

Stream fish occurrence in response to impervious cover, historic land use, and hydrogeomorphic factors

Seth J. Wenger, James T. Peterson, Mary C. Freeman, Byron J. Freeman, and D. David Homans

Abstract: We evaluated competing models explaining the occurrence of five stream fishes in an urbanizing watershed to determine the relative importance of (a) impervious surface and other indicators of current land use, (b) historic land use (e.g., agriculture, impoundments), and (c) hydrogeomorphic characteristics (e.g., stream size, elevation, geology). For four of five species, the best-supported models were those that included both current effective impervious cover and historic land use predictor variables, although models with only effective impervious cover were equally well supported for two of those species. For the best-supported models for three species, occurrence probability was predicted to approach zero at levels of development equivalent to about 2%–4% effective impervious cover in the surrounding region. Data were drawn from 357 fish collections made in the Etowah River basin, Georgia, USA, between 1998 and 2003 and analyzed using hierarchical logistic regression accounting for imperfect species detection. This is the first study we know of to examine the response of individual fish species to both increasing impervious cover and historic land use. Such individual species assessments will be increasingly necessary to guide policies for managing urban effects and preventing extirpations of sensitive species.

Résumé : Nous évaluons plusieurs modèles concurrents explicatifs de la présence de cinq poissons d'eau courante dans un bassin versant urbanisé afin de déterminer l'importance relative (a) de la surface imperméable et des autres indicateurs de l'utilisation actuelle des terres, (b) de l'utilisation des terres dans le passé (par ex., agriculture, barrages) et (c) des caractéristiques hydrogéomorphiques (par ex., taille des cours d'eau, altitude, géologie). Pour quatre des cinq espèces, les modèles les plus solides sont ceux qui incluent à la fois la couverture imperméable effective actuelle et les variables prédictives de l'utilisation des terres du passé; par ailleurs, les modèles qui tiennent compte seulement de la couverture imperméable efficace fonctionnent aussi solidement avec deux de ces espèces. Dans le cas du modèle le plus solide pour trois espèces, il prédit que la probabilité d'occurrence s'approche de zéro à des niveaux de développement équivalents à environ une couverture imperméable effective de 2 % – 4 % dans la région avoisinante. Les données proviennent de 357 récoltes de poissons faites dans le bassin de l'Etowah, Géorgie, É.-U., entre 1998 et 2003 et elles ont été analysées à l'aide d'une régression logistique hiérarchique qui tient compte de la détection imparfaite des espèces. Il s'agit de la première étude, à notre connaissance, qui examine les réactions d'espèces individuelles de poissons à la fois à la croissance de la couverture imperméable et à l'utilisation des terres dans le passé. De telles évaluations d'espèces individuelles deviendront de plus en plus nécessaires afin de guider les politiques de la gestion des effets de l'urbanisation et de prévenir l'extirpation des espèces sensibles.

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Introduction

Many studies have demonstrated that fish assemblages respond to a gradient of urbanization (e.g., Wang et al. 2001; Meador et al. 2005; Roy et al. 2005). Most such studies have used characteristics of the fish assemblage — such as an index of biotic integrity, species diversity, or a ratio of

homogenization — as response variables (but see Olden 2003 and Walsh et al. 2004b, the latter of which is for an amphipod). The limitation of assemblage-level analyses is that they do not provide information about the response of individual species, especially rare ones. Species-level responses can be a matter of significant interest in the management of imperiled fish species. As urban land cover

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S.J. Wenger.¹ University of Georgia River Basin Center, Athens, GA 30602, USA.

J.T. Peterson. US Geological Survey Georgia Cooperative Fish and Wildlife Research Unit, University of Georgia, Athens, GA 30602, USA.

M.C. Freeman. US Geological Survey Patuxent Wildlife Research Center, University of Georgia, Athens, GA 30602, USA.

B.J. Freeman. Georgia Museum of Natural History, University of Georgia, Athens, GA 30602, USA.

D.D. Homans. University of Georgia, Institute of Ecology, Athens, GA 30602, USA.

¹Corresponding author (e-mail: swenger@uga.edu).

increases globally, a growing number of species will be impacted by urbanization, and knowledge of species-specific relationships between indicators of urban cover and fish occurrence or abundance will be essential to develop effective conservation strategies.

In the absence of sufficient long-term data sets relating changes in fish occurrence to land use, most studies employ a space-for-time substitution. That is, variation in species occurrence over space is related to variation in land use patterns at a fixed point in time. The space-for-time substitution requires the assumption that observed species distribution patterns are due to the effects of contemporary land use patterns. However, this assumption may not be supported. Contemporary fish distributions are likely the result of (1) complex interactions between hydrogeomorphic characteristics of streams, the landscape, and other biota (Allan 2004), and (2) past human land use activities (Harding et al. 1998), and the two are often strongly related. For example, cities tend to be built on low-slope, formerly agricultural land, rather than high-slope, formerly forested land. If we fail to account for the influence of hydrogeomorphic influences and historic land use, we risk misinterpreting the role of current land use.

This study involves fish species of the Etowah River basin, Georgia, USA. The Etowah River is a major tributary of the Coosa River system in the Mobile River basin (Fig. 1). The Etowah basin supports a diverse aquatic fauna, with 76 extant native species of fish (Burkhead et al. 1997), including three that are listed under the Endangered Species Act and six others that are considered imperiled but are not currently listed. A significant threat facing these organisms is rapid urbanization from the metropolitan Atlanta region (Wenger 2006). To head off a potential conflict between development and species protection, in 2003 the local governments of the Etowah basin began a process to develop the Etowah Aquatic Habitat Conservation Plan (HCP; Etowah HCP Advisory Committee 2006). The purpose of the plan is to implement a set of growth management policies and ordinances that minimize the impact of future development on the aquatic fauna, thus permitting additional growth without threatening the persistence of federally protected organisms.

This study was designed to evaluate whether there was sufficient evidence of an urban effect on listed fish species to justify controls on stormwater runoff as part of the HCP. Although the occurrence patterns of many Etowah fish species appear to suggest a negative relationship with urbanization, these patterns may also reflect natural landscape characteristics or past land use activities. Historic land use appears especially likely to have influenced distributions because much of the Etowah basin experienced intense row-crop agriculture from the 1800s to the early 1900s. The agricultural practices caused massive erosion and the sedimentation of stream valleys (Trimble 1974), which could have led to extirpation of sensitive fish species from many tributaries. Subsequently, many impoundments were constructed across the basin, which may have prevented recolonization and otherwise influenced (and may continue to influence) fish distributions.

In this study we examine five species native to the Etowah system (Table 1) whose distribution patterns suggest possible negative correlations to urban cover. Two of the

species (*Etheostoma etowahae* and *Etheostoma scotti*) are listed under the Endangered Species Act and are targets of the Etowah HCP. Our objective is to determine the relative importance of hydrogeomorphic characteristics, historic land use, and current urbanization in explaining the distribution of the species. Our focal metric of current land use is effective impervious area (EIA), which other studies have found to be a key indicator of urban effects on aquatic biota (Walsh et al. 2005a). A secondary objective is to identify response thresholds of fish occurrence to increasing EIA.

Materials and methods

Data preparation

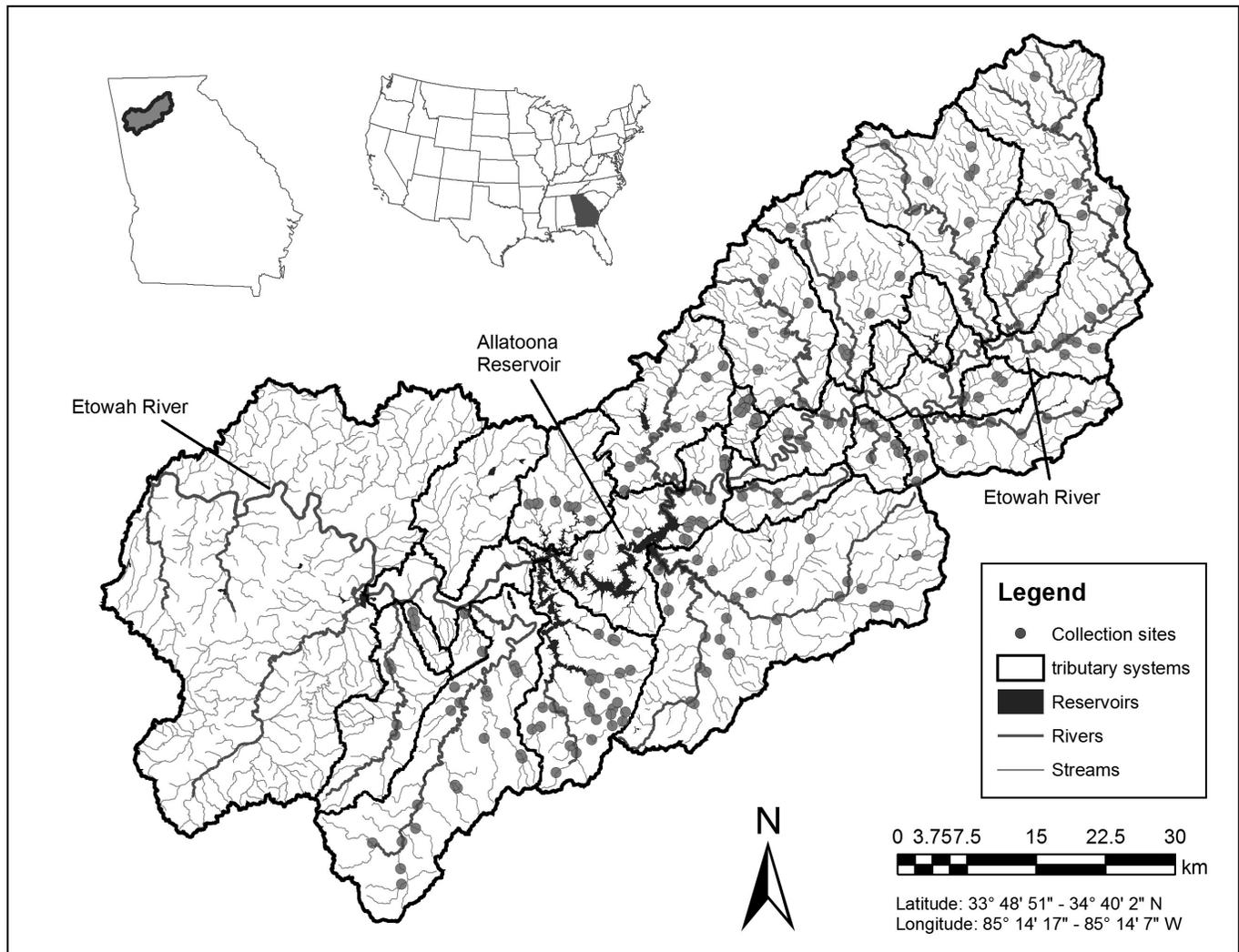
Fish collections

We selected 357 records of fish collections from a database maintained by the Georgia Museum of Natural History (Athens, Georgia). We used collections made in the Etowah basin between 1 January 1999 and 31 December 2003, which we considered approximately contemporaneous with the available “current” land cover data (see below). We selected only collections intended to characterize the full assemblage of sampled habitats using electroshocking, kick-seining, and seine hauling. Some of the data were used in previously published studies (Walters et al. 2003a; Roy et al. 2005). We excluded collections from streams draining less than 0.5 km² and those of uncertain reliability, which included collections targeting only certain species, collections that appeared to be missing information, and collections where notes indicated that an incomplete or low-effort sample had been taken. Sample reaches at sites were 50 m to 200 m in length. Collections from localities that were very close together (less than 0.5 km apart within the same stream, without large intervening tributaries) were assumed to be from the same site. However, collections from the same locality but more than 2 years apart were treated as if they were from independent sites with regard to estimating detection probability, under the assumption that populations could not be considered “closed” across this time period (see below). With these adjustments, the primary data set included 252 distinct sites, each sampled from one to five times.

We selected an additional set of 65 records for collections made at 31 sites to provide supplementary data for estimating species-specific probability of detection (following MacKenzie et al. 2002). We used sites where collections were made twice within 2 consecutive years (28 sites) or three times in 3 years (3 sites; temporal replicates) between 1 January 1990 and 31 December 1998; we also selected pairs of sites that were immediately adjacent and were sampled within a day of one another (spatial replicates) within this time period. We assumed that a species was either present or absent during samplings for each set of replicates, i.e., that the populations were closed.

Hydrogeomorphic predictor variables

For each collection site, we delineated the watershed that drained to the site and assigned it to one of 21 tributary systems (Fig. 1). We derived seven hydrogeomorphic predictor variables: watershed area, downstream link magnitude

Fig. 1. The Etowah River basin (Georgia, USA), showing collection sites and tributary system boundaries.**Table 1.** Species analyzed for occurrence in relation to hydrogeomorphic variables, historic land use, and current land use.

Species	Family	Distribution	Status
<i>Cyprinella trichroistia</i> Jordan and Gilbert, tricolor shiner	Cyprinidae	Mobile River basin, AL, GA, TN	CS; sensitive to increasing turbidity (Burkhead and Jelks 2001); representative of other sensitive minnows
<i>Noturus leptacanthus</i> Jordan, speckled madtom	Ictaluridae	Atlantic and Gulf Slope drainages, SC to LA	CS; potential surrogate for <i>N. sp. cf. munitus</i> , coosa madtom (T)
<i>Etheostoma etowahae</i> Wood and Maiden, Etowah darter	Percidae	Etowah River system, GA	E; federally listed
<i>Etheostoma scotti</i> Bauer, Etnier and Burkhead, Cherokee darter	Percidae	Etowah River system, GA	T; federally listed
<i>Percina palmaris</i> Bailey, bronze darter	Percidae	Coosa and Tallapoosa river systems, AL, GA	CS; potential surrogate for <i>P. antesella</i> Williams and Etnier, amber darter (E)

Note: Status follows Warren et al. 2000: currently stable (CS), threatened (T), and endangered (E).

(d-link), elevation, physiographic province, bedrock geology, surficial geology, and stream slope (Table 2). All were calculated in ArcView 3.3 or ArcGIS 9.0 software (ESRI, Redlands, California). Watershed area was calculated as the total area draining to the collection site and served as an indicator of stream size at the fish sampling location. D-link was used as a way of describing a stream reach's position in a watershed — whether it was a headwater stream or

directly connected to larger main-stem streams, for example. D-link was calculated as the number of unbranched streams draining to the next confluence downstream of the site, using 1:24 000 scale maps (Osborne and Wiley 1992). Elevation was calculated at the collection site from 30 m resolution digital elevation models (DEMs) (US Geological Survey 1988). Physiographic province (Georgia Geologic Survey 1999), bedrock geology summarized by group

Table 2. Summary statistics on continuous predictor variables measured for 252 collection sites used in models of species occurrence.

Variable	Abbrev.	Group	Mean	SD	Min.	Max.
Watershed area (km ²)	area	Hydrogeo	9.3	28.3	0.5	1591
Elevation (m above sea level)	elev	Hydrogeo	305.01	53.06	207.43	536.52
Downstream link magnitude	d-link	Hydrogeo	56.5	118.4	0.00	415
Density of dams in watershed (no.·km ⁻²)	damw	Historic	0.98	0.87	0.00	5.95
% of watershed in impoundments	waterw	Historic	0.70	0.64	0.00	3.73
% watershed in intense historic land use	histw	Historic	33.39	22.48	0.00	90.69
% watershed urban cover	urbanw	Current	16.11	17.60	0.00	73.12
% watershed forest cover	forestw	Current	65.12	17.74	0.00	99.15
% watershed TIA	tiaw	Current	3.83	5.55	0.01	28.37
% TIA in 500 m radius	tia500	Current	3.32	5.39	0.00	29.78
% TIA in 1 km radius	tia1	Current	3.47	5.41	0.00	28.89
% TIA in 1.5 km radius	tia15	Current	3.57	5.23	0.00	26.37
% TIA in 2 km radius	tia2	Current	3.71	5.26	0.02	24.71
% watershed EIA	eiaw	Current	2.49	4.44	0.00	23.67
% EIA in 500 m radius	eia500	Current	2.07	4.33	0.00	26.23
% EIA in 1 km radius	eia1	Current	2.23	4.34	0.00	24.56
% EIA in 1.5 km radius	eia1.5	Current	2.32	4.14	0.00	22.07
% EIA in 2 km radius	eia2	Current	2.44	4.19	0.00	20.41
Mean slope of large streams in tributary system (Δ elev./watershed area)	slope	Hydrogeo	83.75	73.03	14.62	289.64
Density of dams in tributary system (no.·km ⁻²)	damswden	Hydrogeo	0.83	0.41	0.29	1.90
% of tributary system in impoundments	watertr	Hydrogeo	0.58	0.37	0.12	1.35
% tributary system in intense historic land use	histtr	Hydrogeo	32.37	18.60	4.84	61.47
Presence of metamorphic mafic bedrock geology group (binary)	meta. mafic	Hydrogeo	—	—	—	—
Clayey sand / sandy clay quaternary geology (binary)	rck	Hydrogeo	—	—	—	—
Micaceous saprolite quaternary geology (binary)	ssb	Hydrogeo	—	—	—	—
Multiple binary bedrock geology groups	geology	Hydrogeo	—	—	—	—

Note: TIA, total impervious area; EIA, effective impervious area. "Abbrev." indicates the abbreviation used for the variable in other tables. "Group" refers to whether the variable is classed as hydrogeomorphic ("Hydrogeo"), historic land use, or current land use. SD, standard deviation; "Min." and "Max." indicate the minimum and maximum values, respectively.

(Georgia Geologic Survey 1999), and surficial (quaternary) geology (Richmond et al. 1987) were included as candidate measures of the influence of geology on physicochemical properties of streams. Local stream slope data were not available for most collection sites, so we estimated the mean slope of all streams draining at least 10 km² at the scale of each system using 30 m DEMs (US Geological Survey 1988), and assigned the mean to each site in that system.

Impervious area and other measures of current land cover

We focused on impervious area as an indicator of urbanization, as stormwater runoff from impervious surfaces has been identified as the primary source of stressors to urban streams (Walsh et al. 2005b). Previous researchers have suggested that the most problematic impervious surfaces are those that are directly connected to streams via drainage and conveyance systems (Alley and Veenhuis 1983; Booth and Jackson 1997; Walsh et al. 2005a). Studies have demonstrated that this effective impervious area (EIA) is a better predictor of stream biological and chemical response than total impervious area (TIA) (e.g., Wang et al. 2001; Hatt et al. 2004; Walsh et al. 2004a). The 2001 National Land Cover Database Zone 54 Imperviousness Layer (US Geological Survey 2003) was used as the source for TIA. This is a raster coverage with a resolution of 30 m derived

from supervised classification of LandSat satellite imagery. To calculate EIA, we followed Alley and Veenhuis (1983) in developing our own empirical relationship between TIA and EIA, which we applied to the TIA coverage. We hand-delineated both impervious and directly connected impervious surfaces (which we considered EIA) from high-resolution aerial photographs for 15 sites of 25–70 ha in size. Impervious areas included roofs, roads, parking lots, sidewalks, and any other artificial impervious surfaces distinguishable on the aerial photos. Directly connected impervious surfaces were a subset of impervious surfaces that were visually noted to drain to the stormwater conveyance network. Such connections were generally obvious from the high-resolution aerial photographs, although there was occasional ambiguity; uncertain cases were considered directly connected. We then determined the relationship between TIA and EIA by fitting the data to different candidate models. The best model, selected on the basis of the coefficient of determination, was linear with a threshold:

$$(1) \quad EIA = (1.046 \times TIA) - 6.23\%$$

where EIA = 0 for TIA values less than 6.23% ($R^2 = 0.98$).

We applied this formula cell-by-cell to the TIA layer to create a raster EIA layer. For each fish collection site, we then calculated TIA and EIA at five scales: impervious area in the watershed upstream of the site, and impervious area

within 0.5 km, 1 km, 1.5 km, and 2 km radiuses of the site (Table 2). Note that summarizing these values across many cells reduced the differences between EIA and TIA below that expected from the above relationship. The reason was that (especially at low development levels) impervious cover was not distributed evenly across the landscape but tended to occur in patches of cells of moderate TIA surrounded by cells of zero TIA. The transformation calculation of TIA to EIA was applied only to cells with TIA values greater than zero. Therefore, in practice, a watershed of 4% TIA equated to about 2.0%–2.5% EIA. In addition to impervious cover, we also considered urban land cover and forested land cover as indicators of current land use. These variables were calculated for the upstream watershed for each site using 2001 land cover data (Kramer 2004) (Table 2).

Historic land cover

We investigated three candidate indicators of historic land cover, each measured at two scales. The first was historic modified land cover in the basin, which was quantified from 1938 aerial photographs. These were the oldest aerial photographs available for the entire region, and the best representation we could find of land use from the era of cotton production. We georectified scans of 1938 Agricultural Stabilization and Conservation Service (ASCS) 1:100 000 scale aerial photograph index sheets from the Georgia Aerial Photographs database (<http://dbs.galib.uga.edu/gaph/html/>). We classified the resulting images into forested areas and agricultural or developed land based on cell brightness.

The other candidate indicators of historic land use were the number and area of reservoirs, which we expected to correlate with historic land cover. Many reservoirs were built in the 1950s through the 1970s on agricultural lands, and these can be viewed both as indicators of agricultural influences and as potential stressors. All indicators of historic land use (percentage of drainage area in agricultural land cover in 1938, number of reservoirs, and area of reservoirs) were measured at two scales: (1) the watershed above each collection site and (2) the tributary system within which the collection site was nested (Table 2).

Data analysis

One of our goals in the modeling was to obtain covariate parameter estimates with minimal bias by accounting for spatial dependencies in the data and incomplete detectability of species. Failure to account for spatial correlations can lead to underestimates of the variance of parameter estimates (Snijders and Bosker 1999), while failure to correct for incomplete detection can lead to bias in the means of parameter estimates (Gu and Swihart 2004). We constructed logistic regression models using two-level hierarchical modeling to manage spatial correlations (Snijders and Bosker 1999), following the general approach for modeling species distributions outlined by Latimer et al. (2006). We adapted this to account for incomplete detectability using a species occupancy model (MacKenzie et al. 2002). While incorporating both hierarchy and incomplete detectability into a logistic regression model presents significant challenges for conventional maximum likelihood estimation, Monte Carlo Markov Chain (MCMC) model-fitting techniques are able to accommodate such complexity (Conroy et al. 2005; Peter-

son et al. 2005). The disadvantage of MCMC techniques is that model fitting is computer-intensive and time-consuming. Therefore, we used a two-stage modeling approach: (1) We screened potential predictor variables representing hydrogeomorphic characteristics, historic land use, and current land use with ordinary logistic regression that assumed complete detectability. (2) We evaluated the relative fit of the best-supported models from the initial screening using hierarchical species occupancy models.

Screening of candidate predictor variables

For the candidate predictor variable selection, we ignored spatial dependencies and assumed complete detectability. For sites with multiple collections, we assumed a species was present if it was encountered in any of the collections. To increase linearity in the predictor variables, watershed area was square root transformed and d-link was natural log transformed. All continuous predictors were normalized with a mean of 0 and standard deviation of 1 and we included quadratic terms for area, d-link, and elevation as possible predictors.

We evaluated a series of logistic regression models for each of the five species, with species occurrence as the dependent variable. All models were run with the statistical package R 2.0.1 (R Development Core Team 2004). There were four model categories: (1) models with only hydrogeomorphic predictors, or “hydrogeomorphic”, (2) models with hydrogeomorphic predictors plus a historic land use predictor, or “historic”, (3) models with hydrogeomorphic predictors plus a current land use predictor, or “current”, and (4) models with hydrogeomorphic predictors plus a historic and a current land use predictor, or “global”. Our goal was to identify the best-approximating model in each category (1 through 4) for each species, using Akaike’s information criterion modified for small sample size (AIC_c) as the basis for selection (Burnham and Anderson 2002). To identify the most plausible model that included only hydrogeomorphic predictor variables, we fitted a model with all hydrogeomorphic predictors and then performed a series of stepwise removals, selecting the three best-supported models based on AIC_c . Next, we compared 18 models, each of which was based on one of the three best-supported hydrogeomorphic predictor models and included one of the six candidate historic land cover predictor variables. We again performed a stepwise removal of variables to determine whether a reduced model was better supported. We then repeated the process for the 12 candidate predictor variables for current land use (comparing 36 models). Finally, we compared models with different combinations of both a historic land use predictor variable and a current land use predictor variable, to select the best global model. We compared the best-supported models in each category with one another to estimate which was best supported overall.

Hierarchical occupancy modeling

To account for incomplete detection, we jointly modeled species detectability and presence as

$$(2) \quad P(d) = P(d|\psi)P(\psi)$$

where $P(d)$ is the probability that the species is present and detected at the site, $P(\psi)$ is the probability that the species

is present, and $P(d|\psi)$ is the probability that the species is detected given that it is present, i.e., detectability. Detection probability was calculated using a site occupancy model (MacKenzie et al. 2002) based on the encounter history of the species at sites sampled multiple times. Briefly, this method simultaneously estimates species presence and detectability by assuming that the occupancy state (presence or absence) of a site sampled multiple times does not change between samples; thus, if a species is found three out of four times when a site is sampled in rapid succession, its detectability is 75%. In our data set, 63 sites were sampled a second time, 21 of those were sampled a third time, 13 of those were sampled a fourth time, and 8 of those were sampled a fifth time (the remaining 189 sites were sampled only once each). The assumption that populations remain unchanged (“closed”) between samples was likely violated in many cases, which adds slightly to the uncertainty of the detectability estimates. To improve our estimate of detectability, we added a second data set of an additional 31 sites sampled at least twice during the period 1990–1998. We assumed that because collection methods remained relatively consistent through the 1990s and early 2000s, species detectability was also consistent. The MCMC methods we employed permitted us to construct models in which these auxiliary data informed the estimate of $P(d|\psi)$ but not any of the other model parameters. That is, the detectability parameter for each species was estimated across both data sets, but parameters for explaining presence–absence were estimated using only the main data set. It is possible to include covariates of detectability to account for differences in sample effort and methods, but we did not do so because we lacked relevant collection-level data across all samples.

Prior to running the hierarchical occupancy models, we tested for spatial autocorrelation at the level of the tributary systems by performing an analysis of variance on the residuals of each of the best-supported screening models, using the tributary systems as treatments. We detected significant dependence within the tributary systems ($P < 0.001$), indicating that samples within the same tributary system tended to be similar to one another and could not be considered fully independent samples. If ignored, this problem would tend to produce overly narrow credible intervals for model parameters (Snijders and Bosker 1999). We addressed the issue by defining a two-level hierarchical structure with sites nested within the 21 tributary systems, implemented in the model by adding a normally distributed random effect at level two (Snijders and Bosker 1999). Level one of the model can be represented as

$$(3) \quad \text{logit}(P(\psi_{i,j})) = \beta_{0j} + \sum_{s=1}^m \beta_s x_{s,i,j}$$

where $x_{s,i,j}$ are $s = 1, 2, \dots, m$ predictors for site i within tributary system j . The intercept is then modeled as a function of tributary system characteristics (level two):

$$(4) \quad \beta_{0j} = \gamma_0 + \sum_{r=1}^n \gamma_r w_{r,j} + \delta_j$$

where $w_{r,j}$ are the $r = 1, 2, \dots, n$ predictors corresponding to

tributary system j , and δ_j is a random effect that varies normally among reaches with a mean of zero and variance σ_j^2 .

For each of the five species, we fit the best-supported screening model in each of the four categories (hydrogeomorphic, historic, current, and global) to the hierarchical occupancy models. If the screening analyses showed that the second- or third-best models in a category also had considerable support, we also fit these to the hierarchical occupancy models. We used MCMC methods as implemented in WinBUGS 1.4 (Spiegelhalter et al. 2003) for all hierarchical occupancy modeling. We ran six parallel chains and tested each model for convergence using the Gelman–Rubin diagnostic (Gelman and Rubin 1992). Models converged within 8000 iterations, and the values from this “burn in” period were discarded. Models were then run for a further 60000 iterations to estimate parameters and deviance. We used diffuse priors for all parameters. To reduce MCMC autocorrelation, models were thinned by a factor of 10, which means that only every tenth sample was used in calculating statistics. The use of this technique greatly reduced autocorrelation but did not eliminate it in all cases. We tested increased iterations with even greater thinning, up to 600000 iterations with 100× thinning, but parameter estimates, deviance, and convergence diagnostics remained stable throughout the range of iterations evaluated. Therefore, we considered 10× thinning adequate.

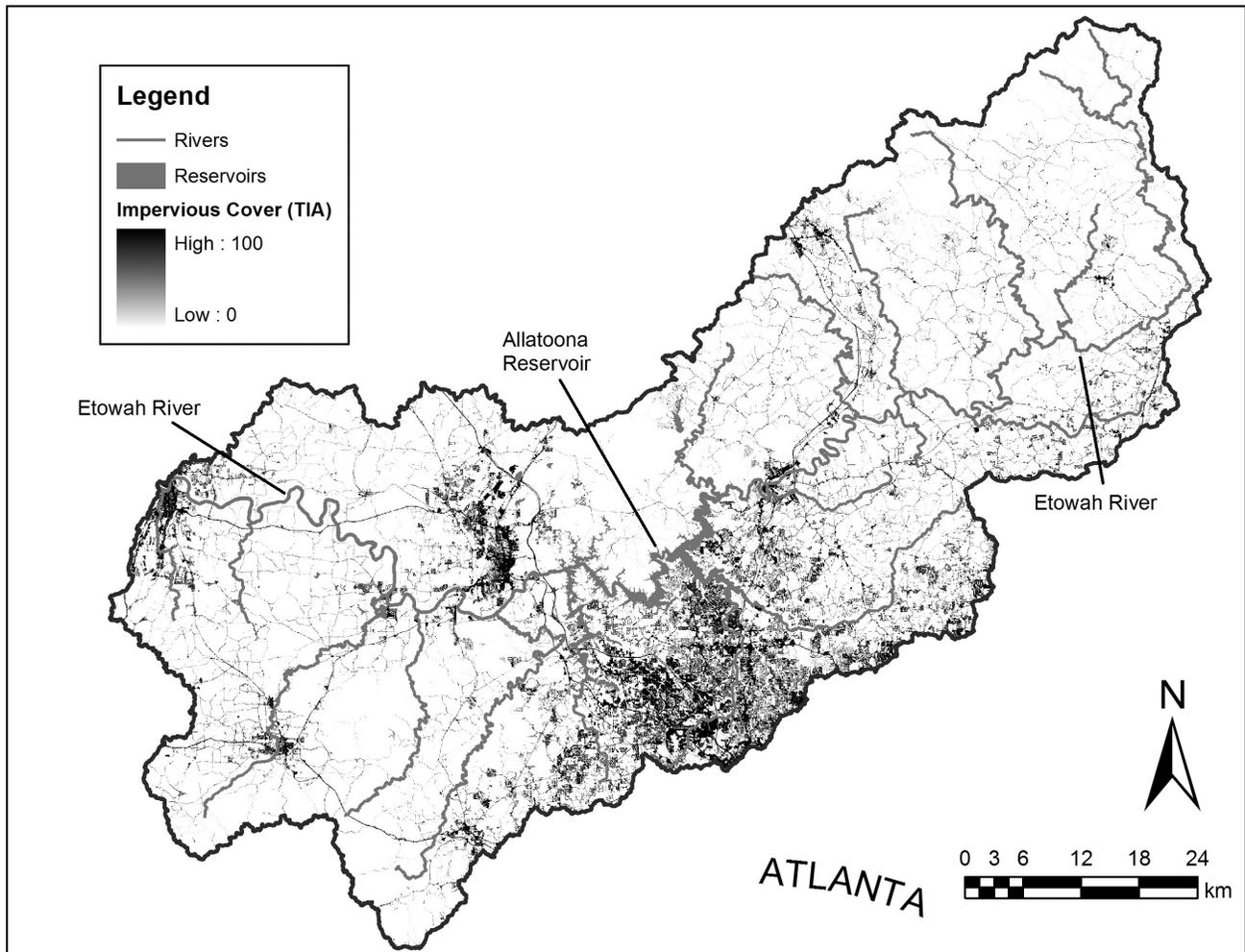
We used threefold cross-validation to select models and estimate their out-of-sample predictive performance. For test sites we assumed that tributary system membership was unknown. We ranked models by their predictive performance using the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot as a summary statistic. The ROC curve is the ratio of true positives to false positives when the species occurrence decision threshold is varied between zero and one; the AUC of the ROC curve is considered a robust measure that is invariant to species prevalence (Manel et al. 2001; Olden et al. 2002; Latimer et al. 2006).

We found that for models with large variances on the random effect, fixed-effect parameter estimates were proportionately large. These large values are a result of the fixed level one variance of logistic regression models, which leads to inflation of parameter estimates to maintain proportionality between levels one (e.g., stream site) and two (e.g., tributary) when random effects are added (Snijders and Bosker 1999). We corrected for this phenomenon by standardizing the parameter estimates of each model by the sum of level one and level two variances. These standardized values were used to calculate odds ratios for the mean and 90% credible intervals for the fixed-effect parameter estimates for all variables of the best-supported current, historic, and global models.

Results

Impervious cover, historic land cover, and reservoir density varied considerably across the basin and among tributary systems (Figs. 2 and 3), resulting in high variances of most variables across the collection sites or watersheds (Table 2). As expected, there were correlations between historic land use predictor variables and current land use pre-

Fig. 2. Total impervious area in the Etowah basin.



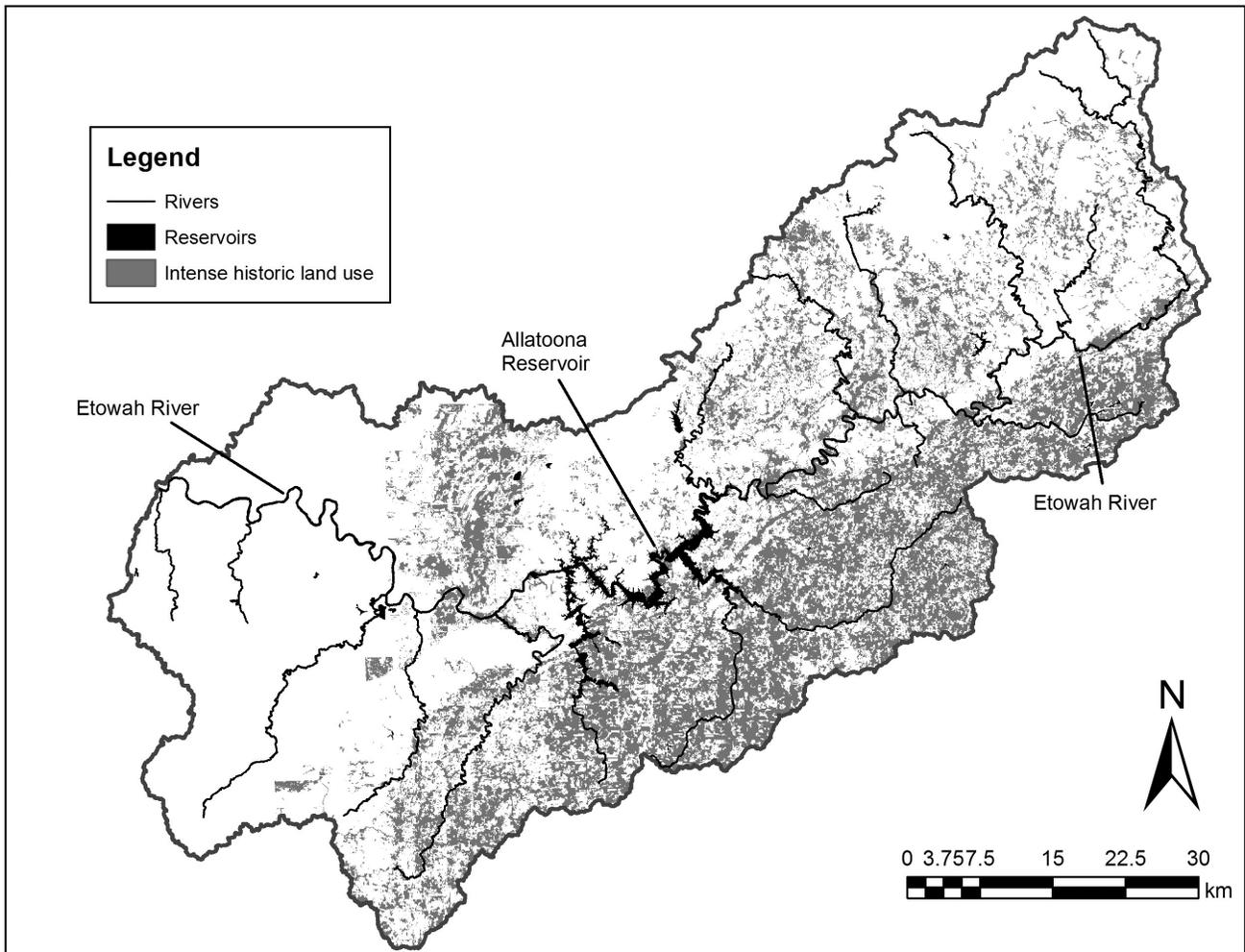
dictor variables, but pairwise Pearson correlations between historic and current land use predictors were less than 0.6 in all cases and we observed no evidence that multicollinearity affected parameter estimates.

Based on the screening model analysis, we selected 7–14 models to run for each species in the hierarchical occupancy modeling (Table 3). Among the hydrogeomorphic predictor variables evaluated, watershed area, downstream link magnitude, tributary system slope, and elevation were the most commonly included in the best-fitting models. Among historic land use predictors, area inundated by impoundments was the most commonly included, but historic land cover was included for at least some models for two species. Effective impervious area (EIA) within 500 m to 1.5 km of the collection site was the most common measure of current land use selected for inclusion in models, based on the screening analysis. The only exception was *E. scotti*, for which forest cover in the watershed was the best current land use predictor.

Gelman–Rubin convergence diagnostics showed that all of the hierarchical occupancy models converged. Based on the AUC values, the best model for each species was a global model, with the exception of *E. scotti*, for which a historic model (i.e., one without a predictor variable for cur-

rent land use) was best supported (Table 3). However, for *N. leptacanthus* and *E. etowahae* the best current land use model (i.e., one without a predictor variable for historic land use) was equally or nearly equally well supported. The best historic land use model was less well supported than the best current land use model for all species except *E. scotti*. For all species, the best hydrogeomorphic model was a poorer predictor than the best global, historic, and current models. The differences among the AUC scores for the best models for each species were small. According to a rule of thumb (Swets 1988), models with AUC values > 0.9 have high accuracy. The best models for three of the species met this threshold, while those for *N. leptacanthus* had slightly lower AUC values and those for *E. scotti* had substantially lower AUC values (Table 3).

Cross-validation inherently penalizes model overfitting, and this was evidenced in our analyses by the higher AUC scores of some models that were subsets of others. For example, *N. leptacanthus* model 8 was a subset of models 1–7, but was ranked equal to or higher than these more complex models, indicating that it was the more parsimonious model. Nevertheless, some highly ranked models included parameters whose credible intervals overlapped 1 (Table 4), indicating uncertainty in whether the direction of

Fig. 3. Historic modified land cover in the Etowah basin.

the correlation was positive (values greater than 1) or negative (values less than 1). For example, for *N. leptacanthus* model 5, the credible interval for historic land use ranged from 0.08 (a strong negative effect) to 1.80 (a moderate positive effect). The historic land use term was therefore of questionable predictive value, and indeed the simpler model 8, which lacked this parameter, had an AUC score equal to that of model 5.

The species with the strongest relationship with current land use was *C. trichroistia* (Table 4). Using the best predicting model, we estimated that the species was almost 20 times less likely to occur for each 1% increase in EIA within 1.5 km (note that this was not a relative increase in EIA, but an absolute increase; e.g., a change from 5% to 6% would be a 1% increase). Occurrence probability approached zero when EIA exceeded about 2% and other predictor variables were held to their mean values (Fig. 4). The presence of *P. palmaris* and the presence of *E. etowahae* also were strongly negatively related to EIA, although the 90% credible interval for *E. etowahae* was very broad (Table 4). For both species the models predicted that the occurrence probabilities approached zero at 4% EIA and above, using the mean estimates for the EIA parameter (Fig. 4). *Noturus leptacanthus* showed a weaker relationship

with EIA, and *E. scotti* showed essentially no relationship, with the mean credible interval for the odds ratio centered near 1 and broadly overlapping on either side (Table 4, Fig. 4).

Under the highest-ranked models, the distributions of three species showed a strong relationship with historic land use (Table 4). Using the mean parameter estimates of the best-supported models for *C. trichroistia*, *E. etowahae*, and *P. palmaris*, species were 1.7 to 2.5 times less likely to occur for each increase of 0.25% in the area of upstream watershed or tributary system that was impounded. *Noturus leptacanthus* was 2.3 times less likely to occur for each 10% increase in the area of the upstream watershed in historic modified land cover, but the credible interval of the odds ratio was very wide and included 1, indicating large uncertainty around the species' response. The odds ratio credible interval for *E. scotti* was centered near 1, suggesting little relationship with historic land use.

The current distribution of four of the five species was positively related to watershed area and downstream link magnitude, usually with a second-order term indicating lower occurrence probability in the largest streams. The exception was *E. scotti* occurrence, which was negatively related to watershed area (Table 4). The best-supported model

Table 3. Hierarchical occupancy models for each species with model selection statistics.

Model No.	Category	Predictor variables	AUC
<i>Cyprinella trichroistia</i>			
2	Global	area, area², d-link, d-link², slope, waterw, eia1.5	0.933
1	Global	area, area ² , d-link, d-link ² , waterw, eia1.5	0.931
4	Global	area, area ² , d-link, d-link ² , histtr, eia1.5	0.929
3	Global	area, area ² , d-link, d-link ² , slope, histtr, eia1.5	0.926
5	Current	area, area², d-link, d-link², eia1.5	0.922
6	Current	area, area ² , d-link, d-link ² , slope, eia1.5	0.922
8	Historic	area, area², d-link, d-link², histtr	0.915
7	Historic	area, area ² , d-link, d-link ² , slope, histtr	0.904
9	Historic	area, area ² , d-link, d-link ² , waterw	0.875
10	Hydrogeomorphic	area, area², d-link, d-link², slope	0.788
<i>Noturus leptacanthus</i>			
5	Global	area, slope, histw, eia1	0.892
8	Current	area, slope, eia1	0.892
7	Current	area, elev, slope, eia1	0.887
4	Global	area, d-link ² , elev ² , slope, histw, eia1	0.885
6	Current	area, d-link ² , elev ² , slope, eia1	0.878
3	Global	area, elev, slope, histtr, eia1	0.875
2	Global	area, slope, histtr, eia1	0.874
1	Global	area, d-link ² , elev ² , slope, histtr, eia1	0.873
12	Historic	area, slope, histtr	0.858
14	Hydrogeomorphic	area, slope	0.855
11	Historic	area, elev, slope, histtr	0.851
9	Historic	area, d-link ² , elev ² , slope, histw	0.843
10	Historic	area, d-link ² , elev ² , slope, histtr	0.834
13	Hydrogeomorphic	area, d-link ² , elev ² , slope	0.814
<i>Etheostoma etowahae</i>			
3	Global	area, d-link, d-link², slope, watertr, eia1.5	0.946
1	Current	area, d-link, d-link², slope, eia1.5	0.945
6	Global	area, d-link, d-link ² , slope, damswden, eia1.5	0.945
4	Global	area, area ² , d-link, d-link ² , slope, watertr, eia1.5	0.943
7	Historic	area, area², d-link, d-link², slope, damswden	0.936
5	Global	area, d-link, d-link ² , watertr, eia1.5	0.932
9	Historic	area, area ² , d-link, d-link ² , watertr, slope	0.931
2	Current	area, d-link, d-link ² , eia1.5	0.927
11	Hydrogeomorphic	area, area², d-link, d-link², slope	0.912
8	Historic	area, d-link, d-link ² , damswden	0.903
10	Hydrogeomorphic	area, area ² , d-link, d-link ² , elev, elev ² , slope	0.896
<i>Etheostoma scotti</i>			
4	Historic	area, elev², meta. mafic, rck, ssb, watertr	0.737
5	Global	area, elev², meta. mafic, rck, ssb, watertr, forestw	0.727
2	Current	area, elev², meta. mafic, rck, ssb, forestw	0.724
7	Hydrogeomorphic	area, elev², meta. mafic, rck, ssb	0.711
3	Historic	area, elev, meta. mafic, rck, ssb, watertr	0.700
6	Hydrogeomorphic	area, d-link ² , elev ² , geology	0.675
1	Current	area, d-link ² , elev ² , forestw	0.624
<i>Percina palmaris</i>			
1	Global	area, area², d-link, d-link², elev, slope, watertr, eia500	0.921
2	Global	area, d-link, d-link ² , elev, watertr, eia500	0.918
6	Current	area, d-link, d-link², elev, eia500	0.908
5	Current	area, area ² , d-link, d-link ² , elev, slope, eia500	0.905
3	Historic	area, area², d-link, d-link², elev, slope, watertr	0.895
4	Historic	area, d-link, d-link ² , elev, watertr	0.891
7	Hydrogeomorphic	area, area², d-link, d-link², elev, slope	0.870
8	Hydrogeomorphic	area, d-link, d-link ² , elev	0.853

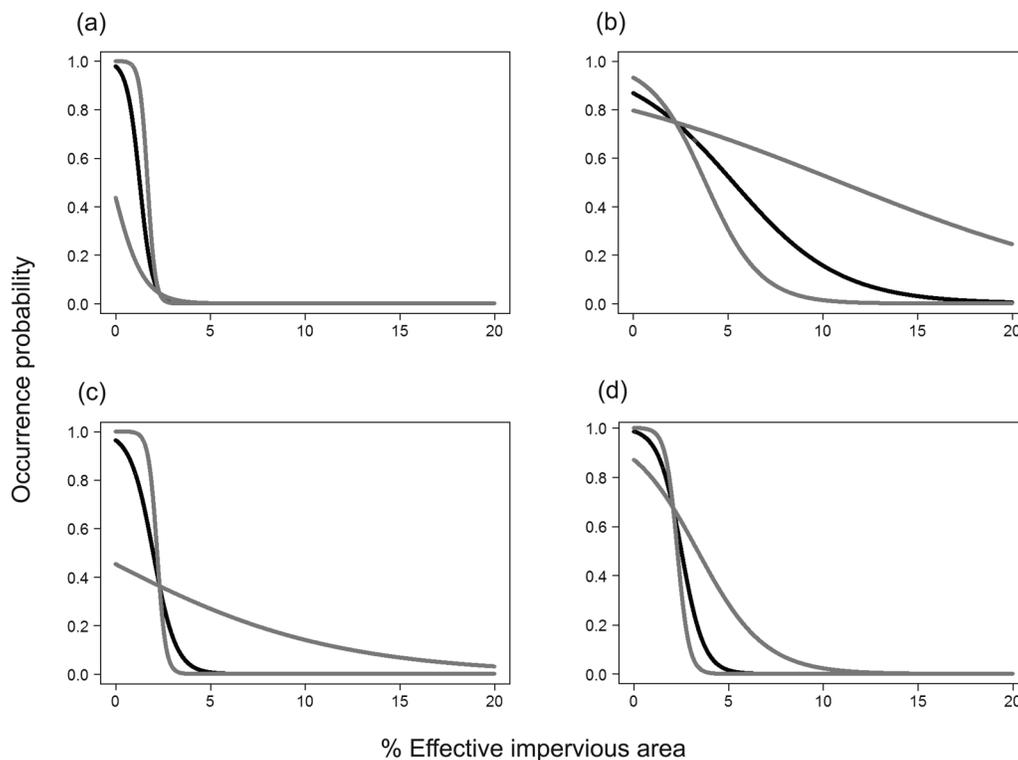
Note: The best model in each category for each species is shown in bold. Models are shown sorted from best to worst fitting based on area under the curve (AUC) of the receiver-operating characteristic plot. Variable abbreviations are defined in Table 2.

Table 4. Parameter estimates for detection probability, intercepts, and fixed effects of best-supported hierarchical occupancy models for each species.

Parameter	Estimate	5% CI	95% CI	Unit of increase
<i>Cyprinella trichroistia</i>				
Detection probability	82%	75%	88%	
Intercept	1%	0%	15%	
area	37.83	5.46	340.22	Standard deviation
area ²	0.48	0.23	0.86	Standard deviation
d-link	1.79	0.59	5.64	Standard deviation
d-link ²	0.22	0.04	0.69	Standard deviation
slope	1.97	0.89	4.31	Standard deviation
waterw	0.57	0.37	0.80	0.25%
eia1.5	0.05	0.01	0.29	1%
Level 2 random effect variance	3.28	0.43	8.08	
<i>Noturus leptacanthus</i>				
Detection probability	55%	44%	67%	
Intercept	24%	10%	46%	
area	9.14	2.85	44.41	Standard deviation
slope	0.11	0.02	0.43	Standard deviation
histw	0.44	0.08	1.80	10%
eia1	0.70	0.50	0.88	
Level 2 random effect variance	27.94	6.46	60.82	
<i>Etheostoma etowahae</i>				
Detection probability	55%	44%	65%	
Intercept	1%	0%	22%	
area	17.13	2.95	372.81	Standard deviation
d-link	80.02	6.39	6664.24	Standard deviation
d-link ²	0.01	0.00	0.16	Standard deviation
slope	4.36	0.93	32.95	Standard deviation
watertr	0.41	0.14	0.95	0.25%
eia1.5	0.19	0.01	0.85	1%
Level 2 random effect variance	15.62	4.64	34.64	
<i>Etheostoma scotti</i>				
Detection probability	81%	75%	86%	
Intercept	73%	55%	86%	
area	0.74	0.50	0.93	Standard deviation
elev ²	0.84	0.66	0.98	Standard deviation
watertr	0.95	0.53	1.67	0.25%
meta. mafic	0.48	0.19	0.88	Present (binary)
rck	121.58	0.12	4.40 × 10 ⁷	Present (binary)
ssb	0.47	0.19	0.85	Present (binary)
Level 2 random effect variance	7.78	3.02	16.86	
<i>Percina palmaris</i>				
Detection probability	86%	79%	92%	
Intercept	6%	0%	41%	
area	47.09	5.67	782.68	Standard deviation
area ²	0.88	0.40	2.20	Standard deviation
d-link	3.23	1.27	9.79	Standard deviation
d-link ²	0.23	0.05	0.77	Standard deviation
elev	1.47	0.79	3.28	Standard deviation
slope	1.55	0.60	3.80	Standard deviation
watertr	0.44	0.23	0.85	0.25%
eia500	0.19	0.04	0.57	1%
Level 2 random effect variance	5.26	1.16	17.39	

Note: CI, credible interval. Detection probability estimates are given as percentages. For the intercept term, estimates correspond to site occupancy (occurrence probability) when other parameters are zero. For fixed effects, values are given as odds ratios per specified unit of increase. A value greater than 1 indicates a positive correlation, and a value less than 1 indicates a negative correlation. For example, *Cyprinella trichroistia* is 95% less likely to occur for each 1% increase in EIA within 1.5 km. A credible interval that overlaps 1 indicates a variable of uncertain effect. For the level 2 random effect, values are variance estimates.

Fig. 4. Occurrence probability of each species under the best-supported model in response to increasing impervious cover. The black line represents the response curve based on the mean parameter estimate for effective impervious area (EIA); gray lines represent the response curves based on the 5% and 95% values for the parameter estimate for EIA. Predictor values for watershed area and d-link are set to one standard deviation larger than the mean, while other predictors are set to mean values. (a) *Cyprinella trichroistia*; (b) *Noturus leptacanthus*; (c) *Etheostoma etowahae*; (d) *Percina palmaris*. *Etheostoma scotti* is not plotted because the best-supported model did not include a current land use predictor variable.



for *P. palmaris* indicated that species occurrence was positively related to elevation, whereas *E. scotti* occurrence was negatively related to elevation. Slope was positively related with the occurrence of *C. trichroistia*, *E. etowahae*, and *P. palmaris*, although in all cases the 90% credible interval overlapped 1. The occurrence of *N. leptacanthus* was negatively related to slope (Table 4).

There was unexplained variation at the tributary system level, as indicated by the level 2 random effect variance estimates (Table 4). Variation was greatest for *N. leptacanthus* and lowest for *C. trichroistia*. The variability among tributary systems is reflected in shifted intercepts, which affect the relationship of fixed effects (such as EIA) by shifting the curve to the left or right of the overall mean (Fig. 5, using *E. etowahae* as an example).

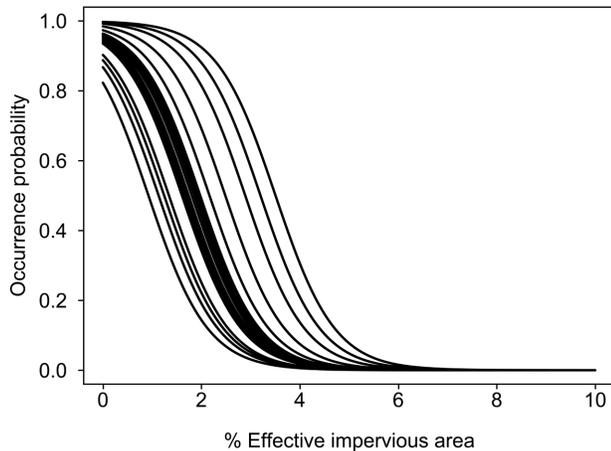
Discussion

We found that for four of the five species evaluated, both historic and current land use variables were included in the best-supported hierarchical occupancy models. For *N. leptacanthus* and *E. etowahae*, the best model was a toss-up between one including current land use (and not historic land use) and one with both current and historic land use, suggesting that historic land use added relatively little explanatory power. The results provide good evidence that both current and historic land use are potentially important

determinants of occupancy patterns for these species. However, the similarity in AUC scores among the best models for each species suggests that caution is warranted in determining which model is best. Although we know of no standard criteria for identifying a candidate set of well-supported models based on AUC scores, we considered it prudent to consider any model with a score within 0.010–0.015 of the top model to be an alternative hypothesis with good support from the data. By this criterion, both the current land use and global models are well-supported alternatives for *C. trichroistia*, *N. leptacanthus*, and *P. palmaris*, while the global, current, and historic models are supported for *E. etowahae* and *E. scotti*.

Based on the top models, the occurrence of several species was strongly related to low levels of EIA. Many previous studies have reported declines in aquatic fauna in watersheds draining more than 10%–12% impervious cover (Klein 1979; Schueler 1994; Wang et al. 2000). Our results indicate that some species become rare at impervious cover levels as low as 2% EIA. For some species there is considerable uncertainty around this value, but for *C. trichroistia* this threshold is consistent across all credible intervals of all well-supported models. We caution that the accuracy of these values is somewhat uncertain because the accuracy and bias of the impervious cover layer (US Geological Survey 2003) on which EIA is based are unreported in the metadata and apparently unmeasured. We anecdotally

Fig. 5. Occurrence probability for *Etheostoma etowahae* in each of 21 tributary systems as a function of increasing EIA under the best-supported model. Coefficients for fixed and random effects are held to their mean estimates. Predictor values for watershed area and d-link are set to one standard deviation larger than the mean, while other predictors are set to mean values.



observed that impervious cover appeared to be underestimated in the data layer in some geographic regions; we suspect this may be a common problem with impervious layers derived from satellite imagery. Nevertheless, our observed 2% EIA threshold value for the most sensitive species is consistent with a recent study that suggested EIA must remain below 2% to maintain natural ecological conditions (Ladson et al. 2006).

We found that for four of five species, models with current land use (and not historic land use) provided slightly more accurate predictions than models with historic land use (and not current land use). Our finding is in contrast to the results of Harding et al. (1998), who found that 1950s land use was a better predictor of fish and invertebrate diversity than current land use. However, Harding et al. (1998) examined only forested and agricultural watersheds, whereas we considered urban watersheds as well. We found that models including both current and historic land use predictors were among the best supported for most species, providing evidence that current fish distributions are the product of past land use legacies and recent activities, especially urban development. We hypothesize that in the Etowah basin, historic agricultural activities caused extirpations of some species from large sections of the basin. The decline in agriculture and subsequent reforestation then allowed a slow recovery of these species, but current urbanization and suburbanization activities are now causing new extirpations. Such a pattern is probably evident in much of North America, owing to the widespread conversion of current and former agricultural land to urban and suburban uses.

Of the historic land use variables, density of and area inundated by impoundments were generally better predictors than historic modified land cover as mapped from aerial photos. Historic land cover may have performed less well because it was only a snapshot at one point in time (1938) and perhaps not an accurate predictor of the locations that suffered the greatest impacts. Cotton agriculture in Georgia

crashed in the early 20th century with the arrival of the boll weevil (Haney et al. 1996), and by 1938 some agricultural areas may already have been abandoned and reforested. Reservoirs (many constructed for sediment control on agricultural lands) may be a better long-term signal of past land use because they are pervasive and because they may prevent recolonization of areas of extirpation. In this sense, reservoirs are both indicators of past land use and current stressors in their own right. In addition to blocking fish movement, reservoirs also eliminate fluvial habitat; alter flows, temperature, and chemistry; and have been shown to affect downstream fish assemblages (Collier et al. 1996; Freeman and Marcinek 2006). In our data set, the number of dams in the tributary system was highly correlated with the historic modified land cover in the tributary system ($r = 0.88$). However, the area inundated by impoundments in the collection watershed, which was a good predictor for some species, was relatively uncorrelated with historic modified land cover ($r = 0.34$).

The appearance of slope in the best-supported models for most species is consistent with the findings of previous studies in the Etowah basin, which identified slope (i.e., stream channel gradient) as a critical variable influencing the distribution of many species (Walters et al. 2003a, 2003b). The strengths of the relationships are somewhat remarkable considering that we were able to use only map slope and not field-measured reach slope, which was unavailable for many sites. We measured slope at the tributary system scale under the assumption that tributary systems with lower average slope had less riffle habitat, which made these systems less suited to riffle-dwelling species such as the five modeled here. Thus, at the tributary system scale mean slope is a potential filtering mechanism (Poff 1997), limiting whether fish species are likely to be present or absent from the system as a whole (we also hypothesized that low slope could indicate high suitability for agriculture, but we found no relationship between slope and historic land cover at the tributary system scale; $r = 0.2$). Reach-scale slope may serve as a second filter, limiting whether a species is locally present, given its presence in the tributary system.

Our study did not evaluate mechanisms by which urbanization affects fishes. Urbanization is a complex phenomenon that can impact fish populations through multiple potentially interacting pathways, including modification of the hydrologic regime, introduction of toxins, physical alteration of habitat, and reduction and shifts in the food base (see Paul and Meyer 2001; Walsh et al. 2005b; Wenger 2006). Past studies in the Etowah basin have related shifts in fish communities across an urban gradient to geomorphic change (Walters et al. 2003a) and to hydrologic alteration associated with imperviousness (Roy et al. 2005). It is possible that the mechanism by which urbanization causes extirpation varies from species to species. Indeed, considering the variability in natural-history characteristics among different fish species, we believe this is quite likely to be the case: some fishes will be sensitive to alteration of spawning habitat and others to toxins in their larval stage, while still others are feeding specialists that will respond to shifts in their food resources. If these responses were better understood, management strategies could be better targeted to the needs of individual species. However, there is consid-

erable value in understanding the overall thresholds of responses of individual species, even without a mechanistic understanding, because these thresholds can be used to inform policies that broadly manage the impacts of urbanization. For example, most of the potential mechanisms are driven by stormwater runoff from impervious surfaces, which can be controlled by stormwater management programs designed to mimic natural hydrology (e.g., Ladson et al. 2006).

In previous studies in the Etowah basin, urban effects were found to be strongest on fish species classified as regional endemics or fluvial specialists (Walters et al. 2003a; Roy et al. 2005). Of the species examined here, *C. trichroistia*, *P. palmaris*, and *E. scotti* were included in both of these categories. Our results provide strong evidence that *C. trichroistia* and *P. palmaris* are indeed sensitive to urban stressors, but that occurrence of *E. scotti* is not strongly related to current land use. We also found that *N. leptacanthus* appears to be influenced by impervious cover, despite the fact that this species had previously been included among cosmopolitan species (i.e., species which as a group responded neutrally or positively to urban impacts; Walters et al. 2003a). These exceptions serve as a reminder that species groupings based on traits and classifications — such as endemics and cosmopolitans, or any of various index of biotic integrity metrics — may contain considerable noise in the form of species that respond in a manner opposite to what is expected. While such groupings may provide some utility in assessing the degree of impact experienced at the level of the fish assemblage, the response of a group as a whole cannot be used as a surrogate for the response of an individual species. However, it is realistic to use groups as a preliminary screen to identify species that are potentially sensitive to urbanization.

Similarly, general ecological correlates of imperilment such as benthic habit and small body size (Burkhead et al. 1997; Reynolds et al. 2005) may also be indicators of potential urban sensitivity. While such characteristics may provide an initial group of candidate species to test for sensitivity, they do not provide much insight into the degree of sensitivity. For example, the life-history traits of the highly sensitive *C. trichroistia* as a small fluvial specialist do not differentiate it from many other minnow species that are robust to urbanization effects.

Ultimately, effective management of the impacts of urbanization requires an understanding of the thresholds of response of individual species. For the two federally protected species we evaluated, we found good evidence for a strong response of *E. etowahae* to impervious cover but little evidence to indicate a relationship between presence of *E. scotti* and urbanization. These findings are consistent with field observations: *E. etowahae* is unknown from urban or suburban streams, while *E. scotti* has been collected in a number of suburban and moderately urban watersheds, albeit at lower abundances than in streams in forested or agricultural catchments. These results have important management implications, as they suggest that aggressive stormwater management policies are justified by the presence of *E. etowahae* but not by the presence of *E. scotti*.

We assert that in evaluating the sensitivity of individual species to urbanization or other hypothesized stressors, it is

important to consider alternative hypotheses. Specifically, historic land use is likely to be of considerable importance in explaining present distribution patterns of many fish species. The extent to which this is true will depend on the magnitude of the historic effect and subsequent recolonization. Recolonization will depend on (1) persistence of effects or degree of habitat recovery, (2) movement potential and propensity of the species, and (3) presence of movement barriers. These factors may be difficult to assess. However, we suggest that in many cases it will be possible to use the type of approach presented here, or a simplified version, to compare the relative support for historic land use, current land use, hydrogeomorphic factors, or a combination of the three in explaining present fish distribution patterns.

This is the first study we know of to quantify the response of individual fish species to both historic and current land use. We found that both factors were important in explaining the distribution of fishes in an urbanizing watershed, and that some species exhibited a strong relationship to impervious cover, with occurrence probability approaching zero at levels above 2% EIA. Assessment of the response of individual species is a necessary step if we are to advance from merely cataloguing urban effects on fish assemblages to developing management policies that prevent extirpation of sensitive fish species.

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