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Fish Assemblage Responses to Forest Cover

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Abstract We investigated whether fish assemblage
structure in southern Appalachian streams differed with
historical and contemporary forest cover. We compared
fish assemblages in 2nd–4th order streams draining water-
sheds that had increased forest cover between 1950 and
1993 (i.e., reforesting watersheds). We sampled fish in 50
m reaches during August 2001 and calculated catch-per-
unit-effort (CPUE) by taxonomic, distributional, trophic,
reproductive, and thermal metrics. We assigned streams to
reforestation categories based on cluster analysis of years
1950 and 1993 near-stream forest cover. The relationship
between forest cover and assemblage structure was asses-
sed using analysis of variance to identify differences in fish
CPUE in five forest cover categories. Streams contained 23
fish species representing six families, and taxa richness
ranged from 1 to 13 at 30 stream sites. Streams with rel-
atively low near-stream forest cover were different from
streams having moderate to high near-stream forest cover
in 1950 and 1993. Fish assemblages in streams having the
lowest amount of forest cover (53–75%) were
characterized by higher cosmopolitan, brood hider, detri-
tivore/herbivore, intermediate habitat breadths, run-pool
dweller, and warm water tolerant fish CPUE compared to
streams with higher riparian forest cover. Our results sug-
gest that fish assemblage's structural and functional
diversity and/or richness may be lower in streams having
lower recent or past riparian forest cover compared to
assemblages in streams having a high degree of near-
stream forest cover.

Keywords Land-use · Agriculture · Forest ·
Riparian zone · Stream · Threshold

Introduction

Land-use has been identified as a major source of distur-
bance to streams worldwide (Matson and others 1997;
NRC 2002; Iwata and others 2003). Agriculture, surface
mining, and urbanization have been identified as detri-
mental land-cover types inducing disturbance to terrestrial
and aquatic ecosystems, whereas undisturbed land-cover
(e.g., natural riparian forest) is often associated with more
natural ecosystem characteristics and higher biotic integrity
(Allan 2004). Stream fauna, including fish, are particularly
affected by deforestation; therefore, the field of bioas-
sessment has developed to study the relationship between
stream fauna and impairment (e.g., Schlosser 1990; Smo-
gor and Angermeier 1999; Scott and Helfman 2001;
Meador and Goldstein 2003). Bioassessment research has
strongly associated urban, agriculture, and suburbanization
land-use/land-cover with lower taxonomic and functional
richness and/or diversity. However, the absolute amount or
intensity of land-use coupled with the temporal extent or
duration of detrimental land-uses has been shown to induce

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a broad range of faunal influence, such that predictions about faunal responses are difficult (NRC 2002; Allan 2004).

Bioassessment studies, whether multimetric (i.e., the Index of Biotic Integrity) or multivariate, have been conducted in a broad range of ecosystems and have associated detrimental land-uses with all ranges of faunal influence from extirpations to enhanced diversity. The baseline hypothesis typically predicts that detrimental land-use (often associated with deforestation in the northeastern deciduous forest) reduces the "biointegrity" of the ecosystem. Biointegrity has been defined multiple ways (Karr 1999) and we include both a taxonomic (i.e., richness and diversity of species or genera) and functional (i.e., representation of a diverse feeding, reproductive habitat or tolerance group or guild) component in our definition. In some southern Appalachian streams it appears that detrimental land-uses are associated with a greater number of species or genera relative to a control (i.e., less impaired) system, although the taxa share similar functional niches. For example, Burcher and Benfield (2006) showed that fish and macroinvertebrate assemblages affected by suburban or agricultural land-uses were comprised of taxa occupying similar trophic and reproductive niches. In other words, organisms in disturbed systems may have similar feeding or reproductive habits to reflect the narrower range of resources available. Biointegrity, thus, should reflect both a broad range of taxa and broad niche representation, reflecting the availability of broad resources, rather than simply taxonomic diversity.

Although decreased forest cover and associated land-uses reduce stream biointegrity worldwide, forest cover is actually increasing in many areas of western North Carolina (Wear and Bolstad 1998). As forest cover increases, landscapes return to a more natural condition and the presence of disturbance-type (e.g., agriculture, urban) land-cover is reduced. Although reforestation is considered terrestrial recovery, it is largely unknown whether terrestrial changes lead to improvement of aquatic biotic integrity.

We asked, generally, whether current fish assemblage structure and function differed in streams that vary in the amount of historic and contemporary forest cover but are generally reforesting. We hypothesized that if fish assemblages differed with forest cover, then the amount of forest cover, or the degree of reforestation, would explain the differences because increased forest cover represents reduced disturbance and improved biotic integrity. In this study, we assumed that biotic integrity reflected broader trophic, reproductive, habitat, and thermal niche occupancy to fish taxa. We predicted that fish assemblages in streams having lower relative forest cover or reforestation would have lower trophic, reproductive, and thermal tolerance

diversity compared to mostly forested sites. We expected more impaired streams to contain fewer endemic fishes, representing a narrower range of reproductive, trophic, habitat, and thermal preferences compared to less impaired systems. We expected assemblages would respond to ecosystem level changes in resource availability reflecting lower food availability and more homogenized habitats. For example, streams in reduced forest cover watersheds often might shift from riffle-pool habitats to more homogenized run or run-pool habitats as riffles are reduced by hydrologic alteration. Fish assemblages in these systems should be comprised of fewer taxa that prefer or require riffle habitats for feeding and/or reproductive success. Following this pattern, our general prediction was that more impaired systems would contain fewer endemic taxa thought to prefer less-available habitat and/or trophic resources, fewer taxa that require clean or varied substrata for spawning, fewer specific feeding niches (e.g., herbivores), fewer trophic or habitat specialists, and fishes tolerant to a broader range of thermal conditions compared to sites with a higher amount of increased forest cover and/ or a greater amount of forest cover in years 1950 and/or 1993. We also predicted that sites with lowest forest cover in 1950 and 1993 would contain the most impaired assemblages, and that intermediate sites would resemble either most or least forested sites and reveal whether time (i.e., 1950 versus 1993 conditions) or intensity (i.e., absolute amount of forest cover) was most associated with assemblage impairment.

Methods

Site Selection

Streams were selected to represent watersheds along a forest cover continuum from mostly forested to least forested. Using ArcView® 3.2 (ESRI), forest cover in 1950 was digitized from maps available from that period that identified areas of either forest cover or nonforest cover. We obtained land-cover maps (open water, forest and nonforest which we considered to be mostly agriculture) of the entire southern Appalachian region in 1993 and coverage for Grayson County, Virginia and Madison, Buncombe, and Macon Counties, North Carolina in 1950. Although imagery from 1950 was summarized by ground observation and aerial photography and imagery from 1993 was summarized by satellite imagery, the simplification of forested versus nonforested categories should have reduced the error in methodology. Because comparable imagery sources were not available, we used the best available data and assumed that the error in each method was comparable. In addition, we determined watershed boundaries for 2nd,

3rd and 4th order streams and used a GIS to determine percent forest cover in 1950 and 1993 by overlaying watershed boundaries on land-cover maps from these years. This analysis produced a database of land-cover in > 5000 watersheds using the hydrotools extension in Arc-View® 8.2 Spatial Analyst to identify flow boundaries to a pour-point representing the stream reach within which fish would be collected. From this database, we generated a list of approximately 120 sites with relatively consistent geomorphic structure by restricting potential sites to defined ranges of elevation, slope, stream order, and watershed area. We eliminated high-elevation (above 4000 ft) streams (typically first order streams) from our survey to avoid targeting cold-water trout/sculpin assemblages typical of the southern Appalachian region (Hocutt and Wiley 1986).

Every effort was made to ensure that sites were as similar as possible in all characteristics except forest cover.

We quantified forest cover in each watershed and visited sites to qualitatively address the current (circa 2001) conditions and compare streamside vegetation to remotely sensed images (i.e., ground-truthing) to ensure accurate representation of forest-cover. We then selected 30 sites that had varying proportions of their watersheds covered by forest in 1950 and 1993 but qualitatively showed a trend of increasing forest cover between those dates (Table 1). The 30 sites were located in either the Upper Tennessee or New River drainage watersheds of southwest Virginia and western North Carolina.

The 30 sites represented varying degrees of historic (i.e., 1950) and contemporary (i.e., 1993) forest cover typical of

Table 1 Percent forest cover in both 1950 and 1993 prescribed within entire watersheds draining to sample reach (FOWS) and 100-m riparian zones beginning 2 km upstream of sample reaches (FO2k)

Stream	Site code	FOWS 1950	FOWS 1993	Forest cover category	FO2k 1950	FO2k 1993
Bournes	BOU	99	100	1	100	88
Corner Rock	COR	100	100	1	100	99
Avery	AVE	100	99	1	100	99
Jones	JON	100	98	1	99	99
Ball	BAL	100	100	1	100	99
Shope	SHO	90	97	2	27	79
Little Pine	LPC	58	87	2	15	48
West Fork Bull	WFB	45	77	2	12	43
Terry	TER	73	96	2	24	62
Knob	KFC	52	79	2	14	58
Lisenbee	LIS	87	94	3	74	84
Little Laurel	LLC	97	99	3	86	87
North Prong Ellijay	NPE	89	97	3	71	92
Tessentee	TES	88	97	3	72	97
Little Foster	LFC	91	96	3	74	90
Meadow	MED	82	91	3	77	86
Rocky	ROC	79	95	3	83	93
Little Ellijay	LEC	89	98	3	76	93
Ripshin	RIP	79	88	3	64	79
Roaring Buncombe	ROB	69	92	3	36	82
Roaring Madison	ROM	85	94	4	81	92
Caler	CAL	84	93	4	30	56
Newfound	NFC	48	78	4	32	54
Gap	GAP	64	71	4	20	39
Little Fox	FOX	48	94	4	48	94
Gouches	GOU	32	54	5	3	29
East Fork Bull	EFB	48	80	5	9	48
Skeenah	SKE	58	79	5	1	29
Rock	ROK	49	75	5	1	13
Paint	PFC	78	90	5	0	16

western North Carolina landscapes. Sites that were mostly forested were all located in national forests and had dense tree cover with vegetation typical of mature mixed hardwood forests (hemlock, yellow poplar, white pine, oaks and rhododendron) during sample year (2001). Sites having intermediate forest cover all had extensive evidence of current agricultural activity but these areas differed in the amount of agriculture across their watersheds and in riparian vegetation. Some streams had intact forest areas with small patches of agriculture, whereas other sites had no woody riparian vegetation, were completely open to sunlight, and had extensive agricultural activity.

The 30 streams were further examined using cluster analysis (PC-ORD v. 4.32, MJM Software, Oregon, USA) to group sites based on near-stream forest cover in 1950 and 1993 to capture both the absolute amount of forest cover on those dates as well as the increase in percent forest cover between both dates. Research has shown that stream responses are related to near-stream land-cover rather than whole watersheds because proximal watershed portions are more likely to affect in-stream responses (Roth and others 1996; Sponseller and Benfield 2001; Strayer and others 2003; Boothroyd and others 2004; Lee and others 2004; King and others 2005; Burcher and Benfield 2006; Burcher and others 2007). Harding and others (1998) also showed that land-cover in areas proximal to stream reaches was most predictive of fish diversity metrics. Similarly, Sponseller and Benfield (2001) showed that leaf breakdown rates were most influenced by agriculture in 100-m riparian corridors 2 km upstream. We therefore elected to focus the area in which we considered forest cover to 100-m riparian corridors beginning 2 km above sample reaches and continuing to the ridgeline defining the watershed. This procedure effectively ignores the riparian area immediately (i.e., within the first 2 km) upstream of the sample location and reflects the longitudinal nature of streams (Vannote 1980; Burcher and others 2007)

Fish Sampling

Fish were sampled once during August 2001 in each stream from 50-m stream reaches using backpack shocking units and a 10-mm mesh seine. Fifty-meter reaches were subdivided into approximately 5-m reaches that were blocked at the downstream end by the seine, and fishes were herded into the seine during a single electrofishing pass. Fifty-meter reaches were selected based on inclusion of a series of habitat types (i.e., riffle-run-pool sequence) and as a function of stream width (Simonson and others 1994). Average stream width among 30 sites was 3.3 m, ranging from 1.7–5.7 m. Hence, stream reaches were between 9 and 29 times stream width. Fifty meters, averaging 14 times

average stream width, was deemed adequate to obtain representative fishes from the dominant taxa common to each stream (Schlosser 1982; Angermeier and Schlosser 1989; Angermeier and Smogor 1995). Angermeier and Smogor (1995) found that only rare fishes were collected beyond a sample reach equivalent to 15–20 stream widths in Copper Creek, Virginia. Most fishes were released after identification.

Fish assemblage structure and function were characterized by several metrics (Table 2). Fish taxa richness was estimated as the number of species found at any site. Fish catch-per-unit-effort (CPUE) was estimated as the number of fish of a species or ecological group per square meter of stream bottom (50-m reach X average stream width). We elected to use CPUE as a proxy measure of density because actual estimates of fish density are complicated by capture rates and difficulties validating true fish density (Angermeier and Schlosser 1989). CPUE was also characterized by distribution status, reproductive habit, trophic guild, and thermal tolerance based on the classification of Etnier and Starnes (1993), Jones and others (1999), Simon (1999), Scott and Helfman (2001), and Jenkins and Burkhead (1994; Table 3). Fish distribution status was assigned according to Scott and Helfman (2001) and reflected whether fishes were endemic to local drainages, restricted to upland areas, or widely distributed throughout the study area and is a measure of invasiveness by native species (Scott and Helfman, 2001 for Appalachian highland fishes). Reproductive habit described the spawning strategy and spawning-substrate requirements for a species. Some taxa require clean substrate for spawning (i.e., nest associates), whereas others are able to clean embedded substrate (i.e., nest guarders). Trophic guild status reflected the known feeding habits of each species. Impaired streams have been shown to be more likely to be dominated by omnivorous species (Jenkins and Burkhead 1994). Habitat type and breadth referred to the particular stream areas where a species is known to spend most of its time. Trophic and habitat breadths reflected the propensity for a species to utilize multiple resources as opposed to requiring a narrow subset of some resource. Thermal tolerance was described as the range of temperatures a species was able to tolerate (Scott and Helfman 2001).

Data Analysis

We followed a multivariate approach to comparing fish assemblages among study streams. CPUE estimates were compared using one-way ANOVA comparisons by forest cover category (SigmaStat v. 3.0, SPSS, Inc.). Multiple comparisons tested the hypothesis that assemblages in at least one forest cover category were different from other

Table 2 Distributional, reproductive, trophic, and thermal tolerance metrics used to classify fishes

Guild / Group	Category	Code	Description
Distribution status			
	Endemic	1	Endemic to Appalachian highlands
	Upland	2	Restricted to upland areas
	Cosmopolitan	3	Cosmopolitan or occur in lowlands
Reproductive habit			
	Brood hider	1	Bury eggs in gravel, no parental care
	Nest guarder	2	Rock crevice nest guarder
	Nest associate	3	Eggs abandoned in chub nest, no parental care
	Broadcast spawner	4	Scatter eggs, no parental care
	Guarder	5	Various nests, guarded
Trophic guild			
	Omnivore	1	Omnivorous
	Detritivore/herbivore	2	Detritivore or herbivore
	General invertivore	3	Collect prey items from drift, benthos, and elsewhere
	Piscivore	4	Eat other fish
	Insectivore	5	Feed on insects
Trophic breadth			
	Specialist	1	Near-obligate feeder
	Narrow	2	More than one potential diet
	Broad	3	Very flexible diet
	Omnivore	4	Eats almost anything
Habitat type			
	Riffle	1	Found primarily in riffles
	Run-pool	2	Found in slower, deeper water
	Riffle-pool	3	Prefer pool/riffle boundary
Habitat breadth			
	Specialist	1	
	Intermediate	2	
	Broad	3	
Thermal tolerance			
	Cold water	1	rainbow, brown and brook trout
	Cool water	2	
	Warm water	3	
	Broad thermal tolerance	4	

systems. The multivariate approach differs from the multimetric approach in that no reference condition is required. CPUE densities were estimated for categories of distributional status, reproductive habit, trophic guild, and temperature tolerance. Holm-Sidak (the most discriminatory post-hoc test available using SigmaStat) pairwise comparisons were made when ANOVA indicated significant differences among forest cover categories. Because the ANOVA test is considered robust, CPUE estimates were not transformed if normality or homogeneity of variance assumptions were not met (Zar 1999). We elected not to Bonferonni adjust significance level because the dependent variable was different for each pairwise comparison.

Results

Forest Cover Categories

Clustering of streams suggested five distinct categories that described groups of streams that were similar within categories, yet different (based on Euclidian distance or similarity) from other categories (Fig. 1; Table 1). We selected five groups because more than 95% of the differences were accounted for (as indicated by distance measures) and represented one group of sites mostly forested in both 1950 and 1993, one group that reflected the least forested streams in both 1950 and 1993, and three

Table 3 Occurrence, reproductive, trophic, habitat, distribution, and thermal tolerance status of fishes collected

Scientific name	Common name	Occurrence (# sites)	Distribution status	Reproductive status	Trophic class	Trophic breadth	Habitat type	Habitat breadth	Thermal tolerance
Rhinichthys atratulus	Blacknose dace	22	3	4	3	3	3	1	4
Cottus bairdi ssp.	Smoky sculpin	18	1	2	5	1	3	1	2
Oncorhynchus mykiss	Rainbow trout	15	2	3	4	3	2	3	1
Campostoma anomalum	Central stoneroller	12	3	3	2	1	3	2	4
Etheostoma flabellare	Fantail darter	12	1	2	5	1	1	2	3
Nocomis micropogon	Bluehead chub	12	3	3	4	3	3	2	4
Hypentelium nigricans	Northern hogsucker	10	3	1	5	3	3	2	4
Salvelinus fontinalis	Brook trout	9	2	3	4	3	2	1	1
Semotilus atromaculatus	Creek chub	9	3	3	4	4	2	1	4
Rhinichthys cataractae	Longnose dace	8	2	4	5	2	1	1	2
Ambloplites rupestris	Rock bass	5	3	5	3	3	2	1	4
Clinostomus funduloides	Rosyside dace	5	1	3	5	1	2	1	2
Notropis rubricroceus	Saffron shiner	5	1	3	5	2	2	1	2
Lepomis macrochirus	Bluegill sunfish	4	3	5	3	2	2	3	4
Phoxinus oreas	Mountain redbelly dace	4	3	3	2	3	2	2	3
Salmo trutta	Brown trout	4	2	3	4	3	2	2	1
Cyprinella galactura	Whitetail shiner	3	2	3	3	2	2	2	4
Luxilus coccogenis	Warpaint shiner	3	1	3	5	1	2	1	3
Ichthyomyzon greeleyi	Mountain brook lamprey	2	3	3	1	3	3	2	3
Notropis leuciodus	Tennessee shiner	2	1	3	5	1	2	2	3
Etheostoma blennioides	Greenside darter	1	1	1	5	1	1	1	2
Etheostoma swannanoa	Swannanoa darter	1	1	1	5	1	3	2	2
Percina evides ssp.	Appalachian gilt darter	1	1	1	5	1	1	1	3

Species are listed in order of decreasing occurrence. Category codes are given in Table 2

Fig. 1 Cluster analysis of 30 streams by forest cover on 2 dates (1950 and 1993) prescribed within 100-m riparian corridors beginning 2 km upstream of sample reaches
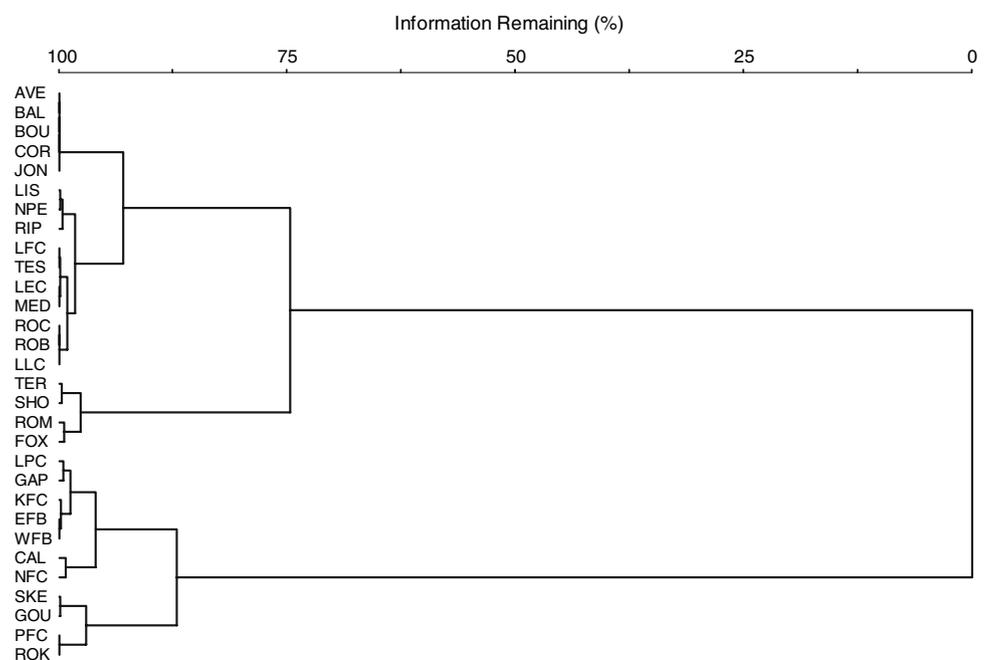
Table 4 Summary statistics for five forest cover categories and percent change in forest cover between 1950 and 1993

Values are percent forest cover within 100-m riparian corridors beginning 2 km upstream of sample reaches. FC = forest cover

Forest Cover Category (high to low)	Mean ± 1 SE 1950 FC	Mean ± 1 SE 1993 FC	% FC change 1950–1993
1	100 ± 0.2	100 ± 0.0	0.1
2	64 ± 17.7	88 ± 9.3	24.7
3	88 ± 6.5	98 ± 3.1	9.4
4	62 ± 15.4	87 ± 9.4	24.1
5	53 ± 16.7	75 ± 12.7	21.8

levels of intermediate sites having different absolute forest cover in 1950, 1993, or both (Table 4).

Fish Assemblage Characteristics

Twenty-three species were collected among 30 sites and 6 of 28 assemblage metrics differed among streams with respect to reforestation categories. Taxa richness varied from 1 (Ball, Lisenbee, and Meadow) to 13 (Gap Creek) species at any single site, averaging 7 taxa at category 4 sites (maximum) and 4 taxa at category 1 sites. Mean taxa richness ranged between 4 and 7 among forest cover categories but did not differ significantly ($f = 0.682$, $p = 0.661$). Total CPUE was not different among forest cover categories but ranged between 0.05 (Meadow) and 5.48 (Rock) individuals m^{-2} (overall $\bar{x} = 0.77$ m^{-2}). CPUE of cosmopolitan species was significantly higher in reforestation category 5 sites when compared to other categories ($f = 3.382$, $p = 0.024$; Fig. 2a). CPUE of upland and endemic species did not differ among forest cover categories.

Reproductive and trophic assemblage structure was also influenced by forest cover. CPUE of fish taxa that hide broods was significantly higher in category 5 streams ($f = 4.569$, $p = 0.007$; Fig. 2b). CPUE of detritivore/herbivore species was also highest in category 5 streams ($f = 4.008$, $p = 0.012$; Fig. 2c). CPUE estimates did not differ among other reproductive trophic classes or breadth categories.

Fish assemblages also differed with respect to habitat preferences and thermal tolerance. CPUE of fishes preferring run-pool habitat was significantly higher in category 5 streams compared to others ($f = 4.338$, $p = 0.008$; Fig. 3a). Species considered intermediate in habitat breadth were significantly more dense in reforestation category 5 streams ($f = 4.336$, $p = 0.008$; Fig. 3b). Warm water fish CPUE was also higher in reforestation category 5 streams and cold water fishes (i.e., trout) were absent from reforestation category 5 streams ($f = 3.690$, $p = 0.017$; Fig. 3c). Estimates of CPUE for fishes in other habitat and thermal categories did not differ with forest cover category.
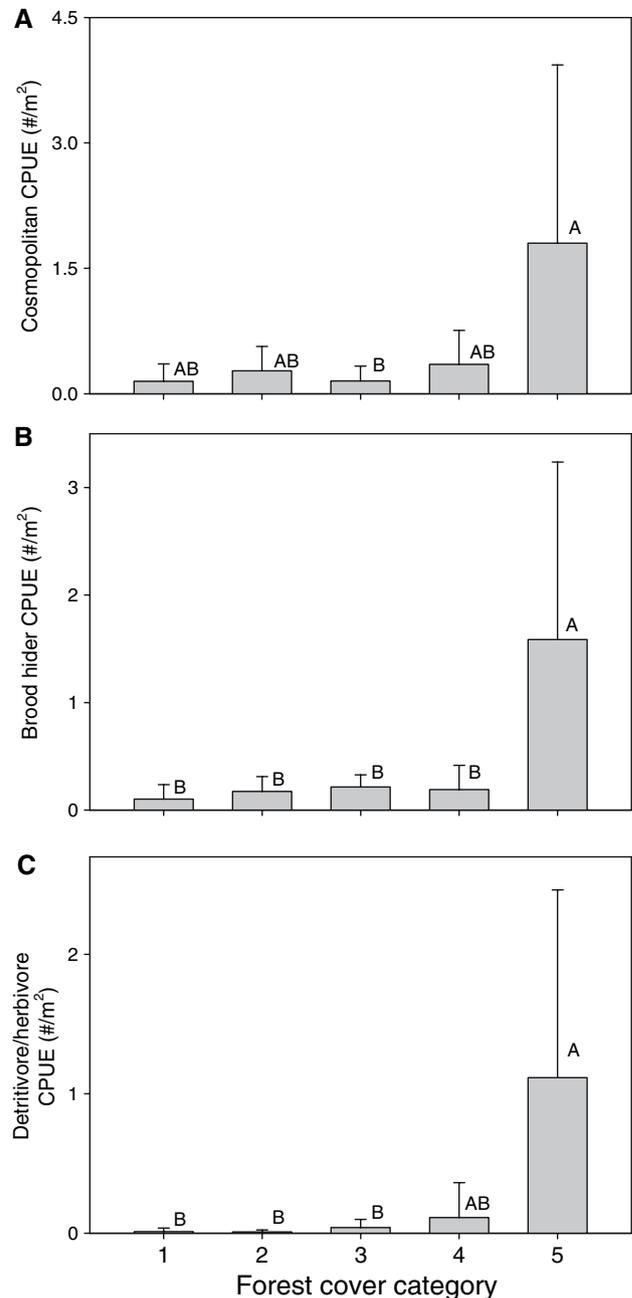

Fig. 2 Cosmopolitan (**a**), brood hider (**b**) and detritivore/herbivore (**c**) species CPUE (mean ± 1 se) by forest cover categories. Significant differences detected with Holm-Sidak post-hoc testing indicated by capital letters near bars
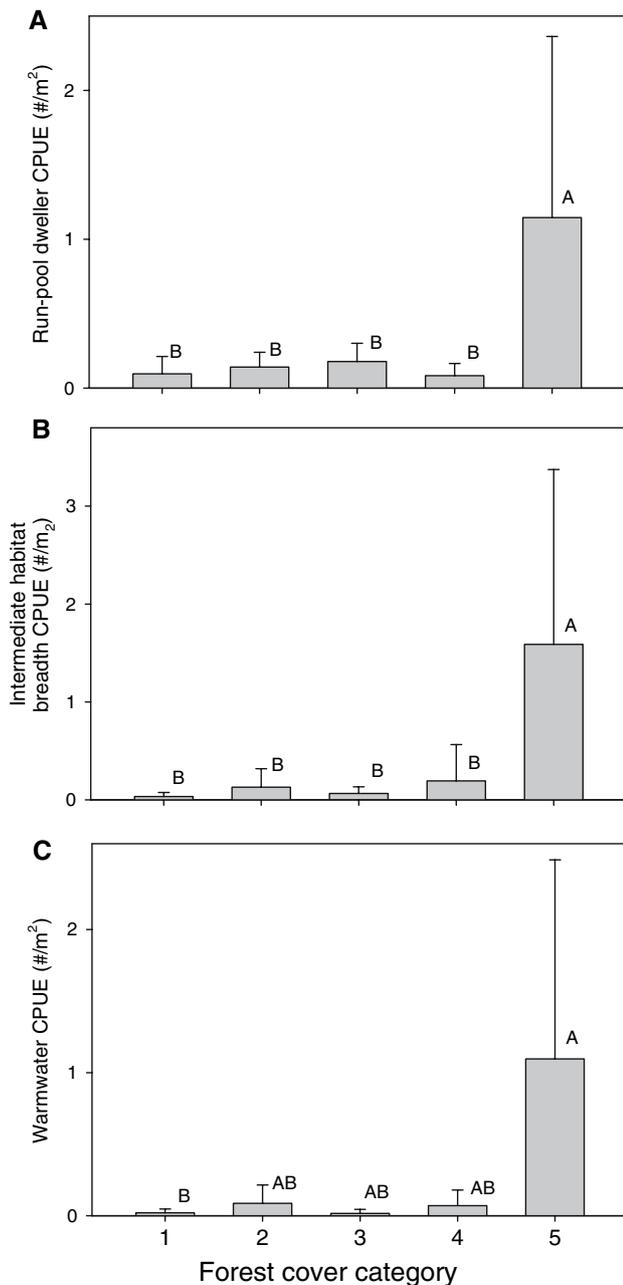
Fig. 3 Run-pool dwellers (**a**), intermediate habitat breadth (**b**) and warm water (**c**) species CPUE (mean ± 1 se) by forest cover categories. Significant differences detected with Holm-Sidak post-hoc testing indicated by capital letters near bars

Discussion

Our analysis of fish assemblages draining landscapes with varying amounts of historic and contemporary forest cover suggested a relationship between forest cover and fish assemblage structure whereby all differences occurred in category 5 sites, and streams in the other four forest cover categories were similar to one another and either category 1 or 5 streams. Category 5 sites were different with respect to distributional status, reproductive habit, trophic guild status, habitat type and breadth, and thermal tolerance. Although taxa richness was higher in streams having the lowest relative forest cover, fish assemblages in lower forest cover sites were characterized by cosmopolitan generalist species.

Assemblage Responses to Reforestation

In all of the six differences in fish assemblage structure and function which we found to be associated with forest cover, the category 1 and 5 streams were different from one another but not to category 2, 3, or 4 streams. Intermediate sites, those with moderate forest cover in 1950 or 1993, were typically similar to one another and to category 1 streams. This response suggests that category 5 streams are unique with respect to forest cover and assemblage structure. Fish assemblages in category 5 streams had higher cosmopolitan taxa that are typically associated with generalist resource use. Category 5 assemblages were dominated by the brood hiding mode of reproduction whereby parents hide eggs to reduce predation. Fishes in category 5 streams were also more likely to be detritivorous or herbivorous species. Category 5 fishes also preferred an intermediate range of habitats most often to include the run-pool series. Lastly, category 5 assemblages differed in that they were numerically dominated by warm water species. These six characteristics suggest that stream conditions in category 5 streams reflected disturbed conditions relative to more forested sites.

Disturbed, low forest-cover streams typically are characterized by higher light penetration and temperature (Meador and Goldstein 2003), reduced riparian vegetation (Jones and others 1999; Lee and others 2004), decreased habitat diversity (Burcher and others 2007), and reduced substrate heterogeneity associated with sedimentation (Nerbonne and Vondracek 2001; Sutherland and others 2002). The assemblage characteristics we found to represent category 5 streams reflect adaptations or acclimations to these types of stream conditions.

Higher CPUE of generalist species in streams that had minimal forest cover and minimum reforestation in 1950 suggests that streams draining minimally forested landscapes did not recover as compared to intermediate or mostly forested sites. Differences in other metrics (e.g., upland, riffle-pool dwelling, broad habitat, and cold water species) were associated with intermediate levels of reforestation or forest cover. These nonlinear patterns suggested that some changes in assemblage structure occurred above a minimal reforestation or forest cover amount but did not suggest a pattern or theme. For example, cosmopolitan fishes able to acclimate to a wider

range of local conditions dominated category 5 streams. These fishes represented a generalist life history strategy, had flexible dietary and spawning requirements and were more successful at exploiting less-favorable conditions than endemic or upland species (Scott and Helfman 2001). Similarly, species having intermediate habitat requirements were more prominent in impaired streams, likely due to their facultative nature of these taxa, with respect to habitat use (Jenkins and Burkhead 1994; Burkhead and Jelks 2001). Similarly, detritivore/herbivore fish CPUE was significantly higher in category 5 sites, which reflected their ability to feed on a commonly available resource (i.e., detritus) rather than being restricted by narrow trophic requirements.

Assemblages in category 5 streams were characterized as having similar richness and taxonomic diversity but lower functional diversity compared to forested systems. Assessment of functional diversity provided more information than simple taxonomic measures and ultimately described fish assemblages in more ecologically relevant detail. Streams draining intermediate levels of forest cover contained assemblages with some aspects of functional diversity in-between least and most forested systems. Whether these differences resulted from increasing agriculture or decreasing forest is unknown. In any case, category 5 streams having the lowest forest cover represented a distinct change to fish assemblages. It is possible that lower relative forest cover (i.e., category 5 streams; 53–75% forest in upstream riparian corridors in 1993; Table 4) associated with higher agriculture (Wear and Bolstad 1998) represented a threshold beyond which impairment to fish assemblages occurred.

Land-cover Thresholds

Stream responses and land-cover thresholds are common in urban literature (Paul and Meyer, 2001). Generally, urban stream research has suggested that a threshold of 10–20% watershed impervious surface cover (ISC) induces dramatic changes to stream ecosystem structure and function (Schueler 1994; Wang and others 2000). Researchers have shown that biotic (Weaver and Garman 1994; Wang and others 2001), geomorphic (Booth 1990), and hydraulic (Poff and Allan 1995) changes occur with urbanization as defined by greater than 10% ISC. Research has suggested that some combination of detrimental effects occurs when urban activity surpasses this threshold (but see Burcher and Benfield 2006).

We identified the threshold of forest cover by the range of mean forest cover in 100-m corridors 2 km upstream of sample reaches (i.e., 53–75%; Table 4). Because corridor forest cover varied among individual streams we estimated

the threshold as the median forest cover proportion among impaired sites. The range of forest cover in the intermediate (categories 2–4) sites we examined was relatively high (Table 4) and may have been subtle enough to inhibit assemblage responses we observed in category 5 streams.

Whether the impairment to fish assemblages we observed is a direct result of lower initial forest cover or lower reforestation remains unknown. Disturbance to fish assemblages in deforested agricultural watersheds is largely associated with sediment inputs that increase after deforestation and agriculture (Ellis 1936; Berkman and Rabeni 1987; Waters 1995; Ryan and Emmett 2002). Sediment fills interstitial spaces, reduces spawning habitat, and interferes with fish feeding success by reducing benthic macroinvertebrate density (Crosbie and Chow-Fraser 1999; Collins and others 2001; Bond and Downes 2003, Roy and others 2003). Further research relating detrimental stream response with agricultural thresholds is necessary to determine whether agricultural thresholds of disturbance are common among systems. Despite the multitude of threshold effects and ISC suggested by the urban literature, we do not yet understand the multivariate factors that influence stream fish assemblages in urban systems (Jennings and Jarnagin 2002). It is likely that multiple factors combine to induce observed detrimental effects and that the combination is significant, or obvious, at some threshold of impairment as measured by land-cover.

Conclusions

In our study of southern Appalachian streams, impairment to fish assemblages (i.e., higher warm water and cosmopolitan CPUE) was observed when less than 75% of proximal, upstream riparian zones were forest (i.e., > 25% nonforest land cover). Our data suggested that a threshold of 75% forest cover defined within near-stream riparian corridors was necessary to significantly impair fish assemblages in southern Appalachian streams. Fish assemblage structure and function in streams draining intermediate levels of forest cover did not respond to forest cover in a linear fashion. Rather, streams draining intermediate forest cover resembled both forest and heavy agriculture streams in some respects. However, we were not able to determine whether increased forest cover (i.e., between 1950 and 1993) or absolute forest cover affected conditions in intermediate streams.

The lack of differences among fish assemblages in intermediate forest cover categories could also suggest that, within the range of forest cover we investigated, intermediate conditions did not create distinctively different levels of disturbance or impact. Similarly, the range of the four intermediate categories of forest cover we assessed, 62–

98% (Table 4) mean forest cover in upstream riparian corridors, is broad and complicated by different reforestation rates and it is possible that forest cover at these intermediate sites affected fishes similarly. Alternatively, our sampling schedule or methods may have been inadequate to detect differences at intermediate disturbance conditions. For example, we sampled across a wide geographic range and collected only once at each site and we may have collected at a site during atypical conditions. Spatial and temporal variation could potentially have influenced our ability to detect differences among sites. However, Scott (2001) found no evidence of significant temporal variation in fish assemblages within sites in a study also conducted in the southern Appalachians, which at least gives us confidence that temporal variation is not likely a significant complication. Our effort choosing similar sites with respect to geomorphic conditions and our standardized methods should have minimized other sampling artifacts.

Our results therefore lead to four possible conclusions with respect to the influence of intermediate land disturbance on fish assemblages in southern Appalachian streams: (1) dramatic disturbance (i.e., forest cover below the threshold of approximately 53–75% in upstream riparian corridors) is necessary before definitive effects are detectable; (2) current response metrics that focus on taxonomic and ecologic structure and function are insufficiently sensitive to detect actual differences among intermediate disturbance categories; (3) variation in geomorphic, geographic, biotic, and other environmental differences among geographically widespread study sites was large and may have overshadowed variation in metrics due to forest cover; (4) in streams draining areas of intermediate forest cover, the variety and complexity of multiple influences are not sufficient to induce consistent, long-term changes to fish assemblage structure and function. Rather, thresholds of impact may have to be surpassed before factors that come into play at low forest cover levels become influential, similar to what has been found for urban land-cover impacts and impervious surface cover (e.g., Peiser 1989; Arnold and Gibbons 1996; Jones and others 1999; Morse and others 2003).

Ours is among the first studies to assess forest cover impacts along a continuum of forest cover intensity on stream fish assemblages. Given that we were able to detect differences of ecological relevance with respect to fish structure and function between the extremes of our forest cover types, we conclude that the intermediate conditions that we assessed are insufficient to cause distinct shifts in stream fish assemblages, although methodological or environmental factors may have affected our ability to detect subtle differences. Comparative or more intensive investigations will be needed to clearly determine whether reforestation leads to fish assemblage recovery in streams draining reforesting landscapes.

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