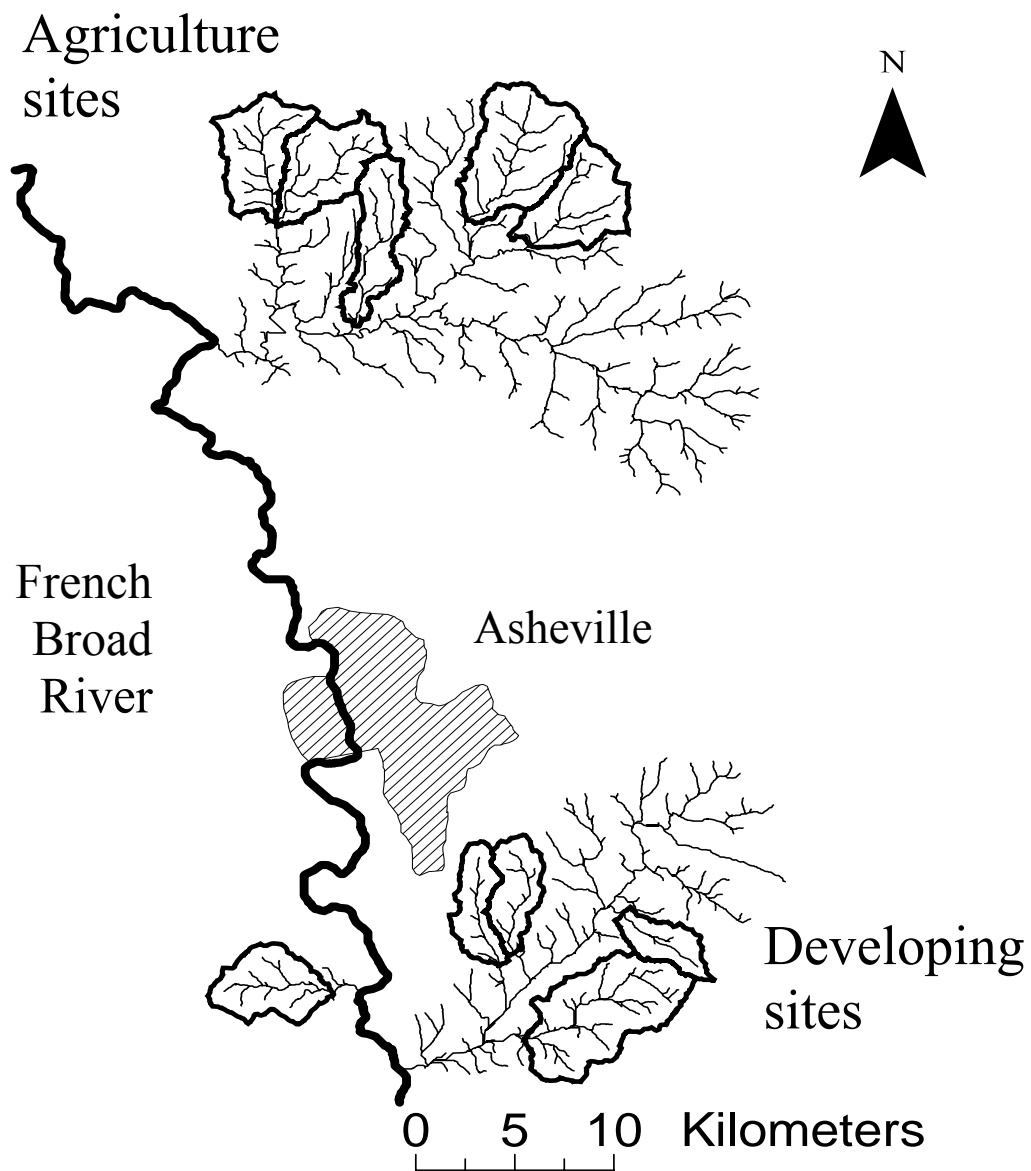


Figure 3.1. Map of study area showing city of Asheville, French Broad River, and study watersheds.

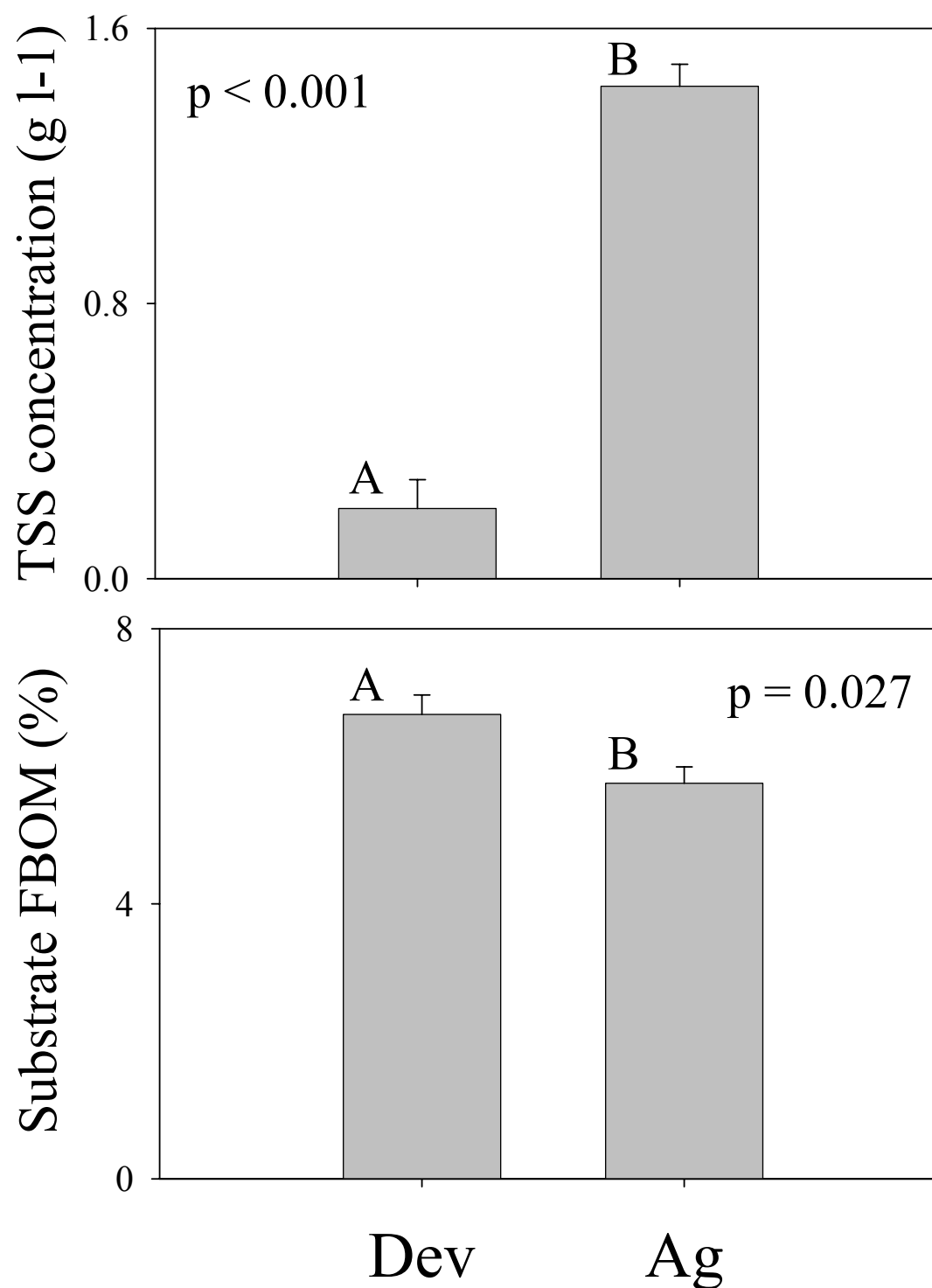


Figure 3.2. Mean (± 1 SE) TSS and FBOM concentration in rural vs. agricultural streams. Letters denote significant differences between stream type. Dev = developing sites, Ag = agricultural sites.

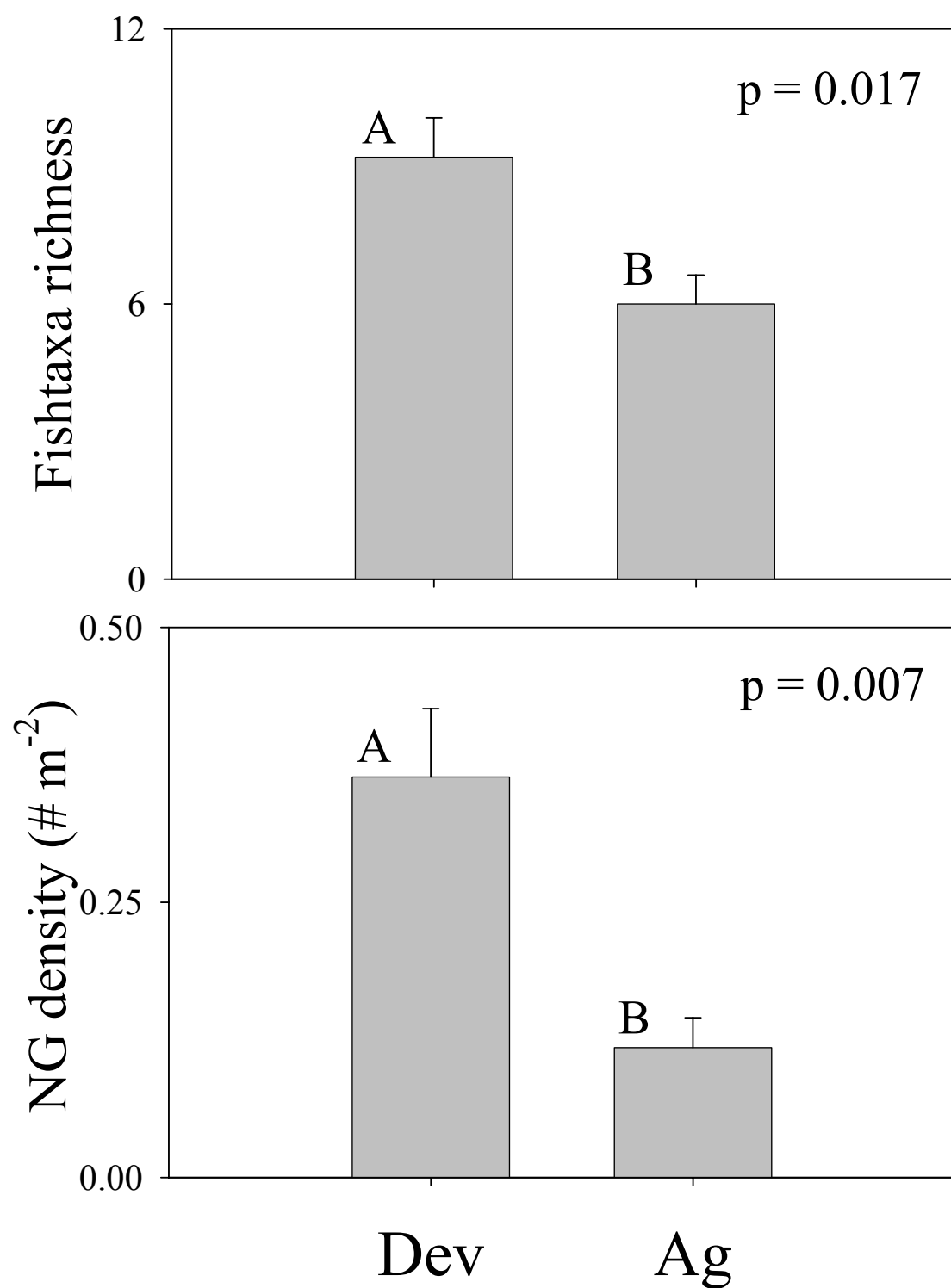


Figure 3.3. Mean (± 1 SE) fish TR and NG density in rural vs. agricultural streams. Dev = developing sites, Ag = agricultural sites.

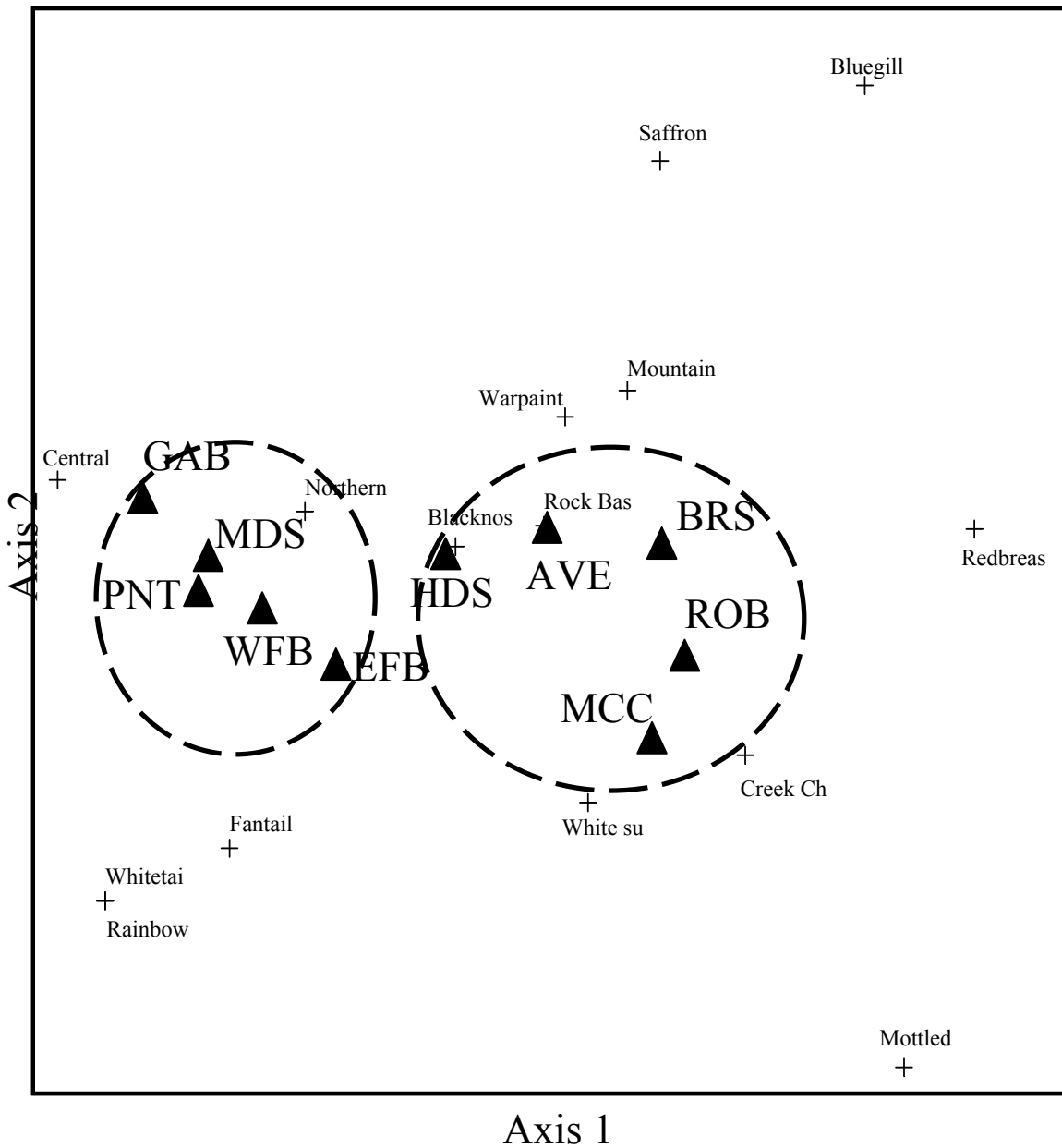


Figure 3.4. Detrended correspondence analysis of streams by fish species density. Triangles indicated locations of streams in the hypothetical space defined by species distribution. Dashed circles indicate grouping of sites by land-use category. Site codes are from table 3.1. Fish common names are truncated to 8 letter abbreviations and can be found in Table 3.6.

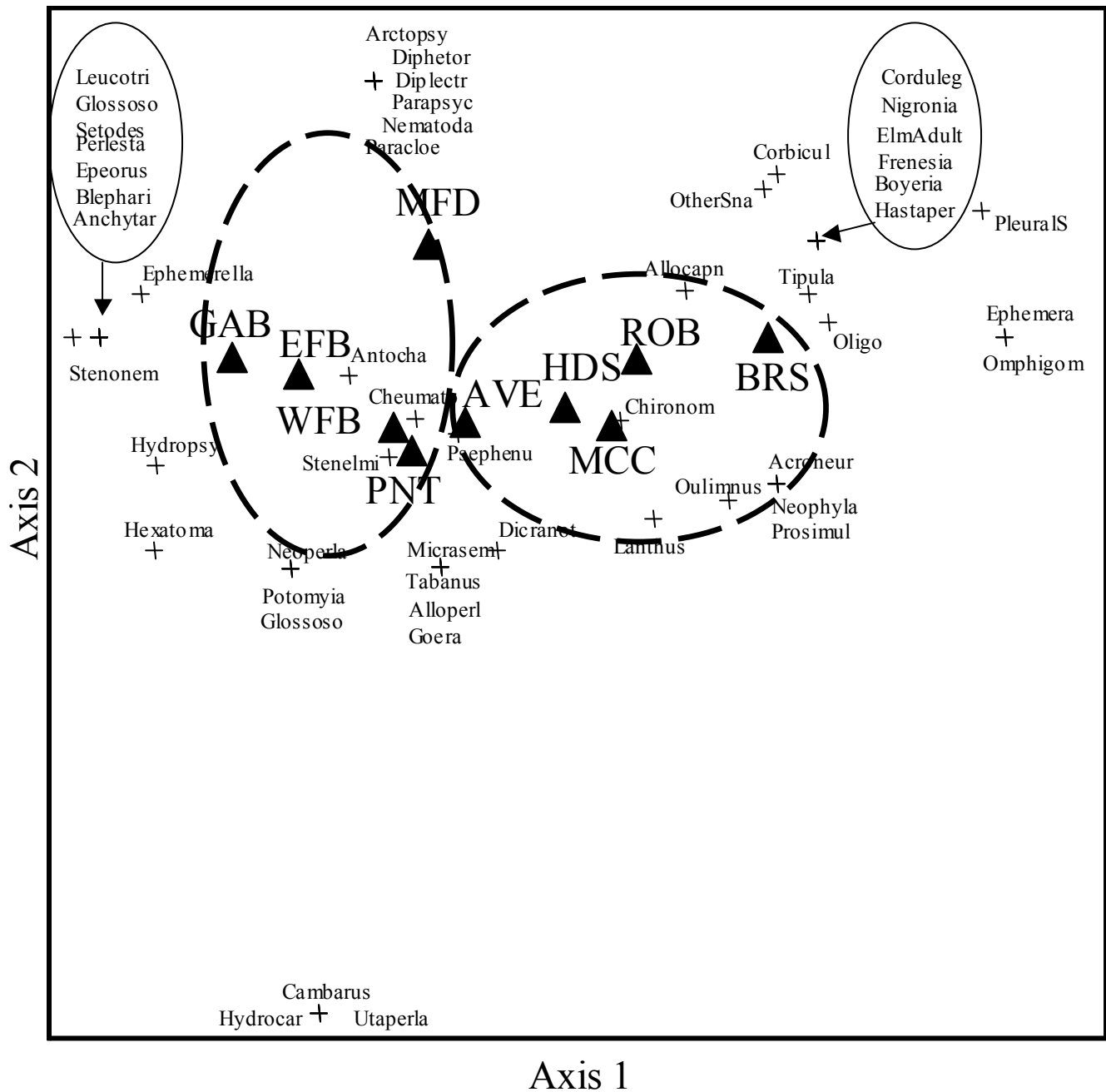


Figure 3.5. Detrended correspondence analysis ordination of streams by macroinvertebrate density. Dashed circles indicate grouping of sites by land-use category. Dotted circles group taxa common to one ordination location. Site codes are from table 3.1. Macroinvertebrate names are truncated to 8 letter abbreviations and can be found in Table 3.8.

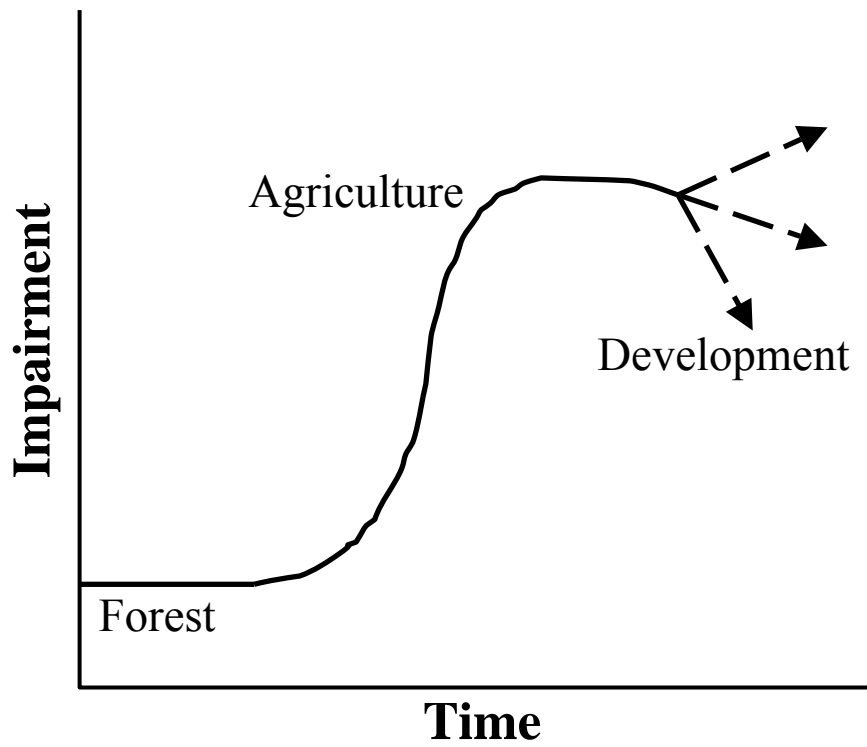


Figure 3.6. Changes to abiotic and biotic stream impairment through time reflecting the change from forest to agriculture, decreased agricultural activity, and 3 theoretical scenarios predicting the influence of rural development.

Chapter 4: Multivariate versus bivariate analysis of land-cover disturbance to stream biota

Abstract

I introduce the land-cover path (LCC) hypothesis as a conceptual framework to organize the transfer of land-cover disturbance to stream biota through a cascading gradient of intermediate abiotic variables. Selected abiotic variables represent key ecosystem features that transform disturbance and pass a reorganized effect to the next variable where the process repeats until ultimately affecting biota. I hypothesized that land-cover affects stream biota indirectly through a hierarchy of stream abiotic components that transform disturbance to biota. I measured 31 hydrologic, geomorphic, erosional, and substrate variables and 26 biotic responses that have been associated with land-use disturbance. Regression analyses reduced this set of variables to include only those abiotic variables that responded to land-cover and/or affected biota. From this reduced variable set, hypotheses were generated that organized the disturbance pathways linking land-cover to each biotic response. I identified a multivariate path model for each biotic response that illustrated the pathway through which land-cover influenced physical variables and ultimately biota. Paths were tested for predictive ability and goodness-of-fit using path analysis and the Amos[®] software program. Biota were influenced both directly (i.e., bivariate linear regressions) and indirectly (i.e., multivariate path analyses) by near-stream urban, agricultural, and forest land-cover as well as by hydrologic, geomorphic, erosional, and depositional substrate features. Multivariate models (indirect effects) were compared to bivariate models (direct effects). Indirect pathways generally predicted biotic responses better than direct effects and always explained more of the associated variance by including intermediate abiotic variables. Path models suggested that fish and macroinvertebrates were influenced by near-stream agricultural disturbance that cascaded through channel geomorphic elements including bank height, incision ratio, and width / depth ratio, inorganic sediment loads, and substrate size and organic matter content. Some bivariate models significantly predicted biotic responses but were not easily translated ecologically. My results suggest that intermediate abiotic variables were important in propagating land-cover disturbance to biota and usually provided more information than bivariate relationships. More generally, the land-cover cascade concept and experimental framework was useful in explaining variation in biotic responses associated with

the propagation of anthropogenic disturbance through intermediate abiotic ecosystem components.

Introduction

The cascade approach could be useful in ecosystem research to organize multivariate interactions occurring at multiple spatial scales. Much is known about the disturbance response of individual ecosystem components, but how components interact, and how disturbance is transformed, is largely unknown (Lake 2000). Ecosystem response to disturbance is difficult to study due to the varying nature, intensity, and duration of both disturbance and ecosystem responses. As the spatial scale of research gets larger the number of important variables or the scale of relevant variables can also increase and weaken our ability to identify mechanisms (Strayer et al. 2003). Ecosystems are also difficult to replicate and the variance associated with ecosystem measures are difficult to quantify. As a result, much of what we know about anthropogenic disturbance to streams has come from small-scale studies that make bivariate inferences of ecosystem scale effects (Downes et al. 2002).

Many bivariate studies have shown that land-cover disturbance induces a series of direct effects to ecosystem structure and function (Meyer and Turner 1992, Jacobson et al. 2001). Land-cover changes have been shown to induce hydrologic, geomorphic, erosional, and biotic responses (Waters 1995, Richards et al. 1996, Harding et al. 1999, Cuffney et al. 2000, Lee and Bang 2000). Bivariate studies typically use regression or correlation analyses to identify relationships between land-cover and abiotic or biotic responses but cannot explain the disturbance pathways involved and thus cannot be used to identify mechanisms. Conclusions generated from such studies have limited use in generalizing relationships among multiple variables and often report direct, bivariate effects of land-cover on biota but do not quantitatively link biotic responses, land-cover, and intermediate variables. The bivariate approach is limited when research questions demand consideration of multiple spatial scales and when significant relationships may involve intermediate variables. A cascade approach to ecosystem disturbance study will help link intermediate variables or acting to propagate land-cover disturbance to biota indirectly (i.e., indirect effects). Cascades imply multivariate path models that join land-cover effects and biota through at least one intermediate variable, or link. Path models may also identify relationships among response variables that facilitate the identification of mechanisms involved in transforming landscape-scale disturbance to biota.

Here I propose a cascade approach to organize how land-cover disturbance is transformed via interacting abiotic variables across multiple spatial scales to ultimately affect stream biota (sensu Frissell et al. 1986; Fig. 4.1). The land-cover cascade (LCC) is a novel design used to organize the series of intermediate variables through which land-cover disturbance energy ‘flows’ along a reducing temporal and spatial gradient before influencing biota (Montgomery 1999). Generally, the LCC describes a 3-tiered hierarchy among land-cover, physical elements, and biotic responses. I constructed individual cascades for each biotic response and tested the predictive ability of multivariate models to bivariate comparisons between land-cover or abiotic variables and biotic responses. To build each LCC model I identified important intermediate abiotic variables between land-cover and biota as being hydrologic, geomorphic, erosional, and substrate elements. I used variables known to respond to land-cover disturbance and/or induce biotic responses to build multivariate models describing relationships among land-cover, biota, and physical ecosystem elements. I considered disturbance effects as originating with land-cover and being transformed by intermediate abiotic variables (i.e., links) to produce a terminal biotic response. Some of the disturbance would be realized at each intermediate variable and some transferred to the next link along the path. Each link is considered a necessary step in the complete translation of land-cover disturbance to a particular biotic community response.

I hypothesized that land-cover disturbance would follow a cascade pattern whereby disturbance was transformed to the next-smaller spatial scale through physical response variables and that cascades would continue until eventually affecting stream biota. I predicted that each bivariate link within a cascade could be quantified and the overall predictive value of a cascade assessed using structural equation modeling (SEM) to quantify cascades as path models. To assess the value of LCC models I compared SEM results to bivariate comparisons (i.e., regression and correlation) between land-cover and individual biotic responses. I predicted that biotic responses would be better explained by multivariate (i.e., indirect effects explained by the LCC and SEM; path models) than bivariate (i.e., direct effects) models. I expected biota to respond strongly to altered substrate and sediment dynamics associated with higher agricultural or urban land-cover.

Methods

Study sites

To develop testable LCC models I measured physical and biotic elements in ten 3rd – 4th order streams in the Blue Ridge physiographic province in western North Carolina that had been historically influenced by row crop and grazing agriculture. The streams were similar in length, gradient, and underlying geology. Watershed areas varied from 1000 – 3500 Ha ($\bar{x} = 1907 \pm 256$ ha). All watersheds contained active agricultural areas since at least 1950, and included 21 – 77 % ($\bar{x} = 47 \pm 18$ %) agriculture and 16 – 62 % ($\bar{x} = 40 \pm 14$ %) forest as of 1993 (Herman 1996, USCB 2002).

Land-cover definition

Land-cover circa 1993 was estimated from National Land-cover Dataset (NLCD; USDI 2002). Whole watershed land-cover classification was calculated as the percentage of a land-cover type in the entire watershed area. Twenty-nine NLCD land-cover categories were reduced to four. Agriculture included active row crop or grazing areas and old fields. Urban included urban and rural areas in addition to roads and other elements of human infrastructure. Forest combined most vegetation categories, and other categories included open water, barren, and others that did not fit into the previous categories.

I considered land-cover along a spatial gradient from near-stream to whole watershed areas. Riparian corridors of 100-m width were estimated in a GIS and land-cover percentages defined within. To examine land-cover along a continuum of spatial proximity to stream channels, overland flow travel time zones (TTZs) were used to constrain the area in which land-cover percentages were estimated, and thus how independent variables were defined. Travel time estimates were calculated using a GIS and defined by gradient, surface roughness, average rainfall, and other criteria (C.L. Burcher, Chapter 2 this dissertation). Travel time zones ranging from 30 to 300-min were used to delimit spatial zones ranging from proximal, near-stream areas to the whole watershed. Percent land-cover in agriculture, light urban, heavy urban, and forest categories were estimated in each of ten TTZs.

Quantifying physical and biotic characteristics

I quantified several metrics that I hypothesized would be important components involved in the LCC of study streams. Metrics were established to capture both the spatial and temporal range of known physical responses that have been shown or inferred to contribute to biotic

responses to land-cover change (*sensu* Ward 1989; Fig. 4.1). Hydrologic metrics captured landscape scale phenomena including discharge and overland-flow travel-time estimates. Geomorphic metrics were calculated from multiple channel cross-section surveys, digital elevation models, and line-transect discharge measurements. Erosional metrics were suspended and bedload sediment concentration and percent fine benthic organic matter (FBOM). Substrate metrics quantified particle size, composition, and percent substrate FBOM.

Fish were sampled during August in 2002 using single pass backpack electrofishing along 100-m stream reaches. Reaches were subdivided into 1 to 10-m sections using natural breaks in habitat units as boundaries between sub-units. Electrofishing herded fish into a seine (5-mm mesh) at the downstream end of each sub-unit. Fish were collected and identified to species after each sub-unit was sampled and returned downstream. Density was estimated as the number of individuals collected per stream area sampled (100-m X average stream width; # m⁻²).

Fishes were assigned to distributional, reproductive, and trophic guilds based on available information for each species. Distribution status reflects historic occurrence of a species within and across drainages (Scott and Helfman 2001). Cosmopolitan species are widely distributed through a drainage and span stream order and habitat gradients. Endemic species are often only found in a small portion of a drainage often in a very localized area. I considered endemic fishes in the southern Appalachian region to be associated with highland areas, or higher gradient, lower-order streams and to have limited geographic distributions relative to cosmopolitans (Scott and Helfman 2001).

Fishes were assigned to reproductive guilds based on known spawning habits of each species. Fishes vary in their mode of reproduction and can build nests, guard eggs, or simply broadcast eggs across the benthos. I placed species into 1 of 5 reproductive guilds (Jenkins and Burkhead 1994, Etnier and Starnes 1993). Nest builders (NB) build and guard nests and included centrarchids and the Fantail darter. Nest associates (NA) often spawn in association with pebble mounds organized by another species and included Whitetail shiner, Warpaint shiner, and Central stoneroller minnows. Burying non-guarders (NG) hide eggs in substrate without further parental care and included species from several families. Broadcast spawners spread eggs and milt over an area of substrate without burying or providing parental care and included Blacknose dace and White suckers.

Fish feeding habits were also used to categorize species by feeding guild based on recorded knowledge of each species (Jenkins and Burkhead 1994, Etnier and Starnes 1993). Herbivores are fishes feeding primarily on living plant material, algae, and detritus and included Bluegill, Redbreast sunfish, Whitetail shiner and Blacknose dace. Invertivores prefer insects and crustaceans and were subdivided by the portion of the water column prey is taken. Benthic invertivores pick prey items from substrata, often have specialized subterminal mouths designed for bottom feeding and included the Northern hogsucker. Drift invertivores lie-and-wait for drifting prey to be delivered to them, and included Warpaint and Saffron shiners. General invertivores are species known to collect prey items from multiple locations within a stream and included Creek chub, Central stoneroller, Rock bass, and Rainbow trout. Detritivores feed primarily on detritus matter and included White sucker and Mountain brook lamprey.

Macroinvertebrates were collected during late April 2003 using twenty quantitative (Surber, 500- μm mesh, 0.09 m^2 , 1.8 m^2 total area sampled per 100-m reach). Density ($\# \text{m}^{-2}$) was estimated from individual samples and average density by taxa calculated for each stream. Macroinvertebrates were preserved in 80% ethanol and identified to the lowest possible taxonomic level (typically genus). Taxa were placed into functional feeding groups (FFG) based on the classification by Merrit and Cummins (1996) or expert opinion of macroinvertebrates in southern Appalachian streams. Functional feeding groups included collector-filterers and collector-gatherers known to remove particulate matter from the water column, shredders that feed on decaying leaves, scrapers that have specialized mouthparts for removing algae from rock surfaces, and predators that consume other animals. I did not consider ontogenetic changes to feeding habit associated with small instars and assumed that individuals of a species could be classified into a single FFG.

Statistical analyses; direct and indirect effects

Variables in were organized according to the conceptual LCC hierarchy (Fig. 1). Thirty-six land-cover variables (twelve each in agriculture, forest, and urban categories) were always considered independent variables. Physical variables (30 total; 6 hydrologic, 10 geomorphic, 11 erosional, and 3 substrate) were considered both dependent variables affected by land-cover and independent variables affecting other physical variables and biotic responses. Biotic variables (21 total; 13 fish and 8 macroinvertebrate) were always considered dependent variables, either directly on land-cover or indirectly through physical variables.

Every possible pairwise combination of variables was analyzed with simple linear regression. Land-cover was compared to every other physical and biotic variable (51 total) for a total of 1836 comparisons. All physical variables were compared with each biotic variable in 630 comparisons. Ecologically significant variables were defined as those that were significantly correlated ($p < 0.05$) to at least one other variable and contained no visible outliers in scatter-plots. Significant relationships were further assessed to determine whether they were ecologically feasible. For example, if a bivariate model predicted that land-cover would be influenced by substrate size then that model would be omitted based on the seemingly impossible scenario implied. Resulting variables represented the strongest potential among measured variables to either link land-cover to biota or predict biotic responses directly (i.e., a direct effect of land-cover to biota). Significant bivariate regressions between land-cover and biotic responses were compared to the path model that predicted the same biotic response.

Path analysis

Path analysis is a form of structural equation modeling and a statistical technique that allows researchers to relate variables and their inferred influence sequentially (Shipley 2000). Similar to multivariate regression, path analysis considers dependent variables potentially influenced by multiple independent variables but allows each independent variable to interact with one another. Path analysis decomposes the total variation in a dependent variable associated with all other variables in a model. Unlike linear or multiple regression methods, however, path analysis also allows consideration of interaction or correlation among independent variables along hypothetical paths. Path analysis provides coefficients similar to r^2 that indicate how much variation in response variables is explained by each independent variable and the entire model. Path analysis also provides correlation coefficients for each bivariate pair providing both direction and a measure of relatedness.

Path models were constructed and assessed using Amos[®] version 5.0 to decompose direct (i.e., bivariate) and indirect (i.e., multivariate path) effects of each path model variable on each biotic response (Arbuckle 2003). Path models were built according to significant direct relationships identified by linear regression whereby variables related to one another in a bivariate sense (i.e., significant with linear regression) were combined to connect land-cover to biota through related abiotic variables. For example, if agriculture was significantly linked (i.e., significant regression) to baseflow discharge and discharge was linked to fish taxa richness, a

path model could be built linking agriculture to discharge and discharge to taxa richness. Path analysis would calculate the correlation between each variable pair and assess the overall predictive capacity of the model. Each link (i.e., bivariate comparison) was known to be significant based on the underlying linear regression analysis completed prior to model building but whether or not a path model would be significant depended on the overall strength of all variables in a model.

Path models indicated the structure of cascading physical and biotic variables that were hypothesized to affect a particular biotic response (Fig. 4.2). Paths included at least 3 variables, but could include all significant relationships. For example, total fish density was hypothesized as being affected by agriculture as delimited within 60-min travel time zones that initially (i.e., prior to affecting fish density) induced a change to bank height and subsequently influenced baseflow total suspended solids (TSS) percent inorganic matter. Models provided measures of direct and indirect effects and indicated the percent variance (analogous to overall r^2 in linear regression) in a biotic response that was explained by an entire pathway. Each model was tested for goodness of fit using chi-squared analysis, root mean squared error approximation (RMSEA), and the normed fit index (NFI) output from Amos[®] (Arbuckle 2003).

Results

Simple linear regression reduced 36 land-cover variables and 51 physical and biotic variables to 11 land-cover, 16 physical, and 15 biotic variables (Table 4.1). The reduced set of variables was used to construct LCC models that were tested using path analysis. Linear regression between land-cover and biotic responses were compared to path analysis results and the utility of each model considered.

Path models

Thirteen of twenty-two hypothesized path models predicted six fish and seven macroinvertebrate responses and described significant cascades between land-cover and biota (Fig. 4.2). The remaining nine models tested were not significant with Amos[®] but were compared with significant bivariate regression models for similar land-cover / biotic response comparisons to assess the relative predictive ability of multivariate versus bivariate approaches. Each significant path model path began with land-cover effects and included at least one physical response. Direct (i.e., bivariate) and indirect (i.e., multivariate) effects were decomposed to estimate the predictive values (analogous to overall r^2) for each path model and for each variable

within a path model (Table 4.2). Multivariate path models explained between 41 % (fish non-guarder density) and 92 % (fish taxa richness and total density) of the variance observed in biotic responses (Fig. 4.2). All path models fit according to chi-square (X^2) analyses, although some models failed RMSEA and NFI fit tests (Table 4.3). Goodness-of-fit tests compared the hypothesized model to data covariance structure to determine how well the hypothesized model fit the actual data. X^2 significance is often considered sufficient criteria to consider a model meaningful and I considered this acceptable despite the failure of some models' fit indicated by RMSEA and NFI (Shipley 2000, Arbuckle 2003, Riseng and Wiley 2004).

Six land-cover, 2 hydrologic, 3 geomorphic, 1 erosional, 3 substrate, 5 fish, and 7 macroinvertebrate variables were included in path models. The remaining pairwise relationships included variables that did not participate in any path model and were not considered in bivariate comparisons of land-cover and biota (Appendices A, B). Fish and macroinvertebrate responses were generally influenced by near-stream land-cover (i.e., described with in 60, 90, or 120-min TTZs or 100-m corridors) although watersheds scale agriculture was important in predicting a change to the density of fish nest associates. Baseflow discharge and the slope of discharge / stage rating curves were significant in several path models including macroinvertebrate total density and collector filterer density but, in general, hydrologic elements were not predictive and did not significantly affect the influence of land-cover to fish responses. Mean bank height measured in year 1, the change to bank incision ratio over 1 year, and the width / depth ratio of baseflow depth were important geomorphic elements in all but two path models. Percent stormflow TSS inorganic matter was the only significant erosional element and was a key entity in path models explaining fish assemblage responses but not included in any macroinvertebrate path. Substrate metrics were important in several models to both fishes and macroinvertebrates.

Fish responses

Path models significantly predicted three fish taxonomic metrics. The path model that summarized the influence of near-stream agriculture on stormflow inorganic matter explained ninety-two percent of the variation in fish taxa richness among streams (IM; Fig. 4.2a). The fish taxa richness path model suggested that agriculture described within 100-m riparian corridors positively influenced storm flow inorganic matter concentration, which in turn negatively influenced fish taxa richness. In other words, higher near-stream agriculture negatively influenced fish taxa richness via the intermediate influence on storm flow IM. The fish total

density path model significantly explained the positive influence of near-stream agriculture to bank height and the direct effects of baseflow TSS inorganic matter (Fig. 4.2b; 92 % variance in total density explained). Density of cosmopolitan fishes (i.e., widely distributed as opposed to localized in distribution) was explained (91%) by a combination of agriculture bank height, and suspended inorganic particles (Fig. 4.2c). The cosmopolitan fish path model indicated that both near-stream (i.e., 60-min travel time zones) and large-scale (i.e., whole watershed) agriculture positively influenced bank height (i.e., streams were deeply incised) and baseflow TSS organic matter. Deeper banks negatively influenced, whereas suspended inorganic TSS positively influenced cosmopolitan fish density.

Fish metrics that summarized reproductive behavior and associated habitat preferences were also significantly modeled using path analysis. Forty-one percent of the variation in fish non-guarder density (fishes that do not guard their eggs after spawning) was explained by a path model whereby near-stream agriculture (i.e., described within 60-min travel time zones) negatively influenced the incision ratio change of stream channels (i.e., whether bank slope changed between sample years), which negatively influenced percent organic matter (OM) in substrata, which positively influenced fish non-guarder density (Fig. 4.2d). In other words, increased agriculture was associated with bank erosion that was related to a higher ratio of substrate organic matter (as compared to IM). Lower IM was significantly related to higher fish non-guarder density. Similarly, increased fish nest-associate density (i.e., fish that spawn in the presence of nests built by other species) was predicted (88%) by watershed-scale agriculture positively influencing TSS % IM (41%; Fig. 4.2e). Combined, models summarizing fish reproductive structure suggested that the reproductive structure of fish assemblages was altered by inorganic sediments and channel shape associated with near-stream and whole-watershed agriculture.

One metric summarizing trophic structure of fish assemblages was significantly predicted by path analysis. Density of herbivorous fishes was higher in association with urban land-cover described within 120-min travel time zones. Urban land-use positively influenced width / depth ratios (i.e., streams were wide and shallow) which led to a decrease in substrate % fines and an increase to fish herbivore density (49 % variance in fish herbivore density explained; Fig. 4.2f).

Fish responses, in general, were predicted by near-stream agriculture (i.e., as described within 60 to 120-min travel-time zones) and were not affected by hydrologic variables in any

path model. Bank height, incision ratio change, and width / depth ratio were important predictors of total, cosmopolitan, non-guarder, and herbivore fish density. Percent IM was important in each path except for herbivore and non-guarder density paths. Substrate inorganic matter and percent fines were only predictive to non-guarder and herbivore density respectively.

Macroinvertebrate responses

Three taxonomic macroinvertebrate metrics; taxa richness, total density, and midge density were significantly predicted by path models. Higher taxa richness was associated with lower cosmopolitan fish density and by higher bank height associated with higher near-stream agriculture (49%; Fig. 4.2g). Fifty-seven percent of variation in macroinvertebrate total density was explained by a path model that summarized the influence of near-stream agriculture and urban land-cover (Fig. 4.2g). Macroinvertebrate total density was lower with higher agriculture due to lower rating curve slope values and smaller D_{50} . Higher urban land-cover, however, appeared to be positively related to total density by inducing wider, shallower streams (i.e., higher w/d ratios) and lower % fine substrata. Eighty percent of the variation in midge density among sites was explained by a path model summarizing the negative influence of near-stream agriculture (i.e., described within 60-min travel time zones), higher baseflow discharge, and higher density of fish nest associates (Fig. 4.2i). Midge density appeared to negatively respond to higher agriculture, deeper stream channels, and predation by nest associates.

Four significant path models were developed that predicted responses of macroinvertebrate functional feeding groups (FFGs) to land-cover. Macroinvertebrate shredders, dependent on allochthonous-derived organic matter (e.g., leaves) were positively influenced by agriculture. Forty-eight percent of the variation in shredder density among sites was explained by a model linking higher agriculture (described within 60-min travel time zones) to bank movement or erosion (incision ratio change) and higher percent benthic organic matter (Fig. 4.2j). Macroinvertebrate scraper density responded similarly to shredders in a model explaining 46% of the variation in scraper density (Fig. 4.2k). Scrapers also appeared to benefit from lower urban activity in 120-min travel time zones and the intermediate influence of urban activity on substrate OM. A positive influence of urban land-use was also apparent in the model predicting collector-filterer density (Fig. 4.2l). Collector-filtering macroinvertebrate density was lower in association with higher agriculture and lower urban land-cover described within 120-min travel time zones. Agriculture was negatively related to rating curve slope and D_{50} was positively

correlated to urban land-use and w/d ratios. In other words, D_{50} was negatively influenced by agriculture and the associated influence on discharge but also positively by urban land-use influencing narrower and deeper stream channels. Urban land-cover negatively influenced collector-gathering macroinvertebrate density (Fig 4.2m). A cascading path model indicated that higher urban activity was associated with wider, shallower streams (i.e., higher w/d ratio) and lower % fine substrata and explained 70% of the variance in collector-gatherer density.

Agriculture and urban land-cover altered hydrology features, substrate D_{50} , and percent fine substrates. Agriculture most strongly influenced macroinvertebrate total density and the presence of agriculture contributed to deeper, flashier streams dominated by small substrates. Macroinvertebrate responses were generally predicted by near-stream agriculture but total, scraper, collector-filterer, and collector-gatherer density was affected by urban land-cover. Near-stream forest cover positively influenced scraper density. Stream hydrology, specifically rating curve slope, affected total density and density of collector filterers. Similar to fishes, macroinvertebrates responded to geomorphic features including bank height, incision ratio change, and width / depth ratio. Substrate characteristics were particularly important in predicting macroinvertebrate responses except for taxa richness and midge density.

Bivariate analyses

Sixty-nine pairwise combinations of all possible variable combinations were significant with linear regression (Table 4.2, Appendix B). I considered these relationships to be ecologically significant (i.e., direct effects) where land-cover or a physical response explained more than 40% of the variation (i.e., $r^2 > 0.4$) in a physical or biotic response. I chose 40% as the rejection level to be conservative enough to consider entities that may contribute to a larger model but permissive enough to reduce the number of entities I considered. Low correlation (i.e., 40 to 60 %) has limited meaning in a bivariate sense but whether a single variable would be more useful in multivariate models was unknown. I wanted to eliminate enough variables to design practical multivariate models but be conservative enough to maintain variables that could potentially contribute to larger models.

Land-cover significantly explained variation in 4 fish and 5 macroinvertebrate responses (Table 4.2). Density of cosmopolitan fishes was negatively related to higher forest cover within 100-m riparian corridors ($p = 0.042$, $r^2 = 0.422$). Fish detritivore density was negatively influenced by higher agriculture within 60-m TTZs ($p = 0.005$, $r^2 = 0.642$). Density of nest

associate fishes was positively associated with 100-m buffer agriculture ($p = 0.024$, $r^2 = 0.489$). Non-guarding fish density was influenced negatively by forest cover (90-min TTZs; $p = 0.013$, $r^2 = 0.556$) and urban land-cover (60-min TTZs; $p = 0.012$, $r^2 = 0.564$). Midge density was significantly predicted by near-stream agriculture (100-m corridors; negative relationship; $p = 0.021$, $r^2 = 0.508$) and positively related to urban land-cover within 60-min TTZs ($p = 0.006$, $r^2 = 0.627$). Shredder density was positively influenced by urban land-cover in 90-min TTZs ($p < 0.001$, $r^2 = 0.893$). Scraper density was influenced positively by urban land-cover (90-min TTZs; $p = 0.015$, $r^2 = 0.541$) and negatively by both forest (90-min TTZs; $p = 0.046$, $r^2 = 0.411$) and agriculture (100-m corridors; $p = 0.03$, $r^2 = 0.466$). Density of collector-filtering macroinvertebrates was negatively influenced by forest cover in 100-m corridors ($p = 0.032$, $r^2 = 0.456$) and predator density by agriculture in 100-m corridors ($p = 0.029$, $r^2 = 0.468$).

Comparisons of bivariate and multivariate techniques

Land-cover was significantly related to a biotic response in twenty-six individual bivariate or multivariate path models representing hypothesized relationships between land-cover and biotic responses suggested by the LCC. In general, path models were considered more useful than bivariate models because at least one intermediate variable was identified that might have propagated or translated land-cover disturbance to biota. However, bivariate and multivariate models typically complimented one another by including different land-cover types in predictions (Table 4.2). Three land-cover / biotic responses models predicted the same combination of land-cover type and biotic response and required interpretation of the ‘better’ or most predictive model. Fish nest associate density was influenced by agriculture by both bivariate and multivariate models although the spatial extent of agriculture was different in each model (Table 4.2). Watershed scale agriculture was a more powerful predictor when combined with baseflow TSS IM in a cascading path model to predict nest-associate density (Fig. 4.2f; 88 percent of variance explained). The bivariate model predicting nest associate density was less powerful (49 % of variance explained) and assumed that near-stream agriculture directly influenced fish nest associates. Similarly, path analysis provided a stronger model to predict macroinvertebrate total density response to near-stream agriculture (Table 4.2, Fig. 4.2i). However, the strength of the macroinvertebrate total density path model may have been higher because urban land-cover helped explain variation in macroinvertebrate total density. Scraper density was influenced by forest and urban land-cover and the relative value of bivariate and

multivariate models was similar (Table 4.2, Fig. 4.2k). The bivariate model linking urban land-cover in 90-min TTZs was actually stronger than the more complex multivariate model. The influence of forest cover to scraper density was similar regardless of the model used. In any case, multivariate models provided more information by identifying potentially critical intermediate variables involved in the transfer of land-cover disturbance to biota.

Discussion

Path models successfully linked land-cover disturbance stimulus to biotic responses through intermediate abiotic links hypothesized by the LCC. Path models (Fig. 4.2) generally explained more variability in biotic responses than simple pairwise comparisons (Table 4.2). Bivariate model utility was considered limited because land-cover does not likely influence biota directly (King et al. 2005). Path models were typically considered more useful in identifying intermediate variables interacting with land-cover to influence biota.

Fish assemblage responses

Fish response path models explain 92% of the variation in fish total density and taxa richness. These metrics have been shown to respond to anthropogenic disturbance and are commonly reported in the literature (Angermeier and Karr 1986, Wang et. al 2001, Sutherland et al. 2002). Taxa richness decreased with inorganic sediment concentration associated with increased near-stream agriculture. This suggests that the erosional load entering streams was largely geologic in origin. The negative influence of inorganic materials to the number of fish taxa was likely related to the filling of benthic interstices reducing spawning and feeding habitat (Sutherland et al. 2002). Fish total density was also affected by near-stream agriculture, baseflow suspended inorganic matter, and channelization as measured by increased bank height. Together these land-cover and erosional changes suggested that increased agriculture led to channelization, which was related to higher erosion. The fish density path model (Fig. 3b) suggested that agricultural channelization and suspended inorganic sediments were very important in determining the total number of fish.

Cosmopolitan fishes are typically generalists in habitat and trophic preferences (Scott and Helfman 2001) and responded negatively to agriculture and channelization but positively to inorganic suspended sediment concentration in my study. Scott and Helfman (2001) showed that cosmopolitan fishes dominated disturbed streams in the southern Appalachians and my results offer an explanation. Path models indicate that inorganic sediment input associated with whole

watershed agriculture favors cosmopolitan fishes over endemics, which are likely more sensitive to inorganic sedimentation that is known to reduce feeding and habitat niches (Mol and Ouboter 2004). However, the same path model suggests that cosmopolitan fishes were negatively influenced by channel deepening associated with agriculture and may be less tolerant to channelization. Apparently, the negative influence of channelization was outweighed by the ability of cosmopolitan fishes to exist in streams influenced by high inorganic sedimentation. It is likely that the negative influence of channelization is related to hydrologic activity though none of my results indicated that the hydrologic features we quantified were important in predicting biotic responses.

Sediments were also important to fish reproduction strategy. Density of nest-associate fishes was higher with both higher agriculture and higher inorganic sediments. The nest-associate path model indicated that agriculture induced higher baseflow sediment concentration, which might have influenced reproductive strategy. The dominance of nest associates might be a result of other reproductive strategies being negatively influenced by sediment and agriculture. Sediments decrease the availability of benthic interstices making building of nests difficult. Similarly, lower substrate organic matter (and relatively higher substrate inorganic matter) was positively related to the density of fishes as non-guarders and may be indicative of embedded substrata (Fig. 4.2d). Higher inorganic matter also negatively influenced fish taxa richness and it is possible that reproductive strategies other than nest-associates and non-guarders were negatively influenced by inorganic sediment.

Fish trophic structure responded to urban and agricultural land-cover, which seemed to favor non-invertivorous feeding strategies and was likely influenced by inorganic sediments. Herbivore density was positively influenced by urban land-use, which contributed to wider, shallower streams and lower fine substrate concentration (e.g., sand; Fig. 2.4f). Similarly, detritivore density was predicted directly (i.e., bivariate regression) by agriculture indicating that higher agricultural land-cover may have stimulated detritivory or the availability of detritus. Invertivore density was not significantly related to land-cover.

Generally, path models showed that fish diversity (e.g., reproductive or trophic guild representation) and density were impaired by near-stream agriculture. Path models identified key mediating variables involved in the transfer of land-use disturbance to fishes that included channel form (i.e., channelization), suspended inorganic sediments (agricultural erosion),

substrate size (i.e., high percent fine substrates), and inorganic sediments in substrata. In summary, fish assemblage structure appeared to be influenced by near-stream land-cover and the associated geomorphic changes that further created substrate conditions suitable for retaining sand, silt, and fine inorganic matter.

Macroinvertebrate assemblage responses

Macroinvertebrate taxa richness and total density path models explained 49% and 57%, respectively, of the variation in these responses related to land-use. These metrics are known to respond to anthropogenic disturbance, especially agriculture. Agriculture is often associated with lower macroinvertebrate diversity and smaller substrate particle size (i.e., D_{50}), and many bivariate models link diversity with particle size (Angradi 1999, Huryn et al. 2002). My study linked substrate size and inorganic matter content to macroinvertebrate responses and to geomorphic (w/d ratio) and hydrologic (rating curve slope) elements and to land-cover. Streams influenced by agriculture exhibited higher taxa richness and deeper banks (i.e., channelized). Total macroinvertebrate density was negatively associated with near-stream agriculture and positively related to near-stream urban land-cover. In these study streams, increased agriculture, decreased urban land-cover, and channelization (associated with rating curve responses) combined with decreased D_{50} and increased fine substrates to negatively affect total macroinvertebrate density.

Shredder density was positively associated with near-stream agriculture. My shredder path model suggested that higher agriculture may have influenced stream channel deepening and that this helped explain higher shredder density. The positive relationship between shredders and agriculture could be explained by a hydrologic change. For example, Smock (1990) demonstrated that hydrologic activity can reintroduce buried organic matter. However, I feel that the scraper path model is of limited use because it does not reflect known ecological relationships.

The shredder model indicated that higher OM (or lower sediment, e.g., IM) was associated with urban land-cover. This could be a result of lower inorganic erosion associated with urban land-cover types (e.g., impervious surface cover, Want et al. 2001). Substrate OM was also positively related to forest cover. Scrapers appeared to be positively influenced by forest cover, which is contradictory to predictions that forest cover may reduce algal production and therefore scraper density. Algal production can be influenced by mechanical abrasion

associated with inorganic sediments (Matthaei et al. 2003). Agriculture appears to induce higher organic sediment input, which negatively influences the availability of algae to scrapers. It is possible that taxa described as scrapers may be more generalist in their feeding habits and eat something other than algae.

Collector-filterers and collector-gatherers are also important to stream energy dynamics. Specifically, decreased collector density has been associated with near-stream agriculture urban and land-cover (Huryn and Wallace 2000). In our models, channelized streams were associated with finer substrates and a decrease in collector-filterer and collector-gatherer trophic groups. Our data could suggest that the combination of impervious surfaces and associated hydrologic changes, shallower streams, and the washing-out of fine substrates were favorable to collector-gatherers (Danger and Robson 2004).

Macroinvertebrate assemblages were impaired by near-stream agriculture according to our path models. However, near-stream urban land-cover was beneficial in some models, likely a result of lower inorganic sediment input associated with increased impervious surface cover and altered watershed hydrology (Morse et al. 2003, Wang and Kanehl 2003). Similar to fishes, macroinvertebrates were likely impaired by near-stream agriculture, which led to deeper stream channels and induced sequestration of inorganic matter and embedding of substrata.

Few path models included hydrologic variables we measured, yet hydrology was likely important in distribution of erosional inorganic sediments to study streams. Observed changes to bank height, incision ratio, discharge / stage rating curves, and inorganic sediment concentration suggested that watershed hydrologic dynamics played an important, yet unobserved, role in influencing biotic assemblages in study streams (Gaines and Denny 1993). Path models rarely included hydrologic variables, largely because they were not significant in our series of pairwise regressions. However, watershed hydrology is notoriously difficult to quantify due to the varying nature, timing, and intensity of storms (Poff and Ward 1989). It is likely that our measures of hydrologic dynamics did not capture organizing events affecting observed geomorphic responses.

The LCC vs. bivariate regression

The LCC successfully modeled known relationships between physical stream elements and biotic responses. Further, path models identified links between land-cover disturbance and critical physical response variables mediating biotic effects. The LCC approach allowed me to

relate multiple variables spanning spatial and temporal scales and provided information that brings us closer to identifying the mechanisms involved in disturbance – response relationships.

My results suggest an alternative approach to exploring relationships when consideration of multiple factors is necessary. The emergent model is a novel framework to organize scientific investigations in systems having multiple interacting variables and includes at least 4 analytical steps. First, inclusive categories are identified within which specific mediating variables can be measured that are known, or hypothesized, to be involved in the transfer of anthropogenic disturbance to biota in specific systems. Second, these variables are quantified and examined for relative predictive value with respect to other variables following the general framework identified a-priori. Third, hypothetical path models are built that reflect measured responses. Fourth, the predictive value and fit of hypothesized models is quantified using path analysis. Variables associated with LCC path models may also suggest mechanisms that could prevent or impede the transfer of disturbance effects to the next hierarchical level. Rather than simply being involved in transferring disturbance effects path links could provide a buffering mechanism whereby disturbance energy is instead realized, exhausted, or absorbed. It is likely that stable, or intact, ecosystems are characterized as having operational buffering links along the path that serve to mediate disturbance responses and provide a feedback mechanisms to perpetuate stable conditions. There may be multiple mechanisms within ecosystems that can provide disturbance-mediating feedbacks under stable conditions. When these mechanisms are overwhelmed by disturbance, the energy is transferred to the next level, where it can be mediated or transferred. In systems where biotic impairment is observed, it follows that disturbance mediation has failed at each critical link.

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Table 4.1. Physical and biotic response variable significant in at least one pairwise linear regression comparison with land-cover in at least one category.

| Metric type | Metric | Units | Mean \pm 1 SE |
|-------------------|---|-------------------|-----------------|
| Hydrologic | | | |
| | Baseflow discharge | L s ⁻¹ | 40 \pm 5.5 |
| | Discharge / stage rating curve slope | - | 0.91 \pm 0.06 |
| Geomorphic | | | |
| | Mean bank height year 1 | m | 1.3 \pm 0.07 |
| | Change in incision ration between years | ° | 3.5 \pm 1.5 |
| | Width / depth ratio | - | 29 \pm 4.8 |
| Erosional | | | |
| | Baseflow TSS Inorganic Matter | g L ⁻¹ | 0.29 \pm 0.20 |
| | Stormflow TSS Inorganic Matter | g L ⁻¹ | 0.39 \pm 0.23 |
| Substrate | | | |
| | Substrate D ₅₀ | mm | 15.9 \pm 2.3 |
| | Substrate percent organic matter | % | 6.3 \pm 0.2 |
| | Substrate percent fines | % | 14 \pm 2.9 |
| Fish | | | |
| Summary | Taxa richness | # m ⁻² | 7.6 \pm 0.7 |
| | Total density | # m ⁻² | 1.1 \pm 0.2 |
| Distributional | Cosmopolitan density | # m ⁻² | 1.8 \pm 0.4 |
| Trophic | Herbivore density | # m ⁻² | 0.24 \pm 0.03 |
| Reproductive | Nest-associate density | # m ⁻² | 0.5 \pm 0.2 |
| | Non-guarder density | # m ⁻² | 0.24 \pm 0.05 |
| Macroinvertebrate | | | |
| Summary | Taxa richness | # m ⁻² | 11 \pm 1.2 |
| | Total density | # m ⁻² | 677 \pm 134 |
| | Midge density | # m ⁻² | 175 \pm 37 |
| | Shredder density | # m ⁻² | 11 \pm 6 |
| Trophic | Scraper density | # m ⁻² | 178 \pm 49 |
| | Collector-gatherer density | # m ⁻² | 192 \pm 53 |
| | Collector-filterer density | # m ⁻² | 90 \pm 19 |

Table 4.2. Comparison of predictive ability assessed with standardized regression coefficients from path models and bivariate regression between bivariate regression and path analysis as used to predict relationships between land-cover and biotic responses. Direction of relationship indicated by +/- . Dashes (-) indicate no significant model was identified. Superscript letters join multivariate models where two types of land-cover interacted to influence a single biotic response. Ag = agriculture, Fo = forest, Urb = urban. WS = watershed, min = minute, corr = 100-m corridor. Biotic metrics are density estimates (# m⁻²) except taxa richness.

| Metric category | Metric | Land-cover type | Land-cover zone | Bivariate model | Multivariate model |
|---------------------|--------------------|-----------------|-----------------|-----------------|------------------------|
| Fish taxonomic | Taxa richness | Ag | Corr | - | 0.92 (-) |
| | Total density | Ag | 60-min | - | 0.92 (-) |
| Fish distributional | Cosmopolitan | Fo | corr | 0.422 (-) | - |
| | | Ag | 60-min | - | 0.91 (-) ^A |
| | | Ag | WS | - | 0.91 (+) ^A |
| Fish trophic | Herbivore | Urb | 120-min | - | 0.49 (+) |
| | Detritivore | Ag | 60-min | 0.642 (-) | - |
| Fish reproductive | Nest associate | Ag | corr | 0.489 (+) | - |
| | | Ag | WS | - | 0.88 (+) |
| | Non-guarder | Fo | 90-min | 0.556 (-) | - |
| | | Urb | 60-min | 0.564 (+) | - |
| | | Ag | 60-min | - | 0.41 (+) |
| Mac taxonomic | Taxa richness | Ag | 60-min | - | 0.49 (-) |
| | Total density | Ag | 120-min | - | 0.57 (-) ^B |
| | | Urb | 120-min | - | 0.57 (+) ^B |
| | Midge | Ag | corr | 0.508 (-) | - |
| | | Urb | 90-min | 0.627 (+) | - |
| | | Ag | 60-min | - | 0.80 (-) |
| FFG | Shredder | Urb | 90-min | 0.541 (+) | - |
| | | Ag | 60-min | - | 0.48 (+) |
| | Scraper | Fo | 90-min | 0.411 (-) | - |
| | | Urb | 90-min | 0.541 (+) | - |
| | | Ag | corr | 0.466 (-) | - |
| | | Fo | 60-min | - | 0.426 (-) ^C |
| | | Urb | 120-min | - | 0.426 (+) ^C |
| | Collector-filterer | Fo | corr | 0.456 (-) | - |
| | | Ag | 120-min | - | 0.42 (-) ^D |
| | | Urb | 120-min | - | 0.42 (+) ^D |
| | Collector-gatherer | Urb | 120-min | - | 0.70 (+) |
| | Predator | Ag | corr | 0.468 (-) | - |

Table 4.3. Indices of model fit explaining how well a model fit our data.

| Metric type | Metric | Chi-squared (X^2 ; $p > 0.05$) | Root mean square error of approximation (RMSEA; ≤ 0.05) | Normed Fit Index (NFI; > 0.9) |
|-------------------|---------------------|--|---|----------------------------------|
| Fish | Taxa richness | $X^2 = 3.597$, $df = 1$, $p = 0.058$ | 0.537 | 0.805 |
| | Total density | $X^2 = 1.204$, $df = 3$, $p = 0.752$ | 0.00 | 0.943 |
| | Cosmopolitan | $X^2 = 7.580$, $df = 6$, $p = 0.271$ | 0.171 | 0.731 |
| | Non-guarders | $X^2 = 6.236$, $df = 3$, $p = 0.101$ | 0.346 | 0.724 |
| | Nest-associates | $X^2 = 1.999$, $df = 1$, $p = 0.157$ | 0.333 | 0.872 |
| | Herbivores | $X^2 = 4.085$, $df = 6$, $p = 0.252$ | 0.200 | 0.836 |
| Macroinvertebrate | Taxa richness | $X^2 = 4.084$, $df = 3$, $p = 0.253$ | 0.200 | 0.765 |
| | Total density | $X^2 = 21.811$, $df = 14$, $p = 0.083$ | 0.249 | 0.727 |
| | Shredders | $X^2 = 5.366$, $df = 3$, $p = 0.147$ | 0.296 | 0.764 |
| | Scrapers | $X^2 = 5.635$, $df = 6$, $p = 0.465$ | 0.00 | 0.840 |
| | Collector-filterers | $X^2 = 6.738$, $df = 10$, $p = 0.750$ | 0.00 | 0.818 |
| | Collector-gatherers | $X^2 = 6.995$, $df = 3$, $p = 0.072$ | 0.385 | 0.785 |
| | Midges | $X^2 = 9.727$, $df = 6$, $p = 0.137$ | 0.263 | 0.652 |

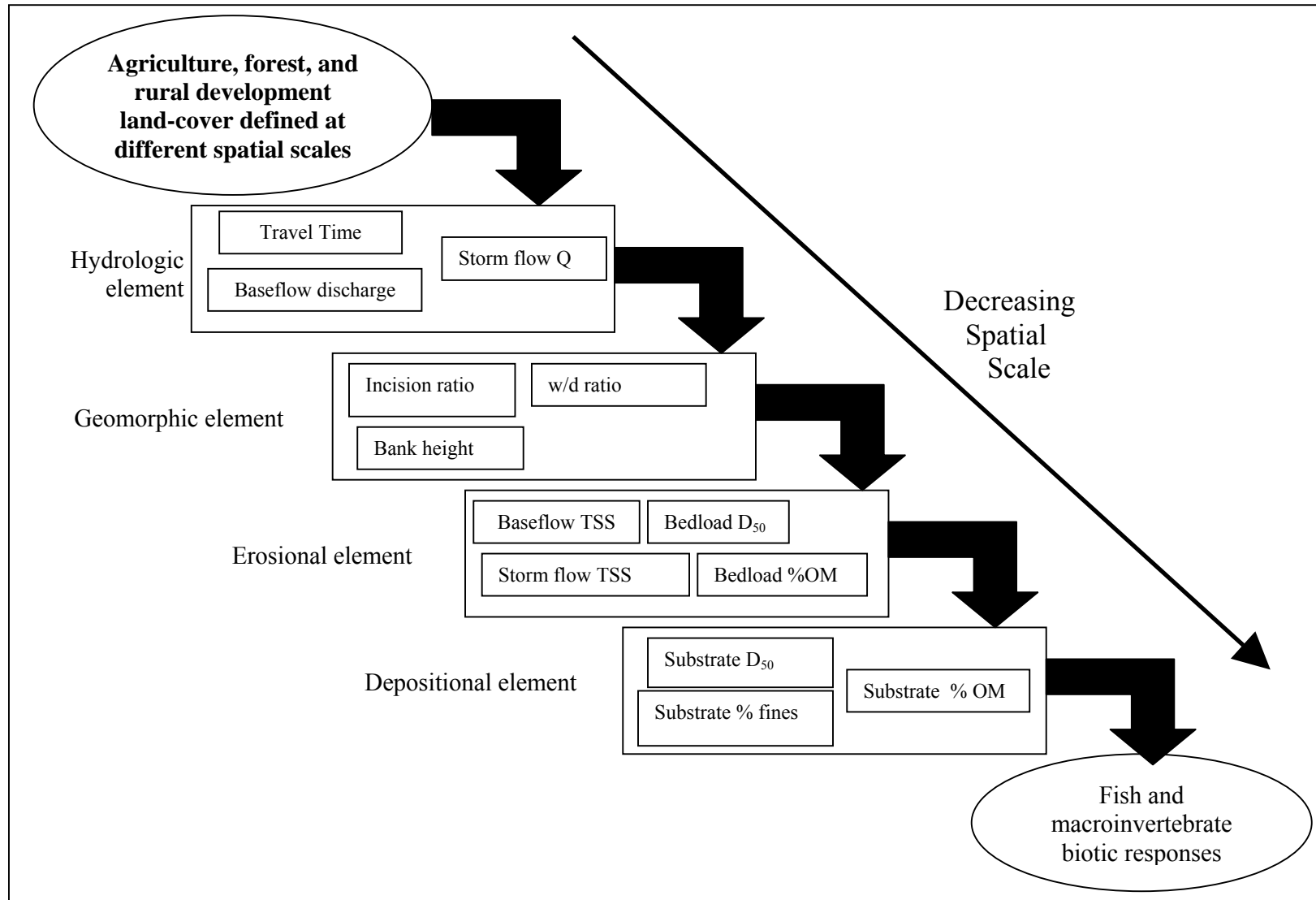
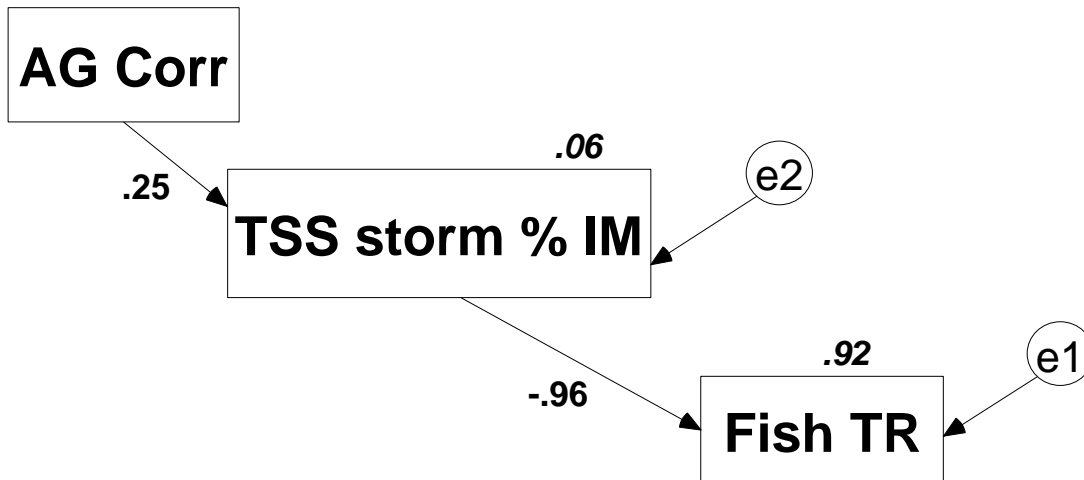


Figure 4.1. Schematic describing the general land-cover path hypothesis. OM = organic matter, , w/d = width / depth ratio, Q = discharge.

a)



b)

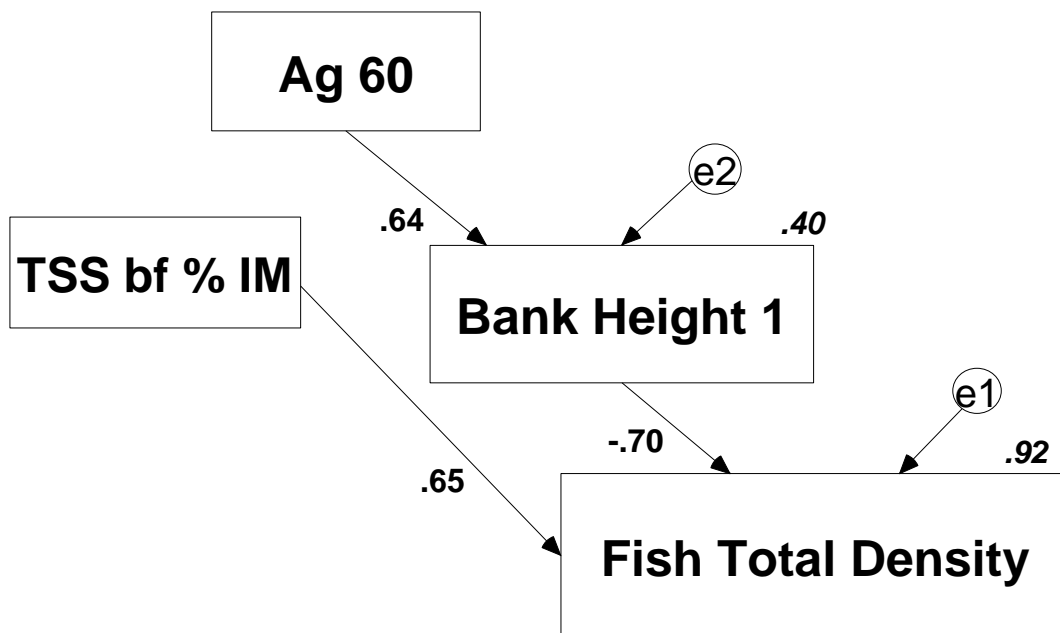
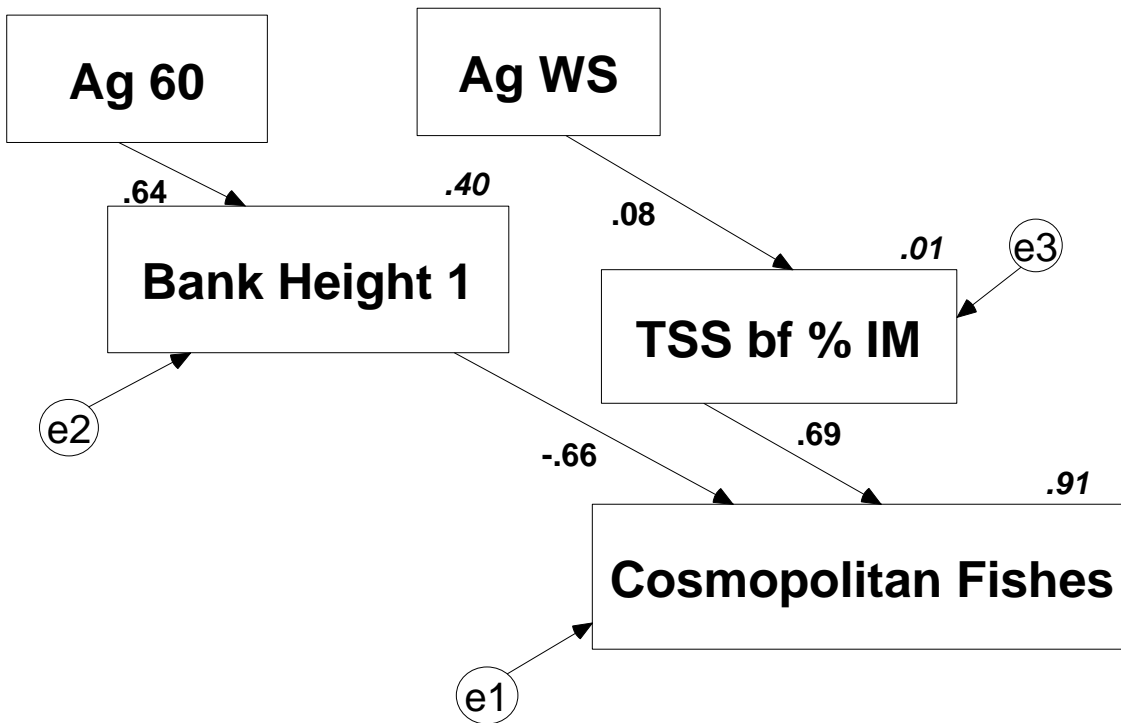
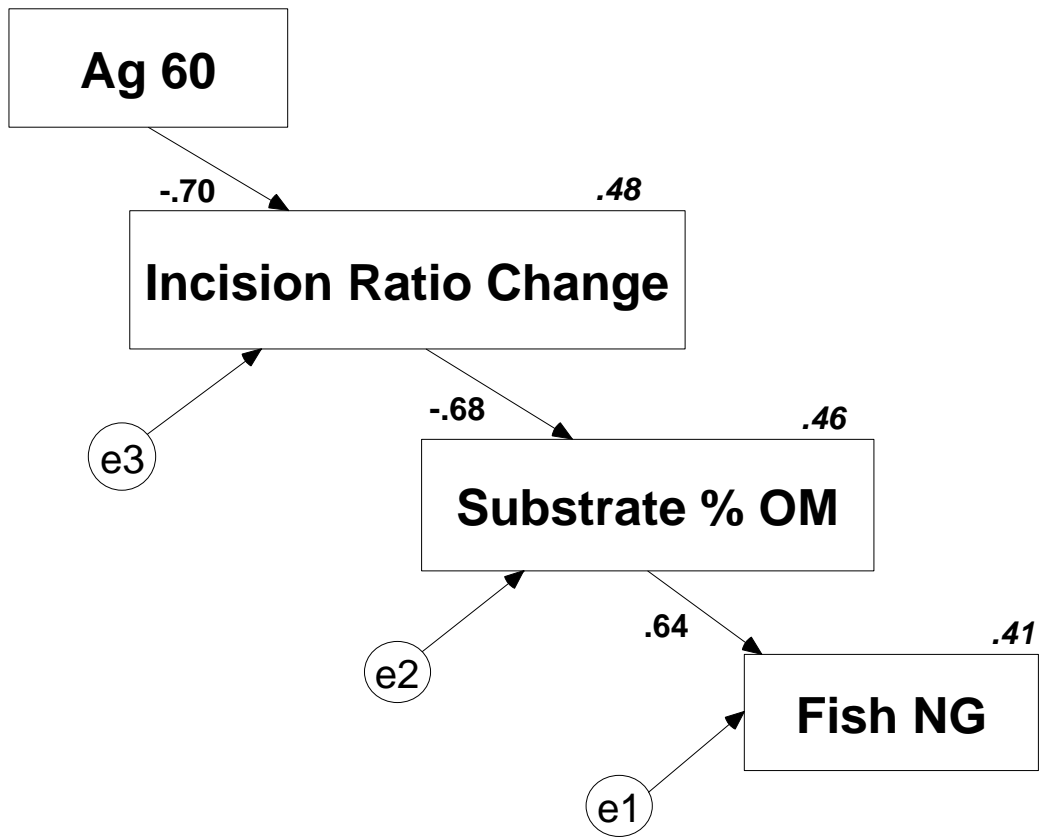


Figure 4.2. Path diagrams reduced to include best-fit predictive models. Numbers along path arrows are path coefficients, and numbers associated with variable boxes are squared correlation coefficients analogous to r^2 . Error terms are denoted by circled e's, and denote error associated with each measured variable. These errors are assumed to be unimportant, except in panel a, where Amos automatically estimated errors. Ag = agriculture, Fo = forest, corr = corridor, numerals with land-cover type indicate duration of travel time zone in which land-cover was prescribed, WS = watershed, TSS = total suspended solids, IM = inorganic matter (%), TR = taxa richness, bf = baseflow, NG = non-guarders, NA = nest associates, Mac = macroinvertebrate (continued).

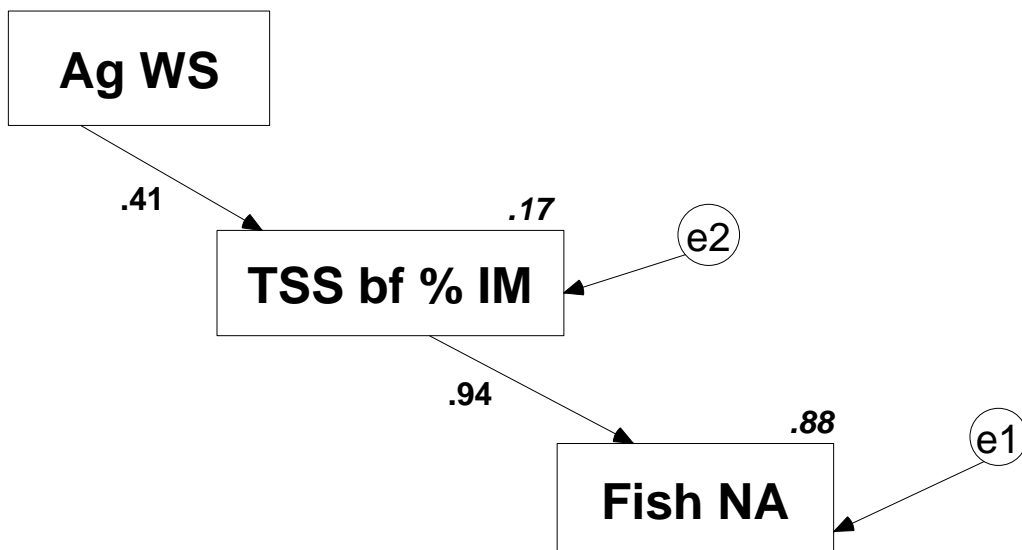
c)



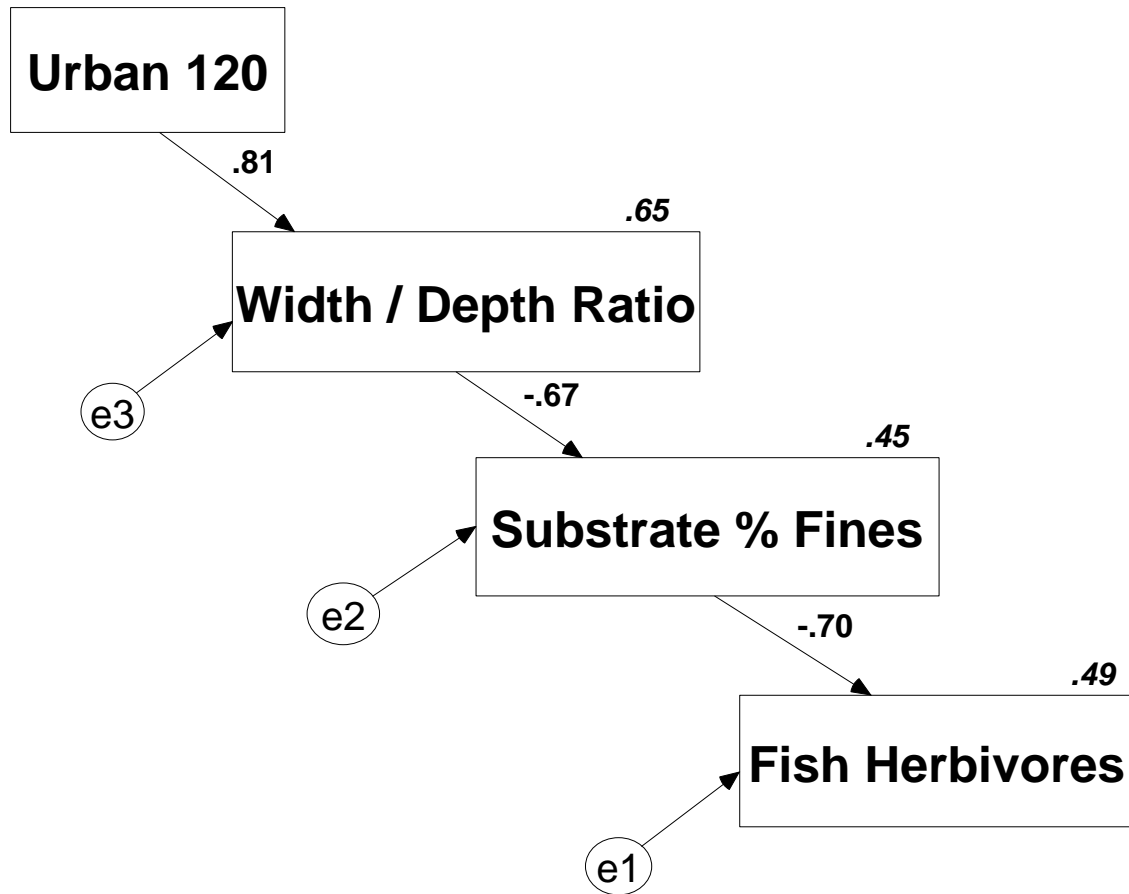
d)



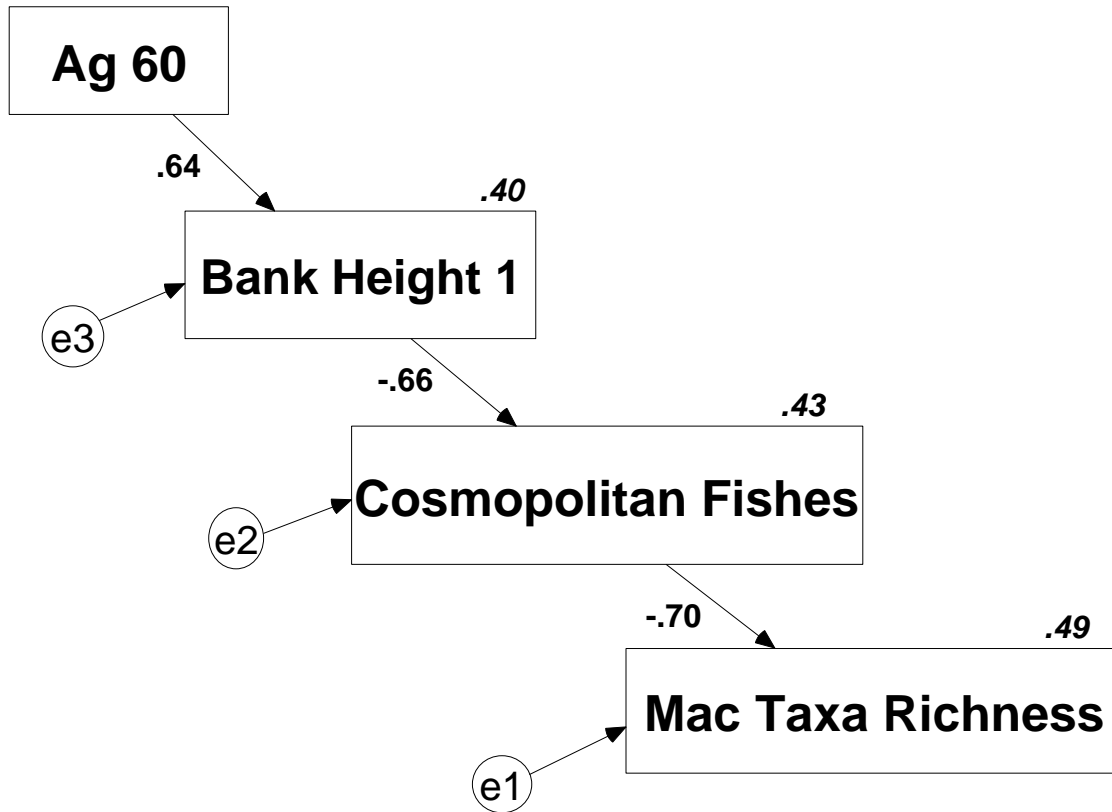
e)



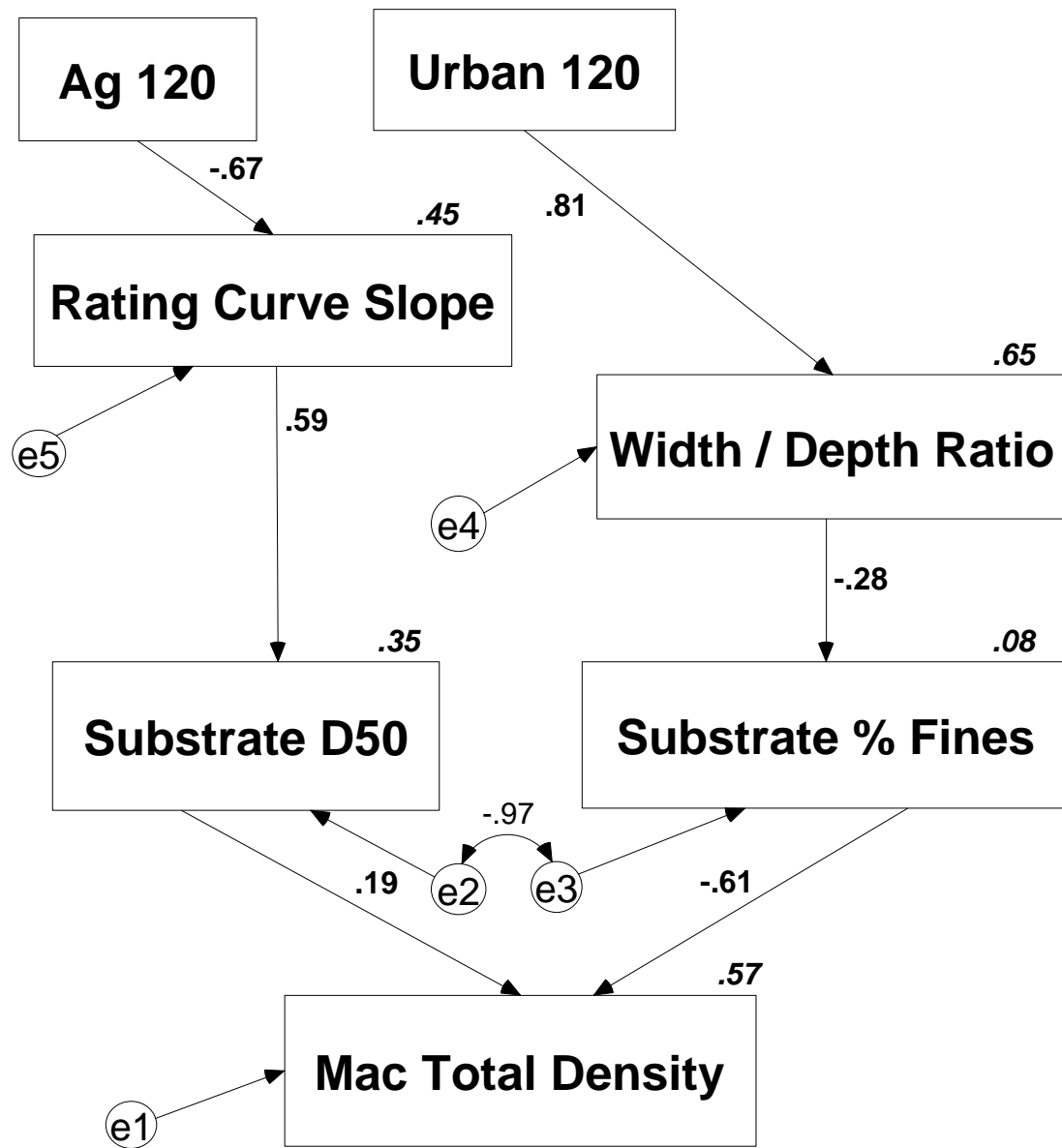
f)



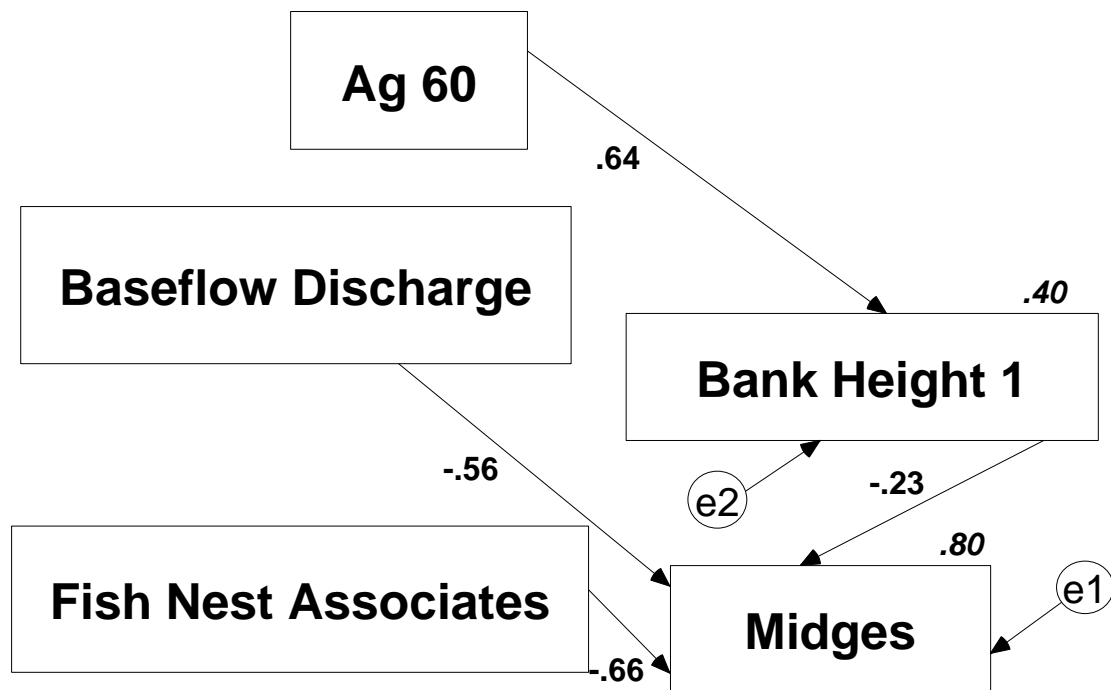
g)



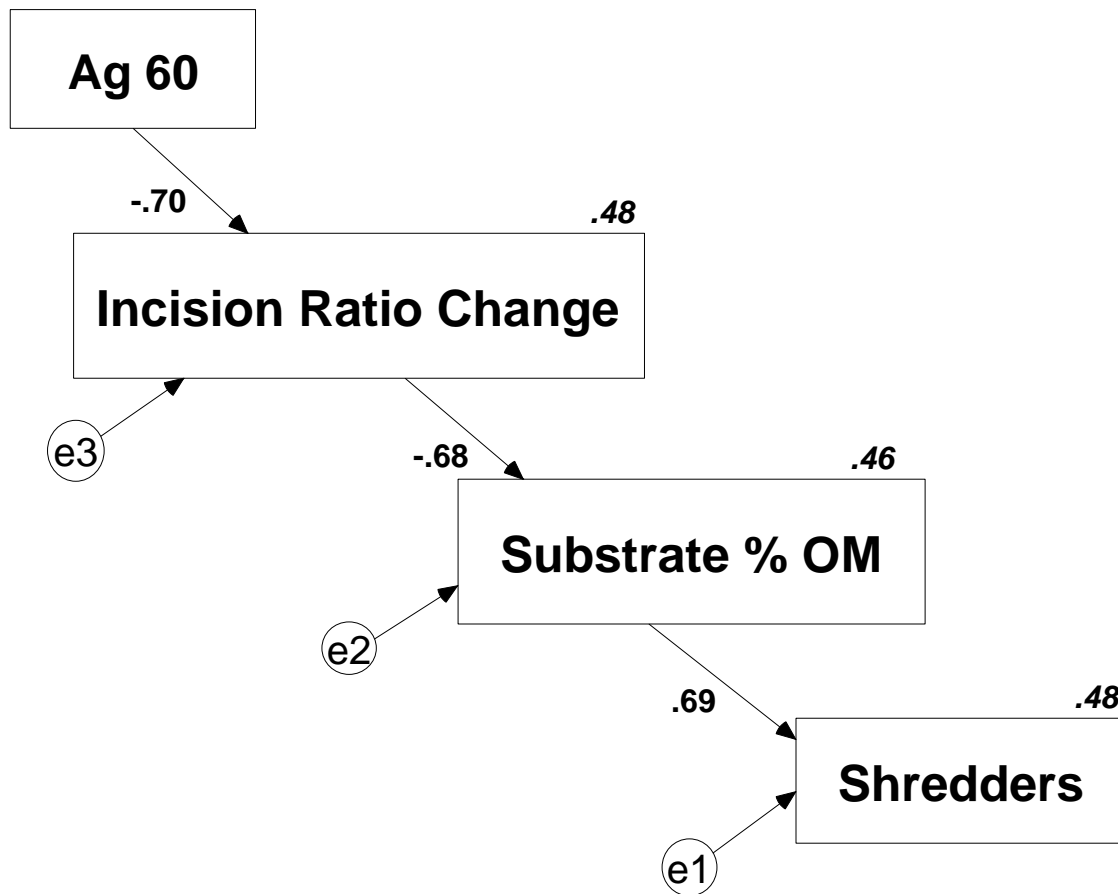
h)



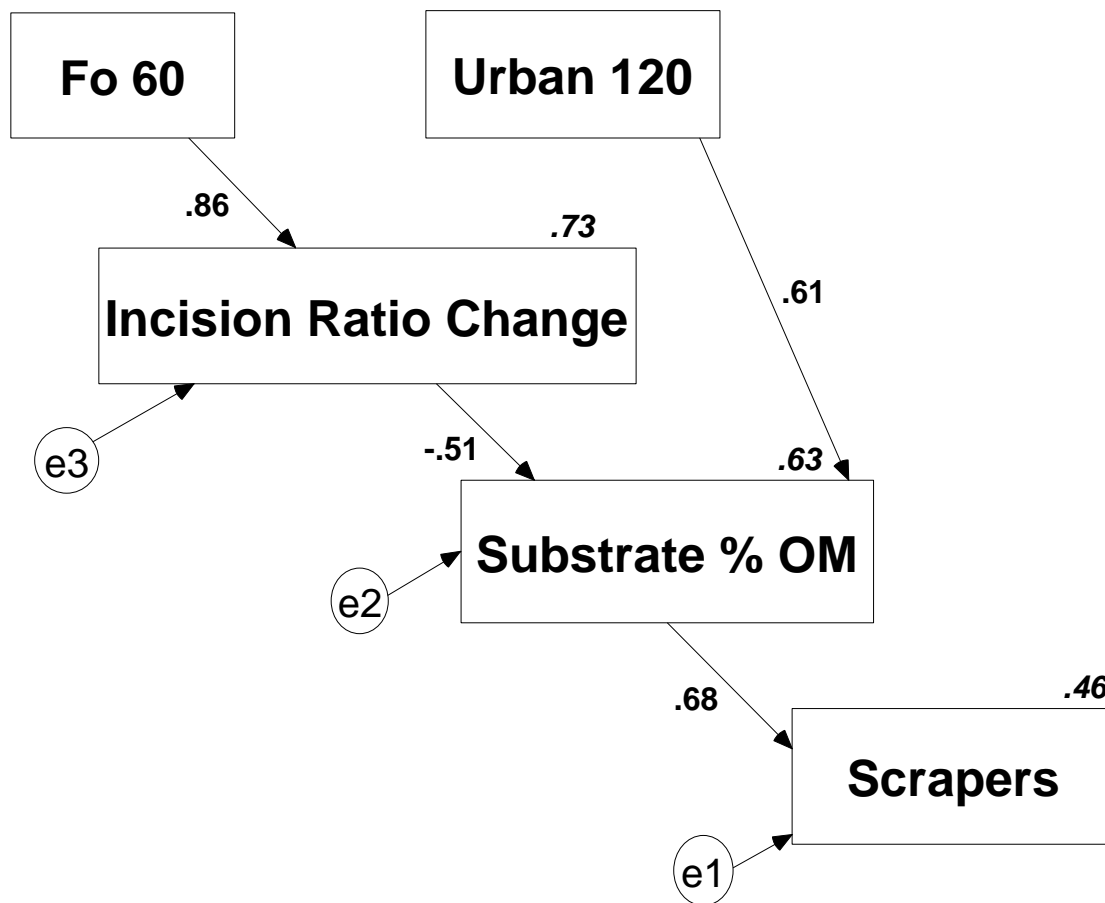
i)



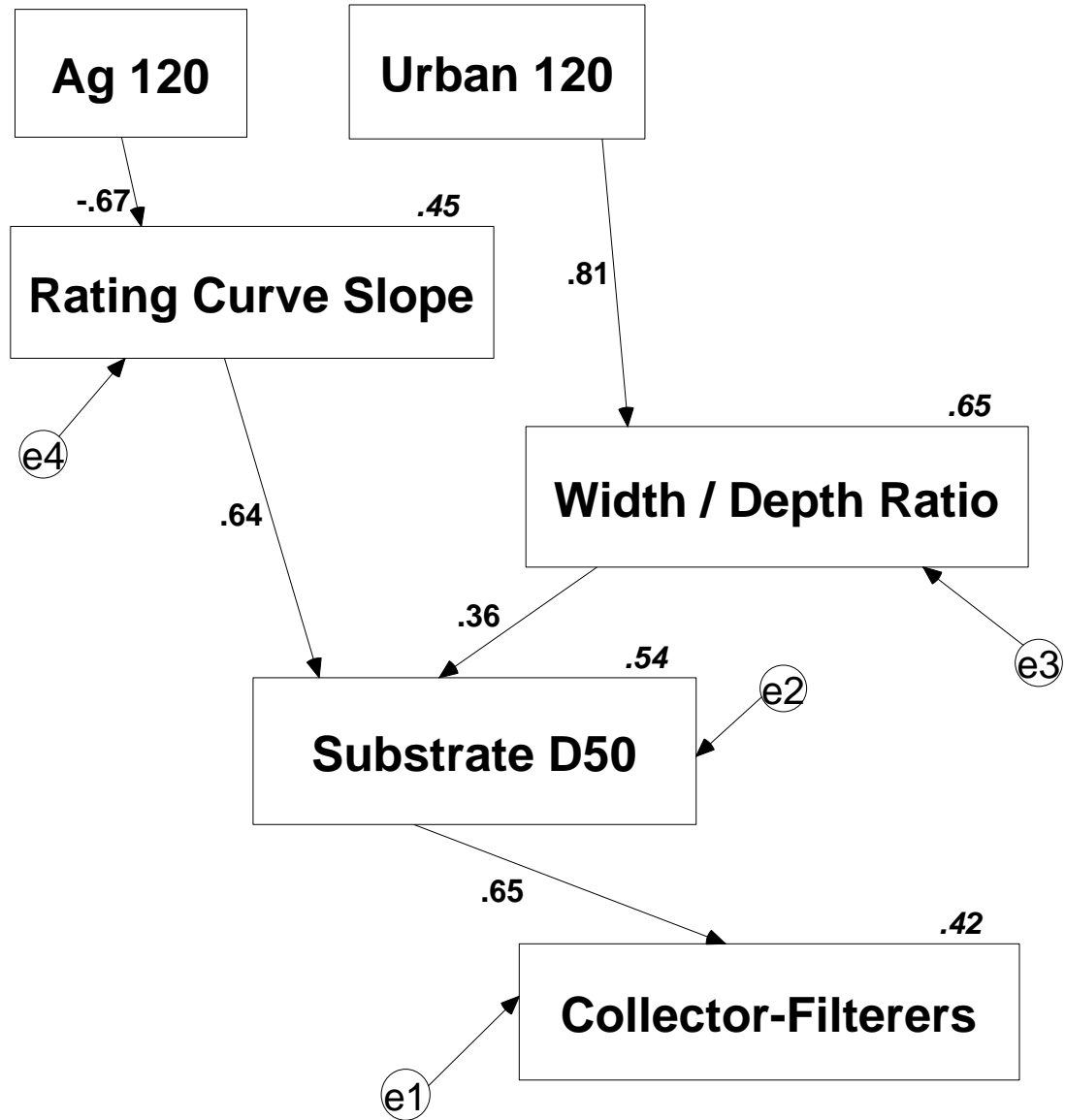
j)



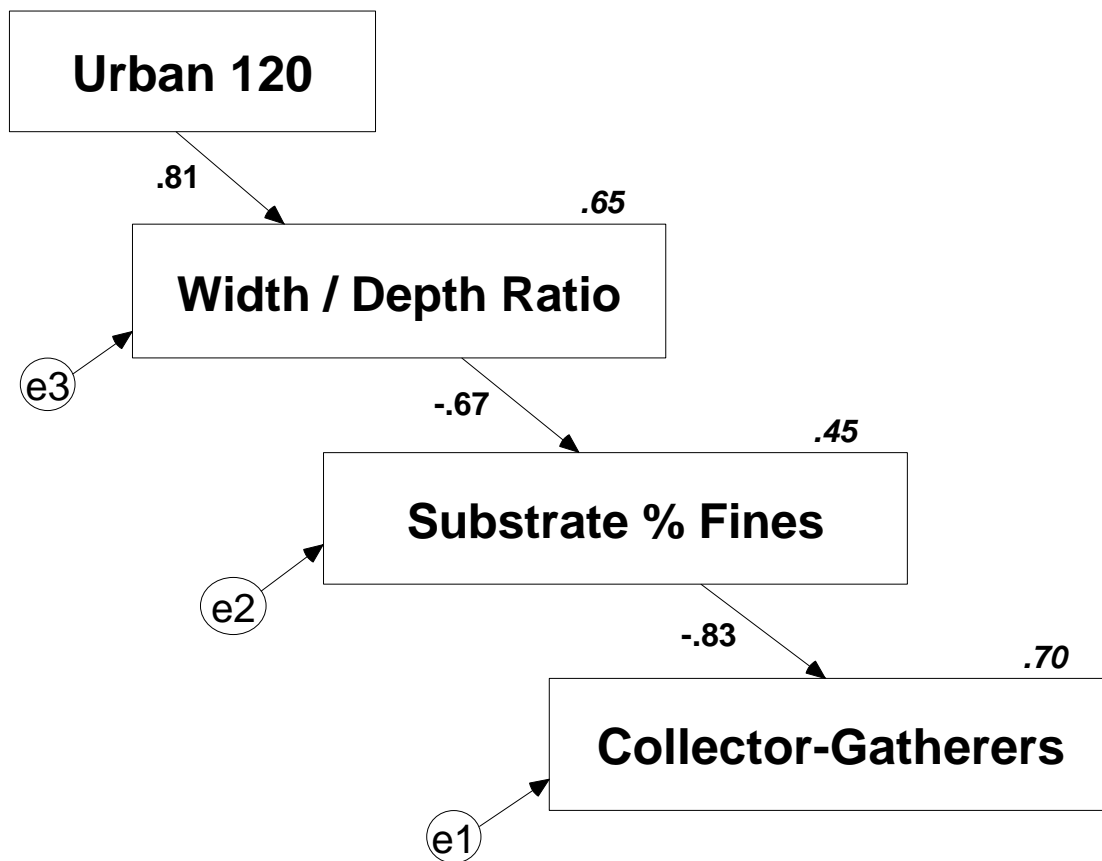
k)



l)



m)



Appendices

Appendix A. Physical and biotic response variables that were not identified as part of any land-cover/biota path.

| Response variable | Units | Mean \pm 1 SE |
|--|-------------------|-------------------|
| Hydro-dynamic | | |
| Storm flow discharge | L s ⁻¹ | 1685 \pm 553 |
| Discharge range | L s ⁻¹ | 1645 \pm 552 |
| Mean travel time | 'minutes' | 146 \pm 26 |
| Maximum travel time | 'minutes' | 678 \pm 164 |
| Geomorphic | | |
| Froude number | - | 0.124 \pm 0.015 |
| Mean bank height year 2 | m | 1.3 \pm 0.06 |
| Change in bank height bet. years | m | 0.11 \pm 0.04 |
| Mean bank incision ratio year 1 | ° | 31 \pm 1.8 |
| Mean bank incision ratio year 2 | ° | 33 \pm 2.7 |
| Mean baseflow width | m | 4.1 \pm 0.35 |
| Mean baseflow depth | cm | 0.17 \pm 0.02 |
| Erosional | | |
| Reach slope from DEM | percent | 0.34 \pm 0.06 |
| TSS baseflow | g L ⁻¹ | 0.37 \pm 0.23 |
| Rising limb TSS Organic Matter | g L ⁻¹ | 0.13 \pm 0.11 |
| Rising limb TSS stormflow | g L ⁻¹ | 0.48 \pm 0.28 |
| Rising limb TSS Stormflow Organic Matter | g L ⁻¹ | 0.13 \pm 0.1 |
| TSS rating curve exponent | - | 0.94 \pm 0.11 |
| Bedload D-50 | mm | 2.7 \pm 0.5 |
| Bedload percent organic matter | % | 11 \pm 2.8 |
| Bedload percent fines | % | 34 \pm 2.9 |
| Fish | | |
| Endemic | # m ⁻² | 0.2 \pm 0.1 |
| Benthic invertivore | # m ⁻² | 0.15 \pm 0.03 |
| General invertivore | # m ⁻² | 0.5 \pm 0.2 |
| Drift invertivore | # m ⁻² | 0.19 \pm 0.03 |
| Detritivore | # m ⁻² | 0.05 \pm 0.02 |
| Nest-builder | # m ⁻² | 0.20 \pm 0.05 |
| Broadcast spawner | # m ⁻² | 0.21 \pm 0.03 |
| Macroinvertebrate | | |
| Predator | # m ⁻² | 0.3 \pm 0.1 |

Appendix B. Set of pairwise comparisons (i.e., direct effects) resulting from significant linear regressions ($p < 0.05$) after reducing models with strong outliers. Only variables found to be significantly related to land-cover and/or biota, and thus appropriate for path analysis, are included. LC = land-cover, numbers associated with land-cover denote travel time zones and minutes, corr = 100-m buffer. G = geomorphic, H = hydrologic, E = erosional, S = substrate, B = biotic. Fo = forest, Ag = agriculture, Urb = urban. Mac. = macroinvertebrate. Biotic response variables were density ($\# \text{ m}^{-2}$) except for taxa richness. IM = inorganic matter, OM = organic matter, w/d = width to depth ratio.

| Categories | Land-cover type and zone | Response variable | Direction (+ / -) | Coefficient of determination (r^2) | p-value |
|------------|--------------------------|-------------------------|----------------------|---|---------|
| LC->G | Fo 60 | Incision ratio change | + | 0.732 | 0.002 |
| LC->G | Fo60 | Depth | + | 0.579 | 0.011 |
| LC->H | Fo120 | Mean travel time | - | 0.545 | 0.015 |
| LC->S | Fo120 | Substrate OM | - | 0.724 | 0.002 |
| LC->B | Fo90 | Fish non-guarders | - | 0.556 | 0.013 |
| LC->G | Urb120 | Depth | - | 0.642 | 0.005 |
| LC->G | Urb120 | w/d | + | 0.650 | 0.005 |
| LC->S | Urb120 | Substrate OM | + | 0.532 | 0.017 |
| LC->G | Ag60 | Bank height year 1 | + | 0.404 | 0.018 |
| LC->G | Ag60 | Incision ratio change | - | 0.484 | 0.025 |
| LC->H | Ag90 | Mean travel time | + | 0.678 | 0.003 |
| LC->H | Ag120 | Rating curve slope | - | 0.446 | 0.035 |
| LC->H | Ag120 | Mean travel time | + | 0.778 | <0.001 |
| LC->G | Ag120 | Width | - | 0.420 | 0.043 |
| LC->E | Agcorr | Baseflow TSS | + | 0.925 | 0.002 |
| LC->E | Agws | Baseflow TSS IM | + | 0.929 | 0.002 |
| LC->E | Agcorr | Stormflow TSS | + | 0.943 | <0.001 |
| LC->E | Agws | Stormflow TSS IM | + | 0.902 | 0.003 |
| LC->B | Ag60 | Fish total density | - | 0.642 | 0.005 |
| H->G | Mean travel time | Froude number | + | 0.464 | 0.030 |
| H->G | Rating curve slope | Width | + | 0.505 | 0.021 |
| H->S | Rating curve slope | Substrate D_{50} | + | 0.569 | 0.012 |
| H->B | Rating curve slope | Mac. collector-filterer | + | 0.407 | 0.047 |

| | | | | | |
|------|---------------------------|---------------------------|---|-------|--------|
| H->B | Baseflow discharge | Mac. total density | - | 0.558 | 0.013 |
| H->B | Baseflow discharge | Midge | - | 0.453 | 0.033 |
| G->S | Incision ratio change | Substrate organic matter | - | 0.464 | 0.030 |
| G->S | Width | Substrate D ₅₀ | + | 0.500 | 0.022 |
| G->S | Depth | Substrate organic matter | - | 0.530 | 0.017 |
| G->S | w/d | Substrate D ₅₀ | + | 0.420 | 0.043 |
| G->S | w/d | Substrate % fines | - | 0.448 | 0.034 |
| G->B | Froude no. | Fish herbivore | + | 0.476 | 0.027 |
| G->B | Bank height year 1 | Fish total density | - | 0.500 | 0.022 |
| G->B | Bank height year 1 | Cosmopolitan fish | - | 0.431 | 0.039 |
| G->B | Depth | Fish herbivore | - | 0.447 | 0.035 |
| G->B | w/d | Fish herbivore | + | 0.419 | 0.043 |
| G->B | Depth | Shredder | - | 0.528 | 0.017 |
| G->B | w/d | Shredder | + | 0.654 | 0.005 |
| E->B | Baseflow TSS | Fish taxa richness | - | 0.980 | <0.001 |
| E->B | Baseflow TSS | Fish nest associate | + | 0.784 | 0.019 |
| E->B | Baseflow TSS IM | Fish taxa richness | - | 0.917 | <0.001 |
| E->B | Baseflow TSS | Fish total density | + | 0.682 | 0.043 |
| E->B | Stormflow TSS | Fish taxa richness | - | 0.986 | <0.001 |
| E->B | Stormflow TSS | Fish nest associate | + | 0.757 | 0.024 |
| E->B | Stormflow TSS IM | Fish taxa richness | - | 0.929 | 0.002 |
| E->B | Stormflow TSS IM | Fish total density | + | 0.658 | 0.05 |
| E->B | Stormflow TSS IM | Cosmopolitan fish | + | 0.719 | 0.033 |
| E->B | Stormflow TSS IM | Fish nest associate | + | 0.872 | 0.006 |
| S->B | Substrate % fines | Fish herbivore | - | 0.485 | 0.025 |
| S->B | Substrate % OM | Fish non-guarder | + | 0.412 | 0.045 |
| S->B | Substrate D ₅₀ | Mac. total density | + | 0.570 | 0.012 |
| S->B | Substrate D ₅₀ | Collector-gatherers | + | 0.588 | 0.010 |
| S->B | Substrate D ₅₀ | Collector-filterers | + | 0.476 | 0.027 |
| S->B | Substrate % OM | Shredder | + | 0.478 | 0.027 |
| S->B | Substrate % OM | Scraper | + | 0.520 | 0.019 |
| S->B | Substrate %fines | Mac. total density | - | 0.637 | 0.006 |
| S->B | Substrate % fines | Collector-gatherer | - | 0.695 | 0.003 |

| | | | | | |
|------|-------------------|--------------------|---|-------|-------|
| B->B | Cosmopolitan fish | Mac. taxa richness | - | 0.490 | 0.024 |
| B->B | Nest associates | Midge | - | 0.405 | 0.048 |

Chapter 5: Synthesis

*Plant a new Truffula. Treat it with care.
Give it clean water. And feed it fresh air.
Grow a forest. Protect it from axes that hack.
Then the Lorax
and all of his friends
may come back.
– Theodor Seuss Geisel in The Lorax.*

My dissertation focused on contemporary issues of stream ecology and continues the legacy of the Virginia Tech Stream Team. Specifically, I was interested in expanding our knowledge of how land-cover disturbance influences streams at the ecosystem scale. Anthropogenic land-use is one of the most detrimental disturbances affecting streams worldwide (Ramankutty et al. 2002), and a central tenet of my dissertation was determining whether rural development influenced streams. Inherent in my approach to stream ecosystems is my use of watersheds as organizational systems appropriate for studying streams. Researchers interested in stream reach-scale responses (e.g., macroinvertebrate communities, nutrient spiraling, habitat sedimentation) are currently focusing on watershed-scale phenomena that potentially influence the responses we measure. Aquatic ecologists are still learning how to study streams at the watershed scale, which variables are important, and what the mechanisms are that inhibit or induce disturbance effects from the landscape to stream responses.

Linking disturbance effects to stream responses is greatly complicated by spatial scale. Currently, research addressing how to consider the relationship between land-use spatial scale and biotic responses is in the pioneer stages. My dissertation contributes to the spatial scale issue by using travel time to subdivide watersheds along a spatial continuum. I designed a method for delimiting watersheds into ecologically relevant sub-portions that could be used as spatially explicit zones of influence to describe land-cover at multiple spatial scales. In the last five years researchers have introduced several methods for considering landscape influence, but travel time zones (TTZs) are the first I am aware of that use ecologically relevant criteria in their design. TTZs helped subdivide watershed land-cover by hydrologic connectivity that I believe represents potential areas of terrestrial-aquatic interaction. Differential land-cover influence to stream biota associated with TTZs reflected differences in proximity and the level of potential interaction appropriate to each biotic response. TTZs are a step toward integrating ecological

meaning and management objectives. Identification of critical areas of terrestrial-aquatic interaction or potential influence could greatly enhance research, conservation, and management.

Rural development had a subtle influence on biotic assemblages and appeared to induce changes to watershed hydrology and erosion dynamics. This relatively recent phenomenon has not yet been well studied and my findings that rural development subtly influenced biodiversity in streams already impaired by agriculture will contribute to our understanding of stream disturbance response. Rural development effects were not strong enough to be detectable with inferential statistics, but distinct biotic assemblages were present in developing and agricultural streams. The influence of rural development appeared to be related to reduced inorganic sediment input that was likely associated with changes to watershed hydrology. I identified suspended solids associated with watershed hydrology and substrate as potential intermediate links influencing biota and being influenced by land-cover.

The Land Cover Cascade design linked large-scale disturbance influence to smaller scale biotic responses through intermediate abiotic variables that helped propagate the land-cover disturbance. Since at least the 1970's researchers have investigated how humans influence streams and I have identified many of the potential cause-effect relationships involved in the propagation of land-cover disturbance. My conclusions were mostly supportive of former findings but unlike past studies I was able to quantify links between land-cover and biota through known intermediate abiotic variables. Using structural equation modeling I also identified some of the intermediate variables linking land-cover to biotic responses that traditional bivariate techniques could not. To manage, conserve, and restore aquatic systems we must identify the mechanisms that propagate or inhibit disturbance from influencing streams. The Land Cover Cascade design brings us closer to identifying these mechanisms and will influence the way we study streams in the future.

To understand relationships between humans and streams, researchers must consider large-scale, multivariate, integrative approaches to science. I have attempted to assemble our current knowledge of landscape/stream relationships with emerging techniques to attain a thorough analysis of land-cover influence to stream biota. Humans continue to alter our influence to the landscape and researchers must likewise continue to alter their approaches to science. Combining the scientific method, past research, and creativity will bring us closer to successful coexistence between natural systems and human needs.

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