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RESEARCH ARTICLE

Riparian influences on stream fish assemblage structure in urbanizing streams

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Abstract We assessed the influence of land cover at multiple spatial extents on fish assemblage integrity, and the degree to which riparian forests can mitigate the negative effects of catchment urbanization on stream fish assemblages. Riparian cover (urban, forest, and agriculture) was determined within 30 m buffers at longitudinal distances of 200 m, 1 km, and the entire network upstream of 59 non-nested fish sampling locations. Catchment and riparian land cover within the upstream network were highly correlated, so we were unable to distinguish between those variables. Most fish assemblage variables were related to % forest and % urban land cover, with the strongest relations at the largest spatial extent of land cover (catchment), followed by riparian land cover in the 1-km and 200-m reach, respectively. For fish variables related to urban land cover in the catchment, we asked whether the influence of riparian land cover on fish assemblages was dependent on the amount of urban development in the catchment. Several fish assemblage metrics (endemic richness, endemic:cosmopolitan abundance, insectivorous cyprinid richness and abundance, and fluvial specialist richness) were all best predicted by single variable models with % urban land cover. However, endemic:cosmopolitan richness, cosmopolitan abundance, and lentic tolerant abundance were related to % forest cover in the 1-km stream reach, but only in streams that had < 15% catchment urban land cover. In these cases, catchment urbanization overwhelmed the potential mitigating effects of riparian forests on stream fishes. Together, these results suggest that catchment land cover is an important driver of fish assemblages in urbanizing catchments, and riparian forests are important but not sufficient for protecting stream ecosystems from the impacts of high levels of urbanization.

Keywords Riparian buffer · Catchment · Urban · Land use/cover · Land–water interface · Piedmont · Stream · Fish

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Introduction

Landscapes are being developed and managed to meet human needs, subsequently altering stream hydrology, geomorphology, and water quality (Allan 2004). These changes, in turn, affect stream biotic assemblages by reducing fish richness, diversity, and density, particularly of endemic and pollution-sensitive species. Such associations between catchment-scale land cover disturbances and stream fish communities have been documented for agricultural (Roth et al. 1996; Lammert and Allan 1999), silvicultural (Davies and Nelson 1994; Stevens and Cummins 1999), and urban (Wang et al. 1997, 2001; Walters et al. 2003) land uses.

While these studies show that overall anthropogenic land cover in the catchment has been linked to declines in fish assemblage integrity, the location and spatial extent of certain land uses within a catchment should have a disproportional influence on stream biota (Turner 1989; Wiens 2002; Allan 2004). For example, many studies have suggested that forested riparian areas, which provide shading, organic inputs, stream-bank protection, nutrient uptake, and other essential functions for stream ecosystems, indirectly maintain fish assemblage integrity (Steedman 1988; May et al. 1997; Lee et al. 2001). Further, the longitudinal scale of riparian land uses (i.e., whether it is adjacent to the stream reach or extends upstream along the stream network) may also influence relations between land cover and in-stream communities (Roth et al. 1996; Lammert and Allan 1999; Wang et al. 2001).

Several previous studies have examined relations between biota and land cover assessed at multiple spatial extents; however, results are conflicting in terms of the relative importance of catchment vs riparian areas for driving differences in fish assemblages (Table 1). For example, some studies have found that catchment land cover variables are the best indicators of fish assemblages (Roth et al. 1996; Snyder et al. 2003), while others have indicated that riparian and reach-scale land cover are most correlated with fish assemblages (Lammert and Allan 1999; Fitzpatrick et al. 2001; Van Sickle et al. 2004). Many have proposed reasons why these results differ, including: (a) resolution and age of land cover data, (b) riparian extents (width and length) measured, and (c) poor statistical resolution of intercorrelated variables (Stauffer et al. 2000; Fitzpatrick et al. 2001; Allan 2004). Further, some studies have been specifically designed to vary reach-scale riparian conditions (e.g., Jones et al. 1999; Lammert and Allan 1999; Stauffer et al. 2000; Lee et al. 2001), while others studies include a range in catchment land cover (Roth et al. 1996; Wang et al. 2001), creating statistical differences in the ability to find significant effects at various spatial extents (Allan et al. 1997).

Most of the studies examining the relative influence of catchment and riparian land cover at multiple spatial extents have occurred in agricultural landscapes; however, the extent to which these results can be applied to urbanizing landscapes is unknown. Despite the lack of research in urban areas, forested riparian areas have been widely applied across the US to protect aquatic resources from *all* anthropogenic land uses (Lowrance 1998; Pusey and Arthington 2003). We hypothesize that streams in urban landscapes are overwhelmed by upstream disturbances, and that forested riparian patches do not influence fish assemblage integrity in urbanizing areas. Our previous research has shown that local forest canopies may not strongly affect fish assemblages in suburban streams (Roy et al. 2005a), so in this study we asked whether cumulative effects of riparian deforestation along urbanizing stream networks are important in driving fish assemblage structure. This study addresses the following questions: (1) What catchment and riparian variables are most strongly related to fish assemblages?, (2) What longitudinal scale of riparian variables (200 m, 1 km, or network) are best predictors of fish assemblages?, and (3) Is the ability of forested riparian areas to mitigate effects of upland disturbance on fish assemblages dependent on the amount of urban development within the catchment?

Methods

The Etowah River basin is a 4,823-km^2 catchment in north-central Georgia which harbors high

Table 1 Selected studies relating catchment (basin) and riparian (along entire upstream network or smaller, ''reach'' spatial extents) land cover to fish assemblage integrity (listed in chronological order)

Citation	# Sites (basin area)	Range of catchment land cover	Land cover data type	Riparian extents[a]	Correlations between basin and riparian land cover and fish assemblage
Steedman 1988	108 (2–895 km^2)	0–~25% forest[b] 0–~75% urban	Topo maps	% network length with intact forest, min 20-m width	Basin and riparian % forest vs IBI (+) Basin % urban vs IBI (–)
Roth et al. 1996	23[c](21–251 km^2)	10–25% forest 1–13% urban 36–84% agriculture	Database[d]—basin Air photos—1.5 km Field transects—150 m	50, 125, and 250 m width 150 m, 1.5 km, and network length	Basin % forest vs IBI (+) Basin % urban and agriculture vs IBI (–) 50 m % forest network vs IBI (+)
Lammert and Allan 1999	18[c] (50–76 km^2)	14–29% forest 1–9% urban 21–73% agriculture	Land cover database[d]	50 and 125 m width for network length and segment to next site (~ 1 km)	50 and 125 m forest vs IBI (+) 50 m agriculture vs IBI (–)
Fitzpatrick et al. 2001	25 (2–250 km^2)	5–56% forest <1% urban 5–82% agriculture	Air photos—reach Satellite imagery—basin and network buffer	Riparian vegetation width—reach 50 m width—network	Riparian vegetation width vs IBI (+) Network % agriculture (–), wetland (+), veg. (+) vs IBI
Stewart et al. 2001	38 (9–71 km^2)	1–34% forest 0–33% urban 19–88% agriculture	Air photos	0–10, 10–20, and 20–30 width for network length forest gaps and length	Basin % forest vs diversity (+) and richness (+) <30 m and basin % forest vs % tolerant (–) Mean gap length vs IBI (–) Basin % urban and 20–30 m grassland vs fish density (–)
Wang et al. 2001	47 (10–101 km^2)	0–18% forest 3–97% urban 0–89% agriculture	Database[e]	<50, 50–100, >100 m width <1.6, 1.6–3.2, >3.2 km radius	<3.2 km impervious vs richness (–), IBI (–) and diversity (–) >3.2 km land cover vs richness (–), IBI (–) and diversity (–)
Snyder et al. 2003	20 (3–85 km^2)	22–53% forest 0–28% urban 38–74% agriculture	Satellite imagery—basin Air photos—400 × Field transects—80 ×	30 m for length 80 × stream width 129 m for length 400 × stream width	Basin % urban and agriculture vs IBI (–)
Strayer et al. 2003	944 (0–22,278 km^2)	2–100% forest 0–93% urban 0–88% pasture	Satellite imagery	135 m width for network length 300 m radius	Basin and 135 m pasture and cultivated vs richness (–)
Lattin et al. 2004	23 (15–87 km^2)	~46% agriculture	Air photos and satellite imagery	25, 50, 100, 150 m width reach, 1 and 10 km, and network length	10 km and network land cover vs IBI

Table 1 continued

Citation	# Sites (basin area)	Range of catchment land cover	Land cover data type	Riparian extents[a]	Correlations between basin and riparian land cover and fish assemblage
Roy et al. (this study)	59 (5–36 km^2)	29–97% forest 0–65% urban 0–31% agriculture	Satellite imagery	50 and 100 m width 200 m, 1 km, and network length	Basin and network % forest vs sensitive (+) and tolerant (–) Basin and network % urban vs sensitive (–) and tolerant (+) 1 km % forest vs cosmopolitan (–) and tolerant (–)

IBI, index of biotic integrity

[a] Widths reported as distance from centerline of stream; double values to obtain riparian corridor widths

[b] Percentages estimated from figures, unknown amount of agriculture land cover

[c] Some subcatchments spatially nested

[d] Land cover from 1978 Michigan Resource Inventory System updated with 1995 aerial photography; resolution ~25 m

[e] Land cover from digital land-use database developed from 1:4,800 air photos; resolution 600–4,000 m^2

species diversity (Burkhead et al. 1997); however, increased urbanization in the basin in the last two decades has impacted biotic integrity within small streams (Roy et al. 2003b; Walters et al. 2003). Current land use/cover is a mixture of forest (secondary growth), agriculture (primarily pasture for hay production and grazing), and urban (primarily suburban residential housing and roads). Counties in the area experienced population growth of 22–123% between 1990 and 2000, including Forsyth and Paulding counties, two of the fastest growing counties in the nation (U.S. Census Bureau 2000).

Sites were selected for this study from a database of 479 fish collections made within the Etowah River basin from 1999 to 2002. From this database, we selected non-nested, small streams (5–27 km^2) that had been sampled for fishes using the same protocol (see fish assemblage methods). When multiple samples were taken from the same location, we selected the most recent, quantitative sample with comparable techniques (e.g., single pass) for analysis. We excluded sites with impoundments within the 1-km reach upstream of the sample site to yield a final data set of 59 streams (Fig. 1). All sites were located in the Piedmont physiographic region, which has some distinct geology and fish species relative to the Ridge and Valley region to the west and Blue Ridge region to the northeast. Streams in this region typically have flat to moderate slopes (0.1–1%) with meandering riffle-pool morphology and primarily cobble–gravel–sand stream beds.

Land use/cover

Land use/cover (hereafter referred to as land cover) was quantified within a 30-m riparian buffer on each side of the stream (i.e., 60 m corridor) and the entire catchment (inclusive of the riparian area) using ArcView© 4.0 Geographic Information Systems (GIS). The buffer width was selected based on resolution of land cover data (30-m pixels) and comparability with typical regional riparian buffer regulations (25–75 ft). The Georgia Erosion and Sedimentation Control Act requires primary and secondary trout streams to maintain an undisturbed 50-ft riparian buffer, and all other streams to maintain 25-ft buffers

(O.C.G.A. 12-7); however, many local governments have adopted more stringent riparian requirements. A drainage network created from Digital Elevation Models (DEMs), which was similar to a 1:24,000 scale stream network, was used to create buffers around (a) the lower 200-m reach at the sampling location, (b) the 1-km reach upstream of the site, and (c) the entire drainage network upstream of the site.

Landsat Thematic Mapper (TM) satellite imagery for 1998 and 2001 (17 land cover classes) were used to calculate percentages of land cover categories within the catchment and riparian areas upstream of sample sites. Land cover was categorized as urban (high density and low density urban), agriculture (cultivated/exposed land and cropland/grassland), and forest (evergreen, deciduous, mixed, and forested wetlands). The most recent prior imagery date corresponding to fish collections was used (e.g., 1998 for collections 1999–2000, and 2001 for collections 2001–2002) for each site. Percent impervious cover (2001) was calculated for each sub-catchment from a classified dataset created by the Georgia Land Use Trends Project (Natural Resources Spatial Analysis Laboratory, Institute of Ecology, University of Georgia, Athens, GA, USA). For five streams, we also classified land cover within the 30-m buffer based on 1999 ortho-rectified aerial photography (1-m resolution) to determine approximate error rates in land cover classification based on satellite imagery (from 1998).

Fish assemblages

Fishes were collected in spring through early autumn (March–October) during low flow conditions using a backpack electroshocker and downstream seine. All samples were from a single pass for a length of *ca*. 35 times the stream width (mean widths = 2.0–6.4 m). Although sampled reach lengths and shock times varied due to stream size and habitat complexity, the protocol was designed to have sufficient length and comparable effort to obtain representative samples for cross-site comparisons. However, because stream size and reach length may affect the number of fish caught, both basin area and reach length were included as

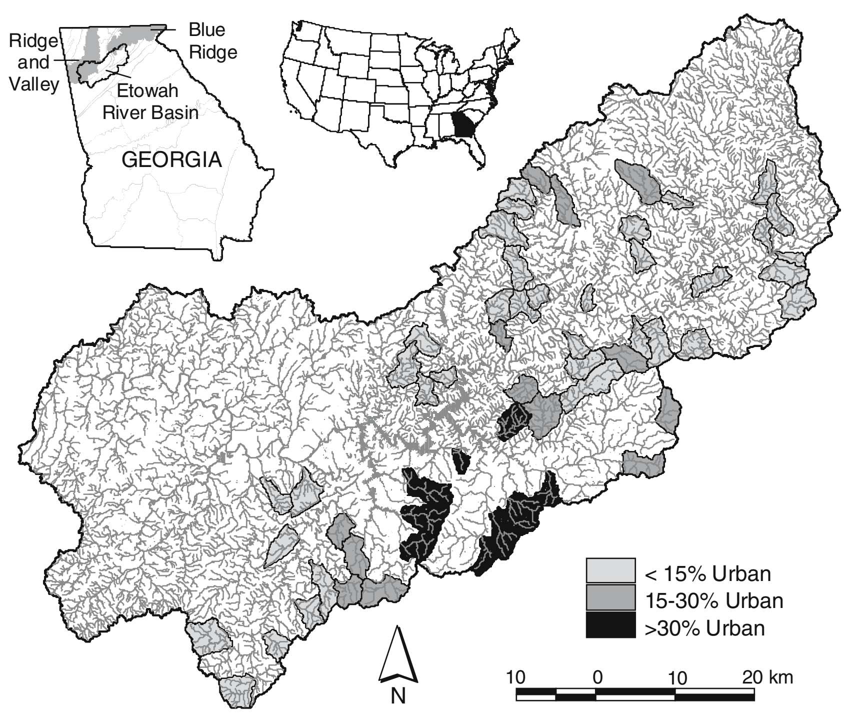

Fig. 1 Map of the 59 study sites in the Etowah River basin, Georgia, USA

potential variables in the multiple regression models. Estimated richness was calculated from species counts using a first-order jackknife which uses the number of species with only one individual collected to estimate species not observed (Burnham and Overton 1979; Nichols et al. 1998). Fish assemblage structure was evaluated based on estimated richness (no. species) and abundance (no. individuals) of groups of species that have been previously used as indicators of disturbance: endemic, cosmopolitan, insectivorous cyprinid, lentic tolerant, and fluvial specialist species, as well as the ratio of endemics to cosmopolitans (Appendix: Table 1). Endemic species are regionally distinct fishes primarily limited to the Coosa River drainage (which includes the Etowah River), whereas cosmopolitan species (i.e., widespread, generalist species) were defined as those fishes native to at least 10 major drainages (Walters et al. 2003). In Southern Appalachian streams, a homogenization of fish assemblages coincident with loss of endemics and expansion of cosmopolitans (as reflected in the ratio of endemics to cosmopolitans) has been demonstrated with increased urbanization (Scott and Helfman 2001; Walters et al. 2003). We also examined insectivorous cyprinids, a subgroup of the family Cyprinidae that have been used as a positive indicator in biotic indices (Miller et al. 1988). Lentic tolerant species are habitat generalists, capable of completing their life cycle in lentic environments (Travnichek et al. 1995), whereas fluvial specialist species require running water habitats; these species were classified using Etnier and Starnes (1993) and Mettee et al. (1996). Changes in the composition and abundances of lentic tolerant and fluvial specialist species have been linked to altered hydrology and sedimentation, respectively, and we expect these two groups will be useful indicators of urbanization impacts (Roy et al. 2005b). Thus, in disturbed streams, we expect to have *higher* composition and abundance of cosmopolitan and lentic tolerant species (reflective of lower biotic integrity), and *lower* composition and abundance of endemic, insectivorous cyprinid, and fluvial specialist species (reflective of higher biotic integrity) relative to less disturbed streams.

Data analysis

We used Pearson's correlation coefficient (r) to analyze relations between catchment land cover and riparian land cover variables assessed at three spatial extents. Although these are not independent variables (i.e., smaller spatial units are incorporated within larger spatial units), we used correlation as a descriptive measure of the relative strengths of relationships. Correlation analysis was also used to determine relations between land cover variables and fish assemblages. All variables were tested for normality using Shapiro–Wilk goodness of fit test and transformed when necessary. All fish abundance metrics were transformed using $\log(x + 1)$ and percentage variables were transformed using arcsin(sqrt (%/100)).

Since catchment land cover may provide an overriding influence on fish assemblages, we asked how strong the evidence is that riparian forest cover influences fishes, and whether that influence is dependent on % urban in the catchment. Plots of % forest in riparian areas vs % urban in catchment were examined to determine if we had sufficient data (e.g., sites with high and low % urban in catchment with high and low % forest in riparian areas) to address this question. For the fish assemblage variables that were correlated with urban land cover, we created linear regression models using individual land cover variables, as well as additive and interactive combinations of catchment urban cover and % riparian forest.

We used Akaike's Information Criterion, adjusted for small sample size (AIC_c), to assess fit of candidate models, with lowest AIC_c indicating the best-supported model for predicting each fish assemblage metric within model sets (Burnham and Anderson 2002). In contrast to hypothesis testing, this information-theoretic approach avoids overfitting models by identifying scientifically appropriate models a priori, and evaluates the relative support for each model within a set of plausible models based on model likelihood and number of parameters included (Burnham and Anderson 2002). Akaike weights (w_i) were computed as $w_i = \exp(-1/2\Delta_i)/\sum\exp(-1/2\Delta_i)$, 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 $\exp(-1/2\Delta_i)$ for all models in the set. We used Akaike weights (which vary from 0 to 1 with the best-fitting model having the highest weight) to measure the weight of evidence for each model given the data (Burnham and Anderson 2002). Although adjusted R^2 values provide useful information about the variance explained in a model, we feel that AIC_c is the best approach to compare candidate models and determine the best-supported model relative to the model set.

We plotted regressions for the best supported models for each fish assemblage variable. Where the best supported model was an interaction term with riparian and urban cover, we divided sites into categories of urban land cover (<15% (n = 37), 15–30% (n = 13), and >30% (n = 10), and ran separate regressions for each category. Urban categories corresponded to literature reported threshold values (Wang et al. 1997; Paul and Meyer 2001) and natural breaks in data points across sites. All analyses were run using JMP Version 4 (SAS Institute, Inc., Cary, NC, USA).

Results

Correlations between land cover and fish assemblages

Sites exhibited a wide range in urban (0.5–65%) and forest (29–97%) land cover across the 59 catchments (Table 2). On average % forest land cover was higher within the 30-m riparian buffer compared to the entire catchment for all longitudinal spatial extents. Mean % urban land cover was lower in riparian areas vs catchment, while mean % agriculture was higher in the riparian areas vs. catchment at the 200-m and 1-km reach extents (Table 2). Land cover classification of five stream buffers using air photos revealed that satellite imagery overestimated urban land cover by an average of 8.2 ± 9.0% and agriculture land cover by 1.4 ± 1.8%, and underestimated forest land cover by 6.5 ± 5.9%.

Catchment land cover was highly correlated with riparian land cover in the upstream network for urban (r = 0.98), forest (r = 0.95), and agriculture (r = 0.90) cover (Table 3). Because of the high correlations between these catchment and riparian network variables, only riparian variables at the 200 m and 1 km reach extent were used in analyses with fish assemblages. Percent forest and % urban land cover were also highly negatively correlated with each other at the largest spatial extents, with r-values ranging from – 0.85 to – 0.87 (Table 3). There were no strong correlations among land cover variables at other spatial extents, so we were able to include land cover variables at the 200-m, 1-km, and catchment scales in all analyses and interpret relationships separately (A. Roy, unpublished data).

Between 6 and 29 fish species were found at each site (subsequent to adjustment with jackknife estimator), with an average abundance of 240 individuals (Table 2). *Hypentelium etowanum* (Alabama hogsucker), *Campostoma oligolepis* (largescale stoneroller), *Lepomis macrochirus* (bluegill sunfish), *Lepomis auritus* (redbreast sunfish), and *Percina nigrofasciata* (blackbanded darter) were the most commonly found species, present at >80% of the sites, and also the species with the highest average abundances (Appendix: Table 1). For the most part, fish assemblages variables were not related to drainage area or reach length sampled (Table 4). Drainage area was incorporated into additional analyses only for the fish variables that indicated strong relationships (i.e., insectivorous cyprinid richness and lentic tolerant abundance).

Fish assemblages were correlated with urban, forest, and agriculture land cover variables, with the greatest number of strong relations with % forest and % urban in the catchment (eight strong models), and % forest and % agriculture in the 1-km riparian network (four strong models; Table 4). Cosmopolitan and lentic tolerant species were the only groups correlated with agriculture, with increased richness and abundance associated with agriculture at some spatial extents. For all except cosmopolitan species, the strongest relationships were with the largest

Table 2 Land cover and fish assemblage summary data for the 59 study sites

Land cover	Mean	Range	Fish assemblage	Mean	Range
Basin area (km^2)	13.1	(5.4–26.8)	Total richness	15.9	(6–29)
Reach sampled (m)	151.3	(98.6–500)	Total abundance[b]	235.7	(58–1,115)
% Impervious (2001)[a]	9.4	(1.7–31.1)	Endemic		
Road crossings (no. km^{-1})	0.4	(0–1.39)	Richness	2.6	(0–9)
Catchment			Abundance[b]	54.2	(0–333)
% Forest[a]	63.7	(28.8–96.5)	Cosmopolitan		
% Urban[a]	18.0	(0.5–65.2)	Richness	8.4	(2–18)
% Agriculture[a]	10.1	(0.1–31.2)	Abundance[b]	107.6	(11–342)
Riparian, 200 m			Endemic:cosmopolitan		
% Forest[a]	68.4	(0–100)	Richness	0.37	(0–1.3)
% Urban[a]	8.1	(0–100)	Abundance[b]	0.89	(0–10.5)
% Agriculture[a]	14.5	(0–100)	Insectivorous cyprinid		
Riparian, 1 km			Richness	2.2	(0–10)
% Forest[a]	75.2	(1.5–100)	Abundance[b]	45.8	(0–485)
% Urban[a]	6.4	(0–98.5)	Tolerant		
% Agriculture[a]	11.8	(0–76.1)	Richness	4.6	(0–14)
Riparian, network			Abundance[b]	54.1	(0–341)
% Forest[a]	75.2	(48.3–98.6)	Fluvial specialist		
% Urban[a]	11.1	(0–44.9)	Richness	11.0	(2–23)
% Agriculture[a]	5.4	(0–17.8)	Abundance[b]	181.6	(1–1,076)

Land cover for catchment and 30-m riparian buffer for three extents of stream length (200 m, 1 km, network) at each site was calculated from *Landsat* TM imagery for closest previous date (1998 or 2001) prior to fish sampling. Abundance is number of individuals collected, and richness is estimated number of species using a first-order jackknife of single-pass collections (Nichols et al. 1998)

[a] Transformed using arcsin(sqrt(x /100)) for analysis

[b] Transformed using log(x + 1) for analysis

spatial extents of land cover (catchment), followed by riparian land cover in the 1-km and 200-m reach, respectively. Endemic richness, endemic:cosmopolitan richness and abundance, insectivorous cyprinid richness and abundance, and fluvial specialist richness were all negatively correlated with % urban cover and positively correlated with % forest cover in the catchment (Table 4).

Importance of riparian forests based on urban land cover

For the eight fish assemblage variables that were significantly related to % urban in the catchment, we asked whether the influence of riparian land cover on fish assemblages was dependent on the amount of urban development in the catchment. Again, riparian forest in the stream network could not be assessed because there were no sites with low catchment urban and low riparian forest, or high catchment urban and high riparian forest (Fig. 2). However, sites with low and high % forest in the riparian area for the smaller spatial extents (1 km and 200 m) had a range in catchment urban land cover. For these land cover variables, we compared multiple regression models with single variables and combinations of variables, and used AIC to compare model support.

Endemic richness, endemic:cosmopolitan abundance, insectivorous cyprinid richness (after accounting for drainage area) and abundance, and fluvial specialist richness were all best predicted by % urban land cover (Table 5). In all cases, these single variable models were weighted at least twice as strong as competing models. Although these models explained a small percent variance in fish assemblages, they indicated that % forest in the 1-km or 200-m riparian area was not important in explaining these aspects of fish assemblages, regardless of the level of urbanization. Plots revealed wedge-shaped relationships, whereby the maximum richness or abundance of

Table 3 Pearson's correlations (r) between catchment scale % land cover and riparian % land cover at three longitudinal spatial extents (network, 1 km, and 200 m)

	% Impervious	Catchment land cover		
		% Urban	% Forest	% Agriculture
Catchment				
% Urban	**0.93**	–	–	–
% Forest	**–0.87**	**–0.87**	–	–
% Agriculture	–0.21	–0.30	–0.12	–
Riparian, network				
% Urban	**0.91**	**0.98**	**–0.85**	–0.30
% Forest	**–0.84**	**–0.86**	**0.95**	–0.06
% Agriculture	–0.25	–0.33	–0.03	**0.90**
Riparian, 1 km				
% Urban	0.41	**0.52**	–0.44	–0.15
% Forest	–0.14	–0.20	0.27	–0.29
% Agriculture	–0.19	–0.22	0.07	0.47
Riparian, 200 m				
% Urban	0.35	0.44	–0.36	–0.17
% Forest	–0.05	–0.12	0.13	–0.17
% Agriculture	–0.13	–0.16	0.07	0.35

Bold type indicates $r \geq 0.50$

Table 4 Pearson's correlations (r) between fish assemblage variables and drainage area, reach length sampled for fish collections, and % land cover for catchment (catch) and riparian areas at two longitudinal extents (1 km and 200 m)

	Drainage area (km^2)	Reach sample (m)	% Urban			% Forest			% Agriculture		
			Catch	1 km	200 m	Catch	1 km	200 m	Catch	1 km	200 m
Endemic (E)											
Richness	–0.04	0.00	**–0.41**	–0.14	–0.07	**0.39**	0.09	0.00	–0.03	–0.01	0.06
Abundance	–0.04	–0.01	–0.16	0.00	0.10	0.20	0.06	–0.02	–0.16	–0.11	–0.10
Cosmopolitan (C)											
Richness	–0.06	0.25	–0.09	–0.09	–0.08	0.07	–0.21	0.15	0.14	**0.34**	**0.28**
Abundance	0.15	0.14	**0.29**	0.26	0.20	**–0.38**	**–0.45**	**–0.31**	**0.33**	**0.34**	0.21
E:C											
Richness	0.00	–0.03	**–0.34**	–0.14	–0.05	**0.32**	**0.32**	0.20	–0.10	–0.25	–0.16
Abundance	–0.09	–0.07	**–0.37**	–0.17	–0.11	**0.41**	**0.26**	0.20	–0.23	–0.18	–0.17
Insectivorous cyprinid											
Richness	**–0.28**	–0.06	**–0.38**	–0.09	–0.04	**0.36**	–0.09	–0.08	0.05	0.05	0.08
Abundance	–0.18	–0.06	**–0.31**	–0.13	–0.01	**0.27**	0.04	0.03	0.00	0.02	–0.01
Lentic tolerant											
Richness	0.01	0.25	0.04	0.01	–0.04	–0.07	–0.23	–0.11	0.10	**0.32**	0.20
Abundance	**0.29**	0.24	**0.35**	0.24	0.21	**–0.38**	**–0.37**	**–0.30**	0.17	**0.33**	0.20
Fluvial specialist											
Richness	–0.23	0.02	**–0.39**	–0.10	–0.04	**0.39**	–0.03	–0.08	0.00	0.08	0.14
Abundance	–0.15	–0.08	–0.23	–0.07	0.02	0.19	–0.02	–0.02	0.06	0.01	0.02

Bold type indicates $r \geq 0.26$

these groups of sensitive species declined with increased urbanization (Fig. 3).

For endemic:cosmopolitan richness and lentic tolerant abundance, the best supported model was % forest in the 1-km riparian area plus an interaction between % riparian forest and % urban in the catchment (Table 5). Cosmopolitan abundance was best supported by a model with % forest in the 1-km riparian area alone; however, the model that also included an interaction term with % urban explained the most variation in abundance of cosmopolitans across sites. The model with the interaction term suggests that these fish assemblage variables are related to % forest in the riparian area, but the slopes of the models are different for different levels of urban land cover. Thus, we plotted the relationships with % forest in riparian areas, and regressed fish variables against riparian forest according to categories of % urban land cover in the catchment (Fig. 4). Interestingly, only sites with <15% urban land cover were related to % forest in the riparian area. In other words, sites with >15% urban land cover have consistently low endemic:cosmopolitan richness and high cosmopolitan and lentic tolerant abundance, regardless of % forest in the riparian area (Fig. 4).

Discussion

What scale of land cover variables best predict fish assemblages?

A majority of the fish assemblage metrics, especially those that were expected to decline with disturbance, were primarily related to catchment-scale (vs riparian-scale) urban and forest land cover. These results support other studies that have highlighted the importance of catchment-scale land cover in influencing biotic assemblages (Roth et al. 1996; Allan et al. 1997; Allan and Johnson 1997; Snyder et al. 2003). Urbanization and the concomitant declines in forest land cover throughout catchments result in hydrologic alteration, increased bank erosion and sedimentation, altered in-stream habitat, and increased delivery of pollutants to streams, among other impacts (Paul and Meyer 2001). These changes, in turn, alter biotic assemblages, resulting in the observed linkages between catchment land cover and fish assemblages in this and other studies (e.g., Wang et al. 1997, 2001; Scott and Helfman 2001; Walters et al. 2003).

Studies that incorporate a range of catchment land cover often demonstrate significant relationships between land cover and stream quality (see Table 1). This study had the greatest differences in % forest and % urban land cover (vs smaller ranges in % agriculture) across sites, and these variables

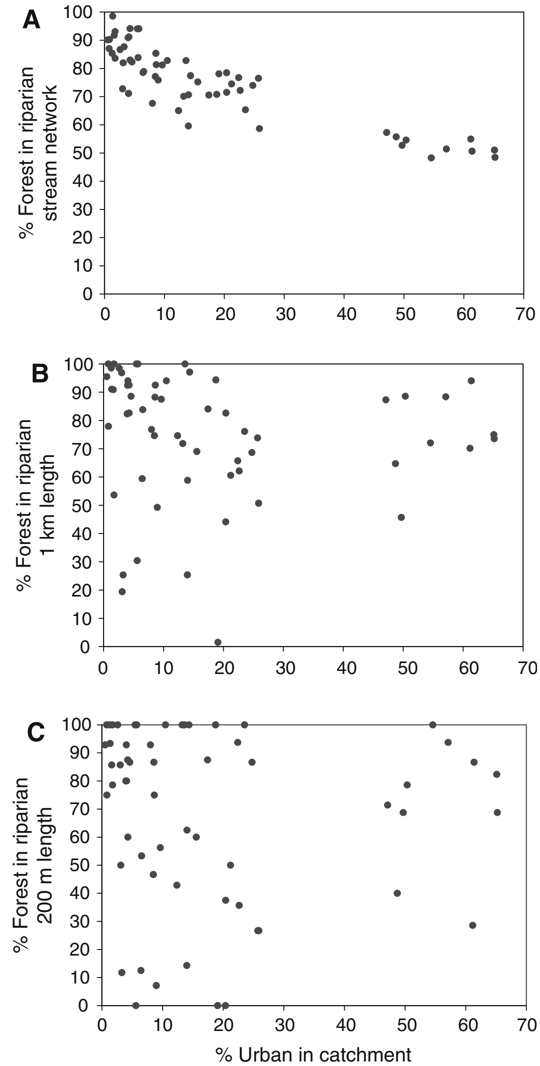

Fig. 2 Relationship between % forest in riparian area at three longitudinal spatial extents (network, 1 km, 200 m) and % urban in catchment

were most important in predicting aspects of fish assemblage integrity. Conversely, in streams with one dominant land cover (and a very small range) we are more likely to observe shifts associated with minor changes in riparian land cover if we look at the appropriate scale. For example, Stauffer et al. (2000) and Lee et al. (2001) found that small increases in local forest cover within the riparian area resulted in shifts toward higher fish assemblage integrity in catchments that were dominated (88–100%) by agricultural land cover. Similarly, Jones et al. (1999) documented changes in fish assem-

Table 5 Multiple linear regression models for fish assemblage indices with % forest in riparian for 1 km length (Rip1km), % forest in riparian for 200-m length (Rip200m), % urban in catchment (Urban), and interaction terms

	Adj. R^2	Δ_i	w_i		Adj. R^2	Δ_i	w_i
Endemic richness				*Cosmopolitan abundance*			
Rip1km	–0.01	4.57	0.03	Rip1km	0.19	0.00	**0.30**
Rip200m	–0.02	4.76	0.03	Rip200m	0.08	3.36	0.06
Urban	0.16	0.00	**0.32**	Urban	0.07	3.67	0.05
Rip1km+Urban	0.14	2.30	0.10	Rip1km + Urban	0.22	0.98	0.18
Rip1km + Rip1km*Urban	0.14	2.39	0.10	Rip1km + Rip1km*Urban	0.23	0.59	0.22
Urban + Rip1km*Urban	0.14	2.30	0.10	Urban + Rip1km*Urban	0.13	3.69	0.05
Rip200m + Urban	0.14	2.22	0.10	Rip200m + Urban	0.13	3.79	0.04
Rip200m + Rip200m*Urban	0.15	2.16	0.11	Rip200m + Rip200m*Urban	0.17	2.56	0.08
Urban + Rip200m*Urban	0.15	2.12	0.11	Urban + Rip200m*Urban	0.07	5.53	0.02
Endemic:cosmopolitan richness				*Endemic:cosmopolitan abundance*			
Rip1km	0.09	0.74	0.13	Rip1km	0.05	1.98	0.08
Rip200m	0.03	2.39	0.06	Rip200m	0.02	2.70	0.06
Urban	0.10	0.33	0.16	Urban	0.12	0.00	**0.22**
Rip1km + Urban	0.15	0.68	0.13	Rip1km + Urban	0.14	1.25	0.12
Rip1km + Rip1km*Urban	0.17	0.00	**0.19**	Rip1km + Rip1km*Urban	0.15	0.90	0.14
Urban + Rip1km*Urban	0.10	2.21	0.06	Urban + Rip1km*Urban	0.12	1.95	0.08
Rip200m + Urban	0.11	1.84	0.08	Rip200m + Urban	0.13	1.59	0.10
Rip200m + Rip200m*Urban	0.15	0.64	0.14	Rip200m + Rip200m*Urban	0.16	0.80	0.14
Urban + Rip200m*Urban	0.09	2.59	0.05	Urban + Rip200m*Urban	0.11	2.18	0.07
Insectivorous cyprinid richness				*Insectivorous cyprinid abundance*			
DA + Rip1km	0.06	10.12	0.00	Rip1km	–0.02	2.63	0.08
DA + Rip200m	0.06	10.14	0.00	Rip200m	–0.02	2.66	0.08
DA + Urban	0.19	0.00	**0.35**	Urban	0.08	0.00	**0.29**
DA + Rip1km + Urban	0.21	1.31	0.18	Rip1km + Urban	0.07	2.29	0.09
DA + Rip1km + Rip1km*Urban	0.20	8.08	0.01	Rip1km + Rip1km*Urban	0.06	2.41	0.09
DA + Urban + Rip1km*Urban	0.20	1.63	0.16	Urban + Rip1km*Urban	0.07	2.30	0.09
DA + Rip200m + Urban	0.19	1.72	0.15	Rip200m + Urban	0.07	2.30	0.09
DA + Rip200m + Rip200m*Urban	0.19	8.26	0.01	Rip200m + Rip200m*Urban	0.08	1.92	0.11
DA + Urban + Rip200m*Urban	0.19	1.77	0.14	Urban + Rip200m*Urban	0.07	2.20	0.10
Fluvial specialist richness				*Lentic tolerant abundance*			
Rip1km	–0.02	4.16	0.04	DA + Rip1km	0.18	0.71	0.14
Rip200m	–0.01	4.01	0.04	DA + Rip200m	0.13	2.22	0.07
Urban	0.14	0.00	**0.30**	DA + Urban	0.16	1.29	0.10
Rip1km + Urban	0.13	1.93	0.11	DA + Rip1km + Urban	0.24	0.70	0.14
Rip1km + Rip1km*Urban	0.14	2.65	0.08	DA + Rip1km + Rip1km*Urban	0.26	0.00	**0.20**
Urban + Rip1km*Urban	0.12	2.26	0.10	DA + Urban + Rip1km*Urban	0.18	2.81	0.05
Rip200m + Urban	0.14	1.80	0.12	DA + Rip200m + Urban	0.21	1.68	0.09
Rip200m + Rip200m*Urban	0.12	2.34	0.09	DA + Rip200m + Rip200m*Urban	0.26	0.27	0.17
Urban + Rip200m*Urban	0.13	1.96	0.11	DA + Urban + Rip200m*Urban	0.16	3.29	0.04

Adjusted R^2, differences in Akaike's Information Criterion from minimum (Δ_i), Akaike weights (w_i) of each model are reported. Bold type indicates best-supported model

blages with local riparian deforestation in primarily forested (96–100%) watersheds. In this study we found minimal evidence that reach-scale riparian forests were driving fish assemblages, possibly because the streams lie within landscapes that have multiple land uses, and because there were large differences in basin land cover across sites. Taken together, these studies suggest that landscape context is critical to understanding the extent of influence of riparian areas on stream ecosystems (Naiman and Decamps 1997).

Reach-scale riparian forest cover was not strongly related to richness or abundances of sensitive fish species. However, high proportions of riparian forests along the lower 1-km reach, and, to a lesser extent, along the 200-m reach were negatively related to the abundance of cosmopolitan and lentic tolerant species. Cosmo-

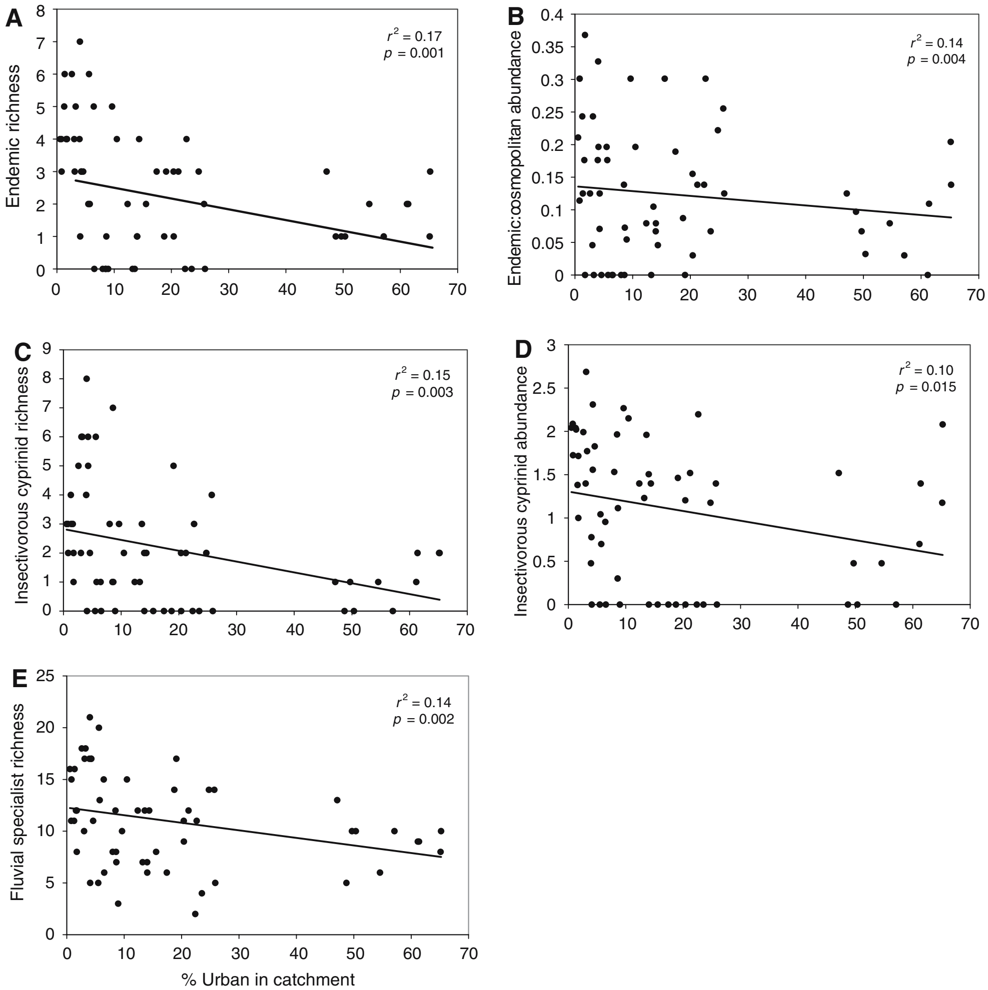

Fig. 3 Regressions (r^2) for the five fish variables where % urban in catchment was the best supported model (see Table 5). Abundance values are log(x + 1) transformed on graph, and urban land cover was arcsin-square-root transformed prior to analysis

politan and lentic tolerant species include ictalurids (e.g., bullheads and catfish) and centrarchids (e.g., sunfish) that are typically tolerant of bed sedimentation, high levels of nutrients, and low dissolved oxygen typical of disturbed streams (Detenbeck et al. 1992; Jones et al. 1999). Further, these groups of species have habitat and trophic requirements conducive to disturbed conditions; they spawn in nests constructed of fine sediment, and they are primarily omnivores or trophic generalists (Etnier and Starnes 1993; Mettee et al. 1996). Cosmopolitans and lentic tolerants were also the only two groups related to % agriculture land cover in this study, suggesting that the conditions created by riparian removal (e.g., increased light, temperature, and productivity) that affect these fishes may also be the same conditions by which these tolerant species thrive in agricultural settings.

Does urbanization influence the relative importance of riparian forests?

We hypothesized that streams in urban settings would not respond to differences in riparian forest cover because catchment-level processes would overwhelm reach-scale land cover and reduce assemblage integrity. Richness of endemic:cosmopolitan species was positively

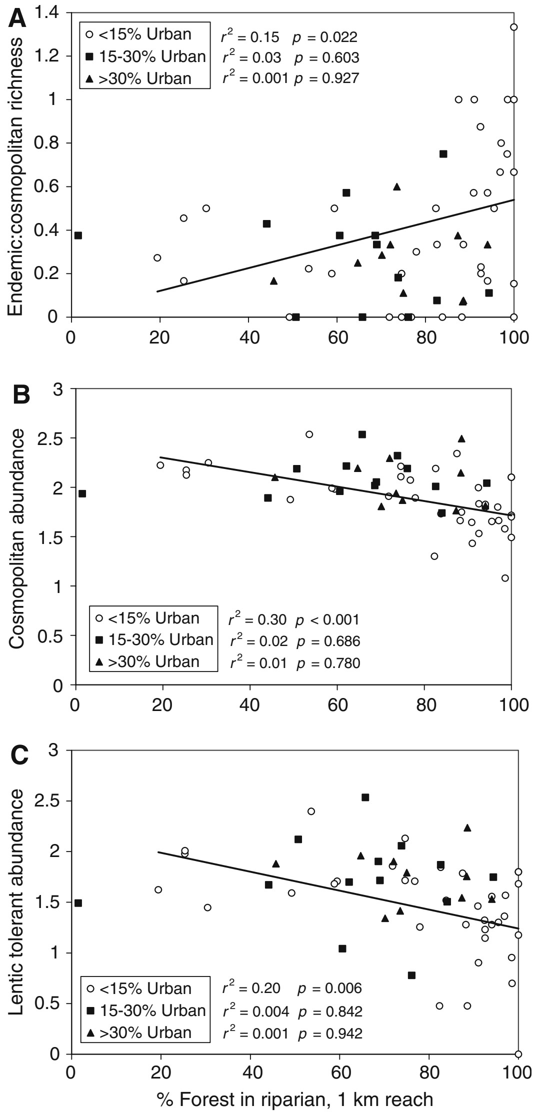

Fig. 4 Regressions between richness and abundance ($\log(x + 1)$ transformed) of fish assemblage variables where % forest in riparian area at 1-km stream length plus an interaction term was the best supported and/or strongest model (see Table 5). Separate linear regressions are reported for sites with <15% ($n = 10$), 15–30% ($n = 13$), and >30% ($n = 37$) urban land cover in catchment (arcsin-square-root transformed prior to analysis)

associated with % forest in the 1-km riparian area *only* in sites with <15% urban cover in the catchment, thus broadly supporting this hypothesis. Similarly, abundances of cosmopolitan and lentic tolerant species declined with increased % riparian forest cover, particularly in sites with low levels of catchment urbanization. This suggests that a forest cover in both catchments and riparian areas is important for moderating effects of relatively low levels of urbanization, but at high levels of catchment urbanization the potential benefits of riparian forests are overwhelmed.

For several fish assemblage metrics, levels of catchment urbanization did not seem to affect responses to reach-scale riparian forest cover; however, the tight correlation between urban and forest cover complicates these analyses. By addressing the mechanism of urban impacts on stream ecosystems, Roy et al. (2006) found that the influence of riparian forest cover was dependent on the level of instream habitat disturbance (i.e., sedimentation in stream beds). Further investigation of this question with specific attention to aspects of urban land cover that might impair streams, as well as aspects of riparian forest cover that may mitigate effects, would help to tease apart mechanisms of fish response to riparian deforestation, while avoiding the problem of correlation between urban and forest land cover.

Potential problems with spatial extent analyses

We were unable to detect differences in the relative importance of catchment vs riparian land cover over the entire upstream network, because these variables were highly correlated within land cover classes. Other studies have also reported significant correlations among land cover variables, especially at the scale of the entire stream network (Lammert and Allan 1999; Wang et al. 2001). We suspect that this problem of colinearity exists in most watersheds and equally restricts the ability to interpret differences in predictive models among landscape variables. Although these observational studies are limited in their ability to distinguish among key variables, large-scale manipulative studies in already disturbed landscapes are unlikely to occur. Van Sickle et al. (2004) suggest that modeling alternative land cover scenarios may be useful at distinguishing differences between spatial extents; however, their data-driven modeling approach was not sensitive enough to detect differences between riparian and catchment land cover. The authors suggest that making predictive models based on ''expert judgment'' may offer discriminatory power between these variables (Van Sickle et al. 2004). We contend that such models may not be useful, since not enough is known about what % riparian forest is necessary to provide sufficient functions (e.g. organic matter inputs, bank stability) to prevent loss of biotic integrity.

Satellite imagery was used to characterize land cover at the multiple spatial extents because these data were available at multiple dates corresponding to fish sampling; however, the results may have been influenced by the poor resolution of satellite imagery (30-m pixels), which may be especially biased at small spatial extents (i.e., 200-m and 1-km reach). Although we found that land cover classification based on satellite imagery overestimated urban cover and underestimated forest cover in the 30 m buffers, these differences were <10% and may not be problematic if error rates are consistent across sites. Many studies have simultaneously varied the land cover data source in order to best characterize land cover within each scale. For example, field transects are sometimes used to characterize land cover in riparian areas along short (i.e., 100–250 m) reaches; aerial photography is often used to assess land cover in 1–2 km reaches; and satellite imagery or other digital land cover databases have been used for network- and catchment-scale land cover (see Table 1). Lattin et al. (2004) tested whether these differences in sources of land cover (aerial photography vs satellite imagery) affected the accuracy and strength of relationships between land cover and biota. Although they found slightly stronger relationships with aerial photography, assessment at multiple spatial extents was more important than the source of imagery for detecting associations between land cover and fish assemblage integrity. The authors suggested that incorporating different imagery sources may mask changes in land cover across spatial extents (Lattin et al. 2004), endorsing our exclusive use of satellite imagery for this study.

Management implications

Riparian forests have been used for managing non-point source disturbances in the US since the late 1960s (Calhoun 1988; Lee et al. 2004), due to their role in ''buffering'' aquatic resources from upland disturbances (e.g., taking up nutrients and other contaminants, retaining sediment, etc.; Lowrance 1998). These regulations imply that upland disturbances can be mitigated by protecting land adjacent to streams (Allan et al. 1997; Harding et al. 1998). However, research continues to suggest not only that catchment land cover is an important driver of biotic assemblages, but also that riparian forests are not sufficient for protecting stream ecosystems in highly disturbed areas (Allan and Johnson 1997; Harding et al. 1998; Roy et al. 2006). Importantly, our results show that at low levels of urbanization (<15%), riparian forests can moderate upland disturbances and help to maintain fish assemblage integrity.

Although forested riparian buffers may not be sufficient for protecting fish assemblages in highly urbanized areas, these results do not imply that riparian forests are unimportant. In addition to buffering streams from upland disturbances, riparian forests have been recognized for their importance in providing shade, organic material, bank stabilization, and other essential functions for stream ecosystems (see reviews Gregory et al. 1991; Sweeney 1992; Naiman and Decamps 1997; Lowrance 1998; Pusey and Arthington 2003). Based on the number of potential linkages between riparian alteration and fish assemblages (Pusey and Arthington 2003), it is not surprising that reach-scale, riparian conditions have been related to some aspects of fish assemblage integrity here and elsewhere (Meador and Goldstein 2003). Since riparian forests provide certain functions such as temperature regulation and organic matter input that are essential for maintenance of stream integrity, complete removal of riparian forests would be detrimental to stream ecosystems.

Results from this study and other studies suggest that human alteration affects stream processes at multiple spatial extents. In addition to % land cover within catchments and riparian areas, the continuity of riparian forests (Stewart et al. 2001) and historic land use in the catchment (Harding et al. 1998) likely also influence fish assemblages. Regardless of what riparian variables are most important, these results lead to similar recommendations for stream protection. Currently, Georgia's stream buffers are protected by the Erosion and Sedimentation Control Act of 1975 (O.C.G.A. 12-7) which requires a minimum of 25 foot riparian buffers on all streams. However, riparian areas exhibited an average 10.3% decrease in forest cover and 8.5% increase in urban land cover between 1973 and 1997 (Roy et al. 2003), suggesting that these regulations and/or current enforcement of these regulations have not been effective at protecting stream ecosystems from continued loss of forest cover and subsequent declines in fish assemblage integrity. High amounts of private land ownership coupled with the inability to require retrofit of riparian buffers limit complete protection of riparian buffers and challenge policymakers to adapt regulations for the existing mosaic of land cover within basin and riparian areas. Efforts to enforce stricter buffer regulations on future developments to restrict loss of forest in the 30-m buffer along stream networks would offer the best protection of stream fishes only if associated with regional planning to minimize catchment-scale disturbances.

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Appendix

Appendix 1 Fishes collected in the 59 study streams in the Etowah River catchment, frequency of occurrence (no. sites), and total abundance

Family name, *Scientific name*	Common name	Composition categories	No. sites	Abundance
Petromyzontidae				
Ichthyomyzon gagei	southern brook lamprey	FLU	12	79
Ichthyomyzon sp.	unidentified lamprey	FLU	22	104
Cyprinidae				
Campostoma oligolepis	largescale stoneroller	COS, FLU	54	1,575
Cyprinella callistia	Alabama shiner	FLU, IC	21	343
Cyprinella trichroistia	tricolor shiner	END, FLU, IC	9	187
Cyprinella venusta	blacktail shiner	FLU, IC	6	49
Hybopsis lineapunctata	lined chub	END, FLU, IC	1	6
Luxilus zonistius	band fin shiner	FLU, IC	7	115
Nocomis leptocephalus	bluehead chub	FLU	18	509
Notemigonus crysoleucas	golden shiner	COS, LEN	9	65
Notropis chrosomus	rainbow shiner	FLU, IC	6	52
Notropis longirostris	longnose shiner	COS, FLU, IC	1	6
Notropis lutipinnis	yellowfin shiner	FLU, IC	16	960
Notropis stilbius	silverstripe shiner	FLU, IC	8	17
Notropis xaenocephalus	Coosa shiner	END, FLU, IC	30	933
Phenacobius catostomus	riffle minnow	END, FLU, IC	1	4
Pimephales vigilax	bullhead minnow	COS, FLU	1	9
Semotilus atromaculatus	creek chub	COS, FLU	48	705
Catastomidae				
Hypentelium etowanum	Alabama hog sucker	FLU	57	1,436
Minytrema melanops	spotted sucker	COS, FLU	2	3
Moxostoma duquesnei	black redhorse	COS, FLU	10	46

Appendix 1 continued

Family name, *Scientific name*	Common name	Composition categories	No. sites	Abundance
Moxostoma erythrurum	golden redhorse	COS, FLU	3	11
Moxostoma poecilurum	blacktail redhorse	COS, FLU	1	1
Ictaluridae				
Ameiurus brunneus	snail bullhead	FLU, LEN	11	43
Ameiurus natalis	yellow bullhead	COS, LEN	5	12
Ameiurus nebulosus	brown bullhead	COS, LEN	5	8
Ictalurus punctatus	channel catfish	COS, LEN	1	1
Noturus leptacanthus	speckled madtom	COS, FLU	8	25
Fundulidae				
Fundulus stellifer	southern studfish	FLU	29	378
Poeciliidae				
Gambusia affinis	eastern mosquitofish	COS, LEN	6	60
Gambusia holbrooki	western mosquitofish	COS, LEN	3	45
Gambusia sp.	unidentified mosquitofish	COS, LEN	8	104
Cottidae				
Cottus carolinae zopherus	Coosa banded sculpin	END, FLU	36	1,268
Centrarchidae				
Lepomis auritus	redbreast sunfish	COS, LEN	52	1,078
Lepomis cyanellus	green sunfish	COS, LEN	33	347
Lepomis gulosus	warmouth	COS, LEN	8	36
Lepomis macrochirus	bluegill	COS, LEN	54	1,331
Lepomis megalotis	longear sunfish	COS, LEN	1	1
Lepomis microlophus	redear sunfish	COS, LEN	6	10
Lepomis cyanellus × *macrochirus*	hybrid sunfish	LEN	2	19
Lepomis microlophus × *punctatus*	hybrid sunfish	LEN	1	11
Micropterus coosae	Coosa bass	FLU	35	240
Micropterus punctulatus	spotted bass	COS, FLU	8	42
Micropterus salmoides	largemouth bass	COS, LEN	21	64
Percidae				
Etheostoma etowahae	Etowah darter	END, FLU	1	1
Etheostoma scotti	Cherokee darter	END, FLU	36	627
Etheostoma stigmaeum	speckled darter	COS, FLU	14	171
Percina kathae	mobile logperch	FLU	12	73
Percina nigrofasciata	blackbanded darter	COS, FLU	50	548
Percina palmaris	bronze darter	END, FLU	10	107

Composition categories include: endemic (END), cosmopolitan (COS), insectivorous cyprinid (IC), lentic tolerant (LEN), and fluvial specialist (FLU). The primary sources for composition designations were Etnier and Starnes (1993), and Mettee et al. (1996), Walters et al. (2003)

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