RESPONSES OF INSTREAM HABITAT AND FISHES TO MODEST CHANGES IN FOREST COVER IN SOUTHEASTERN STREAMS

by

ALLISON VOGT

(Under the Direction of Gene S. Helfman)

ABSTRACT

This study investigated relationships among forest cover, instream habitat diversity, and the prevalence of endemic species in tributaries of the Upper Little Tennessee River basin. Comparisons were also made of various qualitative and quantitative methods of habitat assessment to test their sensitivity to changes in forest cover and fish assemblage composition. Faunal homogenization, measured as the proportion of endemic fishes relative to the entire assemblage, was best predicted by higher levels of deforestation. The prevalence of endemic fishes declined in streams with greater proportions of glide habitat and fine streambed particles. Our findings suggest that (1) conversion of riffle to glide habitat, via deposition of fines, is occurring in response to forest cover removal; and that (2) this conversion of preferred to less suitable habitat affects the balance between endemic specialist and more widespread generalist species.

INDEX WORDS: mountain streams, habitat diversity, endemic, stream fishes, human impact, basin-scale, Blue Ridge

RESPONSES OF INSTREAM HABITAT AND FISHES TO MODEST CHANGES IN FOREST COVER IN SOUTHEASTERN STREAMS

by

ALLISON VOGT

B.S. University of Notre Dame, 1999

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

MASTER OF SCIENCE

ATHENS, GEORGIA

2004

RESPONSES OF INSTREAM HABITAT AND FISHES TO MODEST CHANGES IN FOREST COVER IN SOUTHEASTERN STREAMS

by

ALLISON VOGT

Major Professor: Gene S. Helfman

Committee: Mary C. Freeman
David S. Leigh

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
December 2004

ACKNOWLEDGEMENTS

Successful completion of this thesis could not have happened without the patient and generous advisement of Gene Helfman. Mary Freeman and David Leigh provided ample, significant feedback through the entire duration of this project, for which I am very grateful. The research was strongly improved by collaboration with Katie Price and the interdisciplinary nature of the Coweeta LTER Research Program, which provided funding (NSF Award DEB-0218001).

TABLE OF CONTENTS

Page

CHAPTER 1

INTRODUCTION

A long held notion of ecology is that organismal diversity is directly and positively related to habitat diversity. Positive correlations between species richness and the complexity of habitat structure have been documented for temperate and tropical birds, desert rodents, lizards, as well as coral reef and stream fishes (Macarthur et al. 1966, Pianka 1967, Rozenzweig and Winakur 1969, Gorman and Karr 1978, Garcia-Charton and Perez-Ruzafa 2001). Diverse habitat is thought to facilitate the apportionment of limiting resources and thus promote greater specialization (Brown and Lomolino 1998). Among endemic fish species, highly specific habitat requirements may be a liability where widespread land use change has occurred. The presumed mechanism driving loss among many fish species is escalated habitat simplification (Miller et al. 1989, Jones et al. 1999).

The particular susceptibility of stream fishes in the southern Appalachian highlands to habitat alteration originates in the region's geologic history (Mayden 1987). Compared to much of the contiguous U.S., the southern Appalachians were largely unaffected by massive disturbances during the Pleistocene era (1.6 to 0.01 mybp). Thick deposits of glacial ice, permafrost, and loess (glacially-derived clay and silt sized sediments) eliminated aquatic life in affected streams further north (Christopherson 1997). Thus spared, southern Appalachian fishes continued to evolve relatively undisturbed, developing ecological requirements particular to highland stream morphology (Mayden 1987). This uninterrupted speciation helps account for the over 609 species of fishes native to the Southeastern US, a hotspot of temperate fish diversity. A high proportion of these are endemic to one or a few river basins (Warren et al. 1997; 2000). However, several attributes of specialists, including feeding habits and naturally low population densities, render these endemic fishes particularly vulnerable to extirpation via insularization that can result from habitat destruction (Angermeier 1995, Scott 2001).

Habitat alteration is often a catalyst for faunal homogenization (Rahel 2000). Homogenization describes a process by which regionally diverse faunal assemblages are replaced with a lower number of widespread, tolerant, typically invasive species (McKinney and Lockwood 1999). In southern Appalachian fish assemblages, homogenization has occurred via shifts in the proportion of highland endemic fishes relative to cosmopolitan generalist fishes and has accompanied increasing development (e. g., Scott and Helfman 2001, Walters 2003a,b).

Threats related to human development are escalating in the southern Appalachians. For example, Macon County in western North Carolina has experienced a 31% population increase between 1990 and 2003 compared with a national average of 16% (NCDC 2004). With increased population density comes intensified building and clearing of land. Published accounts linking urbanization to the declining integrity of stream fish populations are common (reviewed by Paul and Meyer 2001). However, human disturbance in the southern Appalachians is unique because the region’s ‘natural’ esthetic is integral to the attraction of tourists and second home owners. Development is occurring without the extensive increases in impervious surface and loss of forest cover that typify urbanization in most regions (Wear and Bolstad 1998).

Research on the ecological effects of this pattern of deforestation accompanying sub-urbanization is limited. One observed effect is that, with increasing land use intensity, endemic and habitat-specialist fishes are replaced by more cosmopolitan, generalist, lowland species (Scott and Helfman 2001). These biotic changes are accompanied by increases in suspended sediments, nutrient enrichment, and thermal pollution that are brought about by deforestation (Scott et al. 2002, Sutherland et al. 2002, Price 2004). Understanding the mechanisms by which changes in land use elicit an instream biotic response is directly applicable to conservation needs. To curb mounting anthropogenic threats, managers will likely be charged with formulating and implementing protective watershed regulations and instream restoration plans.

Fish-focused restoration efforts often center on supplementing local habitat diversity by manipulating channel morphology via such methods as alteration of the streambed and banks (Cowx and Welcomme 1998). Two presumed relationships provide the basis for these practices. First, higher degrees of physical habitat diversity or heterogeneity support more biologically diverse and stable assemblages (Gorman and Karr 1978, Jones et al. 1999). Second, instream habitat homogenization is assumed to result from land use activities in the catchment. Recovery of fish assemblages via habitat ‘enhancement’ is a logical outgrowth of these ecological concepts. However, documented success of instream habitat restoration is rare and the success of such efforts remains a matter of debate (Frissell and Nawa 1992). Failure of projects targeting recovery of fishes indicates either incorrect ecological assumptions or application of inappropriate methodologies. We explored these ecological assumptions in southern Appalachian streams by testing the hypothesis that alterations in stream morphology associated with deforestation simplify instream habitats and consequently homogenize stream fish assemblages.

We also investigated whether accepted methods of assessing instream habitat appropriately reflect anthropogenically induced changes. Measuring ‘habitat diversity’ requires a method of classifying and quantifying individual instream habitat types. In spite, or perhaps because of, a variety of habitat classification schemes, little uniformity exists among concepts or methodologies underlying current protocols (Osborne et al. 1991, Heinz Center 2002). Popular classification methods run the gamut from qualitative visual habitat assessment to quantitative, field intensive data collection. Poole et al. (1997) evaluated several studies that assessed the efficacy of habitat unit classification and concluded that broad application of these protocols was unjustified. Poole’s analyses described two principal inadequacies of qualitative habitat unit classification. First, visual classification of instream habitat led to observer bias. Consequently, the precision, reliability, and repeatability of habitat category designations were questionable. Second, important physical changes in stream morphology were often not manifested as alterations in habitat unit frequency (e.g., % riffle). To combat these potential problems, several studies have supported the incorporation of quantifiable parameters into visual habitat classification schemes (e. g., Jowett 1993, Danehy et al. 1998, Vadas and Orth 1998). However, no agreement exists as to which parameters best reflect catchment level land use changes and consequent shifts in the biotic assemblage. These discrepancies led us to test for possible differences in the responsiveness of both qualitative and quantitative metrics of instream habitat diversity to varying levels of forest cover. Similarly, we investigated the capabilities of the two metrics of habitat diversity to predict biotic response, measured as the proportion of endemic species in the assemblages.

Although removal of forest cover elicits numerous watershed responses including alterations of water quality, flow, and sediment regimes, we focused on morphological habitat changes because of their relevance to the field of stream restoration. Although we acknowledge the potential impact of these other factors, the objectives of this study were to 1) assess if measurable differences in fish assemblage composition and habitat diversity exist along a gradient of forest loss in a predominantly forested landscape; 2) determine if homogenization of habitat due to deforestation is a key predictor of endemic fish occurrence; and 3) compare the utility of various metrics describing instream habitat in terms of their responsiveness to land cover change and ability to reflect biotic change.

CHAPTER 2

METHODS

Study Sites

Sites consisted of nine stream segments in tributaries to the Little Tennessee and French Broad rivers of western North Carolina and northern Georgia (Figure 2.1). The watersheds of all sites are in the Blue-Ridge physiographic province and have similar geologic and land-use histories. All study streams exhibit pool-riffle morphology with cobble-dominated stream beds. Streams with step-pool or sand-dominated beds were excluded from analyses. Human impacts in these basins include both agricultural and suburban uses, with an increasing trend towards suburban second home development supporting a burgeoning population. A decline in the economic importance of agriculture has prompted significant reforestation in the last 20 years throughout the Blue Ridge, and recent development within a substantial portion of the Upper Little Tennessee basin has been restricted due to the Nantahala National Forest. Despite these factors slowing the pace of development, analyses of demographic trends indicate continued regional growth and conversion of forested land cover to suburban uses (Wear and Bolstad 1998). To capitalize on this opportunity to study streams before and during the urbanization process, a 30-year investigation of changes in stream geomorphology and biota was launched in 2000. The study is part of the collaborative research effort within the Coweeta Long Term Ecological Research (LTER) program. Several of these sites, each predicted to undergo significant development in coming decades, were included in the present study (e. g., Gardiner 2002). Catchments upstream of the study sites represented the full range of current forest cover in the majority of tributaries of the Little Tennessee and French Broad rivers, and ranged between 67 and 98% (Table 2.1). We treated non-forested percentage as a proxy for the percentage of land affected by human impact, including but not limited to roads, pasture, cropland, and residential and urbanizedareas. Forest cover in the basins was measured using ESRI ArcView and ERDAS Imagine software for both 1950 and 1998. Land use change during these two temporal endpoints was also calculated from forest cover data. We were interested in 1950 forest coverage because Harding et al. (1998) determined that in some southern Appalachian streams, historical land use was a more effective indicator of present-day biotic assemblage composition than current land cover data.

Four sites, grouped into two pairs, were highly similar with regard to reach slope (± 0.002) and drainage area (Table 2.1). Stream reach slope was measured as the average slope projected through the tops of riffles in the reach. Drainage area and reach slope are known to influence the composition of instream habitat, macroinvertebrates, and fish assemblages in lotic systems (Hubert and Kozel 1993, Roy et al. 2003, Walters et al. 2003a, b). Additionally, flood discharge and reach slope are controlling factors in a stream’s capacity for erosion and sediment transport. Reach slope was measured using a Topcon high precision electronic total station and standard survey techniques. Within each of the paired sites, the two streams have experienced contrasting levels of deforestation. ArcView software and USGS 7.5 minute Digital Raster Graphs (DRGs) were used for drainage basin delineation and calculation of drainage area. Study reaches were located so that all sites had at least 50% vegetation coverage in their riparian zones. Length of study reaches was a function of stream size and approximated at 40 times the average wetted channel width as measured in the field.

Physical Habitat Characterization

Sampling points

A longitudinal profile of the thalweg was sampled along the entirety of each study reach according to U.S. Environmental Protection Agency (EPA) protocols (Kaufman and Robison 1998). Thalweg observations were made at 81 equally-spaced points at intervals of one-half the average channel width. Data were also collected at 81 points located at equally-spaced distances along the 40X reach but at randomly selected positions ('random points') across the wetted width to adequately represent all habitat units in the reach (Figure 2.2).

Quantitative Variables

Water depth, velocity, and bed sedimentology were recorded at each point. Velocity was measured using a Marsh-McBirney Flowmate™ electromagnetic flow meter at 0.6 depth. To quantify stream bed particle size, the intermediate axis of a randomly selected particle was measured at each random point. Additionally, the modal phi size class (phi= $-\log_2$ diameter in mm) of stream bed particles within a 50 cm radius of each sample point was visually assessed at all 162 points to depict dominant particle size by area. Depth measurements were also recorded at all thalweg and random points.

Based on previous findings of potential watershed responses to deforestation, we calculated several habitat parameters to test relationships with land cover and fishes. Parameters included average depth of pools, and d_{84}/d_{50}, where d_i represents particles larger than *i* percent of particles in the riffles and therefore d_{50} is the median particle size. This heterogeneity metric provides a simple measure of structural stream bed architecture, at scales relevant to aquatic fauna (Brooks et al. 2002).

Qualitative Habitat Assessment

Visual classification of instream mesohabitat units was determined for all random and thalweg points according to the U.S. EPA classification scheme (Kauffman and Robison 1998) (Table 2.2). Mesohabitats are generally defined as moderately large instream units exhibiting relatively homogenous depth and flow characteristics (Hawkins et al. 1993, Vadas and Orth 1998). In light of the myriad available habitat categorization protocols, we chose to use the EPA scheme because of its frequent, nationwide application. At all points, in addition to habitat unit, we noted the presence or absence of woody debris.

Additionally, channel habitat unit coverage was hand mapped using the U.S. EPA habitat classification scheme (Kauffman and Robison 1998). These units were digitized using ArcView®, and percentages of total surface area for each habitat were calculated.

Hydraulic Variables

Froude and Reynolds numbers, two variables not typically included in habitat assessment protocols, have received attention in the literature as potentially useful predictors of fishes (Jowett 1993, Vadas and Orth 1998). The Froude number is a dimensionless velocity/depth ratio $Fr= V_m/\sqrt{(gY)}$, where V_m is the mean water column velocity taken at 0.6 depth. Y is the water depth, and g is the constant acceleration due to gravity ($9.81\ m \cdot s^{-2}$). Froude number estimates water surface turbulence. Similarly, Reynolds' number describes water column turbulence as $Re= V_m (Y)/ K$, where K equals kinematic viscosity.

Studies have successfully used Froude and Reynolds numbers to distinguish among pools, riffles, and other habitat units (Jowett 1993, Vadas and Orth 1998). Advocacy for integration of the Froude number into instream habitat classification and analysis is increasing (Jowett 1993, Lamouroux 1999, 2002). Furthermore, canonical correspondence analysis indicates that coefficient of variation for the Froude number, used as a proxy for habitat complexity, is strongly correlated with fish assemblage composition (Danehy et al. 1998). Other studies have achieved similar results for benthic macroinvertebrate assemblages (Jowett et al. 1991, 2003). By incorporating velocity and depth, we anticipate better descriptions of instream conditions as experienced by fishes and hence subsequent improved prediction of fish assemblage composition using Froude and Reynolds numbers. However, we know of no studies investigating whether Froude and Reynolds numbers respond to watershed alteration.

Calculations of Habitat Diversity

The term 'habitat diversity' is widely used but inconsistently defined in the stream ecology literature. For the purposes of this study, we utilized diversity metrics that incorporate the composition of mesohabitats within a study reach. Although often interchanged with habitat diversity, habitat heterogeneity implies consideration of not only the composition but also the configuration, or spatial arrangement, of mesohabitats within a channel. In spite of the documented importance of spatial heterogeneity to organisms in the field of landscape ecology, methods of calculating spatial heterogeneity of instream habitats are not well developed (Turner 1989). We used more traditional metrics of habitat diversity in this study for ease of comparison with previous studies.

For comparison, we used two data sets to calculate separate values for habitat diversity at each site. Using the Shannon-Weiner diversity index, H', we calculated diversity values based on both the qualitative and quantitative data sets (as described above). For the quantitative dataset, mesohabitat categories constructed from point data for depth, velocity, and streambed particle size were constructed following Gorman and Karr (1978) and Jones et al (1999). Higher diversity values characterize streams with a greater number of habitat units present.

Fish Collection and Analysis

Fishes at each site were sampled once in the summer of 2003 along a reach length of 20X stream width. Each collection was made at baseflow using backpack electrofishing units and seines. All habitat units were thoroughly sampled in a single pass (Simonson and Lyons 1995). Block nets were not used. Fishes were identified to species, counted, and released. Specimens that could not be positively identified were preserved and returned to the lab for identification.

Assemblage homogenization was calculated as the proportion of individuals of endemic species to that of cosmopolitan and endemic species combined (e: (e+c)). Higher values represent a greater proportion of endemic fishes in the assemblage and a lower level of homogenization. We defined endemic and cosmopolitan species according to Scott and Helfman (2001) following Mayden (1987).

Data Analysis

Because natural landscape factors may influence instream habitat and fish assemblage composition, we wanted to evaluate the importance of catchment land cover after accounting for drainage area and reach slope. To do this, we created least-squares linear regression models using catchment land cover, stream reach slope, and drainage area individually and in combination. Variance inflation factors were computed for each predictor in the models as an assessment of multicollinearity. All variables met conditions of normality, or were transformed to satisfy normality according to the Shapiro- Wilk test. White's test was used to assure homoskedasticity within the dataset (Hamilton 1992). STATA statistical software (version 8) was used for all data analyses.

For two sets of models, one predicting habitat diversity and the other fish assemblage composition, we used Akaike's Information Criterion, adjusted for small sample size (AIC_c), to assess relative fit of candidate models. Lower AIC_c values indicate a better supported model for predicting the dependent variable, relative to other models in the model (Burnham and Anderson 2002). Whereas adjusted R^2 and accompanying p values provide useful information about the variance explained by a model, we feel that AIC_c is the best approach to compare candidate models and determine which independent variables supply the most reliable explanation of trends in the data. Akaike weights (w_i) were computed as $w_i = \exp(-½\,\Delta_i)/\sum\exp(-½\,\Delta_i)$, where Δ_i equals the difference in AIC_c for each model compared to the best-supported model (i.e.$\Delta_i = 0$ for best-supported model) and the denominator is a sum of $\exp(-½\Delta_i)$ for all models in the set. Comparing Akaike weights (which vary from 0 to 1 with the best-fitting model having the highest weight) allows the investigator to determine which independent variables, or combination thereof, best predict the variable of interest (Burnham and Anderson 2002).

We used Pearson's correlation coefficients and linear regression to assess relationships among land cover, landscape, habitat, and fish variables for which we did not designate *a priori* models.

CHAPTER 3

RESULTS

Changes in assemblage as a function of changes in land cover and landscape variables

The best supported model for predicting the proportion of endemic species was a single variable model of catchment forest cover (Table 3.1(a)). An apparently strong influence of forest cover on the proportion of endemic species is further suggested by data from sites paired by drainage area and reach slope. Fully 81% of individuals collected at the Coweeta Church site (96% forest cover) were endemics compared with 49% at its paired site, Skeenah (77% forest). For these sites, drainage area and reach slope varied by only 3.4 km^2 and 0.0003 respectively. Similarly, the fish assemblage at Keener (90% forest) was composed of 92% endemic individuals versus 54% at its pair, Rocky Branch (73% forest). Drainage area for Rocky Branch and Keener varied by 0.4 km^2 and differed in reach slope by 0.0002. These four data points represent values near the end points from all study sites of the (e: (e+c)) values that ranged from 41% to 92%.

Across the nine sites, total number of individuals collected ranged from 92 to 337 representing six to 16 species (Appendix A). Values of (e: (e+c)) ranged from 40.5 to 91.9%. *Cottus bairdi* ssp. (smoky sculpin), a highland endemic, dominated assemblage composition at eight of the nine sites. Proportions of endemic species calculated first including and then excluding smoky sculpin revealed only a weak relationship between the two values (r=0.39), indicating that assemblage trends primarily represent changes in sculpin abundance. Furthermore, when smoky sculpin were excluded from the calculations of (e: e+c)), no relationship existed between (e: (e+c)) and forest cover (r= -0.05).

Species richness was negatively correlated with proportion of endemic individuals (r = -.74; p =.02). At regional scales, increased species richness has been found to characterize the faunal mixing that leads to biotic homogenization (reviewed by Sax and Gaines 2003). In the southern Appalachians, sites highest in species diversity supported the lowest proportion of endemic fishes (Scott and Helfman 2001).

Forest cover values from 1950 and 1998 were highly and positively correlated (r=0.96). A strong positive relationship was also present between land cover change and forest cover data. As a result, we assumed the potential effect of historic land use was negligible for these sites and used only land cover data for 1998 in analyses (Harding et al. 1998). No strong correlations existed between the three metrics of land cover (1950, 1998, and land cover change) and any of the landscape variables (Table 3.2). Although strongly correlated (r= 0.62), levels of deforestation tended to be higher in watersheds with streams exhibiting less steep reach slopes, in keeping with regional patterns (Scott et al. 2002).

Alterations of habitat diversity as a function of land cover and landscape variables

Our findings above suggested a relationship between species occurrences and forest cover. Because fish distribution has commonly been associated with habitat type, we hypothesized that instream habitat diversity would also be responsive to land cover variables, thus linking fishes, habitat, and land use. Analyses of the composition of instream habitat revealed that individual components of the diversity metrics correlated with varying levels of forest cover (Table 3.3(a)). The proportion of glides, riffles, and rapids per reach responded to varying levels of deforestation, although the percentage of pools per study reach was strongly correlated only with reach slope. With less forest cover, we found fewer riffles and rapids but more glides (Figure 3.1(c)). Furthering the case for the influence of forest cover on glides and riffles, neither stream reach slope nor drainage area were significant predictors of the frequency of these habitat units (Table 3.3 (a)).

However, the model containing only reach slope was identified by AIC as most parsimonious in revealing correlates of habitat diversity (Table 3.1 (b)). Similar results were achieved for both the qualitative method, based on EPA habitat classification data, and the quantitative method calculated from depth, velocity, and particle size data (Table 3.1 (c)). Similarly, results from the four paired sites showed no pattern in differences in habitat diversity among highly and less forested sites when reach slope was held constant. H' for all sites ranged from 0.63 to 1.46. Coweeta, the more highly forested site, had an H' value of 1.14 in comparison with 1.17 for Skeenah, its pair. Similarly, Keener, the more heavily forested basin, had an index value of 0.88 whereas Rocky Branch had a value of 0.67.

Habitat diversity was also calculated for each quantitative variable independently. For depth data, reach slope and forest cover in 1998 predicted diversity nearly equally well. Habitat diversity measured using dominant stream bed particle size was not related to either reach slope nor forest cover. However, diversity calculated from velocity data was highly and positively correlated with forest cover but not with reach slope (Table 3.3(b)).

A comparison of habitat diversity values derived from the qualitative and quantitative habtiat information revealed little congruence between the two methods (r=0.37). Analyses of each of the quantitative variables (depth, velocity, and particle size) individually revealed that only depth data had significant positive relationship with habitat diversity values based on EPA classification data. Instream habitat composition based on the mapped surface area of each habitat unit was highly similar to the frequency of each habitat type based on point observations.

Responses of geomorphic and hydrologic variables to forest cover

Forest cover was the best predictor of the proportion of particles less than 2 mm (% fines) (r= -0.68, p= 0.05) (Figure 3.3(c)). There were no significant relationships between % fines and drainage area (r = 0..38, p=0.02) or reach slope (r = -0.17) (Table 3.3 (c)). Values of d84/ d50 were related to neither land cover nor landscape variables.

Mean values of Froude numbers, a hydrologic variable that integrates velocity and depth, increased significantly with greater percentages of forest cover. Mean Reynolds number and the coefficient of variation for these two parameters did not correlate with forest cover (Table 3.3(d)). There was no significant relationship between the presence of woody debris as a habitat characteristic and any of the landscape variables (all r<0.38). Furthermore, correlation analysis indicated no relationship between mean pool depth and forest cover (r=0.09).

Relationships between habitat variables and fish assemblage composition

We selected the instream habitat variables most responsive to land cover change to predict (e:(e+c)). The proportion of glides in the study reach and the percentage of stream bed particles less than 2 mm were most strongly related to the proportion of endemic species (Table 3.4). We saw a greater proportion of endemic fishes in streams with both fewer glides and fewer fine particles. Both % glide and % fines were also negatively correlated with forest cover, suggesting that alteration of these habitat characteristics may play a key role in initiating biotic homogenization (Table 3.3 (a & c)).

CHAPTER 4

DISCUSSION

Stream characteristics that are at once easy to measure, responsive to changes in watershed alteration, and indicative of potential biotic imperilment remain elusive to stream ecologists. The multitude of pathways by which land use practices generate instream changes are too complex to distill into a few, easily obtained metrics. Still, managers and policymakers rely on scientists to provide utilitarian tools to aid in the reversal of anthropogenic impacts influencing stream integrity. Metrics currently in use or advocated in the literature are discussed below in relation to deforestation in the southern Appalachians, instream habitat diversity, and stream fish assemblage composition.

Influence of forest cover on fish assemblage composition

In our findings, modest differences in basin forest cover elicited a measurable response in fish assemblage composition. Fewer endemic and more native generalist fishes were collected in basins with lower levels of catchment forest cover, in concordance with other results from this region (Scott and Helfman 2001, Sutherland et al. 2002, Gardiner 2002).

We found that forest cover alone best predicts the proportion of endemic fishes within assemblages. In contrast, previous studies indicated that stream reach slope acts as a predominant controller of fish assemblage composition (Lyons 1996, Walters et al. 2003b). Our sites exhibit a smaller range of both reach slopes and with respect to those in Walters et al. (2003b), but our ranges of drainage areas and urban land cover are smaller. This difference may possibly explain the differential level of influence; presumably our narrower range of drainage areas and urban land cover better revealed the influence of forest cover. Additionally, stream reaches used by Walters et al. (2003b) had stream beds dominated by sand-sized particles in contrast to the predominantly cobble stream beds in this study. Similarly we found neither drainage area nor wetted width had significant predictive power with respect to fish assemblage composition.

Both catchment wide and more localized (riparian) land cover patterns play an important role in predicting stream condition (Richards et al. 1996, Lammert and Allan 1999, Stewart et al. 2001). In the southern Appalachians, catchment forest cover has successfully predicted physicochemical, sedimentological, and biotic parameters (Scott et al. 2002, Sutherland et al. 2002). Agricultural lands that formerly dominated this region were concentrated in lower relief riparian lands; conversely, emerging development in the region is distributed throughout both high and low relief portions of the watershed (Wear and Bolstad 1998). Thus, we chose to focus on catchment level effects to more closely reflect this regional conversion from watersheds with concentrated agricultural lands to more widespread suburban development.

Changes in stream biotic integrity are typically studied in basins undergoing intensive urbanization or agricultural development (Roth et al. 1996, Wang et al. 1997). The relatively low intensity of development that currently exists in the southern Appalachians makes it possible to explore the initial impacts that landscape alterations are likely to cause. Indicators of such impacts may include early symptoms of faunal decline or thresholds of disturbance beyond which sensitive species cannot persist. Sutherland et al. (2002), also working in the southern Appalachians, detected a potential threshold between 10 and 20% non-forested land cover. At greater levels of deforestation, fishes that spawn in benthic crevices or over gravel-sized stream bed particles were missing (Sutherland et al. 2002). Similar patterns were evident in our data: streams flowing through catchments with only 67 - 82% forest cover housed fish assemblages consisting of only 54% endemic fishes whereas streams that are were at least 90% forested housed 87% endemics (Figure 3.1(a)). Our data indicate that greater than 10-20%

deforestation is likely to cause a reduction of perhaps 40- 50% in the number of endemic individuals. If representative, such thresholds may be useful for regional conservation planning.

These responses of the fish assemblage to forest cover hold only when Cottus bairdi ssp., the most abundant fish collected, is included in the calculation. One possible explanation is that levels of deforestation affecting these study sites are not extensive enough to elicit a response from most endemic species, suggesting a particular sensitivity of Smoky sculpin to deforestation.

Interestingly, an analysis of most life history traits and ecological attributes do not distinguish the Smoky sculpin from other endemic species in the region (based on Scott 2001). Maximum body size and foraging habitat best differentiated endemic fishes from cosmopolitan species (Scott 2001). Smoky sculpin have a maximum body size of 11 cm in comparison with a median of 10 cm for all endemic species, well within one standard deviation. Cosmopolitan species in the region, in contrast, have a median body size of 25 cm. Similarly, the benthic foraging habit utilized by Smoky sculpin is shared with 35% of other endemics in the region (based on Scott 2001). Neither of these traits successfully distinguishes Smoky sculpin from other endemic species.

However, a recent study investigating the instream movement of sculpin in the Upper Little Tennessee basin revealed one of the lowest movement rates recorded for stream fishes. For example, over the course of 45 days, sculpin moved a mean of 1.3 m (Petty and Grossman 2004). Although studies of movement for non-salmonid fishes are limited, the findings of Petty and Grossman (2004) are orders of magnitude smaller than movement distances recorded for smallmouth bass, northern hog suckers, and central stonerollers (Todd and Rabeni 1989, Matheney and Rabeni 1995, Lonzarich et al. 2000). Petty and Grossman (2004) surmised that the poor swimming ability of sculpin accounts for their limited movement. This may provide a possible explanation for their apparent sensitivity to low levels of deforestation. Whereas other endemic fishes are capable of migrating further upstream to potentially less-disturbed sites, sculpin may remain in the degraded habitat and their numbers would thus decline. Additionally, Burkhead et al. (1997) identified limited mobility along with small size and benthic habits as traits characterizing southern Appalachian fish species that are most vulnerable to extinction. Presumably, the applicability of this suite of characters to Smoky sculpin may help explain their apparent sensitivity to land disturbing activities in our study.

Growing evidence suggests that particular groups of fishes, such as endemics or those with distinct breeding or feeding habits, are particularly susceptible to habitat alteration resulting from deforestation (Scott and Helfman 2001, Walters et al. 2003a & b). For example, in watersheds averaging 85% agricultural land use, Berkman and Rabeni (1987) found fish assemblages contained fewer riffle-specific species than in less disturbed watersheds. Similarly, at sites along a gradient of deforestation from six to 82%, rare fish species were positively correlated with canopy cover. Nevertheless, species richness measures revealed no differences among sites (Bojsen and Barriga 2002).

Another, related trend emerging from our data is one of increased species richness in streams with lower values of (e:(e+c)) (r= -0.74)(Rahel et al. 2000; see also Scott and Helfman, Walters et al. 2003a). Analogously, a pattern of increased species richness caused by the introduction of non-native species followed impoundment in streams in southern Illinois (Taylor et al. 2001).

Effects of forest cover removal on instream habitat

Homogenization of fish assemblages and an accompanying decline in sensitive species are often facilitated by alterations of habitat (Miller et al. 1989, Rahel 2000). Rahel (2000) proposed that homogenization of freshwater faunas may be slowed by the rehabilitation of aquatic habitats important to native species. In fact, a goal of restoration is to combat effects of detrimental land use through the enhancement of habitat diversity. However, our data indicate that habitat diversity, calculated using both qualitative and quantitative metrics, responds best to stream reach slope, not forest cover, i.e., the relationship between habitat diversity per se and watershed alteration is weak at best. These results are in agreement with Wang et al. (2001) who found percent impervious surface to be the best predictor of fish integrity but failed to identify significant relationships between percent impervious surface and fish habitat quality.

Using quantitative metrics of habitat diversity similar to those in this study, Jones et al. (1999) investigated the influence of riparian forest cover on instream habitat diversity. Significant decreases in diversity of instream habitat due to riparian deforestation were shown, suggesting that restoration efforts targeted at localized sources of disturbance such as road crossings may be more effective than efforts directed at catchment-wide land use practices.

Few rigorous tests have focused on whether habitat unit classification schemes respond to changes in land use at the watershed level. Poole et al. (1997) looked for trends in the frequency of occurrence of habitat types relative to watershed disturbance but were unable to find any differences between two sites that experienced drastically dissimilar levels of disturbance. However, they were readily able to discern differences between a logged watershed and its undisturbed pair member by using quantitative measures of hydrologic processes and channel morphology. In contrast, we showed that diversity values based on quantitative data performed no better overall than the qualitative data set in this study. The exception is the diversity of (H') of flow velocities, calculated using water column velocity data. Flow diversity increased significantly in more highly forested basins (Table 3.3b).

We found no differences in the presence of woody debris along the gradient of forest cover at our sites. In contrast, even at the modest levels of forest cover removal that we studied and that typify the southern Appalachians, changes in sediment regime are apparent (Figure 3.1b). A detailed, companion sedimentological study of the four paired sites included in this study revealed stream beds were composed of smaller particles in less forested sites (Price 2004). Because drainage area and reach slope were held constant at these sites, we assume the differences can be attributed to forest cover. Many studies have established connections between catchment deforestation and decreasing bed particle size (Berkman and Rabeni 1987, Waters 1995, Jackson et al. 2001, Sutherland et al. 2002). Fine sediments were also more prevalent in riffles of streams adjoining deforested riparian patches in another investigation in this same region (Jones et al. 1999).

These decreases in median particle size are largely driven by an influx of fine sediments (< 2 mm) introduced by removal of vegetation and by road construction in urbanizing watersheds (Johnson and Besctha 1980, Sah and Mazari 1998). Chamberlin et al. (1991) predicted fewer pools in association with decreasing forest cover. In the present study, the proportion of pools was related to stream reach slope rather than to forest cover, although we observed more glides and fewer riffles and rapids per reach with increasing levels of forest cover.

Fine sediments are capable of being transported and deposited within the stream channel at near base flows. As a result of this high potential for mobility, streams with high levels of fine sediment experience an infilling of riffle habitat by the small particles. High levels of fine sediments are often a consequence of lower levels of catchment scale forest cover. Conversion of riffle habitat units to glides is suggested by a strong negative relationship between the frequency of glides and the frequency of riffle/rapid combinations (r= 0.77).

Effects of habitat diversity on fish assemblage composition

The complexity of habitat within a stream segment has been shown to have a strong influence on the associated fish assemblages (Schlosser 1991, Danehy et al 1998, Harvey et al 1999). Gorman and Karr (1978) hypothesized that the positive correlative relationship between habitat diversity and species diversity is because structurally complex streams maintain the buffering capacity to withstand disturbance events. Various life stages and different species of stream fishes require an array of habitat types (Etnier and Starnes 1993). Even within a single species and size/age class, individuals may prefer different habitats for overwintering, spawning, and feeding (Schlosser 1991). However, and contrary to anticipated relationships, none of our measures of habitat diversity were significant predictors of the proportion of endemic fishes in stream assemblages. Our data do agree with Stauffer and Goldstein's (1997) evaluation of the predictive capabilities of three qualitative habitat assessment indices in that no significant correlations were identified between any metric of fish assemblage integrity and scores for habitat quality calculated by the indices.

This lack of correlative relationship may shed light on the failed track record of many instream restoration projects whose aim is to enhance fish populations. Our results support findings that failed to observe an improvement in invertebrate metrics as a result of enhanced habitat diversity. For example, macroinvertebrate community structure did not respond to experimental manipulation of particle size diversity (Brooks et al. 2002). Similarly, in streams where stream bed diversity was enhanced with the placement of boulders there were only minimal effects on macroinvertebrates. Short-term gains in abundance and richness were recorded for only one year following restoration (Negishi and Richardson 2003). One exception to this lack of effect was Brown (2003), who found a decrease in temporal variability and an increase in taxon richness of macroinvertebrates as a function of increasing habitat heterogeneity.

At scales smaller than the channel unit, termed 'subunits', Inoue and Nakano (1999) suggested that the preference of Masu salmon for one subunit over another may be in part due to its spatial position relative to other subunit types, in addition to the attributes of the subunit itself. This interpretation suggests that fishes may respond to the spatial heterogeneity of instream habitat units. Measures of habitat diversity typically apply to only composition of channel units in a reach but not spatial distribution or configuration. Palmer et al. (2000) found that stream invertebrates respond not only to patch type but also to the arrangement or configuration of instream habitats, providing further evidence that spatial dispersion of habitats may influence biotic responses. All aspects of habitat, including composition and spatial configuration, contribute to habitat heterogeneity, but research on the importance of habitat heterogeneity to fishes remains limited.

Although endemic fishes did not respond to characteristics of habitat diversity as we measured them, both the percentage of fines and the proportion of glides were sensitive to varying levels of forest cover and were strong predictors of fish assemblage composition (Figures 3.1(a),(b), &(c); 4.1(a) &(b)). As discussed above, increases in fine sediments in streams often accompany anthropogenic land use change. Increased sedimentation is thought to impair fish assemblages via three mechanisms: disruption of normal reproduction, destruction of food supply, and reduction of available instream habitat (Berkman and Rabeni 1987).

In highland streams of the Blue Ridge province, we found evidence suggesting that fine sediments reduce the amount of riffle habitat and convert those areas to glide habitat (Figure 4.2). This is potentially a preliminary step in habitat homogenization, too subtle to be detected by the metrics of habitat diversity used in this study. It is not clear from our data whether decreasing habitat diversity plays a dominant role in the decline of southern Appalachian fishes, but our data strongly point to impacts of sedimentation as a causative factor. We therefore urge caution during restoration efforts that focus on techniques to enhance habitat diversity in response to catchment wide disturbance rather than on alleviating the disturbance itself. Controlling sources of sediment throughout a watershed and especially at point sources of disturbance may provide a superior approach to fisheries restoration than enhancement of instream habitat diversity.

REFERENCES

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

Berkman, H.E. and C.F. Rabeni. 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18: 285- 295.

Bojsen, B.H. and R. Barriga. 2002. Effects of deforestation on fish community structure in Ecuadorian Amazon streams. Freshwater Biology 47: 2246-2260.

Brooks, S.A., M.A. Palmer, B.J. Cardinale, C.M. Swan, and S. Ribblett. 2002. Assessing stream ecosystem rehabilitation: limitations of community structure data. Restoration Ecology 10: 156-168.

Brown, B.L. 2003. Spatial heterogeneity reduces temporal variablilty in stream insect communities. Ecology Letters 6: 316-325.

Burkhead, N. M., S. U. 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 (editors). Aquatic Fauna in Peril: the Southeastern Perspective. Special Publication 1, Lenz Design and Communications, Decatur, GA

Burnham K. P. and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, Inc., New York, New York.

Chamberlin, T.W., R.D. Harr, and F.H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. pp. 181-205 in: Meehan, W.R. (editor). Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats. American Fisheries Society Special Publication 19.

Christopherson, R.W. 1997. Geosystems: an introduction to physical geography. 3rd edition. Prentice-Hall, Inc. Upper Saddle River, New Jersey

Cowx, I.G. & R.L. Welcomme, eds. 1998. Rehabilitation of rivers for fish, Oxford, Fishing News Books.

Danehy, R. J., S.V. Stehmanm, and J.M. Hasset. 1998. Variability of fish densities in a small catchment. Ecology of Freshwater Fish. 7:36-48

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

Frissell, C.A. and R.K. Nawa. 1992. Incidence and causes of physical failure of artificial habitat structures in the streams of western Oregon and Washington. North American Journal of Fisheries Management 122:182-197

Garcia-Charton, J.A. and A. Perez-Ruzafa. 2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Marine Biology. 138: 917-934.

Gardiner, E.P. 2002. Geospatial techniques for stream research in the southern Blue Ridge Mountains. Doctoral Dissertation. The University of Georgia, Athens, Georgia

Gorman, O. T., and J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology 59: 507-515.

Gorman, O.T. and J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology, 59: 507-515.

Hamilton, L.C. 1992. Regression with graphics: a second course in applied statistics. Wadsworth, Inc.

The H. John Heinz Center for Science, Economics, and the Environment. 2002. The State of the nation's ecosystems: measuring the lands, waters, and living resources of the United States. Cambridge University Press, New York, 276 pp.

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 of the United States of America 45:14843-14847.

Harvey, B.C., R.J. Nakamoto, and J.L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Onchorynchus clarki*) during fall and winter. Canadian Journal of Fisheries and Aquatic Sciences 56: 2161-2166

Hawkins, C.P., J.L. Kershner, P.A. Bisson, M.D. Bryant, L.M. Decker, S.V. Gregory, D.A. McCullough, C.K. Overton, G.H. Reeves, R.J. Steedman, and M.K. Young. 1993. A hierarchical approach to classifying stream habitat features. Fisheries 18: 3-12

Hubert, W.A. and S.F. Kozel. 1993. Quantitative relations of physical habitat features to channel slope and discharge in unaltered mountain streams. Journal of Freshwater Ecology 8(2): 177-183.

Inoue, M., and S. Nakano. 1999. Habitat structure along channel-unit sequences for juvenile salmon: a subunit-based analysis of in-stream landscapes. Freshwater Biology 42: 597-608

Jackson, C.R., C.A. Sturm, and J.M. Ward. 2001. Timber harvest impacts on small headwater Stream channels in the coast ranges of Washington. Journal of the American Water Resources Association 37: 1533-1549.

Johnson, M.G. and R.L. Beschta. 1980. Logging, infiltration, and surface erodibility in western Oregon. Journal of Forestry 78: 334-337.

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.

Jowett, I.G. J. Richardson, B.J.F. Biggs., C.W. Hickey, and J.M. Quinn.1991. Microhabitat preferences of benthic invertebrates and the development of generalized *Deleatidium* spp.

habitat suitability curves, applied to 4 New Zealand streams. New Zealand Journal of Marine and Freshwater Research 25: 187-199.

Jowett, I.G. 1993. A Method for objectively identifying pool, run, and riffle habitats from physical measurements. New Zealand Journal of Marine Freshwater Research. 27: 241-248

Jowett, I.G. 2003. Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed rivers. River Research and Applications 19:495-507.

Kaufmann, P.R. and E.G. Robison. 1998. Physical habitat characterization. Section 7 – Field Operations and Methods for Measuring the Ecological condition of Wadeable Streams. PA/620/R-94/004F, U.S. Environmental Protection Agency, Research Triangle Park, North Carolina

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.

Lamouroux, N., J.M. Olivier, H. Persat, M. Pouilly, Y. Souchon, and B. Statzner. 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. Freshwater Biology. 42:275-299

Lamouroux, N. and Y. Souchon. 2002. Simple predictions of instream habitat model outputs of fish habitat guilds in large streams. Freshwater Biology 47: 1531-1542.

Lonzarich, D.G., M.R. Lonzarich, and M.L. Warren Jr. 2000. Effects of riffle length on the short-term movement of fishes among stream pools. Canadian Journal of Fisheries and Aquatic Sciences 57: 1508-1514.

Lyons, J. 1996. Patterns in the species composition of fish assemblages among Wisconsin streams. Environmental Biology of Fishes 45:329-341.

Osborne, L.L., Dickson, B., Ebbers, M., Ford, R., Lyons, J., Kline, D., Rankin, E., Ross, D., Sauer, R., Seelbach, P., Speas, C., Stefanavage, T., Waite, J., and Walker, S., 1991, Stream habitat assessment programs in states of the American Fisheries Society North Central Division: Fisheries, v. 16, p. 28-35.

MacArthur, R., H. Recher, and M. Cody. 1966, On the relation between habitat selection and species diversity. American Naturalist 100: 319-332.

Matheney, M.P. IV and C.F. Rabeni. 1995. Patterns of movement and habitat use by northern hog suckers in an Ozark stream. Transactions of the American Fisheries Society 124: 886-897.

Mayden, R.L. 1987. Historical ecology and North American highland fishes: a research program in community ecology. Pages 210-222 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. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14:450-453.

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

NCDC (North Carolina Department of Commerce, Economic Policy and Research Division). 2004. Economic Development Information System- Macon County. http://cmedis.commerce.state.nc.us/countyprofiles/default.cfm

Negishi, J.N. and J.S. Richardson. 2003. Responses of organic matter and macroinvertebrates to placements of boulder clusters in a small stream of southwestern British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 60:247-258.

Palmer, M.A., Swan, C.M., Nelson, K.,Silver, P., Alvestad, R. 2000. Stream bed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. Landscape Ecology 15: 563-576

Paul, M. J. and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32: 333-365.

Petty, J.T. and G.D. Grossman. 2004. Restricted movement by mottled sculpin (pisces: cottidae) in a southern Appalachian stream. Freshwater Biology 49: 631-645.

Pianka, E.R. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:331-351.

Poole, G.C., C.A. Frissell, and S.C. Ralph. 1997. In-stream habitat unit classification: inadequacies for monitoring and some consequences for management. Journal of the American Water Resources Association 33: 879-896.

Price, K. 2004. Stream response to human impact in the southern blue ridge mountains. Masters Thesis. University of Georgia, Athens.

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

Richards, C., L.B. Johnson, and G.E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Science 53 (Suppl. 1), 295-311.

Rosenzweig, M.L. and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50: 558-572.

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

Roy, A.H., A.D. Rosemond, M.J. Paul, D.S. Leigh, and J.B. Wallace. 2003. Stream macroinvertebrate response to catchment urbanisation (Georgia, U.S.A.). Freshwater Biology 48: 329-346.

Sah, M.P. and R.K. Mazari. 1998. Anthropogenically accelerated mass movement, Kulu Valley, Himachel Pradesh, India. Geomorphology 26,: 123-138.

Sax, D.F. and S.D. Gaines. 2003. Species diversity: from global decreases to local increases. Trends in Ecology and Evolution 18: 561-566.

Schlosser, I.J. 1991. Stream fish ecology- a landscape perspective. Bioscience 41: 704-712.

Scott, M.C. 2001. Integrating the stream and its valley: land use change, aquatic habitat, and fish assemblages. PhD Dissertation, University of Georgia.

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

Scott, M.C., Helfman, G.S., McTammany, M.E., Benfield, E.F., and P.V. Bolstad. 2002. Multiscale influences on physical and chemical stream conditions across Blue Ridge landscapes. Journal of the American Water Resources Association 38:1379-1392.

Simonson, T. D., and J. Lyons. 1995. Comparison of catch per effort and removal procedures for sampling stream fish assemblages. North American Jou

Stauffer, J.C. and R.M. Goldstein. 1997. Comparison of three qualitative habitat indices and their applicability to prairie streams. North American Journal of Fisheries Management 17: 348-361

Stewart, J.S., L. Wang, J. Lyons, J.A. Horwatich, and R. Bannerman. 2001. Influences of watershed, riparian-corridor, and reach-scale characteristics on aquatic biota in agricultural watersheds. Journal of the American Watershed Association 37: 1475-1487.

Sutherland, A.S., J.L. Meyer, and E.P. Gardiner. 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams.
Freshwater Biology 47: 1791-1805.

Taylor, C.A., J.H. Knouft, and T.M. Hiland. 2001. Consequences of stream impoundment on fish communities in a small North American drainage. Regulated Rivers: Research & Management 17: 687-698.

Todd, B.L., and C.F. Rabeni. 1989. Movement and habitat use by stream-dwelling small mouth bass. Transactions of the American Fisheries Society 118: 229-242.

Turner, M.G. 1989. Landscape ecology- the effect of pattern on process. Annual Review of Ecology and Systematics 20:171-197

Vadas, R.L., and D.J. Orth. 1998. Use of Physical Habitat Variables to Discriminate Visually Determined Mesohabitat Types in North American Streams. Rivers 6: 143-159

Walters, D. M., D. S. Leigh, and A. B. Bearden. 2003a. Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River Basin, USA. Hydrobiologia 494: 5-10.

Walters, D. M., D. S. Leigh, M. C. Freeman, B. J. Freeman, and C. M. Pringle. 2003b. Geomorphology and fish assemblages in a Piedmont river basin, U.S.A. Freshwater Biology 48:1950-1970.

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.

Wang, L., J. Lyons, P. Kanehl, and R. Bannerman. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28: 255-266.

Warren, M.L., B.M. Burr , S.J. Walsh , H.L. Bart , 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: 7-31.

Warren, M. L., Jr., P.L. Angermeier, B.M. Burr, and W.R. Haag. 1997. Decline of a diverse fish fauna: patterns of imperilement and protection in the southeastern United States. Pages 105-164 in: G.W. Benz and D.E. Collins (editors). Aquatic Fauna in Peril: the Southeastern Perspective. Special Publication 1, Lenz Design and Communications, Decatur, GA

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

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

Appendix A. Fishes collected within tributaries to the French Broad and Upper Little Tennessee river basins

Site	Species Name	Common Name	Count
Coweeta Boundary	*Ambloplites rupestris*	Rock Bass	2
	Campostoma anomalum	Central Stoneroller	13
	Clinostomous funduloides	Rosyside Dace	9
	Cottus bairdi	Mottled Sculpin	211
(e:(e+c))= 0.898	*Hypentelium nigricans*	Northern Hogsucker	4
	Luxilus coccogenis	Warpaint Shiner	3
	Nocomis micropogon	River Chub	7
	Onchorynchus mykiss	Rainbow Trout	4
	Rhinichthys cataractae	Longnose Dace	12
	Semotilus atromaculatus	Creek Chub	1
Coweeta Church	*Ambloplites rupestris*	Rock Bass	1
	Campostoma anomalum	Central Stoneroller	43
	Clinostomous funduloides	Rosyside Dace	5
	Cottus bairdi	Mottled Sculpin	262
(e:(e+c))= 0.814	*Hypentelium nigricans*	Northern Hogsucker	3
	Luxilus coccogenis	Warpaint Shiner	1
	Nocomis micropogon	River Chub	8
	Notropis Leuciodus	Tennessee Shiner	3
	Notropis lutipinnis	Yellowfin Shiner	3
	Onchorynchus mykiss	Rainbow Trout	5
	Percina evides	Gilt Darter	1
	Petromyzon greeleyi	Brook Lamprey	2
	Rhinichthys cataractae	Longnose Dace	4
	Semotilus atromaculatus	Creek Chub	2
Darnell	*Campostoma anomalum*	Central Stoneroller	15
	Clinostomous funduloides	Rosyside Dace	2
(e:(e+c))= 0.849	*Cottus bairdi*	Mottled Sculpim	240
	Nocomis micropogon	River Chub	3
	Notropis lutipinnis	Yellowfin Shiner	10
	Onchorynchus mykiss	Rainbow Trout	16
	Rhinichthys atratulus	Blacknose Dace	15

Site	Species Name	Common Name	Count
Gap (e:(e+c))= 0.405	*Campostoma anomalum*	Central Stoneroller	35
	Catostomus commersonii	White Sucker	1
	Cottus bairdi	Mottled Sculpin	33
	Etheostoma blennioides	Greenside Darter	9
	Etheostoma swannanoa	Swannanoa Darter	4
	Hybopsis amblops	Bigeye Chub	2
	Hypentelium nigricans	Northern Hogsucker	2
	Lepomis cyanellus	Green sunfish	1
	Lepomis punctatus	Spotted Sunfish	1
	Nocomis micropogon	River Chub	2
	Notropis rubricroceus	Saffron Shiner	13
	Percina evides	Gilt Darter	5
	Petromyzon greeleyi	Brook Lamprey	3
	Rhinichthys atratulus	Blacknose Dace	15
	Rhinichthys cataractae	Longnose Dace	8
	Semotilus atromaculatus	Creek Chub	35
Keener (e:(e+c))= 0.919	*Campostoma anomalum*	Central Stoneroller	6
	Clinostomous funduloides	Rosyside Dace	10
	Cottus bairdi	Mottled Sculpin	157
	Hypentelium nigricans	Northern Hogsucker	3
	Luxilus coccogenis	Warpaint Shiner	1
	Nocomis micropogon	River Chub	3
	Notropis Leuciodus	Tennessee Shiner	2
	Notropis Leuciodus	Tennessee Shiner	2
	Notropis lutipinnis	Yellowfin Shiner	3
Robinson (e:(e+c))= 0.782	*Cottus bairdi*	Mottled Sculpin	123
	Luxilus coccogenis	Warpaint Shiner	17
	Nocomis micropogon	River Chub	1
	Semotilus atromaculatus	Creek Chub	33
	Hypentelium nigricans	Northern Hogsucker	3
	Rhinichthys cataractae	Longnose Dace	32
	Petromyzon greeleyi	Brook Lamprey	16
	Campostoma anomalum	Central Stoneroller	5
	Ambloplites rupestris	Rock Bass	3
	Etheostoma blennioides	Greenside Darter	5
	Notropis rubricroceus	Saffron shiner	18
	Etheostoma swannanoa	Swannanoa Darter	10

Site	Species Name	Common Name	Count
Rocky Branch	*Campostoma anomalum*	Central Stoneroller	3
	Cottus bairdi	Mottled Sculpin	45
	Hypentelium nigricans	Northern Hogsucker	2
	Luxilus coccogenis	Warpaint Shiner	5
(e:(e+c))= 0.543	*Nocomis micropogon*	River Chub	12
	Notropis lutipinnis	Yellowfin Shiner	1
	Notropis photogenis	Silver Shiner	5
	Onchorynchus mykiss	Rainbow Trout	1
	Rhinichthys atratulus	Blacknose Dace	15
	Semotilus atromaculatus	Creek Chub	4
Skeenah	*Ambloplites rupestris*	Rock Bass	4
	Campostoma anomalum	Central Stoneroller	40
(e:(e+c))= 0.493	*Catostomus commersonnii*	White Sucker	2
	Clinostomous funduloides	Rosyside Dace	4
	Cottus bairdi	Mottled Sculpin	109
	Hypentelium nigricans	Northern Hogsucker	8
	Lepomis auritus	Redbreast Sunfish	12
	Luxilus coccogenis	Warpaint Shiner	30
	Nocomis micropogon	River Chub	30
	Notropis Leuciodus	Tennessee Shiner	19
	Notropis lutipinnis	Yellowfin Shiner	67
	Percina evides	Gilt Darter	2
	Petromyzon greeleyi	Brook Lamprey	4
	Phenacobius crassilabrum	Fatlips Minnow	2
Watauga	*Ambloplites rupestris*	Rock Bass	2
	Campostoma anomalum	Central Stoneroller	23
(e:(e+c))= 0.577	*Cottus bairdi*	Mottled Sculpin	56
	Cyprinella nivea	Whitefin shiner	3
	Lepomis megalotis	Longear Sunfish	2
	Micropterus	Smallmouth Bass	2
	Nocomis micropogon	River Chub	9
	Percina evides	Gilt Darter	6
	Phenacobius crassilabrum	Fatlips minnow	2
	Rhinichthys atratulus	Blacknose Dace	6

Appendix B. Habitat data values for all study sites.

Site	Qualitative Habitat Diversity	Quantitative Habitat Diversity	Diversity of Velocity values	Diversity of Depth values	Diversity of Particle size values	% Glide	% Riffle	%Riffle & %Rapid	% Fines	Mean Froude	Coefficent of variation of Froude number
Coweeta Boundary	1.46	5.76	1.46	1.09	1.27	0.43	0.31	0.37	0.185	0.3483	19.878
Coweeta Church	1.14	4.69	1.45	1.00	0.93	0.43	0.43	0.49	0.074	0.3676	18.169
Darnell	1.03	5.31	1.43	0.70	1.42	0.56	0.33	0.41	0.321	0.2709	19.099
Gap	0.91	4.75	1.12	0.73	1.34	0.59	0.35	0.35	0.346	0.2444	23.068
Keener	0.88	4.06	1.16	0.71	1.07	0.51	0.44	0.44	0.148	0.3882	8.118
Robinson	1.12	4.74	1.03	0.84	1.29	0.60	0.26	0.26	0.346	0.3994	10.963
Rocky Branch	0.67	4.40	1.12	0.72	0.90	0.74	0.23	0.23	0.185	0.3342	6.300
Skeenah	1.17	5.14	1.01	0.80	1.45	0.59	0.25	0.26	0.358	0.3611	19.893
Watauga	0.63	5.13	1.21	0.91	1.20	0.68	0.32	0.32	0.356	0.2287	17.267

Table 2.1. Study site characteristics, Little Tennessee and French Broad river drainages. Lower case letters following site name represent sites paired by stream reach slope and basin drainage area.

Site	Reach Characteristics		Basin Characteristics			
	width (m)	gradient	drainage area (km^2)	% forested 1950	% forested 1998	Δ forest cover 1950-1998
Keener [a]	3	0.0056	7.2	92	90	-2.0
Rocky Branch [a]	2	0.0058	7.7	67	73	5.9
Robinson	5	0.0075	14.8	64	67	3.4
Watauga	4	0.0082	16.8	77	82	5.0
Gap	5	0.0084	20.3	64	73	9.3
Coweeta Church [b]	6	0.009	18.5	95	96	1.0
Skeenah [b]	4	0.0093	15.1	63	77	14.3
Darnell	6	0.0155	14.7	98	94	-4.0
Coweeta Boundary	6	0.0179	16.6	98	98	0.0

Table 2.2. U.S. EPA instream habitat unit classification scheme, taken from Kaufman and Robison 1998

Class (Code)	Description
Pools	Still water, low velocity, smooth, glasssy surface, usually deep compared to other parts of the channel
Plunge Pool (PP)	Pool at base of plunging cascade or falls
Trench Pool (PT)	Pool-like trench in the center of the stream
Lateral Scour Pool (PL)	Pool scoured along a bank
Impoundment Pool (PD)	Pool formed by constriction resulting from impoundment
Backwater Pool (PB)	Pool separated from main flow in side channel
Pool (P)	Pool (unspecified type)
Glide (GL)	Water moving slowly, with smooth, unbroken surface. Low turbulence.
Riffle (RI)	Water moving, with small ripples, waves, and eddies -- waves not breaking, surface tension not broken. Sound: 'babbling', 'gurgling'
Rapid (RA)	Water movement rapid and turbulent, surface with intermittent white-water with breaking waves. Sound: continuous rushing, but not as loud as cascade.
Cascade (CA)	Water movement rapid and very turbulent over steep channel bottom. Most of the water surface is broken in short, irregular plunges, mostly whitewater. Sound: roaring.
Falls (FA)	Free falling water over a vertical of near vertical drop into plunge, water turbulent and white over high falls. Sound: from splash to roar
Dry Channel (DC)	No water in the channel

Table 3.1. Multiple linear regression models predicting proportion of endemic fishes and habitat diversity with forest cover in 1998, stream reach slope, and basin drainage area. Habitat diversity in (b) was calculated from EPA habitat classification data ("Qualitative Habitat Diversity") and from depth, velocity, and particle size data ("Quantitative Habitat Diversity") in part (c). Boldface lines indicate the best supported model.

(a) Proportion of Endemic Fishes	AICc	Δ AICc	w_i	adj. R^2
Forest Cover 1998	**-4.148**	**0.000**	**0.592**	**0.420**
Gradient	-1.680	2.468	0.172	-0.090
Drainage Area	-1.790	2.359	0.182	0.070
Forest Cover 1998, Gradient	2.116	6.264	0.026	0.470
Forest Cover 1998, Drainage Area	2.789	6.938	0.018	0.360
Drainage Area, Gradient	4.214	8.362	0.009	0.080
Forest Cover 1998, Drainage Area, Gradient	14.063	18.211	0.000	0.370

(b) Qualitative Habitat Diversity	AICc	Δ AICc	w_i	adj. R^2
Forest Cover 1998	-0.885	1.539	0.237	0.060
Gradient	**-2.425**	**0.000**	**0.511**	**0.370**
Drainage Area	-0.690	1.734	0.215	0.010
Forest Cover 1998, Gradient	4.718	7.142	0.014	0.270
Forest Cover 1998, Drainage Area	5.770	8.195	0.008	0.050
Drainage Area, Gradient	4.713	7.137	0.014	0.270
Forest Cover 1998, Drainage Area, Gradient	16.687	19.112	0.000	0.130

(c) Quantitative Habitat Diversity	AICc	Δ AICc	w_i	adj. R^2
Forest Cover 1998	1.154	2.422	0.160	0.080
Gradient	**-1.268**	**0.000**	**0.537**	**0.500**
Drainage Area	0.190	1.458	0.259	0.280
Forest Cover 1998, Gradient	5.900	7.168	0.015	0.420
Forest Cover 1998, Drainage Area	6.373	7.641	0.012	0.350
Drainage Area, Gradient	5.723	6.991	0.016	0.450
Forest Cover 1998, Drainage Area, Gradient	17.573	18.841	0.000	0.370

Table 3.2. Pearson's correlation coefficients (*r*) between landscape and land cover variables used as predictors in models; * indicates $p < 0.05$.

	width (m)	reach slope	drainage area (km^2)	% forested 1950	% forested 1998
Reach Slope	0.73*				
Drainage Area (km^2)	0.77*	0.40			
Forest Cover 1950	0.48	0.58	-0.01		
Forest Cover 1998	0.50	0.62	0.10	0.96*	
Δ Land Cover 1950-1998	-0.33	-0.36	0.23	-0.84*	-0.66*

Table 3.3. Correlation coefficients between instream habitat characteristics and landscape and land cover variables; * indicates $p < 0.05$

	reach slope	drainage area (km^2)	% forested 1998
(a) Qualitative Habitat Units			
% pool	0.67*	0.32	0.31
% glide	0.48	-0.31	-0.77*
% riffle	0.06	0.07	0.63
% riffle + % rapid	0.24	0.18	0.82*
(b) Habitat diversity calculated from quantitative data			
Depth diversity	-0.68*	0.41	0.66*
Velocity diversity	-0.63	0.28	0.90*
Streambed particle size only	-0.56	0.50	-0.11
Depth, velocity, & particle size	-0.75*	0.61	0.48
(c) Sedimentological variables			
% particles less than 2 mm	-0.17	0.38	-0.66*
Mean particle size (mm)	0.27	0.68*	0.09
(d) Hydraulic variables			
Mean Froude number	0.12	-0.23	0.77*
Coefficient of variation Froude	0.73	0.72	0.06
Mean Reynolds number	0.53	0.60	0.39
Coefficient of variation Reynolds	0.09	-0.02	0.09

Table 3.4. Pearson's correlation coefficients for instream habitat variables and the proportion of endemic fishes; * indicates p <0.05

Independent Variable	r
Velocity Diversity	0.59
Depth Diversity	0.31
% glide	- 0.67 *
% riffle	0.54
% riffle + % rapids	0.64
% particles less than 2 mm	- 0.67 *
Mean Froude number	0.68 *

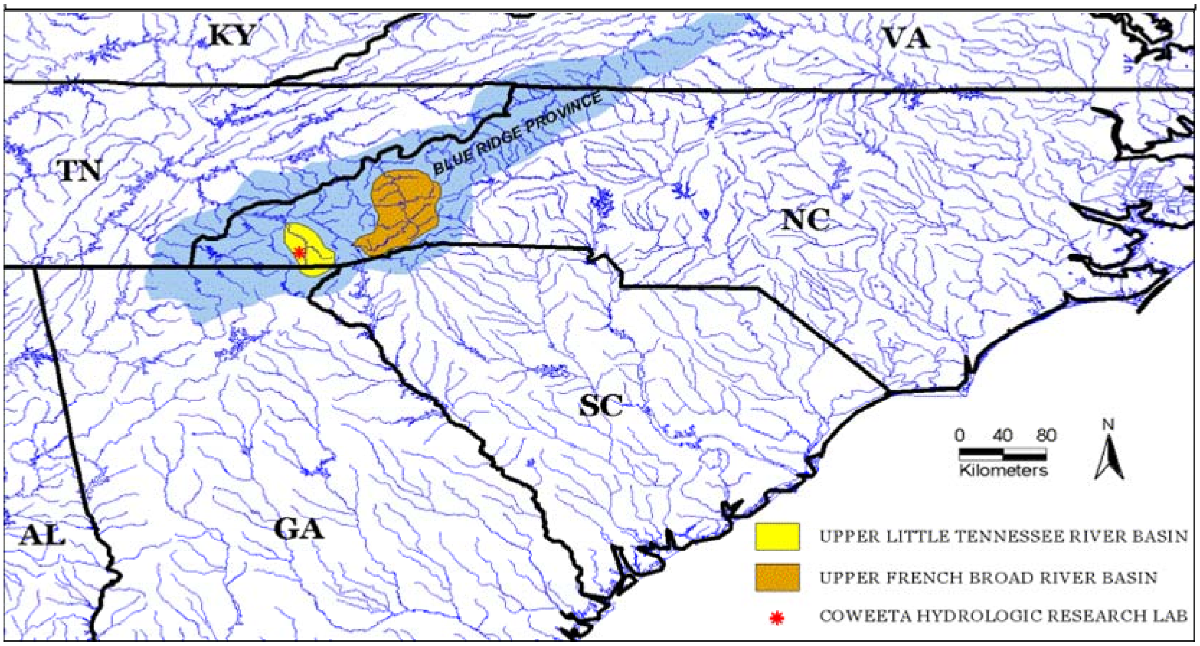

Figure 2.1. Study Area: sampling locales were situated in the Upper Little Tennessee and French Broad river basins. Shaded blue portion denotes the southern Appalachian region.

THALWEG SURVEY
-Particle size (dominant phi class) *n* = 81
-Depth *n* = 81
-Velocity *n* = 81
-Habitat unit (e.g. pool, glide, riffle, or rapid) *n* = 81

0.5X RANDOM POINTS SURVEY
-Particle size (mm) *n* = 81
-Particle size (dominant phi class) *n* = 81
-Depth *n* = 81
-Velocity *n* = 81
-Habitat unit *n* = 81

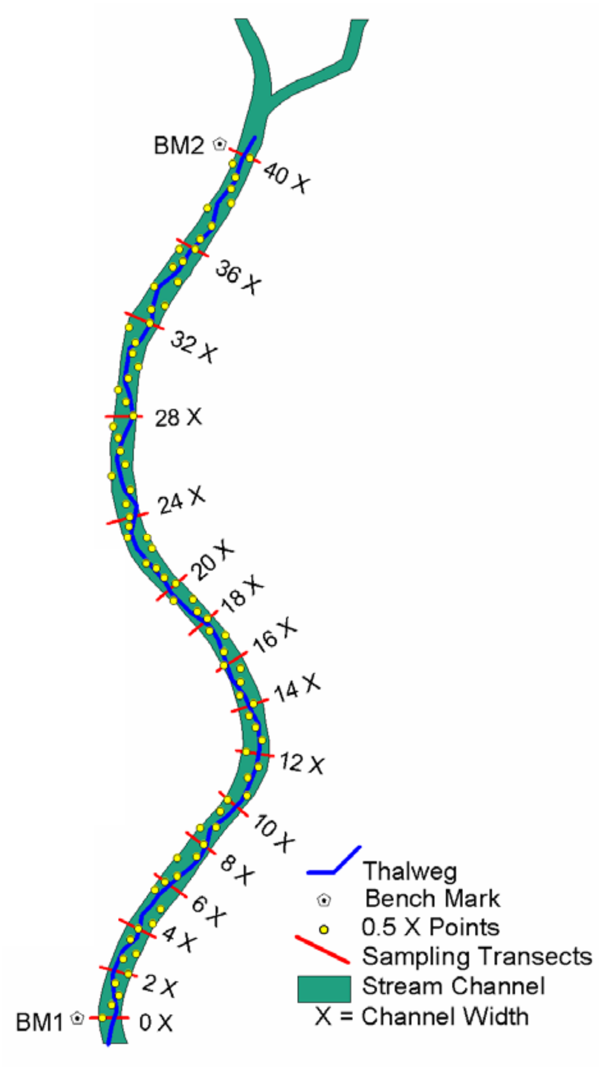

Figure 2.2. Field data collection protocol; see text for details

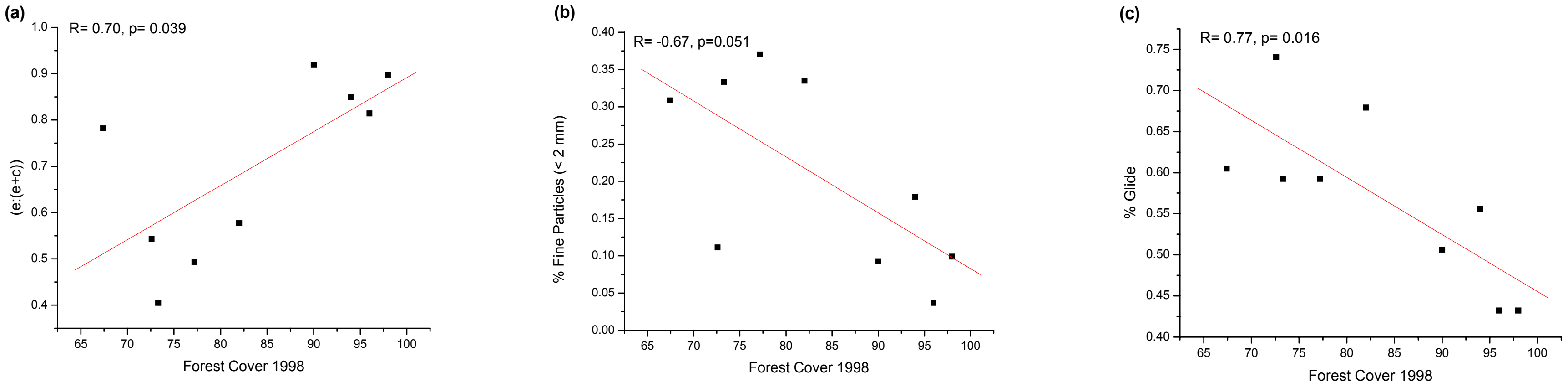

Figure 3.1. Linear regression of **(a)** the homogenization index e:(e+c)), where e is the abundance of endemic fishes and c is abundance of cosmopolitan species; **(b)** percentage of stream bed particles less than 2 mm; and **(c)** percentage of instream habitat composed of glides as a function of forest cover.

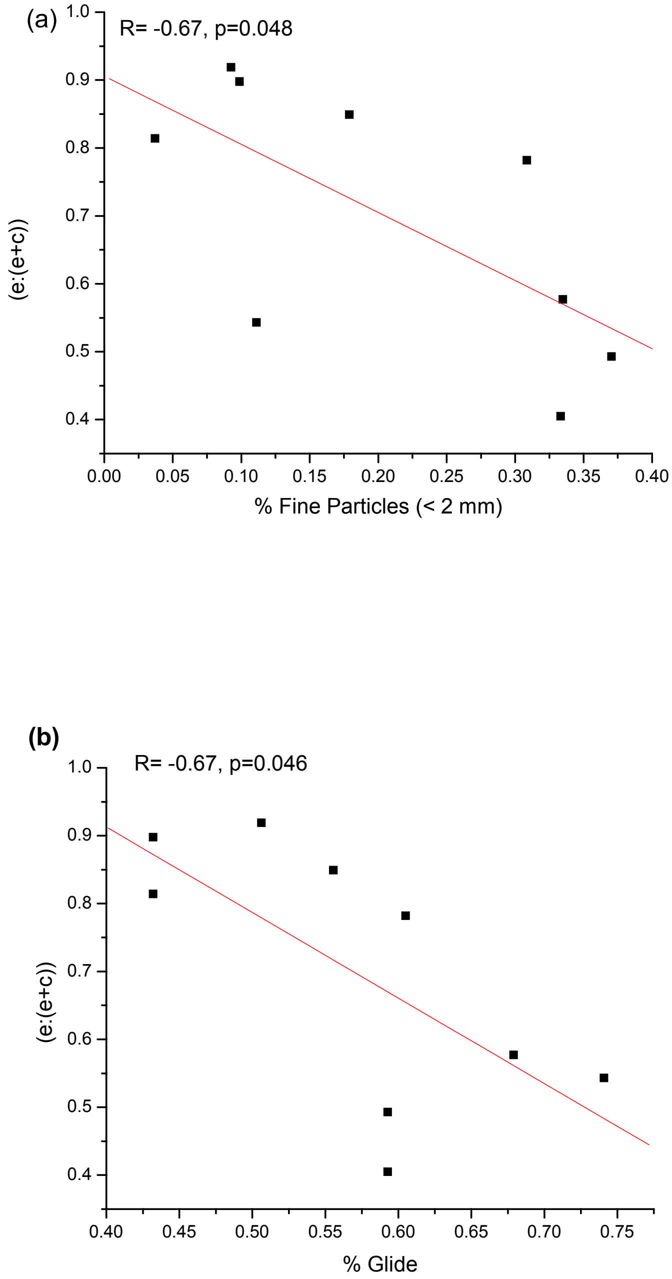

Figure 4.1. Linear regression of the relationship between the homogenization index e:(e+c)), where e is the abundance of endemic fishes and c is abundance of cosmopolitan species and **(a)** the percentage of stream bed particles less than 2 mm and **(b)** the percentage of instream habitat composed of glides.

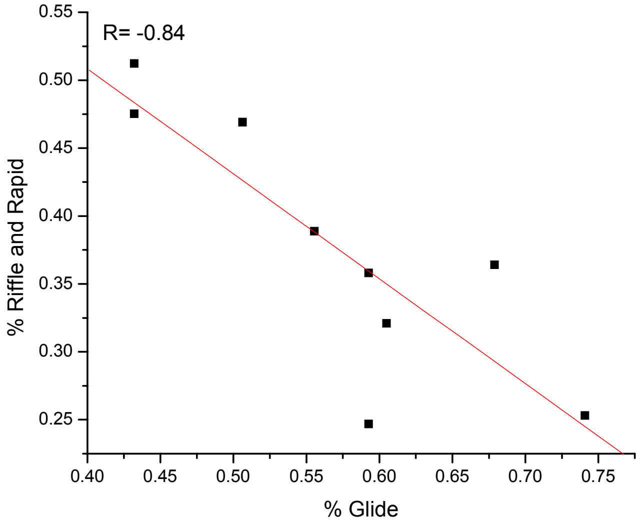

Figure 4.2. Linear regression of the percentage of instream habitat composed of riffles and rapids and the percentage of instream habitat composed of glides.