Linking stream and landscape trajectories in the southern Appalachians

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Abstract A proactive sampling strategy was designed and implemented in 2000 to document changes in streams whose catchment land uses were predicted to change over the next two decades due to increased building density. Diatoms, macroinvertebrates, fishes, suspended sediment, dissolved solids, and bed composition were measured at two reference sites and six sites where a socioeconomic model suggested new building construction would influence stream ecosystems in the future; we label these "hazard sites." The six hazard sites were located in catchments with forested and agricultural land use histories. Diatoms were species-poor at reference sites, where riparian forest cover was significantly higher than all other sites. Cluster analysis, Wishart's distance function, non-metric multidimensional scaling, indicator species analysis, and *t*-tests show that macroinvertebrate assemblages, fish assemblages, *in situ* physical measures, and catchment land use and land cover were different between streams whose catchments were mostly forested, relative to those with agricultural land use histories and varying levels of current and predicted development. Comparing initial results with other regional studies, we predict homoge-

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nization of fauna with increased nutrient inputs and sediment associated with agricultural sites where more intense building activities are occurring. Based on statistical separability of sampled sites, catchment classes were identified and mapped throughout an 8,600 km^2 region in western North Carolina's Blue Ridge physiographic province. The classification is a generalized representation of two ongoing trajectories of land use change that we suggest will support streams with diverging biota and physical conditions over the next two decades.

Introduction

Because urbanization affects so many streams in the U.S. and around the world, many authors (Lenat and Crawford 1994; Paul and Meyer 2001; Wang et al. 2003; Allan 2004) point out the need to examine streams whose catchments are in the early phases of suburban or urban land use change, i.e., before impervious surfaces dominate the hydrologic response, water chemistry, and geomorphology of streams. Such catchments are likely to be at the margins of urban centers, for example in suburban areas shifting from low density housing surrounded by forest, pasture, or row crops to higher density housing, commercial, or industrial land uses. Many biological, chemical, and physical processes in streams change in response to land use and land cover transitions that occur over large areas. These landscape-level changes include increased sediment loading (Waters 1995; Wood and Armitage 1997), contaminant loading, and nutrient loading (Delong and Brusven 1998; Hampson et al. 2000), as well as altered flow regime (Poff et al. 1997), elevated stream temperature (Scott et al. 2002), increased channel incision (Doyle et al. 2000), riparian clearing (Jones et al. 1999), loss of large woody debris (Erhman and Lamberti 1992) and habitat homogenization (Berkman and Rabeni 1987). Landscape changes in turn manifest themselves through altered invertebrate and fish assemblage structure

(Berkman and Rabeni 1987; Sutherland et al. 2002).

Agricultural land use negatively impacts streams by increasing non-point sources of sediment, nutrients, pesticides and other toxins. The percentage of agricultural land cover is a correlate of change in local-scale fish and invertebrate abundance and diversity, and large-scale fish assemblage homogenization (Scott 2001; Walters et al. 2003). When agricultural land use exceeded 50% of overall catchment land use, fish biotic integrity was notably lower in Wisconsin streams, relative to that observed in forested catchments; further, agricultural catchments supported streams with higher biological integrity than urban catchments (Wang et al. 1997). Increased impervious surface cover, which often brings increased stormflow runoff, channel scouring, and sediment supply, is often associated with decreased biological integrity in streams (Waters 1995). When impervious surfaces cover more than approximately 10% of a catchment, hydrologic and geomorphic changes have been shown to alter stream geomorphology (Booth and Jackson 1997; Doyle et al. 2000), thereby affecting biological assemblages (Paul and Meyer 2001; Roy et al. 2003; Wang et al. 2003). As land uses change, for example from rural to suburban or other developed land uses, stream ecosystem processes and biota may follow predictable trends. Scientists and managers have a sustained interest in the socioeconomic factors associated with catchment land cover and land use changes and, in turn, their effects on physical and biological processes in freshwater ecosystems (Carpenter et al. 1999; Strange et al. 1999; Wilson and Carpenter 1999; Grimm et al. 2000; Gergel et al. 2002). Understanding trajectories of land use change is necessary in order to forecast associated impacts to the physical, chemical and biological structure and function of stream ecosystems.

To address this challenge, we initiated a 30-year study comprised of (a) forecasting building activity, (b) observing catchment land use change, and (c) simultaneously measuring physical, chemical, and biological characteristics of streams in target watersheds. This linked approach will facilitate forecasting stream ecosystem response to land use change, especially in forested headwaters

of the southern Appalachians. We used an empirical model of future land use (Wear and Bolstad 1998) to identify sites throughout a large study area that are likely to support higher density housing in the future. Catchments in different regions had different land use histories (described below), and those land use legacies are likely reflected in current biological and physical properties of streams (Harding et al. 1998; Scott et al. 2002; Allan 2004). Using past research as a guide, we designed this study to infer how invertebrate and fish assemblages will diverge among catchments with different land use trajectories, where "trajectories" refers to the past, present, and expected future land use characteristics of those catchments.

In this paper, we document physical, chemical, and biological conditions among streams with distinct catchment land use histories at the beginning of a long-term study. We hypothesize that catchments with differing land use histories support streams with differing physical templets (sensu Southwood 1977) and therefore biota. We test this hypothesis through whole-assemblage and landscape-level analyses. First, ordination of diatom, macroinvertebrate, and fish assemblages provides groupings of sites with distinct taxa. We compare landscape-level descriptors as well as physical characteristics of streams among groups of sites, as defined by the ordinations. Second, we describe the biological changes that are likely to accompany two common trajectories of land use and land cover change occurring in western North Carolina: forested land cover giving way to low density residential land use; and agricultural land use yielding to higher density suburban. Third, we use cartographic modeling to map the spatial arrangement of catchments throughout a large study area that are likely to have similar flora and fauna, relative to the collections described here.

Study area and methods

The study area includes most of western North Carolina's major river systems in the Blue Ridge physiographic province in four sub-catchments of

the upper Tennessee River: the upper Little Tennessee (LT; 1,154 km^2), Tuckaseegee (1,706 km^2), Pigeon (1,403 km^2), and Upper French Broad (FB; 4,309 km^2) basins (Fig. 1). The backwater reaches of Lake Fontana, a 41 km^2 reservoir on the Little Tennessee River, define the downstream limits of the LT and Tuckaseegee River basins considered here. The Tuckaseegee was historically a major tributary of the Little Tennessee but now feeds directly into the Lake Fontana impoundment. The North Carolina border with Tennessee defines the northern extent of the Pigeon and FB study basins. Elevation in the study area ranges from 400 to 2,000 m a.s.l. In high gradient catchments, land cover is predominantly forested while land use is mostly rural and low density residential. Row crops (small farms), pasture, light industry, tourist-oriented businesses, small urban centers, and suburban land uses predominate in the valleys. The Coweeta Long Term Ecological Research (LTER) site is near Franklin, N.C. in the LT basin. Asheville (population approx. 70,000), located in the north-central portion of the FB basin, is the largest city in the region. Franklin is a small urban center (population approx. 3,500) in the LT basin. Canton (population approx. 4,000) is a comparably sized city in the Pigeon River basin.

Two basins in our study area, LT and Cane Creek (a sub-basin within the FB), typify two distinct land use histories and trajectories (see Wear and Bolstad 1998). In the LT, the most common land cover change between 1950 and 1990 was the conversion of non-forested to forested land cover and from forested without buildings to forested with buildings. Wear and Bolstad (1998) concluded that agricultural, timber production, and recreational land uses in the LT had shifted toward low density residential development associated with vacation homes. The Cane Creek catchment had higher proportions of agricultural land use in both 1950 and 1990 as well as substantially higher housing density (occasionally exceeding eight building ha^{-1}) than the LT watershed. In the Cane Creek basin, land use transitions between 1950 and 1990 were split equally between forest clearing and reforestation, but both land cover transitions supported equal increases
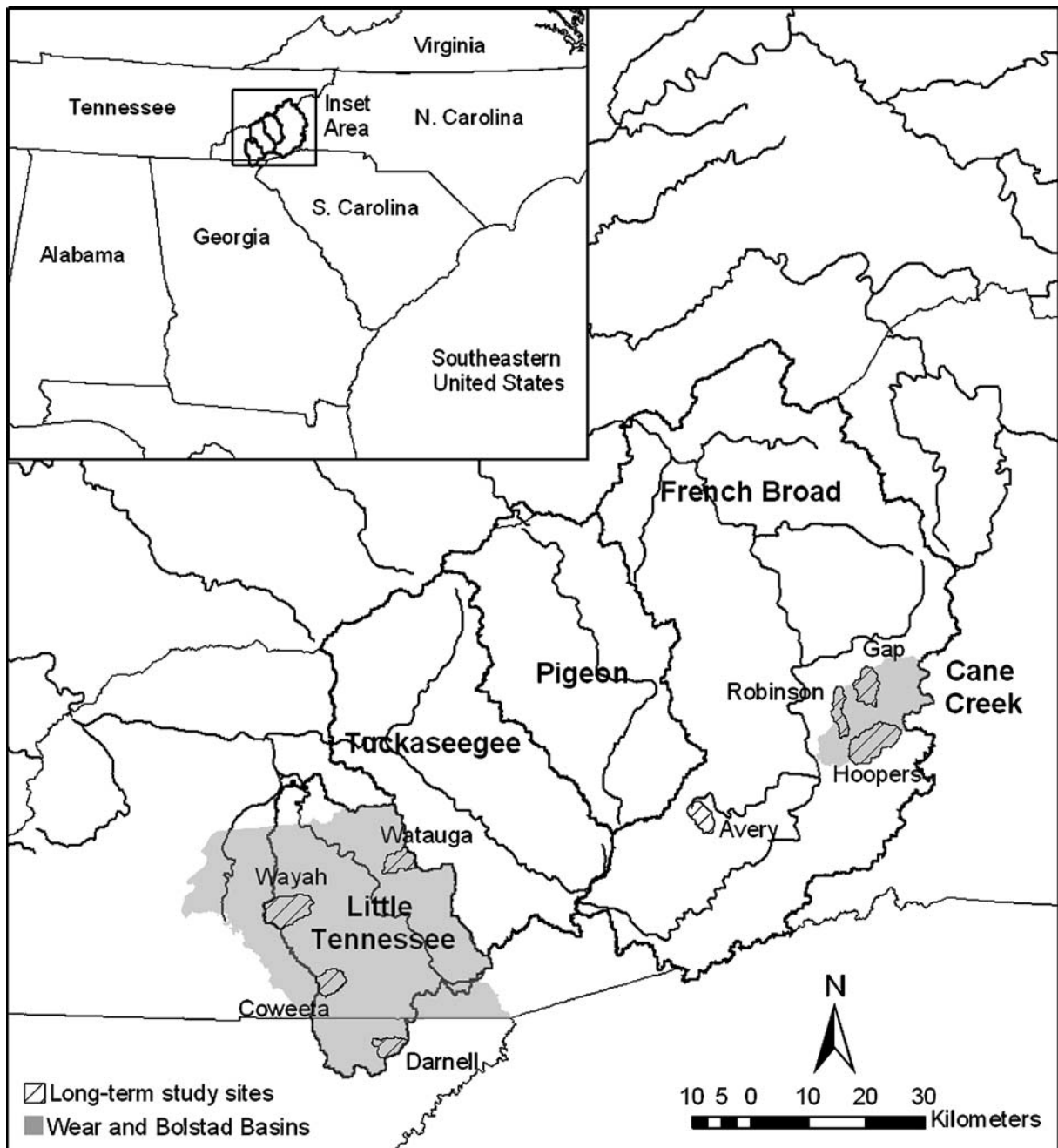
Fig. 1 Sampling catchments and study area in the southern Blue Ridge province of western North Carolina

in housing density. Whereas rural second home development in forested catchments was evident in the LT, suburban land use was replacing agricultural land use in Cane Creek at the outset of this study.

Site selection

We used projected growth in building density from the LT and Cane Creek (Wear and Bolstad 1998) to establish a set of stream research

sites where ecosystem changes will likely occur in coming years. In the southern Blue Ridge physiographic province, streams in forested catchments are typically cool, clear, low in nutrients and primary productivity, and have relatively low fish diversity (Wallace et al. 1992; Scott and Helfman 2001). Headwater streams may be important refugia for endemic fish species as well as sensitive riverine taxa that migrate to small streams to spawn, or for thermal refugia. Decreased forest cover in a catchment can raise temperatures, increase nutrient supply (Scott and Helfman 2001; Scott et al. 2002), and lead to increased suspended and bedload sediment yield in streams (Lenat and Crawford 1994; Harding et al. 1998; Sutherland et al. 2002). We therefore expect increases in sediment flux, nutrient supply, and runoff when forested land with no buildings is converted to non-forested land with buildings. In streams that drain watersheds that change from agricultural to urban land cover we expect to see a long-term reduction in sediment, increased metal concentration, increased temperature due to riparian loss, channel incision, and lower baseflow accompanied by greater discharge immediately following storms.

Two metrics were used to identify sites with a high likelihood of increased building density. The first metric, the difference between building density projected for 1990 and building density observed in 1990 (Wear and Bolstad 1998), was a measure of the uncapitalized value inherent in land parcels that were accessible and in desirable locations in 1990. The second metric, the difference between building density projected for 2030 and observed building density for 1990 (Wear and Bolstad 1998), was a measure of expected future trends in land use. Where both indices exceeded three buildings in a 9 ha neighborhood, we inferred a high likelihood that building activity would proceed by 2030. Observable changes to streams are expected where building activities are concentrated near streams, so pixels meeting each of these criteria were mapped if they lay within 100 m of streams on previously undeveloped land parcels. The 100 m distance was chosen in order to include construction activities near streams but not confined to active floodplains. Our definition of "undeveloped" was a land parcel that had been

forested since 1950 and that had fewer than one building per 9 ha in both 1950 and 1990. This 40-year horizon was intended to limit the confounding influence of the "ghost of land use past," a concept that posits biota may differ in catchments that have similar present-day catchment land use but different historic land use (Harding et al. 1998; Allan 2004). Pixels that met all the criteria described above were included in the Composite Hazard Index used henceforth.

Potential study catchments were restricted to sizes between 10 and 40 km^2 in area and outlet elevations between 550 and 720 m a.s.l. because these size and site elevation ranges were associated with shifts in assemblage structure for fishes in this region (Scott 2001). Watersheds containing relatively large numbers of Composite Hazard Index pixels were identified and visited. At the beginning of this study, buildings were already being constructed in many of those catchments, indicating our land use trajectory model had merit. Six catchments with numerous Composite Hazard Index pixels but which did not show evidence of recent building activity near streams were selected for long-term study (Fig. 1, Table 1). These are henceforth termed "hazard sites." Two reference streams were located on land owned and managed by the US Forest Service (USFS) where land use was not expected to change over the projected 30-year duration of the study. The reference stream located in the LT basin is Coweeta Creek and is at the entrance of the USFS Coweeta Hydrologic Laboratory. Further evidence for the efficacy of Wear and Bolstad's (1998) empirical model was that the Composite Hazard Index predicted the location of forest service buildings erected at Coweeta in 2002, well after the publication date of the model. The reference stream located in the FB basin is Avery Creek, and is in the Pisgah National Forest near Brevard, N.C. Both reference sites are on public lands supporting recreation and land management research.

Ecosystem assessments

Biological assessments

Biological and physical assessments were conducted during the summer of 2000 at the six

Table 1 Land use, % composite hazard index pixels within 100 m of streams, algal, and geomorphic factors among the eight "hazard" sites chosen for long-term research

	Upper Little Tennessee River basin				Upper French Broad River basin			
	Darnell	Wayah	Watauga	Coweeta[a]	Avery[a]	Gap	Robinson	Hoopers
Land use and projected development								
% Forest 1993	98	98	85	98	100	72	65	72
% Developed 1993	0.0	0.11	5.3	0	0.02	0.86	6.2	0.63
% Agriculture 1993	1.5	2.2	8.8	1.2	0.44	27	28	28
% Forest—10 m Buffer, 1993	80.3	56.6	44.9	88.9	83.6	46.9	36.6	67.4
% Forest 1970	99	98	84	100	99	70	64	73
% Forest 1950	97	98	76	98	100	64	64	68
% Composite Hazard Index in 100 m Stream Buffer	<1	2.2	2.0	<1	<1	7.7	7.6	3.4
Algal and geomorphic conditions								
AFDM (mg m^{-2}; s.d.; $n = 3$)	1.1 (1.3)	4.8 (11)	1.7 (0.84)	0.85 (1.1)	0.88 (0.29)	2.2 (0.90)	0.8 (0.84)	1.2 (0.98)
chl-a (µg m^{-2}; s.d.; $n = 3$)	115.7 (112.4)	89.1 (42.8)	109.1 (119.7)	35.1 (21.2)	60.4 (47.4)	299.6 (226.9)	42.4 (29.6)	48.7 (18.1)
Average ϕ ($n = 100$)	−4.4	−5.3	−3.8	−4.6	−5.5	−5.1	−2.9	−2.6
D$_{90}$ (mm)	200	200	120	150	280	400	72	22
% Fines ($n = 3$ per site)	9.6	10.0	15.5	3.3	13.7	13.1	18.4	36.1
TSS (mg l^{-1}; s.d.; $n = 3$)	14.7 (22.7)	13.3 (6.1)	132.3 (14.0)	6.1 (4.7)	3.2 (0.8)	14.7 (2.8)	8.0 (2.8)	19.2 (7.6)

[a] Reference site

hazard sites and two reference sites. Benthic periphyton was quantitatively sampled with a modified Loeb sampler (Loeb 1981). Three samples were collected and composited from representative rocks at 10-m intervals along a 100-m transect above the downstream end of each sampling reach. Samples were preserved on ice, bulked, and later sub-sampled to determine chlorophyll *a* concentration and ash-free dry mass (AFDM) using standard methods (Wetzel and Likens 1991). Subsamples were processed using standard methods (Lowe and LaLiberte 1996) and prepared as permanent slides to enumerate diatom species composition and densities to the lowest taxonomic unit possible using algal floras from the southeastern USA (Camburn et al. 1978; Kociolek and Kingston 1999). Only diatoms were quantified because they comprise the majority of periphyton in southern Appalachian streams (Lowe et al. 1986; Greenwood and Rosemond 2005). Macroinvertebrates were collected by quantitative kick net sampling within each sample reach (see Harding et al. 1998). Macroinvertebrates were identified to genus, and densities were recorded. At each site, fishes were collected and identified to species from representative 50-m reaches between April 16 and July 6, 2000 using a backpack electroshocker, seines, and dip nets. Fishes were enumerated and classified as "cosmopolitan" or "highland endemics" which generally refer to widespread species and those restricted to high gradient, headwater streams in the southern Appalachians (see Scott and Helfman 2001).

Specimens for all taxa have been accessioned at the Georgia Museum of Natural History for future reference. For diatoms, this includes permanent slides and the remainder of samples (preserved in formalin). All macroinvertebrates were preserved in alcohol and archived. Voucher fish specimens have previously been catalogued. These museum records establish an important reference collection for future efforts.

Physical assessments

Sediments were sampled using a 60 cm high × 25 cm diameter stainless steel cylinder in three riffles and three pools at each site to a depth of 10 cm wherever bedrock or boulders were not reached first. Large sediment (>64 mm) was weighed in the field; remaining sediment was dried and weighed in a laboratory to calculate % by weight of coarse (2 to 64 mm) and fine (<2 mm) fractions. Medial axes of one hundred particles from the stream bed were measured (Gordon et al. 1992) while traversing a "zig-zag" pattern in riffle habitats at each site. Measurements were converted to phi size (ϕ; negative base two logarithm). Average ϕ and the 90th percentile for medial axis lengths (D_{90}) were calculated for comparison among sites.

Three 125 ml water samples were collected from the thalweg of run habitat. Water samples were filtered with a hand pump in the field onto pre-ashed, pre-weighed 47 mm diameter, 0.45 μm mesh Whatman® glass fiber filters. These were placed in aluminium foil envelopes, dried in a 105°C oven for 24 h, and weighed to determine total suspended solids (TSS, mg l^{-1}). Filtrates were placed on ice and subsequently analyzed for NH_4, NO_3, SO_4, PO_4, K, Na, Ca, and Mg using methods outlined in Deal (2001). Stream temperature was collected at all eight sites from August 3 to September 15, 2000. The total range (maximum–minimum) of late summer temperature was determined for each site as an indicator of temperature variability.

Land cover data were compiled previously (Wear and Bolstad 1998). Because riparian forest data were not sufficiently resolved at the 30 m resolution of those data, false color digital orthophoto images acquired in 1993 were downloaded from the U.S. Geological Survey (seamless.usgs.gov) and analyzed using a semi-automated contextual classification procedure (Laacke 2000). Each stream bank and individual trees were clearly visible in the images, so use of high resolution aerial photographs allowed precise estimates of riparian cover within 10 m of each side of river channels (Table 1). Excluding road density measures, land cover data were largely multicollinear across all sites (see King et al. 2005 for more discussion on multicollinearity of land cover parameters), with *r*-values of 0.7 or more. A principal component, henceforth termed "PC1," encapsulated 98.8% of the variation in elevation, riparian forest cover in 1970 and in 1990, building densities during both epochs,

catchment-wide % forested area, and catchment-wide % agricultural land cover in the 1970s and 1990s. To assess land cover differences among groups of sites identified through ordination (as described in the following section), PC1 was used in lieu of those individual, multicollinear measures.

Statistical analyses

Differences among diatom, macroinvertebrate, and fish assemblages at all sites were analyzed using cluster analysis (Wishart 1969; Greig-Smith 1983), Wishart's objective function (Wishart 1969), and nonmetric multidimensional scaling (NMS; Kruskall and Wish 1978) in PC-Ord (McCune and Mefford 1999). Both cluster analysis and NMS require a measure of similarity or dissimilarity between all possible pairs of sites, so a Bray–Curtis dissimilarity matrix was calculated from fourth-root transformations of diatom density (cells/ml), macroinvertebrate density ($\#/m^2$), and fish abundance (#/sample). This transformation reduced the influence of the most abundant taxa on site scores, allowing less common species to contribute to site rankings (Clarke 1993). The group average distance function was used to calculate between-site distances in the *n*-dimensional space defined by Bray–Curtis dissimilarities (UPGMA in McCune and Mefford 1999) so that sites were given equal weight regardless of the number of observations per site.

Wishart's (1969) objective function indicates how much of the total sum of squared distances between sites (based on Bray–Curtis dissimilarity) is captured by that group of sites. The % Information Remaining statistic indicates the relative distance, in Bray–Curtis dissimilarity space, between individual sites or between groups of sites defined by branching points in a dendrogram. If a given group spans a large proportion of the objective function distance, that group consists of sites with heterogeneous assemblages. If the objective function's span for a group is small, that group is relatively homogeneous. In cluster analysis, it is customary to prune a cluster dendrogram, a process whereby the analyst defines

unique clusters based on the maximum allowable difference between sites within a given group. The Wishart objective function (Wishart 1969) provides a standard measure against which to prune dendrograms. If a dendrogram is pruned at so that there is a large % Information Remaining, the resulting groups are homogeneous. Conversely, as % Information Remaining decreases for a given dendrogram node, groups of sites in adjacent dendrogram branches are biotically more similar. If groups of sites branch at 0% Information Remaining, there is no floral or faunal affinity among groups in those branches. Due to small sample sizes, we pruned trees with narrowly defined clusters at 75% Information Remaining.

Ordination plots from NMS provided another representation of between-site similarity and dissimilarity for each taxonomic group. To ensure an optimal NMS solution, PC-Ord's (McCune and Mefford 1999) "autopilot/slow and thorough" mode was used in which 40 iterations were performed on the Bray–Curtis matrix; 50 additional runs were performed with randomized data so that the final solution could be compared to solutions that might be obtained by chance alone. These methods are well represented in ecological literature comparing aquatic assemblages to one another and to environmental gradients (McRae et al. 1998; Ford and Rose 2000; Hawkins et al. 2000; Hawkins and Vinson 2000; McCormick et al. 2000; Heino et al. 2003; Mykra et al. 2004; Ilmonen and Paasivirta 2005). Clarke (1993) discussed in detail several advantages of the NMS methodology employed here. Cluster dendrograms and NMS ordination plots visually and quantitatively demonstrate assemblage differences among sites in this study.

For all of the ordinations and classifications described above, indicator species analysis (Dufrene and Legendre 1997) highlighted taxa that contributed to similarity and differences within and between groups of sites. Monte Carlo tests of significance based on 1,000 randomizations of the original species matrices were used to indicate the level of significance of indicator values (McCune and Mefford 1999). Physical and chemical differences between site groupings were analyzed using *t*-tests and ANOVA in S-plus (Mathsoft 1999)

based on the groups identified through cluster analysis and NMS ordination.

Inferring landscape and stream trajectories

We compared the fish data already described with fish collections from 1995 and 1996 (see Scott 2001) from eight sites meeting the elevation range and catchment size criteria established at the outset. We recognize that abundance, presence, and absence of taxa vary at a site year to year (Freeman et al. 1988), but ordination examines the ranking of species across sites; our fourth-root transformation (see above) of raw data further emphasized presence and absence within each sites flora and fauna. If only a few taxa are present one year but not another, then ordination should be robust for analyzing landscape correlates of entire assemblages. Previous studies suggested that fish assemblage structure may be considered stable in this context, especially compared to macroinvertebrates (Desmond et al. 2002). Because land use and land cover are not generally changing rapidly in our study area, land use data used in this study were valid for the data collected in 1995 and 1996. Scott's (2001) fish collection methods were identical to those described above. By viewing more sites, we were able to examine fish assemblage differences in catchments with more residential land use but which were otherwise similar to the hazard sites' catchments. For heuristic purposes, these data were pooled with the collections from 2000 and ordinated using methods described above. The additional sites extended the gradient of development intensity sampled for this study, thus providing a space-for-time substitution that allowed us to explore possible future biotic states in hazard site catchments. Using the methods described above, ordination was used to identify distinct assemblages of fishes. We identified land use factors that were correlated with groups of sites identified through ordination. We classified catchments based on the land use factors that were strong predictors of fish assemblage structure in this pooled data set, thus providing a whole-landscape set of predictions about fish assemblages across a large portion of western North Carolina.

Table 2 Summary of ordination results: most of the inter-site differences in Bray–Curtis space were encapsulated in two-axis NMS solutions with minimal stress

| % Variance in distance matrix represented by NMS axes			
Focal group	Final stress	Axis 1	Axis 2
Diatoms	3.9	45%	40%
Macroinvertebrates	3.2	7%	86%
Fishes	2.5	18%	79%

Results

Assemblage ordinations

All three NMS ordinations of assemblage data produced two-axis solutions with low instability (i.e., instability <0.00001) and stress values below 5 (Table 2). The patterns represented by each graph accurately represent between-site dissimilarity based on Bray–Curtis distance (Clarke 1993).

The NMS ordination and indicator species analysis using diatom species data separated the reference sites (Coweeta and Avery) from all other sites (Fig. 2a and b). Three sites (Gap, Robinson, and Wayah) comprised a second, distinct cluster evident at the 75% Information Remaining level (Fig. 2b). Six diatom species were found at both reference sites and not found at any other sites (Table 3). Three of those species typically dominate assemblages in oligotrophic, heavily shaded habitats (Greenwood and Rosemond 2005; Potapova and Charles 2007). One species is known to be shade-tolerant and endemic to southern Appalachian streams and wetlands (Brant 2003). Species richness was low at the reference sites. One reference site, Coweeta, had only 24 diatom species whereas the other sites collectively had between 42 and 59 species each. Not surprisingly, less-forested sites were dominated by diatoms that are shade-intolerant and are associated with streams having moderate nutrient inputs. Riparian forest cover was significantly greater at the cluster of reference sites (86.3%) than at the other group of tightly clustered sites (46.6%; t-test, $p <$ 0.01). Contrasting with both of those groups were the remaining sites, which collectively had an intermediate level of riparian forest cover (64.9%).

Fig. 2 Nonmetric multidimensional scaling ordination results for diatoms sampled from benthic periphyton at eight hazard sites. A plot of site scores (**a**) shows that the two reference sites are very distinct from the remainder of sites in the study. Cluster analysis (**b**) confirmed this pattern
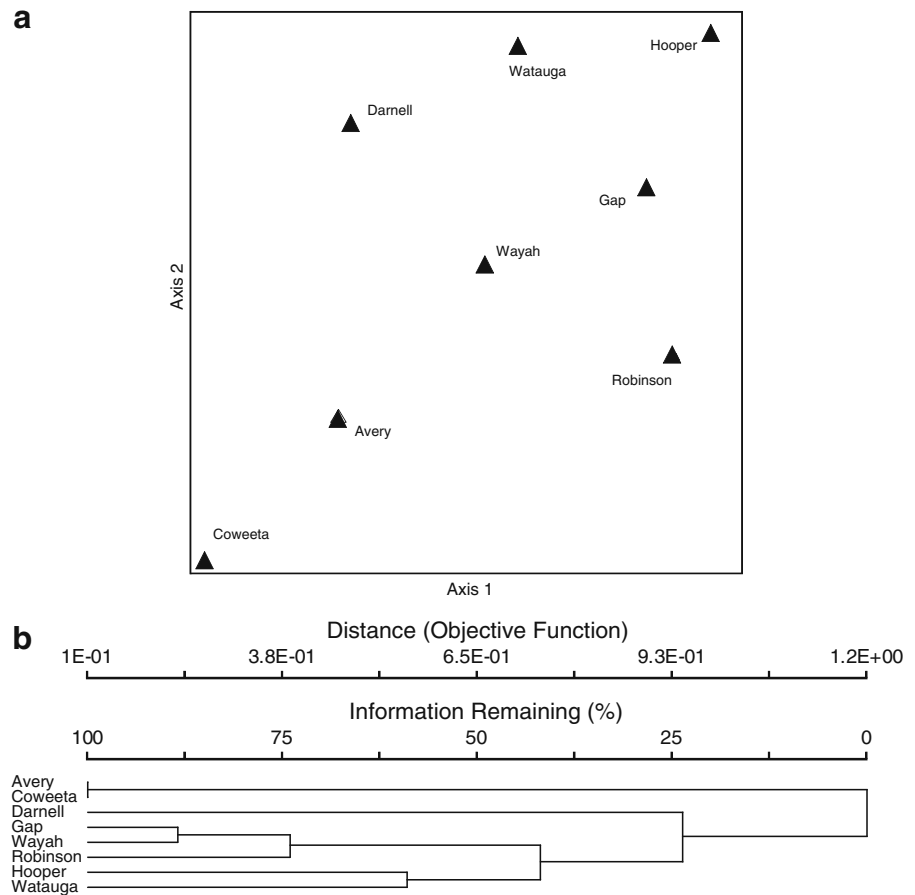
In other words, there was a detectable difference in diatom assemblages in forested vs. non-forested catchments, and catchments with intermediate forest cover included species found in both of those other groupings, i.e., cosmopolitan taxa. Analysis of variance showed that the gradient from high to low riparian forest was statistically significant ($p = 0.04$) across those three sets of sites. No other physical descriptor of stream habitats or their catchments was statistically different among the groups of sites identified through cluster analysis of diatom assemblages.

Clustering among macroinvertebrates yielded different groupings than those observed based on diatoms. One relatively tight cluster, consisting of the reference sites and two others from the LT basin, is evident in the NMS ordination and cluster analysis of macroinvertebrate densities (Fig. 3). This cluster spanned less than 20% of the Wishart objective function (Fig. 3b) owing to the simi-

larity of density and diversity of taxa amongst these sites. Macroinvertebrate assemblages at the remaining sites were not similar to one another nor to the tightly grouped sites. Seven macroinvertebrate genera were found among the tightly grouped sites and nowhere else (Table 3), a result that did not likely occur by chance alone (Monte Carlo permutation test $p = 0.033$ for each). The tight cluster of sites was more speciose than the remaining sites (59 vs. 33 species on average; one-tailed t-test, assuming unequal variance $p = 0.005$). The density of individuals in orders Ephemeroptera, Plecoptera, and Trichoptera (EPT) was significantly higher in the tight group of sites than among all other sites (t-test, $p = 0.04$ based on log-transformed data). The land cover and terrain metric PC1 was significantly different (t-test, $p = 0.002$) between the clustered and unclustered sites. Greater catchment-wide forest cover (and less agricultural area) was associated

Table 3 Taxa associated, via indicator species analysis Monte Carlo permutation tests, with groups of sites identified by NMS and cluster analyses (Figs. 2, 3, and 4)

Diatoms at reference sites	Diatoms in other cluster (Gap, Robinson, and Wayah)	Macroinvertebrates at reference sites	No macro-invertebrate clusters among other sites	Fishes only at less developed sites	Fishes only in more developed sites (Gap, Hooper, Robinson)
Achnanthes hungarica	Achnanthes suchlandtii	Acentrella (Ephemeroptera Baetidae)		Rhinichthys cataractae	Notropis rubricroceus
Diatoma mesodon (Ehr.) Kütz.[a]	Cymbella affinis	Paraleptophlebia (Ephemeroptera Leptophlebiidae)		Oncorynchus mykiss	Rhinichtys atratulus[d]
Eunotia incisa W. Sm.[a]	Fragilaria crotonensis	Cinygmula (Ephemeroptera Heptageniidae)			Hypentelium nigricans[d]
Eunotia pectinalis var. minor (Kütz.) Rabeh[a]	Geissleria decussis(Østrup) Lange–Bert and Metzeltin in Lange–Bert.[c]	Tallaperla (Plecoptera Peltoperlidae)			Etheostoma flabellare
Meridion alansmithii Brant[b]	Melosira varians Agardh[c]	Glossosoma (Trichoptera Glossosomatidae)			Semotilus atromaculatus[d]
Synedra acus	Navicula cryptocephala Kütz.[c]	Lepidostoma (Trichoptera Lepidostomatidae)			
		Atherix (Diptera Athericidae)			

Due to sample sizes, p-values differ for Monte Carlo tests differ by taxonomic group: diatoms ($p < 0.1$); macroinvertebrates ($p < 0.033$); and fishes ($p < 0.1$)

[a]Taxa identified by Greenwood and Rosemond (2005) and Potapova and Charles (2007) as indicative of forested, oligotrophic headwater streams

[b]Shade-tolerant, endemic to southern Appalachian streams (Brant 2003)

[c]Somewhat shade-intolerant, mesotrophic diatoms

[d]Cosmopolitan fishes listed by Scott and Helfman (2001)

Fig. 3 Nonmetric multidimensional scaling ordination (**a**) and cluster analysis (**b**) results for macroinvertebrates from eight hazard sites
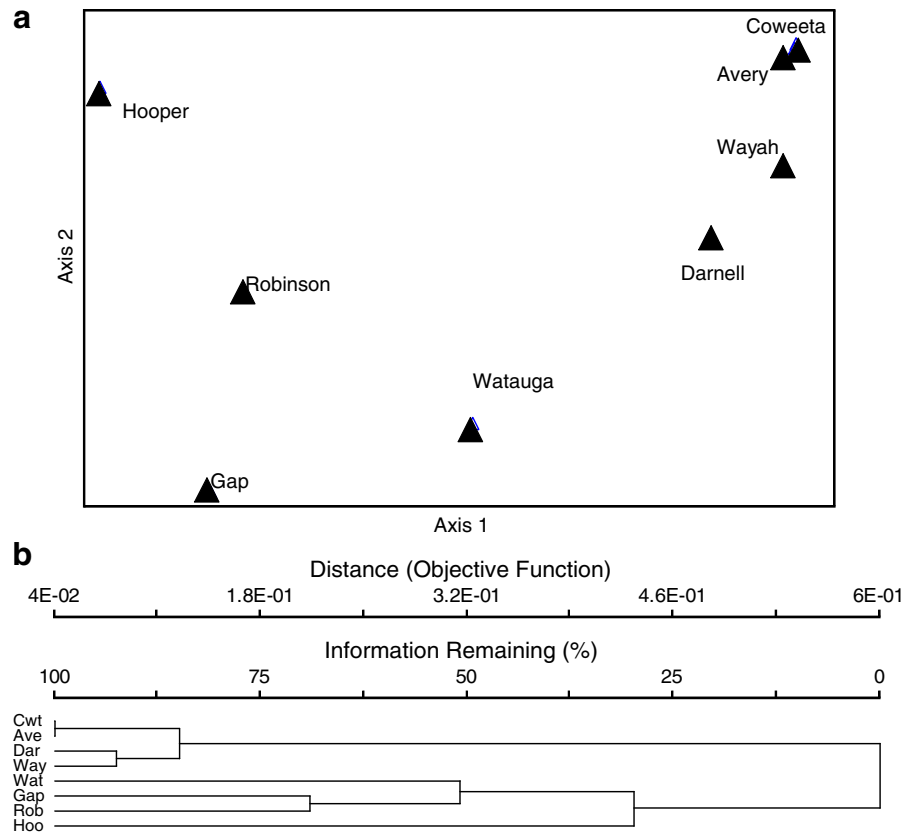
with the tight cluster of sites. Nitrate ($p < 0.001$) and sodium ($p = .001$) were higher in the tight cluster; cations (K, $p < 10^{-6}$; Ca, $p = 0.001$; Mg, $p = 0.001$), SO$_4$ ($p = 0.006$), temperature range ($p = 0.02$), and substrate particle size (ϕ, $p = 0.006$) were all lower in the tight cluster of sites relative to the remaining sites.

Two groups comprising three sites each are readily apparent in the NMS ordination graph (Fig. 4a) as well as at the 75% Information Remaining level of the cluster analysis (Fig. 4b) of fish observations. Coweeta, Wayah, and Darnell creeks had more (*t*-test on angular transformation of proportions; $p < 0.001$) highland endemic fishes (76% by abundance) than the three sites in the lower right in Fig. 4a (46%, by abundance). The group in the upper left also had fewer cosmopolitan fishes (1%, by abundance, of fauna) than the group to the lower right (42%, by abundance; *t*-test, $p = 0.0035$). The group to the upper left (Fig. 4a) had significantly fewer species than the group depicted in the lower right (mean

richness 8.3 vs. 13 species; *t*-test $p = 0.024$). The land cover and terrain metric, PC1, was significantly different between the groups of sites distinguished by fish abundance and diversity ($p < 0.0001$). Nutrients and trace metals had lower concentrations for the group with more highland endemics: NO$_3$ ($p < 0.005$), K ($p < 0.0005$), Na ($p < 0.005$), Mg ($p < 0.05$), and S0$_4$ ($p < 0.01$). Most of the fishes found in the tight cluster of sites with higher ion concentrations and less forest cover were cosmopoloitan taxa (Table 3; Scott and Helfman 2001). While not endemic highland species per se (Scott and Helfman 2001), both fish species found in the more forested sites (Coweeta, Wayah, and Darnell) are commonly associated with headwater streams with clean substrate (Jenkins and Burkhead 1994).

Landscape-level inferences

An NMS ordination (NMS) of fish assemblages at 16 sites (Fig. 5a)—including eight sites not

Fig. 4 Nonmetric
multidimensional scaling
ordination (**a**) and cluster
analysis (**b**) results for
fishes from eight hazard
sites
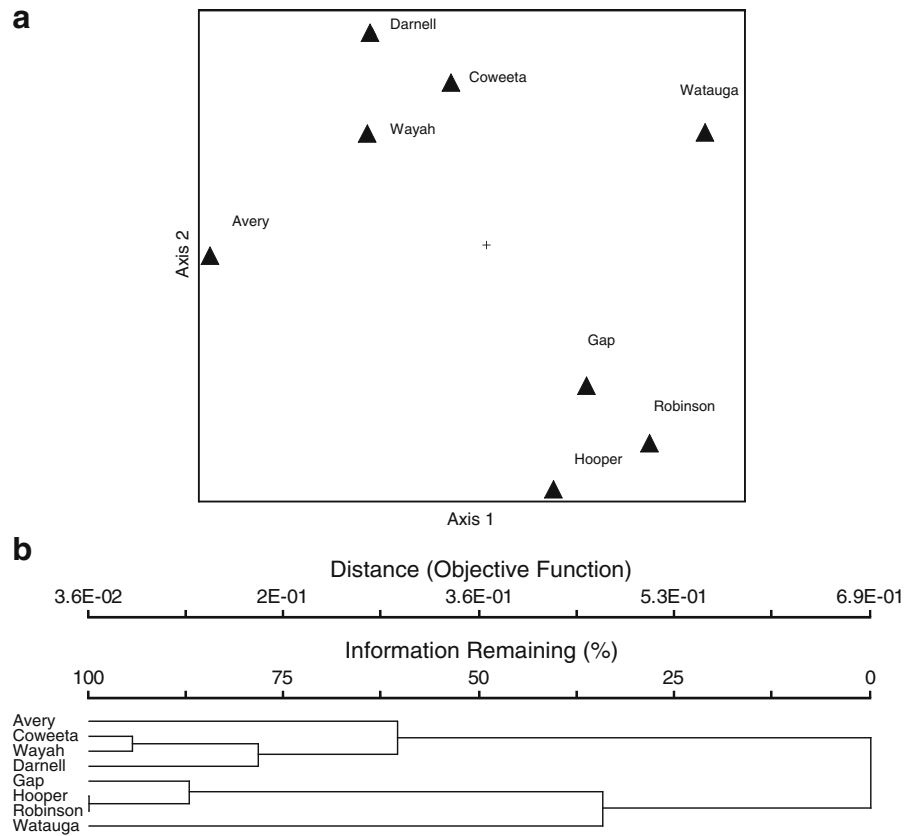
analyzed in the previous analysis—encapsulated about 90% of the variation present in the matrix of Bray–Curtis dissimilarities between all sites. The positions of sites where future development is expected, relative to reference sites, was identical to that observed prior to analyzing the eight additional sites (Fig. 4a). Similarly, the cluster analysis dendrogram positions for sites were very similar between analyses (Figs. 4b and 5b). Four clusters are apparent at the 50% information remaining level (Fig. 5a dotted lines; Fig. 5b). The two groups with positive Axis 2 scores all had catchments with greater than 85% forested area, road density less than 3 km/km^2, and catchment-wide agricultural land use less than 3%. Sites with negative Axis 2 scores had less forested area and greater road density. This difference in land cover was accompanied by a suite of differences in water chemistry and temperature range (Table 4).

The distinctions observed among groups of sites depicted in Fig. 5 can be used to derive

a decision tree that can be used to hypothesize ecosystem states likely to occur across the region (Fig. 6a). Compared to Forested sites, catchment-wide agricultural land use ($p < 0.01$) was greater among sites depicted in the upper left corner of Fig. 5a. These are labeled "Rural." Sample sizes were too small to yield statistically powerful results for the sites with negative Axis 2 scores. It appeared there were more roads in the sites to the lower right of Fig. 5a (hereafter termed "Suburban/Urban") than in the lower left (hereafter termed "Suburbanizing Agriculture"; t-test, $p = 0.16$). Haw Creek was an outlier in this analysis; its channel is dominated by concrete, boulders used for stabilization, and its catchment consists mostly of urban land use. There were clear breaks in this data set that separated Forested, Rural, Suburbanizing Agriculture, and Suburban/Urban sites (Fig. 6a) which were used to classify watersheds of comparable size throughout the study area (Fig. 6b). Land use characteristics of each classification (Table 5) show that these classes

Fig. 5 Nonmetric multidimensional scaling ordination (**a**) and cluster analysis (**b**) results for fishes observed at 16 sites with comparable catchment size and outlet elevation. *Dotted lines* in **a** represent the 50% Information Remaining criterion
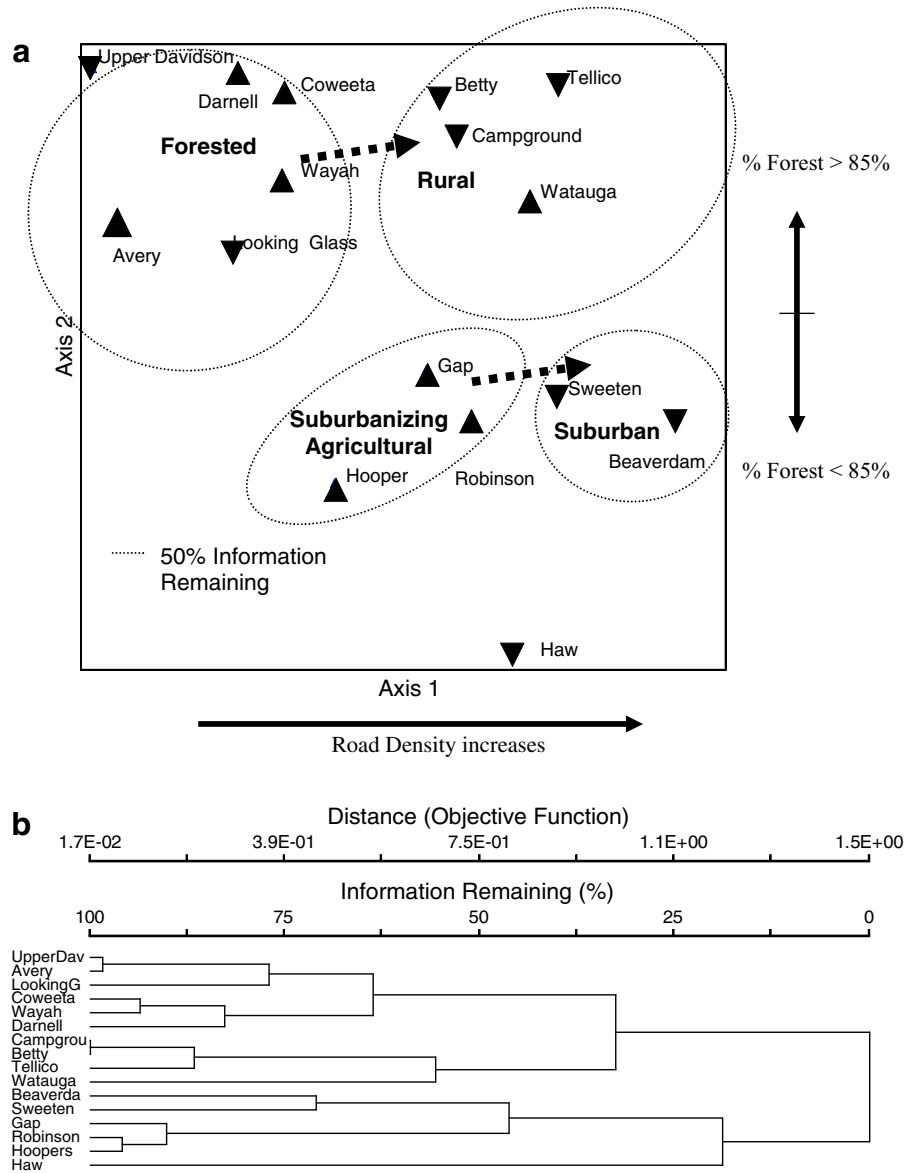

Table 4 Nutrient chemistry and temperature range ANOVA results for streams in four catchment classes identified through fish ordination

	Forested (n = 6)	Rural (n = 4)	Suburbanizing agriculture (n = 3)	Urban (n = 3)
NO_3 (mg l^{-1})	0.044	0.083	0.33	0.69
NH_4 (mg l^{-1})	0.011	0.014	0.021	0.059
PO_4 (mg l^{-1})	0.018	0.024	0.021	0.025
K (mg l^{-1})	0.53	0.69	1.83	2.01
Na (mg l^{-1})	1.52	1.44	4.85	4.84
Ca (mg l^{-1})	0.98	1.29	5.36	6.59
Mg (mg l^{-1})	0.41	0.48	1.73	2.84
SO_4 (mg l^{-1})	0.97	1.14	2.75	4.92
Late summer temp. range (°C)	17.8	19.3	18.9	21.0

Fig. 6 Catchments with similar areas and outlet elevations were compared to sampled streams to infer possible stream ecosystem states through the study area. Decision rules are outlined in (**a**) while the resultant catchment classes are mapped onto the landscape in (**b**)
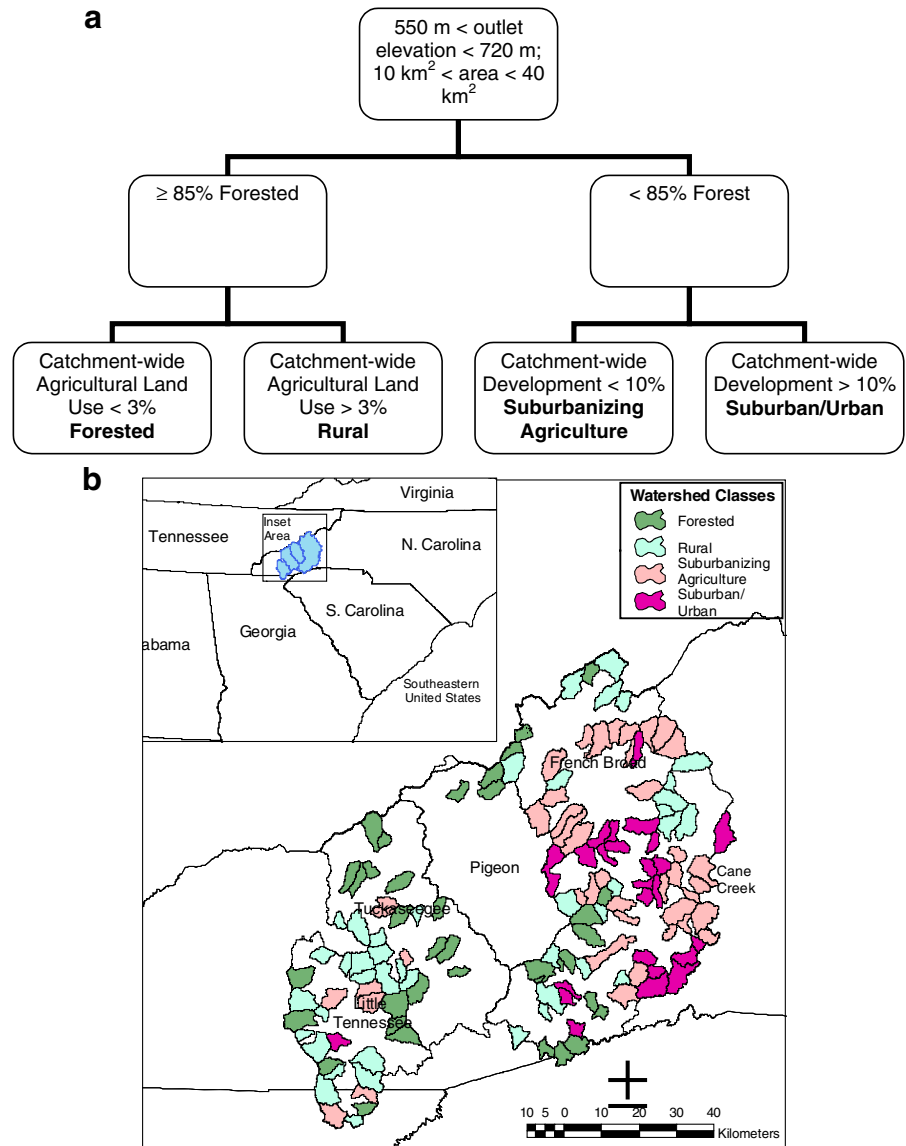
represent a gradient of development intensity. We mapped these decision rules onto the entire population of catchments throughout the study area whose elevation and size matched those of the study sites (Fig. 6b).

Discussion

The distinctiveness of algal flora between the forested reference sites and the remaining catchments, all of which had lower riparian forest cover than the reference sites, points to diatoms' sensitivity to light availability. Low diatom species richness observed at the reference sites set them apart from all other sites and is consistent with the expectation that highly forested sites with low light and nutrient inputs should have lower primary productivity and low diversity of algal taxa (Lowe et al. 1986). This study and others (Lowe et al. 1986; Mosisch et al. 2001; Greenwood and Rosemond 2005) demonstrate that canopy cover plays a major role in influencing algal community structure and growth and can be the primary

Table 5 Land cover and land use attributes of clusters of comparably sized catchments with similar outlet elevations

	n	Area (%) with given land cover				1993 Ag. 100 m buffer	1993 Ag. in catchment	1993% Developed catchment	Road density (km km^{-2})		
		1970 Forest in catchment	1970 Forest in 100 m buffer	1993 Forest in catchment	1993 Forest in 100 m buffer				Improved	Unimproved	Total
Forested	37	97.1	95.1	97.1	94.3	2.0	1.2	1.7	1.5	0.46	1.5
Rural	42	90.7	84.4	92.3	85.6	9.6	5.4	2.4	1.7	0.57	1.7
Suburbanizing agriculture	45	73.6	65.2	79.6	61.4	30.7	21.4	5.8	2.4	0.45	2.4
Urban	25	56.6	48.1	59.1	52.6	22.1	19.1	21.8	5.0	0.3	5.0

driver of periphyton biomass and communities compared to parameters such as temperature or nutrient inputs. Additionally, the combination of both increased irradiance and nutrients (which we predict will accompany deforestation that accompanies increased building density) is likely to cause increases in periphyton biomass and shifts in community structure (Rosemond 1993). We predict that assemblages typified by endemic (i.e., *Meridion alansmithii*), shade-tolerant, and oligotrophic taxa in largely forested catchments will include more cosmopolitan taxa if those catchments become more developed and have less riparian forest cover through time.

Macroinvertebrate and fish assemblages also suggest broad differences between stream segments in catchments with differing land use, water chemistry, and physical habitats. Prior research (Scott and Helfman 2001) suggests lower macroinvertebrate diversity and higher fish diversity will follow building activities within forested catchments. For example, Darnell and Wayah Creeks both had low Composite Hazard Index values (Table 1) and high forested area in the 1950s and in 1993; they also clustered with the reference sites (Fig. 4). Forested catchments that undergo limited development are expected to support somewhat higher fish diversity as cosmopolitan taxa (prevalent in low-elevation, warmer streams) invade but do not displace highland endemic fishes found in headwater streams (Harding et al. 1998; Scott and Helfman 2001; Walters et al. 2003).

Biologists point to the need for cost effective means of quickly assessing whether one stream segment is likely to support more sensitive taxa than another (Hawkins et al. 2000). To generate a spatial hypothesis about stream conditions throughout the study area at the start of this long-term study, we used simple decision rules to separate similarly sized catchments with outlet streams having similar elevation ranges throughout the study region (Fig. 6). Details on watershed database construction can be found elsewhere (Gardiner 2002). The largely forested LT basin contains mostly "Forested" and "Rural" catchment categories while the FB has more "Suburbanizing Agricultural" and "Suburban/Urban" ones.

Some catchments of comparable size and elevation in this study area contain agricultural areas approaching 50% (data not shown), a threshold Wang et al. (1997) associated with loss of biotic integrity among streams in southern Wisconsin. These more agricultural catchments are found in areas that are currently undergoing suburbanization and urbanization, and therefore represent useful targets for sampling efforts. In the Forested and Rural catchments, road density was below the 1.1 km km^{-2} density threshold associated with substantial hydrologic changes by others (Forman and Alexander 1998). Thus these two classes represent a distinct trajectory. The other two classes, which are each beyond that threshold, represent another land use trajectory from agricultural land use to Suburban and Urban land uses. Ecologists have emphasized the need for research examining streams whose watersheds consist of 6% to 12% impervious surface area (Paul and Meyer 2001; Wang et al. 2003) to understand ecosystem states below, at, and above the threshold beyond which hydrologic impairment and lowered biotic integrity often occur (Booth and Jackson 1997). This study is well-poised to detect and describe physical, chemical, and biological changes in streams whose catchments will likely exceed impairment thresholds in the near future.

Conclusion

Sampling at the hazard sites in the next two decades aims to link specific physical and biological changes within streams to accompanying catchment-wide land use changes. We infer likely future conditions within catchments and their associated stream biota. Prior research on land use patterns and socioeconomic drivers of those land use patterns suggests that the LT and Cane Creek basins are on different land-use-change trajectories (Wear and Bolstad 1998). One trajectory can be described as starting from highly forested catchments (in the mid-twentieth century) with only a few buildings and transitioning toward mostly forested catchments with some residential development over the next two decades. A second trajectory, exemplified in the Cane Creek basin, is characterized by suburban development in histor-

ically agricultural catchments (Wear and Bolstad 1998).

We show that a gradient of catchments— from Forested to Rural and from Suburbanizing Farmland and to Urban—exists in western North Carolina. Diatoms were low in species numbers at forested reference sites but increased in diversity at sites with more open riparian cover. Macroinvertebrate and fish ordinations both separated forested catchments from agricultural ones. Suburbanizing Farmland catchments, which had lower EPT richness, fewer highland endemic fishes, and more cosmopolitan fishes, were ecologically distinct from Forested catchments. Urban catchments supported mostly tolerant fishes and macroinvertebrates and did not have many sensitive taxa.

In addition to summarizing current findings and anticipating future biological and physical changes, the data presented here will contribute to retrospective analyses to be conducted in future decades, after time-series observations are available. When low density housing is built in an otherwise forested setting, productivity and diversity increase (Scott and Helfman 2001). Our analyses suggest that this transition would be marked by a sharp increase in diatom diversity. The transition from agricultural to suburban and urban land uses, however, would likely be typified by increases in dissolved solids and decreases in biotic integrity (see Scott et al. 2002), such as when both non-native (Rahel 2000) and native (Scott and Helfman 2001) invasive fish species flourish at the expense of native ones (also see Wang et al. 2000; Scott et al. 2002; Wang et al. 2003; Walters et al. 2003). Because much greater building density is predicted in the French Broad basin, the hazard sites there (Table 1) are expected to diverge from the other hazard sites and reference sites. Scott and Helfman (2001) have proposed a mechanism whereby habitat homogenization would lead to biotic homogenization, even in the absence of non-native invasive species.

This study establishes a sampling protocol to track biological and physical consequences for freshwater ecosystems due to predicted land use changes. Examining land use patterns as they change as well as and their socioeconomic context within a large region provides a template for

understanding the relationships among landscape position, catchment land use, water quality, and biological integrity of streams. In turn, knowledge of socioeconomic determinants of land use can help identify consequent inputs and therefore changes to river systems in the region (Turner et al. 1996; Grimm et al. 2000; Pickett et al. 2001). We identified a set of sites that currently lies below important thresholds of road density and impervious surface area but where catchment development is likely to surpass those thresholds over the coming decades. Land use and land cover data were used to classify all watersheds of comparable size and elevation in the region into categories identified through detailed stream assessments. These classes provide a snapshot of overall conditions in the study area and shed light on possible future conditions in streams as they are influenced by human land use decisions. The consequences of land use change for stream ecosystem change depends on the historical context of streams and their watersheds. Current land use and ecosystem states indeed reflect "the ghost of land use past" (Harding et al. 1998), but they also suggest the specter of what is to come.

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