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Winners and losers among stream fishes in relation to land use legacies and urban development in the southeastern US

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ABSTRACT

The southeastern United States is a center of aquatic species diversity and endemism in North America, but many taxa are imperiled or in decline. Proactive conservation strategies depend on developing sensitive measures of ecological response to environmental degradation early in the process. In the southern Appalachian highlands, much of the region has reforested following extensive logging and agriculture in the last century, but recently exurban development has surged. Patterns of aquatic ecosystem response to these changes were examined in 36 watersheds along a gradient of forest cover from moderately to heavily forested. A linear combination of watershed-scale measures reflecting the extent contemporary forest cover, the trajectory of forest cover change over time, and building and road density were stronger predictors of fish assemblage composition than topographic features. A measure of biotic homogenization relating the abundance of endemic highland fishes to abundance of broad-ranged fishes was sensitive to the gradient of anthropogenic disturbance. Across the watershed disturbance gradient, cosmopolitan species were clear winners as forms unique to the Appalachian highlands were lost. Similar measures of homogenization may be suitable elsewhere for tracking early warning signs of ecosystem stress, particularly in regions with significant endemism. Quantification of the homogenization process in response to urban development and other stressors is a promising avenue for proactive conservation, land use planning, and sustainable development efforts.

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1. Introduction

Biological diversity declines in freshwaters have been well-described, producing a narrative that is at once compelling and alarming (e.g., Moyle and Leidy, 1992; Allan and Flecker, 1993; Bruton, 1995; Richter et al., 1997; Ricciardi and Rasmussen, 1999; Boon et al., 2000). Threats to native biota include exotic species introductions and overexploitation, but by nearly all accounts the most pervasive is habitat alteration. Aquatic systems are integrated with surrounding terrestrial systems through the processes of runoff, sedimentation, and transport of chemical and biotic elements (Fisher, 1997). Conversion of landscapes from indigenous cover to urban and suburban uses disrupts those processes, altering hydrologic regimes, channel morphology, and water quality to the detriment of dependent biological communities (Paul and Meyer, 2001; Miltner et al., 2004). For example, fish density, species richness, and biotic integrity in streams draining highly developed watersheds have been reported to be lower compared to less developed watersheds (Limburg and Schmide, 1990; Weaver and Garman, 1994; Wang et al., 2001). Complications arise, however, with the recognition that the biota may reflect influences other than contemporary watershed disturbance. Faunal structure and organization may be more indicative of past rather than current conditions (Harding et al., 1998). Moreover, anthropogenic and natural

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topographic gradients often covary in the landscape, confounding empirical associations between land use and ecological response (Allan, 2004).

The southeastern US is unique among temperate regions in possessing a highly diverse freshwater fauna and an abundance of endemic forms, with the southern Appalachian highlands being particularly rich. The region has not been glaciated as have areas to the north nor inundated by rising seas as have areas in each of the other cardinal directions, which has allowed this ancient fauna a lush evolutionary history of speciation (Mayden, 1987). Species composition can be quite variable from one physiographic region to the next and among river drainages, creating a mosaic of distinctive assemblages across landscapes. The uniqueness of the southeastern highland ichthyofauna can be attributed to the high level of endemism, with close to 90 species that are found nowhere else and more currently in the process of being formally described (Mayden, 1987; Warren et al., 2000). Brooks et al. (1992) noted that the oldest ecosystems containing the largest numbers of endemic species are most likely to be vulnerable to environmental change, and most in need of immediate conservation. The fact that the southern US has the fastest rate of urbanization of any region in the country (Alig et al., 2004) has sparked concerns over loss of the irreplaceable evolutionary heritage the regional fauna represents (Burkhead et al., 1997; Warren et al., 2000).

Small geographic range is a well-known correlate of species vulnerability to imperilment (Angermeier, 1995; Purvis et al., 2000). Fishes that have evolved within a particular region often show specialized behaviors, ecologies, and/or physiologies that are adaptive to indigenous environmental regimes (Matthews, 1987; Fausch et al., 2001). Specialization is a liability when habitat alterations (e.g., hydrologic disruption, pollution) create a set of new selective pressures that operate on populations; species with more generalized requirements often find the new conditions more suitable (Scott and Helfman, 2001). Through this non-random process of substitution and replacement, unique local communities disappear and widespread 'weedy' species that can tolerate human activities take their place, a process known as biotic homogenization (McKinney and Lockwood, 2001). The need to identify vulnerable taxa before they are in precipitous decline is a high priority for proactive conservation (Angermeier and Karr, 1994), as is early recognition of threats to habitats and species (Moyle and Leidy, 1992; Warren and Burr, 1994).

Direct measures of homogenization that can be shown to be sensitive to threats such as urban development present an opportunity for proactive conservation. That is, if we know how the homogenization process responds to specific threats, mitigation of those threats and, more importantly, conser- vation planning to avoid the impacts in the first place are possible. Here, I explore the sensitivity of a measure of homogenization to watershed characteristics using field data from western North Carolina. I compare the influences of natural topographic variation with anthropogenic gradients of forest cover change over time and intensity of watershed development on a measure relating endemic highland fish abundance to abundance of species with broad geographic ranges.

2. Methods

2.1. *Data collection*

As part of the Coweeta Long-Term Ecological Research (LTER) Program sponsored by the National Science Foundation, affiliated researchers collected data on land use/land cover and stream ecosystems as part of a larger study of land-use change in the southern Appalachians (e.g., Harding et al., 1998; Wear and Bolstad, 1998; Scott et al., 2002). Forest cover began to be systematically cleared in the 1800s in the southern Appalachian mountains, and virtually no virgin forest tracts remain today. Nevertheless, the majority of the region remains covered in subsequent forest regrowth. In the last 20 years, the region has seen significant population growth, and the general trend in landuse has been away from the agriculture prevalent in the mid 1900s. There has been an overall increase in forest cover since that time due to succession in abandoned fields, but building densities have also increased, indicative of an increasing market for residential development and associated commercial uses (Wear and Bolstad, 1998). Asheville, NC is the major urban center in the study area.

Researchers selected 36 streams for aquatic sampling that spanned a gradient in watershed land use from mostly forested to higher percentages of agricultural or urban use (Scott et al., 2002). Study streams are tributaries of the Little Tennessee and French Broad rivers, adjacent drainages in the upper Tennessee River system draining the Blue Ridge region of western North Carolina (Fig. 1). Due to the inert nature of the predominantly crystalline rocks, highland streams are naturally low in dissolved ions and nutrients, are clear, and have circumneutral pH. Stream channels are typically bedrock-constrained, with boulder-cobble substrates prevalent. Watersheds ranged from 5 to 320 km^2 in drainage area. Scott et al. (2002) further described features of the study area and documented empirical relations between watershed land use, water quality, and channel geomorphology.

Landscape data within study stream catchments were assembled in a GIS as part of the LTER effort (P. Bolstad, unpublished data) from which I selected several topographic and land cover variables for this analysis (Table 1; see Scott et al. (2002) for a more detailed description). Catchment area in hectares, elevation in meters, and channel gradient in percent over a 1 km reach above each sample site were derived from digital elevation models (DEMs). Proportion of forest cover within each catchment was obtained for two time periods: the early 1970s from Landsat Multi-Spectral Scanner scenes and for 1993 from Landsat Thematic Mapper satellite imagery. A measure of forest cover change was calculated by subtracting proportion of catchment in forest cover at the earlier period from the later period, hence positive values indicated forest cover recovery and negative values loss of forest over time. Road and building location data were measured by digitizing the most recent available 1:24,000-scale USGS topographic maps. I calculated catchment road density as km per ha and building density as number per ha. An index of watershed development was created for each catchment by normalizing building and road densities to their maximum

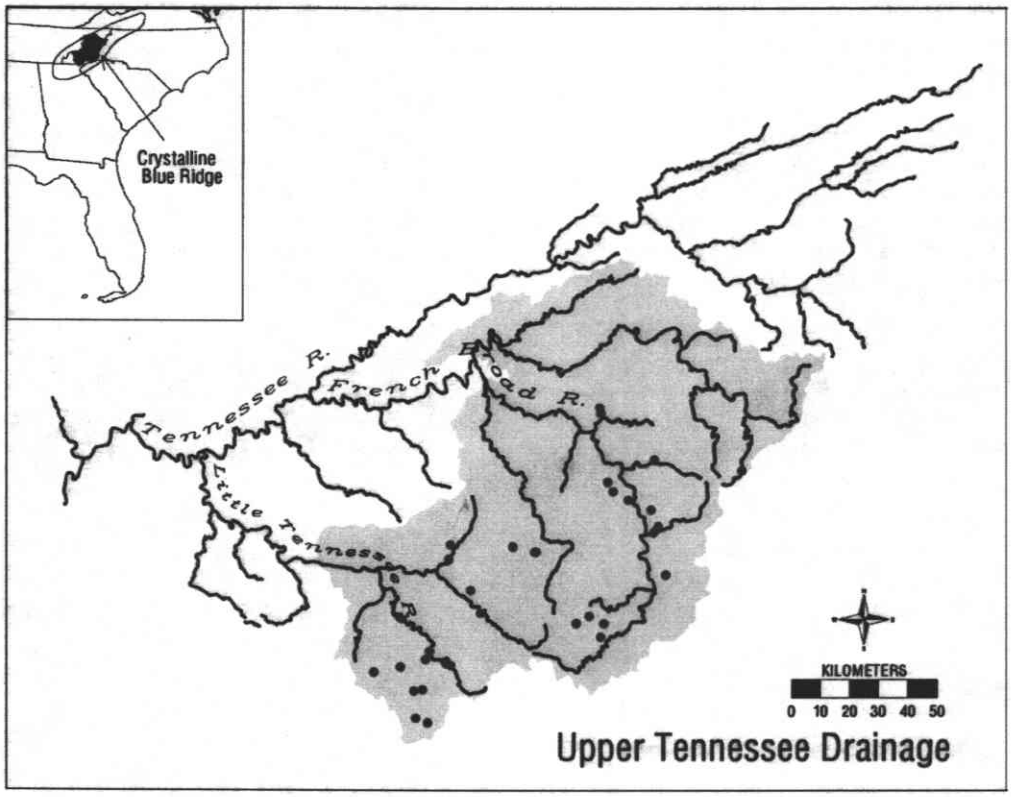

Fig. 1 – Map of the Upper Tennessee River system. Shading indicates drainage area of the upper Little Tennessee and French Broad Rivers. Points indicate locations of 36 sampling sites on tributary streams in the study area.

Table 1 – Landscape measures of study watersheds (see Scott et al., 2002 for additional details)

Landscape variable	Measurement unit	Data source	Mean (SD)	Range
Channel gradient	% over 1 km	USGS 30 digital elevation model (DEM)	7.69 (4.34)	1.7–20.3
Catchment area	ha	USGS 30 m DEM	8397 (6745)	511–32,125
Elevation	m	USGS 30 m DEM	657 (104)	489–981
Urbanization intensity	Index score	Normalized catchment building + road density from 1:24 K USGS topographic maps	0.336 (0.459)	1.82–0.02
Catchment forest cover (1993)	Proportion of total land cover	1993 Thematic Mapper satellite imagery	0.85 (0.18)	0.40–1.0
Catchment forest cover (early 1970s)	Proportion of total land cover	LandSat Multi-Spectral Scanner satellite imagery	0.67 (0.34)	0.03–1.0
Forest cover change	Difference in proportions above	See above	0.18 (0.33)	−0.19 to +0.94

values (i.e., scores were expressed as a proportion of maximum) and summing the two.

Field collection of fishes took place at 24 of these sites in spring and fall 1995 and 1996 (E. B. Dale Jones III, unpublished data); I collected fishes at 12 additional sites in spring and fall of 1997 and 1998. We used backpack electrofishing units in combination with seines to thoroughly cover all habitats in a 50 m segment from downstream to upstream, collecting all juvenile and adult individuals encountered. Researchers typically electrofished into seines set in riffles and chutes, a particularly useful technique for collecting fishes in high gradient streams. Fishes were identified to species or subspecies, counted, and released. Specimens that could not be positively identified in the field were preserved and returned to the lab for identification. Taxonomy of fishes followed Warren et al. (2000); even though some of the recognized forms await formal taxonomic descriptions, they were included because many are localized endemics and thus of importance in evaluating biotic homogenization. In sum, we sampled each of the 36 sites four times by the same method for a total of 144 collections. Variation in fish assemblage structure due to seasonal and annual effects was negligible compared to

variation due to environmental differences among sites (Scott, 2001). Therefore, I pooled collections within sites to obtain a total catch per species per site.

2.2. Data analysis

From the list of 49 species collected during the study, I compiled two groups to contrast for this analysis (Table 2) based on descriptions and discussion of their evolutionary history in Mayden (1987) and supplemented with additional information on geographical distributions (Warren et al., 2000; Lee et al., 1980). One group comprises 17 species and subspecies endemic to the Appalachian highlands under the hypothesis that this group is more likely to possess adaptations to the cool-to-cold water, rocky substrates, and low nutrient conditions of these high-gradient streams (Scott and Helfman, 2001). The second group of 27 species is more broad-ranged; essentially I considered as cosmopolitan those species whose native ranges included Coastal Plain, Mississippi Valley, or other lowlands under the assumption that these species are

Table 2 – Endemic Appalachian highland fishes and more cosmopolitan fishes (i.e., distributed more widely across North America) collected in streams of the Little Tennessee and French Broad river basins listed by family (modified from Scott and Helfman, 2001)

Endemic highland species	
Cyprinidae	
Clinostomus sp. cf. *funduloides* smoky dace	
Erimystax insignis eristigma, mountain blotched chub	
Luxilus coccogenis, warpaint shiner	*Notropis leuciodus*, Tennessee shiner
N. rubricroceus, saffron shiner	*N. spectrunculus*, mirror shiner
Phenacobius crassilabrum, fatlips minnow	
Salmonidae	
Salvelinus fontinalis, southern brook trout	
Cottidae	
Cottus bairdi ssp., smoky sculpin	
Percidae	
Etheostoma blennioides gutselli, Tuckasegee darter	
E. chlorobranchium, greenfin darter	*E. rufilineatum*, redline darter
E. swannanoa, Swannanoa darter	*E. vulneratum*, wounded darter
Percina evides ssp., Appalachian gilt darter	*E. flabbellare* ssp., fantail darter
P. squamata, olive darter	
Widely distributed species	
Petromyzontidae	
Ichthyomyzon greeleyi, mountain brook lamprey	
Cyprinidae	
Campostoma anomalum, central stoneroller	*Hybopsis amblops*, bigeye chub
Nocomis micropogon, river chub	*Notemigonus crysoleucas*, golden shiner
Notropis lutipinnis, yellowfin shiner	*Notropis photogenis*, silver shiner
Carassius auratus, goldfish	*Rhinichthys atratulus*, blacknose dace
Semotilus atromaculatus, creek chub	
Catostomidae	
Catostomus commersoni, white sucker	
Hypentelium nigricans, northern hog sucker	
Moxostoma duquesnei, black redhorse	
M. erythrurum, golden redhorse	
Ictaluridae	
Ameiurus melas, black bullhead	*A. natalis*, yellow bullhead
Poecilidae	
Gambusia affinis, western mosquitofish	
Centrarchidae	
Ambloplites rupestris, rock bass	*Lepomis auritus*, redbreast sunfish
Lepomis cyanellus, green sunfish	*L. macrochirus*, bluegill sunfish
L. gibbosuss, pumpkinseed	*L. gulosus*, warmouth
Micropterus salmoides, largemouth bass	*Micropterus dolomieui*, smallmouth bass
Percidae	
Etheostoma zonale, banded darter	
Perca flavescens, yellow perch	

Designations are based on Mayden (1987) and Warren et al. (2000).

more likely to possess adaptations to the warmer, more silty, and nutrient-rich habitats resulting from watershed disturbance. I calculated relative abundance of endemic and cosmopolitan fishes per site by taking the total number of individuals in each group and dividing by the total number of fish collected at that site. The resulting two numbers are not reciprocals because other species were collected that I considered neither Appalachian highland endemic nor cosmopolitan and thus do not strictly conform to the hypotheses stated above concerning differential response to habitat alteration. These species are more or less common forms that are restricted to the uplands in the southeastern US but are also distributed elsewhere. For example, two species of non-native trout were present in many collections (rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*). These are native to cold water habitats of the western US and Europe, respectively, but widely introduced worldwide, including the Appalachian mountains where their occurrence and abundance are highly influenced by stocking and harvest rates. The remaining three species excluded from this analysis are native to the southern Appalachians but are also distributed elsewhere, such as across the Canadian shield (i.e., longnose dace *Rhinichthys cataractae*) or the Ozark highlands (i.e., whitetail shiner *Cyprinella galactura* and telescope shiner *Notropis telescopus*).

I created a measure of homogenization (E–C) from the assemblage relative abundance matrix by subtracting the relative abundance of cosmopolitan fishes from that of highland endemics. Therefore a value of 1.0 indicates an assemblage composed entirely endemics at that site (i.e., low homogenization) and −1.0 indicates complete dominance of cosmopolitan fishes (i.e., highly homogenized with surrounding regions). The E–C value was used in subsequent analyses.

I evaluated the response of the E–C homogenization measure to watershed conditions with respect to both natural topographic and anthropogenic land use gradients. First, I examined scatter plots of the dependent and independent variables and determined that linear models would be appropriate. I applied the Box-Cox procedure for finding an optimum power transformation (Sokal and Rohlf, 1995) to improve the normality and error structure of the variables. Even with transformation most of the variables were non-normal (Shapiro–Wilk test, $p < 0.05$). Multiple regression using ordinary least squares estimation assumes variables are from a normal distribution, the violation of which does not bias parameter estimates but renders *t*- and *F*-tests invalid and inflates the variance of parameter estimates (Sokal and Rohlf, 1995). Therefore I took an information-theoretic approach to multiple regression using maximum likelihood methods that reduces reliance on statistical significance tests (Burnham and Anderson, 1998). Akaike's Information Criterion, adjusted for small sample size (AICc), is a model performance statistic that balances statistical fit with model parsimony, useful for determining the number of predictors involved and as a criterion for selecting between competing models. Model-building consists of sequentially dropping alternate terms from the full model until AICc is minimized, resulting in the best approximating regression model (Burnham and Anderson, 1998). I proceeded to model homogenization as a function of untransformed topographic and land use variables using maximum-likelihood estimation in the GENMOD procedure of SAS® software, specifying normal distributions and the identity link function. Preliminary inspection of the data indicated weak correlations between channel gradient and urban intensity ($r = -0.38$) and 1993 forest cover ($r = 0.35$), and a stronger correlation between urban intensity and 1993 forest cover ($r = -0.76$). Therefore, I calculated variance inflation factors (VIF) to assess the extent of colinearity among the correlated predictors; all VIF were less than 3.0, indicating that colinearity was not strong enough to adversely affect parameter estimates (Draper and Smith, 1981). I first modeled E–C with all predictors included as terms and sequentially removed and retained the topographic variables (channel gradient, elevation, and catchment area) and watershed disturbance variables (forest cover in 1993 and the early 1970s, forest cover change, and development intensity) to compare the fit of various model.

Finally, I used ordination as a graphical aid to help visualize relationships among multiple variables. I conducted a principal components analysis of the untransformed land use variables catchment urbanization intensity, 1993 catchment forest cover, and catchment forest change over time. The correlation matrix was used and the axes were orthogonally rotated to maximize structural correlations. The homogenization measure E–C was plotted against the first principal component to assess the form of the relationship.

3. Results

The maximum-likelihood analysis showed that the biotic homogenization measure E–C is negatively related to watershed development and positively related to forest cover, indicating that assemblages were most homogenized in sites where watershed development is most dense and forest cover is reduced (Table 3). The best approximating model included urbanization intensity, 1993 forest cover, and forest cover change from the 1970s to the 1990s. Multiple regression employing these three predictors yielded an R^2adj = 0.64, indicating that nearly two-thirds of the variation in E–C values among sites was explained with these three land use measures. Land use variables were superior to topographic factors as predictors of homogenization (Table 3). Channel gradient was the superior predictor among all topographic factors (ranked model 8), but no combination of topographic variables improved fit beyond the model employing land use alone. These results indicate that the homogenization measure E–C is more responsive to the anthropogenic disturbance gradient than to natural topographic variation.

The contribution of catchment forest change over time to predictive ability appeared to be relatively minor because the second ranked model was nearly equivalent to the first, according to AICc (Table 3). This conclusion is supported by the fact that the second and third ranked models were nearly equivalent. Forest cover in 1993 (ranked model 2) fit only slightly better than forest cover in the early 1970s (ranked model 3), as long as catchment urbanization was included in the model. However, when urbanization was not included, forest cover in the early 1970s alone (ranked model 7) was a

Table 3 – Linear models of biotic homogenization measure E–C (relative abundance of Appalachian highland endemic fishes minus relative abundance of cosmopolitan fishes) as a function of topographic and land use variables, ranked by the model performance statistic, Akaike's Information Criterion adjusted for small sample size (AICc; Burnham and Anderson, 1998)

Model rank	AICc	Model predictors	Standardized estimates	Adjusted R^2
1	36.02	Catchment forest cover (1993)	0.46	0.64
		Urbanization intensity	−0.42	
		Forest cover change	−0.21	
2	37.69	Urbanization intensity	−0.46	0.61
		Catchment forest cover (1993)	0.38	
3	38.48	Urbanization intensity	−0.68	0.60
		Catchment forest cover (1970s)	0.24	
4	40.56	Urbanization intensity	−0.76	0.56
5	42.93	Catchment forest cover (1993)	0.74	0.53
6	44.02	Catchment forest cover (1993)	0.50	0.62
		Urbanization intensity	−0.35	
		Forest cover change	−0.23	
		Channel gradient	0.03	
		Elevation	−0.03	
		Catchment area	0.10	
7	62.49	Catchment forest cover (1970s)	0.46	0.19
8	66.81	Channel gradient	0.33	0.08
9	69.06	Channel gradient	0.35	0.11
		Elevation	0.08	
		Catchment area	0.27	

Parameters estimates are standardized by unit of measure for comparison of predictors within each model; R-squares are adjusted for the number of terms in each model.

far weaker predictor than recent forest cover (ranked model 5). Interestingly, the standardized estimate of forest cover change is negative in ranked model 1, although weak, signifying that recovery of forest over time has not overcome the legacy of past land use impacts on aquatic biota. These results are congruent with a process of reforestation in some study catchments accompanied by exurban growth, and they further suggest that urban development is having a negative effect on the homogenization measure regardless of forest recovery.

Principal components analysis results illustrated the overall negative correlation between forest cover and urbanization intensity. Urbanization and forest cover in 1993 loaded with structural correlations of 0.95 and −0.93, respectively, on the first component axis, which accounted for 61% of variation among sites in the three land use variables. Forest cover change over time was less important (0.07). The second component accounted for 32% of variation in land use variables, and was 99% correlated with forest cover change. A plot of E–C on the rotated first principal component clearly illustrates that the linear combination of urbanization and forest cover has a strong negative relationship with the homogenization measure (Fig. 2). Although the relationship is fairly noisy, its form appears linear. Sites with less disturbed watersheds (i.e., higher forest cover and lower building and road densities) are located toward the negative end of the x-axis, and sites with more disturbed watersheds are located toward the positive end. Least disturbed sites presented here are characterized by a 30–90% greater representation of endemic fishes than cosmopolitan fishes. As the gradient of disturbance increases, E–C becomes more variable and falls to around 0 (equal representation of the two groups). There is also a possible breakdown point, or threshold response, as the principal component turns positive. In this area of the plot, E–C has its greatest variance. Further toward the positive end, in streams with more disturbed watersheds, the fish assemblages are dominated by cosmopolitan fishes.

4. Discussion

The altered biota observed in the disturbed catchments is troubling precisely because it is uncharacteristic of the region. Endemic fishes represent a substantial component of aquatic biological diversity across scales, and constitute an important element of the ecological integrity of the region. Land disturbance, and development in particular, clearly is associated with loss of ecological integrity in these streams, as revealed by declines in endemic fishes and their replacement with widespread species. The trend emphasizes the need to manage and conserve this fauna. The progression of the homogenization process over time will propel sensitive endemic forms toward imperilment. The early detection of declines in these unique forms, none of which are listed as threatened or endangered, should be a call to action to stop and reverse the poor land use practices that degrade aquatic habitats or else their decline toward future listing is foreseeable.

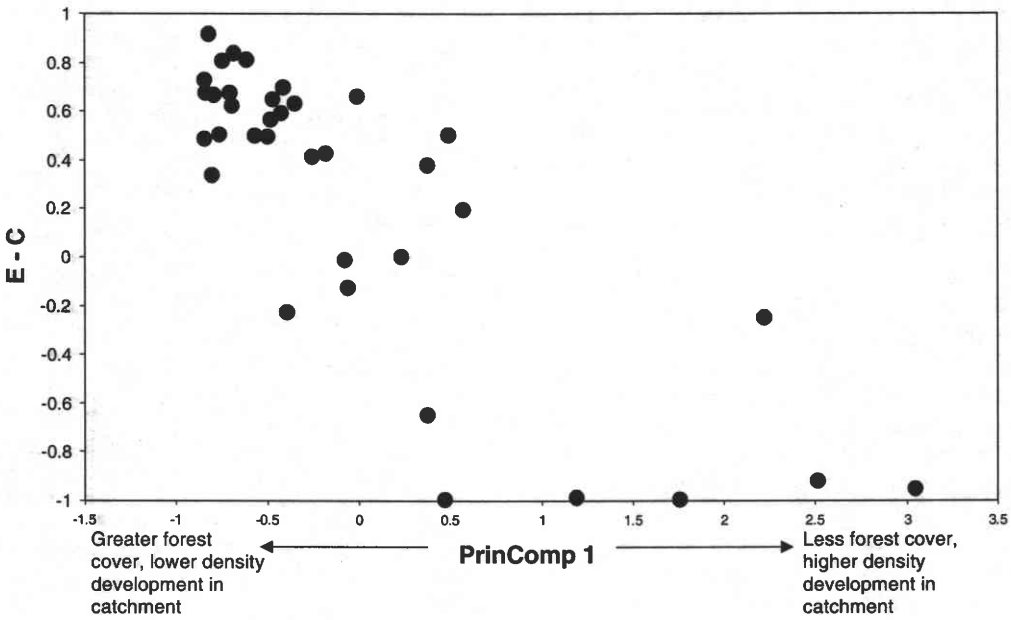

Fig. 2 – Plot of a measure of biotic homogenization (E–C: relative abundance of Appalachian highland endemic fishes minus relative abundance of cosmopolitan fishes) on the first axis from a principal components analysis of catchment land use variables. The axis explained 61% of variation in three land use measures among the 36 sites. Forest cover in 1993 loaded on the negative end ($r = -0.93$) and urban intensity loaded on the positive end ($r = 0.95$) of the axis. Forest cover change over time was not significantly correlated with the first component axis.

The significance of endemism is well recognized in conservation literature as indicative of distinctive biotas, biodiversity "hotspots", and as a criterion in protected area selection (Saunders et al., 2002; Mehlman et al., 2004; Tognelli, 2005). The results I presented here, as well as those of Walters et al. (2003), suggest another useful role for endemic taxa: indicators of biotic homogenization and ecological integrity. Measures of homogenization typically have focused on assemblage similarity or turnover among different geographic areas (Rahel, 2002; McKinney, 2004). More direct measures such as the one I used do not rely on paired comparisons. Walters et al. (2003) found ratios of endemic to widespread species, measured both as ratios of abundance and of number of taxa, were sensitive to urbanization in Georgia streams near Atlanta. Similar homogenization measures may be useful with other faunas in other areas of high endemism such as the tropics or mountain regions. Moreover, since endemism may be defined based on a series of spatial scales (e.g., single stream, drainage unit, river basin, physiographic region(s), continent), others might rank and classify organisms of interest according to range size, in keeping with the underlying principle that restricted range is an indicator of ecological attributes that place species at risk of imperilment (Angermeier, 1995; Purvis et al., 2000). Other direct measures of homogenization may be useful as well, including proportions, ratios, or differences in measures of native vs. introduced species in a given assemblage.

Building and road density as a combined index of urban intensity emerged along with forest cover as the strongest predictors of homogenization, pointing to the long. One of the challenges in assessing the effects of land use is the frequent covariation among anthropogenic gradients and natural landscape features (Allan, 2004). Although urban intensity and forest cover were correlated with channel gradient, the relationship was weak enough that the independent variation could be modeled. The modeling results indicated that E–C was sensitive to the anthropogenic gradient rather than topographic features, an independence that is certainly a desirable feature in an ecological indicator.

Regeneration of forest cover across these landscapes was not a major factor influencing homogenization. Endemic fishes are not significant components of the assemblage in watersheds that have made large gains in forest cover over two decades, suggesting a lack of biological recovery in these systems. The evidence suggests two possible reasons. One is that some of the catchments that have recovered from past deforestation have concomitantly undergone exurban development. The impacts of ongoing development activities negate the aquatic habitat recovery presumably associated with reforestation. The other possibility is that the habitat impacts that are legacies of the old disturbance (fine sediments, lack of large woody debris) are still present, a situation termed the "ghost of land use past" by Harding et al. (1998). Long term monitoring of such systems is desirable to establish what the rates of recovery in the physical, chemical, and biological components of the aquatic ecosystem might be.

Going into the future, direct measures of homogenization present an opportunity for proactive conservation. Conservation strategies to sustain native aquatic biota must focus on

landscapes. Protected-area conservation strategies for freshwater systems are necessary and most useful in headwater areas or catchment-wide reserves (Pringle, 2000; Collares-Pereira and Cowx, 2004). Unfortunately, protected areas are inadequate as the sole national or regional strategy due to the cumulative nature of point and non-point source pollutants, the mounting economic pressures to develop and utilize land, the need for connectivity among drainage networks, and the sheer size of area needed to sustain diverse faunas. As Miller and Hobbs (2002) note, effective conservation must take place where people live and work. A more holistic and proactive conservation effort to sustain southern aquatic ecosystems must involve identification of early impacts and their causes on a landscape scale, then setting policies and establishing management practices that prevent degradation of habitat and loss of ecological integrity from occurring. As the results presented here show, a promising avenue of research is to quantitatively link biotic homogenization to specific aquatic threats such as watershed deforestation and development. A primary goal then is to get information on likelihood of impacts given land use scenarios to policy makers, resource managers, land-use planners, developers, and private landowners.

Jablonski (2001) noted that the evolutionary effects of biotic homogenization may depend to some degree on how it occurs. In a worst case, elimination of endemics will leave behind a residue of already widespread taxa that may be more or less resistant to geographic isolation and diversification, which could channel subsequent evolution into narrower regional pathways than would otherwise be expected. Time is short to implement actions to avoid this scenario of long-term biological simplification. Armed with an understanding of when and how susceptible native species begin to be replaced by human-commensal forms as habitat alteration increases, we can better manage and pass on our natural heritage.

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