Regional differences in patterns of fish species loss with changing land use

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ABSTRACT

Human-centered land use causes ecosystem degradation and loss of biodiversity in streams, yet such processes may be highly heterogeneous among species and regions. We quantified fish species sensitivity to several classes of land use and determined if trends varied among three geoclimatic regions of Maryland, USA. Our approach compares the cumulative frequency distribution (CFD) of sites where a species was expected to occur to the CFD of those where it was collected to estimate the species-specific maximum degree of land use tolerated and the minimal amount that may induce an impact. Fishes were most vulnerable to urban land use gradients, though trends were region-specific with heightened sensitivity in the Piedmont (64–72% of species negatively affected) relative to the Coastal Plain (45–52% negatively affected). Species found in both regions exhibited greater vulnerability to urbanization in the Piedmont. Responses to agricultural land use were less severe though trends were region-specific as well with the least sensitive in the Piedmont and the greatest negative impact in the Highlands region. In many cases, reduced population abundances were detected at lower levels of land use relative to the range where the species was apparently extirpated. Our results demonstrate that population reduction and species loss due to land use change differs substantially among regions, even within a single species. Greater sensitivity observed in abundance-weighted analyses implies that further loss of fish diversity may be impending in impacted streams. Our results have direct application to prioritize conservation resources and forecast future declines in species distributions and biodiversity.

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1. Introduction

Land use change and consequential habitat degradation ranks as the dominant driver in the global biodiversity decline across multiple biomes and ecosystems (Sala et al., 2000), yet the relationship may be nuanced and complex. Differences among ecoregions may render one locale more sensitive to species loss from the same form and magnitude of land use change than another, even when species composition is similar between regions (Huggett, 2005). Species loss may occur decades or centuries after patch isolation and fragmentation (Hilderbrand, 2003; Lindborg and Eriksson, 2004; Vellend et al., 2006), making its true magnitude difficult to detect. Further, invasions of non-native species and/or species compositional shifts from sensitive to tolerant taxa in degraded habitats may obscure responses by mitigating biodiversity declines when comparing commonly used measures such as species richness against gradients of land use change (Walters et al., 2005).

A broad suite of land use associated stressors influences stream biodiversity as streams are tightly linked to past and present activity in their watersheds (Harding et al., 1998; Gergel et al., 2002). Substantial physicochemical degradation in streams may occur at multiple temporal and spatial scales due to land use change (Allan, 2004), and these in turn may influence distributions of aquatic organisms. Common stressors include altered hydrologic regimes (Konrad et al., 2005), elevated nutrient and pollutant loads (Jones et al., 2001; Sprague and Nowell, 2008), shifts in temperature extremes and variability (Price and Leigh, 2006; Wehrly et al., 2006), and reductions in substrate and habitat heterogeneity (Waters, 1995; Jones et al., 2001; Sutherland et al., 2002). A substantial number of aquatic taxa are imperiled due to such stressors (Sala et al., 2000; Wilcove et al., 2000; Abell, 2002; Strayer, 2006). In North America, 39% of all described freshwater fish species are considered imperiled in part due to land use change, a number that has nearly doubled in the past 20 years (Jelks et al., 2008). Though comprehensive species status assessments in other regions are often less complete, estimates of imperilment are consistently alarming. For example, as much as 50% of the Mediterranean and Malagasy freshwater fish fauna are in danger of extinction, partially as a result of forest clearing, agriculture, and urban expansion (Darwall et al., 2008).

Due to the multivariate nature of land use associated stressors, broad landscape classifications may be effective surrogates for

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quantifying degradation. Physicochemical changes are often correlated with one another in developed catchments (Gergel et al., 2002; Joy and Death, 2004; Short et al., 2005; Potopava et al., 2005; Meador et al., 2008). For example, urbanization may simultaneously elevate water temperatures, substantially alter the hydrologic regime, and increase pollutant loads, each of which may independently or interactively impact aquatic organisms (Walsh et al., 2005). Therefore, at large spatial scales, broad land cover classes stand as useful measures of disturbance and allow for analyses of species sensitivity over the entire stressor gradient. Such landscape-scale approaches complement analyses of species sensitivity to component physicochemical stressors (Eaton and Scheller, 1996; Pollard and Yuan, 2006) to comprehensively assess the conservation needs of threatened taxa.

Geoclimatic variability among ecoregions also may complicate the relationship between land use change and biodiversity. Physicochemical changes induced by urbanization such as hydrologic regime shift (Poff et al., 2006) and elevation in pesticide concentrations (Sprague and Nowell, 2008) may vary substantially among geoclimatic locations along analogous urban land use gradients. Similarly, nutrient concentrations may not be uniformly affected by agricultural intensity even among adjacent physiographic settings (Jordan et al., 1997; Liu et al., 2000). Biological assemblages may therefore respond differently to the same landscape stressor among ecoregions. For instance, in the Mid-Atlantic United States, fish and macroinvertebrate biotic integrity metrics (Morgan and Cushman, 2005; Goetz and Fiske, 2008) as well as individual macroinvertebrate taxa (Utz et al., 2009) show heightened sensitivity to urbanization in the eastern Piedmont physiographic province relative to the Coastal Plain. Yet despite explicit calls for further inquiry into physiographic mediation in landscape–stream interactions (Walsh et al., 2005), interregional comparisons of landscape stressor sensitivity remain scarce.

Given the rapid expansion of urban land (Brown et al., 2005) and ongoing degrading impact of agricultural practices on streams (Barker et al., 2006) in the eastern United States, we sought to quantify how fishes are distributed along land use gradients and whether such distributions differ between distinct, yet adjacent, geoclimatic regions. Our study area was the state of Maryland in the Mid-Atlantic region of the United States, a region experiencing rapid urban and exurban growth with substantial fish diversity (including 31 species considered vulnerable to local extirpation). Study objectives included: (1) quantify sensitivity (i.e., risk of population reduction and extirpation) of fish taxa to land uses by analyzing fish distributions along urban and agricultural land use gradients; (2) identify both general and species-specific differences in patterns among regions; and (3) address landscape-scale conservation implications for current and future species of concern.

2. Methods

2.1. Study area

The state of Maryland encompasses about 32,000 km^2 of land in the mid-Atlantic United States. Nearly all watersheds in the state drain to the Chesapeake Bay; a small area ($\sim$1100 km^2) empties to the Ohio River in the western portion of the state and some tributaries (430 km^2 area) drain directly to the Atlantic Ocean on the eastern shore. Three general geoclimatic regions are found in the state: the Coastal Plain physiographic province, the Eastern Piedmont physiographic province (hereafter Piedmont), and the Highlands (a conglomerate of the Appalachian Plateau, Ridge and Valley, and Blue Ridge physiographic provinces, Fig. 1; Omernick, 1987).

Stream physicochemistry and geomorphology varies considerably among these three regions (Table 1). Topographic relief typically decreases on a west-to-east gradient from the Highlands to the Coastal Plain. As a result, mean channel slopes decreases and percent wetland cover increases categorically among regions from west-to-east. Climatic variability influences stream temperature such that the warmest streams are found in the Coastal Plain and
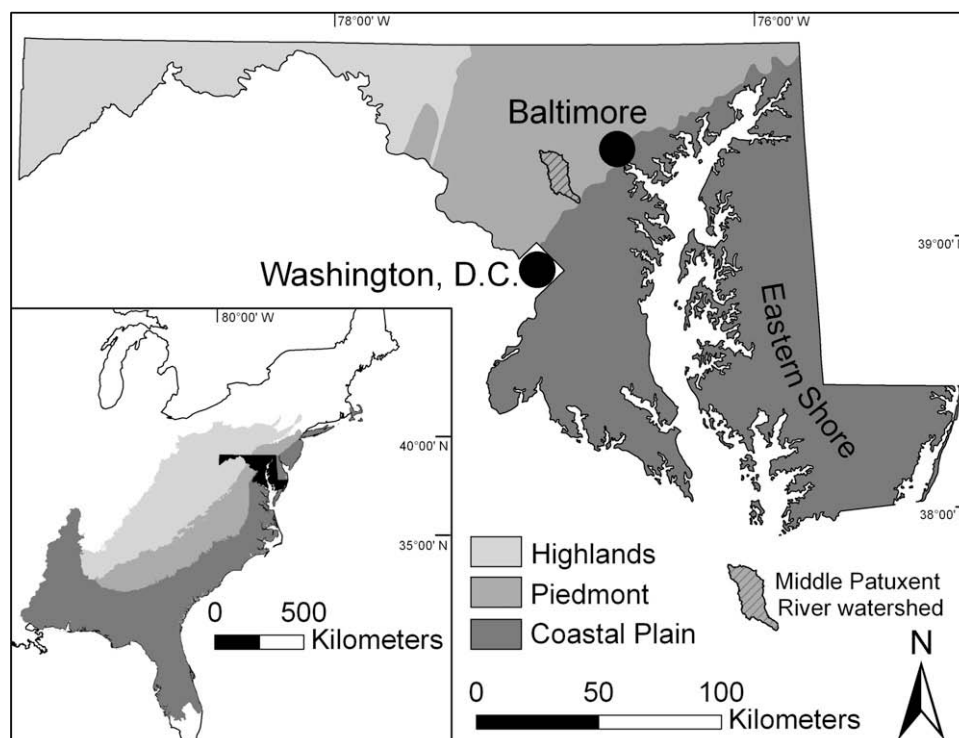

Fig. 1. Map of the state of Maryland and the eastern United States illustrating the physiographic regions delineated for species-specific analyses.

Table 1
Means and ranges (in parentheses) of study watershed attributes delineated by region.

Variable	Coastal Plain	Piedmont	Highlands
Physicochemical			
Size (km^2)	34.9 (0.1–379.9)	38.2 (0.1–429.5)	55.0 (0.3–424.3)
Slope	0.4 (0.1–4.5)	0.9 (0.1–10.5)	1.4 (0.1–18.0)
pH	6.7 (4.0–9.1)	7.5 (6.3–9.6)	7.4 (4.9–8.7)
Mean summer temperature[a] (°C)	21.0 (15.5–28.5)	19.4 (12.8–27.9)	18.1 (12.0–24.6)
Land cover (%)			
Forest	38.6 (0.1–100)	26.4 (0.0–98.5)	69.5 (0.0–100)
Wetlands	3.2 (0.0–49.2)	1.1 (0.0–14.2)	0.5 (0.0–4.8)
Agriculture	40.4 (0.0–99.4)	59.0 (0.5–100)	22.2 (0.0–91.1)
Urban	16.3 (0.0–96.7)	12.9 (0.0–98.5)	7.1 (0.0–80.7)

[a] Derived from a subset of round two (2000–2004) MBSS sites; data loggers were typically deployed June 1–September 1.

coolest in the Highlands. Geologic variation among the three regions alludes to substantial differences in benthic substrate structure. Basement rock in the Coastal Plain is buried by unconsolidated siliclastic sediment ten to hundreds of meters thick (Ator et al., 2005); stream sediments consist of a heterogeneous mix of cobble, sand, silt and clay. Siliclastic and carbonate bedrock dominates in the Highlands while Piedmont bedrock is primarily composed of gneiss-schist; basement rock in both provinces is typically overlain by a 0.5–2 m thick layer of soil (Swain et al., 2004). Highland and Piedmont stream sediments range from boulder to cobble, with finer grains on average found in the Piedmont. Piedmont streams are highly buffered, while tannic wetlands and a lack of buffering bedrock renders Coastal Plain streams the most acidic in the study region.

2.2. Biological data

Data were derived from rounds one (1995–1997) and two (2000–2004) of the Maryland Biological Stream Survey dataset (MBSS; Klauda et al., 1998). The MBSS is a statewide stream monitoring system with >2000 site collections. The survey uses a probability-based design to maximize representativeness of sites. Each wadable 75 m stream reach within the state has a non-zero probability of being selected over a 3 year sample frame that is stratified by major river basins. No specific watershed size criteria was applied to filter sites chosen by the MBSS program, however >99.5% of those sampled were fifth Strahler-order or smaller ($\leqslant$282 km^2; Knighton, 1998) and mean catchment areas among sites in the three regions were similar (Table 1).

Fishes were collected during summer baseflow using equal effort, two-pass depletion electrofishing (Kazyak, 2001). The top and bottom of each section were blocked using nets to prevent fish movement during sampling. All fishes were identified to species. A number of water quality attributes (including pH) were measured at each site during summer fish sampling. Further detail concerning sampling of fish and water quality may be found in Kazyak (2001). Data analyzed in the current study were derived from 2227 fish collections, of which 528 were sampled more than once (271 of these were sampled twice).

2.3. Land cover data

For each site, watershed boundaries upstream from each sampling site were delineated using a flow corrected, 30 m resolution National Digital Elevation dataset (USGS, 2008), and the respective land covers from the 2001 National Land Cover Database (NLCD) were extracted in a GIS. To simplify analyses of catchment land

cover, land cover designation was limited to Class-I categories (see EPA, 2008 for a full description of all classes). Urban land represents low-, medium-, and high-intensity developed land along with open space urban development. Agricultural cover represents the sum of the pasture/hay and row crop categories. The area of each summed category (urban and agricultural land cover) was divided by the area of each watershed to estimate the percentage of developed and agricultural land. The 2001 NLCD dataset also includes an estimate of percent impervious surface cover (ISC) from 0 to 100; the total percent of impervious surface covering each watershed was calculated from this layer. Though urban cover and ISC are strongly correlated (Pearson correlation coefficients = 0.91–0.96 in sample sites among the three regions, $p < 0.0001$ in each case), we ran analyses on both coverages for several reasons. Both classes of land use are commonly used to quantify environmental impacts on streams and we wished to provide quantitative data on each to ease comparisons of our findings to related work. Additionally, the classes may account for somewhat different stressors. For instance, elevated nitrogen concentrations in urban streams may largely originate from sewage and fertilizer derived from structurally pervious urban areas rather than storm flow delivered by impervious surfaces (Groffman et al., 2004). We therefore wished to determine if any consistent differences were found in fish sensitivity between the two classes.

The two major metropolitan regions of Maryland (Baltimore and Washington, DC) are located at the border of the Coastal Plain and Piedmont (Fig. 1). As a result, the degree of urban land cover is similarly divided between the two regions, a trend reflected in the distribution of urban land in watersheds sampled by the MBSS program (Utz et al., 2009). In both the Coastal Plain and Piedmont, agriculture and urbanization are more negatively correlated with one another than either is with natural cover (Utz et al., 2009). Urbanization and agriculture are positively correlated in the Highlands and urban cover is rare as metropolitan centers are absent in the region. Though the average percent urbanization of MBSS-sampled Highland watersheds was 7.1%, this value was substantially inflated by a minority of intensely urbanized catchments (Utz et al., 2009).

Relationships between watershed size and land use intensity (agricultural or urban) are absent or weak. Among the three regions and two classes of tested land use, five out of six correlations between watershed size and land use are not significant (Pearson correlation p-values = 0.0543–0.6206). Watershed size is correlated with urbanization in the Piedmont, but only weakly (Pearson correlation coefficient = −0.0834, $p = 0.0154$).

2.4. Statistical analysis

Prior to the analysis of distributions, we used a filtering process (Fig. 2) to include only sites expected to possess a species in the absence of landscape stressors. Low pH from atmospheric deposition and mine drainage may limit many fishes in the mid-Atlantic (McClurg et al., 2007). For each species, a quantile analysis of pH levels for species' occurrences identified sites that fell below the 5% quantile of pH and were omitted from further analysis. We also used a biogeographic filter to exclude watersheds where a species would not be expected to occur naturally due to catchment boundaries and/or spatial limitations of distributions. Only watersheds where the species was collected among the 18 major basins within the state (shown in Heimbuch et al., 1999) were included for analysis. We also removed sites located in the Eastern Shore for four species with relict populations there (*Catostomus commersoni*, *Clinostomus funduloides*, *Notropis procne* and *Rhinichthys atratulus*; Jenkins and Burkhead, 1994). If a fish was biogeographically restricted to basins without substantial urban cover, we did not perform distributional analyses (this occurred for five fishes in the
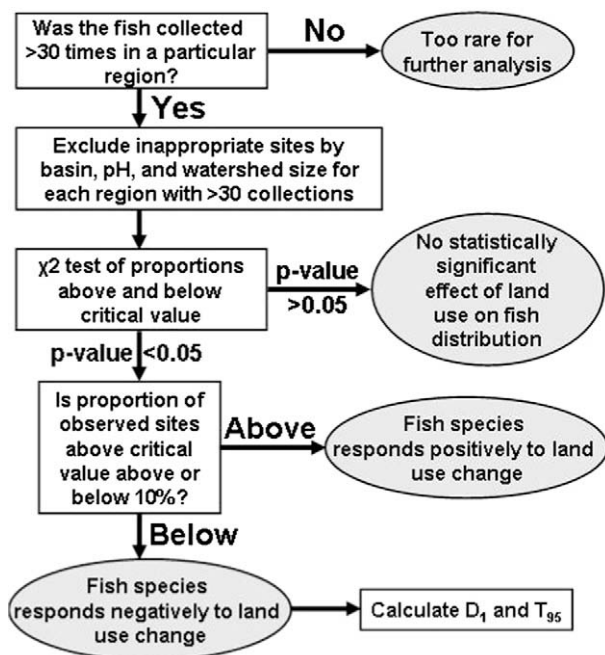
Fig. 2. Flow chart representing the process conducted for determining species-specific response with respect to land cover change. Ovals with grey fill represent endpoints for the three potential relationships along land use gradients.

Coastal Plain and two in the Piedmont). Sites below the minimum and above the maximum basin area size where each species was collected by the MBSS program were excluded from further analysis. These large-scale filters (*sensu* Poff, 1997) typically account for a substantial amount of variation in lotic community composition at the landscape scale (Hawkins et al., 2000; De Zwart et al., 2006; Kennard et al., 2006) and thus were considered adequate to select the appropriate watersheds of analysis for each species. A number of other factors such as riparian or instream habitat, water quality, and temperature may potentially affect the abundance and distribution of stream fishes. Yet such variables are likely to be impacted by land use change and were therefore considered inappropriate for the preliminary filtering process.

We implemented a cumulative frequency distribution (CFD) analysis that compared the distribution of land cover at the sites where the organism was collected to the distribution where the organism would be expected if the effects from land use did not (positively or negatively) influence the species. Our main objective was to quantify species sensitivity to land use; we therefore used land cover classes as univariate environmental stress variables that are surrogates for the physicochemical responses which are multivariate and interactive. Though multivariate approaches are often used for similar large-scale analyses, our goal was to identify response thresholds to land uses rather than estimate component contributions of stressors to fish species occurrence. Other factors not related to or influenced by land use (such as interspecific interactions) may influence fish community structure and population abundance. The CFD approach assumes that such factors not accounted for by the filtering process described above are spatially independent of land use. One advantage of using cumulative frequencies in concert with landscape-scale filtering is that species need not be present at every site where suitable habitat is available. Rather, the distribution of sites where a taxon was collected is compared to those where it is expected (inclusive of observed sites) with respect to a land use gradient. Thus rare and common species are treated equally. Because of the considerations above,

our approach is meant to complement, rather than replace, related multivariate studies exploring environmental sensitivity of fishes as we are asking a different question.

To perform the CFD analysis once pH-, biogeographic-, and size-inappropriate sites were excluded, the actual and expected occurrences of each species were compared in relation to land cover. Within each physiographic region, the CFD of all sites arranged by percent land cover (i.e., agricultural, urban or ISC) was calculated. This 'expected' group included all sites where the species was and was not collected. The land cover percentage at the 90th percentile (termed the critical value) for the expected set of sites was determined and compared to the suite of the sites where the species was collected, hereby termed the 'observed' group. Two observed CFD curves for each species were constructed: (1) a presence/absence curve where each occurrence was equally weighted and (2) an abundance-weighted (by number of individuals collected at each site) curve where each occurrence was assigned a value based on the formula:

$$\% = 100 * (\# \text{ of species A at specific site})$$
$$/(\# \text{ of species A collected across all sites})$$

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The abundance-weighted analysis was used to detect if land use affected trends in population size, which may be a more subtle response than outright population loss. A Chi-square goodness of fit test on the proportions above and below the critical value was performed between the expected group (10% above and 90% below the critical value) and observed group (% above and % below). Since only two proportions were tested between stream sets, all such tests had one degree of freedom despite varying numbers of observed and expected sites among species. If the analysis showed no significant difference ($\alpha > 0.05$) between proportions, the land cover was assumed to have no relationship to the occurrence of the species. However, if the test did find a significant difference, analysis of the CFD curves continued.

If a species' distribution was found to be significantly affected by land cover, two scenarios were possible. First, the species may have responded positively to the particular land cover, and populations were consequently more frequently observed in catchments with high percentages of agricultural, urban, or impervious land cover. Such was the case when the percentage of observed streams above the critical value was significantly higher than 10%. Alternatively, the species may be negatively associated with the particular land cover gradient. Here the percent occurrence or abundance above the critical value was significantly lower than 10% (in many cases 0%).

When a significant negative response was detected, two values were calculated to describe the severity of response. The first was the 95th percentile of land cover in the observed stream set, termed the T_{95} (i.e., 95% threshold). This was considered the maximum percentage for a specific land cover in a catchment that could conceivably retain the species. The second calculated value estimated the point of divergence between the observed and expected CFD curves and is considered to be the minimum detectable effect, or the D_1. Each quantile (specific cumulative frequency) of land cover in the observed site group was matched to the closest possible quantile in the expected stream group. The percent land cover values of both groups were then compared by matched quantile, starting from zero. Once the difference in percent land cover for the same quantile on both curves exceeded (and remained above) 1%, the curves were considered divergent. At this point, the land cover percentage on the observed group curve was assumed to be where the land cover could negatively affect the species. Fig. 3 presents a graphical example of the critical value, D_1 and T_{95}.
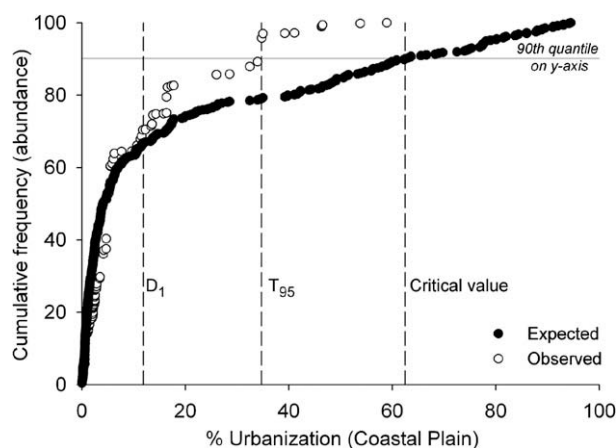
Fig. 3. Cumulative frequency distribution of margined madtom (*Noturus insignis*) abundance and expected sites along an urban land use gradient in the Coastal Plain. All values used to quantify the distributional response are illustrated as dashed vertical lines; the 90th quantile on the *y*-axis (used to calculate the critical value) is also shown as a horizontal grey line.

In our approach we sought to quantify sensitivity using both presence/absence and abundance data and allow for comparisons of sensitivity at both scales. The substantial variation in collection frequency among fish species required that analyses were robust to species rarity. Values representing sensitivity (D_1 and T_{95}) were selected to represent the upper bound of land use tolerance (T_{95}) and minimal detection of effect (D_1), rather than the inflection point of most rapid loss in abundance or probability of occurrence. All three quantitative values (the critical value, D_1 and T_{95}) were, to some degree, arbitrarily selected to descriptively depict species sensitivity. Those implementing our methodology in future work may adjust the reported values to derive more conservative or moderate estimates of species sensitivity.

We also summarized species responses based on taxa deemed in greatest conservation need (GCN; taxa considered imperiled by the Maryland Department of Natural Resources) for fish with collection frequencies high enough to permit analyses. GCN status was designated by the state of Maryland (Kazyak et al., 2005) with the exception of American eel *Anguilla rostrata* (listed as a GCN species due to widespread population decline, Haro et al., 2000).

One concern pertaining to our analyses was that species rarity may artificially inflate landscape sensitivity due to the limited distribution of infrequently collected species. We therefore ran linear regression models relating the abundance-T_{95} values of sensitive fishes to species sample size by region and land use class (urbanization and agriculture) to assess if patterns of land use sensitivity was influenced by collection frequency.

2.5. Forecasting biodiversity

We spatially modeled both the status of an urban-sensitive fish and the projected loss of species richness in a Piedmont watershed as an example of biodiversity forecasting using D_1 and T_{95} values. Exurban growth in the Middle Patuxent River, a 150 km² tributary of the Patuxent River (Fig. 1), is likely to be particularly acute as the watershed is situated between the two metropolitan areas of Maryland. Urban land use for the year 2030 was approximated using a spatially-explicit projected housing density model (Theobald, 2005). Any cell with ⩽0.7 hectares (1.7 acres) of land per unit of housing was classified as urban and integrated into the 2001 NLCD land use grid. The resulting layer projected urban land use based on the expansion of (medium to high density) residential urban land in 2030 and commercial/industrial urban cover during

2001. A suite of subwatersheds was derived by dividing the Middle Patuxent perennial stream network into 65 approximately equally spaced reaches, and percent urban cover was calculated for each.

The likelihood of extirpation and population status for the common, but urban-sensitive, fallfish (*Semotilus corporalis*) was forecasted in each subwatershed. Urbanization-driven extirpation and population reduction likelihood (using presence/absence and abundance analyses, respectively) was deemed negligible if urban development in the subwatershed was below the D_1 value, moderate if between the D_1 and T_{95} values, and high if greater than the T_{95} value. Only watersheds large enough (based on MBSS sites where the species was collected) to support fallfish were assessed.

Ichthyofaunal biodiversity was also forecasted using presence/absence D_1 and T_{95} values. Twenty-two fish species assessed for land use sensitivity were collected in the Middle Patuxent River by the MBSS program; 11 of these 22 are urban-tolerant. Maximum potential diversity was spatially modeled in two forms: least sensitive, which assumed subwatersheds would support a sensitive fish if urban cover fell below the T_{95} value, and most sensitive, where sensitive fish were extirpated if subwatershed urbanization exceeded their D_1 value. Species were only included in a subwatershed if it exceeded the minimum watershed size where the fish was collected.

3. Results

Distributions of 54 freshwater fish species across the three regions were tested against land use gradients (Appendices A–C and Table 2). Due to a lack of urbanization only agriculture was assessed in the Highlands region. Land use sensitivity of ichthyofauna varied substantially among both regions and classes of land use. We discovered the presence of all three hypothetical responses (negative, neutral, and positive associations) to land use gradients (see Fig. 4 for examples of each). In some cases no response was detected when presence/absence CFD curves were compared, but differences were evident for abundance-weighted data (Fig. 4A). Additionally, while some taxonomic groups exhibited a uniform response to a given land use gradient (cottids and percids), many congeners responded heterogeneously (Appendices A–C). For example, the ictalurids *Noturus* and *Ameirus* had both sensitive and tolerant species to given land uses.

### 3.1. Urbanization and ISC

Urban and ISC gradients exerted a pronounced effect on the distributions of fishes in the Coastal Plain and Piedmont overall, though responses often differed substantially between the regions (Fig. 5).

In the Piedmont, a majority of fish species (26 out of 36 when abundance-weighted) were negatively affected along an increasing urban gradient; no species were collected more frequently or in greater numbers in urbanized watersheds (Table 2 and Fig. 5). When presence/absence data were analyzed, the majority of urbanization-sensitive species possessed T_{95} values between 40% and 55%. In contrast, T_{95} values for abundance-weighted data ranged relatively evenly between 8% and 60% (Fig. 5). River chub (*Nocomis micropogon*), rosyface shiner (*Notropis rubellus*), and brook trout (*Salvelinus fontinalis*) were found to be most sensitive, possessing T_{95} values between 6% and 20%. Sculpin (Cottidae, genus *Cottus*) and darters (Percidae, members of the genus *Etheostoma*) were also consistently sensitive to urban gradients. Several species such as the golden shiner (*Notemigonus crysoleucas* – Fig. 4a) exhibited no response along the urban gradient when presence/absence data were considered but were found to be sensitive when curves were abundance-weighted.

Table 2
Regional summaries of tested fish species responses by count and percent of regional tested species pool (provided in parentheses) to land cover gradients delineated by region.

| Land cover	Region	n Species	Presence/absence			Abundance		
			Negative	Neutral	Positive	Negative	Neutral	Positive
Urbanization								
	Coastal Plain	31	8 (25.8)	19 (61.3)	4 (12.9)	14 (45.2)	10 (32.2)	7 (22.6)
	Piedmont	36	20 (55.6)	16 (44.4)	0 (0.0)	26 (72.2)	10 (17.8)	0 (0.0)
Impervious surfaces								
	Coastal Plain	31	9 (29.0)	18 (58.1)	4 (12.9)	16 (51.6)	12 (38.7)	3 (9.7)
	Piedmont	36	18 (50.0)	18 (50.0)	0 (0)	23 (63.9)	13 (36.1)	0 (0)
Agriculture								
	Coastal Plain	36	7 (19.4)	27 (75.0)	2 (5.6)	12 (33.3)	19 (52.8)	5 (13.9)
	Piedmont	38	1 (2.7)	37 (94.6)	1 (2.7)	7 (18.4)	24 (63.2)	7 (18.4)
	Highlands	25	5 (20.0)	18 (72.0)	2 (8.0)	11 (44.0)	12 (48.0)	2 (8.0)
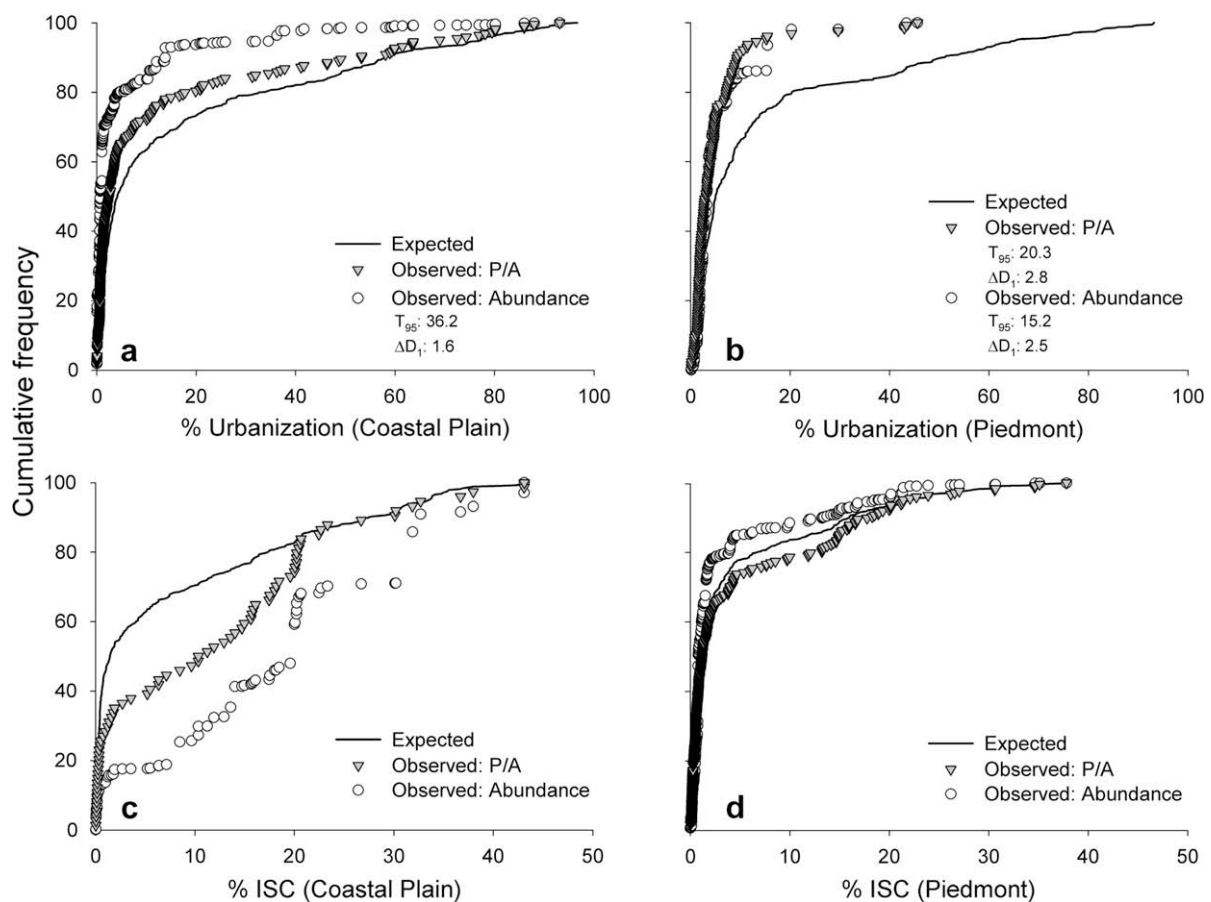
Fig. 4. Examples of varying species-specific distributions along urban and impervious surface (ISC) gradients. When the observed curves were found to be significantly different than the expected, the T_{95} and D_1 values are listed in the legend. Shown are examples of: (a) no significant difference in the presence/absence curve but a negative response of abundance along an urban gradient of golden shiner (*Notemigonus chrysoleucas*) in the Coastal Plain, (b) a rapid, negative response relative to an urbanization gradient for both presence/absence and abundance curves of Piedmont river chub (*Nocomis micropogon*), (c) evidence of a positive association with impervious surface cover in Coastal Plain green sunfish (*Lepomis cyanellus*), and (d) no apparent response of either curve along an impervious surface gradient in Piedmont American eel (*Anguilla rostrata*).

Fishes in the Coastal Plain were less affected by urban land use than in the Piedmont. A smaller but still sizable proportion of species (14 out of 31 when abundance-weighted) were negatively associated with the urban cover gradient (Table 2 and Fig. 5). The distribution of Coastal Plain T_{95} values was relatively uniform between 12% and 60% (Fig. 5). A number of fishes were found to be acutely sensitive, including the margined madtom (*Noturus insignis*), redfin pickerel (*Esox americanus*), least brook lamprey (*Lampetra aepyptera*), and pirate perch (*Aphredoderus sayanus*). Several species were collected more frequently and/or were more abun-

dant in urban watersheds, including the mummichog (*Fundulus heteroclitus*), satinfin shiner (*Notropis analostanus*), creek chub (*Semotilus atromaculatus*), and the non-native green sunfish (*Lepomis cyanellus* – Fig 4c).

For species collected in both the Coastal Plain and Piedmont, a greater sensitivity to urban gradients was observed in the Piedmont, almost without exception (Table 3). In some cases, such as the brown bullhead (*Ameiurus nebulosus*), both presence/absence and abundance analyses suggested sensitivity in the Piedmont while neither analysis did in the Coastal Plain. Not only was sensitivity
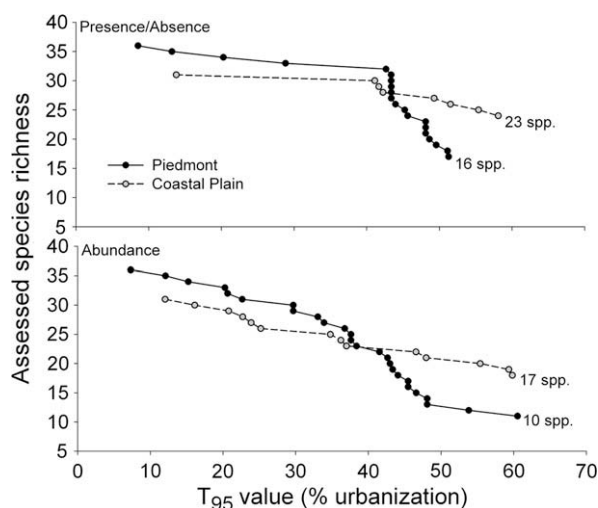
Fig. 5. Decline in region-specific species richness (those common enough to allow assessment) along a watershed urbanization gradient represented by the distribution of T_{95} values of Coastal Plain and Piedmont fishes. The number of species that did not show a significant deviance or responded favorably to urbanization is listed at the far right of the curve.

Table 3
Comparison of T_{95} values with respect to urbanization by fish common to both the Piedmont and Coastal Plain physiographic provinces. Only fish that were found to be sensitive to urbanization in at least one province are listed. Bold values indicate greater sensitivity; if curves were not divergent the value is listed as non-significant (n.s.).

Species	Presence/absence		Abundance	
	Coastal Plain	Piedmont	Coastal Plain	Piedmont
Ameiurus natalis	n.s.	n.s.	n.s.	**48.1**
Ameiurus nebulosus	n.s.	**48.1**	n.s.	**45.5**
Clinostomus funduloides	n.s.	n.s.	59.8	**33.0**
Etheostoma olmstedi	n.s.	**51.3**	n.s.	**43.3**
Lepomis gibbosus	n.s.	n.s.	n.s.	**48.1**
Luxilus cornutus	n.s.	**45.2**	59.3	**20.3**
Notropis hudsonius	n.s.	**48.1**	n.s.	**37.6**
Notemigonus crysoleucas	n.s.	n.s.	**36.2**	45.5
Noturus insignis	**41.1**	43.4	34.8	**22.6**
Petromyzon marinus	n.s.	**53.8**	n.s.	**45.6**
Semotilus corporalis	51.5	**48.1**	48.0	**38.4**

greater in the Piedmont, but species disappeared more rapidly across the urban land use gradient (Fig. 5).

As expected, responses of fish to ISC gradients were very similar to those observed along the urbanization gradient except that responses occurred at much lower levels of ISC. T_{95} values for ISC-sensitive fishes ranged from 1.8% to 20.5%, corresponding D_1 values were between 0.3% and 14.1%. Most fishes sensitive to urbanization were sensitive to ISC. As with urbanization, some species were more common (redbreast sunfish, *Lepomis auritis* and swallowtail shiner, *N. procne*), in greater abundance (green sunfish), or both more common and abundant (mummichog and satinfin shiner, *N. procne*) in Coastal Plain watersheds with high ISC.

3.2. Agriculture

Though overall the effects of the agricultural land cover gradient were reduced relative to responses to the urban gradient, a number of species were affected, both positively and negatively. The effects from agriculture varied among regions and species.

Among regions, Highland ichthyofaunal distributions were the most affected by agriculture. Nearly half (44%) of species tested in the Highlands were found in lower abundances as agriculture increased, while 20% were found to be reduced when comparing presence/absence curves (Table 2). All tested species of salmonids and cottids were negatively affected by agriculture. Three species were positively associated along the agricultural gradient: the central stoneroller (*Campostoma anomalum*), common shiner (*Luxilus cornutus*) and largemouth bass (*Micropterus salmoides*).

In contrast to the Highlands, fish distributions in the Coastal Plain and especially the Piedmont were less affected by agriculture. In these regions, no more than one-third of species were negatively associated (presence/absence or abundance) with agriculture, and in the Piedmont the number of species that were positively associated matched the number of negatively affected species (Table 2). Interestingly, a number of species that were found to be reduced in Highlands agricultural watersheds were insensitive to the same land use in Piedmont streams, including the Blue Ridge sculpin (*Cottus caeruleomentum*) and brook trout (collected with apparently no reduced abundance in watersheds with 98% and 100% agricultural cover, respectively).

3.3. Effect of sample size on sensitivity

Land use sensitivity values appear to be unaffected by species rarity. For four out of five tests (all regressions of T_{95} values for agriculture and for urbanization in the Piedmont), no significant relationship was apparent (*F*-value range = 0.03–3.04, *p*-value range = 0.1119–0.8755). The exception was the relationship between Coastal Plain urbanization abundance-T_{95} values and species collection frequency (*F*-value range = 4.89, *p*-value range = 0.0471, $r^2 = 0.23$); however, the relationship was negative.

3.4. Greatest conservation need fishes

Responses of GCN fishes to land cover varied considerably by land use class and species (Table 4). Urbanization negatively affected 7 out of 8 GCN species. However, some GCN species, such as the rosyside dace and silverjaw minnow (*Notropis buccatus*), were moderately tolerant to urbanization, responding negatively only with abundance and possessing high T_{95} values (60% for the silverjaw minnow). Agriculture affected proportionally fewer GCN species than urbanization (two exhibited positive associations). Several species without GCN status were more sensitive to urbanization than nearly all GCN fishes; these included the pirate perch, redfin pickerel, river chub, and rosyface shiner.

3.5. Forecasted change in the Middle Patuxent River

Urban expansion between 2001 and 2030 will likely induce substantial decline in the distribution and abundance of fallfish in the Middle Patuxent River (Fig. 6). In 2001, fallfish potentially inhabited the entire watershed, including seven first-order tributaries where urban cover fell below the D_1 value. By 2030, fallfish will likely be extirpated from the lower Middle Patuxent mainstem, Cricket Creek, and portions of two tributaries in the north of the watershed. Only one first-order tributary lacking urban-associated risk of population decline will remain classified as such.

Portions of the Middle Patuxent River are projected to lose substantial representative ichthyofaunal diversity due to urbanization by 2030 (Fig. 7). All of the following richness estimates include the 11 urban-tolerant species. Least sensitive estimates (based on presence/absence T_{95} values) predict a subwatershed average species richness decline of 12% and a maximum of 50%. Under most sensitive estimates (using D_1 values), average and maximum species richness loss is 26% and 45%, respectively. The slightly lower

Table 4
Summary of responses to land use for fishes designated as greatest conservation need (GCN) and those deemed most vulnerable by our analysis (Abundance T_{95} values <20 for urbanization or agriculture) that currently lack GCN status in Maryland. Species are deemed GCN by Kazyak et al. (2005) except *Anguilla rostrata*, included due to widespread decline (Haro et al., 2000). Species not tested for responses to urbanization are filled grey, those not found to be significantly different than expected are listed as not significant (n.s.), positive responses are noted with a plus sign (+).

Classification	Species	Region	Urbanization T_{95}		Agriculture T_{95}	
			P/A	Abun	P/A	Abun
GCN	*Acantharchus pomotis*	CP			75.5	72.0
	Anguilla rostrata	CP	n.s.	n.s.	n.s.	n.s.
		Pied	n.s.	n.s.	n.s.	n.s.
	Clinostomus funduloides	CP	n.s.	59.8	n.s.	n.s.
		Pied	n.s.	33.0	n.s.	n.s.
	Enneacanthus gloriosus	CP	49.3	37.0	n.s.	72.0
	Enneacanthus obesus	CP			72.0	66.7
	Etheostoma blennioides	Pied	43.4	29.7	n.s.	+
		H			n.s.	65.1
	Etheostoma fusiforme	CP			74.1	72.0
	Hypentenlium nigricans	Pied	43.4	37.6	n.s.	n.s.
	Lampetra aepyptera	CP	42.2	22.7	n.s.	n.s.
	Lepomis gulosus	CP			55.9	40.4
	Notropis buccatus	Pied	n.s.	60.5	n.s.	+
	Salvelinus fontinalis	Pied	13.2	12.1	n.s.	n.s.
		H			34.8	22.5
Most vulnerable w/o GCN status	*Aphredoderus sayanus*	CP	13.8	12.0	n.s.	n.s.
	Esox americanus	CP	41.7	16.1	n.s.	n.s.
	Nocomis micropogon	Pied	20.3	15.2	n.s.	n.s.
	Notropis hudsonius	Pied	8.5	7.3	n.s.	74.9
	Notropis rubellus	Pied	48.1	37.6	n.s.	+
		CP	n.s.	n.s.	n.s.	19.4

maximum estimate under the most-sensitive scenario occurs because the 2001 species pool is relatively smaller than in the least-sensitive scenario. Average loss of sensitive species richness in most- and least-sensitive assessments is 28% and 91%, respectively. Projected richness decline is spatially heterogeneous. For instance, fish biodiversity is most likely to decline in the lower mainstem and Cricket Creek, while upper mainstem reaches and some tributaries (particularly in the west) may retain many sensitive species.

4. Discussion

Distinct patterns of fish species responses to land use exist among contiguous regions in Maryland. For example, Piedmont ichthyofauna are acutely vulnerable to urbanization: nearly three-fourths of tested species respond negatively. In contrast, though a sizable proportion of Coastal Plain fishes are urbanization-sensitive, more fishes in this region exhibit a neutral response and some even show a positive response to ISC and urban cover. Regional disparities in sensitivity to land use also frequently occur at the species scale. For instance, the brook trout is the most agriculture intolerant species in the Highlands but exhibits no apparent sensitivity to agriculture in the Piedmont; however, it is sensitive to impervious surfaces across the state of Maryland (Stranko et al., 2008).

Studies exploring fish community responses to land use offer conflicting evidence for regionally distinct response patterns. Meador et al. (2005) compared stream fish community change along urban gradients in Boston and Birmingham area streams. Some metrics (such as loss of endemic or fluvial species) exhibited region-specific patterns, but the rate of decline in species richness was similar between regions though species composition was dissimilar. Conversely, using indices of biotic integrity developed separately for Maryland Coastal Plain and Piedmont fishes, Morgan and Cushman (2005) reported regional differences in biotic degradation along urban gradients that correspond with our findings. The disparity was partially attributed to a lack of congruency be-

tween indices. Our results (Fig. 5 and Table 3), however, suggest that substantial differences in fish sensitivity to urbanization (and other classes of land use) exist among regions, even within a species.

The observed differences may reflect the spatially and temporally complex nature of agricultural and urban land use in Maryland. Agriculture in the Coastal Plain and Piedmont grew rapidly in the early 18th century and dominated the landscape until widespread farmland abandonment started around 1930 (Jacobson and Coleman, 1986; Waisanen and Bliss, 2002; Jackson et al., 2005). As a result, fine sediment deposition in streams remained orders of magnitude above baseline levels for about 200 years and still exerts a legacy in the region's streams (Walter and Merritts, 2008). Agriculture was never as extensive in the Highlands region, though nearly all old-growth forests were lost to logging (Brown et al., 2005). Thus agriculture-sensitive fishes in the Coastal Plain and Piedmont may have been severely reduced in range or extirpated in the past and are not currently present in watersheds where forests have regenerated, as hypothesized in streams elsewhere (Harding et al., 1998; Harding, 2003; Wenger et al., 2008).

The mechanisms behind the different sensitivities to urban land use between Coastal Plain and Piedmont streams remain unclear. Streams between these geomorphically distinct regions may vary in rates of physicochemical change as watersheds urbanize. For example, flood flow magnitudes increase more in Coastal Plain urban streams relative to those in the Piedmont, yet Piedmont streams experience substantially higher absolute magnitude floods (Moglen et al., 2006). Alternatively, the inherent physicochemical and geomorphic differences between the two provinces may buffer biological assemblages from the effects of urbanization. For instance, low topographic relief and wetland cover in the Coastal Plain may mediate the hydrologic impact of urbanization in moderately urbanized watersheds. Unfortunately, comparative studies on the effects of urbanization between the two regions have not been conducted for the majority of physicochemical attributes. Our findings, along with related efforts using multimetric biotic indices (Morgan and Cushman, 2005; Goetz and Fiske, 2008) and those that compare physicochemical responses among regions,
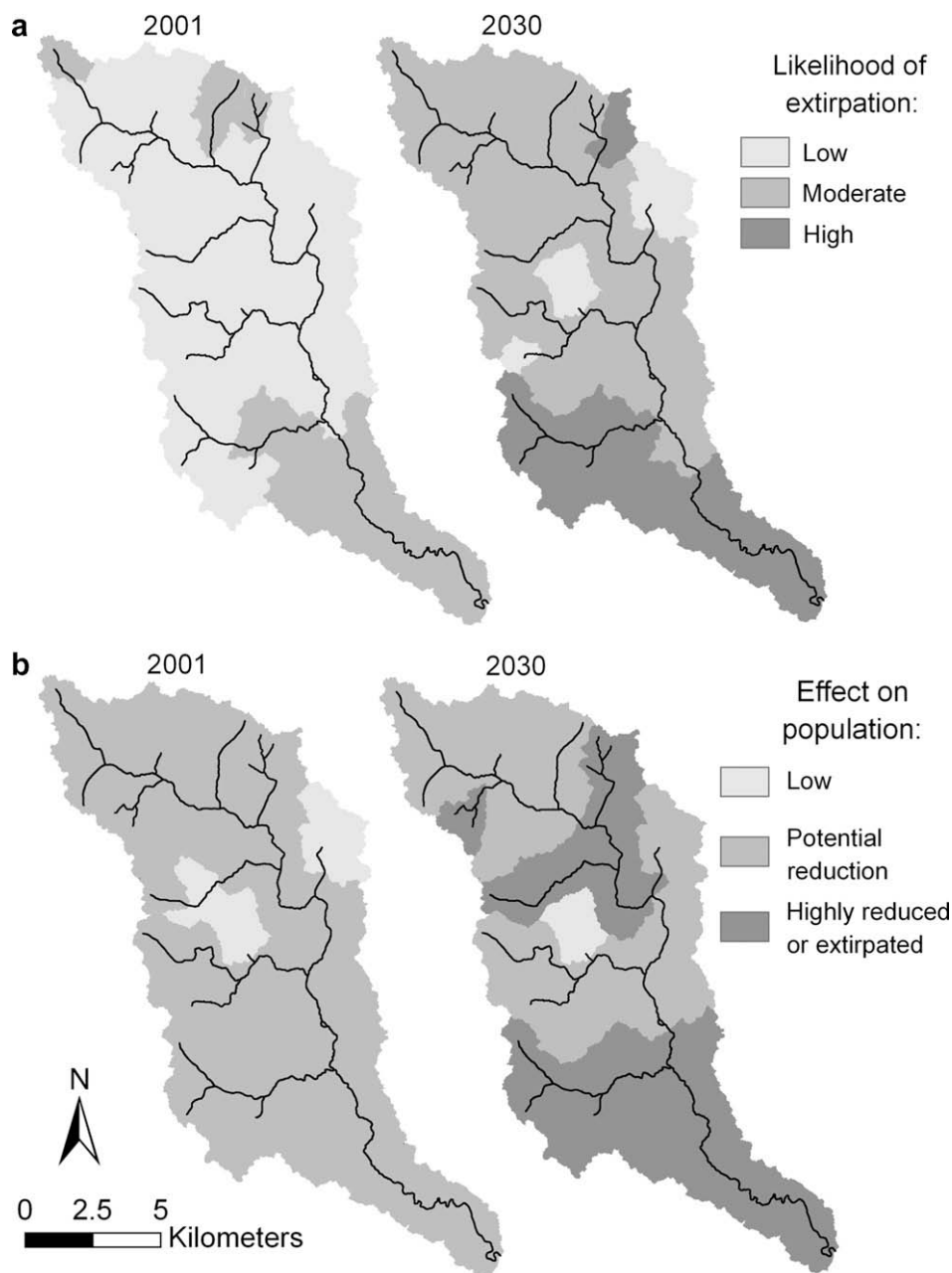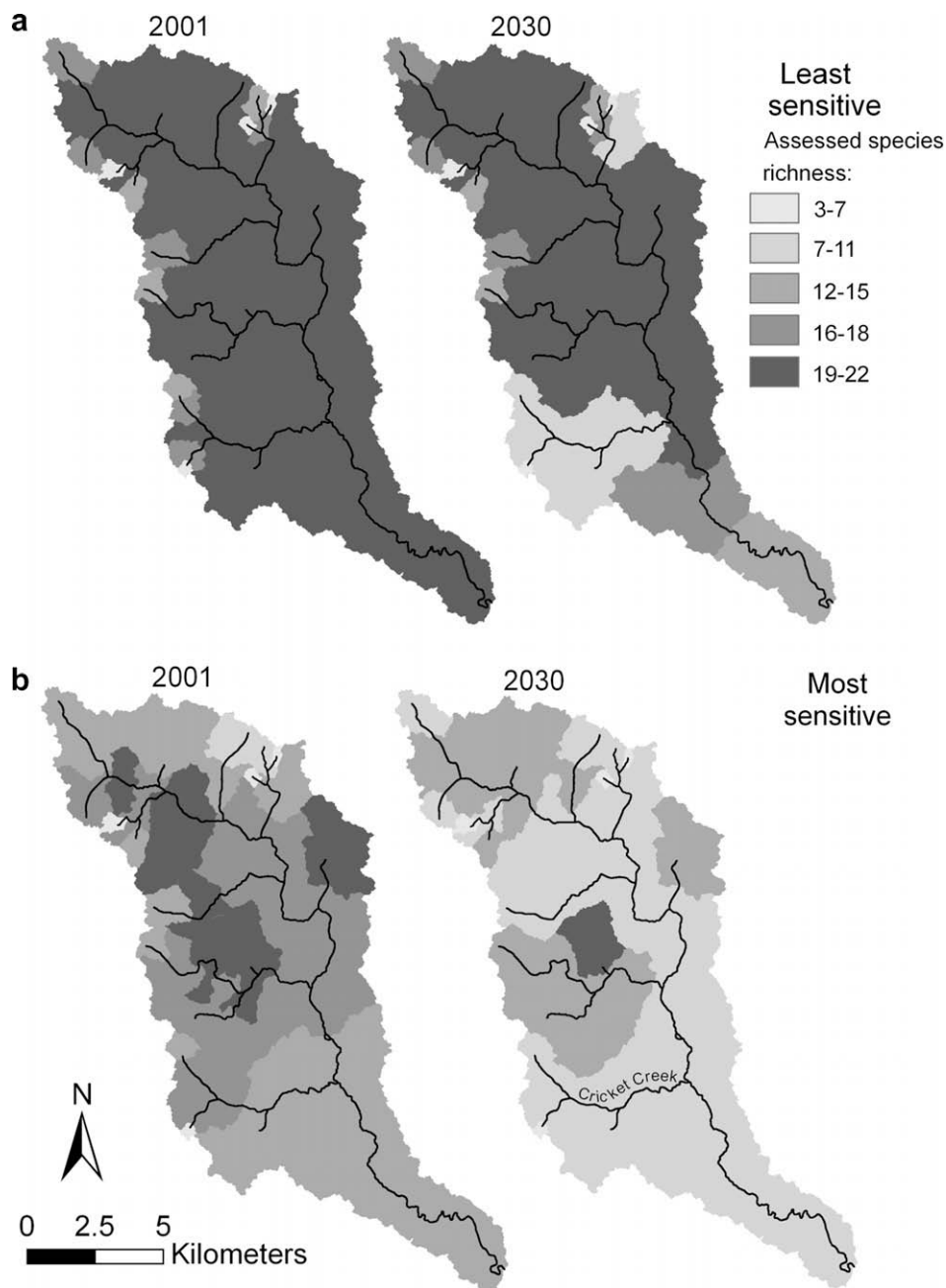
Fig. 6. Effect of urban development between 2001 and 2030 on fallfish (*Semotilus corporalis*) (a) distribution and (b) abundance in the Middle Patuxent River watershed. Extirpation and population reduction likelihood were based on presence/absence and abundance assessments, respectively. Extirpation or population reduction risk was considered low if a reach was urbanized less than the fallfish D_1 value, moderate if between the D_1 and T_{95}, and high if greater than the T_{95}.

suggest that interregional comparisons of ecological change in urban streams among these and other geoclimatic regions may prove insightful.

As demonstrated in the Middle Patuxent River watershed, our methodology may be used to forecast biodiversity loss with high spatial and biological resolution. Though freshwater fish community change has been forecasted previously at coarse spatial and biological scales (i.e., degree of biotic homogenization; Olden et al., 2006), the species-specific quantification of landscape sensitivity provided in the response catalog permits detailed prediction of change. The projected decline in species richness in the Middle Patuxent highlights the need for such efforts; despite the conservative (lacking commercial/industrial and transportation) estimates of urban growth used for forecasting, a substantial, but spatially heterogeneous, loss of biodiversity can be expected as a result of urban encroachment. Other means of biological degradation such as habitat fragmentation may also be deduced from such efforts. For instance, the high likelihood of extirpation in the lower mainstem reaches suggest that Middle Patuxent fallfish populations will likely become isolated from other Patuxent River populations by 2030. Though our results allow for such forecasting only within the ecoregions of the Mid-Atlantic United States, the methodology allows for creation of additional stressor response assessments in other regions and/or assemblages.

Furthermore, the response catalog can be used to assess the effectiveness of GCN status in highlighting those species most vulnerable to land use change. While all tested Maryland GCN fishes were found to be urbanization-sensitive, species such as the rosyside dace and silverjaw minnow are only moderately so (Table 4) and likely respond to a different suite of stressors. In contrast,

Fig. 7. Effect of urban development between 2001 and 2030 on species richness (those tested for landscape stressor sensitivity) in the Middle Patuxent River watershed based on presence/absence D_1 and T_{95} values for each species. Least sensitive estimates (a) assume a fish is present if the level of subwatershed urbanization was less than species T_{95} values. Most sensitive estimates (b) include fish species only when subwatershed urbanization fell below D_1 values for each species.

acutely sensitive fishes without GCN status, such as the river chub, fallfish and rosyface shiner, may experience widespread distributional decline with encroaching urbanization. Therefore a number of currently common species (those listed as most vulnerable without GCN status in Table 4) may require conservation efforts due to urban encroachment in the future. Considering that only 22% of freshwater flora and fauna (fishes, odonates, amphibians, crabs, and plants) globally have been assessed for conservation status (Darwall et al., 2008) and that our technique was capable of identifying highly sensitive species not classified as GCN, application of our methodology may prove valuable as a first step in identifying other species in need of conservation efforts.

Because of the inherent complexity and variation of ecosystem and taxa responses, ecological thresholds should never be treated

as static or absolute, but rather as guidelines. A general rule has been that stream fish communities rapidly degrade as watershed ISC exceeds 10–15% (Klein, 1979; Wang et al., 2000, 2001). Our results suggest that degradation and biodiversity loss may occur even at the lowest levels of land use conversion, which has been shown for communities elsewhere (Meador et al., 2005; Moore and Palmer, 2005). In other cases, community-level changes may not be expressed until a sufficient number of taxa are already severely affected and well beyond their species-specific tolerance thresholds (Wang et al., 1997; Roy et al., 2003; King et al., 2005). For Maryland's freshwater fishes, response thresholds appear to be region-dependent and probably also depend on site-specific characteristics such as the configuration of land use within watersheds, and/or potential interactive effects of multiple landscape

stressors (Sponseller et al., 2001; Booth, 2005; King et al., 2005). Such likely render thresholds difficult to detect if indeed present and allowing development up to an absolute value may endanger many populations. However, our results can be used to assess the relative vulnerabilities among species, regions and classes of land use, as well as providing guidance on strategies to prevent fish biodiversity loss.

Landscape-scale analyses may have limitations due to their large spatial extent. At large scales, land use classes may not be independent of one another, and more than one may simultaneously affect stream ecosystems (King et al., 2005). In our dataset, urban and agricultural uses were more negatively correlated with one another relative to natural cover in the Piedmont and Coastal Plain while urban watersheds were rare in the Highlands (Utz et al., 2009). Potential stressors may also interact (Woodward et al., 2002; Merovich and Petty, 2007) and make interpretations difficult even in large datasets. Our approach did not directly consider the full suite of land use induced physicochemical stressors and interactions that simultaneously affect lotic organisms, but that was not our objective. Rather than quantify the amount of variance explained by each stressor, we used land uses as surrogates for the many potential stressors to identify the minimum detectable effects of a land use as well as when an organism is expected to disappear. Thus our approach implicitly incorporates additive and/or interactive effects of multiple physicochemical stressors that exist in impacted streams. A final consideration is that our assessment point thresholds (the critical value, D_1 and T_{95}) need not be considered fixed points, because there is uncertainty associated with any analysis; each of these assessment points can be altered to accommodate one's comfort with uncertainty.

In summary, we identified highly variable patterns in fish distributions along land use gradients both within and among species and regions. Piedmont fishes appear to be considerably more vulnerable to urbanization relative to those of the Coastal Plain, while Highland fishes are most affected by agricultural land use. The regional trends may partly result from different land use history, but also suggest dissimilar rates of physicochemical change with land conversion among regions. Several species show increased sensitivity to land use when samples are abundance-weighted, implying that further reductions in distributions from existing urban and agricultural development may be imminent. Additionally, species both with and without current conservation priority status may experience substantial reductions in distributions if current trends in land use change continue. In light of the increasing human population growth and land conversion in the mid-Atlantic region, our results cataloging regional land use sensitivity of fishes should prove useful for establishing conservation priorities and planning future development to help minimize biodiversity loss.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.12.006.

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