MARK CHANDLER SCOTT
Integrating The Stream And Its Valley: Land Use Change, Aquatic Habitat, And Fish Assemblages
(Under the Direction of GENE S. HELFMAN)

Streams integrate landscape processes across multiple spatial and temporal scales. Human activities have extensively altered landscapes in North America, with serious consequences for aquatic ecosystems. I investigated land use in southern Appalachian watersheds to identify proximate effects on stream habitat and ultimate effects on fish assemblage structure and organization. I examined how catchment land use type, extent, spatial pattern, and history affect physical and chemical characteristics of streams, and how instream factors (i.e., habitat) influence distribution and abundance of stream fishes. Field data were used to test predicted relationships and to construct empirical models of relationships among landscape and stream variables. Forest cover accounted for the most variation in nearly all models, supporting predictions of nutrient enrichment, thermal pollution, and sedimentation caused by landscape disturbance. Physicochemical models fit better when landscape predictors were catchment-wide rather than localized, indicating cumulative impacts. Four faunal associations were identified across the landscape. Three classes were dominated by endemic Appalachian highland fishes, forming a continuous gradient in assemblage structure from smaller, cooler, higher-elevation streams to larger, warmer, lower-elevation streams. A fourth association was characterized by non-endemic fishes where habitats were affected by nutrients and sediment in association with forest cover loss in streamside buffers and high density of buildings and roads. Endemic, small-bodied (low fecundity), cool-water trophic specialists that depend on coarse substrate for spawning declined where stream habitats were modified. They were supplanted by cosmopolitan, large-bodied (long-lived, high-fecundity), warmwater trophic generalists that do not require rocky substrates for successful spawning. Streams draining urbanizing catchments, or those that had been severely disturbed in the past, had lower ratios of endemic to widespread taxa even though riparian buffers were largely forested, suggesting legacy effects from past catchment disturbance. Replacement of unique locally-adapted taxa with widespread generalized species has been termed biological homogenization, and may severely affect regional and continental biodiversity, particularly in regions with rich endemic faunas such as the Southeast. Research identifying functional responses to cumulative effects of landscape change is needed to promote proactive conservation at the watershed scale, management that is critical to maintaining the integrity of aquatic habitat and biodiverse communities.

INDEX WORDS: Watershed management, Water quality, Cumulative impacts, Aquatic habitat alteration, Biodiversity of southeastern fishes, Endemism, Biotic homogenization, southern Appalachian Mountains, North Carolina, USA

INTEGRATING THE STREAM AND ITS VALLEY: LAND USE CHANGE, AQUATIC HABITAT, AND FISH ASSEMBLAGES

by

MARK CHANDLER SCOTT

B.S., Wofford College, 1987

M.S., Virginia Tech, 1994

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2001

INTEGRATING THE STREAM AND ITS VALLEY: LAND USE CHANGE, AQUATIC HABITAT, AND FISH ASSEMBLAGES

by

MARK CHANDLER SCOTT

Approved:

Major Professor:	Eugene S. Helfman
Committee:	Judith L. Meyer Mary C. Freeman Catherine M. Pringle C. Ronald Carroll

Electronic Version Approved:

Gordhan L. Patel
Dean of the Graduate School
The University of Georgia
December 2001

DEDICATION

To my wife Tina for her unflagging support, to those whose lives are dedicated to protecting our natural heritage, and to all those who find beauty and solace at the river's edge.

ACKNOWLEDGMENTS

I thank my advisor Gene Helfman for his support and insight over the years; committee members Mary Freeman, Cathy Pringle, Judy Meyer, and Ron Carroll for their comments and guidance on this research; Paul Bolstad and Ned Gardiner for providing geographic data; Steve Rathbun for advice on statistical methods; Dale Jones, Ned Gardiner, Matt McTammany, Douglas Toole, Buddy Farmer, Josh Harper, Kate Schofield, Brandon Staub, Andrew Sutherland, Shane Kornberg, Heather Russell, Paula Marcinek, and Tina Scott for field assistance. This research was supported by National Science Foundation grant DEB-9632854 to the University of Georgia Coweeta Long Term Ecological Research Program.

TABLE OF CONTENTS

Page

CHAPTER

CHAPTER 1

INTRODUCTION AND BACKGROUND LITERATURE

As part of the National Science Foundation-sponsored Regionalization Initiative, researchers with the Coweeta Long-Term Ecological Research Program began an investigation in 1995 into consequences of land-use change in the southern Appalachians. The regionalization work shifted the traditional focus from the Coweeta Hydrological Laboratory, an experimental watershed in western North Carolina, to the surrounding region, thereby encompassing the human community and its effects on landscapes and ecosystems. The aquatics section of this effort comprises work on various lotic system components, one of which is fish fauna. The Blue Ridge physiographic province of North Carolina provides an excellent location for studies of fish biodiversity since it drains primarily into the Tennessee River which is among the richest examples of freshwater faunal diversity in the temperate world (Warren and Burr 1994). Two major sub-basins, the Little Tennessee and French Broad river systems, were selected for study and samples for various physical, chemical, and biological parameters were collected during 1995-1999.

The establishment of the Regionalization Program was well-timed given the rapid rate of environmental change in this region (Wear and Bolstad 1998). Ecological communities worldwide are undergoing rapid modification due to ongoing human actions (Vitousek 1994); current rates of landscape change create an imperative for scientists to understand and quantify anthropogenic impacts on ecosystems (Lubchenco et al. 1991). Habitat alteration is a root cause of biodiversity loss and shifts in community structure (Chapin et al. 1998, Wilcove et al. 1998). Habitat degradation due to human activities within a catchment has been recognized as a particularly important contributor to species imperilment and loss of ecological integrity in running waters (Karr et al. 1985, Carpenter et al. 1992, Allan and Flecker 1993, Warren and Burr 1994).

I investigated land use in southern Appalachian watersheds to identify effects on stream habitat and fish assemblages. Specifically, I examined how catchment land-use type, intensity of use, spatial pattern, and history of land-use affect physical and chemical characteristics of streams, and how these instream factors (i.e., habitat) relate to the distribution and abundance of stream fishes. Field data were used to test relationships predicted by current understanding of watershed processes and to construct empirical models indicating interrelationships among landscape and local instream conditions. Assemblage structure was examined within the context of regional geologic and evolutionary history with regard to composition, diversity, behavioral and ecological attributes, and life-history traits. I attempted to account for landscape influences on aquatic systems, and the relative magnitude of effects, using a statistical variance-partitioning approach (Richards et al. 1997; Roth et al. 1996; Allan et al. 1997; Lammert and Allan 1997). Several researchers have made the case that habitat is dependent on conditions in the catchment, providing a linkage between terrestrial conditions and aquatic communities (Richards and Host 1994; Imhof et al. 1996). My goal was to assess the ability of this general model to explain the structure of fish assemblages in the southern Appalachians.

Conceptual Model

A framework depicting linkages among landscape and stream processes provides a context for observed patterns in stream geomorphology, water quality, and faunal structure (Figure 1.1). The watershed is a natural way to organize landscapes, particularly from a lotic perspective (Lotspeich 1980). My approach was to test predictions of a hierarchical model that links streams to their catchments (or "valley"; Hynes 1975). While the River Continuum Concept (Vannote et al. 1980) provides a view of the upstream-downstream linkage and the importance of physicochemical features to stream biota, an emerging paradigm in lotic research expands this concept and views the stream as an integrator of the landscape (Frissell et al. 1986; Imhof et al. 1996; Fisher 1997). The form assumed by the stream system is the result of a dynamic process involving water and sediment supply that is a function of climate, geology, and land cover (Leopold et al. 1964; Hunsaker and Levine 1995; Church 1996). These relationships form a hierarchy of regional, landscape, reach, and local-scale factors. Physical and chemical conditions (i.e., habitat), observed at any site along the upstream-downstream continuum, are functions of these spatial factors, and biological communities are constrained by their habitat. Figure 1.1 is a simplified schematic illustrating the hierarchy of influences ultimately affecting community structure (modified from Karr 1991). In essence, watershed- and reach-scale factors influence local conditions, which in turn comprise habitat for organisms.

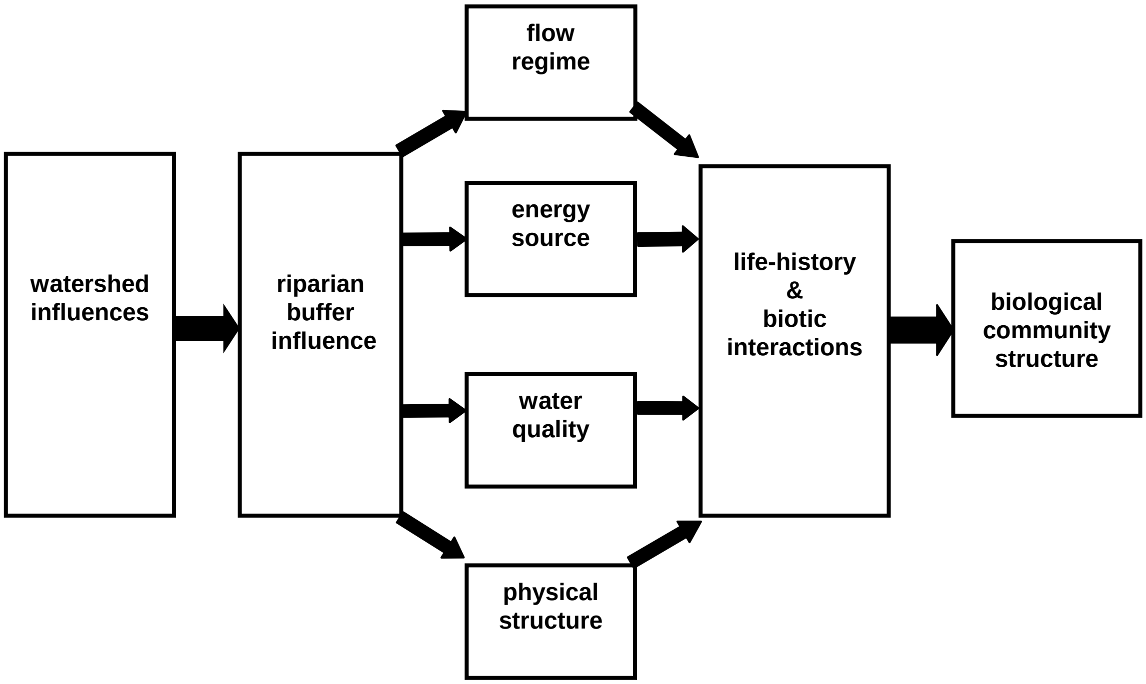

Figure 1.1. Conceptual model of watershed influences on aquatic habitats and biota (modified from Karr 1991).

Patterns of occurrence and abundance of organisms are fundamentally determined by abiotic constraints, described by Southwood (1977) as the habitat template. Species possessing traits suited to these abiotic "filters" may be constrained further by biotic interactions (Poff 1997). The outcome of interactions such as competition and predation may shift as the habitat template is altered in response to landscape change, providing a second means, in addition to physicochemical tolerance, by which community structure is modified.

Application to the southern Blue Ridge physiographic province

A consideration of a region's history is a prerequisite to understanding its ecology. Prior to intensive, widespread disturbance associated with European colonization, southern Blue Ridge watersheds originally featured rugged highland topography and densely forested landscapes; the associated stream habitat template included coarse sediments and cool to cold water with low concentrations of dissolved ions and nutrients (Wallace et al. 1992). Species physiologies, life histories, and ecological traits have evolved under this selection regime for the region's 200 million years of above-sea history (Hack 1969). As a result of this unique history, the region is a major center of aquatic biodiversity and endemism in the temperate world (Warren and Burr 1994). I hypothesize that some native species, particularly endemics, evolved specialized adaptations to the distinctive southern Appalachian environmental regimes. These adaptations might include greater metabolic efficiency at low temperatures and/or use of coarse substrates at one or more life-stages.

With anthropogenic change in habitat conditions, life-history strategies that evolved under natural environmental regimes may no longer be adaptive. This may be particularly stressful for species endemic to the Appalachian Highlands (Mayden 1987), since these species evolved with the distinctive flow regime, geomorphology, and water chemistry found in the region. If the types of anthropogenic change occurring in southern Appalachian watersheds include, as literature suggests, an increase in sediment loading, water temperature, and nutrient levels in streams (Waters 1995; Hunsaker and Levine 1995; Peierls et al. 1991), then species whose evolution was influenced by lowland conditions may be favored. This process of endemic species loss and their replacement by geographically widespread species has been described as *biotic homogenization* (Lockwood and McKinney 2001). Thus one of the key questions I address is: Are highland endemics being supplanted by other fishes in streams draining modified basins? In this context, lowland warm-water fishes would be functioning as exotic species; their invasion at the expense of endemics would constitute a decline in ecological integrity (Karr 1991) and a loss of regional, or gamma, diversity. Evidence for this would be indicated by greater abundance of widely-distributed, lowland species relative to highland endemic fishes in disturbed watersheds. This line of reasoning has been suggested by research on species imperilment and conservation in Virginia (Angermeier 1995). Taxonomically-rich systems such as the Tennessee River are excellent field sites for tests of this hypothesis.

To study anthropogenic effects, other “natural” (i.e., non-anthropogenic) influences structuring stream biota must be taken into account. I therefore first describe variation in fish assemblages along natural gradients (e.g., stream size, elevation) in the study region, and then determine whether an anthropogenic “signal” can be detected against the backdrop of these natural patterns. A gradient of land use intensity present among study streams, from relatively undisturbed forest to urban, provides a means for detecting the signal and provides insight into the form of ecological response along the gradient (McDonnell and Pickett 1990).

Research Overview

I proceed under the hypothesis that the level of human activity in the watershed is altering physicochemical habitat, and test the relative roles of land use/land cover characteristics at various scales to determine which best explain stream habitat conditions. Patterns in fish assemblage structure (composition and abundance) are examined with respect to landscape and habitat influences, under the hypothesis that environmental change affects fish composition and distribution either by exceeding physiological tolerances or by shifting the outcome of biological interactions. Particular life history and ecological attributes are investigated to determine if endemic fishes can be distinguished from geographically-widespread species, and further to determine if attributes are related to watershed disturbance. Finally, historical change in land use is related to faunal change determined from historical fish collections. Turnover in species composition and the ratio of endemic to widespread species are analyzed with respect to change in forest cover over the latter part of the 20th century.

Bibliography

Allan, J.D., and A.S. Flecker. 1993. Biodiversity conservation in running waters. BioScience 43(1):32-43.

Allan, J.D., D.L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biol. 37:149-161.

Angermeier, P.L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. Conserv. Biol. 9:143-158.

Carpenter, S.R., S.G. Fisher, N.B. Grimm, and J.F. Kitchell. 1992. Global change and freshwater ecosystems. Ann. Review Ecol. & Systematics 23:119-139.

Chapin, F.S., III, and 13 coauthors. 1998. Ecosystem consequences of changing biodiversity. BioScience 48(1):45-52.

Church, M. 1996. Channel morphology and typology. pp. 185-202 *in* G. Petts and P. Calow, eds. River flows and channel forms. Blackwell, Oxford.

Fisher, S.G. 1997. Creativity, idea generation, and the functional morphology of streams. J. N. Am. Benthol. Soc. 16:305-318.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage. 10:199-214.

Hack, J.T. 1969. The area, its geology: Cenozoic development of the southern Appalachians. pp. 1-17 *in* P.C. Holt, ed. The distributional history of the biota of the southern Appalachians. Part I: invertebrates. Research Division Monograph 1, VPI&SU, Blacksburg, Virginia.

Hunsaker, C.T. and D.A. Levine. 1995. Hierarchical approaches to the study of water quality in rivers. BioScience 45:193-203.

Hynes, H.B.N. 1975. The stream and its valley. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 19:1-15.

Imhof, J.G., J. Fitzgibbon, and W.K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 312-326.

Karr, J.R., L.A. Toth, and D.R. Dudley. 1985. Fish communities of midwestern rivers: a history of degradation. BioScience 35:90-95.

Karr, J.R. 1991. Biological integrity: a long-neglected aspect of water resource management. Ecol. Appl. 1:66-84.

Lammert, M. and J.D. Allan. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ. Manage. 23:257-270.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial processes in geomorphology. W.H. Freeman, San Francisco.

Lockwood, J.L., and M.L. McKinney, eds. 2001. Biotic homogenization. Kluwer Plenum/Academic Press, New York. 289 pp.

Lotspeich, F.B. 1980. Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. Water Res. Bull. 16:581-586.

Lubchenco, J.A., and 15 coauthors. 1991. The sustainable biosphere initiative: an ecological research agenda. Ecology 72:371-412.

Mayden, R.L. 1987. Historical ecology and North American highland fishes: a research program in community ecology. pp. 203-222 *in* W.J. Matthews and D.C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

McDonnell, M.J. and S.T.A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71:1232-1237.

Peierls, B.L., N.F. Caraco, M.L. Pace, and J.J. Cole. 1991. Human influence on river nitrogen. Nature 350:386-387.

Poff, N.L. 1997. Landscape filters and species traits: towards a mechanistic understanding and prediction in stream ecology. J. N. Am. Benthol. Soc. 16:391-409.

Richards, C. and G.E. Host. 1994. Examining land use influences on stream habitats and macroinvertebrates: a GIS approach. Water Resources Bulletin 30:729-738.

Richards, C., R.J. Haro, L.B. Johnson, and G.E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. 37:219-230.

Roth, N.E., J.D. Allan, and D.L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecol. 11:141-156.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46:337-365.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Vitousek, P.M. 1994. Beyond global warming: Ecology and global change. Ecology 75(7):1861-1876.

Wallace, J.B., J.R. Webster, and R.L. Lowe. 1992. High-gradient streams of the Appalachians. pp. 133-191 *in* Hackney, C.T., S.M. Adams, and W.H. Martin, eds. Biodiversity of the southeastern United States: Aquatic communities. John Wiley & Sons, New York.

Warren, M.L. Jr., and B.M. Burr. 1994. Status of freshwater fishes of the United States: Overview of an imperiled fauna. Fisheries 19(1):6-17.

Waters, T.F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph 7.

Wear, D.N., and P. Bolstad. 1998. Land-use change in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States: assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. BioScience 48(8):607-615.

CHAPTER 2

MULTISCALE INFLUENCES ON PHYSICAL AND CHEMICAL STREAM CONDITIONS ACROSS SOUTHERN APPALACHIAN LANDSCAPES [1]

---

[1] Scott, M. C., G. S. Helfman, M. E. McTammany, E. F. Benfield, P. V. Bolstad. Submitted to *Journal of The American Water Resources Association.*

ABSTRACT -- Streams integrate multiple biogeochemical processes operating at broad to local spatial scales and long- to short-term time scales. Human activities have extensively altered those processes in North America, with serious consequences for aquatic ecosystems. We collected data on Upper Tennessee River tributaries in North Carolina to: 1) compare anthropogenic landuse to landscape geomorphology in ability to explain regional variation in water quality, sedimentation measures, and large woody debris; 2) determine if landscape change over time contributed significantly to explaining present stream conditions; and 3) assess the importance of spatial scale in examining landuse influences on streams. Both landuse and landscape geomorphology were useful predictors of stream variables. Forest cover accounted for the most variation in nearly all models, supporting predictions of nutrient enrichment, thermal pollution, and sedimentation caused by landscape disturbance. Legacy effects from past catchment disturbance were apparent in sedimentation measures. Nitrogen and phosphorus concentrations, as well as stream temperature, tended to decrease with forest recovery. Empirical models of physicochemistry fit better when predictors were catchment-wide rather than more localized (i.e., within 2 km of a site). Cumulative impacts to streams due to changes in landuse must be managed from an ecosystem perspective with quantitative models integrating across scales.

Keywords: watershed management; highland water quality; sedimentation; catchment landuse; nonpoint source pollution; southern Appalachian Mountains; North Carolina, USA

Introduction

Stream form and function have long been known to depend on conditions within the drainage basin (Leopold et al., 1964; Hynes, 1975). A conceptual framework has emerged that views terrestrial-aquatic linkages from a hierarchical perspective (Frissell et al., 1986; Hunsaker and Levine, 1995; Poff, 1997; Allan et al., 1997). This framework recognizes that a variety of factors at multiple spatial and temporal scales influence variation in stream biogeochemistry. For example, regional patterns in climate, geology, and topography are primary determinants of watershed processes over geologic time, producing environmental regimes such as stream hydroperiod, channel geomorphology, and water chemistry. Thus physicochemical conditions observed at a given point along the stream continuum reflect the influence of geophysical variables at regional, catchment, and reach scales. Extensive alteration of land cover by humans has forced many watershed processes toward new states. The resulting changes in aquatic systems have intensified concern over non-point source impacts to surface waters, driving legislation such as the federal Clean Water Act and a host of state regulations.

An examination of landscape influences on stream systems requires consideration of scale (Frissell et al., 1986). The spatial configuration of landforms and land covers affects water quality (Hunsaker and Levine, 1995). Intact riparian buffers have been shown to reduce nutrient and sediment movement from uplands to streams in small agricultural watersheds (Schlosser and Karr 1981; Lowrance et al., 1984; Peterjohn and Correll, 1984). But some investigation into cumulative effects at landscape scales has suggested that catchment-wide patterns are also important (Omernik et al., 1981;

Richards et al., 1996; Wang, 1997; Jones et al., 1999). Thus uncertainty remains about the relative importance of localized riparian *vs*. catchment-wide implementation of land management practices for mitigation and restoration.

Conditions at a stream site may also be influenced by the disturbance history of the watershed. Time lags in the response of stream characteristics such as sediment load (Meade et al., 1990; Brooks and Brierley, 1997) and large woody debris (Likens and Bilby, 1982) suggest that past landscape patterns may explain variation in some stream conditions better than the present landscape. Altered biological communities have been detected as a legacy of past landuse in the southern Blue Ridge by Harding et al. (1998), who implicated persistent fine sediment as a factor contributing to lack of ecological recovery. We therefore considered landscape disturbance history as an additional factor that may help explain present-day physicochemical conditions.

Long-term investigations at the U.S. Forest Service's Coweeta Hydrologic Laboratory have demonstrated a variety of stream changes in response to disturbance in a southern Appalachian catchment. Webster et al. (1992) summarized the results of decades of work examining stream response following experimental catchment deforestation. Important stream responses and associated mechanisms included increased water temperature due to loss of shading, elevated streamwater concentrations of nutrients due to reduced vegetative uptake and accelerated water movement through soils, higher sediment inputs due to soil disturbance and loss of the protective litter layer, and decreased inputs of organic matter, with particularly long-lasting effects on large woody debris in channels due to timber removal. Many of these responses were short-lived, returning to normal levels over decadal or shorter time spans as forest succession progressed and the canopy closed (Webster et al., 1992). However, over much of the broader Blue Ridge deforestation has been prolonged as people developed the land and maintained it for agricultural, residential, or industrial/commercial uses. Surface waters draining these landscapes undergo cumulative, long-term impacts.

In western North Carolina, landuse change has taken place over century-to-decade time scales against a background of landscape heterogeneity. Variables such as slope, elevation, and drainage area are the result of geomorphic processes operating at geologic time scales, and human activity is superimposed on this non-anthropogenic (or "natural") template of spatial variation (Vannote et al., 1980). Failure to account for natural variability can confound comparisons of landuse effects among streams or watersheds. Much of the research cited above examined terrestrial-aquatic relations in areas of low relief such as the Gulf-Atlantic Coastal Plain or Midwestern U.S. We are not aware of published studies relating landform and cover patterns to stream physicochemical conditions in a region with landscapes as heterogeneous as the Blue Ridge.

Cause-effect relationships are difficult to document in large-scale observational studies, but the usefulness of a particular approach or model may be determined by how well the data fit model predictions (Pickett et al., 1994). We evaluated how well the relationships reported by Webster et al. (1992) predicted patterns observed across the region. Our objectives were to : 1) assess whether landuse could explain regional variation in stream physicochemistry beyond that explained by natural landscape features, 2) determine if land cover change between 1970 and 1990 could contribute significantly to explaining present patterns in stream physicochemistry, and 3) compare the relative ability of current landuse at different spatial scales to explain physicochemical variation in southern Blue Ridge streams.

Methods

Study area-- The study region is located within the Blue Ridge physiographic province in western North Carolina (Figure 2.1), with a climate classified as marine humid temperate (Swift et al., 1988). Blue Ridge landscapes are characterized by pronounced topographic relief; the highest peaks (>1800 m) found east of the Rockies occur in the study area. The area is drained primarily by two major Upper Tennessee River systems: the Little Tennessee and French Broad rivers (areas of 4,117 and 11,194 km^2, respectively; Figure 2.1). Most streams are permanent because of abundant rainfall. Bedrock geology is late Precambrian in origin and occurs in complex patterns dominated by metamorphic crystalline rocks resistant to mechanical and chemical weathering (Hack, 1969). Nonresistant mica schists occupy extensive areas of low relief, and some carbonate rocks occur on the western edge of the Blue Ridge. Due to the inert nature of the predominantly crystalline rocks, waters are naturally low in dissolved ions and nutrients, are clear, and have circumneutral pH (Wallace et al., 1992). Stream channels are typically bedrock-constrained and have boulder-cobble-gravel substrates.

Forest cover was systematically cleared in the 1880's in the southern Appalachian mountains, although the Cherokee farmed the valley bottoms prior to European colonization (Bartram, 1794). Virtually no virgin forest tracts remain today. Nonetheless, the majority of the region today is covered in subsequent forest regrowth. In the last 20 years, the region has undergone significant population growth (SAMAB, 1996), and the general trend in regional landuse has been away from the agriculture prevalent in the mid 1900's (Harding et al., 1998). There has been an overall increase in forest cover since that time due to succession in abandoned fields, but building density has also increased, indicating residential and commercial development (Wear and Bolstad, 1998).

Data collection -- Thirty-six stream sites (Figure 2.1) were selected to represent catchment landuse ranging from primarily forested to agricultural to suburban/urban. Several data sources were used to collect information from each catchment (Table 2.1). Two geormorphic features of the terrain, site elevation and channel slope (1 km upstream of each site), were quantified using 30-m digital elevation models. Forest cover data were derived using satellite imagery from two periods: Landsat Multi-Spectral Scanner scenes from the early 1970's and Thematic Mapper scenes from 1993 (see geographic information details in Wear and Bolstad, 1998). A measure of the trajectory of land cover change was obtained by subtracting the proportion of riparian non-forested area in 1993 from the proportion in the 1970's, with positive values corresponding to increases in forest cover and negative values corresponding to losses. Catchment drainage areas as well as road and building location data were obtained by digitizing 1:24,000-scale USGS topographic maps. The recent landuse data (i.e., forest cover from 1993, buildings and roads) were tabulated at four different spatial scales (Figure 2.2). The broadest scale (denoted with variable prefix WS) comprised the entire area draining to a stream site (Figure 2.2A). The second scale (prefix MB) comprised landuse within a 100 m riparian buffer on either side of the stream extending along the entire mainstem corridor to the source (Figure 2.2B). At the third scale (prefix 2K), landuse was measured within a 100 m riparian buffer extending 2 km upstream of the site (Figure 2.2C). Finally, at the most local scale (prefix 1K), landuse was measured in the 100 m riparian buffer extending 1 km above the site (Figure 2.2D). Forest cover in the 1970's was also determined from sattelite imagery at WS, MB, and 1K scales. At each scale and time period, the area of non-forested land was divided by the total area of land in the catchment or buffer to give proportion of non-forested land (variable suffix DEF70 or DEF90). Likewise, the number of buildings and kilometers of paved road were divided by total area to give a density of buildings ($number \cdot ha^{-1}$) and roads ($km \cdot ha^{-1}$) at each scale. Building density was normalized by the maximum value (i.e., scores were expressed as a proportion of maximum). Road density was similarly normalized. Normalized building and road densities were then added together into an index of landuse intensity (denoted with suffix INTENS) for each stream at the four spatial scales (Table 2.1).

Physical and chemical features of the stream were measured during 1995 – 1999 within a 50 m sampling segment established at each stream site (Table 2.2). Channel substrate was characterized by pebble counts (Wolman, 1954). This method involved walking a zig-zag pattern throughout the segment, randomly selecting 100 bed particles, and measuring the intermediate axis of each. The coarse fraction (>64 mm in diameter) of this distribution is reported here as an estimate of the streambed area covered by coarse-grained particles, important as foraging and refuge habitat for stream organisms (Waters, 1995). The proportion of coarse particles reflects the extent to which streambeds were covered by fine sediments. The number of pieces of large wood (wood at least 10 cm diameter and 1 m length) that occurred in the segment was counted. Large wood and substrate particle size were quantified once at each site in summer 1998.

Temperature data loggers (Onset Corp.®) were deployed at all sites in February 1999 and recorded stream water temperatures hourly until October 1999, except for two sites near Coweeta Hydrologic Laboratory. Temperature data for a comparable period in 1998 were used for these two sites. We were interested in evidence of elevated temperatures. The maximum temperatures at each site occurred in the period 14 July-18 August, so we calculated the mean temperature from all data collected during this period. This mean summer temperature was used in the analysis.

Streamwater was collected by grab sample at baseflow six to eight times at each site from 1995 to 1999. Samples were analyzed at Coweeta Hydrologic Laboratory's Analytical Lab according to procedures described in Bolstad and Swank (1997). The following chemical variables were measured as concentrations ($mg.L^{-1}$): nitrate-N, ammonium-N, soluble reactive phosphorus (SRP), Ca^{++}, Mg^{++}, Na^{+}, K^{+}, Cl^{-}, SO_4^{2-}, HCO_3^{-}, and SiO_2. The concentration of listed solutes Ca^{++} through SiO_2 were added together and reported for each site as total dissolved solids (Allan, 1995). Turbidity, an indication of suspended sediment, was determined with a turbidimeter and recorded in nephelometric turbidity units (NTU's). Mean values by site for all water quality variables were used in analyses.

Data analyses—To address the first two objectives, we constructed models of a temporal sequence in landscape influences. Geomorphic variables represented geologic time scales, whereas the two time frames of forest cover data (1970's and 1990's) represented change in human activity on the landscape over time. For the third objective we examined the influence of spatial scale using the 1990's landuse data. Each objective was addressed by constructing linear models that reflected specific hypotheses, and then assessed the fit of the alternative models to the data using several indicators. Coefficients of determination adjusted for the number of terms in each model (r^2_{adj}) were calculated to reflect the amount of variation explained by each model. F-ratio tests were used to assess the fit of nested models (Draper and Smith, 1981), and for non-nested models the Bayesian information criterion (BIC; Schwarz, 1978) was used to compare the fit of alternative models. All model parameters were estimated by least squares regression, except abundance of large wood, which was modeled as a Poisson process using maximum likelihood estimation (MLE). By including multiple predictor terms in each model, our approach permits examination of the effect of each factor after accounting for the effect of other terms in the model.

The first objective was to compare the ability of anthropogenic and natural landscape features to explain regional variation in stream physicochemistry. The hypothetical models in the comparison were:

$$M_1 : \; y_i = b_0 + b_1 x_{\text{GRAD}} + b_2 x_{\text{ELEV}} + b_3 x_{\text{WSAREA}} + e_i$$

$$M_2: \; y_i = M_1 + b_4 x_{\mathrm{MBDEF90}}$$

where y_i are dependent stream variables (Table 2.2), x_i are predictor landscape variables (Table 2.1), b_i are parameters fit by multiple regression, and e_i is a random error term. In M_2, the proportion of non-forest within the mainstem riparian buffer was used as a measure of human disturbance. In this analysis, M_1 was compared to M_2 using F-ratio tests (or in the case of wood, a likelihood ratio test) to determine whether addition of land cover information contributed significantly to prediction for each dependent physicochemical variable.

The second objective was to determine if an indicator of landscape change between the 1970's and 1990's was a significant additional predictor. The model :

$$M_3: \; y_i = M_2 + b_5 x_{\Delta\mathrm{MBFOR}}$$

included a term for loss or gain of forest cover in the mainstem riparian buffer. The parameter estimate was determined as above using multiple regression (or MLE), then F- (or likelihood) ratio tests were used to compare M_3 to M_2.

The final objective was to compare the influence of landuse at four different spatial scales (Figure 2.2). Landuse data at all 4 scales were available for only 34 of the 36 streams; therefore, only 34 sites were used in this analysis. We assumed that landscape geomorphology influenced streams; accordingly, channel slope, site elevation, and drainage area were included in all models. Two landuse terms (forest cover and landuse intensity index, Table 2.1) were varied by scale in each alternative model, corresponding to spatial hypotheses depicted in Figure 2.2:

$$M_{4\mathrm{A}}: y_i = M_1 + b_4 x_{\mathrm{WSDEF90}} + b_5 x_{\mathrm{WSINTENS}}$$

M_{4B}: $y_i = M_1 + b_4x_{\mathrm{MBDEF90}} + b_5x_{\mathrm{MBINTENS}}$

M_{4C}: $y_i = M_1 + b_4x_{\mathrm{2KDEF90}} + b_5x_{\mathrm{2KINTENS}}$

M_{4D}: $y_i = M_1 + b_4x_{\mathrm{1KDEF90}} + b_5x_{\mathrm{1KINTENS}}$

Model M_{4A} employs the landuse data from the entire watershed, M_{4B} uses data calculated from within a 100 m riparian buffer along the length of the mainstem channel, M_{4C} uses data from the 100 m buffer within 2 km upstream of the site, and M_{4D} reflects the landuse within the 100 m buffer 1 km upstream of the site.

Linear relationships, normal distributions (except woody debris counts), and homogeneous variances are the main assumptions implicit in the statistical approach outlined above. The majority of dependent stream variables were transformed using the Box-Cox method (Krebs, 1989), which employs an iterative algorithm to find a power transformation that improves univariate normality. The fraction of coarse streambed particles was arcsine-square root transformed. We screened the data by viewing multivariate normal quantile-quantile plots to check for serious deviations from normality and also plotting model residuals against predicted values to check for trends in the error structure. Only mean summer temperature did not appear normal after transformation. After rank-transforming the temperature data (Iman and Conover, 1979), we found similar regression model performance. Results using the Box-Cox transformed temperature data are reported here. We suspected that correlations among some of the predictors might be problematic, so separate models were run for the spatial-scale comparison to avoid multicollinearity. Variance inflation factors were computed for all predictors in each model as an indicator of multicollinearity; inflation factors never exceeded 4 (Draper and Smith, 1981).

In addition to the three objectives outlined above, we examined all possible subset models employing the landscape predictors (Table 2.1), using BIC to select the most parsimonious model that gave the best fit to each physical and water chemistry variable. We present these models simply as empirical insights into the regional and watershed processes governing stream quality. Their purpose is not for inference or prediction because site selection was not based on a probability-based sampling design.

Results

Several landscape variables were interrelated, as correlation coefficients indicate (Table 2.3). Channel slope was the only one of the geomorphic features that was significantly related to landuse. Building and road density tended to be higher and forest cover tended to be reduced with lower gradient slopes. Landuse was strongly correlated among several spatial scales. In particular, landuses were highly correlated at the two broadest scales (catchment-wide and mainstem buffer, $r > 0.97$) and the two local scales (2 km and 1 km buffers, $r > 0.97$).

Both landscape geomorphology and landuse explained significant variation in physical and chemical conditions among streams (Table 2.4). Geomorphic features alone were generally weak predictors, as no adjusted r-squares exceeded 0.51. Nonetheless, half of the geomorphic models were significant at the $\alpha=0.01$ level. Channel slope, elevation, and catchment area were significant predictors of ammonium-N, stream temperature, turbidity, and substrate coarseness, but stream temperature was the only variable for which over 50% of variation was explained.

The addition of 1993 land cover within the mainstem buffer as a predictor significantly improved most models. The amount of variation explained increased dramatically in nitrogen, total dissolved solids, water temperature, turbidity, and substrate coarseness models. The soluble reactive phosphorus model improved significantly but less dramatically when land cover was included. Addition of a riparian land cover change term to the models contributed significantly to prediction of only soluble reactive phosphorus (Table 2.4). Lower concentration of SRP in streamwater was associated with a trajectory of increasing forest cover over time. Information on land cover change was not informative in any remaining physicochemical models.

The examination of spatial scale influences on the models had to be modified in light of the high correlations among scales noted above. We were unable to distinguish the relative contributions of all four spatial scales, but correlations were lower between the broad- and local-scale landuse variables ($r<0.70$; Table 2.3). Thus enough independent variation existed in the data to make the comparison at a coarser grain: basin *vs*. local scale. Regression results indicated that the broader spatial scales produced better-fitting models (Table 2.5). Highest r-squares, and lowest BIC values, were consistently produced in physical and chemical models that included landuse either catchment-wide or in the 100 m riparian buffer along the entire mainstem. Local landscape conditions (i.e., within 2 km) were in most cases inferior predictors. However, models of substrate particle size were similar regardless of the scale of landuse.

We used the BIC to select parsimonious models that accounted for the most regional variation in stream physical and chemical variables. Standardized regression coefficients are presented for each model (Table 2.6; except the MLE-derived wood model, Figure 2.5) to show direction and magnitude of predictor influence. Standardized coefficients facilitate comparisons among predictors in a model because they account for the differences in measurement units. Variation in dependent stream variables explained by landscape predictors ranged from 61% in soluble reactive phosphorus to 84% in total dissolved solids. All of the models included geomorphic as well as anthropogenic terms. Substrate particle size increased with channel slope. Larger drainage areas were associated with higher mean summer temperatures and occurrence of large woody debris. Elevation was a significant predictor of several water quality variables. Higher elevations were associated with lower temperatures and lower concentrations of several stream water constituents.

Overall, anthropogenic landscape variables accounted for more variation than geomorphic variables, as indicated by standardized coefficients (Table 2.6). Forest cover along the mainstem in 1993 was the most predictive variable, contributing to 5 out of the 8 models. It was the top predictor in models of nitrate-N, total dissolved solids, mean summer temperature, and turbidity. History of land cover change further contributed to models of nitrate-N, soluble reactive phosphorus, and mean summer temperature. Lower nutrient concentrations were associated with an increase in forest cover in the riparian buffer along the mainstem, and lower temperatures were associated with increased catchment forest cover over time (Table 2.6). The turbidity and coarse substrate models indicated that past land cover was a useful predictor of sedimentation impacts. Turbidity was positively related to the proportion of non-forested land in the catchment in the 1970's, and coarse substrate was best predicted by riparian forest cover in the 1970's (Table 2.6). Abundance of large woody debris was negatively related to building and road density, but no forest cover variables were significant predictors of wood (Figure 2.5).

Some effects apparent in Table 2.6 are contrary to those expected, and may give some indication of more complex interactions among the landuse variables. For example, in the case of turbidity, non-forest cover in the catchment was positively related to turbidity whereas the catchment landuse index had an opposite effect (Table 2.6). Similarly, the ammonium-N and soluble reactive phosphorus models indicated that local forest cover had an opposite effect to broader scale measures of cover. Such departure from expected relationships may reflect differences in the extent of agricultural and urban/suburban development among catchments. Further classification of land cover into land use types (i.e., agriculture, low-density residential, etc.) such as an Anderson classification may be necessary to clarify these effects.

Discussion

The relationships Webster et al. (1992) described linking stream physical and chemical quality to terrestrial conditions in the catchment appeared to be detectable across the region using fairly coarse landscape data. Thus, even though comparative studies such as ours cannot establish cause-and-effect relationships, they can provide support for or against conceptual models. Our results indicated that although stream conditions naturally varied on the Blue Ridge landscape, land disturbance due to human activities were impacting the environmental quality of streams. The clear, cool, low-nutrient waters and coarse substrates of less-disturbed streams contrasted with turbid, warm, nutrient-enriched, and fine substrates in streams where riparian or catchment forests were replaced with other landuses. Human impacts are discussed below in relation to landscape heterogeneity, temporal trends of change, and spatial scale of disturbance.

Landscapes and human alteration -- The landscape features that have influenced surface waters over geologic time were important predictors of current physicochemical conditions. High topographic relief in the region produces strong longitudinal effects in stream conditions, as slope, elevation, and drainage area vary along stream continua and across landscapes (Vannote et al., 1980). Channels with greater slopes featured coarser (e.g., boulder-cobble) substrates. Stream channel gradient is directly related to water velocity and tractive force, increases in which cause the stream to transport particles of larger sizes (Bagnold, 1973). Elevation was an important predictor of water quality in this study. Mechanistically, elevation may reflect the accumulation of dissolved and suspended materials at lower elevation or correlate with some aspect of geology (e.g., mineralogy or groundwater outflows). Lower elevation streams with larger drainage areas were also generally warmer, likely due to air temperature differences related to elevation and increased insolation in larger streams, but groundwater may also be important.

While geomorphic landscape patterns have influenced watershed processes over geologic time scales, human effects have been more recently superimposed. Our results agree with evidence from many areas of the world, suggesting that human transformations of landscapes are significantly impacting surface waters (Carpenter et al., 1992). We found that anthropogenic alteration of indigenous forest cover was strongly and consistently related to physical and chemical aspects of stream quality, accounting for significant variation beyond that explained by natural landscape features. The association of elevated nutrient and dissolved solids concentrations with deforestation is in agreement with the idea that forests regulate inputs to streams (Bormann et al., 1969) and wetlands (Crosbie and Chow-Fraser, 1999), an idea that has been corroborated in multiple empirical studies at broader scales (Smith et al., 1987; Caraco, 1995; Bolstad and Swank, 1997; Herlihy et al., 1998). We observed elevated water temperature in relation to deforestation; this has also been reported elsewhere (Swift and Messer, 1971; LeBlanc et al., 1997). Increased turbidity and finer substrate particle size distributions were additional correlates of anthropogenic activity in this study. Altered erosion and sedimentation processes contributing to higher suspended and substrate silt loads are well-documented as a result of landuse change (see Waters, 1995 for a review).

Webster et al. (1992) reported that deforestation reduced inputs of large woody debris (LWD) to streams. We did not find LWD to be related to forest cover, although greater abundance was associated with few buildings and sparse road density. Figures 2.4 and 2.5 illustrate that our ability to forecast LWD abundance is quite weak, although there is an effect of landuse. There are at least two possible reasons why the association was so weak. The first possibility is a time lag in recovery to normal wood input rates. Because forests across the region were logged within the last 100 years or so, the regeneration and succession process has still not progressed to maturity. The time until significant tree mortality occurs may exceed a century (Likens and Bilby, 1982). The second possibility is that simply counting the occurrences of LWD was not an adequate measure of inputs for comparison among streams. A better-quantified measure such as volume may have been necessary for a strong association to be observed. Additional sampling is necessary to rule out inappropriate sampling as the reason for the weak LWD-landuse association.

Trajectory of land cover change -- Few studies have partitioned the variance in stream variables associated with landuse into past and present contributions. Geomorphological literature generally takes past conditions into consideration more often than does the water chemistry literature (e.g., Brooks and Brierley, 1997). This is reasonable since sediment transport and storage processes operate over longer time scales (Meade et al., 1990). We found that turbidity and substrate particle size were measures indicative of past disturbance in the drainage basin. Water chemistry and temperature, in contrast, were more influenced by recent landscape conditions and appeared to respond to trajectories of land cover change. Studies at Coweeta also showed rapid recovery of water chemistry and temperature following clearcutting (Webster et al., 1992). Harding et al. (1998) reported, for a subset of the streams presented here, that the biological community was related more to past than recent landuse, and they suggest that sedimentation may be a primary factor affecting ecological communities in these streams.

The differences in response of sediment and water quality measures also have implications for stream rehabilitation and recovery efforts; one might expect mitigation efforts to achieve more rapid improvements in water quality compared to sediment-related problems.

Spatial Scale -- Broad-scale measures of landuse were the best predictors of stream variables. More localized conditions within a 2 km riparian buffer generally produced inferior models for water quality. The relative influence of local- versus broad-scale factors on stream quality has been debated in recent years, especially in the Midwest (Hunsaker and Levine, 1995; Richards et al., 1996; Johnson et al., 1997; Lammert and Allan, 1999). Richards et al. (1996) suggested that sediment-related habitat variables may be influenced more by stream buffers, whereas channel dimensions are more likely a function of geomorphic features at the catchment scale. Johnson et al. (1997) reported that water chemistry in Michigan was generally more dependent on riparian ecotone conditions than catchment-wide factors. In our data, landuse at the two broadest scales - catchment and mainstem corridor - were highly correlated ($r > 0.95$). Thus, even though the riparian models were often the most explanatory, there were no situations where large sections of riparian zone forest were intact but uplands were deforested, or vice versa, allowing us to examine the relative effects statistically. As a consequence, we cannot conclude that stream quality management may simply focus on the riparian corridor while ignoring the uplands. Nonetheless, the importance of stream buffers is certainly apparent in this and many other studies (Lowrance et al., 1984; LeBlanc et al., 1997).

The results of Jones et al. (1999), working in the Little Tennessee river drainage, suggested that immediately local conditions may be important in this region. They detected increased fine sediments in channel substrate and altered fish assemblages at sites below deforested riparian patches one kilometer or more in length. We observed the converse of this finding, that the fraction of coarse substrate particles (>64mm) decreased with riparian deforestation, although past conditions were more informative (Table 2.5). The buffer 2 km upstream of the site yielded a substrate model basically equivalent to the mainstem buffer (Table 2.4), which does not conflict with the conclusions of Jones et al. (1999) regarding the importance of locally intact riparian zones to substrate quality.

Generally, however, patterns of nutrient enrichment, thermal pollution, and sedimentation observed in southern Blue Ridge streams support the idea of cumulative impacts. Given the association of stream variables with landuse further upstream than 2 km (Figures 2.3 and 2.4), we suggest that management concerns not be limited to immediate landuse, but take a more prudent holistic view of the entire stream corridor. Stream restoration efforts that focus on relatively short stream sections while failing to consider conditions further upstream may be inadequate to achieve desired results. The data presented here suggest that streams respond to cumulative impacts, hence efforts to improve streams require a broad view of the stream system.

The ability to extrapolate fine-scale observations (e.g., Webster et al., 1992) to broader scales (this study), at least within major drainages and physiographic regions, suggests useful applications in sampling design and statistical inference. The hierarchical, nested structure of subcatchments, drainage basins, and river systems over physiographic regions points to a natural organization of landscapes (Lotspeich, 1980; Frissell et al., 1986; Maxwell et al., 1995). Probabilistic sampling designs exploiting such a framework would allow statistically-valid estimation of regional stream responses to non-point source pollution based on remotely-sensed geographic data and past landuse information (e.g., Basnyat et al., 1999). Spatially-explicit forecasting of water resource quality, implemented within a geographic information system, would allow quantification of the likelihood and magnitude of environmental effects caused by proposed developments and landuse plans, information that is generally lacking in the decision-making process.

Conclusions

Our results show that models considering both natural landscape variation and human activities on broad spatial scales are feasible and effective in relating the aquatic environment to landscape factors in regions of pronounced topographic relief. An examination of empirical relationships between landscapes and stream physicochemical conditions supported a hierarchical framework for addressing terrestrial-aquatic interactions. Spatial heterogeneity among streams in the southern Blue Ridge was related to landscape features, including both geomorphic and anthropogenic factors. Landuse effects on stream resources typically dominated natural geomorphic effects in our analysis, indicating that the relatively recent transformation of landscapes by humans is currently a significant determinant of streamwater nutrient levels, thermal properties, and channel sediment processes in the region. Past landuse had more influence on measures of sedimentation processes, whereas recent landuse accounted for more variation in stream chemistry and temperature variables. These differences suggest that stream sediment is to some extent a legacy from historical human activity, and that water quality is likely to respond more rapidly to mitigation efforts and best management practices. Broad-scale measures of landuse explained more variation in regional stream quality than more localized measures, supporting the idea that streams respond to cumulative impacts. While the issue of the relative influence of whole-catchment *vs*. riparian landuse remains unresolved, results from this study certainly support the current emphasis on contiguous protection of riparian corridors. The environmental quality and integrity of freshwaters is dependent on maintenance of stream buffers throughout the stream system.

The associations of stream variables with landscape disturbance that we observed at a regional scale were similar to those documented by earlier experimental work in the region on stream response to catchment-scale deforestation (Webster et al., 1992). The ability to broadly extrapolate should be exploited in probabilistic designs that will allow regional inferences to be drawn from sampling and monitoring results. Development of quantitative regional models would provide valuable tools in landuse planning and water resource management. Given that freshwater biodiversity is now gravely threatened (Allan and Flecker, 1993; Ricciardi and Rasmussen, 1999), our documentation of associations between human activity in the landscape and environmental change in streams is a strong argument for holistic, proactive protection of water resources. Amassed evidence shows that surface waters are affected by the way people use the land; likewise, quality of life is linked to clean and sustaining water.

Acknowledgments

We thank J. Meyer, C. Pringle, and M. Freeman for comments on an earlier draft, S. Rathbun for advice on statistical methods, and B. Farmer, N. Gardiner, J. Harper, D. Jones, S. Kornberg, P. Marcinek, K. Schofield, B. Staub, A. Sutherland, H. Russell, and D. Toole for assistance in data collection. This research was supported by National Science Foundation grant DEB-9632854 to the University of Georgia Coweeta Long Term Ecological Research Program. Data reported here are available at the following url: http://sparc.ecology.uga.edu/webdocs/

Literature Cited

Allan, J.D. 1995. Stream Ecology: Structure and Function of Running Waters. Chapman and Hall, London, England.

Allan, J. D., and A. S. Flecker. 1993. Biodiversity Conservation in Running Waters. BioScience 43(1):32-43.

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The Influence of Catchment Land Use on Stream Integrity Across Multiple Spatial Scales. Freshwater Biology 37:149-161.

Bagnold, R. A. 1973. Bedload Transport by Natural Rivers. Water Resources Research 13:303-312.

Bartram, W. 1794. Travels Through North & South Carolina, Georgia, East & West Florida, the Cherokee Country, the Extensive Territories of the Muscogulges, or Creek Confederacy, and the Country of the Chactaws; Containing an Account of the Soil and Natural Productions of those Regions, Together with Observations on the Manners of the Indians. James & Johnson, Philadelphia, Pennsylvania.

Basnyat, P., L. D. Teeter, K. M. Flynn, B. G. Lockaby. 1999. Relationships Between Landscape Characteristics and Nonpoint Source Pollution Inputs to Coastal Estuaries. Environmental Management 23:539-549.

Bolstad, P. V. and W. T. Swank. 1997. Cumulative Impacts of Landuse on Water Quality in a Southern Appalachian Watershed. Journal of the American Water Resources Association 33:519-533.

Bormann, F. H., G. E. Likens, and J. S. Eaton. 1969. Biotic Regulation of Particulate and Solution Losses from a Forest Ecosystem. BioScience 19:600-611.

Brooks, A. P., and G. J. Brierley. 1997. Geomorphic Responses of Lower Bega River to Catchment Disturbance, 1851-1926. Geomorphology 18:291-304.

Caraco, N. F. 1995. Influence of Human Populations on P Transfers to Aquatic Systems: A Regional Scale Study Using Large Rivers. *In*: Phosphorus in the Global Environment, H. Tiessen (Editor). John Wiley & Sons, New York, New York, pp. 235-244.

Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global Change and Freshwater Ecosystems. Annual Review of Ecology & Systematics 23:119-139.

Church, M. 1996. Channel Morphology and Typology. *In*: River Flows and Channel Forms, G. Petts and P. Calow (Editors). Blackwell, Oxford, England, pp. 185-202.

Draper, N. R., and H. Smith. 1981. Applied Regression Analysis. John Wiley, New York, New York.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A Hierarchical Framework for Stream Habitat Classification: Viewing Streams in a Watershed Context. Environmental Management 10:199-214.

Hack, J. T. 1969. The Area, its Geology: Cenozoic Development of the Southern Appalachians. *In*: P. C. Holt (Editor). The Distributional History of the Biota of the Southern Appalachians. Part I: Invertebrates. Research Division Monograph 1, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, pp. 1-17.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream Biodiversity: The Ghost of Land Use Past. Proceedings of the National Academy of Sciences 95:14843-14847.

Herlihy, A. T., J. L. Stoddard, and C. B. Johnson. 1998. The Relationship Between Stream Chemistry and Watershed Land Cover Data in the Mid-Atlantic Region, U.S. Water, Air, and Soil Pollution 105:377-386.

Hunsaker, C. T. and D. A. Levine. 1995. Hierarchical Approaches to the Study of Water Quality in Rivers. BioScience 45:193-203.

Hynes, H. B. N. 1975. The Stream and its Valley. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 19:1-15.

Iman, R. L., and W. J. Conover. 1979. The Use of the Rank Transform in Regression. Technometrics 21:499-509.

Johnson, L. B., C. Richards, G. E. Host, and J. W. Arthur. 1997. Landscape Influences on Water Chemistry in Midwestern Stream Ecosystems. Freshwater Biology 37:193-208.

Jones, E. B. D. III, G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of Riparian Forest Removal on Fish Assemblages in Southern Appalachian Streams. Conservation Biology 13:1454-1465.

Krebs, C. J. 1989. Ecological Methodology. Harper & Row, New York, New York.

Lammert, M. and J. D. Allan. 1999. Assessing Biotic Integrity of Streams: Effects of Scale in Measuring the Influence of Land Use/Cover and Habitat Structure on Fish and Macroinvertebrates. Environmental Management 23:257-270.

LeBlanc, R. T., R. D. Brown, and J. E. FitzGibbon. 1997. Modeling the Effects of Land Use Change on the Water Temperature of Unregulated Urban Streams. Journal of Environmental Management 49(4):445-469.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial Processes in Geomorphology. W. H. Freeman, San Francisco, California.

Likens, G. E., and R. E. Bilby. 1982. Development, Maintenance and Role of Organic Debris Dams in New England Streams. *In*: F. J. Swanson, R. J. Janda, T. Dunne, and D. N. Swanston (Editors). Sediment Budgets and Routing in Forested Drainage Basins. USDA Forest Service General Technical Report PNW-141, Portland, Oregon, pp. 122-128.

Lotspeich, F. B. 1980. Watersheds as the Basic Ecosystem: This Conceptual Framework Provides a Basis for a Natural Classification System. Water Resources Bulletin 16:581-586.

Lowrance, R., R. Todd, J. Fair Jr., O. Hendrickson Jr., R. Leonard, and L. Asmussen. 1984. Riparian Forests as Nutrient Filters in Agricultural Watersheds. BioScience 34:374-377.

Meade, R. H., T. R. Yuzyk, and T. J. Day. 1990. Movement and Storage of Sediment in Rivers of the United States and Canada. *In*: Surface Water Hydrology. The Geology of North America, Vol. O-1, M. G. Wolman and H. C. Riggs (Editors). Geological Society of America, Boulder, Colorado, pp. 255-280.

Omernik, J. M., A. R. Abernathy, and L. M. Male. 1981. Stream Nutrient Levels and Proximity of Agricultural and Forest Land to Streams: Some Relationships. Journal of Soil and Water Conservation 36:227-231.

Osborne, L. L., and M. J. Wiley. 1988. Empirical Relationships Between Land Use/Cover and Stream Water Quality in an Agricultural Watershed. Journal of Environmental Management 26:9-27.

Peterjohn, W. T., and D. L. Correll. 1984. Nutrient Dynamics in an Agricultural Watershed: Observations on the Role of a Riparian Forest. Ecology 65:1466-1475.

Pickett, S. T. A., J. Kolasa, and C. G. Jones. 1994. Ecological Understanding: The Nature of Theory and the Theory of Nature. Academic Press, New York.

Poff, N. L. 1997. Landscape Filters and Species Traits: Towards a Mechanistic Understanding and Prediction in Stream Ecology. Journal of the North American Benthological Society 16:391-409.

Ricciardi, A., and J. B. Rasmussen. 1999. Extinction Rates of North American Freshwater Fauna. Conservation Biology 13:1220-1222.

Richards, C. and G. E. Host. 1994. Examining Land Use Influences on Stream Habitats and Macroinvertebrates: A GIS Approach. Water Resources Bulletin 30:729-738.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-Scale Influences on Stream Habitats and Biota. Canadian Journal of Fisheries and Aquatic Sciences 53 (Supplement 1):295-311.

Southern Appalachian Man and the Biosphere (SAMAB). 1996. The Southern Appalachian Assessment Summary Report. Report 2 of 5. USDA Forest Service, Southern Region, Atlanta, Georgia, 166 pp.

Schlosser, I. J., and J. R. Karr. 1981. Water Quality in Agricultural Watersheds: Impact of Riparian Vegetation During Base Flow. Water Resources Bulletin 17:233-240.

Schwarz, G. 1978. Estimating the Dimension of a Model. Annals of Statistics 6:461-464.

Smith, R. A., R. B. Alexander, and M. G. Wolman. 1987. Water-Quality Trends in the Nation's Rivers. Science 235:1607-1615.

Swift, L. W., Jr., and J. B. Messer. 1971. Forest Cuttings Raise Temperatures of Small Streams in the Southern Appalachians. Journal of Soil and Water Conservation 26:111-116.

Swift, L. W., Jr., G. B. Cunningham, and J. E. Douglass. 1988. Climatology and Hydrology. *In*: Forest Hydrology and Ecology at Coweeta, Ecological Studies, Vol. 66, W. T. Swank and D.A. Crossley, Jr. (Editors). Springer-Verlag, New York, New York, pp. 35-55.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Wallace, J. B., J. R. Webster, and R. L. Lowe. 1992. High-Gradient Streams of the Appalachians. *In*: Biodiversity of the Southeastern United States: Aquatic Communities, C. T. Hackney, S. M. Adams, and W. H. Martin, (Editors). John Wiley & Sons, New York, New York, pp. 133-191.

Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of Watershed Land Use on Habitat Quality and Biotic Integrity in Wisconsin Streams. Fisheries 22:6-12.

Waters, T. F. 1995. Sediment in Streams: Sources, Biological Effects, and Control. American Fisheries Society Monograph 7, Bethesda, Maryland, 251 pp.

Wear, D. N., and P. Bolstad. 1998. Land-use Change in Southern Appalachian Landscapes: Spatial Analysis and Forecast Evaluation. Ecosystems 1:575-594.

Webster, J. R., S. W. Golladay, E. F. Benfield, J. L. Meyer, W. T. Swank, and J. B. Wallace. 1992. Catchment Disturbance and Stream Response: An Overview of Stream Research at Coweeta Hydrologic Laboratory. *In*: River Conservation and Management, P. J. Boon, P. Calow, and G. E. Petts (Editors). John Wiley & Sons, New York, New York, pp. 231-253.

Wolman, M. G. 1954. A Method of Sampling Coarse River-Bed Material. Transactions of the American Geophysical Union 35:951-956.

Table 2.1. Landscape variables measured in 36 southern Blue Ridge stream catchments.

Variable description (VARIABLE NAME)	Units	Data Source	Range of values
catchment area WSAREA	ha	1:24,000 USGS topo map	511 - 32,125
elevation ELEV	m	USGS 30 m DEM	489 - 981
channel slope GRAD	%	USGS 30 m DEM	1.7 - 20.0
1970's deforestation - 3 spatial scales WSDEF70 – throughout catchment MBDEF70 - 100 m mainstem buffer 1KDEF70 - 100 m buffer 1 km above site	proportion	LS Multi-Spectral Scanner satellite imagery from early 70's	0.0 - 0.97
1990's deforestation - 4 scales WSDEF90, MBDEF90, 2KDEF90, 1KDEF90	proportion	1993 TM satellite imagery	0.0 - 0.99
forest cover change - 3 scales ΔWSFOR, ΔMBFOR, Δ1KFOR	proportion	difference in 1970's and 1990's deforestation	-0.41 - +0.94
1990's building density - 4 scales	number·ha^{-1}	1:24,000 USGS topo map	0.0 - 0.97
1990's road density - 4 scales	km·ha^{-1}	1:24,000 USGS topo map	0.002 - 0.15
landuse intensity index - 4 scales WSINTENS, MBINTENS, 2KINTENS, 1KINTENS	index score	normalized building + road densities	0.02 - 2.0

Table 2.2. Chemical and physical variables measured at 36 stream sites.

Variable Description VARIABLE NAME	Units	Data Source	Range of values
nitrate-N NO3-N	mg.L^{-1}	ion chromatography	0.03 - 1.46
ammonium-N NH4-N	mg.L^{-1}	Technicon AutoAnalyzer	0.003 - 0.15
soluble reactive phosphorus SRP	mg.L^{-1}	ion chromatography	0.001 - 0.11
total dissolved solids TDS	mg.L^{-1}	ion chromatography, atomic absorption spectrophotometry	10.5 - 88.4
turbidity TURB	NTU	Hack Model 2100A turbidimeter	0.3 - 25.0
mean summer temperature TEMP	° C	Onset Corp.® HOBO data loggers	16.7 - 23.3
fraction of coarse (>64 mm) substrate particles COARSE	proportion	field pebble counts	0.09 - 0.80
large woody debris WOOD	counts	field counts	0 - 9

Table 2.3. Correlations among landscape variables used as predictors in hypothesized models. Variable descriptions are found in Table 2.1. Asterisk denotes significance at *P*<0.05 level.

	WSAREA	ELEV	GRAD	WSDEF90	WSINTENS	MBDEF90	⊿MBFOR	MBINTENS	2KDEF90	2KINTENS	1KDEF90
WSAREA	-										
ELEV	-0.29	-									
GRAD	-0.04	-0.03	-								
WSDEF90	-0.13	-0.14	-0.35*	-							
WSINTENS	-0.29	0.04	-0.38*	0.77*	-						
MBDEF90	-0.07	-0.15	-0.37*	0.98*	0.74*	-					
⊿MBFOR	-0.12	-0.17	-0.37*	-0.13	0.06	-0.10	-				
MBINTENS	-0.25	0.08	-0.38*	0.72*	0.97*	0.73*	0.03	-			
2KDEF90	0.20	-0.09	-0.55*	0.63*	0.54*	0.68*	0.12	0.58*	-		
2KINTENS	-0.01	0.03	-0.34*	0.36*	0.66*	0.41*	0.15	0.73*	0.68*	-	
1KDEF90	0.16	-0.06	-0.43*	0.57*	0.53*	0.62*	0.12	0.58*	0.96*	0.71*	-
1KINTENS	-0.32	0.05	-0.32	0.26	0.53*	0.34*	0.16	0.62*	0.62*	0.94*	0.66*

Table 2.4. Comparison of adjusted r^2 from modeling the influence of landscape geomorphology on stream physicochemical variables and after sequentially adding recent and historical landuse factors to the models. Variable names follow Tables 2.1 and 2.2.

	Variance explained by:		
Dependent stream variable	landscape geomorphology (GRAD, ELEV, WSAREA)	1990's land cover (MBDEF90)	Land cover change (ΔMBFOR)
NO3-N	0.07	0.77 ***	0.81
NH4-N	0.30 *	0.62 ***	0.62
SRP	0.12	0.27 *	0.50 **
TDS	0.19	0.81 ***	0.81
TEMP	0.56 ***	0.77 ***	0.79
TURB	0.31 *	0.54 **	0.52
COARSE	0.26 *	0.60 ***	0.66
WOOD	*N/A*	*N/A* *	*N/A*

* = significant effect at $\alpha = 0.01$, ** $\alpha=0.001$, *** $\alpha= 0.0001$, based on *F*- or likelihood ratio tests

Table 2.5. Comparison of the fit of linear models using 1993 landuse (forest cover, building and road density) at four different spatial scales to predict physicochemical stream variables. R-squares are presented for each model, except the MLE-derived large woody debris model, which lists the order of best fit according to the Bayesian information criterion (BIC). Model fit ranked by r^2 concords with the ranking by BIC for each dependent variable.

Spatial Scale	*NO3-N*	*NH4-N*	*SRP*	*TDS*	*TEMP*	*TURB*	*COARSE*	*WOOD*
Catchment (WS)	0.78	0.69	0.44	0.78	0.76	0.64	0.63	1
mainstem riparian buffer (MB)	0.80	0.66	0.47	0.85	0.78	0.69	0.65	2
2k buffer (2K)	0.43	0.37	0.26	0.49	0.61	0.58	0.65	4
1k buffer (1K)	0.35	0.36	0.25	0.43	0.57	0.53	0.57	3

Table 2.6. Best-fitting linear models of stream physicochemical variables and their landscape predictors as selected by the BIC. Predictors are listed in order of model influence, as indicated by the standardized regression coefficients. Variable abbreviations are explained in Tables 2.1 and 2.2. All models were significant at $\alpha = 0.0001$ (F-test).

Dependent variable	Predictors	standardized coefficients	r^2
NO3-N	*MBDEF90*	0.77	0.83
	ELEV	-0.28	
	ΔMBFOR	-0.27	
NH4-N	*WSDEF90*	0.85	0.76
	1KDEF90	-0.47	
	ELEV	-0.39	
	1KINTENS	0.31	
SRP	*ΔMBFOR*	-0.53	0.61
	ELEV	-0.44	
	MBDEF90	0.40	
	1KDEF90	-0.28	
TDS	*MBDEF90*	0.78	0.84
	ELEV	-0.30	
	1KINTENS	0.11	
TEMP	*MBDEF90*	0.53	0.82
	ELEV	-0.42	
	WSAREA	0.42	
	ΔWSFOR	-0.18	

Dependent variable	Predictors	standardized coefficients	r^2
TURB	*MBDEF90*	0.92	0.79
	WSINTENS	-0.71	
	WSDEF70	0.34	
	ELEV	-0.33	
COARSE	*MBDEF70*	-0.60	0.71
	GRAD	0.19	
	1KDEF90	-0.18	

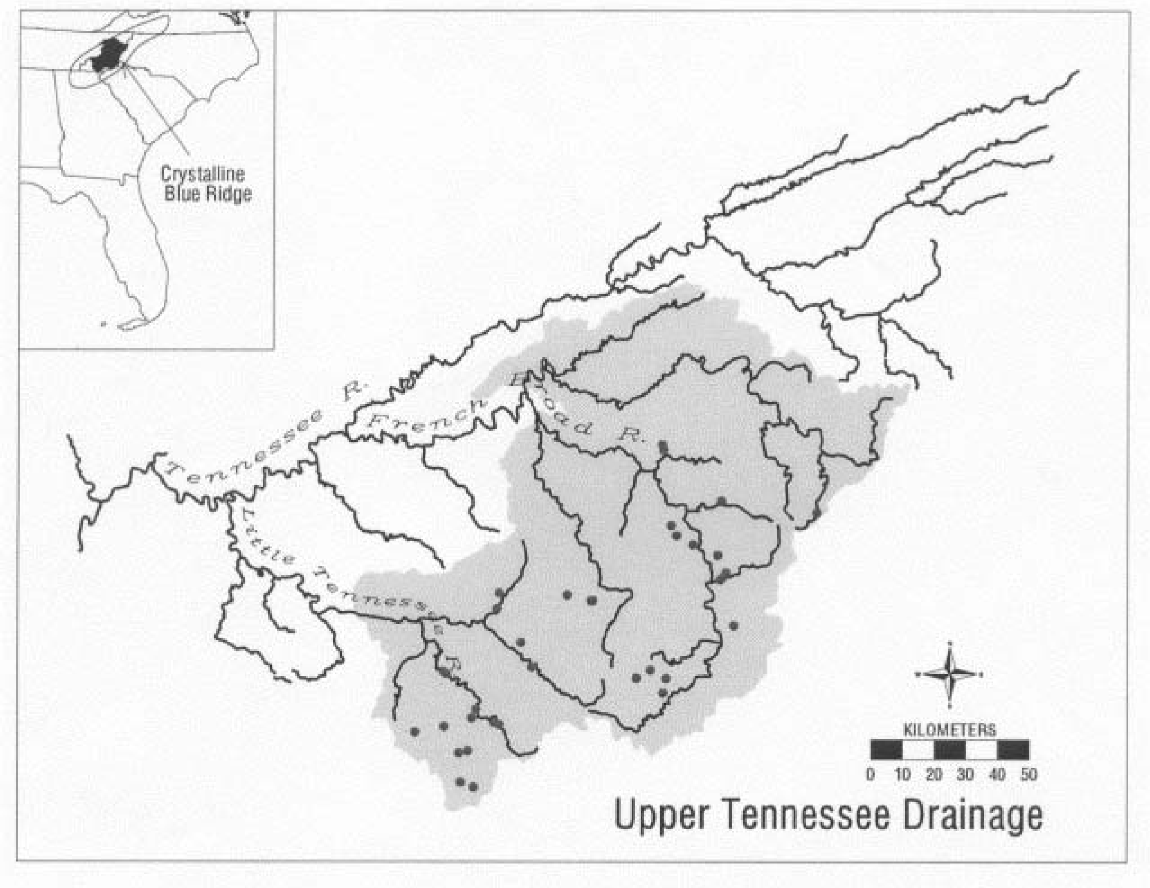

Figure 2.1. Map of the upper Tennessee River system, including location of the Little Tennessee and French Broad river basins in the crystalline Blue Ridge physiographic province (inset). Points mark the location of 36 sampling sites in the study area.

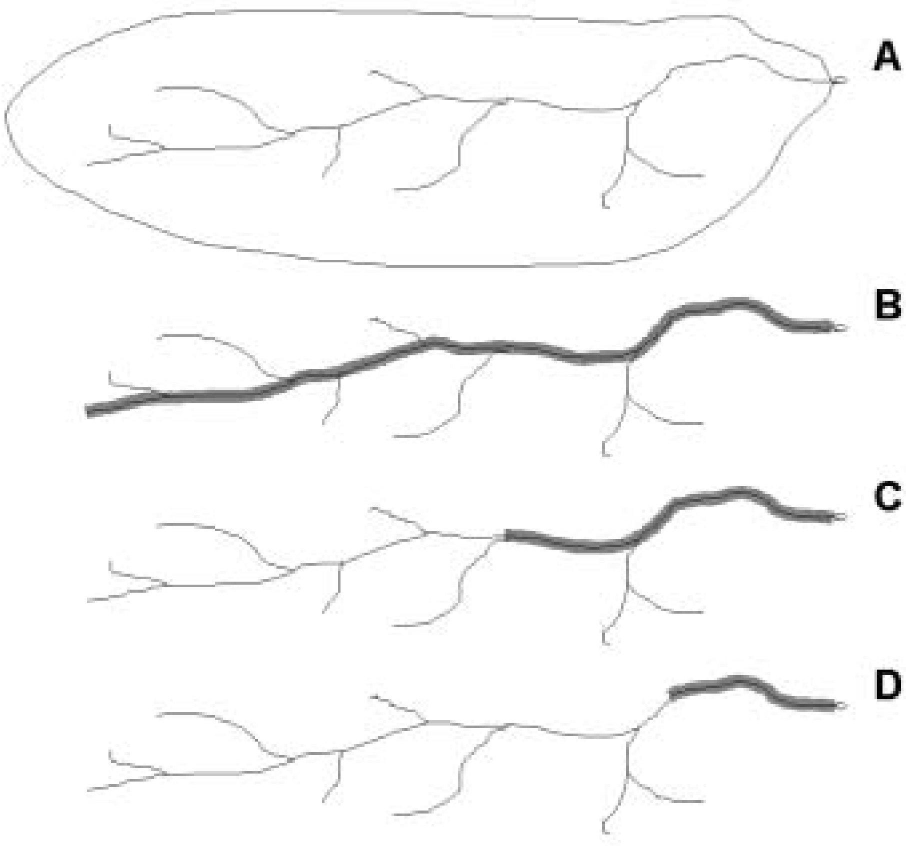

Figure 2.2. The four spatial scales at which landuse was characterized. The open circle denotes a stream site; A - within the entire catchment, B - within a 100 m buffer along the mainstem corridor, C - within the 100 m buffer along a corridor extending 2 km upstream of the site, D - within the 100 m buffer extending 1 km upstream.

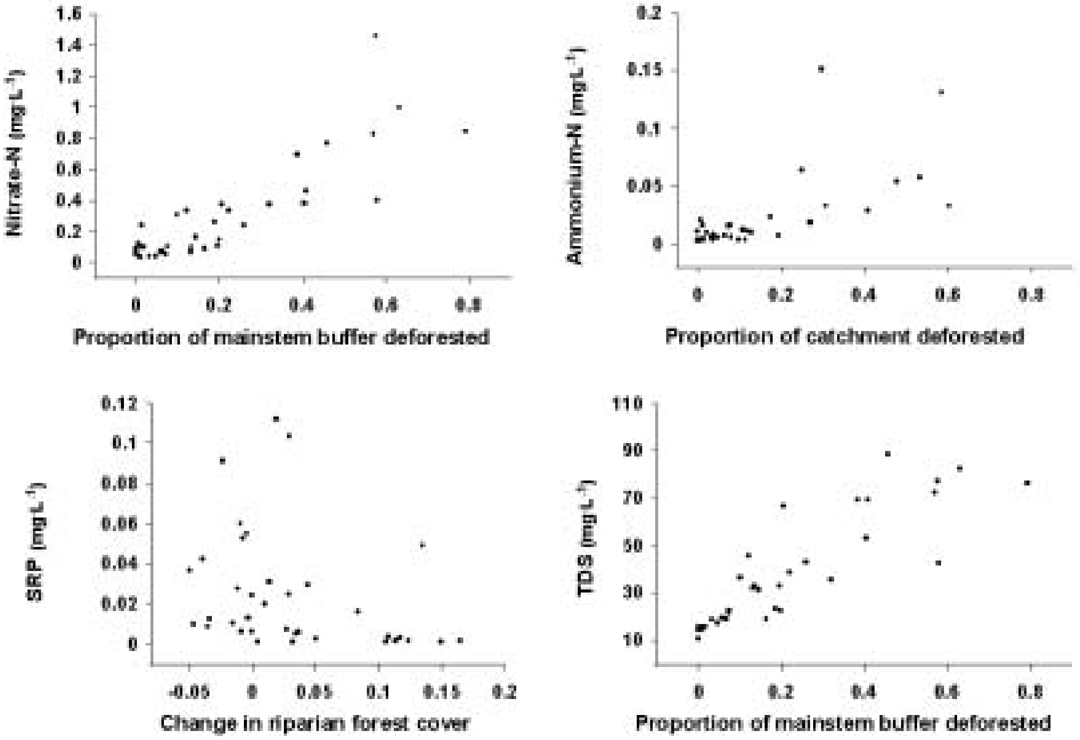

Figure 2.3. Plots showing the form of relationship between chemical variables and forest cover.

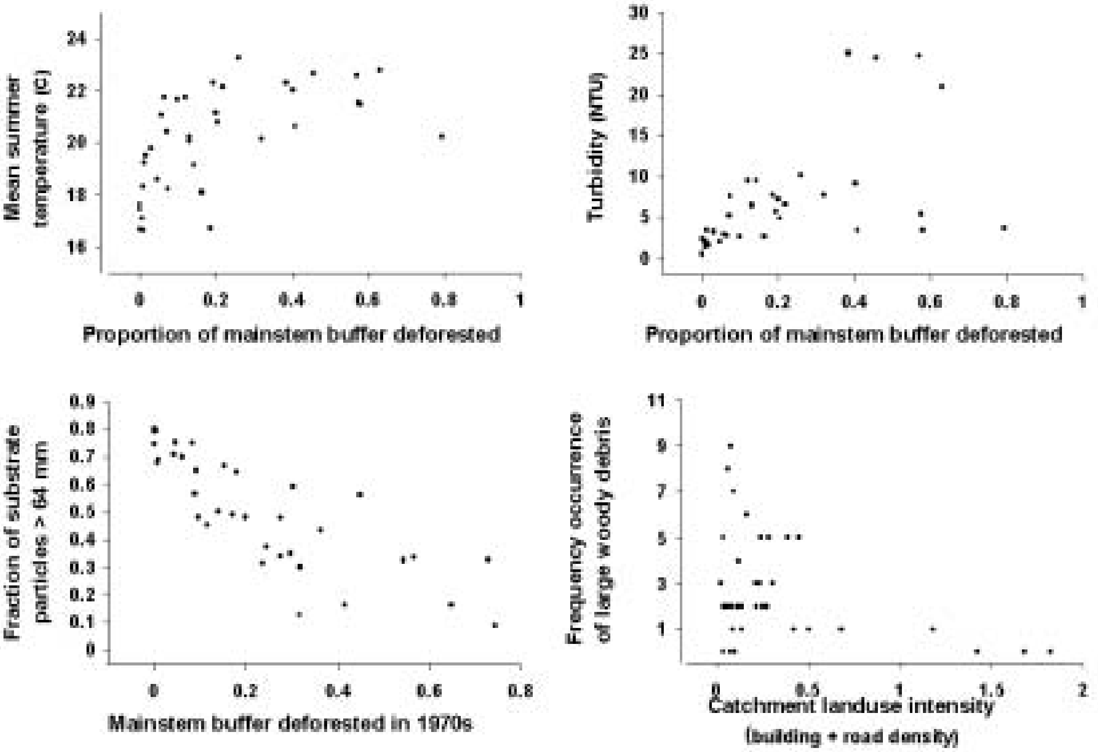

Figure 2.4. Plots showing the form of relationship between physical variables and landuse.

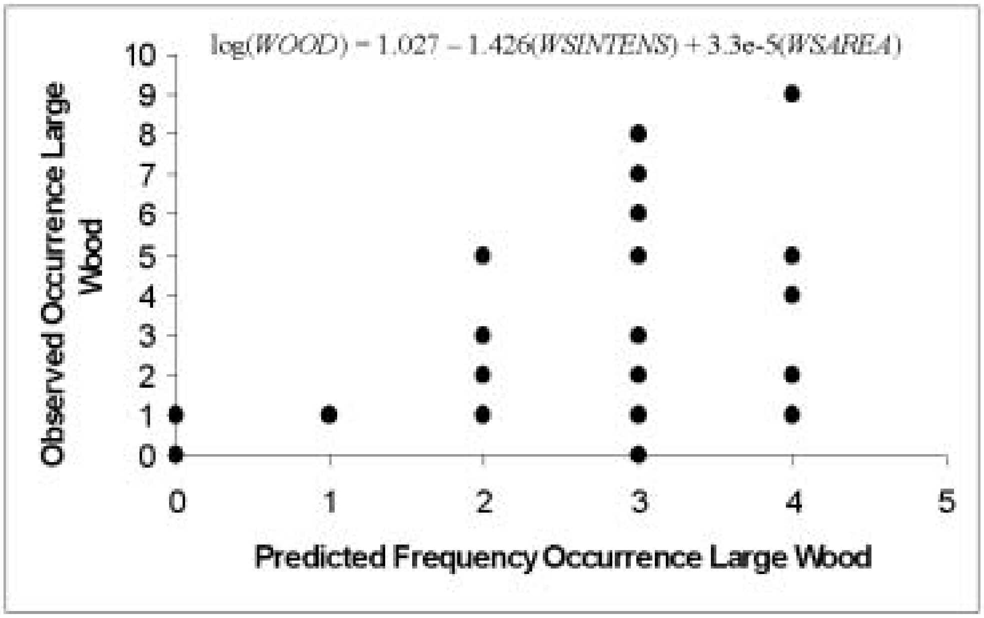

Figure 2.5. Observed counts of large woody debris *vs*. values predicted from a linear model based on the Poisson distribution and estimated by maximum-likelihood.

CHAPTER 3

PATTERNS IN ASSEMBLAGE STRUCTURE OF SOUTHERN APPALACHIAN FISHES IN RELATION TO CATCHMENT AND STREAM HABITAT FACTORS [1]

---

[1] Scott, M. C. To be submitted to *Ecological Applications*

ABSTRACT -- Our ability to predict species distribution and abundance will be facilitated if we can identify the multiscale, hierarchical structure of processes organizing communities and incorporate this structure into theoretical and empirical models. In streams, fish populations respond to the physical and chemical conditions of their habitat, and habitat conditions are in turn influenced by catchment-scale patterns and processes. I examined fish species composition and abundance using ordination and classification methods in 36 streams of the upper Tennessee River system in North Carolina to evaluate the utility of this hierarchical framework for understanding variation in assemblage structure. Faunal similarities among collections were ordinated using non-metric multidimensional scaling, and resulting site scores were analyzed for within-site temporal effects and among-site spatial effects. Seasonal and annual variation in assemblage structure over a 4 y period was minor (<5%) compared to spatial variation (>95%). I used partial redundancy analysis to examine the spatial variation among ordination scores. Environmental variables were classed according to scale, with site-level reflecting instream habitat (channel geomorphology and water chemistry), and catchment-level representing landscape setting (basin size, elevation/slope, land cover). Instream habitat variables unrelated to landscape setting explained 21% of variation, landscape variables unrelated to habitat explained 22%, and landscape-influenced habitat conditions explained 28%, in total accounting for 71% of variation in biotic scores. Four faunal associations were identified from a cluster analysis of fish abundance. Three classes, dominated by endemic Appalachian highland fishes, formed a continuous gradient in assemblage structure from smaller, cooler, higher-elevation streams to larger, warmer,

lower-elevation streams in this topographically diverse region. A fourth association was characterized by non-endemic fishes dominating where habitats were enriched by nutrients and affected by siltation in association with forest cover loss in streamside buffers and high density of buildings and roads. The results suggest that landscape setting exerts a broad influence on local stream conditions and habitat-dependent fauna. Human activities on the landscape have cumulative effects that alter stream habitats and thereby shift biological assemblages to states uncharacteristic of the region. The patterns I observed may reveal early stages of biodiversity loss via homogenization of a unique highland fauna as habitats become more suitable for species from surrounding regions.

Introduction

A primary goal in ecology is to gain an understanding of how the distribution and abundance of organisms varies in space and time. Calls for predictive theory in ecology have emphasized the need to incorporate the nested hierarchy of interacting abiotic and biotic factors that influence species patterns (Allen and Starr 1982, Ricklefs 1987, Menge and Olson 1990, Ricklefs and Schluter 1993). A hierarchical framework for understanding running water ecosystems has been emerging over the last few decades (Hynes 1975, Vannote et al. 1980, Lotspeich 1980, Frissell et al. 1986, Maxwell et al. 1995, Schlosser 1995, Imhof et al. 1996, Poff 1997, Ward 1998). The framework recognizes that smaller-scale systems are embedded within larger-scale systems and that more localized conditions develop under the constraints imposed by higher-level phenomena. Native biota adapted to the environmental conditions and disturbance regimes characteristic of a locale suffer declines when human activities shift the habitat template to new states (Matthews 1987). This process constitutes one of the root causes of species decline and loss of biological integrity (Karr 1991, Allan and Flecker 1993).

The term ‘hierarchical filters’ has been proposed to describe the multiple factors that influence and limit populations at different scales (Tonn et al. 1990, Poff 1997). For example, at continental to regional scales (10^4 - 10^2 km), geophysical processes such as climate and geology generate broad environmental gradients, influence nutrient availability, and affect evolutionary rates of dispersal, adaptation, speciation, and extinction. Landscape-scale phenomena (10^0 - 10^2 km) include physiographic and drainage basin differences in aquatic faunas reflecting particular geological and evolutionary histories. At more local scales (<1 km), habitat structure, physical disturbance and biological interactions such as competition and predation further regulate survival, growth, and reproduction over time scales of one or a few generations. Within drainages, longitudinal shifts occur along flowpaths (Vannote et al. 1980), as well as between different habitat types within a single stream reach (Gelwick 1990). While biotic variability across spatial scales has long been acknowledged, the majority of ecological research and theory operates at local scales. A primary goal in the development of the hierarchical concept is to identify the roles and interactions of local habitat conditions, landscape setting, and regional context as determinants of community structure (used here to refer to composition and abundance of species).

Highland streams in southeastern North America provide an excellent setting for examining hierarchical patterns influencing fish assemblages. The streams of the upper

Tennessee River system drain ancient Appalachian landscapes (> 250 million y old), and contain a distinctive fauna with many endemics (McCallister et al. 1986, Mayden 1987) indicative of a long evolutionary history uninterrupted by sea level rise or Pleistocene glaciation (Hack 1969). Moreover, landscape features influence physical and chemical conditions in streams (Scott et al. in review). Regionally, the stream systems are spatially heterogeneous due to topographic relief and, because water flow is perennial and climate is warm-temperate, they are relatively stable through time. Nonetheless, Grossman et al. (1998), working in a southern Blue Ridge stream, noted that environmental variability in the form of drought and flood had a greater effect on assemblage structure than interspecific competition or predation. No published studies have analyzed spatial variation in fish assemblage structure among streams of the Blue Ridge physiographic region, a unique portion of the diverse upper Tennessee River system.

Physical, chemical, and biological data collected over four years from catchment- to site-level scales were organized under a hierarchical framework to examine how fish assemblages varied across Blue Ridge landscapes of western North Carolina. Because study areas were within a single physiographic province and also within the upper Tennessee River drainage, I was not concerned with variation above the landscape scale. My objectives were to: 1) compare the roles of temporal (seasonal and annual within-site variation) and spatial scale (between-site variation) in explaining assemblage patterns; 2) assess the relative roles of local habitat conditions and broader landscape setting in explaining assemblage patterns; and 3) identify assemblage patterns and relationships among biotic, instream habitat, and landscape features.

Methods

Study area-- The study area is located within the Blue Ridge physiographic province in western North Carolina (Fig. 3.1). Environmental characteristics of the region bearing on stream ecosystems were described in Scott et al. (in review). Streams were selected for study in two major basins of the upper Tennessee River system, the Little Tennessee and French Broad rivers. Twenty-four stream sites were established and sampling was initiated in 1995, and an additional 12 were established in 1997 for a total of 36 study sites. Stream sites ranged from 489 to 981 m in elevation, from 1.7% to 20% in channel slope, and drained catchments with areas of 5 to 321 km^2.

Data collection-- Stream variables were measured at three spatial scales: 1) site, 2) 100 m riparian buffer extending 1 km upstream of the site, and 3) entire catchment. Variables were classified either as local stream habitat or broader landscape features. More detailed description of physicochemical and catchment variables of these streams and methods used in their collection appears in Scott et al. (in review); they are simply listed here. Sites consisted of 50 m stream segments; habitat variables were measured within the channel in this segment. Channel geomorphology variables were measured at all sites in summer 1998, including mean wetted width, estimated proportion of riffle habitat, and maximum depth within the segment. Substrate was characterized using the pebble count method of Wolman (1954), and the coarse (> 6.4 cm) fraction of substrate particles was estimated from a distribution of 100 particle measurements. The embeddedness of substrate particles within fine sediments was visually estimated in riffle habitat in the site segment. Large woody debris was defined as wood in the channel >10 cm in diameter and >25 cm in length (Dolloff and Webster 2000); all occurrences in the segment were counted. Grab samples of streamwater were collected at baseflow 6-8 times at each site between 1995 and 1998 and chemically analyzed (Scott et al. in review). Water quality variables reported here include mean values for concentrations of nitrate-N, total dissolved solids, and turbidity. Water temperature was logged hourly at all sites from February 1999 until October 1999, except for two sites near Coweeta Hydrologic Laboratory. Temperature data over the same period in 1998 were used for these two sites. The mean temperature during the period 14 July-18 August was calculated, as maximum temperatures at each site occurred during this period.

Landscape variables were measures of topography and land cover, obtained from a geographic information system containing data from digital elevation models (DEMs), Landsat Thematic Mapper satellite imagery, and 1:24,000 topographic maps (see Scott et al. in review for details). At the catchment level these included drainage area, the proportion of deforested area in a 100 m wide riparian buffer along the channel mainstem, building and road density in the buffer, and forest cover change in the buffer from 1970 to 1993. Elevation was obtained for each site from DEMs. Additional landscape variables were measured over a 1 km reach extending upstream of the site, including channel slope, the proportion of deforested area in a 100 m riparian buffer along the 1 km reach, building and road density in the 1 km buffer, and forest cover change in the 1 km buffer from 1970 to 1993. A landuse index was created at both catchment and 1 km scales by first normalizing building and road densities to their maximum values (i.e., scores were expressed as a proportion of maximum) and then adding them together with proportion of riparian deforested area at the respective scale. I used the indices of landuse intensity at two scales as variables in further analysis.

Fishes at 24 of the sites were sampled in spring and fall 1995 and 1996 (E.B.Dale Jones III, unpublished data); twelve additional sites were sampled in spring and fall 1997 and 1998. Thus, each of the 36 sites was sampled four times for a total of 144 collections. All collections were made by the same method. Backpack electrofishing units and seines were used to thoroughly cover all habitats in the segment from downstream to upstream, collecting all juvenile and adult individuals encountered. Fishes were identified to species or subspecies, counted, and released. Specimens that could not be positively identified were preserved and returned to the lab for identification.

Data analyses-- A multivariate approach was used to examine spatiotemporal patterns in biological and environmental data: 1) biotic patterns were analyzed by ordination and classification; 2) temporal and spatial variation in the biota were examined by analysis of variance; and 3) biotic patterns were related to habitat and catchment factors by partial redundancy analysis. Predominant patterns in species composition and abundance among collections were extracted by an indirect-gradient ordination method, non-metric multidimensional scaling (NMS). Raw fish abundances in each collection were fourth-root transformed prior to analysis to reduce the influence of very abundant species (Clarke 1993), and then Bray-Curtis dissimilarity values were calculated for each pair of collections as a measure of ecological distance (Faith et al. 1987). NMS requires no assumptions about distributions or forms of relationships in biological data (Minchin 1987). Only the rank order of dissimilarities (distances) among samples is used, thus NMS estimates nonlinear monotonic relationships in the data. NMS was performed using the software PC-Ord® (McCune and Mefford 1997), which implements the algorithm of Mather (1976). The number of dimensions necessary to express the variation in the faunal data was determined by plotting the stress of the solution (stress is a measure of how well the multivariate data are represented by a reduced set of dimensions) against the number of dimensions in a six-dimensional solution. Very little reduction in stress occurred after three dimensions, justifying use of a three-dimensional solution for the final analysis. The patterns in the ordination reflected by the dimensions (=axes) were evaluated against a null model of random assemblage with a Monte Carlo randomization test (100 simulations), which tested the likelihood that the final stress could be obtained by chance. Interpretation of the multivariate axes was achieved by examining correlations with species abundances and by plotting classification results onto NMS space (see below). Scores for each fish sample on NMS axes reflected biological variation among samples and were used as biotic response variables in further analyses of temporal and spatial factors.

Temporal and spatial variation in fish assemblage structure were compared using analysis of variance (Wiley et al. 1997). Variance in the three NMS ordination axes was decomposed into temporal (season and year), spatial (site), and time-site interaction components using a three-way ANOVA. Ordination scores met the normality requirements of the method. The 144 fish collections were divided into two sets, one including the 24 sites sampled in 1995-1996 and the second with 12 sites sampled in 1997-1998. Sites were sampled two seasons over two years. Separate ANOVAs were run on the two sets. The variance in the fish assemblage data explained by spatial effects was determined by combining the sums-of-squares (SS) for the site term from both analyses, and by dividing by the model SS combined from the two analyses to get a proportion of explained variance. Likewise, SS for the season and year terms were combined and divided by the combined model SS to determine temporal effects on assemblages in the region. Finally, site-specific temporal effects were evaluated by combining site-time interaction terms and relating these SS to the combined model SS. The ANOVA results indicated the relative amount of variation among collections that is due to spatial effects, seasonal effects, and interannual effects.

The relative influence on assemblage structure of instream habitat vs. catchment variables reflecting broader landscape features was compared using partial redundancy analysis (RDA; Borcard et al. 1992). RDA is a canonical technique that describes variation between multivariate data sets, in this case between the three ordination axes and values for ten habitat and seven landscape variables. A series of redundancy analyses was run (PROC CANCORR in SAS®) with scores on three ordination axes as the dependent variable set as follows: 1) landscape variables as an independent variable set; 2) repeat step 1 with the effect of instream habitat variables partialled out of the analysis; and 3) repeat step 1 with instream habitat variables as the independent set, partialling out landscape variables (Borcard et al. 1992). The output from this series of analyses included squared multiple correlations between dependent variables and a set of canonical variates that were linear combinations of the environmental variables, similar to principal components analysis. The average squared multiple correlation of each environmental canonical variate with the scores on the three ordination axes was multiplied by the corresponding canonical correlation coefficient to yield a redundancy coefficient for each canonical variate. The redundancy coefficients were summed to yield a measure of how much of the variance in the biotic variable set was accounted for by the environmental variables. By performing the three separate RDA's described above, I was able to calculate how much of the variance in the assemblage ordination was explained purely by habitat measures (result from step 3), and how much was explained purely by landscape variables (result from step 2). Finally, the portion of variance that is shared by both habitat and landscape factors was obtained by subtracting 2) from 1). Results indicated the degree to which habitat conditions reflect their landscape context and thus how both scales jointly influenced biotic communities. Because RDA assumes multivariate normality in at least one of the data matrices, the independent environmental variables were transformed using the Box-Cox method (Krebs 1989), which employs an iterative algorithm to find a power transformation that improves univariate normality and homogeneity of variances.

I used cluster analysis to objectively classify sites on the basis of species associations present in the fish assemblage data. Bray-Curtis dissimilarities among sites were calculated from the mean number of individuals per 100 m^2 of stream, and cluster analysis was performed using unweighted pair-group arithmetic averages with $\beta = -0.1$

(Belbin and McDonald 1993). The species indicator method of Dufrêne and Legendre (1997) was used to determine the appropriate number of clusters as well as to identify fish species characteristic of the different associations. The method uses the abundance of each species at sites in a cluster relative to other sites, as well as relative frequency of occurrence in that cluster class, and multiplies these measures to create an indicator value for each species. Indicator values were compared to those obtained from 1000 Monte Carlo simulations; observed values larger than more than 95% of simulated values identified significant indicator species. Indicator species were found mostly in a single class and were present at the majority of sites belonging to that class. The decision regarding the number of classes to best represent the faunal associations present in the data was made by summing the significant indicator values from two to eight cluster typologies; the maximum of the summed indicator values indicates the cluster typology with the most distinctive classes (Dufrêne and Legendre 1997).

Faunal associations identified in the cluster analysis were plotted in the multivariate space defined by NMS ordination. Environmental variables were displayed as vectors on joint plots that reflected the direction and magnitude of Pearson correlations with the ordination axes. Vectors on the graph indicate the direction of the labeled environmental gradient; that is, sites distributed along the length of a vector differ in terms of that variable from one end to the other (extending past the origin in the opposite direction). Length of vectors indicate strength of relationship with axes. Instream habitat and landscape features were displayed on separate joint plots.

Results

Ordination of fish abundances

Forty-nine species of fish were collected in 144 collections at the 36 sites. An NMS ordination of transformed fish abundances in each collection yielded a three-dimensional solution with final stress = 11.3. The three axes together explained 91% of variation in the dissimilarity matrix, with Axis 1 accounting for 45%, Axis 2 for 37%, and Axis 3 for 9% of variance in ordination scores. Monte Carlo simulations indicated that each of the dimensions obtained in the analysis was significant at the p=0.01 level. Species that were correlated most strongly with the ordination axes are presented in Table 3.1 to facilitate axis interpretation. A plot of collections on the first two NMS axes depicts ecological distance among collections (Figure 3.2), thus sites closer together are more similar faunally. Although the plot is noisy, the distribution of sites along the two dimensions showed two properties of interest. The points are individual collections labeled with a 3-character site code. It is apparent that the four samples collected over two years at each site typically group together in the same area of the ordination space, indicating similarity in assemblages among visits. Second, the cloud of points forms a triangular pattern, with most of the variation on the *y*-axis located on the left side of the plot. The triangular pattern representing species associations are related to environmental variables below.

Temporal variability vs. spatial pattern

Variation in fish assemblage structure was decomposed into within-site (seasonal, annual) and among-site (spatial) components. Analysis of variance showed that spatial variation among sites overwhelmed any seasonal or annual effects (Table 3.2). The proportion of variance explained by site terms in the three NMS axis models ranged from 95 - 97%, compared to 1 - 3% for temporal or site-by-time interaction terms. This result indicates significant faunal variability among sites, but no distinct seasonal or annual patterns. The ANOVA results, coupled with the apparent clustering of collections by site in Figure 3.2, suggest that similarity of the assemblage at a given site was high during the two-year study period, and thus assemblages were temporally stable relative to spatial variation.

Because repeated collections were relatively consistent at sites, I utilized pooled collections at a site for the remaining analyses. The central tendency of biotic structure at each site was obtained by averaging scores on each of the three NMS axes. Combining repeated collections at sites reduced the dimensions of the biotic data matrix to the same rank as the environmental data, which was necessary for an examination of influences contributing to the strong spatial pattern observed.

Drainage basin differences

Because the Little Tennessee and French Broad are adjacent drainages in the Upper Tennessee river system, most species were shared. However several species were unique to one or the other basin. Six native species were collected in the Little Tennessee basin but not the French Broad: *Notemigonus crysoleucas* golden shiner, *Clinostomus funduloides* ssp. ‘smoky dace’, *Moxostoma erythrurum* golden redhorse, *Etheostoma vulneratum* wounded darter, *E. zonale* banded darter, and *Percina squamata* olive darter. An additional species introduced to the Upper Tennessee system was found in the Little Tennessee but not the French Broad drainage: *Notropis lutipinnis* yellowfin shiner. The native-status of another fish collected only in the Little Tennessee drainage, *Gambusia affinis* western mosquitofish, is uncertain. Eight native species were collected in the French Broad basin but not the Little Tennessee: *Erimystax insignis eristigma* mountain blotched chub, *Hybopsis amblops* bigeye chub, *Notropis rubricroceus* saffron shiner, *Ameiurus natalis* yellow bullhead, *Lepomis gulosus* warmouth, *Etheostoma flabellare* fantail darter, *E. rufilineatum* redline darter, and *E. swannanoa* Swannanoa darter. Two introduced species were found only in the French Broad: *Carassius auratus* goldfish and *Lepomis gibbosus* pumpkinseed.

Despite these differences in species composition, assemblage structure was quite similar between the basins in streams with similar habitats. This can be determined from Figure 3.2 by examining the distribution of sites with respect to the second letter of the site code: ‘T’ for Little Tennessee and ‘F’ for French Broad. No clear separation of basins was apparent in the ordination plot.

Spatial patterns: effects of local habitat conditions vs. landscape setting

Significant correlations ($P<0.01$) existed between environmental variables and biotic ordination scores (Table 3.3). The first NMS axis (accounting for 48% of variation in site similarities) was most strongly correlated with dissolved materials and nitrate-N in stream water. Channel substrate coarseness tended to be higher at sites with low scores on Axis 1, and more embedded substrates were prevalent at sites with higher scores. At the landscape level, land use in the riparian buffer was correlated with Axis 1. The second axis (accounting for 37% of variation) was most strongly related to mean summer temperature differences among sites, which was related to elevation and stream size. The third axis (6% of variation) was weakly correlated with turbidity (Table 3.3). The relations among ordination axes, classifications obtained from cluster analysis, and environmental variables are outlined in the next section.

Partial redundancy analysis revealed that habitat and landscape variables explained nearly 72% of total variance in biotic ordination scores (Figure 3.3). Variables measuring features of the landscape independently accounted for over 22% of variance in axis scores, and the contribution of instream variables unrelated to landscape setting was similar in magnitude (21%). However, the joint effect of landscape and associated instream habitat accounted for an additional 28% of assemblage variation (Figure 3.3). These results indicate that habitat differences among sites, primarily associated with topographic and land cover characteristics of the catchment, strongly influenced similarities in fish composition and abundance among sites.

Species associations and environmental correlates

Three distinct associations were identified from the cluster analysis using the indicator species method (Dufrêne and Legendre 1997). Here, I present results on four classes because separating the fourth class demonstrates an interesting gradient in species associations across Blue Ridge landscapes, while retaining the pattern displayed by the three classes. Significant indicator species were identified for each of the classes except class A (Table 3.4, Table 3.5), which combined with class B when three instead of four clusters were generated. Class A exhibited a considerable amount of compositional overlap with B, differing apparently because of lower fish density at class A sites and species additions at class B sites (Table 3.4). However, a continuous gradient in assemblage structure between classes A - B - C was suggested by a plot of sites in NMS ordination space (Figure 3.4), primarily on the left side of the plot along Axis 2. Vectors on the joint plot representing the magnitude of axis correlations with landscape variables indicated that axis 2 is related to a gradient in elevation ($r = -0.71$) and stream size ($r = 0.52$; Table 3.3). Class A sites were characterized by an association of rainbow and brown trout, sculpin, and dace (Table 3.4, Table 3.5). Sites in class A tended to be smaller streams at higher elevation compared to class C sites (Figure 3.4), which tended to be larger streams at lower elevations and were characterized by a more diverse assemblage composed of minnows and darters (Table 3.4). Class B sites were located intermediately along this gradient and separated poorly from classes A and C in the ordination plot (Figure 3.4), suggesting continuously intergrading composition and abundance along Axis 2. Two of the class B indicator species, *Clinostomus funduloides* ssp. smoky dace and *Notropis lutipinnis* yellowfin shiner, were unique to the Little Tennessee basin, indicating that most sites in this group were located in that drainage. Results from the classification of fish density agreed well with the ordination based on abundance, as indicator species of class A and C resemble the gradient of species correlated with NMS Axis 2 (compare Table 3.1 and Table 3.5).

Several species were indicative of two classes rather than a single class (Table 3.4), further evidence of a continuous faunal gradient from class A to class C sites. As noted above, class A sites were compositionally similar to class B sites, particularly in terms of *Salmo trutta* brown trout, *Oncorhynchus mykiss* rainbow trout, and *Cottus* *bairdi* ssp. smoky sculpin. A number of species occurred frequently and were relatively abundant in both class B and C sites, including *Ichthyomyzon greeleyi* mountain brook lamprey, *Nocomis micropogon* river chub, *Phenacobius crassilabrum* fatlips minnow, *Moxostoma duquesnei* black redhorse, *Etheostoma blennioides gutselli* Tuckasegee darter, *E. zonale* banded darter, and *Percina evides* ssp. Appalachian gilt darter. This pattern suggests a longitudinal gradient in fish assemblage structure across the region at the landscape level, from smaller, higher elevation streams to larger valley rivers. Species additions rather than turnover occur along this gradient (Table 3.4). Ordination Axis 2 scores were strongly positively correlated with species richness (r = 0.79) and Shannon diversity (r = 0.77).

Sites in class D were located toward the positive end (right side) of NMS Axis 1 (Figure 3.4), which is related to an index of landuse intensity within a 100 m riparian buffer at two scales: within 1 km of the site (r = 0.55) and, more strongly, catchment-wide (r = 0.81; Table 3.3). Species of this association resembled the list of species positively correlated with Axis 1 (Table 3.1) and included *Rhinichthys atratulus* blacknose dace, *Semotilus atromaculatus* creek chub, *Hypentelium nigricans* northern hogsucker, *Catostomus commersoni* white sucker, *Micropterus salmoides* largemouth bass, and *Lepomis auritus* redbreast sunfish (Table 3.5). These species were strong indicators, based on frequency occurrence and abundance at class D sites relative to other sites (Table 3.4). Class D sites are clearly separate in ordination space (Figure 3.4), exhibiting little biological overlap with other classes. However, several species appeared to grade between classes C and D, including *Cyprinella galactura* whitetail shiner, *Ambloplites rupestris* rock bass, and *Etheostoma swannanoa* Swannanoa darter (Table 3.4).

Habitat variables indicate the environmental conditions that prevailed among the different classes of sites (Figure 3.5). Axis 2 scores were related to mean summer water temperature ($r = 0.73$; Table 3.3), reflecting the elevational gradient along this axis (Figure 3.4). Axis 1 was related to measures of channel substrate (embeddedness, $r = 0.66$; coarse fraction, $r = 0.68$) and water chemistry (nitrate-N, $r = 0.74$; total dissolved solids, $r = 0.82$). These habitat conditions reflected the intensity of landuse upstream of the sites (Figure 3.4).

Discussion

Spatial patterns and environmental correlates

The observed relationships among assemblage patterns and environmental variables at multiple scales support a conceptual model of aquatic ecosystems in which landscape-level factors influence stream conditions, and fish assemblages in turn are influenced by their habitats (Matthews 1987, Schlosser 1995, Imhof et al. 1996, Poff 1997). Empirical studies supporting this ecological model have been reported in the midwestern U.S. (Richards and Host 1994, Richards et al. 1996, Allan et al. 1997, Johnson and Gage 1997, Richards et al. 1997, Lammert and Allan 1999), but similar studies are appearing elsewhere (e.g., Australia; Davies et al. 2000). According to a hierarchical framework, spatial variation in aquatic faunas may generally be classified into continental, regional, landscape, drainage basin, and local habitat components. At all scales, species distributions are very much tied to geologic and evolutionary histories

(Brooks et al. 1992). Physicochemical regimes at a stream site are influenced by the interactions among channel, drainage network, and catchment geomorphologies, and further modified by biological processes. Geomorphologies in turn develop according to the interactions of climate, geology, and land cover (Leopold et el. 1964). Hence, ranges of conditions at a given scale are often constrained by their context within higher levels (Frissell et al. 1986).

Classification and ordination results indicated that two major spatial patterns influence fish distribution and abundance in the southern Blue Ridge. The majority of variation in faunal similarity among sites was accounted for by an anthropogenic gradient related to land use/land cover. A natural gradient of elevation and stream size was also apparent. Where streams are unimpacted by deforestation and urban development, habitats in larger, lower-elevation streams tend to be warmer, wider, and channel substrates somewhat more embedded compared to smaller, higher-elevation streams (Figures 3.4 and 3.5). Fishes associated with the higher and cooler streams include two introduced (and widely stocked) species of trout and an endemic Blue Ridge form of the mottled sculpin. The warmer rivers at lower elevations support a more diverse assemblage including many endemic minnows and darters (Table 3.2). Thus, composition of fishes and their relative abundance were related to features of stream habitat, and physical and chemical aspects of habitat were associated with site position in the landscape.

A land use/land cover gradient reflected differences among sites in loss of forest cover and development near the stream. Physical and chemical conditions associated with intensive land use include high concentrations of nitrate-N and total dissolved solids in streamwater and filling of channel substrates with fine sediments (see Scott et al. in review). These conditions correspond to nutrient enrichment and sedimentation processes resulting from land-disturbing practices and other human activities. Fishes associated with disturbed habitats include creek chub, blacknose dace, white sucker, and sunfishes (Table 3.2), species which are widespread in North America but constitute a minor assemblage component in less disturbed Blue Ridge streams. Thus, where humans have transformed large areas of forested landscapes to agricultural or urban uses, streams exhibit physical, chemical, and biological patterns uncharacteristic of the region. The shift in assemblage structure may be because the physicochemical tolerances of endemic species are exceeded by the environmental changes and their fitness in terms of reproductive success, growth, and survivorship is reduced. Another possible pathway is that the outcome of interactions such as competition and predation may shift as the habitat is altered in response to landscape change. Regardless of the mechanisms, declines in numbers and abundance of endemic fishes appear to indicate loss of ecological integrity in these highland systems (Karr 1991).

Temporal variation

Temporal variation in assemblage structure was minor relative to spatial variation among sites, hence fish assemblages in each stream appeared stable over the two years of collections (Table 3.1). Faunal variation over time at a site may be viewed as fluctuating within a given geophysical setting. Over time, species composition may change (Orth and Maughn 1984, Schlosser 1985, Freeman et al. 1988, Gelwick 1990) and population sizes of stream fishes may vary considerably (Elliot 1987) due to a number of factors including immigration/emigration, reproductive success, interactions among species such as predation or competition for resources, and responses to local environmental disturbance (e.g., floods; Poff and Allan 1995). Grossman et al. (1998) reported that environmental variability in the form of hydrologic regime was more important than interspecific competition or predation in structuring fish assemblages in Coweeta Creek, a Blue Ridge stream I also sampled. Freeman et al. (1988) reported that habitat differences (=spatial variation) affected assemblage dynamics among three sites within the Coweeta Creek drainage. I found that when ecological similarities among spatially-extensive collections in the region were ordinated, variation in repeated collections at sites was minor compared to differences among sites. Moreover, patterns in assemblage structure were strongly related to environmental variation among sites, supporting Grossman et al.'s (1998) conclusion that environmental variation interacts with species-specific evolutionary constraints on behavior, morphology, and physiology to structure fish assemblages in the region.

Few studies have been both intensive and extensive enough to sort out long-term variation from spatial variation due to heterogeneous geography. Wiley et al. (1997) suggested that an accurate assessment of temporal structure of trout populations in Michigan required at least 15-20 y of data collection. Obviously, the data I presented were more spatially extensive than temporally intensive, therefore my assessment of temporal stability applies only to the two-year period over which each site was sampled. Because hydrologic variability has been reported to be a primary determinant of assemblage structure (Grossman et al. 1998), I examined discharge recorded at several U.S.Geological Survey gauging stations in the Little Tennessee and French Broad river basins for the period 1980 - 1998 (data available from the National Water Information System at http://waterdata.usgs.gov/nwis-w/US/). These records indicate that peak flows in the region for the years 1995 - 1998 were within historical norms, hence no major disturbance events appeared to take place during the study. Matthews (1998) recently reviewed the literature on assemblage stability and concluded that, although no simple answer to the question of assemblage stability is likely to exist, assemblage structure in most streams is relatively resistant to change or may cycle about some relatively stable condition when viewed over many years. Streams of the Blue Ridge Province appear to conform to that description, absent acute or chronic stressors shifting environmental conditions to new states.

Biodiversity and landscape change

North America is noted for its high diversity of temperate aquatic organisms, a major contributor being the species richness found in the southeastern U.S. (Neves et al. 1997, Morse et al. 1997, Warren et al. 2000). The upper Tennessee River system harbors one of the richest and most distinctive fish faunas on the continent, largely because of the high proportion of endemic species found in Appalachian highland drainages (McCallister et al. 1986, Warren et al. 1997). Mayden (1987, 1988) made a strong case based on phylogenetic and geological evidence that the Appalachian highlands are remnants of an extensive highland region encompassing much of the central U.S. prior to Pleistocene glaciation. Mayden’s findings suggest that fishes that today are endemic to the southern Appalachians are descendents of ancient highland fishes and have evolved under highland environmental regimes. Endemic species may be particularly susceptible to changes in water and habitat quality (Angermeier 1995; Scott and Helfman 2001).

The altered biota observed in streams with modified habitats are troubling precisely because they are uncharacteristic of the region. Endemic fishes represent a substantial component of continental biodiversity, and constitute an important part of the ecological integrity of the region. Yet in disturbed streams endemic fishes were absent or greatly reduced in abundance. Land disturbance clearly is associated with loss of ecological integrity in these streams, as revealed by altered habitats and declines in endemic fishes. The status of endemic fishes would make an appropriate indicator of biological integrity in eastern highland streams (Miller et al. 1988), and such an indicator may also apply to other regions of high endemism such as the western U.S. (McCallister et al. 1986).

The southern Appalachian region is expected to grow in human population, and residential land use is expected to increase (Wear and Bolstad 1998). If the current model of economic growth and land development as practiced in the U.S. holds in this region, the future bodes ill for organisms that are intolerant of habitat alteration. The expected trajectory of faunal change can be illustrated (Figure 3.6) based on Figures 3.4 and 3.5. Essentially, the natural diversity of faunas across Blue Ridge landscapes collapses into a fauna tolerant of the habitat change brought on by anthropogenic modification of the landscape (Jones et al. 1999, Marchetti et al. 2001). High elevation streams gain species richness through invasion by tolerant generalists while low elevation streams lose richness as endemic fishes are eliminated. This process may be viewed as homogenization of a distinct regional fauna into a common assemblage with generalized distributions (Rahel 2000, McKinney and Lockwood 2001). Grossman et al. (1990) urged caution in using fish population data to detect the effects of anthropogenic disturbances in streams, citing variability in many assemblages so high that the effects of human disturbances were not distinguishable from natural variation. I found similar patterns in analyses of both assemblage similarity and fish density which suggested that structure was stable relative to spatial differences. Hence, anthropogenic effects were detectable. Strong and concerted efforts must be made to mitigate the environmental effects of human activity, including protection of riparian zones, maintenance of large proportions of indigenous land cover, and adherence to best management practices whenever land disturbance activity takes place. If management is to be effective, watersheds must be the focus of conservation efforts so that the entire ecosystem is considered (Warren and Burr 1994). Continuation of current trends will likely put today's endemics on tomorrow's lists of threatened and endangered species.

Conclusions

A hierarchical model of aquatic ecosystems was useful in organizing physical, chemical, and biological data and for integrating results over multiple scales. Fish assemblages appeared stable over two years of collections relative to variability among sites. Landscape features influenced habitat conditions across the Blue Ridge, and variability in assemblage structure was associated with the environmental variation, in agreement with model predictions. Several species associations were identified with landscape settings and habitats. Species composition and abundance shifted along a continuous gradient of elevation and stream size, increasing in species richness and diversity from headwater streams to valley rivers. A trout/sculpin association in cool headwaters accrued species along the longitudinal gradient to form a complex association of minnows, suckers, and darters (including many endemics). An assemblage comprising fishes tolerant of anthropogenic landscape disturbance was also evident, in effect replacing the endemic species typical of the region. The disturbed streams were characterized by loss of forest cover and building/road development in the riparian zone, and by nutrient-enriched, sediment-laden stream channels.

The patterns associated with anthropogenic disturbance suggest that poor land-use practices are reducing the ecological uniqueness of the region by altering stream habitats. In disturbed streams, the increased abundance among species with widespread distributions concomitant with endemic species decline may signal the early stages of biodiversity loss (Scott and Helfman 2001). The process may be viewed as ecological homogenization as distinctive elements are replaced by common elements. Averting future imperilment of a whole suite of highland species requires that research, management, and conservation efforts be focused on entire drainage systems. The interconnected patterns and processes of aquatic ecosystems cannot be disengaged from their terrestrial setting, which increasingly include human decisions and actions.

Acknowledgments

I thank G. Helfman, M. Freeman, C. Pringle, and J. Meyer for comments on an earlier draft, P. Bolstad for providing geographic data, S. Rathbun for advice on statistical methods, and F. Benfield, D. Jones, N. Gardiner, M. McTammany, D. Toole, B. Farmer, J. Harper, K. Schofield, B. Staub, A. Sutherland, S. Kornberg, H. Russell, and P. Marcinek for field assistance. This research was supported by National Science Foundation grant DEB-9632854 to the University of Georgia Coweeta Long Term Ecological Research Program. Data reported here are available at the following url: http://sparc.ecology.uga.edu/webdocs/

Literature Cited

Allan, J.D., D.L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biol. 37:149-161.

Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters. BioScience 43(1):32-43.

Allen, T.F.H., and T.B. Starr. 1982. Hierarchy. University of Chicago Press, Chicago.

Angermeier, P.L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. Conserv. Bio. 9:143-158.

Belbin, L., and C. McDonald.1993. Comparing three classification strategies for use in ecology. J. Veg. Sci. 4:341-348.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045-1055.

Brooks, D.R., R.L. Mayden, and D.A. McLennan. 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. Trends in Ecology and Evolution 7(2):55-59.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Austral. J. Ecol. 18:117-143.

Davies, N.M., R.H. Norris, and M.C. Thoms. 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics. Freshw. Biol. 45:343-369.

Dolloff, C. A., and J. R. Webster. 2000. "Particulate organic contributions from forests to streams: debris isn't so bad." Pp. 125-138 *in* E. S. Verry, J. Hornbeck, and C. A. Dolloff, eds. Riparian management in the eastern continental United States. CRC-Lewis Publishers, FL.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345-366.

Elliot, J.M. 1987. Population regulation in contrasting populations of trout, *Salmo trutta*, in two Lake District streams. J. Anim. Ecol. 56:83-98.

Faith, D.P., P.R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57-68.

Freeman, M.C., M.K.Crawford, J.C. Barrett, D.E. Facey, M.G. Flood, J. Hill, D.J. Stouder, G.D. Grossman. 1988. Fish assemblage stability in a southern Appalachian stream. Can. J. Fish. Aquat. Sci. 45:1949-1958.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage. 10:199-214.

Gelwick, F.P. 1990. Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma Ozark stream. Copeia 1990:1072-1082.

Grossman, G.D., J.F. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes: a review. Environ. Manage. 14:661-671.

Grossman, G.D., R.E. Ratajczak, Jr., M. Crawford, and M.C. Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. Ecol. Monogr. 68:395-420.

Hack, J.T. 1969. The area, its geology: Cenozoic development of the southern Appalachians. pp. 1-17 *in* P.C. Holt, ed. The distributional history of the biota of the southern Appalachians. Part I: invertebrates. Research Division Monograph 1, VPI&SU, Blacksburg, Virginia.

Hynes, H.B.N. 1975. The stream and its valley. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 19:1-15.

Imhof, J.G., J. Fitzgibbon, and W.K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 312-326.

Johnson, L.B., and S.H. Gage. 1997. Landscape approaches to the analysis of aquatic ecosytems. Freshw. Biol. 37:113-132.

Jones, E.B.D, III, G.S. Helfman, J.O. Harper, and P.V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conserv. Biol. 13:1454-1465.

Karr, J.R. 1991. Biological integrity: a long-neglected aspect of water resource management. Ecol. Appl. 1:66-84.

Krebs, C. J. 1989. Ecological Methodology. Harper & Row, New York, New York.

Lammert, M. and J.D. Allan. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ. Manage. 23:257-270.

Leopold, L.B., M.G. Wolman, and J.P. Miller. 1964. Fluvial processes in geomorphology. W.H. Freeman, San Francisco.

Lotspeich, F.B. 1980. Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. Water Res. Bull. 16:581-586.

Marchetti, M. P., T. Light, J. Felicano, T. Armstrong, Z. Hogan, and P. B. Moyle. 2001. Homogenization of California's fish fauna through abiotic change. Pp. 259-278 *in* J. L. Lockwood and M. L. McKinney, eds. Biological homogenization. Kluwer Plenum/Academic Press, New York.

Mather, P.M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley & Sons, London.

Matthews, W.J. 1987. Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. pp. 111-120 *in* W.J. Matthews and D.C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman & Hall, New York.

Maxwell, J.R., C.J. Edwards, M.E. Jensen, S.J. Paustian, H.Parrott, and D.M. Hill. 1995. A hierarchical framework of aquatic ecological units in North America (Nearctic Zone).

General Tech. Report NC-GTR-176, USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.

Mayden, R.L. 1987. Historical ecology and North American highland fishes: a research program in community ecology. pp. 203-222 *in* W.J. Matthews and D.C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Mayden, R.L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. Syst. Zool. 37:329-355.

McCallister, D.E., S.P. Platania, F.W. Schueler, M.E. Balwin, and D.S. Lee. 1986. Ichthyofaunal patterns on a geographic grid. pp.17-51 in C.H. Hocutt and E.O. Wiley, eds. The zoogeography of North American freshwater fishes. John Wiley & Sons, New York.

McCune, B., and M.J. Mefford. 1997. PC-ORD. Multivariate analysis of ecological data, Ver. 3.0. MjM Software Design, Gleneden Beach, Oregon.

McKinney, M.L. and J.L. Lockwood. 2001. Biotic homogenization: a sequential and selective process. Pp. 1-17 *in* J.L. Lockwood and M.L.McKinney, eds. Biotic homogenization. Kluwer Plenum/Academic Press, New York.

Menge, B.A., and A.M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5(2):52-57.

Miller, D. L., and 13 coauthors. 1988. Regional applications of an index of biotic integrity for use in water resource management. Fisheries 13(5) :12-20.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69:89-107.

Morse, J. C., B. P. Stark, W. P. McCafferty, and K. J. Tennessen. 1997. Southern Appalachian and other southeastern streams at risk: implications for mayflies, dragonflies and damselflies, stoneflies, and caddisflies. Pp. 17-30 *in* G.W. Benz and D.E. Collins, eds. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.

Neves, R.J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt, and P. W. Hartfield. 1997. Status of aquatic mollusks in the southeastern united states: a downward spiral of diversity. Pp. 31-85 *in* G.W. Benz and D.E. Collins, eds. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.

Orth, D.J., and O.E. Maughan. 1984. Community structure and seasonal changes in standing stocks of fish in a warm-water stream. Amer. Midl. Nat. 112: 369-378.

Poff, N.L. 1997. Landscape filters and species traits: towards a mechanistic understanding and prediction in stream ecology. J. N. Am. Benthol. Soc. 16:391-409.

Poff, N.L., and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. Ecology 76:606-627.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288:854-856.

Richards, C. and G.E. Host. 1994. Examining land use influences on stream habitats and macroinvertebrates: a GIS approach. Water Resources Bulletin 30:729-738.

Richards, C., L.B. Johnson, and G.E. Host. 1996. Landscape-scale influences on stream habitats and biota. Can. J. Fish. Aquat. Sci. 53 (suppl. 1):295-311.

Richards, C., R.J. Haro, L.B. Johnson, and G.E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. 37:219-230.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. Science 235:167-171.

Ricklefs, R.E., and D. Schluter. 1993. Species diversity: regional and historical influences. pp. 350-363 *in* R.E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities: historical and geographic perspectives. University of Chicago Press.

Schlosser, I.J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66: 1484-1490.

Schlosser, I.J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303:71-81.

Scott, M.C., G.S. Helfman, M. McTammany, E.F. Benfield, and P.V. Bolstad. In review. Spatial and temporal influences on stream physicochemistry across southern Blue Ridge landscapes. Journal of the American Water Resources Association.

Scott, M.C., and G.S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26(11):6-15.

Tonn, W.M., J.J. Magnuson, M. Rask, and J. Toivonen. 1990. Intercontinental comparison of small-lake fish assemblages: local processes and regional patterns. Freshw. Biol. 136:345-375.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Ward, J.V. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. Biological Conservation 83:269-278.

Warren, M.L. Jr., and B.M. Burr. 1994. Status of freshwater fishes of the United States: Overview of an imperiled fauna. Fisheries 19(1):6-17.

Warren, M.L. Jr., P.L. Angermeier, B.M. Burr and W.R. Haag. 1997. Decline of a diverse fish fauna: patterns of imperilment and protection in the southeastern United States. pp. 105-164 *in* G.W. Benz and D.E. Collins, eds. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.

Warren, M.L. Jr., B.M. Burr, S.J. Walsh, H.L. Bart Jr., R.C. Cashner, D.A. Etnier, B.J. Freeman, B.R. Kuhajda, R.L. Mayden, H.W. Robison, S.T. Ross, and W.C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25(10):7-31.

Wear, D.N., and P. Bolstad. 1998. Land-use change in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Wiley, M.J., S.L. Kohler, and P.W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. Freshw. Biol. 37:133-148.

Wolman, M.G. 1954. A method of sampling coarse river-bed material. Transactions of the American Geophysical Union 35:951-956.

Table 3.1. Species whose abundances were most correlated with three ordination axes derived by non-metric multidimensional scaling. The three axes accounted for 91% of variation in the matrix of Bray-Curtis similarities among collections (contribution of each axis in parentheses). A positive correlation with an axis indicates that sites where that species is more abundant tend to have high scores on that axis, whereas sites with few or none of that species tend to score lower on the axis. A negative correlation indicates the opposite relations.

Species	Pearson correlation coefficient
Axis 1 (45%)	
Rhinichthys atratulus	0.75
Semotilus atromaculatus	0.74
Cottus bairdi ssp.	-0.74
Catostomus commersoni	0.56
Lepomis auritus	0.50
Oncorhynchus mykiss	-0.50
Axis 2 (37%)	
Luxilus coccogenis	0.81
Notropis leuciodus	0.77
Nocomis micropogon	0.76
Oncorhynchus mykiss	-0.64
Cyprinella galactura	0.61
Etheostoma chlorobranchium	0.51
Axis 3 (9%)	
Etheostoma swannanoa	-0.78
E. flabellare	-0.67
Hybopsis amblops	-0.48
Cyprinella galactura	-0.41
Clinostomus funduloides ssp.	0.41

Table 3.2. Results of analysis of variance showing percentage of variance in ordination axis scores accounted for by spatial and temporal factors. Time factors are combined seasonal (late spring, early fall), annual, and seasonal*annual interaction terms. Each ordination axis is an ordering of sites along a multivariate dimension representing similarities in faunal composition and abundance.

	1995-96 collections *n*=96		1997-98 collections *n*=48			
	df	*SS*	*df*	*SS*	Combined Model *SS*	Percent of variance explained by factor
Axis 1					37.28	
site	23	23.15	11	12.78		96.0
time	3	0.26	3	0.05		1.0
site*time	46	0.67	22	0.37		3.0
Axis 2					55.75	
site	23	43.83	11	9.97		97.0
time	3	0.12	3	0.65		1.0
site*time	46	0.61	22	0.57		2.0
Axis 3					26.07	
site	23	18.83	11	6.06		95.4
time	3	0.18	3	0.17		1.4
site*time	46	0.35	22	0.48		3.2

Table 3.3. Environmental variables at site and landscape scales that correlated significantly with axes of variation in faunal similarity among sites, as extracted by non-metric multidimensional scaling. Pearson correlation coefficients >0.50 ($P<0.01$) are presented.

Variable	Axis 1	Axis 2	Axis3
Instream habitat			
total dissolved solids	0.82		
nitrate-N	0.74		
turbidity			-0.53
coarse substrate	-0.68		
substrate embeddedness	0.66		
channel wetted width	-0.57		
stream temperature	0.50	0.73	
Landscape			
riparian land use index	0.81		
1km land use index	0.55		
elevation		-0.71	
basin area		0.52	

Table 3.4. Four fish species associations (classes A, B, C, and D) that occur across southern Blue Ridge landscapes as identified by cluster analysis of mean number of individuals collected per 100 m^2 of stream. Species are listed along with 1) indicator values (abundance x occurrence) for each class, 2) percentages showing their average abundance in the class relative to their abundance at all sites, and 3) their percent frequency of occurrence in that class. Species marked with an asterisk are significant indicators of a class (largest indicator value), as determined by 1000 Monte Carlo simulations.

Table 3.4.	Species Indicator Value by class				Abundance in class relative to all sites				Frequency occurrence in class			
	A	B	C	D	A	B	C	D	A	B	C	D
Number of sites:	7	7	12	10								
Ichthyomyzon greeleyi	1	38	16	0	3	66	31	0	29	57	50	0
Notemigonus crysoleucas	0	1	0	9	0	6	0	94	0	14	0	10
Clinostomus funduloides ssp. *	2	47	1	1	8	82	4	6	29	57	25	10
Rhinichthys cataractae	11	40	2	24	11	46	3	40	100	86	75	60
R. atratulus *	1	17	0	77	2	20	1	77	43	86	33	100
Campostoma anomalum	2	28	14	50	2	28	14	56	86	100	100	90
Semotilus atromaculatus *	0	3	1	66	0	4	2	94	0	71	50	70

Table 3.4.	Species Indicator Value by class				Abundance in class relative to all sites				Frequency occurrence in class			
	A	B	C	D	A	B	C	D	A	B	C	D
Number of sites:	7	7	12	10								
Nocomis micropogon	0	49	39	7	1	49	39	11	29	100	100	70
Erimystax insignis eristigma	0	0	12	3	0	0	70	30	0	0	17	10
Hybopsis amblops	0	0	6	13	0	0	35	65	0	0	17	20
Cyprinella galactura	0	0	36	44	0	1	36	64	0	29	100	70
Luxilus coccogenis *	0	9	81	4	0	11	81	8	29	86	100	50
Notropis leuciodus *	0	14	73	2	0	16	80	4	0	86	92	40
N. rubricroceus	2	3	22	1	7	20	65	7	29	14	33	10
N. lutipinnis *	0	41	0	0	0	95	0	5	0	43	8	10
N. photogenis	0	7	4	0	0	48	52	0	0	14	8	0
N. telescopus *	0	0	42	0	0	0	100	0	0	0	42	0
N. spectrunculus *	5	12	56	0	16	17	67	0	29	71	83	0
Hypentelium nigricans *	3	17	16	56	4	17	16	63	71	100	100	90
Moxostoma duquesnei	0	19	24	2	0	44	49	8	0	43	50	20

Table 3.4.	Species Indicator Value by class				Abundance in class relative to all sites				Frequency occurrence in class			
	A	B	C	D	A	B	C	D	A	B	C	D
Number of sites:	7	7	12	10								
M. erythrurum	0	2	29	0	0	14	86	0	0	14	33	0
Catostomus commersoni *	0	1	0	78	0	2	1	98	0	43	25	80
Ameiurus natalis												
A. melas	0	0	7	6	0	0	44	56	0	0	17	10
Salvelinus fontinalis	0	2	1	24	0	11	7	81	0	14	17	30
Salmo trutta *	28	45	1	3	33	53	4	11	86	86	17	30
Oncorhynchus mykiss *	39	49	1	2	39	49	2	11	100	100	50	20
Gambusia holbrooki	0	0	0	10	0	0	0	100	0	0	0	10
Cottus bairdi ssp. *	14	76	8	0	14	76	10	0	100	100	83	10
Ambloplites rupestris	1	7	20	23	2	16	24	58	29	43	83	40
Micropterus dolomieu	0	0	23	21	0	0	47	53	0	0	50	40
M. salmoides *	0	0	0	39	0	0	2	98	0	0	8	40
Lepomis gulosus	0	0	0	10	0	0	0	100	0	0	0	10
L. cyanellus	0	0	1	47	0	1	5	94	0	29	25	50

Table 3.4.	Species Indicator Value by class				Abundance in class relative to all sites				Frequency occurrence in class			
	A	B	C	D	A	B	C	D	A	B	C	D
Number of sites:	7	7	12	10								
L. auritus *	0	0	3	55	0	2	6	92	0	29	42	60
L. macrochirus	0	0	2	38	0	1	3	96	0	14	50	40
L. gibbosus												
Perca flavescens	0	0	2	8	0	0	25	75	0	0	8	10
Percina evides ssp.	1	26	33	0	5	46	50	0	14	57	67	0
P. squamata	0	0	8	0	0	0	100	0	0	0	8	0
Etheostoma swannanoa	0	0	14	34	2	3	28	67	29	14	50	50
E. blennioides gutselli	1	26	33	0	5	50	46	0	14	57	67	0
E. zonale	0	4	21	0	0	16	84	0	0	29	25	0
E. chlorobranchium *	0	1	80	0	1	3	96	0	29	43	83	0
E. rufilineatum *	0	0	33	0	0	0	100	0	0	0	33	0
E. vulneratum	0	0	17	0	0	0	100	0	0	0	17	0
E. flabellare	3	0	7	20	12	0	21	67	29	14	33	30

Table 3.5. Indicator species of fish associations identified in a cluster analysis of fish densities, taken from Table 3.4. Class A was not substantially different from class B, except class A sites were dominated by trout to a greater extent.

Class A

N/A

Class B

Cottus bairdi ssp.
Oncorhynchus mykiss
Salmo trutta
Clinostomus funduloides ssp.
Notropis lutipinnis

Class C

Luxilus coccogenis
Etheostoma chlorobranchium
Notropis leuciodus
N. spectrunculus
N. telescopus
E. rufilineatum

Class D

Catostomus commersoni
Rhinichthys atratulus
Semotilus atromaculatus
Hypentelium nigricans
Lepomis auritus
Micropterus salmoides

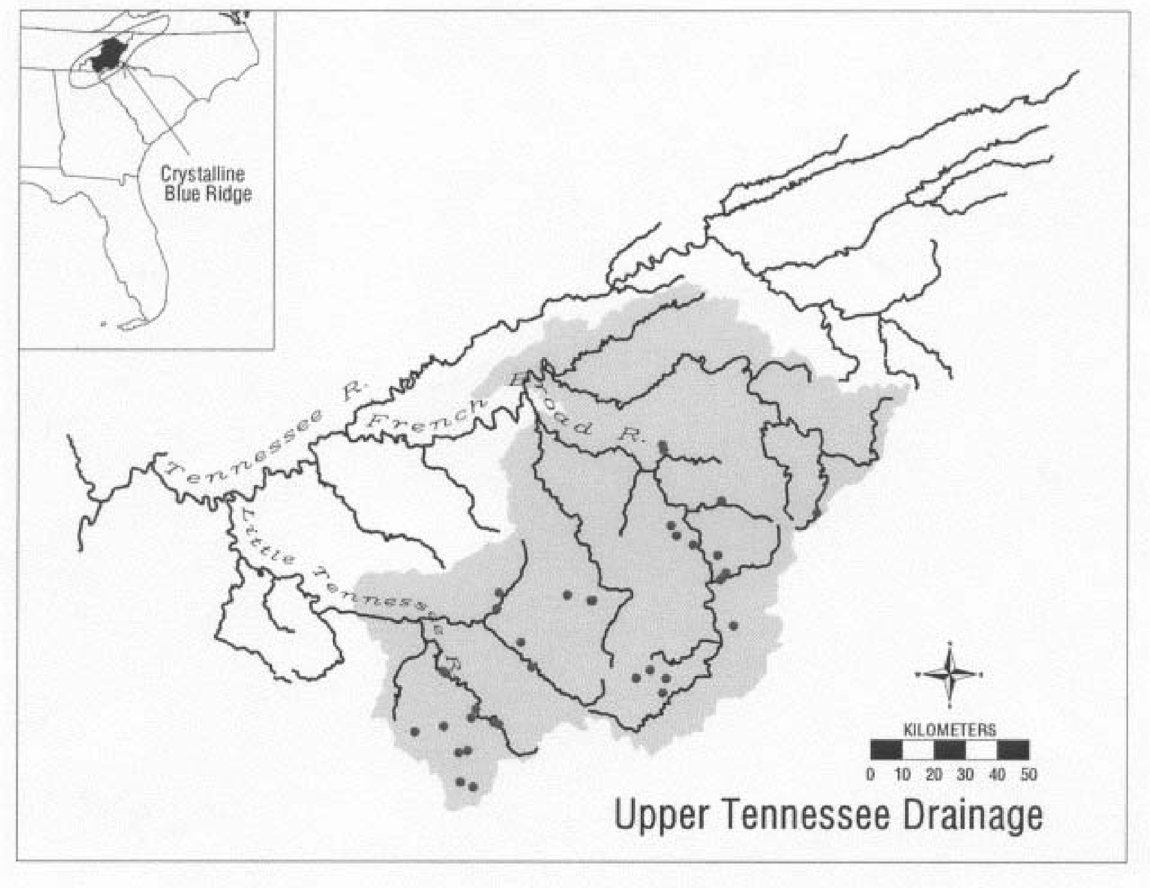

Figure 3.1. Location of the Little Tennessee and French Broad river basins in the Blue Ridge physiographic province. Sampling site locations on tributaries in the study area are indicated with closed circles.

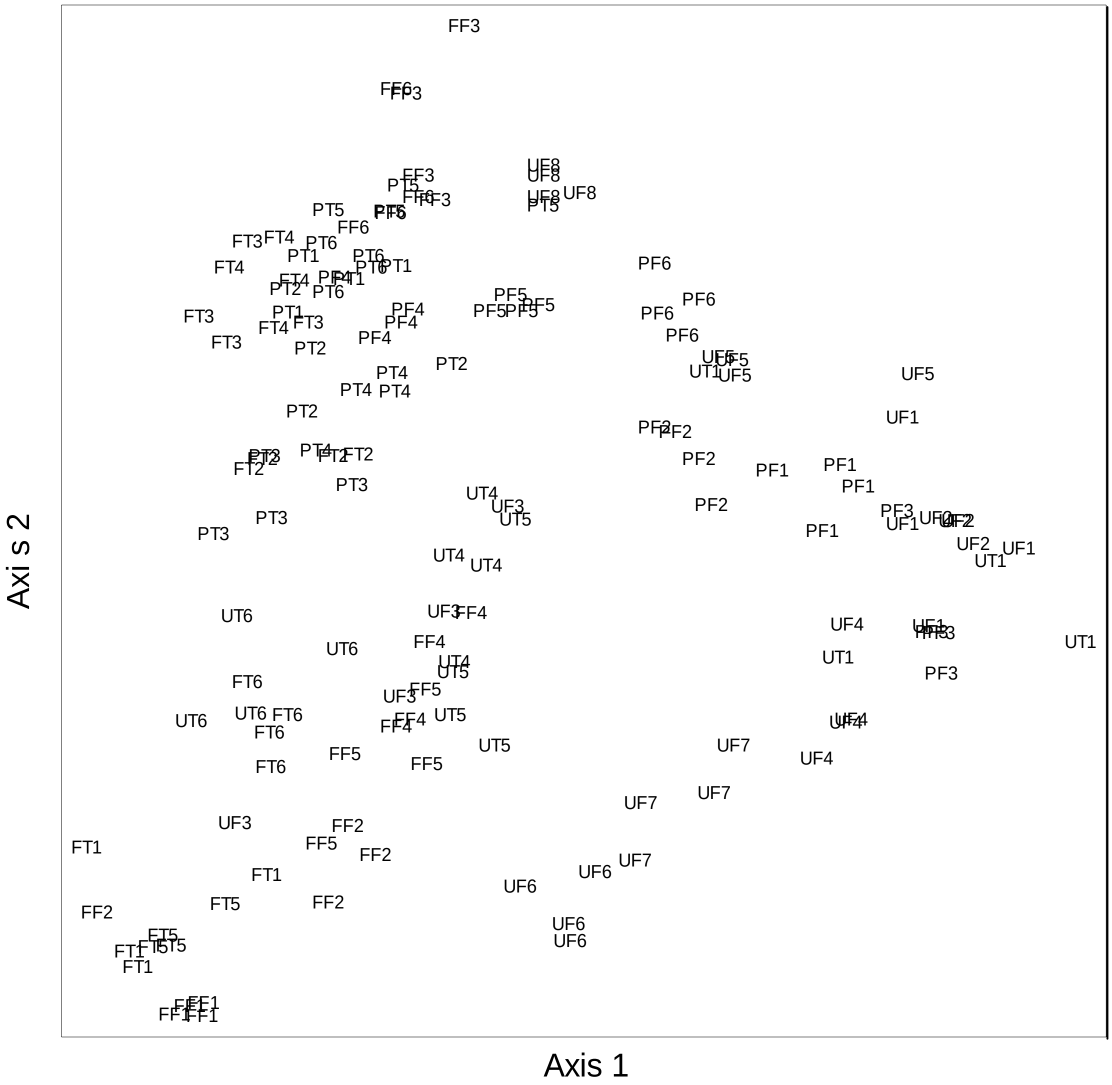

Figure 3.2. Plot of 144 collections at 36 sites according to scores on the first two ordination axes derived from non-metric multidimensional scaling of Bray-Curtis similarities in fish abundance. Axes 1 and 2 accounted for 45% and 37% of variation, respectively, in the original matrix. Three-letter code specifies individual sites. First letter indicates land use visible at the site: F – forest, P – pasture or agricultural field, U – urban/suburban setting. Second letter indicates major drainage basin: T – Little Tennessee, F – French Broad. The last number is an arbitrary specifier.

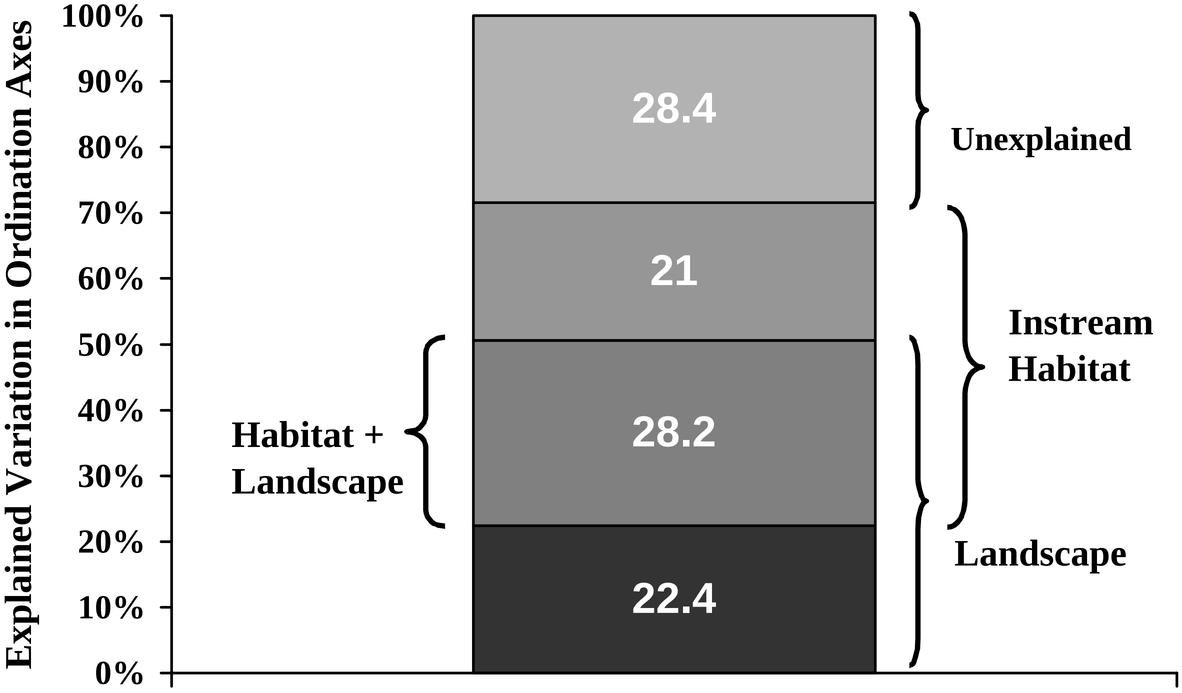

Figure 3.3. Variance partitioning of the scores on three biotic ordination axes according to landscape and instream habitat components. Combined environmental variables (Table 3.3) accounted for almost 72% of variation in ordination scores among sites. Stream habitat characteristics influenced by their landscape context explained the most variation (28.2%), whereas pure landscape and pure habitat variables each accounted for similar magnitudes of variance (21-22%).

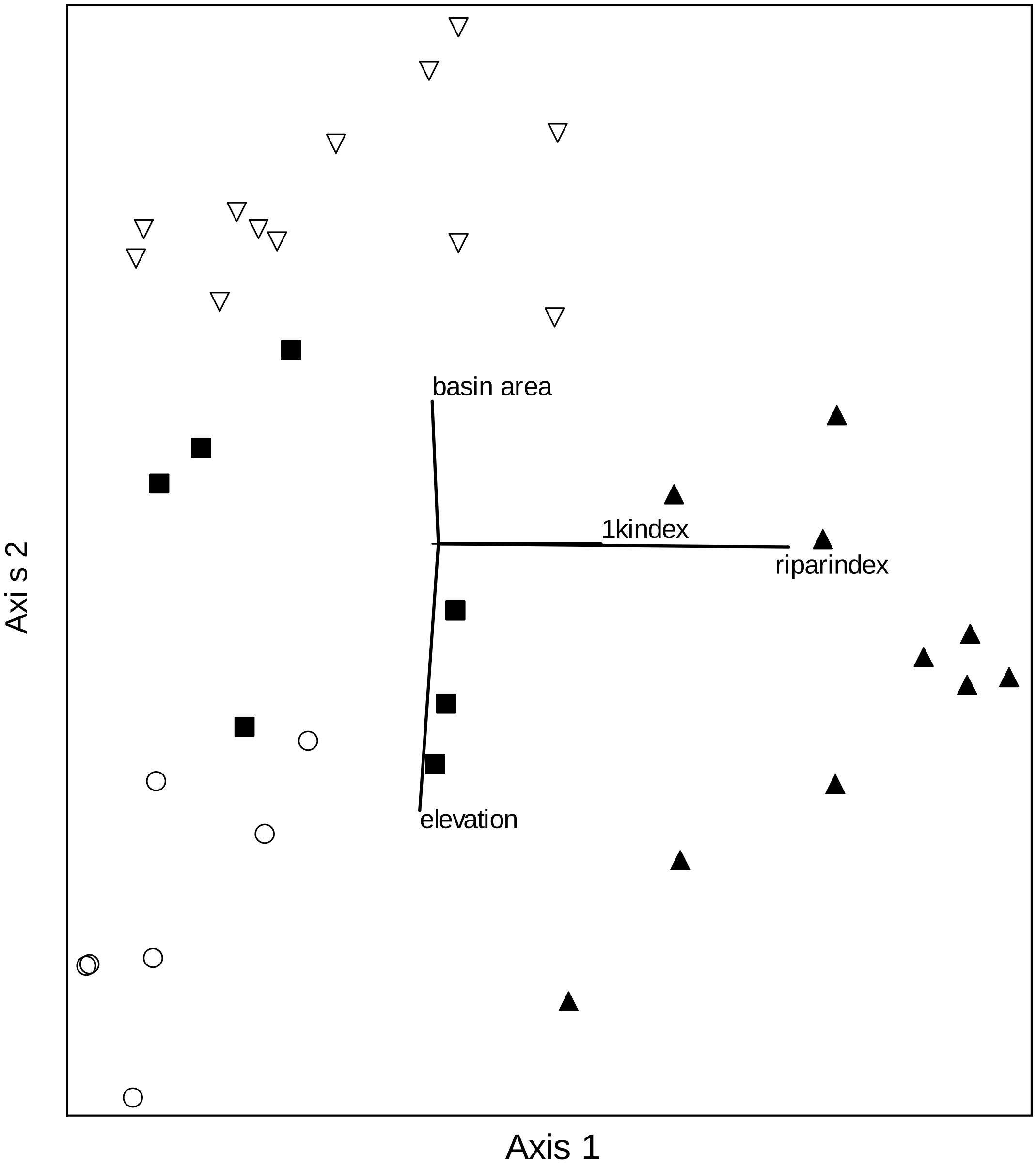

Figure 3.4. Plot of 36 sites on first two NMS axes, according to groups identified in cluster analysis. Symbols for points are open circle - Class A; closed square - Class B; open triangle - Class C; closed triangle - Class D. See Table 3.4 for species associated with each Class. Vectors represent the direction and magnitude of axis correlations with landscape variables (Table 3.3).

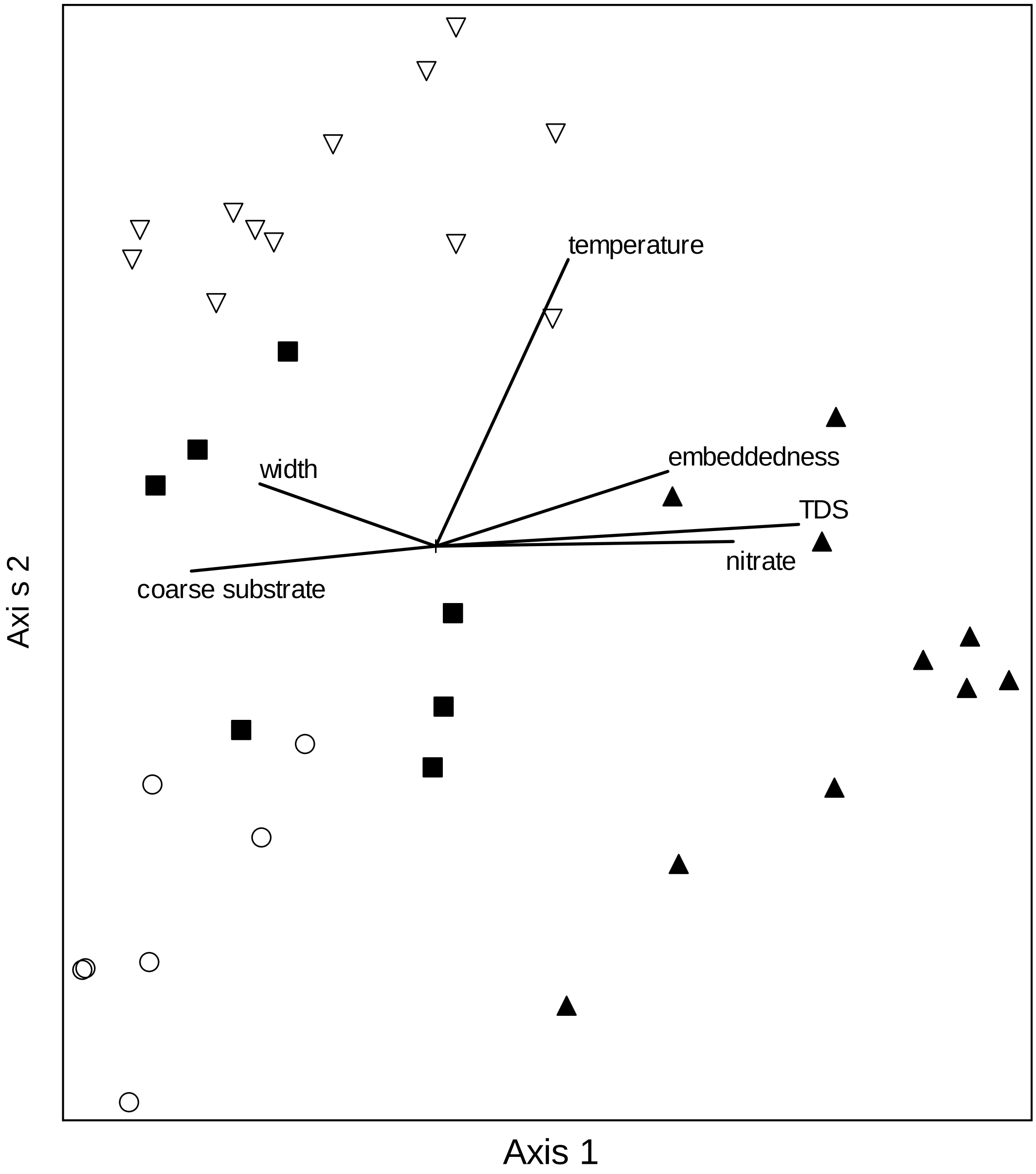

Figure 3.5. Plot of 36 sites on first two NMS axes, according to Classs identified in cluster analysis. Symbols for points are the same as in Figure 3.4. Vectors represent the magnitude of axis correlations with instream variables (Table 3.3).

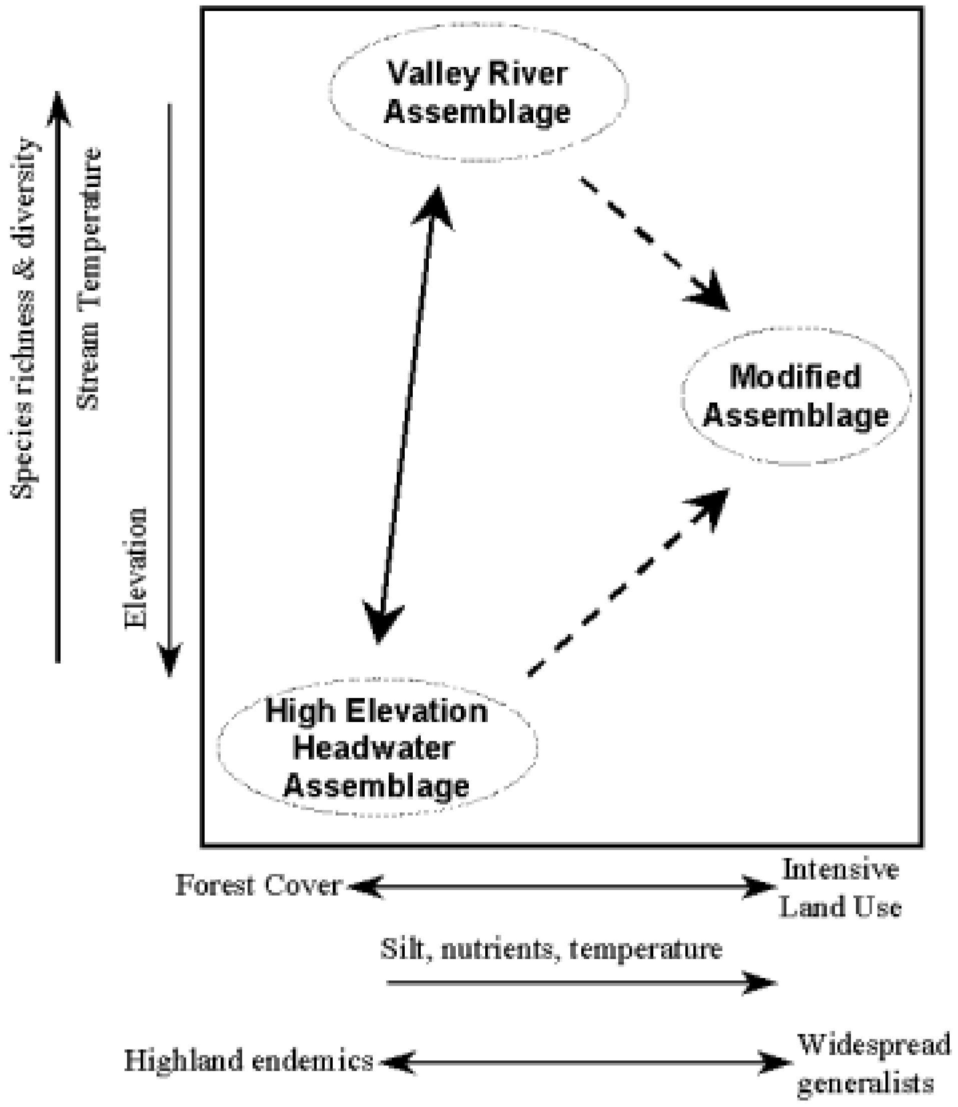

Figure 3.6. Major spatial patterns in assemblage structure of fishes in upper Tennessee River tributaries draining the Blue Ridge physiographic province. The *y*-axis reflects natural variation across Blue Ridge landscapes, whereas the *x*-axis reflects the influence of human activities.

CHAPTER 4

MODIFIED AQUATIC HABITATS AND THE DECLINE OF FISHES ENDEMIC TO THE HIGHLANDS OF EASTERN NORTH AMERICA [1]

---

[1] Scott, M. C. To be submitted to *Conservation Biology*.

ABSTRACT -- Complex and pervasive habitat degradation is the suspected cause of decline in the North American freshwater fish fauna. Literature suggests that taxa with limited distributions are at inordinate risk of imperilment. The following questions were addressed: 1) are endemic fishes different from widely-distributed taxa with respect to important life-history and behavioral traits or attributes, and 2) does the distribution of traits/attributes across the landscape relate to abiotic measures of the stream environment, indicating adaptiveness to indigenous environmental regimes *vs*. anthropogenically-altered conditions? Differences in life-history and ecological attributes of highland endemic (n=16) and geographically widespread (n=27) fishes were identified using multiple logistic regression. Small body size and specialized benthic or drift foraging habits increased the probability that fishes were endemic to the highlands; the model produced 94% concordance in predicted and observed responses. Field data from 36 highland streams were used to evaluate how fishes with risk-associated attributes were distributed in relation to abiotic conditions. Relative abundance of species attributes in streams were regressed against measures of riparian buffer condition, channel substrate particle size, streamwater nitrate-N concentration, turbidity, and temperature. In streams with modified habitats, endemic, small-bodied (low fecundity), cool-water trophic specialists that depend on coarse substrate for spawning decline. They are supplanted by cosmopolitan, large-bodied (long-lived, high-fecundity), warmwater trophic generalists that do not require rocky substrates for successful spawning. Cumulative effects of landscape disturbance alter aquatic habitat to the detriment of the organisms adapted to natural conditions. Loss of locally-adapted taxa may severely affect regional and

continental biotic diversity, particularly in regions with rich endemic faunas such as the Southeast. Proactive conservation at the watershed scale, particularly protection of riparian buffers, is critical to maintaining the integrity of aquatic habitat and associated communities.

Introduction

> “*The oldest ecosystems containing the largest numbers of endemic species are those least likely to survive human intervention, and thus are the most in need of immediate conservation.*”
>
> *Brooks et al. 1992*

Growing concern over the decline of global biological resources has stimulated awareness of the status of freshwater rivers and streams (Allan and Flecker 1993; Ricciardi and Rasmussen 1999). In North America, conservation of native fishes has been the subject of numerous reviews (Deacon et al. 1979; Williams et al. 1989; Moyle and Leidy 1992; Frissell 1993; Warren and Burr 1994), particularly the extraordinary diversity and high density of imperiled fishes in the southeastern U.S. (Lydeard and Mayden 1995; Burkhead et al. 1997; Warren et al. 1997; Warren et al. 2000). A center for biodiversity of North American fishes is located in the uplands of the southern Appalachians, where faunas are typified by high levels of endemism (Mayden 1987, 1988). Large numbers of endemic species in a region translate into a highly distinctive fauna, one that contributes disproportionately to continental diversity compared to regions equally rich in taxa but with fewer endemics. For example, the upper Tennessee

River system, which primarily drains the highlands of eastern Tennessee, southwestern Virginia, and western North Carolina, contains at least 147 native fish species (nearly 20% of the entire U.S. fauna; Warren et al. 1997). Fifteen of the fishes are found nowhere else, a level of endemism exceeded only by the Coosa-Tallapoosa River systems (16 endemic fishes) that drain the uplands of northeastern Alabama and northwestern Georgia (Warren et al. 1997). In fact, the eastern highlands harbor at least 53 endemic fishes (Mayden 1987), not including species known but lacking formal description. This constitutes the highest concentration of combined biodiversity and biological uniqueness on the North American continent, and perhaps the temperate world.

Mayden (1987, 1988) presented geological, biogeographic, and phylogenetic evidence that current distributions of many fishes reflect an ancient highland fauna once widespread across east-central North America. Pleistocene glaciation eliminated large northern areas of the contiguous highlands, leaving disjunct populations of this ancestral fauna in the remaining southern Appalachian, Ozark, and Ouachita mountains. Phylogenetic systematics suggest that a number of sister species occurring in these remaining highlands are descendants of a common ancestor that once was widely distributed. Isolated populations radiated into an impressive array of species, particularly within the families Cyprinidae and Percidae. Where phylogenies exist, endemic highland species often show derived character states (Mayden 1987). The indications are that these endemics speciated *in situ*, under the environmental regimes characteristic of the highlands, rather than having evolved elsewhere and dispersed into these regions. Thus, because of the great age of the fauna (dating to at least the Tertiary; Mayden 1987), endemic members are more likely than other taxa to possess special adaptations to highland environments.

Evidence also suggests that taxa with limited distributions are at inordinate risk of imperilment (Angermeier 1995; Burkhead et al. 1997). If we assume that range-restricted, endemic species are adapted to the environmental regimes found in their native habitats, we may then reason that they will be more susceptible to anthropogenic habitat change than taxa with more generalized requirements. The causes of decline in our native fishes are manifold, but habitat deterioration and loss are primary (Allan and Flecker 1993). Habitats become altered not only by direct manipulation (e.g., dams, channelization), but also as a consequence of cumulative effects that accrue with rapid and large-scale transformation of landscapes. Scott et al. (in review) showed that loss of forest cover on southern Appalachian landscapes was related to increased fine sediments, nutrient concentrations, and temperature in streams. Moreover, patterns in the composition of fish assemblages in the region are associated with landscape and habitat features (Jones et al. 1999, see Chapter 3). I hypothesize that species that evolved ‘in place’ (i.e., endemics) are more sensitive to the environmental change that accompanies anthropogenic activities, and are therefore at greater risk of suffering negative effects from habitat alteration as compared to widely-distributed or generalized species (Scott and Helfman 2001).

Here, I test assumptions about the adaptiveness of behavioral and life-history traits compiled from published literature for fishes that were collected in upper Tennessee River tributaries. I relate their relative abundance in streams to landscape and habitat features indicative of anthropogenic disturbance. The trait-environment relationships were evaluated with respect to hypotheses about adaptation and susceptibility versus two different null models: random distribution or phylogenetic constraint. Several other studies have examined life-history and ecological attributes of fishes (Winemiller and Rose 1992), mostly attempting *a posteriori* to identify risk factors for imperiled or extirpated species (Angermeier 1995; Parent and Schriml 1995; Burkhead et al. 1997). Richards et al. (1997) found that stream habitat conditions were highly predictive of macroinvertebrate species traits. I am not aware, however, of studies relating the attributes of fish taxa to environmental variables as a means of assessing their risk of becoming imperiled. My objectives were to address the following questions: 1) are endemic fishes different from widely-distributed taxa with respect to important life-history and behavioral traits or attributes; and 2) does the distribution of traits/attributes across the landscape relate to abiotic measures of the stream environment, indicating adaptiveness to indigenous environmental regimes *vs*. anthropogenically-altered conditions?

Methods

Data collection-- Data were collected from 1995-1999 during a study of land-use change in the southern Appalachians (Harding et al. 1998; Wear and Bolstad 1998; Scott et al. in review). Fishes were collected as well as data on stream temperature, water chemistry, channel geomorphology, and catchment geography in 36 streams that ranged from 5 - 320 km^2 in catchment area draining the Blue Ridge region of western North Carolina.

Streams were tributaries of the Little Tennessee and French Broad rivers, adjacent drainages in the upper Tennessee River system. Field and laboratory collection of these data are described elsewhere (Scott et al. in review; Chapter 3). Taxonomy of fishes follows Warren et al. (2000). Caveats noted therein on uncertainty regarding known species and subspecies that lack formal descriptions hold here as well; nonetheless, many undescribed taxa are localized endemics and thus of importance in evaluating my thesis so they were included. Life-history and behavioral/ecological attributes for adults of each taxon were derived from regional ichthyology texts (Jenkins and Burkhead 1994; Etnier and Starnes 1993) and environmental monitoring literature (Simon 1999). Several fishes are little-known; in some instances I utilized information on closest congeneric relatives as surrogates and identified them in footnotes. This introduces the potential for error into my analyses; however, given that life-history traits are phylogenetically conservative (Brooks and McLennan 1991; Johnston 1999), and that much of the information I compiled was aggregated into broader categories (see below), I am confident that my method for describing ecological variation among these fishes utilized the best information currently available. In the case of *Ichthyomyzon* and *Phenacobius*, I found no information on fecundity in the genera, so those taxa were omitted in analyses involving that variable. Trophic ecology of *I. greeleyi* was compiled from descriptions of ammocoetes, because adults are not known to feed.

Species attributes fell into roughly six categories: distribution, body size, reproduction, trophic ecology, habitat use, and thermal tolerance (Table 4.1). The following attributes were selected because they have been reported as correlates of species imperilment in the southeastern U.S. (Angermeier 1995; Burkhead et al. 1997; Warren et al. 1997).

Phylogeny – Family designations for each taxon were coded to broadly indicate phylogenetic history (Table 4.1, Table 4.2).

Distribution – Following Mayden (1987) and Warren et al. (2000), I classified each taxon as to its geographic range (Table 4.1, Table 4.2). Fishes received the following codes: 1 if they are range restricted to the eastern highlands (sensu Mayden 1987); 2 if they occur only in highland regions at the latitude of the study area; 3 if they occur in lowland regions; and 4 if they occur in multiple physiographic regions (Table 4.2). Several studies have reported that restricted geographic range was associated with imperilment in fishes (Moyle and Leidy 1992; Angermeier 1995; Burkhead et al. 1997). I also tested the corollary of this, namely that more widely-distributed taxa are comparatively more adaptable to environmental change.

Body size and reproduction – Small body size has been associated with imperilment in fishes, reportedly correlated with low dispersal capabilities, short longevity, and low reproductive potential (Angermeier 1995; Burkhead et al. 1997). I included maximum body size (total length) that each taxon is likely to achieve in running waters at similar latitude, along with expected age at sexual maturity, longevity, and fecundity. Spawning behaviors were compiled because some have been reported as sensitive to riparian disturbance, and reproductive success may be negatively impacted by sedimentation (Berkman and Rabeni 1987; Johnston 1999; Jones et al. 1999).

Behaviors were coded according to the importance of unsedimented, coarse substrates to the success of the behavior (Table 4.1, Table 4.2).

Trophic ecology – All taxa were classified according to predominant food resource, foraging habitat, and breadth of resource use. Fishes were classified for trophic breadth according to the number of trophic classes they reportedly utilize (e.g., coded 1 for a single class, 4 for four or more classes; Table 4.1). Generalized food requirements have been associated with the ability to withstand environmental disturbance (Karr 1991; Simon 1999). In addition, benthic orientation in foraging and habitat use (see below) has been cited as a risk factor for stream fishes (Burkhead et al. 1997; Warren et al. 1997).

Habitat use – Each taxon was classified according to reported habitat type preferred (riffle, pool/run, or unrestricted; Table 4.1, Table 4.2) and the size of the water body typically inhabited. Habitat breadth was coded as follows: 1 – single habitat type and two water sizes, or unrestricted type and one size; 2 – unrestricted type and two sizes; 3 – three or more sizes. Angermeier (1995) considered specialization in habitat requirements as a factor increasing a taxon's risk of imperilment.

Thermal preference/tolerance – Thermal preference/tolerance was determined from the literature (Etnier and Starnes 1993; Jenkins and Burkhead 1994). Thermal studies quantifying preferenda or maxima tolerated by most species are nonexistent, so most classifications are based on distribution. Nonetheless, thermal elevation is a documented consequence of catchment and riparian disturbance on forested landscapes (LeBlanc et al. 1997; Scott et al. in review), so the concordance between perceived thermal tolerance and stream temperature was of interest.

Data analysis-- Multiple logistic and linear regression techniques were used to evaluate two primary hypotheses. First, I postulated that life-history and ecological differences exist between fishes endemic to the Appalachian highlands versus widely-distributed taxa (combined lowland and cosmopolitan classes, Table 4.1). This hypothesis was tested against a null model in which species attributes are distributed randomly among the two groups. Evidence to reject this null hypothesis took the form of significant models that differentiated the attributes of the two groups. The probability that a given taxon was an Appalachian endemic was modeled with the attribute classes as predictors using percent concordance and the Bayesian information criterion (BIC; Schwarz 1978) to compare the fit of the different models to the data. 'Best-fit' models employing different numbers of predictors were constructed, representing the most likely of the hypotheses I considered. The BIC was used in this process to balance model likelihood with parsimony in selecting predictors that best separated endemic and lowland-cosmopolitan taxa. Body size was log-transformed prior to analysis.

Non-random patterns in species attributes revealed by the above analysis may be due to phylogenetic structure that was historically present in the taxocene and not necessarily due to current ecological adaptiveness (Mayden 1987). This formed another null model which was addressed in analyzing the second hypothesis: some life-history/ecological attributes (e.g., distribution, body size, resource use) were adaptive either to natural indigenous habitats or to anthropogenically-modified habitats. Significant relationships in field data between relative abundance of ecological attributes and environmental variables which conformed to expected associations between habitat modification and organism response (see attribute descriptions above) were taken as evidence of adaptive traits that either increase or decrease fitness of individuals in changing environments. Although observational studies cannot establish cause-effect mechanisms, corroboration of conceptual models with data can provide strong support for such models.

Fishes in field collections were combined into the attribute classes to obtain the relative abundance of attributes across the landscape. Two distributional classes were used (Appalachian endemic, lowland-cosmopolitan), and only the extremes of attributes that were ranked ordinally were included. The ordinal classes included small and large size, early- and late-maturing, long- and short-lived, high and low fecundity, and specialized and broad resource use attributes. Each of the remaining coded attributes were included (Table 4.1) for a total of 28 attributes. Relative abundance was obtained for each attribute class by summing the number of member taxa collected at each of the 36 stream sites sampled and dividing by the total number of fishes collected at that site. Relative abundances were transformed by arcsine-square root prior to further analysis.

First, I tested whether any relationship existed between the matrix of attribute abundances and the matrix of stream environmental variables. The two matrices were both converted to Bray-Curtis dissimilarities among each pair of streams, and the congruence of these two distance matrices was evaluated with a non-parametric Mantel test (Sokal and Rohlf 1995). The standardized Mantel statistic (r) is analogous to the Pearson correlation coefficient for two distance matrices. Significance of the Mantel r

was determined by 9999 Monte Carlo permutations. (PC-Ord®, McCune and Mefford 1997).

I then examined relationships among the abundances of each attribute class to measures of riparian condition and stream habitat using multiple regression. The proportions of each attribute were arcsine(square root)-transformed to improve normality. Environmental predictors included riparian buffer condition in the catchment, channel substrate variables, and measures of water quality (see Scott et al. in review for details). Riparian condition was quantified by an index combining the non-forested proportion of a 100 m riparian zone along the mainstem of the stream with building and road density in the buffer. Variables reflecting sedimentation at a stream site included % substrate embeddedness, the fraction of coarse (>64 mm) substrate particles, and turbididty. Nitrate-N and ammonium-N (mgL^{-1}) reflected nutrient loads in stream water, and the maximum 7-d average temperature at each site was used to evaluate the effects of thermal pollution. Further details on environmental data collection and their relationships are found in Scott et al. (in review). Several of the predictors were correlated (e.g., riparian land use related to substrate and water quality), so variance inflation factors (VIF) were computed as a multicollinearity diagnostic. Model VIFs were in all cases less than 4, indicating that colinearity was not problematic. Bonferonni adjustments were made in alpha levels to correct for the large number of models being tested (alpha = 0.05/28 = 0.0018).

I illustrated the multivariate inter-relationships among life-history/ecological attributes and environmental variables by non-metric multidimensional scaling (NMS), an ordination technique useful for summarizing information in multiple variables with a few multivariate axes. Similar to principal components analysis, it differs from PCA in that instead of analyzing the covariance or correlation structure of the data matrix, NMS analyzes ecological distances (here, Bray-Curtis dissimilarities) among each pair of sites and requires no assumptions about variable distributions (Clarke 1993). I used NMS to compare similarities in abundance of fish attributes among streams, and determined the significance of extracted patterns by comparing them with a null model of random pattern generated by 100 Monte Carlo permutations. Each attribute was scored in the multivariate space by weighted averaging using PC-Ord® software (McCune and Mefford 1997). Vectors representing the relationships of environmental variables with the NMS axes were overlaid onto the plot of attributes in the multivariate space defined by the first two ordination axes.

Results

Differences in endemic vs. widely-distributed species-- Multiple logistic regression results indicated that highland endemic fishes could be differentiated from more cosmopolitan fishes by their body size and foraging habits (Table 4.3). Of the best-fit models with various numbers of parameters developed using the Bayesian information criterion, the most parsimonius in predicting the probability that a given taxon was endemic was the two-variable model. Body size and foraging habitat produced a model in which the concordance of predicted and observed responses was 94%. Controlling for the effect of foraging habitat, small body size increased the probability of endemism. Likewise, holding body size constant, lower values of the foraging habitat attribute (benthic-drift; Table 4.1) increased the likelihood that a taxon was endemic to the highlands. Endemics also tended to be specialized feeders on benthic or drift invertebrates (three-variable model), and use a more narrow range of habitats (four-variable model), but these attributes added little to predictive capability. Classification of individual species with the two-variable logistic model was more precise for widely-distributed taxa (88.5%) than for endemics (76.5%). Phylogeny was not a significant predictor in the logistic models, but all 16 endemic taxa fell into three of the nine families: Cyprinidae (7 taxa or 44%), Percidae (8 taxa or 50%), and Cottidae (one taxon, Table 4.2).

Evaluation of adaptiveness in species traits/attributes-- Abundance of life-history and ecological attributes were non-randomly distributed among streams, being significantly related to conditions of the stream environment (standardized Mantel test, r=0.54, *p*=0.0001). Regression models relating attribute abundance to riparian condition in the catchment, nitrate-N concentrations, turbidity, fraction of coarse substrate, and maximum 7-d mean temperature revealed several strong associations with model r^2 exceeding 0.50 (Table 4.4). The riparian land-use index was negatively related to the proportional abundance of fishes possessing the following attributes: highland endemic, small-bodied, low fecundity, rock crevice-nesting, benthic invertivorous, trophic specialist, coolwater. Thus, fishes with these attributes declined in streams where land use within a 100 m riparian buffer was intensive. In contrast, the following attributes became significantly more abundant with increased land-use intensity: cosmopolitan, long-lived, high fecundity, generalized invertivore, warmwater-tolerant (Table 4.4).

Nitrate-N concentration in streamwater was a significant predictor in one model, where the nutrient was positively related to abundance of general invertivores. Turbidity exhibited significant negative relationships with short-lived taxa, fishes that spawn in gravel/pebble nests, drift-feeding invertivores, and fishes that are cool-warm tolerant. In one counterintuitive result in the analysis, benthic invertivores were positively related to stream turbidity. Coarse substrate was a significant predictor in three models, and was borderline statistically significant in several others. Early-maturing and cool-warm tolerant taxa were positively related to substrate coarseness, whereas warmwater fishes exhibited a negative relationship.

Stream temperature was a strong predictor in several regression models (Table 4.4). The strong influence of temperature on biotic variables is likely associated with strong longitudinal zonation in Blue Ridge streams (Chapter 3), with lower temperatures associated with smaller, higher elevation streams, so the relationships of temperature with ecological attributes are influenced by this underlying pattern and are less clearly interpretable. The regression results indicated that the following attributes were related to higher stream temperatures: early maturation, short-lived, low fecundity, rock/gravel spawner with no parental care, drift-feeding invertivore, and cool-warm tolerant. Attributes with significant negative relations to stream temperature were: large size, rock crevice nesting habits, broadcast spawner with pelagic embryos, benthic-feeding invertivore, habitat specialist and generalist, cold and coolwater.

A more holistic view of the joint occurrence and abundance of these attributes among sites on the landscape is provided by the plot of ordination results (Figure 4.1).

The NMS analysis resulted in a two-dimensional solution (final stress=8.2) that explained nearly 96% of the variation in the original distance matrix. Monte Carlo results indicated that both dimensions extracted non-random patterns in the field data ($P<0.01$). Most of the variation occurred along axis 2 (69.4%). Weighted-average scores of attributes that were significantly related to environmental variables (Table 4.4) are plotted in the two dimensional space (Figure 4.1). The location of attributes in the space reflects their abundance in streams, such that attributes in closer proximity on the plot tend to occur together across the landscape. Vectors representing environmental variables that are related to the two axes are overlaid onto the plot. The direction and length of the vectors are proportional to the direction and magnitude, respectively, of their correlations with the two axes. Vertical separation of attributes is related primarily to riparian landuse (MBINDEX), coarse substrates, and nitrate-N concentrations in streams, whereas a diagonal separation from lower right to upper left is related to stream summer temperatures. Thus in the lower portion of the plot a grouping can be identified in which fishes posess the following: lowland/cosmopolitan distributions, long-lived, warmwater tolerance, high fecundity, detritivorous and generalized invertivorous, no requirement for coarse substrate in spawning. These attributes tended to occur in streams with disturbed riparian buffers, sedimented substrates, and stream water enriched with nitrate-N. The upper region of the plot represents the opposite of these environmental conditions and so represent less-disturbed streams. The upper group is characterized by the following attributes: highland endemic, small body, early maturation, short longevity, low fecundity, requirement for rock crevices or gravel/pebbles for spawning, specialized benthic or drift invertivore, and prefer cool to cold water. Within these two groupings, some separation is found along the lower-right to upper-left diagonal related to thermal influence. The plot thus illustrates factors that appear to increase the relative success of organisms under modified environmental regimes (lower grouping, Figure 4.1) and those factors that appear to decrease relative success in modified environments (upper grouping).

Discussion

Endemic fishes could be fairly well differentiated from widely-distributed species by smaller body size and specialized benthic or drift foraging habits (Table 4.3). Small size in fishes was noted by Burkhead et al. (1997) to be correlated with reduced reproductive potential. I found that body size was negatively related to fecundity (Spearman's r_s=0.73) and to the number of reproductive years (longevity minus years to maturity; r_s=0.80), supporting their observation. Contrary to the upper Midwest, where small fishes are reported to be r-selected (i.e., high fecundity, fast growing, short generation times; Parent and Schriml 1995), southeastern small fishes have low reproductive output. Also, many small southern species are benthic rather than pelagic. Burkhead et al. (1997) considered benthic orientation an important correlate of imperilment. The data support the view of small benthic fishes as particularly sensitive to siltation and potential contaminants in sediments (Etnier 1997).

The occurrence and abundance of life-history and ecological attributes were not distributed randomly among streams. Rather, they were associated with measures of habitat condition that reflected cumulative impacts due to catchment disturbance. Water quality and channel habitat in the Blue Ridge region are altered most where land use is most intense (Scott et al. in review). Highland endemics respond in a negative fashion to habitat alteration (Chapter 3), and results suggest that this is related to certain behavioral and life-history traits. Taxa with specialized spawning behaviors (i.e., taxa utilized rock crevice nests, buried eggs in gravel or attached them to stones) declined in association with disturbed habitats. Specialization in the use of trophic and physical habitat resources was another ecological characteristic negatively affected by disturbance. Angermeier (1995) argued that for ecological specialists even small shifts in environmental conditions may be enough to reduce habitat suitability or food availability to the detriment of the populations, whereas generalists simply shift their resource use to coincide with availability. Although the thermal classifications of taxa were not determined experimentally and thus were to some degree redundant with distribution classes, thermal preferenda/tolerance was related to habitat disturbance. This raises the possibility that some effects may be energetically-based. For example, it may be that highland fishes are more energetically efficient than lowland fishes at low temperatures in converting food to calories and in their metabolic activity. These observations, while speculative, provide testable hypotheses.

The historical approach to ecology first looks to phylogeny and vicariance for explanations of species distributions before considering present-day ecological interactions. For example, a species may be distributed as it is now not because it is specially adapted to a particular habitat or coevolved in a tightly interacting community, but because of vicariant events of history that determined the distribution of its ancestors.

Long-term studies of southern Appalachian streams have in fact concluded that the fish assemblages are regulated more by environmental factors than species interactions (Grossman et al. 1990, Freeman et al. 1988). Although highland endemic fishes were primarily in the families Percidae (darters) and Cyprinidae (minnows), family-level phylogeny was not a significant predictor of the distribution of species attributes across the landscape. Rather, the evidence suggests that highland endemic fishes possess behavioral and life-history adaptations to indigenous habitat features. Irrespective of familial lineage, small fishes with low reproductive output and specialized ecologies decline under disturbed catchment conditions and altered stream habitats whereas fishes with more generalized requirements thrive. Other research has also linked fish distributions to the environmental regimes in which they evolved (Matthews and Hill 1980; Matthews 1987; Fausch et al. 2001).

Patterns of faunal decline are not isolated, random phenomena, but embedded in a larger context of environmental change (Angermeier 1995; Burkhead et al. 1997; McKinney 1997). Habitat conditions prior to extensive modification by humans formed the habitat template on which life-history and behavioral strategies were forged (Southwood 1977). Over evolutionary timescales, southern Blue Ridge watersheds featured heterogeneous topography and densely forested landscapes; the associated stream habitat template included coarse sediments and cool to cold water with low concentrations of dissolved ions and nutrients, with food webs supported by allochthonous inputs (Wallace et al. 1992). Given the level of adaptation to these environments exhibited by highland endemic fishes, I suggest these habitat conditions were the norm over evolutionary time (since at least the Tertiary). Aided by explosive population growth and modern technology (Angermeier 2000), humans in North America over the last several hundred years have pursued extensive development and rapid conversion of indigenous land cover to various uses. Species respond to the types of habitat change engendered by humans in ways that reflect their biogeographic history and adaptations, a process that produces clear losers (imperiled taxa) and winners (invasives) (McKinney and Lockwood 2001). Widespread, lowland-adapted fishes appear to find the increased fine sediments, nutrient concentrations, and temperature suitable habitat whereas the highland endemics do not. My observations lend strong support to an emerging view that ascribes the catastrophic loss of aquatic biodiversity and ecosystem integrity in North America and elsewhere to extensive, pervasive habitat degradation (Warren et al. 1997, 2000; Richter et al. 1997; Scott and Helfman 2001).

The concept of ecological integrity (Karr 1991) hinges on accurate identification of a reference condition. This simply means an ecosystem has not been modified by human technology from the geophysical and evolutionary patterns and processes historically present at that particular locale. Obviously, this concept is problematic in many locations because of the long-term intensive influence of humans. The natural condition in some areas is a past unknown state; the ecosystem has since coevolved with human influence (e.g., western Europe). I argue that the presence of localized endemic species, where they still occur, is a powerful indicator of ecosystem integrity. Their loss has been documented repeatedly in the conservation literature, and may constitute the main route to extinction, biological simplification, and homogenization of formerly unique regions of the planet (McKinney 1997; McKinney and Lockwood 2001; Marchetti et al. 2001; Scott and Helfman 2001).

Avenues of research needing immediate attention include identification of mechanisms linking non-point source, cumulative impacts to population decline, and quantification of environmental stressor-biotic response relationships. The relationships I observed between behavioral and life-history attributes and cumulative impacts, although they do not establish cause-effect, do provide some specific hypotheses amenable to manipulative experiments. Erosion and sedimentation, hydrologic disruption, nutrient enrichment, thermal and chemical pollution are some of the processes that potentially cause negative effects. But little information exists on levels or concentrations at which ecological effects are manifested in native biota (but see Burkhead and Jelks 2001), much less how these effects interact in streams. Little is known about the form of functional responses to these impacts (e.g., are they linear, exponential, thresholds?).

While the threats to aquatic ecosystems are profound, all hope is by no means lost. The majority of streams in my data set, although not pristine, have little detectable loss in the richness, structure, and organization of the fish assemblages. Action now to develop science-based ecosystem management strategies can help promote a sustainable society (Meyer and Helfman 1993). The evidence presented here and elsewhere suggests that cumulative impacts could be reduced by maintenance of forested stream buffers throughout the catchment, thereby mitigating a primary threat to the ecological integrity of aquatic systems in forested landscapes (Peterjohn and Correll 1984; Rabeni and Smale 1995; Jones et al. 1999; Crosbie and Chow-Fraser 1999; Scott et al. in review). Efforts should include enactment of sound policies protecting riparian zones, and watershed–based programs to educate landowners about the importance of stream-side protection and the value of native biodiversity and endemic species.

Acknowledgments

I thank G. Helfman, M. Freeman, J. Meyer, C. Pringle, and for comments on an earlier draft, P. Bolstad for sharing geographic data, S. Rathbun for advice on statistical methods, and D. Jones, M. McTammany, N. Gardiner, D. Toole, B. Farmer, J. Harper, K. Schofield, B. Staub, A. Sutherland, H. Russell, and P. Marcinek for assistance in data collection. This research was supported by National Science Foundation grant DEB-9632854 to the University of Georgia Coweeta Long Term Ecological Research Program. Data reported here are available at the following url: http://sparc.ecology.uga.edu/webdocs/

Literature Cited

Allan, J.D., and A.S. Flecker. 1993. Biodiversity conservation in running waters. BioScience 43(1):32-43.

Angermeier, P.L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. Conserv. Biol. 9:143-158.

Angermeier, P.L. 2000. The natural imperative for biological conservation. Conserv. Biol. 14:373-381.

Berkman, H.E., and C.F. Rabeni. 1987. Effects of siltation on stream fish communities. Environ. Biol. of Fishes 18:285-294.

Brooks, D.R., and D.A. McLennan. 1991. Phylogeny, ecology, and behavior: a research program in comparative biology. University of Chicago Press, Chicago.

Brooks, D.R., R.L. Mayden, and D.A. McLennan. 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. Trends in Ecology and Evolution 7(2):55-59.

Burkhead, N.M., S.J. Walsh, B.J. Freeman, and J.D. Williams. 1997. Status and restoration of the Etowah River, an imperiled southern Appalachian ecosystem. pp. 375-444 *in* G.W. Benz and D.E. Collins, eds. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.

Burkhead, N.M., and H.L. Jelks. 2001. Effects of suspended sediment on the reproductive success of the tricolor shiner, a crevice-spawning minnow. Trans. Amer. Fish. Soc. 130:959–968.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Austral. J. Ecol. 18:117-143.

Crosbie, B., and P. Chow-Fraser. 1999. Percentage Land Use in the Watershed Determines the Water and Sediment Quality of 22 Marshes in the Great Lakes Basin. Canadian Journal of Fisheries and Aquatic Sciences 56:1781-1791.

Deacon, J.E., G. Kobetich, J.D. Williams, and S. Contreras. 1979. Fishes of North America endangered, threatened, or of specieal concern: 1979. Fisheries 4(2):30-44.

Etnier, D.A., and W.C. Starnes. 1993. The fishes of Tennessee. University of Tennessee Press, Knoxville.

Etnier, D.A. 1997. Jeopardized southeastern freshwater fishes: a search for causes. Pp. 86-104 *in* G.W. Benz and D.E. Collins, eds. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.

Fausch, K.D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11:1438-1455.

Freeman, M.C., M.K.Crawford, J.C. Barrett, D.E. Facey, M.G. Flood, J. Hill, D.J. Stouder, G.D. Grossman. 1988. Fish assemblage stability in a southern Appalachian stream. Can. J. Fish. Aquat. Sci. 45:1949-1958.

Frissell, C.A. 1993. Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (USA). Conserv. Biol. 7:342-354.

Grossman, G.D., J.F. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes: a review. Environ. Manage. 14:661-671.
Harding, J.S., E.F. Benfield, P.V. Bolstad, G.S. Helfman, and E.B.D. Jones III. 1998. Stream biodiversity: The ghost of land use past. Proc. Natl. Acad. Sci. 95:14843-14847.

Jenkins, R.E., and N.M. Burkhead. 1994. The fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

Johnston, C.E. 1999. The relationship of spawning mode to conservation of North American minnows (Cyprinidae). Environmental Biology of Fishes 55:21-30.

Jones, E.B.D, III, G.S. Helfman, J.O. Harper, and P.V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conserv. Biol. 13:1454-1465.

Karr, J.R. 1991. Biological integrity: a long-neglected aspect of water resource management. Ecol. Appl. 1:66-84.

LeBlanc, R.T., R.D. Brown, and J.E. FitzGibbon. 1997. Modeling the effects of land use change on the water temperature of unregulated urban streams. J. Environ. Manage. 49(4):445-469.

Marchetti, M. P., T. Light, J. Felicano, T. Armstrong, Z. Hogan, and P. B. Moyle. 2001. Homogenization of California's fish fauna through abiotic change. Pp. 259-278 *in* J. L. Lockwood and M. L. McKinney, eds. Biological homogenization. Kluwer Plenum/Academic Press, New York.

Matthews, W.J. 1987. Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. pp. 111-120 *in* W.J. Matthews and D.C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Matthews, W.J., and L.G. Hill. 1980. Habitat partitioning in the fish community of a southwestern river. Southwest. Nat. 25:51-66.

Mayden, R.L. 1987. Historical ecology and North American highland fishes: a research program in community ecology. pp. 203-222 *in* W.J. Matthews and D.C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Mayden, R.L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. Syst. Zool. 37:329-355.

McCune, B., and M.J. Mefford. 1997. PC-ORD. Multivariate analysis of ecological data, Ver. 3.0. MjM Software Design, Gleneden Beach, Oregon.

McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495-516.

McKinney, M.L., and J.L. Lockwood. 2001. Biotic homogenization: a sequential and selective process. Pp. 1-17 *in* J.L. Lockwood and M.L.McKinney, eds. Biotic homogenization. Kluwer Plenum/Academic Press, New York.

Meyer, J.L., and G.S. Helfman. 1993. The ecological basis of sustainability. Ecol. Appl. 3: 569-571.

Moyle, P.B., and R.A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. pp. 127-169 in P.L. Fiedler and S.K. Jain, eds. Conservation biology: the theory and practice of nature conservation, preservation and management. Chapman and Hall, New York.

Parent, S., and L.M. Schriml. 1995. A model for the determination of fish species at risk based upon life-history traits and ecological data. Can. J. Fish. Aquat. Sci. 52:1768-1781.

Peterjohn, W.T., and D.L. Correll. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. Ecology 65:1466-1475.

Rabeni, C.F., and M.A. Smale. 1995. Effects of siltation on stream fishes and the potential mitigating role of the buffering riparian zone. Hydrobiologia 303:211-219.

Ricciardi, A., and J.B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conserv. Biol. 13:1220-1222.

Richards, C., R.J. Haro, L.B. Johnson, and G.E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshw. Biol. 37:219-230.

Richter, B.D., D.P. Braun, M.A. Mendelson, and L.L. Master. 1997. Threats to imperiled freshwater fauna. Conserv. Biol. 11:1081-1093.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics 6:461-464.

Scott, M.C., G.S. Helfman, M. McTammany, E.F. Benfield, and P.V. Bolstad. In review. Spatial and temporal influences on stream physicochemistry across southern Blue Ridge landscapes. Journal of the American Water Resources Association.

Scott, M.C., and G.S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26(11):6-15.

Simon, T.P., ed. 1999. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry : the principles and practice of statistics in biological research. Freeman, New York.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46:337-365.

Wallace, J.B., J.R. Webster, and R.L. Lowe. 1992. High-gradient streams of the Appalachians. pp. 133-191 *in* Hackney, C.T., S.M. Adams, and W.H. Martin, eds. Biodiversity of the southeastern United States: Aquatic communities. John Wiley & Sons, New York.

Warren, M.L. Jr., and B.M. Burr. 1994. Status of freshwater fishes of the United States: Overview of an imperiled fauna. Fisheries 19(1):6-17.

Warren, M.L. Jr., P.L. Angermeier, B.M. Burr and W.R. Haag. 1997. Decline of a diverse fish fauna: patterns of imperilment and protection in the southeastern United States. pp. 105-164 *in* G.W. Benz and D.E. Collins, eds. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.

Warren, M.L. Jr., B.M. Burr, S.J. Walsh, H.L. Bart Jr., R.C. Cashner, D.A. Etnier, B.J. Freeman, B.R. Kuhajda, R.L. Mayden, H.W. Robison, S.T. Ross, and W.C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25(10):7-31.

Wear, D.N., and P. Bolstad. 1998. Land-use change in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States: assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. BioScience 48(8):607-615.

Williams, J.E., J.E. Johnson, D.A. Hendrickson, S. Contreras-Balderas, J.D. Williams, M. Navarro-Mendoza, D.E. McAllister, and J.E. Deacon. 1989. Fishes of North America endangered, threatened, or of specieal concern: 1989. Fisheries 14(6):2-20.

Winemiller, K.O., and K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49:2196-2219.

Table 4.1. Resource-use classifications of spawning behavior, fecundity, trophic ecology, habitat use, and thermal tolerance attributes. Codes are used to assign species to each class for statistical analyses (Table 4.2).

Family	*Distribution*
1 – Petromyzontidae	1 – Endemic to Appalachian highlands
2 – Cyprinidae	2 – restricted to uplands
3 – Catastomidae	3 – occur in lowlands
4 – Ictaluridae	4 – cosmopolitan
5 – Salmonidae	
6 – Poeciliidae	
7 – Cottidae	
8 – Centrarchidae	
9 – Percidae	

Reproductive Ecology

Spawning Behavior	*Fecundity*
1 - Bury eggs in gravel or attach to rocks – no care	1 - less than 100 ova
2 - Rock crevice nest guarder	2 - 100-300
3 - Eggs hidden in prepared gravel/pebbles – no care	3 - 300-1,000
4 - Broadcast over substrate – pelagic embryos	4 - 1,000-10,000
5 - Guard nest depressions or holes, attach eggs to plants, or viviparous	5 – greater than 10,000

Trophic Ecology

Trophic Class	*Foraging Habitat*	*Trophic Breadth*
1 - Detritivore	1 - Benthic	1 - Specialist
2 - Herbivore	2 - Water column	2 - Narrow
3 – General invertivore	3 - Benthic/midwater/surface	3 - Broad
4 - Carnivore/Piscivore		4 - Omnivore
5 – Invertivore: Drift		
6 – Invertivore: Benthic		

Habitat Use and Thermal

Habitat Type	*Waterbody size*	*Habitat Breadth*	*Thermal Tolerance*
1 - Riffle	1 – Creek	1 - Specialist	1 – Cold (trout)
2 - Run-Pool	2 - Stream	2 - Intermediate	2 - Cool
3 - Riffle-Pool	3 – River	3 - Broad	3 - Cool-warm
	4 - Lake		4 - Warm
			5 - Eurythermal

Table 4.2. Life-history and ecological attributes of upper Tennessee River fish taxa collected. Classes and codes are defined in Table 4.1.

Species	Family	Distribution	Max. body size-cm	age-at-maturity	longevity-yrs	Spawning Class	Fecundity class	Trophic Class	Foraging Habitat	Trophic Breadth	Habitat Type	Water Body Size	Habitat Breadth	Thermal Tolerance
Ambloplites rupestris	8	3	25	3	8	5	4	3	3	3	2	2	1	4
Ameiurus melas	4	4	42	2	9	5	4	3	1	4	2	3	3	5
Ameiurus natalis	4	4	46	2	7	5	4	3	1	4	2	3	2	5
Campostoma anomalum	2	3	28	3	6	3	4	4	1	1	3	2	2	4
Carassius auratus	2	4	50	2	7	5	5	2	1	4	2	3	2	5
Catostomus commersoni	3	3	40	3	15	4	5	1	1	3	2	1	1	3
Clinostomus funduloides ssp.	2	1	11	1	4	3	3	5	2	1	2	1	1	2
Cottus bairdi ssp.	7	1	11	2	6	2	1	6	1	1	3	1	1	2
Cyprinella galactura	2	2	15	2	4	3	4	2	3	2	2	2	2	4
Erimystax insignis eristigma	2	1	10	1	3	1	4	2	1	2	1	2	2	4
Etheostoma blennioides gutselli	9	1	13	1	5	1	4	6	1	1	1	2	1	2
Etheostoma chlorobranchium	9	1	11	1	4	1	*2	6	1	1	1	2	1	2
Etheostoma flabellare ssp.	9	1	9.5	1	5	2	2	6	1	1	1	2	2	3
Etheostoma rufilineatum	9	1	9	1	4	1	1	6	1	1	3	2	1	3
Etheostoma swannanoa	9	1	10	1	4	1	*1	6	1	1	3	2	2	2
Etheostoma vulneratum	9	1	8	2	4	2	1	6	1	1	1	2	1	3
Etheostoma zonale	9	3	8	1	4	1	2	6	1	1	1	2	1	4
Gambusia affinis	6	4	6	0	2	5	3	2	3	2	2	3	3	5
Hybopsis amblops	2	3	9	1	*3	1	*2	6	3	1	2	2	2	4
Hypentelium nigricans	3	3	45	3	10	1	*5	6	1	3	3	2	2	4
Ichthyomyzon greeleyi	1	3	16	4	6	3	?	1	1	3	3	2	2	3
Lepomis auritus	8	4	20	2	8	5	4	2	3	2	2	3	3	5
Lepomis cyanellus	8	4	20	1	7	5	4	2	3	2	2	3	3	5
Lepomis gibbosus	8	4	25	1	8	5	4	2	3	2	2	3	3	5
Lepomis gulosus	8	4	23	1	8	5	5	2	3	2	2	3	3	5
Lepomis macrochirus	8	4	22	1	6	5	5	2	3	2	2	3	3	5
Luxilus coccogenis	2	1	13	2	4	3	3	5	2	1	2	2	1	3
Micropterus dolomieu	8	3	50	3	11	5	5	3	3	3	2	3	3	4
Micropterus salmoides	8	4	55	2	12	5	5	3	3	3	2	3	2	5
Moxostoma duquesnei	3	3	43	2	10	1	4	6	1	2	2	2	1	3

Species	Family	Distribution	Max. body size-cm	age-at-maturity	longevity-yrs	Spawning Class	Fecundity class	Trophic Class	Foraging Habitat	Trophic Breadth	Habitat Type	Water Body Size	Habitat Breadth	Thermal Tolerance
Moxostoma erythrurum	3	3	50	3	11	1	5	6	1	2	2	3	2	4
Nocomis micropogon	2	3	28	2	5	3	3	3	3	3	3	2	2	4
Notemigonus crysoleucas	2	4	23	1	8	5	5	2	2	2	2	3	2	5
Notropis leuciodus	2	1	8	1	*4	3	*4	5	2	1	2	2	2	3
Notropis lutipinnis	2	3	8	1	*4	*3	*3	*5	2	1	2	1	1	4
Notropis photogenis	2	3	14	1	3	*4	*4	5	3	2	2	2	1	4
Notropis rubricroceus	2	1	8	1	5	3	3	5	3	2	2	1	1	2
Notropis spectrunculus	2	1	7	1	*3	*1	*3	5	2	2	2	1	1	2
Notropis telescopus	2	2	8	*1	3	*4	*4	2	2	1	2	2	2	3
Oncorhynchus mykiss	5	2	45	1	7	3	4	3	3	3	2	3	3	1
Perca flavescens	9	4	26	2	8	5	5	3	3	3	2	3	3	3
Percina evides ssp.	9	1	8	1	4	1	2	6	1	1	1	2	1	3
Percina squamata	9	1	13	*1	4	1	*3	6	1	1	1	2	1	2
Phenacobius crassilabrum	2	1	11	1	3	3	?	6	1	2	1	2	1	2
Rhinichthys atratulus obtusus	2	3	9	2	4	4	3	2	3	3	3	1	1	4
Rhinichthys cataractae	2	2	13	2	5	4	4	6	1	2	1	2	1	2
Salmo trutta	5	2	55	2	9	3	4	3	3	3	2	3	2	1
Salvelinus fontinalis	5	2	40	2	4	3	4	3	3	3	2	1	1	1
Semotilus atromaculatus	2	3	30	1	7	3	4	3	3	4	2	1	1	4

* Information from surrogate species as follows: *E. acuticeps* for *E. chlorobranchium*; *E. blennius* for *E. swannanoa*; *H. amnis* or *H. lineapunctata* for *H. amblops*; *Moxostoma* spp. for *Hypentelium*; other members of *Notropis* subgenus *Hydrophlox* for *N. leuciodus* and *N. lutipinnis*; *N. atherinoides* for *N. photogenis*; *N. volucellus* for *N. spectrunculus*; *N. scabriceps* for *N. telescopus*; *P. phoxocephala* for *P. squamata*.

Table 4.3. Summary of multiple logistic regression models to estimate probability of endemism in a taxon collected in the upper Tennessee River system. Sixteen endemic and 27 widespread taxa were included in the analysis.

Number of Predictors	*Variable*	*Parameter Estimate*[a]	*Model Chi-square*	*df*	*Concordance of Predicted/Observed*	*BIC*
1	Intercept	8.16	17.3*	1	84.3%	42.5
	Body Size	-3.29				
2	Intercept	12.75	24.0*	2	94.0%	35.8
	Body Size	-3.81				
	Foraging Habitat	-1.89				
3	Intercept	9.07	25.9*	3	94.7%	36.7
	Body Size	-3.50				
	Foraging Habitat	-1.64				
	Trophic Class	0.55				
4	Intercept	10.61	26.0*	4	95.1%	39.9
	Body Size	-3.47				
	Foraging Habitat	-1.64				
	Trophic Class	0.44				
	Habitat Breadth	-0.71				

[a] Parameters are maximum likelihood estimates.
* Significant model at *P*=0.0001.

Table 4.4. Summary of multiple linear regression models predicting abundance of fishes possessing life-history and ecological attributes as dependent variables using abiotic variables. Parameter *t*-statistics with absolute values greater than 2.0 indicate significant individual predictors. Asterisk denotes significance at alpha=0.05/28=0.0018 level.

Dependent Variable	Independent Variables	Parameter Estimate	Parameter *t*-statistic	Model *F*-statistic (5, 30 *df*)	Model r^2
Highland Endemic	Riparian Land-Use Index	-0.4384	-3.395	9.803*	0.62
	NO_3-N	-0.1333	-0.556		
	Turbidity	-0.0106	-1.049		
	Coarse Substrate	0.3236	0.948		
	Max. 7-day mean temperature	0.0602	1.834		
Lowland/ cosmopolitan distribution	Riparian Land-Use Index	0.3741	3.371	14.51*	0.71
	NO_3-N	0.0523	0.254		
	Turbidity	0.0015	0.168		
	Coarse Substrate	-0.5385	-1.836		
	Max. 7-day mean temperature	0.0147	0.521		
Large-bodied (30+ cm)	Riparian Land-Use Index	0.0981	1.907	3.76	0.39
	NO_3-N	0.0893	0.935		
	Turbidity	0.0025	0.628		
	Coarse Substrate	0.0434	0.319		
	Max. 7-day mean temperature	-0.0357	-2.730		
Small-bodied (<15 cm)	Riparian Land-Use Index	-0.2243	-2.545	6.76*	0.53
	NO_3-N	-0.0383	-0.234		
	Turbidity	0.0021	0.300		
	Coarse Substrate	0.1743	0.748		
	Max. 7-day mean temperature	-0.0182	-0.812		
Late-maturing (>3yr)	Riparian Land-Use Index	0.1202	1.434	3.89	0.39
	NO_3-N	0.0163	0.105		
	Turbidity	0.0036	0.557		
	Coarse Substrate	-0.2834	-1.279		
	Max. 7-day mean temperature	0.0007	0.033		

Table 4.4. Continued.

Dependent Variable	Independent Variables	Parameter Estimate	Parameter *t*-statistic	Model *F*-statistic (5, 30 *df)*	Model r^2
Early-maturing (1 yr or less)	Riparian Land-Use Index	0.0222	0.304	11.86*	0.66
	NO_3-N	-0.0274	-0.201		
	Turbidity	-0.0073	-1.285		
	Coarse Substrate	0.5791	2.992		
	Max. 7-day mean temperature	0.1343	7.217		
Long-lived (>7yr)	Riparian Land-Use Index	0.2515	3.768	8.05*	0.57
	NO_3-N	0.0579	0.468		
	Turbidity	-0.0006	-0.117		
	Coarse Substrate	0.0220	0.125		
	Max. 7-day mean temperature	-0.0278	-1.640		
Short-lived (<5yr)	Riparian Land-Use Index	-0.0820	-0.980	17.42*	0.74
	NO_3-N	0.2181	1.405		
	Turbidity	-0.0165	-2.530		
	Coarse Substrate	0.3400	1.537		
	Max. 7-day mean temperature	0.1715	8.063		
Highly fecund (>10k ova)	Riparian Land-Use Index	0.1160	2.763	8.28*	0.58
	NO_3-N	0.0566	0.726		
	Turbidity	0.0012	0.351		
	Coarse Substrate	-0.0776	-0.699		
	Max. 7-day mean temperature	-0.0004	-0.040		
Low fecundity (<2k ova)	Riparian Land-Use Index	-0.3292	-2.843	4.25	0.41
	NO_3-N	0.0460	0.214		
	Turbidity	-0.0100	-1.106		
	Coarse Substrate	0.0215	0.070		
	Max. 7-day mean temperature	0.0679	2.308		
Spawn Class 1	Riparian Land-Use Index	-0.0774	-1.040	4.77	0.44
	NO_3-N	0.0078	0.056		
	Turbidity	-0.0002	-0.035		
	Coarse Substrate	0.0670	0.341		
	Max. 7-day mean temperature	0.0709	3.753		

Table 4.4. Continued.

Dependent Variable	Independent Variables	Parameter Estimate	Parameter *t*-statistic	Model *F*-statistic (5, 30 *df)*	Model r^2
Spawn Class 2	Riparian Land-Use Index	-0.0774	-2.361	8.13*	0.58
	NO_3-N	-0.0078	-0.731		
	Turbidity	0.0002	0.917		
	Coarse Substrate	-0.0670	-1.172		
	Max. 7-day mean temperature	-0.0709	-3.460		
Spawn Class 3	Riparian Land-Use Index	0.0510	0.632	9.38*	0.61
	NO_3-N	-0.0015	-0.010		
	Turbidity	-0.0149	-2.357		
	Coarse Substrate	0.2063	0.967		
	Max. 7-day mean temperature	0.1250	6.095		
Spawn Class 4	Riparian Land-Use Index	0.1925	2.225	7.79*	0.56
	NO_3-N	0.2444	1.522		
	Turbidity	0.0110	1.632		
	Coarse Substrate	-0.0471	-0.206		
	Max. 7-day mean temperature	-0.0928	-4.223		
Spawn Class 5	Riparian Land-Use Index	0.0753	1.815	4.89	0.45
	NO_3-N	0.0196	0.254		
	Turbidity	-0.0041	-1.259		
	Coarse Substrate	-0.1137	-1.036		
	Max. 7-day mean temperature	0.0108	1.023		
Detrivitore	Riparian Land-Use Index	0.0470	1.451	3.92	0.40
	NO_3-N	0.0641	1.066		
	Turbidity	-0.0048	-1.915		
	Coarse Substrate	-0.0335	-0.391		
	Max. 7-day mean temperature	0.0073	0.888		
General Invertivore	Riparian Land-Use Index	0.1312	2.217	18.59*	0.76
	NO_3-N	0.3096	2.819		
	Turbidity	-0.0011	-0.227		
	Coarse Substrate	-0.2343	-1.498		
	Max. 7-day mean temperature	0.0079	0.523		

Table 4.4. Continued.

Dependent Variable	Independent Variables	Parameter Estimate	Parameter *t*-statistic	Model *F*-statistic (5, 30 *df)*	Model r^2
Carnivore	Riparian Land-Use Index	0.1205	1.759	1.66	0.22
	NO_3-N	-0.0253	-0.199		
	Turbidity	-0.0048	-0.892		
	Coarse Substrate	0.0648	0.358		
	Max. 7-day mean temperature	0.0162	0.930		
Drift-feeding invertivore	Riparian Land-Use Index	-0.1822	-1.926	11.08*	0.65
	NO_3-N	-0.0337	-0.192		
	Turbidity	-0.0246	-3.329		
	Coarse Substrate	0.3665	1.466		
	Max. 7-day mean temperature	0.1628	6.771		
Benthic-feeding invertivore	Riparian Land-Use Index	-0.2102	-2.278	15.79*	0.72
	NO_3-N	-0.1413	-0.825		
	Turbidity	0.0207	2.874		
	Coarse Substrate	-0.0411	-0.169		
	Max. 7-day mean temperature	-0.1286	-5.485		
Trophic specialist	Riparian Land-Use Index	-0.2908	-2.610	5.94*	0.50
	NO_3-N	-0.1389	-0.672		
	Turbidity	-0.0035	-0.400		
	Coarse Substrate	0.1774	0.602		
	Max. 7-day mean temperature	0.0354	1.251		
Trophic generalist	Riparian Land-Use Index	0.2857	2.761	7.11*	0.54
	NO_3-N	0.1308	0.681		
	Turbidity	-0.0035	-0.117		
	Coarse Substrate	-0.1774	-0.685		
	Max. 7-day mean temperature	-0.0354	-0.387		
Habitat generalist	Riparian Land-Use Index	0.0778	1.580	3.78	0.39
	NO_3-N	0.0434	0.475		
	Turbidity	-0.0040	-1.042		
	Coarse Substrate	0.0536	0.412		
	Max. 7-day mean temperature	-0.0289	-2.309		

Table 4.4. Continued.

Dependent Variable	Independent Variables	Parameter Estimate	Parameter *t*-statistic	Model *F*-statistic (5, 30 *df*)	Model r^2
Habitat specialist	Riparian Land-Use Index	-0.0371	-0.357	6.35*	0.51
	NO_3-N	-0.0732	-0.379		
	Turbidity	-0.0069	-0.848		
	Coarse Substrate	-0.1762	-0.641		
	Max. 7-day mean temperature	-0.0880	-3.330		
Coldwater fishes (trout)	Riparian Land-Use Index	-0.0172	-0.459	11.01*	0.65
	NO_3-N	0.0348	0.502		
	Turbidity	0.0002	0.076		
	Coarse Substrate	0.0797	0.808		
	Max. 7-day mean temperature	-0.0458	-4.822		
Coolwater fishes	Riparian Land-Use Index	-0.2257	-2.729	29.6*	0.83
	NO_3-N	-0.3009	-1.961		
	Turbidity	0.0128	1.981		
	Coarse Substrate	-0.1023	-0.468		
	Max. 7-day mean temperature	-0.1380	-6.566		
Cool-warm tolerant	Riparian Land-Use Index	-0.1168	-1.514	19.9*	0.77
	NO_3-N	0.0653	0.456		
	Turbidity	-0.0164	-2.718		
	Coarse Substrate	0.6024	2.955		
	Max. 7-day mean temperature	0.1825	9.310		
Thermally-tolerant fishes (eurytherms)	Riparian Land-Use Index	0.0875	2.129	5.4*	0.47
	NO_3-N	0.0095	0.124		
	Turbidity	-0.0045	-1.405		
	Coarse Substrate	-0.1213	-1.117		
	Max. 7-day mean temperature	0.0069	0.660		

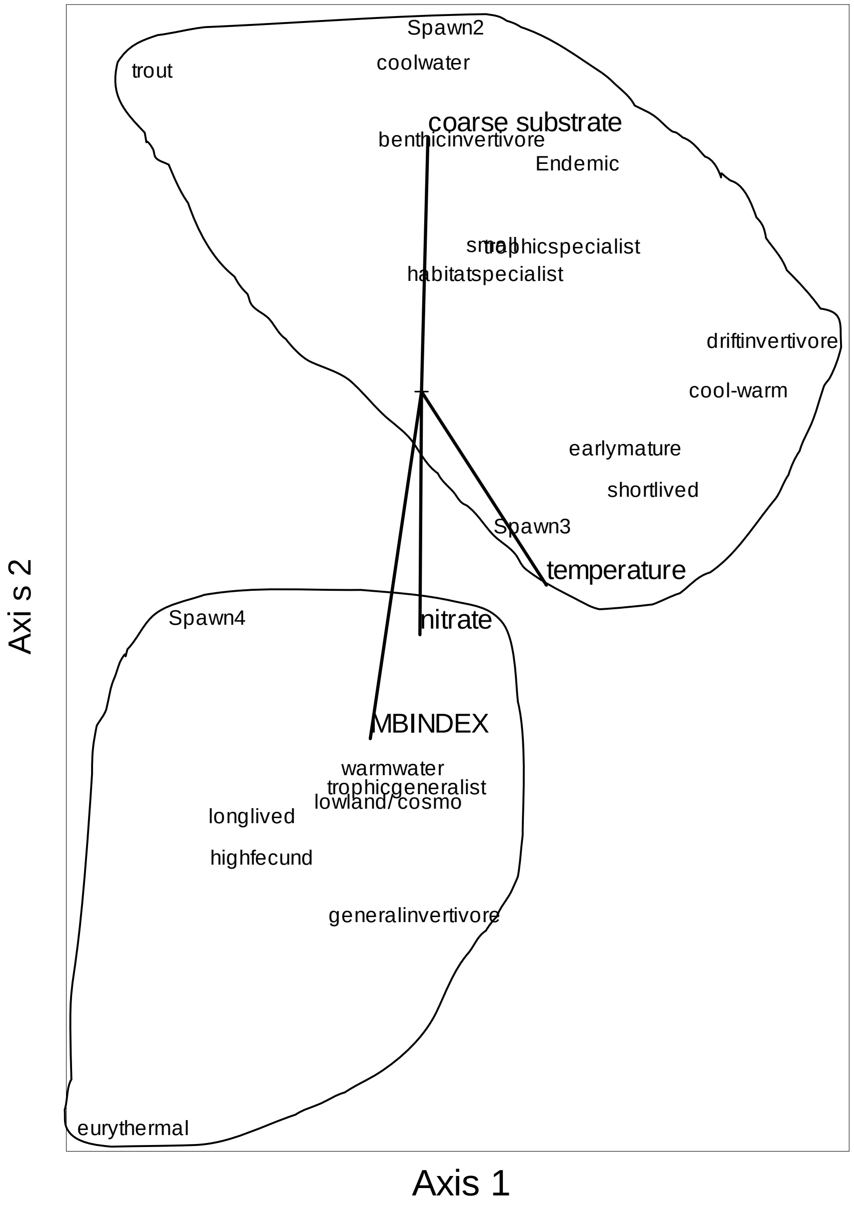

Figure 4.1. Plot of life-history and ecological attributes according to their weighted-average scores on the first two dimensions of an ordination by non-metric multidimensional scaling. Environmental vectors represent correlations of the abiotic variables with ordination axes (MBINDEX is an index reflecting intensity of riparian land use).

CHAPTER 5

LAND COVER CHANGE AND SPECIES COMPOSITION OF FISHES IN SOUTHERN BLUE RIDGE STREAMS OVER 40 YEARS[1]

---

[1] Scott, M. C. To be submitted to *Southeastern Naturalist*

Abstract—Biological homogenization is the loss of unique biotic elements and their replacement with common widespread ones. Potential trends of homogenization were assessed in southern Appalachian fish faunas by an examination of historical collections, available from museum records, made from the 1930s to the 1960s in the same streams that were sampled again in the 1990s. Species turnover and differences in ratio of endemic highland species (e.g., certain darters and minnows) to widely distributed species (e.g., sunfishes) were analyzed to identify relationships with forest cover change in the catchments since the 1950s. A significant positive correlation was observed between forest cover and the number of endemic species relative to widespread taxa. The 1990s ratio of endemic to widespread species was more closely related to 1970s land cover than to 1990s land cover, suggesting that contemporary faunal composition remains influenced by the legacy of past landscape conditions. No significant relationship was observed between species turnover and land cover change. Overall, the pre-1970 ratio of endemics to widespread taxa was not significantly different from the 1990s ratio, suggesting that there had been no general replacement of endemics over the period. Although comparisons of past and recent fish collections are complicated by methodological differences, the data indicate that composition of fishes responds to a complex of factors involving landscape change, riparian buffer condition, and aquatic habitat. Streams that drained urbanizing catchments had lower endemic to widespread taxa ratios even though riparian buffers were largely forested, suggesting that urbanization has more negative impacts on stream biota than other types of land uses. Research is needed to identify possible thresholds of response to land use change, and to

quantify the catchment versus riparian forest cover levels necessary to avoid negative impacts on native fishes and their habitats.

Introduction

Native freshwater fish faunas of southeastern North America are highly diverse, largely because of an abundance of endemic forms (Warren and Burr 1994). The highlands of the Southeast have not been glaciated as have areas to the north nor inundated by rising seas as have areas to the south. This ancient fauna has a lush and unique history of speciation, particularly within the families Percidae and Cyprinidae. Trends of decline in the rich fauna of the southern Appalachians have sparked concerns over loss of the irreplaceable evolutionary heritage represented by biological diversity at scales from genes to landscapes (Brooks et al. 1992, Angermeier and Schlosser 1995, Burkhead et al. 1997, Warren et al. 2000).

Fishes that evolved in specific areas often show specialized behaviors, ecologies, and/or physiologies adaptive to the environmental regimes of their native regions (Matthews 1987, Fausch et al. 2001, Chapter 4). Specialization is a liability when habitat alterations due to hydrologic change and pollution create a set of new selective pressures that operate on populations; species with more generalized requirements often find the new conditions more suitable (Scott and Helfman 2001). Through this non-random process of substitution and replacement, the fauna becomes homogenized as unique local communities disappear and widespread species that can tolerate human activities take their place (McKinney and Lockwood 2001). The need to identify vulnerable taxa before they are in precipitous decline is a high priority for proactive conservation (Angermeier and Karr 1994), as is early recognition of threats to habitats and species (Moyle and Leidy 1992, Warren and Burr 1994).

One way to assess faunal trends is with historical information. Collections made over the years by ichthyologists and accessioned into museum archives are valuable sources of information about assemblges in the past. Comparisons of past and present conditions can provide insights about long-term status and trends in biological communities. I examined data from historical fish collections made 35-70 y ago in the same streams sampled again during a recent investigation (Chapter 3) for evidence of temporal trends in species composition. Changes in species composition were assessed with respect to land cover change within stream catchments. I attempted to address the following questions: Is turnover in species composition related to land cover change? Is biotic homogenization, measured as the ratio of endemic highland species to widely-distributed species, detectable over time? Is the current (1990s) ratio of endemic to widespread fishes related to forest cover or cover change?

Methods

Data were collected during 1995-1998 in the French Broad and Little Tennessee river drainages of western North Carolina as part of a larger effort within the Coweeta Long Term Ecological Research program to examine the consequences of land cover change in the southern Blue Ridge physiographic region. Stream fishes were sampled with seines and electrofishing gear four times at each of 36 streams (see Chapter 3 for detailed description of collection methods). Land cover data within study stream catchments were assembled in a GIS as part of that LTER effort (P. Bolstad, unpublished data). They are reported here as proportion of forest cover in stream catchments from three separate time periods: 1950’s, 1970s, and 1990’s. The 1950’s data were developed by cover typing aerial photos and then digitizing them. A 5 ha minimum mapping unit was used to accommodate the scale of the photos. The digitized data were then corrected for tilt and relief displacement using the single photo resection technique, edited for accuracy, and then attributed. Land cover data from the 1950s were not available for all catchments. The 1970’s data were developed from Landsat Multi-Spectral Scanner (MSS) scenes classified using supervised maximum likelihood classification techniques in Erdas Imagine 8.2. Multiple MSS scenes were classified individually and mosaiced together to produce the final product with a resolution of 60 m. The 1990’s data were obtained through the Southern Appalachian Assessment initiative (Hermann 1996), which includes land cover from 1993 Thematic Mapper imagery at a resolution of 30 m. A measure of land cover change was calculated by subtracting proportion of catchment in forest cover at earlier periods from those at later periods; hence positive values indicated increased forest cover and negative values loss of forest over time.

Museum records were searched via the World Wide Web to locate historical fish collections in the study streams. Two institutions with records from the study area permitted access to their museum records over the Internet: Cornell University (http://www.cumv.cornell.edu/) and University of Michigan (http://ummz1.ummz.lsa.umich.edu/ummzindex.html). Records were retrieved by county and descriptions were examined for stream name and collection location. Historical collections that appeared to be within approximately 10 km of existing study sites were retained for analysis; more than half (13 of 22) of historical collection sites were within 1 km of LTER sites. Species names were in some cases updated, and in the case of

Etheostoma chlorobranchium greenfin darter, specimens collected prior to 1972 were identified as *E. camurum* bluebreast darter (Zorach 1972).

Two primary obstacles exist when comparing past with contemporary collections: uncertainty about sampling effort and the natural fluctuations in fish assemblage composition and structure through time. Although fish assemblage structure may be highly variable over decadal time scales, presence or absence of species may be less variable than species abundance (Matthews 1998, Patton et al. 1998). To avoid the potentially greater variability associated with abundance data, I restricted the analysis to species composition.

Data Analysis—Compositional changes were quantified using a measure of species turnover, T_s, that was developed to measure spatial turnover (Russell 1999, modified by Duncan and Lockwood 2001); here it was used to measure changes in species in a stream over time:

$$T_s = (H_s + C_s) / \alpha$$

where H_s is the number of species unique to the historical collection, C_s is the number of species unique to the contemporary collection, and α is the total number of species collected in the stream. Hence T_s is a proportional measure of change in species composition, with values of 0 indicating identical species composition among samples, and values of 1 indicating complete turnover of species. Land cover data from the 1950s were not available for all catchments; therefore species turnover was obtained by combining all collections in a stream prior to 1970 and calculating change through the 1990s collections. The relationship between turnover and land cover change over 1970s-

1990s was assessed using the distribution-free Spearman correlation coefficient (r_s), which can be used when relationships are potentially non-linear (Sokal and Rohlf 1995).

The list of species (Table 5.1) was compiled based on descriptions in Mayden (1987). Endemic highland species and subspecies endemic to the upper Tennessee River system or the Blue Ridge Mountains were included (Warren et al. 2000). The list of species with broader geographic distributions (Table 5.1) was also compiled based on Mayden's (1987) discussion of highland fishes and supplemented with information in Warren et al. (2000). The ratio of endemic to widespread fish taxa (E/W) was compared in paired historical (pre-1970s) and contemporary (1990s) collections in all streams using the Wilcoxon signed-ranks test, a non-parametric alternative to the paired t-test (Sokal and Rohlf 1995). The relationship of change in E/W between pre-1970s and 1990 with land cover change over the 20-y period was assessed using r_s. The relationships between 1990s E/W and forest cover in 1970 and forest cover in 1990 was also assessed using r_s.

Results

Twenty-two collections at 16 historical sites made from 1934 to 1968 were identified from museum records as taking place on the same stream and within 10 km of where collections were made in the 1990s (Table 5.2) . Stream size and elevation of historical sites, two important variables influencing fish composition (Chapter 3), did not differ appreciably from LTER sites on the same stream. Where multiple collections were taken over time, they were combined according to the time frames of land cover data: pre-1950, 1950-1970, and 1990s (Table 5.3) .

Forest cover in the 15 study catchments was generally extensive, ranging from 69% to nearly 100% (Table 5.3) . Most catchments changed little over the 40 year period, with net changes generally showing reforestation over time. In the three catchments that changed the most over 1970s-1990s, 1950s data were not available. The bulk of forest recovery in these areas apparently took place recently, judging from the magnitude of change since the 1970s (Table 5.3) .

Species richness in the study streams ranged from 8 to 32 species (Table 5.4). The lowest and highest richness occurred, respectively, at the highest elevation stream (Nantahala River, 981 m asl) and the largest stream (Swannanoa River, drainage 321 km^2). At 14 out of 16 streams, more unique species were collected in the 1990s collection period than in historical collections. Over all sites, one species (pumpkinseed, non-indigenous to the Tennessee River system) was collected prior to 1970 that was absent in the 1990s collections. The following species were collected in the 1990s but not before 1970: goldfish, golden shiner, yellowfin shiner, black bullhead, yellow bullhead, brown trout, green sunfish, wounded darter, and banded darter. Creek chub was collected at 50% of sites in the 1990s, but at only 1 site (6% of sites) in historical collections. Turnover in assemblage composition ranged from 0.40 to 0.75 (Table 5.4). No significant relationship was found between turnover in species composition and land cover change over the period 1970-1990 (r_s=0.45, P=0.09).

Numbers of endemic highland species and geographically widespread species were tallied for each stream and collection period (Table 5.5). When the ratio of endemic to widespread species (E/W) at streams historically (pre-1970) was compared to E/W from 1990s collections, there was no significant difference (P=0.72, Table 5.5), indicating an overall lack of temporal trend. A similar result was obtained when the number of endemic species was analyzed instead of the ratio. Historical collections in two streams (Cane Creek and Swannanoa River) were made prior to 1950 and just prior to 1970, corresponding well to the chronology of land cover data. Both of these streams were less forested historically relative to the majority of study streams. Unfortunately, 1950s land cover data was not available for the Swannanoa River. Nonetheless, it is apparent the E/W did not closely track the trajectory of forest cover change over time in these streams (Fig. 5.1). If anything, E/W decreased in the two streams with catchment forest recovery, contrary to expectation.

The change in E/W from historical to contemporary collections did not correlate significantly with land cover change from 1970 to 1990 (r_s=0.03, P>0.05), and a similar result obtained for change in number of endemics species instead of the ratio. Forest cover in the 1990s was correlated with 1990s E/W (r_s=0.52, P=0.03), but 1970s forest cover yielded a stronger correlation with 1990s E/W (r_s=0.83, P<0.001; Fig. 5.2). I determined whether the relationship of E/W with historical forest cover would hold in the larger LTER data set (n=35, one site contained no widespread species so no ratio could be calculated) and observed a significant positive relationship in these data as well (r_s=0.67, P<0.001; Fig. 5.2). The seemingly disparate results, in which no change in E/W was observed through time yet contemporary E/W was primarily related to historical catchment conditions, suggested more complex interactions.

The complexity is apparent in the non-linearity of the relationship (Figure 5.3) and raised the question of why streams that were largely deforested in the 1970s would have higher E/W in the 1990s. An examination of riparian forest cover within a 100 m stream buffer may provide some clarification (see Ch. 1 for details on riparian buffer measures). Table 5.6 lists riparian forest cover for two groups of streams with 1970s catchment cover less than 65%: those streams with E/W of 0.5 or greater and those with E/W less than 0.5. Riparian buffers of the four streams with higher E/W were at least 70% forested at the two measurement periods, indicating some measure of stream-side protection. In contrast 6 out of 10 of the riparian zones of streams with low E/W were less than 60% forested in both the 1970s and 1990s (Table 5.6). Of the four low-E/W streams with greater riparian cover, two of those catchments were more than 90% deforested in 1970 (Scott Cr. and Jonathan Cr.), suggesting that faunal recovery may take longer after impacts of greater magnitude. The remaining two streams, Beaverdam Cr., Asheville and Richland Cr., Waynesville, respectively ranked 5th and 6th among the 36 LTER streams in terms of building and road density in the 100 m riparian buffer, reflecting their urban settings. The assemblage of Beaverdam Cr. may also be influenced by migrants from a nearby pond.

Discussion

Intensive land uses (logging, agriculture, urban/suburban development) cumulatively impact aquatic ecosystems by affecting physical and chemical conditions (Brooks and Brierly 1997, LeBlanc et al. 1997, Herlihy et al. 1998, Basnyat et al. 1999, Crosbie and Chow-Fraser 1999, Davies et al. 2000). Hence, intensive land uses have negative consequences for aquatic biodiversity via their effects on habitat quality (Richards and Host 1994, Roth et al. 1996, Allan et al. 1997, Jones et al. 1999, Lammert and Allan 1999). Previous studies have been able to identify extirpated or declining fish species using historical data (Miller et al. 1989, Williams et al. 1989, Weaver and Garman 1994, Patton et al. 1998). Biotic homogenization, defined as loss of specialized or endemic species and their replacement by widely-distributed and generalized taxa, is a process that has been reported to result from habitat alteration in eastern highland fish faunas (Duncan and Lockwood 2001, Scott and Helfman 2001). I observed no general pattern of decline in highland endemic fishes over the latter part of the 20th century, based on the presence-absence data used. Although some endemic fishes collected historically in certain streams were not collected in those streams during the 1990s, all endemic fishes collected prior to 1970 were found in the 1990s, therefore overall no extirpation was obserrved.

One endemic fish was collected in the 1990s but not in the earlier collections (*Etheostoma vulneratum* wounded darter). Moreover, richness was generally higher in the 1990s collections (Table 5.4). If additional species were in fact added to the fauna over the intervening decades, an examination of their identity with respect to the homogenization hypothesis is worthwhile. Of the nine fishes collected in the 1990s but not historically, one-third were nonnative to the Tennessee River drainage (goldfish, yellowfin shiner, brown trout; Lee et al. 1980). All but one of the others have broad geographic ranges (Table 5.1). Hence, 8 of 9 fishes appearing recently in the fauna are either exotic to the drainage or are considered widely distributed. These observations are consistent with the view presented by Scott and Helfman (2001) that widespread species pose an invasion threat to highland systems.

Forests in the southern Blue Ridge region generally underwent significant regeneration during the 20th century as the extent of small-scale agriculture diminished (Wear and Bolstad 1998). I found that contemporary ratios of endemic to widespread fishes were positively related to catchment forest cover, and that this relationship was stronger with 1970s cover than 1990s cover. The central question at issue: do fish faunas recover with restoration of forest cover? The evidence suggests that recovery depends on several factors including the severity of past catchment disturbance, the condition of riparian buffers, and degree of urban development. Wang et al. (2000) reported that urban development degraded fish communities in Wisconsin to a greater extent than other land uses. As noted above, several stream catchments with low endemic to widespread taxa ratios had gained forest over time but also underwent urban/suburban development, which may preclude recovery of aquatic habitat. Furthermore, ecological recovery from non-point source impacts may be hampered by the magnitude or severity of earlier influences. Where catchments were over 90% deforested in the past, reforestation was not associated with higher E/W, suggesting a threshold beyond which faunal recovery is delayed or perhaps even prevented. There is evidence to suggest that riparian buffers maintained largely in forest may have played a mitigative role. Streams in which at least 70% of the riparian zone was forested had higher E/W than streams with less than 70%, with a few exceptions likely related to urbanization as noted above. Other long-term impacts to aquatic systems may be unrelated to forest cover, such as effects of dams or point sources of pollutants. Research is needed to identify possible thresholds of response to land cover, and to quantify the levels of catchment versus riparian forest cover necessary to avoid negative impacts on native fishes and their habitats (Roth et al. 1996, Jones et al. 1999).

Legacy effects of past land use on aquatic biota have been reported in the southern Appalachians (Harding et al. 1998). In an analysis of some of the same streams I have reported on here, Harding et al. (1998) noted that diversity of benthic invertebrates and fishes was lower in catchments that had been in agricultural use in the 1950s, regardless of forest recovery since, and suggested that effects of large-scale land use impacts on aquatic communities may persist for many decades. Although elevation is the dominant influence on fish species richness and diversity in the Blue Ridge (Chapter 3), present-day ratios of endemic to widespread taxa were indeed related less to contemporary forest cover than to past cover. Measures of sedimentation are better explained by past catchment conditions than current conditions (Chapter 1), therefore persistent biotic changes are likely tied to this persistent type of habitat alteration. Catchment conditions are important, as noted by Harding et al. (1998), but the evidence presented here suggests that the history of riparian conditions can be an important modifier of catchment influences.

Some caveats regarding the use of these data must be discussed. While the historical approach has the potential to detect temporal trends, uncertainties about equal effort in biological sampling complicate comparisons through time unless historical methods and locations are closely matched by subsequent sampling. Consequently, firm conclusions are problematic because of questions about the comparability of historical and recent collection efforts and the rather small sample size (n=16).

Summary

Faunal changes in response to landscape modification are difficult to document because of complex histories and spatial mosaics of land cover. Although temporal trends in land cover were not related to either turnover in species composition or the ratio of endemic to widespread fishes, the ratio was strongly related to forest cover in the 1970s, suggesting a legacy effect of past catchment disturbance. The composition of fishes as reflected in ratios of endemic highland to widespread fishes appeared to respond to a complex of factors involving to landscape reforestation, riparian buffer condition, urbanization, and aquatic habitat. Ecological recovery from the legacy of past land uses and abuses may be a long-term process, but evidence suggests that maintenance of some minimum amount of protective forest cover in catchments and riparian zones will do much to preserve the unique aquatic ecosystems of the southern Appalachians.

Acknowledgments

I thank G. Helfman, M. Freeman, C. Pringle, and J. Meyer for comments on an earlier draft, S. Rathbun for advice on statistical methods, and B. Farmer, N. Gardiner, J. Harper, D. Jones, S. Kornberg, P. Marcinek, K. Schofield, B. Staub, A. Sutherland, H. Russell, and D. Toole for assistance in data collection. This research was supported by National Science Foundation grant DEB-9632854 to the University of Georgia Coweeta Long Term Ecological Research Program. Data reported here are available at the following url: http://sparc.ecology.uga.edu/webdocs/

Literature Cited

Allan, J.D., D.L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biol. 37:149-161.

Angermeier, P.L., and I.J. Schlosser. 1995. Conserving aquatic biodiversity: beyond species and populations. American Fisheries Society Symposium 17:402-414.

Basnyat, P., L.D. Teeter, K.M. Flynn, B.G. Lockaby. 1999. Relationships between landscape characteristics and nonpoint source pollution inputs to coastal estuaries. Environ. Manage. 23:539-549.

Brooks, D.R., R.L. Mayden, and D.A. McLennan. 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. Trends in Ecology and Evolution 7(2):55-59.

Brooks, A.P., and G.J. Brierley. 1997. Geomorphic responses of lower Bega river to catchment disturbance, 1851-1926. Geomorphology 18:291-304.

Burkhead, N.M., S.J. Walsh, B.J. Freeman, and J.D. Williams. 1997. Status and restoration of the Etowah River, an imperiled southern Appalachian ecosystem. pp. 375-444 *in* G.W. Benz and D.E. Collins, eds. Aquatic fauna in peril: the Southeastern perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, Georgia.

Crosbie, B. and P. Chow-Fraser. 1999. Percentage land use in the watershed determines the water and sediment quality of 22 marshes in the great lakes basin. Canadian Journal of Fisheries and Aquatic Sciences 56:1781-1791.

Davies, N.M., R.H. Norris, and M.C. Thoms. 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics. Freshw. Biol. 45:343-369.

Duncan, J.R., and J.L. Lockwood. 2001. Spatial homogenization of the aquatic fauna of Tennessee: extinction and invasion following land use change and habitat alteration. Pp. 245-258 *in* J.L. Lockwood and M.L.McKinney, eds. Biotic homogenization. Kluwer Plenum/Academic Press, New York.

Fausch, K.D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11:1438-1455.

Harding, J.S., E.F. Benfield, P.V. Bolstad, G.S. Helfman, and E.B.D. Jones III. 1998. Stream biodiversity: The ghost of land use past. Proc. Natl. Acad. Sci. 95:14843-14847.

Herlihy, A.T., J.L. Stoddard, and C.B. Johnson. 1998. The relationship between stream chemistry and watershed land cover data in the mid-Atlantic region, U.S. Water, Air, and Soil Pollution 105:377-386.

Hermann, K.A. 1996. The Southern Appalachian assessment GIS data base CD ROM set. Southern Appalachian Man and the Biosphere Program, Norris, Tennessee.

Jones, E.B.D, III, G.S. Helfman, J.O. Harper, and P.V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conserv. Biol. 13:1454-1465.

Lammert, M. and J.D. Allan. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ. Manage. 23:257-270.

LeBlanc, R.T., R.D. Brown, and J.E. FitzGibbon. 1997. Modeling the effects of land use change on the water temperature of unregulated urban streams. J. Environ. Manage. 49(4):445-469.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. North Carolina Biological Survey, North Carolina State Museum of Natural History, Publication Number 1980-12.

Matthews, W.J. 1987. Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. pp. 111-120 *in* W.J. Matthews and D.C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman & Hall, New York.

Mayden, R.L. 1987. Historical ecology and North American highland fishes: a research program in community ecology. pp. 203-222 *in* W.J. Matthews and D.C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

McKinney, M.L. and J.L. Lockwood. 2001. Biotic homogenization: a sequential and selective process. Pp. 1-17 *in* J.L. Lockwood and M.L.McKinney, eds. Biotic homogenization. Kluwer Plenum/Academic Press, New York.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fish during the past century. Fisheries 14(6):22-38.

Moyle, P.B., and R.A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. pp. 127-169 in P.L. Fiedler and S.K. Jain, eds. Conservation biology: the theory and practice of nature conservation, preservation and management. Chapman and Hall, New York.

Patton, T.M., F.J. Rahel, and W.A. Hubert. 1998. Using historical data to assess changes in Wyoming’s fish fauna. Conservation Biology 12:1120-1128.

Richards, C. and G.E. Host. 1994. Examining land use influences on stream habitats and macroinvertebrates: a GIS approach. Water Resources Bulletin 30:729-738.

Roth, N.E., J.D. Allan, and D.L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecol. 11:141-156.

Russell, G.J. 1999. Turnover dynamics across ecological and geological scales. In M.L. McKinney and J.A. Drake, eds. Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia University Press, New York.

Scott, M.C., and G.S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26(11):6-15.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry : the principles and practice of statistics in biological research. Freeman, New York.

Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22:6-12.

Warren, M.L. Jr., and B.M. Burr. 1994. Status of freshwater fishes of the United States: Overview of an imperiled fauna. Fisheries 19(1):6-17.

Warren, M.L. Jr., B.M. Burr, S.J. Walsh, H.L. Bart Jr., R.C. Cashner, D.A. Etnier, B.J. Freeman, B.R. Kuhajda, R.L. Mayden, H.W. Robison, S.T. Ross, and W.C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25(10):7-31.

Wear, D.N., and P. Bolstad. 1998. Land-use change in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Weaver, L.A., and G.C. Garman. 1994. Urbanization of a watershed and historical changes in a stream fish assemblage. Trans. Amer. Fish. Soc. 123:162-172.

Williams, J.E., J.E. Johnson, D.A. Hendrickson, S. Contreras-Balderas, J.D. Williams, M. Navarro-Mendoza, D.E. McAllister, and J.E. Deacon. 1989. Fishes of North America endangered, threatened, or of specieal concern: 1989. Fisheries 14(6):2-20.

Zorach, T. 1972. Systematics of the percid fishes, *Etheostoma camurum* and *E. chlorobranchium* new species, with a discussion of the subgenus *Nothonotus*. Copeia 1972:427-447.

Table 5.1. Endemic, highland fishes and fishes distributed more widely across North America collected in 3rd to 5th order streams of the Little Tennessee and French Broad river basins (from Scott and Helfman 2001). Designations are based on Mayden (1987) and Warren et al. (2000).

Highland Endemic Species

CYPRINIDAE

*Clinostomus funduloide*s ssp., smoky dace
Erimystax insignis eristigma, mountain blotched chub
Luxilus coccogenis, warpaint shiner
N. rubricroceus, saffron shiner
Phenacobius crassilabrum, fatlips minnow
Notropis leuciodus, Tennessee shiner
N. spectrunculus, mirror shiner

SALMONIDAE

Salvelinus fontinalis, brook trout

COTTIDAE

*Cottus bairdi*ssp., smoky sculpin

PERCIDAE

Etheostoma blennioides gutselli, Tuckasegee darter
E. chlorobranchium, greenfin darter
E. swannanoa, Swannanoa darter
*Percina evide*s ssp., Appalachian gilt darter
P. squamata, olive darter
E. rufilineatum, redline darter
E. vulneratum, wounded darter

Widely Distributed Species

CYPRINIDAE

Hybopsis amblops, bigeye chub
Notemigonus crysoleucas, golden shiner
Notropis photogenis, silver shiner
Rhinichthys atratulus, blacknose dace
Nocomis micropogon, river chub
Notropis lutipinnis, yellowfin shiner
Carassius auratus, goldfish
Semotilus atromaculatus, creek chub

CATOSTOMIDAE

Catostomus commersoni, white sucker
Hypentelium nigricans, northern hog sucker
Moxostoma duquesnei, black redhorse
M. erythrurum, golden redhorse

ICTALURIDAE

Ameiurus melas, black bullhead
A. natalis, yellow bullhead

POECILIIDAE

Gambusia affinis, western mosquitofish

CENTRARCHIDAE

Ambloplites rupestris, rock bass
Lepomis cyanellus, green sunfish
Micropterus salmoides, largemouth bass
Lepomis auritus, redbreast sunfish
L. macrochirus, bluegill sunfish

PERCIDAE

Etheostoma zonale, banded darter
Perca flavescens, yellow perch

Table 5.2. Historical collection information obtained from ichthyology records at Cornell and University of Michigan museums. Location of collection site in relation to LTER sampling locations is also presented.

Collection Number	Year	Collector	Stream and Location
ADH40-17	1940	Holloway	Coweeta Creek approx. same location as LTER site
CLH36-3	1936	Hubbs	Oconuluftee R. 1 km upstream of LTER site
CLHM37-934	1937	Hubbs	Oconuluftee R. 0.5 km downstream of of LTER site
CLHM40-229	1940	Hubbs	Richland Cr. 4.5 km upstream of LTER site
CLHM40-230	1940	Hubbs	Scott Cr. 0.5 km upstream of LTER site
JRB47-1	1947	Bailey	Davidson R. <0.5 km downstream of LTER site
JRB47-126	1947	Bailey	Little Tennessee R. 8 km downstream of LTER site
JRB47-142	1947	Bailey	Cartoogechaye Cr. < 0.5 km downstream of LTER site
JRB47-154	1947	Bailey	Nantahala R. 5 km downstream of LTER site
JRB47-158	1947	Bailey	Jones Cr. <0.5 km downstream of LTER site
JRB47-164	1947	Bailey	Scott Cr. 1 km upstream of LTER site
TZ196	1968	Zorach	Cullasaja R. 4 km upstream of LTER site
JRB47-63	1947	Bailey	Ivy Cr. 8 km downstream of LTER site
JRB47-65	1947	Bailey	Big Laurel Cr. 0.5 km downstream of LTER site
LMO52-17	1952	Outten	Little Ivy Cr. within 1 km of LTER site
LMO53-18	1953	Outten	Little Ivy Cr. within 1 km of LTER site
RVM-162	1962	Miller	Jonathan Cr. 8 km downstream of LTER site
JRB47-19	1947	Bailey	Cane Cr. approx. same location as LTER site
RFD67-153	1967	Denoncourt	Cane Cr. approx. same location as LTER site
RMB34-26	1934	Bailey	Swannanoa R. 8 km upstream of LTER site
ECR0727	1940	Raney	Swannanoa R. 10 km upstream of LTER site
RFD67-95	1967	Denoncourt	Swannanoa Cr. 10 km upstream of LTER site

Table 5.3. Proportion of forest cover in each stream catchment and cover change over 40 years.

Stream	Catchment Forest cover 1993	Change in proportion of catchment forested		
		1950-1970	1970-1993	1950-1993
Cartoogechaye Cr.	0.890	0.026	0.074	0.100
Davidson R.	0.989	-0.007	0.001	-0.006
Big Laurel Cr.	0.922	0.225	-0.024	0.201
Coweeta Cr.	0.978	0.030	0.030	0.061
Cullasaja R.	0.963	0.056	0.019	0.075
Nantahala R.	0.996	-0.008	0.016	0.009
Ocunaluftee R.	0.997	0.010	-0.001	0.009
Big Ivy Cr.	0.893	0.056	0.054	0.110
Little Ivy Cr.	0.732	0.238	0.008	0.246
Jones Cr.	0.951	0.067	0.061	0.128
Little Tennessee R.	0.872	0.027	0.061	0.088
Cane Cr.	0.693	0.053	0.022	0.074
Jonathan Cr.	0.902	N/A	0.829	N/A
Richland Cr.	0.806	N/A	0.646	N/A
Scott Cr.	0.921	N/A	0.825	N/A
Swannanoa R.	0.825	N/A	0.615	N/A

Table 5.4. Historical collections either prior to 1950 or during 1950-1970 are compared to recent collections. Number of species unique to a given sampling period for each stream, total species richness from all collections, and proportional turnover in species composition (Ts) between sampling periods are listed.

	Number of Species Unique to Time Period			Total Richness	Turnover Ts
Stream	prior to 1950	1950-1970	1990s		
Cartoogechaye Cr.	1	-	10	17	0.65
Davidson R.	3	-	6	17	0.53
Big Laurel Cr.	1	-	5	15	0.40
Coweeta Cr.	0	-	17	23	0.74
Cullasaja R.	-	0	12	21	0.57
Nantahala R.	3	-	3	8	0.75
Ocunaluftee R.	8	-	2	19	0.53
Big Ivy Cr.	2	-	9	20	0.55
Little Ivy Cr.	-	0	9	20	0.45
Jones Cr.	0	-	13	23	0.57
Little Tennessee R.	3	-	16	27	0.70
Jonathan Cr.	-	3	3	11	0.55
Richland Cr.	0	-	9	13	0.69
Scott Cr.	0	-	10	15	0.67
		prior to 1950	1990s		
Cane Cr.		6	5	27	0.41
Swannanoa R.		8	9	32	0.53

Table 5.5. Number of endemic highland (E) and widespread (W) species occurring in historical and recent collections.

Stream	prior to 1950		1950-1970		1990s	
	E	W	E	W	E	W
Cartoogechaye Cr.	5	1	-	-	7	7
Davidson R.	4	5	-	-	6	5
Big Laurel Cr.	5	4	-	-	7	3
Coweeta Cr.	2	3	-	-	9	10
Cullasaja R.	-	-	4	4	9	8
Nantahala R.	1	4	-	-	1	1
Ocunaluftee R.	8	6	-	-	5	3
Big Ivy Cr.	2	8	-	-	8	6
Little Ivy Cr.	-	-	5	5	8	9
Jones Cr.	5	4	-	-	9	14
Little Tennessee R.	6	5	-	-	9	11
Jonathan Cr.	-	-	1	5	1	4
Richland Cr.	0	3	-	-	0	8
Scott Cr.	1	2	-	-	3	8
Cane Cr.	11	8	9	5	9	11
Swannanoa R.	9	9	5	5	8	13

Wilcoxon signed-ranks test of the hypothesis that pre-1970s and 1990s ratios of E/W are equal: *W*=14.0, *P*=0.72.

Table 5.6. For streams in which less than 65% of the catchment was forested in the 1970s (from the LTER data set of 36 sites), the extent of forest in the riparian buffer (100 m) at two time periods is shown. Streams are separated into two groups: those with an endemic to widespread fishes ratio (E/W) of 0.5 or greater and those with an E/W less than 0.5. Streams with higher E/W had greater forest cover in riparian zones over time, except for streams that were in urban areas or severely disturbed in the past.

1970s riparian forest cover	1990s riparian forest cover
Streams with E/W of 0.5 or greater	
0.80	0.84
0.94	0.93
0.73	0.74
0.70	0.87
Streams with E/W less than 0.5	
0.73 [a]	0.68
0.46	0.59
0.26	0.21
0.76 [a]	0.79
0.35	0.37
0.85 [b]	0.81
0.43	0.43
0.27	0.42
0.83 [b]	0.86
0.46	0.42

[a] urbanized

[b] catchment >90% deforested in 1970

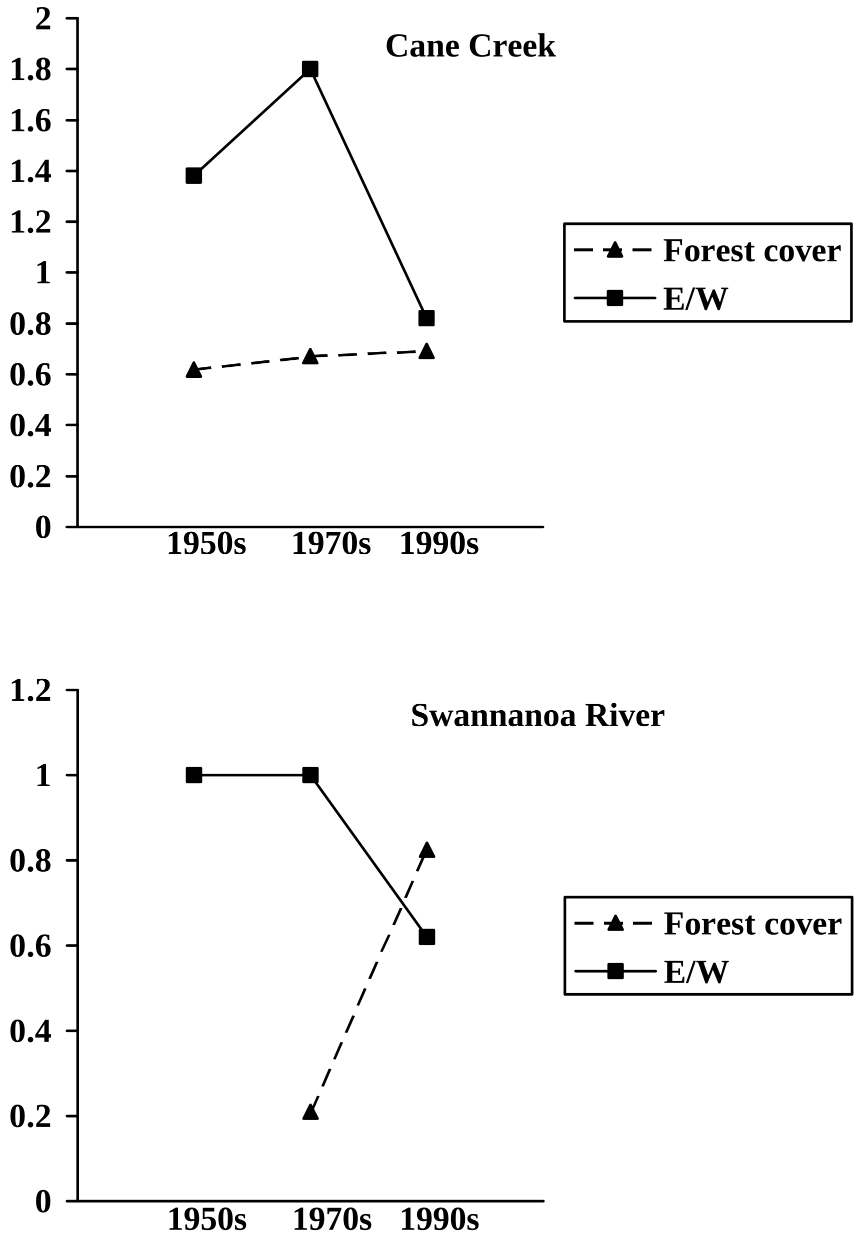

Figure 5.1. Trajectory of the proportion of forest cover at different times in the latter 20th century in two stream catchments, and ratio of endemic highland fish species to widely distributed species present in collections made in the streams before 1950, 1950-1970, and during the 1990s.

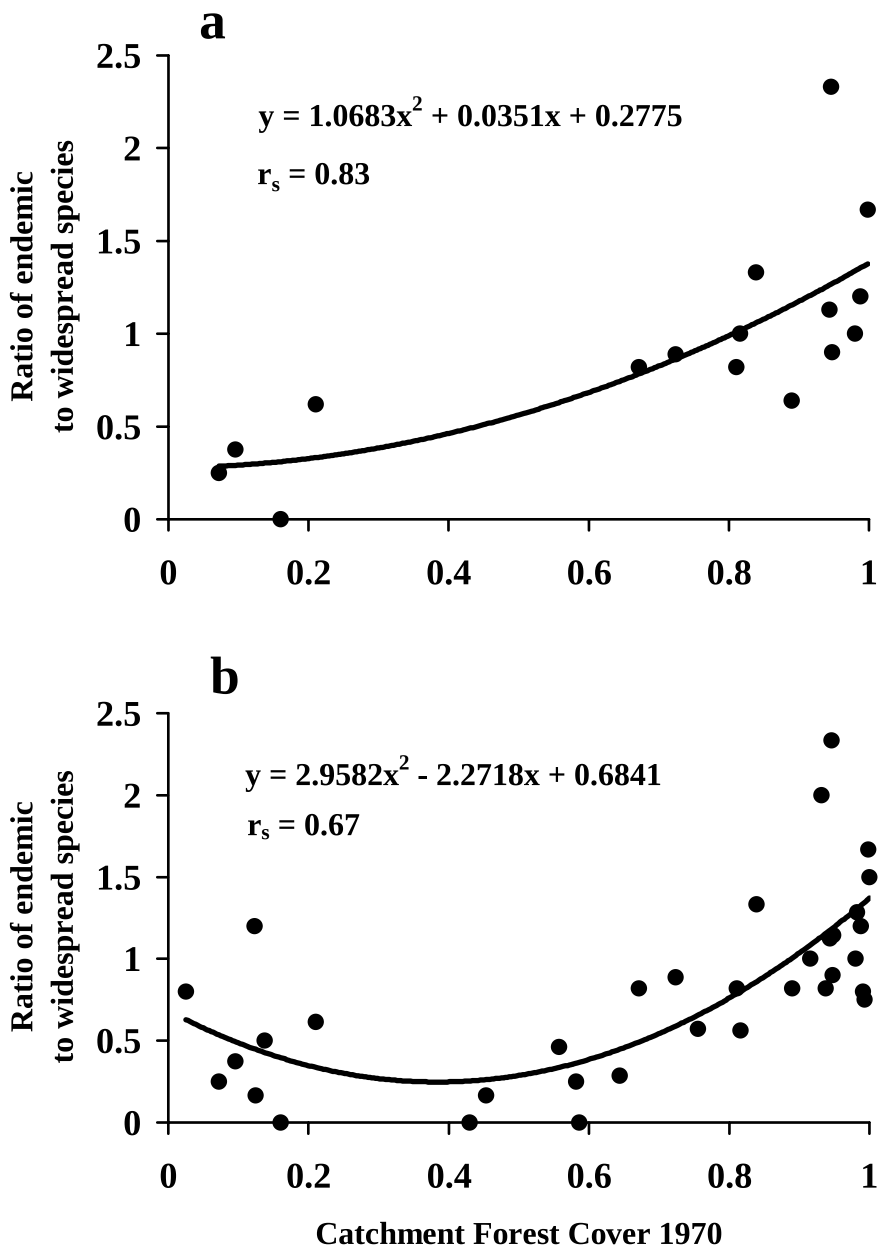

Figure 5.2. Relationship of the ratio of endemic highland species to widely distributed species (1990s collections) with 1970s catchment forest cover; a) only the sixteen streams with historical collections are plotted; b) streams from the larger LTER data set are plotted (n=35).

CHAPTER 6

SUMMARY AND CONCLUSIONS

Understanding patterns in the distribution and abundance of freshwater fishes requires consideration of multiple scales (Frissell et al. 1986, Tonn et al. 1990, Matthews 1998). Rapidly declining ranges and population sizes of many native fishes have generated much concern about the future integrity of the North American freshwater fauna (Deacon et al. 1979, Williams et al. 1989, Moyle and Leidy 1992, Warren and Burr 1994, Ricciardi and Rasmussen 1999, Warren et al. 2000), and habitat loss due to the cumulative impacts of non-point sources has been implicated as a serious and pervasive threat to aquatic ecosystems (Allan and Flecker 1993, Warren and Burr 1994). Models that integrate stream ecosystems with their landscape context are needed for conservation of biological diversity and effective management of aquatic resources. One such model (Fig. 1.1) proved useful for investigating influences on fish assemblage structure and organization in upper Tennessee River tributaries draining the Blue Ridge physiographic region. Primary ecological patterns among streams within the region were related to topography and land cover. Topographic variation across the landscape, as indicated by elevational differences among sites, was a strong predictor of stream temperature. A gradient in fish assemblage structure was identified that tracked the topographic variation among streams with less intensive land use; a relatively simple faunal association consisting largely of trout and an endemic sculpin inhabited the forested headwaters, and a more diverse association of minnows, suckers, and darters was found in valley rivers and streams. Broad-scale measures of forest cover, either throughout a drainage basin or in the riparian zone along the entire channel, accounted for significant amounts of variation among streams in a number of physicochemical variables. Nutrient concentrations and mean summer temperature were higher where forest cover was reduced, and the heterogeneity normally present among the coarse substrate particles was reduced by deposited fine sediment. An association of non-endemic fishes occurred under altered habitat conditions, indicating a loss of highland endemic taxa and their replacement by geographically widespread fishes where landscapes were more disturbed.

Certain behavioral and life-history traits were relatively more abundant in modified vs. unmodified habitats. Hence, habitat alteration associated with transformed landscapes appeared to select for autecologies of some taxa and against others. Small-bodied fishes with cool-water preferences and specialized resource use (trophic and habitat) declined in relative abundance at sites with greater intensity of land use. Small body size and specialized foraging habits were indicative of highland endemic fishes. In contrast, large-bodied fishes (positively correlated with longevity and fecundity) with warmwater preferences and more generalized resource use were relatively more abundant at disturbed locations. The decline of endemic fishes concomitant with the rise in more generalized and widespread fishes fits the pattern resulting from the process described as biotic homogenization (McKinney and Lockwood 2001). Many species are disappearing from former geographic ranges (Channel and Lomolino 2000) while species that are favored by ecological conditions associated with modern human-dominated ecosystems are expanding (Bright 1996). The erosion of regionally distinctive forms that define biogeographic regions amounts to continental- and global-scale simplification of natural biological communities.

Generalized model of environmental change and altered selection pressures

A generalized model of community structure change in response to habitat alteration can be constructed (Fig. 6.1). On the *y*-axis, fitness represents the rates of critical life-support functions such as growth and reproduction in populations of organisms occurring there. The *x*-axis represents the multidimensional environment (e.g., temperature, nutrient availability, spatial heterogeneity) that forms the habitat with which organisms interact. Ranges of conditions are specified along this axis rather than points because environmental conditions are dynamic over time and best considered as regimes. Over evolutionary time (many generations), environmental regimes have central tendencies and patterns of variability that exert selection pressures on populations (Fig. 6.1 a), although certainly these regimes naturally shift in response to broad-scale geophysical changes and may be punctuated by catastrophic disturbances. The position of the habitat suitability curves reflects the niche of each taxon and the shape of the curve indicates niche breadth. Southwood (1977) suggested that the habitat forms a template on which evolution forges organismal life-history strategies. A simplified biological community represented by three species illustrates this idea, as well as the hypothetical effects of altering the habitat (Fig. 6.1). In the top panel (a), Species A possesses adaptations highly suited for the local habitat, with the narrowness of the curve indicating specialization to that habitat. An example of this sort of relationship found in this study is *Etheostoma chlorobranchium* greenfin darter, restricted to Blue Ridge streams characterized by cool water, low nutrients, and coarse substrates (necessary for its eggburying mode of reproduction). Species B may be at the edge of its range or non-indigenous and thus finds the location marginally suitable, whereas Species C is more generalized in its habitat requirements. An example of Species B in this study is *Lepomis auritus* redbreast sunfish, native to Atlantic slope drainages and introduced to the Tennessee River drainage. An example of Species C is *Semotilus atromaculatus* creek chub, native to many physiographic regions in eastern North America including the Coastal Plain and Blue Ridge. Both species, if present, are minor components in the community where habitats are unaltered (Fig. 6.1 a). However, where landscape transformation or other environmental change has forced habitat conditions toward new regimes (e.g. temperature elevation, nutrient enrichment, sedimentation), Species A finds the new conditions unsuitable and fitness undergoes decline (Fig. 6.1 b). In contrast, the new conditions improve the suitability of the habitat for Species B and its fitness increases. Species C finds the new habitat equally suitable. Community structure shifts at this locale by reduction in population size or extirpation of Species A, gain in the population of Species B, while Species C maintains its fitness and population levels. Biological interactions such as predation, competition, or symbioses may also be affected by the habitat modifications and generate community changes as well.

New hypotheses and research needs

Particular hypotheses emerge from the results I have presented, as do several lines of questioning for future research on terrestrial-aquatic interactions. Resolution of these issues is necessary before cause-effect models can be developed to inform management and conservation efforts. The patterns I observed point to two main hypotheses about mechanisms responsible for ecological change, which may be testable via experimental manipulations:

(1) Erosion of disturbed uplands and sedimentation of streams fills in coarse channel substrates, reducing the spatial heterogeneity of the interstices found among stones, thus reducing foraging and reproductive success (Berkman and Rabeni 1987, Waters 1995, Jones et al. 1999), particularly for endemic highland fishes adapted to clear water and coarse substrates.

(2) Nutrient enrichment increases the energy available to organisms in nutrient-poor highland systems; when combined with increased solar radiation due to loss of shading, the trophic basis of production may shift from heterotrophy to autotrophy (Young and Huryn 1999). Highland fishes may be adapted to low-productivity environments (Vitousek 1994), and thus less successful than fishes with more cosmopolitan distributions as energy becomes more available.

Additional questions arising from this research include: What role does hydrological regime play in the interaction of terrestrial land cover with aquatic communities (Poff and Allan 1995)? Can independent effects of different land use classes be isolated, and if so what is the nature of the relationships? Are land-use effects dependent on their spatial arrangement on the landscape (e.g., near-stream *vs*. upslope, patchy *vs*. contiguous; Hunsaker and Levine 1995)? How important is hydrological connectivity (Pringle 2000) in providing refugia and recolonization routes as aquatic systems become fragmented? The processes at issue occur at catchment and landscape scales; therefore, although aspects of these questions can be addressed with small-scale experimental manipulations, localized experimental results should be compared and integrated with carefully designed sampling programs addressing problems at broader scales. Even though comparative studies cannot establish cause-and-effect, they can provide support for or against conceptual models. The hierarchical, nested structure of subcatchments, drainage basins, and river systems is exploitable as an organizational framework for research protocols and resource management programs (Lotspeich 1980, Frissell et al. 1986). Probabilistic sampling designs would allow statistically-valid estimation of stream responses to non-point source pollution based on remotely-sensed geographic data and past landuse information. The evidence presented here indicates that with a proper design, relationships such as those presented above could be used to draw regional inferences. Combination of geographical non-point source data with the location of point source inputs has the potential to be a comprehensive evaluation model for watersheds. Model implementation within a geographic information system could provide spatially-explicit predictions of water resource quality. Such a system would allow quantification of the likelihood and magnitude of effects generated by proposed developments and landuse plans. The increasing availability of high-resolution satellite imagery, together with sophisticated geographic information systems useful for organizing multiscale data, hold much promise as effective research tools for examining and hopefully answering many of these and other questions. Managing human activities for long-term sustainability will require scientific understanding of the ecological consequences of different land uses, and will require effective applications of that knowledge to inform policy and planning decisions.

Literature Cited

Allan, J.D., and A.S. Flecker. 1993. Biodiversity conservation in running waters. BioScience 43(1):32-43.

Berkman, H.E. and C.F. Rabeni. 1987. Effects of siltation on stream fish communities. Environ. Biol. of Fishes 18:285-294.

Bright, C. 1996. Understanding the threat of bioinvasions. Pp. 95-113 *in* L. Starke, ed. State of the World, 1996. W.W. Norton, New York.

Channel, R., and M.V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84-86.

Deacon, J.E., G. Kobetich, J.D. Williams, and S. Contreras. 1979. Fishes of North America endangered, threatened, or of specieal concern: 1979. Fisheries 4(2):30-44.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage. 10:199-214.

Hunsaker, C.T. and D.A. Levine. 1995. Hierarchical approaches to the study of water quality in rivers. BioScience 45:193-203.

Jones, E.B.D, III, G.S. Helfman, J.O. Harper, and P.V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conserv. Biol. 13:1454-1465.

Lotspeich, F.B. 1980. Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. Water Res. Bull. 16:581-586.

Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman & Hall, New York.

McKinney, M.L. and J.L. Lockwood. 2001. Biotic homogenization: a sequential and selective process. Pp. 1-17 *in* J.L. Lockwood and M.L.McKinney, eds. Biotic homogenization. Kluwer Plenum/Academic Press, New York.

Moyle, P.B., and R.A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. pp. 127-169 in P.L. Fiedler and S.K. Jain, eds. Conservation biology: the theory and practice of nature conservation, preservation and management. Chapman and Hall, New York.

Poff, N.L., and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. Ecology 76:606-627.

Pringle, C.M. 2000. Threats to U.S. public lands from cumulative hydrologic alterations outside of their boundaries. Ecol. Appl. 10: 971-989

Ricciardi, A., and J.B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conserv. Biol. 13:1220-1222.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46:337-365.

Tonn, W.M., J.J. Magnuson, M. Rask, and J. Toivonen. 1990. Intercontinental comparison of small-lake fish assemblages: local processes and regional patterns. Freshw. Biol. 136:345-375.

Vitousek, P.M. 1994. Beyond global warming: Ecology and global change. Ecology 75(7):1861-1876.

Warren, M.L. Jr., and B.M. Burr. 1994. Status of freshwater fishes of the United States: Overview of an imperiled fauna. Fisheries 19(1):6-17.

Warren, M.L. Jr., B.M. Burr, S.J. Walsh, H.L. Bart Jr., R.C. Cashner, D.A. Etnier, B.J. Freeman, B.R. Kuhajda, R.L. Mayden, H.W. Robison, S.T. Ross, and W.C. Starnes. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25(10):7-31.

Waters, T.F. 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph 7.

Williams, J.E., J.E. Johnson, D.A. Hendrickson, S. Contreras-Balderas, J.D. Williams, M. Navarro-Mendoza, D.E. McAllister, and J.E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. Fisheries 14(6):2-20.

Young, R.G., and A.D. Huryn. 1999. Effects of land use on stream metabolism and organic matter turnover. Ecol. Appl. 9:1359-1376.

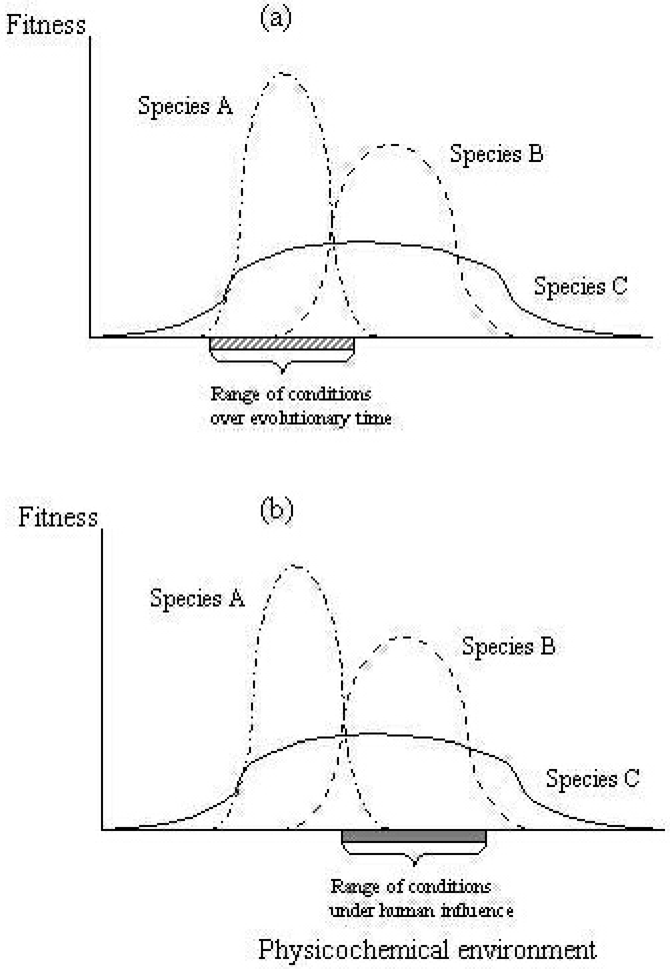

Figure 6.1. Graphical representation of fitness in (a) an undisturbed environment and (b) after alteration of the environment. Environmental change shifts habitat conditions outside of the suitability range for Species A with specialized requirements (e.g., endemic taxon) and populations decline. Populations of two other taxa, Species B with adaptations for another region and generalized Species C, respond positively to the human-modified range of physicochemical conditions. Community structure shifts as a result.