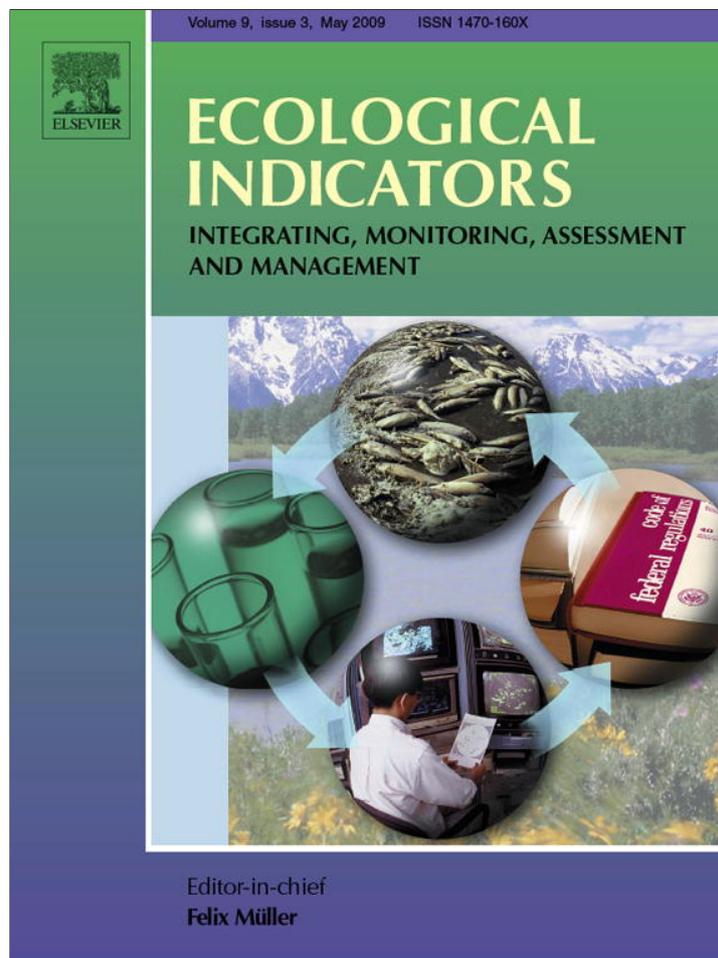


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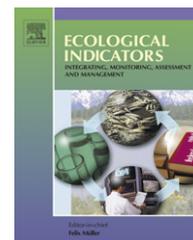


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# Identifying regional differences in threshold responses of aquatic invertebrates to land cover gradients

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## ARTICLE INFO

### Article history:

Received 11 April 2008

Received in revised form

7 August 2008

Accepted 12 August 2008

### Keywords:

Macroinvertebrates

Land use

Thresholds

Physiography

Streams

## ABSTRACT

Conversion of land from natural to urban or agricultural cover degrades stream ecosystems and results in loss of biodiversity. We compared cumulative frequency distributions to measure responses to land use gradients for aquatic invertebrate taxa to agricultural, urban, and impervious surface cover gradients across the state of Maryland, USA. The technique identifies the upper limit threshold above which taxa cease to occur as well as a lower limit of detection of effect for negatively affected taxa. Urban development and impervious surface cover negatively affected the distributions of 44–56% of the 180 taxa tested, depending on region. Across similar taxa, negative responses occurred at lower levels of urban land covers in the Piedmont compared to the Coastal Plain physiographic province, which suggests that Piedmont aquatic biodiversity may be more vulnerable to urbanization. Most taxa were capable of tolerating high levels of agricultural development, although a number of common taxa in the Coastal Plain and Highlands regions were found to be agriculture-sensitive. Some taxa traditionally used as indicators were tolerant of very high levels of human-altered land uses, suggesting that such taxa require examination prior to use as indicators of landscape stressors. Our analysis method appears to be sufficiently flexible and sensitive to be used for a variety of taxa and systems for stressor detection, ecosystem monitoring, and spatially explicit forecasts of taxa loss as watershed land cover changes.

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## 1. Introduction

Indicator taxa can be viewed as ecological threshold detectors. Each taxon may exhibit a unique response to a particular stressor (Gibbs, 1998; Fahrig, 2001), and we can use their different sensitivities to assess how far a system has departed from its base state. Such information can also be used to forecast biodiversity loss as conditions change along a disturbance gradient. In addition to the modern idea of ecological thresholds where a rapid nonlinear response occurs (e.g., Huggert, 2005; Groffman et al., 2006), at least two additional ecological

thresholds are important for monitoring and assessment: lower and upper response limits. The lower response limit represents the stressor value at which a negative effect initiates. We believe this to be important because a response can negatively affect a population long before it enters into the phase of rapid nonlinear change, particularly for those systems that respond linearly. Identifying the initiation of impact can be quite important to planning, management, and conservation. Similarly, the upper limit threshold is valuable as it signals the point along a disturbance gradient where an indicator essentially disappears from the landscape.

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doi:10.1016/j.ecolind.2008.08.008

Stream-dwelling benthic macroinvertebrates are commonly used for indicator purposes (see Rosenberg et al., 2008 for a thorough review) and represent a group of organisms that are increasingly under threat (Strayer, 2006). Benthic macroinvertebrates are ubiquitous in aquatic habitats (Vinson and Hawkins, 1998), widely diverse in both species richness (Allan and Castillo, 2007) and sensitivity to pollution (Barbour et al., 1999), and are easily collected in the field. Despite the widespread use of these organisms as indicators, however, the information regarding sensitivities of specific taxa to particular stressors is limited in scope. The most readily available macroinvertebrate sensitivity information are unit-less tolerance values meant to estimate relative sensitivity either to targeted stressors such as organic pollution or sedimentation (Hilsenhoff, 1987; Lenat, 1993; Blinn and Ruiters, 2006) or to multiple disparate stressors (Barbour et al., 1999; Yuan, 2004; Bessler et al., 2006). Such tolerance values are useful for constructing and applying many community-based systems for biomonitoring use. However, basic ecological questions concerning a taxon may be difficult to answer with tolerance values alone. For instance: at what level of a particular stressor do organisms disappear? Which organisms respond to a potential stressor negatively, positively, or not at all? Are there additional taxa that may be good candidates for detecting degradation?

Conversion of land cover from forest to human-altered forms is a major driver in the degradation of stream ecosystems (Abell, 2002; Strayer, 2006). Urban-associated cover induces substantial change in multiple physicochemical properties of streams (reviewed by Paul and Meyer, 2001 and Walsh et al., 2005) and local loss of biodiversity. Agricultural land use also affects stream form and function, often with consequential loss of biota (Cuffney et al., 2000; Jones et al., 2001; Sutherland et al., 2002; Donohue et al., 2006), though the effects from urbanization appear to be more severe (Allan, 2004; Poff et al., 2006).

Because streams differ substantially in form and function with variations in topography, geology, and climatic characteristics (Poff and Ward, 1989; Rosgen, 1996), the effects of land cover on aquatic organisms may differ among regions. Regional differences may also occur in responses of benthos (Stanfield and Kilgour, 2006), but not be detected with many methods (Cuffney et al., 2005), or assessment methods are adjusted so that indices respond similarly to stressors among regions (Astin, 2006; Southerland et al., 2007). A more thorough examination using individual taxa is warranted because response differences among regions could have large implications for ecological assessments and their applications.

Here, we present a method to assess taxa responses along a stressor gradient. Specifically, we analyze benthic macroinvertebrate taxa collected in different regions and their responses to land cover, but the method is sufficiently flexible to assess a wide range of organisms to numerous stressors. Our objectives are to (1) introduce a robust technique that describes the response distribution of a taxon along a stressor gradient; (2) catalogue macroinvertebrate responses as supplemental material to aid future assessment approaches and for baseline response information for conservation and management; and (3) assess the influence of spatial scale on ecological thresholds.

## 2. Methods

### 2.1. Study area

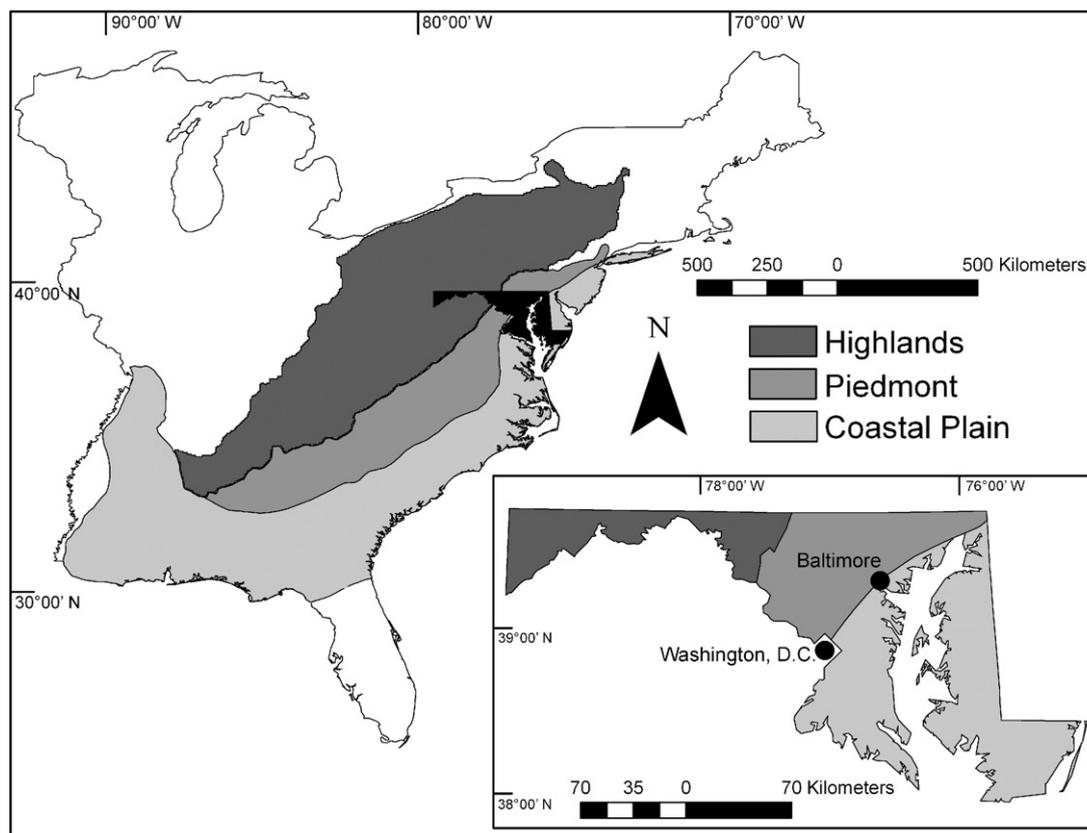
The state of Maryland encompasses about 32,000 km<sup>2</sup> of land in the mid-Atlantic United States. Nearly all watersheds in the state drain into the Chesapeake Bay, with a small area (~1100 km<sup>2</sup>) draining into the Ohio River watershed in far western Maryland, and some emptying directly into the Atlantic Ocean in southeastern Maryland (430 km<sup>2</sup>). Three broad regions fall within the state: the Coastal Plain, Eastern Piedmont (both true physiographic provinces) and the Highlands (a conglomerate of the Appalachian Plateau, Ridge and Valley, and Blue Ridge physiographic provinces, Fig. 1). The Coastal Plain comprises land below the fall line in eastern Maryland and consists of land adjacent to the Chesapeake Bay. The Piedmont province is located above the fall line and west to the Blue Ridge Mountains.

Each region possesses differing physical and ecological attributes. Cluster analyses of both fish and invertebrate data have shown that these regions are ecologically distinguishable (Stribling et al., 1998; Roth et al., 2000; Killian, 2004; Southerland et al., 2007). Some benthic invertebrate genera are only found either above or below the fall line (i.e., Coastal Plain versus Piedmont and Highlands) or exclusively in one region. Differences in ecological characteristics between regions may be partly explained by the physical attributes of each zone. Coastal Plain streams are characterized by low gradient, high sinuosity, and small substrate particle sizes such as silt and sand (King et al., 2005; Barker et al., 2006) while most streams in the Highlands feature the opposite characteristics (high gradient, low sinuosity, and larger substrate particle sizes such as cobble and boulders). Piedmont streams typically represent intermediate physical conditions between the Coastal Plain and Highlands provinces, although many feature steep gradients and a larger sediment particle size composition as in the Highlands.

### 2.2. Biological data

Macroinvertebrate data were extracted from rounds one (1995–1997) and two (2000–2004) of the Maryland Biological Stream Survey dataset (MBSS, Klauda et al., 1998). The MBSS uses a probability-based design for site selection in order to maximize representation of conditions statewide. The 75 m-reach sites are randomly selected for sampling and stratified within a subset of major river basins each year. As a result, each 75-m stream reach within the state has a non-zero probability of being selected for sampling over a 3-year interval.

Macroinvertebrates were collected at all MBSS sites during spring base flow (March and April), when the likelihood of collecting all representative taxa is greatest. Sites were limited to wadable streams; most were first- through third-Strahler order with a small number ( $n = 36$ ) exceeding third-order. Within each 75 m reach, 1.86 m<sup>2</sup> (20 ft<sup>2</sup>) of site-specific characteristic habitat were sampled using a D-net (Kazyak, 2001). Substrate upstream of the D-net was disturbed by kicking and moving by hand, and organic debris such as wood and leaves was rubbed by hand or a small brush. Large organic matter collected in the net was inspected for organisms and



**Fig. 1** – Map of the eastern United States and the state of Maryland illustrating the physiographic regions delineated for taxon-specific analysis.

then removed. Samples were preserved in a 70% ethanol solution. The collected benthic organisms were subsampled and identified to genus or lowest practical taxon, with the exception of Oligochaeta (to family level). All organisms were identified using stereoscopes except Chironomidae and Oligochaeta, which were slide-mounted and identified using a compound microscope. Further detail on taxonomic identification procedures and quality control may be found in [Boward and Friedman \(2000\)](#). Data for the current study were derived from 2303 invertebrate samples from 1953 stream reaches (350 sites were sampled more than once). Of these sites, 873 were collected in the Coastal Plain, 862 in the Piedmont, and 568 in the Highlands region.

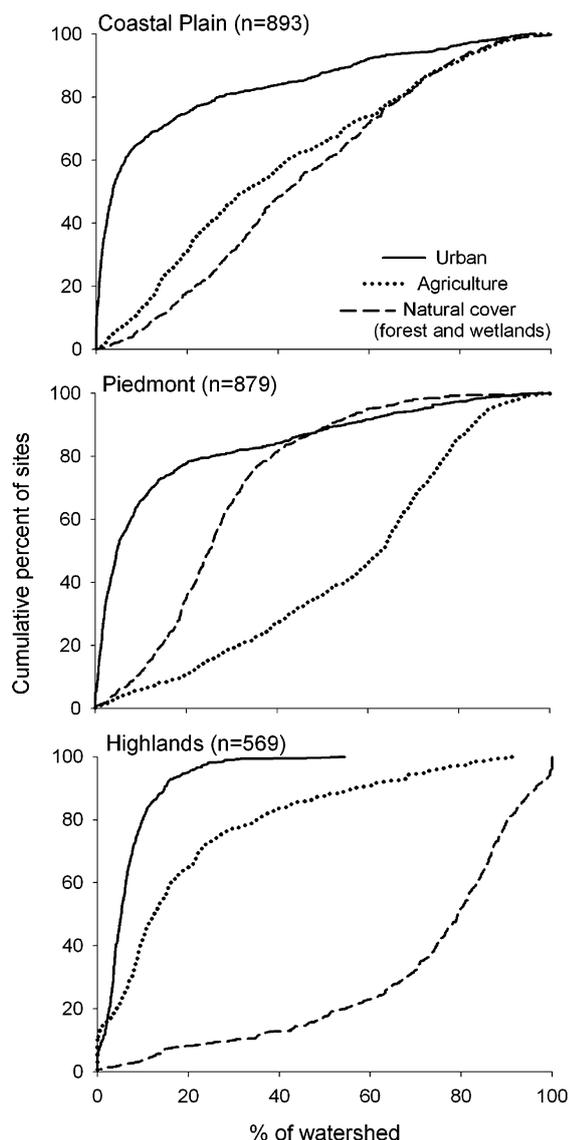
### 2.3. Land cover data

Catchment land cover was calculated for all MBSS sites. Watershed boundaries were determined using the 30 m resolution national digital elevation dataset (U.S. Geological Survey). The land cover layer was provided by the National Land Cover Database (NLCD), a 30-m resolution raster data set taken via thematic imaging during 2001 ([USEPA, 2008](#)). Land covers within each watershed were extracted from the NLCD in a GIS.

To simplify analyses of catchment land cover, land cover designation was limited to Class-I categories (see [USEPA, 2008](#) for a full description of all classes described below).

Urban land represented low, medium, and high intensity developed land along with open space urban development. Agricultural land cover represented the sum of the pasture/hay and cultivated 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 NLCD dataset also includes an estimate of percent impervious surface cover (ISC-pavement, rooftops, and other surfaces that prohibit water permeation) from 0 to 100 on a 30 m<sup>2</sup> pixel scale; the total percent of impervious surface covering each watershed was calculated from this layer. Though urban cover is highly correlated with ISC (Pearson correlation coefficient = 0.94,  $p < 0.0001$  in sampled sites), the latter is considered a more parsimonious land cover class to predict the impact of urban development on stream ecosystems ([Arnold and Gibbons, 1996](#)). We therefore assessed sensitivity to both ISC and urbanization. The percentages of cover for each category were those used in testing for catchment land cover effects on invertebrate distributions.

The distribution of land cover classes in sampled streams among the three regions varied in some instances but was similar in others. Largely due to growth of the Baltimore and Washington, DC metropolitan areas ([Fig. 1](#)), urban land coverage is concentrated in the Coastal Plain and Piedmont regions of Maryland. Sites in these two provinces sampled by the MBSS program were very similarly distributed along an



**Fig. 2 – Cumulative distribution of watershed land use classes for sites sampled by the MBSS program delineated by region. The number of sites sampled per region is provided in the upper left corner.**

urbanization gradient (Fig. 2). Urban watersheds were rarely sampled in the Highlands due to an absence of metropolitan centers in this region (Fig. 2). Agricultural cover was more uniformly distributed among regions, though Piedmont watersheds tended to possess more agricultural cover, and many Highlands watersheds were composed of natural cover (forests and wetlands; Fig. 2). Table 1 provides Pearson correlation coefficients of sample site land use classes by region.

Although climate varies moderately throughout Maryland, agriculture is largely homogeneous among regions. In all three regions the dominant crops are soybeans and corn (MDA, 2003). Agricultural productivity varies more among counties than among the three regions delineated for the current study (MDA, 2003).

**Table 1 – Pearson correlation coefficients of watershed land use classes among regions**

	Coastal Plain		Piedmont		Highlands	
	Urban	Ag	Urban	Ag	Urban	Ag
Ag	-0.542		-0.746		0.282	
Natural	-0.374	-0.551	-0.274	-0.435	-0.535	-0.959

Natural cover includes forests and wetlands; 'Ag' refers to agricultural cover. *p*-values for all correlations are <0.0001.

## 2.4. Data analysis

We compared the cumulative frequency distributions (CFD) of land cover between those sites where a taxon would be expected to occur and the actual group of sites in which a taxon did occur, allowing both rare and common taxa to be compared independent of the collection frequency. The process is described below and in Fig. 3. All genera tested for an effect from land cover required a minimum of twenty-five collection occurrences before being tested; genera collected <25 times within a region were considered too rare for analysis. Urban and impervious cover relationships were calculated for taxa in the Coastal Plain and Piedmont physiographic provinces, but not in the Highlands region, where the total amount and distribution of urban land was considered too sparse for analysis. Responses to agricultural land cover were examined for each region.

### 2.4.1. Acidic streams

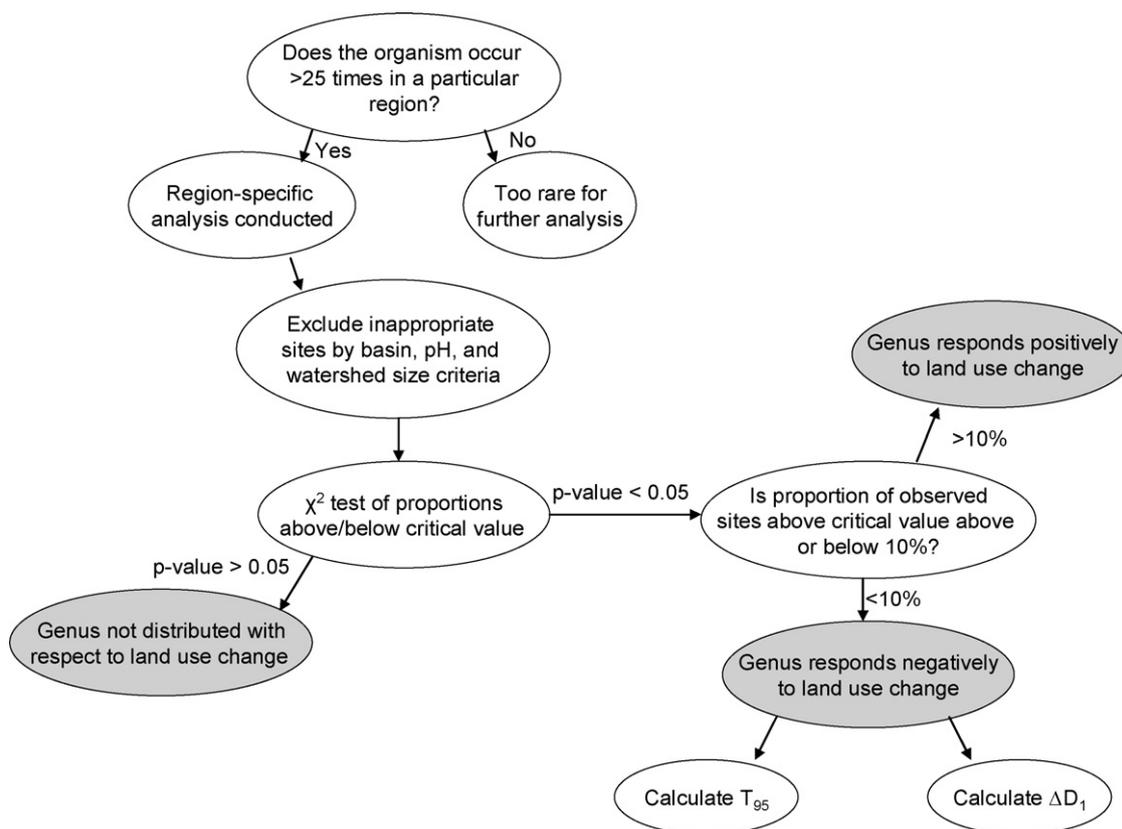
The mid-Atlantic region of the United States receives the most severe acidic precipitation in the United States, and streams with naturally poor buffering capacity are affected as result (Herlihy et al., 1993). Additionally, acidic mine drainage from coal mines in the Highlands region of Maryland may dramatically alter the chemical and biological properties of streams (Simmons et al., 2005; Merovich and Petty, 2007). A water sample taken during macroinvertebrate collections and chemically analyzed for pH in a laboratory was used to filter out sites that were too acidic for each taxon. For each taxon, a quantile analysis of pH levels across sites where the organism was collected was performed, and all sites that fell below the 5% quantile of pH values were omitted from further analysis in both observed and expected sets of streams.

### 2.4.2. Major basin and stream size

We used a hierarchical filtering process to exclude watersheds where a taxon did not likely occur historically. To account for biogeographic effects, we also used a biogeographic filter to exclude watersheds where a species did not likely occur historically. Only watersheds where the species was collected at the Maryland 6-digit hydrologic unit code (17 major basins within the state, Heimbuch et al., 1999) scale were included for analysis. Sites below the minimum and above the maximum basin area size where each taxon was collected by the MBSS program were excluded as well.

### 2.4.3. Distribution with land cover change

Once pH-, biogeographic-, and size-inappropriate sites were excluded, the actual and expected occurrences of each taxon



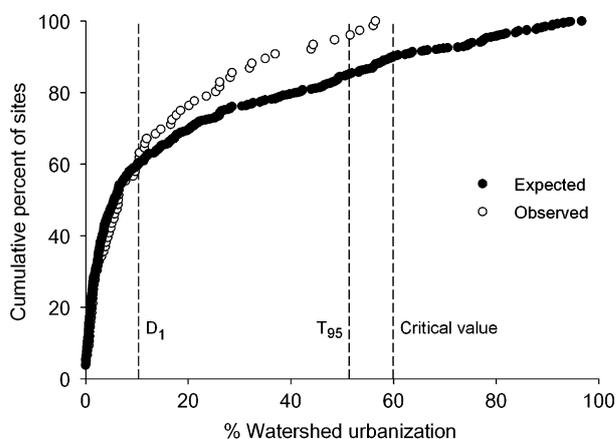
**Fig. 3 – Flow chart representing the process conducted for determining taxon-specific response with respect to land cover change. Ovals with grey fill represent endpoints for the three potential relationships with land covers.**

were compared in relation to land cover. For each respective region, the cumulative frequency distribution (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 taxon 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 taxon was collected, hereby termed the ‘observed’ group. A chi-square goodness of fit test on the frequencies 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). If the chi-square test showed no significant difference ( $\alpha \geq 0.05$ ) between proportions, the land cover was assumed to have no relationship to the occurrence of the taxon. However, if the chi-square test resulted in a significant difference between frequencies, analysis of the CFD curves continued.

If a taxon’s distribution was found to be significantly affected by land cover, two scenarios were possible. First, the taxon 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 number of observed sites above the critical value was significantly higher than 10%. Alternatively, the taxon may be negatively affected by the particular land cover gradient.

Here the number of occurrences above the critical value was significantly lower than 10% (in many cases 0%).

When a significant negative response occurred, two values were calculated to describe the severity of response. The  $T_{95}$  (i.e., 95% threshold) is the land cover value at which 95% of the



**Fig. 4 – The effect of watershed urbanization on the distribution of *Nigronia* (Megaloptera: Corydalidae) in the Coastal Plain of Maryland. Each dot represents a sample. The three values calculated to determine the severity of response are shown as dashed lines.**

occurrences fall below and represents the maximum percentage for a specific land cover in a catchment that could conceivably retain the taxon. The second value,  $D_1$ , estimates the point of divergence between the two CFD curves and represents the minimum detectable land use affect. Each cumulative frequency quantile of land cover in the observed site group was matched and compared to the closest possible quantile in the expected stream group. 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 and was assumed to be the point where the land cover negatively affects the taxon. Fig. 4 presents a graphical example of the critical value,  $T_{95}$ , and  $D_1$ .

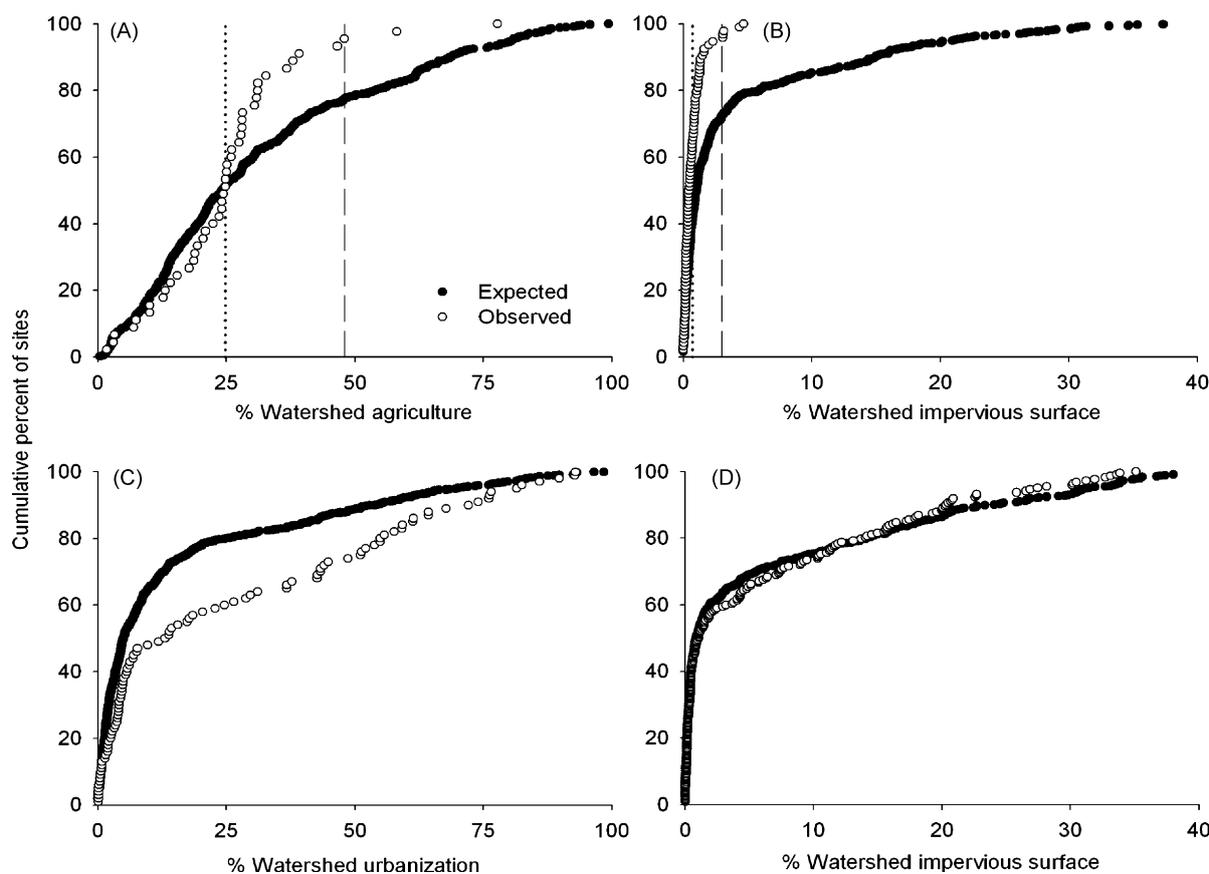
### 3. Results

Among the three regions, 180 benthic macroinvertebrate taxa were analyzed for distributions relative to land cover categories (see Appendix A for all taxon-specific results and Table 1 for a summary of responses by land cover and region). The number of analyses conducted within each region differed, with 126 genera and 3 families analyzed in the Coastal Plain, 102 genera

and 3 families analyzed in the Piedmont, and 77 genera and 3 families analyzed in the Highlands. Due to low levels of urbanization and ISC in the Highlands, only responses to agriculture were assessed in this region. All three hypothetical responses (no effect, positive distribution, negative distribution) with respect to land cover were observed (see Fig. 5 for examples of each). The responses of benthic organisms varied broadly by type of land cover and physiographic region.

#### 3.1. Urbanization

In the Piedmont the majority of taxa responded negatively to urban land cover as well as nearly half of tested taxa in the Coastal Plain (Table 2). The magnitude of the response varied by taxonomic group. For instance, nearly all Plecoptera responded negatively to catchment urbanization (89% in Coastal Plain and 100% in Piedmont), while less than a third of Chironomidae (from all tested subfamilies) were negatively affected in either physiographic province (Fig. 6). Some notable differences in group sensitivity to urban land use between physiographic provinces occurred. All Ephemeroptera were negatively affected by urban land cover in the Piedmont, yet in the Coastal Plain one-third (from various



**Fig. 5** – Examples of taxon-specific distributions in relation to land cover change. Relationships shown include (A) an example of a delayed negative response to agriculture (Plecoptera: Leuctridae: *Leuctra*) in the Coastal Plain, (B) a rapid negative response to impervious surfaces (Ephemeroptera: Heptageniidae: *Epeorus*) in the Piedmont, (C) a positive response to urbanization (Malacostraca: Crangonyctidae: *Crangonyx*) in the Piedmont, and (D) no relationship to impervious surfaces (Trichoptera: Hydropsychidae: *Cheumatopsyche*) in the Coastal Plain. When the relation to land cover is negative, the  $D_1$  and  $T_{95}$  values are shown as dotted and long dashed lines, respectively.

**Table 2 – Summary of the taxa examined for a distributional relationship with land use change by region and cover type**

Land cover	Physiographic province	n taxa	Number (percent) of taxa with negative response	Number (percent) of taxa with positive response	Number (percent) of taxa with neutral response
Urbanization	Coastal Plain	129	57 (44.2)	13 (10.1)	59 (45.7)
	Piedmont	105	59 (56.2)	15 (14.3)	31 (29.5)
Impervious surface	Coastal Plain	129	59 (45.7)	12 (9.3)	58 (45.0)
	Piedmont	105	59 (56.2)	14 (13.3)	32 (30.5)
Agriculture	Coastal Plain	129	12 (9.3)	27 (20.9)	90 (69.8)
	Piedmont	105	1 (0.9)	13 (12.4)	91 (86.7)
	Highlands	80	24 (30.0)	11 (13.8)	45 (56.2)

families) were tolerant of urban cover. Similarly, all but one Coleopteran (*Stenelmis*) in the Piedmont was negatively affected by urban cover contrasted with only half of those tested in the Coastal Plain (*Agabus* and *Hydroporus* in the family Dytiscidae, commonly collected only in the Coastal Plain, were urbanization tolerant).

Regional differences were observed in specific values as well. Both  $T_{95}$  and  $D_1$  values were typically greater for organisms inhabiting the Coastal Plain than those in the Piedmont. Many genera common to both the Coastal Plain and Piedmont also responded differently between provinces, with consistently higher  $T_{95}$  and  $D_1$  values in the Coastal Plain (see examples of Plecoptera in Table 3). The majority of taxa negatively impacted by urbanization disappeared between 10 and 45% urbanization in the Piedmont, whereas in the Coastal Plain the majority disappeared at 15–60% urbanization (Fig. 7). In both provinces, however, no taxon had a  $T_{95}$  value greater than 60%. Thus once ~60% urbanization in a watershed is realized, apparently all taxa remaining in sites respond either neutrally or positively with respect to urbanization.

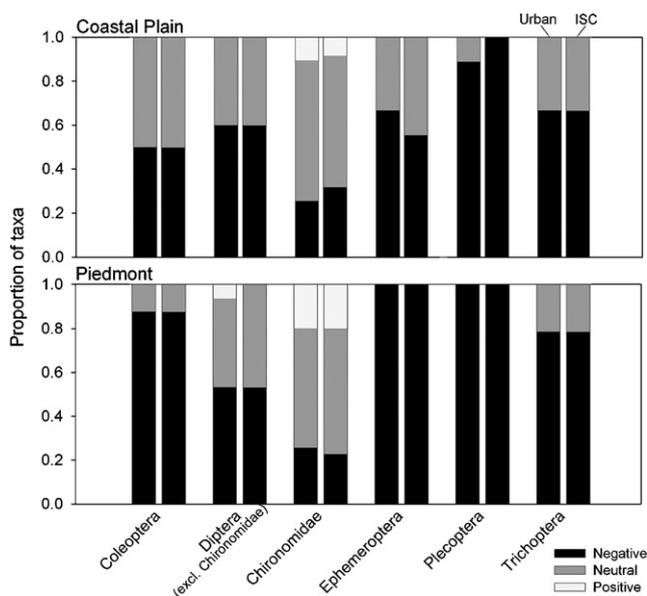
Some genera were more frequently collected in urbanized watersheds. Several Oligochaeta, Diptera, Odonata, and Gastropoda were found to be positively associated with urbanized land cover (Appendix A, Fig. 6). Proportionally, Oligochaeta was the largest group that responded positively to urban development (three-fifths and two-thirds of tested genera or families in the Coastal Plain and Piedmont, respectively).

**3.2. Impervious surface cover**

Organisms responded to impervious surface cover at much lower levels within catchments compared to urban cover. However, differences in  $T_{95}$  and  $D_1$  values between physiographic provinces existed and were consistent with patterns observed for urban cover (Table 3, Appendix A). Taxa sensitive to impervious cover were generally lost between 2.5 and 15% cover in the Piedmont while sensitive taxa in the Coastal Plain possessed  $T_{95}$  values between 4 and 23% cover (Fig. 7). The proportions of major groups that were affected by ISC were similar to those observed for the urban cover gradient (Fig. 8), and the total number of taxa sensitive to impervious cover was similar to the number of urban-sensitive taxa (Table 2); in almost all cases if a taxon was negatively affected by urban development it was negatively affected by ISC (Appendix A).

**3.3. Agriculture**

Relatively few organisms were negatively impacted by agriculture (Appendix A); a strong majority of genera in all three regions showed no distributional response (Table 2). In the Piedmont and Coastal Plain, the number of genera that were positively associated with agricultural development exceeded the number negatively impacted. The Highlands region possessed the greatest number of taxa that were intolerant of agriculture, with greater than one-fourth of those tested exhibiting negative associations. Ephemeropterans in the families Heptageniidae and Ephemerellidae appear to be especially sensitive to agriculture in the Highlands region. All organisms that were negatively associated with increasing agricultural development were insects, with genera in the order Plecoptera representing multiple families most consistently adversely affected (5, 1, and 7 agriculture-sensitive taxa in the Coastal Plain, Piedmont, and Highlands, respectively). Similar numbers of Ephemeropterans (8) and Trichopterans (5) from various representative families in the Highlands were negatively affected (Fig. 8).



**Fig. 6 – Summarized responses to urban land covers of some insect groups in the Piedmont and the Coastal Plain. For each taxonomic group, bars on the left represent the response to urbanization, bars on the right sum the response to impervious cover.**

**Table 3 – Examples of urban and impervious surface (ISC)  $T_{95}$  and  $D_1$  values for Plecoptera genera common to both the Piedmont and Coastal Plain**

Family	Genus	Coastal Plain					Piedmont				
		Urban			ISA		Urban			ISA	
		n	$D_1$	$T_{95}$	$D_1$	$T_{95}$	n	$D_1$	$T_{95}$	$D_1$	$T_{95}$
Capniidae	<i>Allocaupnia</i>	33	3.5	16.9	0.5	5.1	51	5.2	14.3	1.3	3.8
Leuctridae	<i>Leuctra</i>	55	3.6	47.2	1.5	10.6	45	1.0	31.7	1.2	12.3
Nemouridae	<i>Amphinemura</i>	150	6.5	47.0	1.2	15.0	310	1.7	26.7	1.2	5.9
	<i>Prostoia</i>	113	6.1	45.0	1.5	15.9	218	2.7	20.3	1.5	4.7
Perlidae	<i>Eccopteryx</i>	61	3.6	26.1	0.6	5.7	42	7.2	40.0	4.6	9.9
Perlodidae	<i>Isoperla</i>	135	4.1	45.7	0.7	14.6	41	1.0	10.1	0.4	1.9
Taeniopterygidae	<i>Strophopteryx</i>	39	13.4	34.5	2.9	9.7	90	2.7	13.4	1.1	3.5

The number of times each genus was collected per province (n) is provided. A full listing can be found in Appendix A.

Taxa that responded negatively to agricultural development were capable of tolerating higher levels of agriculture relative to those seen with urbanization; the lowest  $T_{95}$  score for agricultural development was ~21% (Plecoptera: Taeniopterygidae: *Oemopteryx* in the Highlands) compared to 4.6% for urbanization (*Clinotanypus* in the Coastal Plain) and 1.6% for ISC (*Drunella* in the Piedmont). In contrast to the findings along urban gradients, many taxa present in agriculture-dominated watersheds included those in groups usually considered stressor sensitive, such as Plecoptera, Ephemeroptera, and Trichoptera (Appendix A), especially in the Piedmont province. For instance, both tested Plecopterans in the family Capniidae (*Allocaupnia* and *Paracaupnia*) were quite sensitive to urbanization and ISC (both possessed  $T_{95}$  ISC values of 3.8) but were significantly positively associated with highly agricultural watersheds.

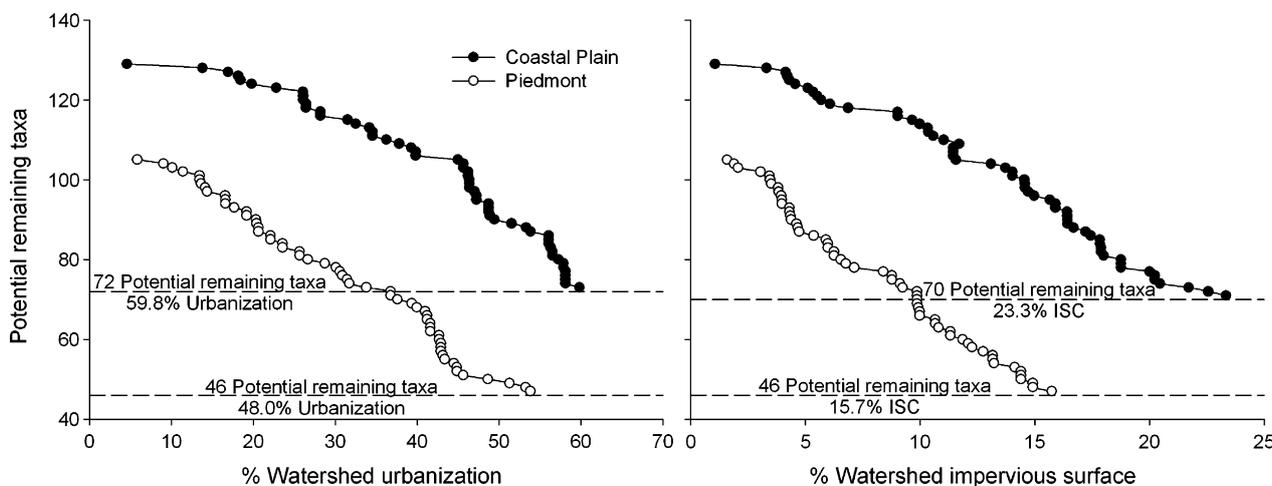
### 3.4. $T_{95}$ and taxa rarity

To assess the influence of rarity of a taxon on the  $T_{95}$  values (i.e., more rare taxa possessing lower  $T_{95}$  values), we regressed

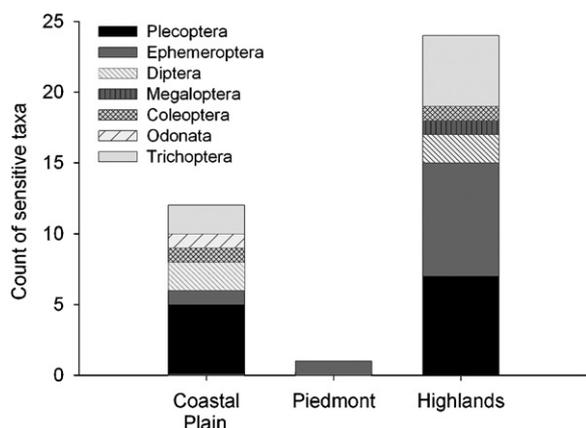
$T_{95}$  values of sensitive organisms against the collection frequency. Separate regressions were run for urban and ISC  $T_{95}$  values in the Piedmont and Coastal Plain, and agriculture  $T_{95}$  values in the Highlands. None of the relationships were significant ( $n = 24-59$ ,  $F = 0.00-2.17$ ,  $p = 0.147-0.966$ ).

## 4. Discussion

Our analytical approach identified a wide array of benthic macroinvertebrate responses, ranging from complete tolerance to acute sensitivity, along human-altered land use gradients. The diversity of responses implies that our methodology is capable of identifying potential indicator taxa as well as differentiating sensitivity within indicators. The approach is straightforward and does not require permutation tests or computer intensive operations to arrive at relative sensitivity values among taxa. The method also is more robust to variations in sample size than techniques such as the Kolmogorov–Smirnov test. While the analyses were targeted to benthic macroinvertebrates, the method can be generalized



**Fig. 7 – The number of taxa remaining given the distribution of urbanization and impervious surface cover as represented by  $T_{95}$  values by physiographic province. Each point represents a  $T_{95}$  value for a taxon collected  $\geq 25$  times; dashed lines denote where all urbanization- or impervious surface-sensitive species have been accounted for. The number of tolerant genera remaining after all sensitive genera have been extirpated is also provided.**



**Fig. 8 – Summary (by physiographic region) of taxa that were negatively distributed with respect to watershed agricultural cover.**

to other taxa or even entire assemblages, and its use is not restricted to aquatic environments. The results are easily interpreted with decision points that can be adjusted up or down to account for uncertainty;  $T_{95}$  values estimate the degree of watershed development where the taxon is no longer expected to be collected, and  $D_1$  values indicate the minimum detectable amount of development that may negatively affect a taxon. The difference between the two descriptor values also conveys meaning: a small range between the  $D_1$  and the  $T_{95}$  indicates a rapid loss of particularly sensitive taxa while a large difference suggests that the taxon is capable of survival in altered watersheds, but will eventually disappear in highly altered watersheds.

The diversity and number of sensitive taxa in Maryland streams point to the presence of ecological thresholds. Our analyses suggest that threshold detection is scale dependent on a number of levels. Across the entire stressor gradient, clear thresholds exist in responses of individual taxa to urbanization, impervious surfaces, and agriculture (e.g., Fig. 5b). However, thresholds may not be detected if only a portion of a stressor gradient is analyzed, particularly if the portion is at the low-disturbance end. Although threshold responses were evident for individual taxa, scaling up by aggregating across taxa showed linear declines in richness (Fig. 7). Groffman et al. (2006) concluded that little consistent evidence for thresholds exists and that aquatic community degradation with land use may be linear, whereas others report threshold responses at 10–15% watershed impervious surface (Paul and Meyer, 2001). Our findings support both contentions depending on the scale of analysis.

Differences in tolerance thresholds also appear to be influenced by spatial scale. We found substantial response differences to urbanization measures between the Piedmont and Coastal Plain for individual taxa and richness declines when aggregating across taxa. Although taxa loss was nearly linear across urban gradients in both regions (Fig. 7), losses occurred at much lower stressor levels along the gradients in the Piedmont. Increasing the spatial extent of analysis would have obscured differences between the regions as well as altered threshold responses of indicators. Similar differences

between these two regions were reported for analyses using a multimetric approach for fishes by Morgan and Cushman (2005), who partially attributed the result to ineffectively constructed indices of biotic integrity. Later work adjusted the metrics to obtain a more homogeneous response to environmental stress between regions (Southerland et al., 2007). Our results suggest the differences are real, and the effects of urbanization may be less severe on stream biota in the Coastal Plain, but we have not identified specific mechanisms for the responses.

In contrast to urbanization, few taxa distributions were negatively affected by increasing agricultural land cover. Effects were most evident in the Highlands where agriculture has never been widespread, whereas only one taxon in the Piedmont responded negatively. The relative lack of response in the Piedmont and Coastal Plain may be due the centuries-long legacy of agriculture and settlement in these areas (Jacobson and Coleman, 1986; Waisanen and Bliss, 2002; Jackson et al., 2005) that may have eliminated the more agriculture-sensitive taxa decades ago. Such artifacts of land use past (*sensu* Harding et al., 1998; Harding, 2003) complicate inferences drawn from current conditions. Additionally, organisms with moderate sensitivity to stressors may have adapted to degraded environmental conditions (Lopes et al., 2005). The relationship is further complicated because agriculture-dominated watersheds in the Maryland Piedmont may possess high invertebrate diversity in streams (Moore and Palmer, 2005), and agriculture generally appears to be less damaging to aquatic taxa than urbanization (Wang et al., 2000; Poff et al., 2006).

The broad classes of urban and agriculture are surrogates for the specific mechanisms that cause the loss of sensitive taxa from streams and thus form convenient yet relevant measures for analysis. Urbanization and associated impervious surfaces dramatically alter hydrologic regimes (Booth and Jackson, 1997; Schuster et al., 2005; Konrad and Booth, 2005), increase organic and inorganic pollutant concentrations (Lenat and Crawford, 1994; Rogers et al., 2002; Chadwick et al., 2006; Morgan et al., 2007), promote prolonged geomorphologic adjustment (Wolman, 1967; Pizzuto et al., 2000; Colosimo and Wilcock, 2007), and cause shifts in temperature regimes (Klein, 1979; Arnold and Gibbons, 1996; Leblanc et al., 1997). Agriculture may cause relatively less severe change, but may cause increased sedimentation (Cuffney et al., 2000; Donohue et al., 2006), elevated nutrient levels (Jones et al., 2001), shifts in water temperature dynamics (Werhly et al., 2006), and altered hydrologic regimes (Poff et al., 1997; Poff et al., 2006). While specific stressors are important to benthic responses, analysis of individual stressors over large spatial scales will likely increase the noise, whereas surrogate measures such as urbanization can integrate the suite of correlated stressors.

A valuable application from our analysis is the catalog of macroinvertebrate responses to land use change (Appendix A). While an exhaustive comparison of existing indicators with thresholds determined by our technique is not the purpose of this paper, the reported sensitivities in the appendix can be used to assess if a given taxon or composite metric will be sufficiently sensitive to land use. Further, our response catalog can be used to forecast biodiversity losses for specific watersheds or to

examine if some taxa may eventually become regionally threatened due to land conversion in the increasingly urbanized mid-Atlantic region (Brown et al., 2005; Grimm et al., 2008). Though our results should not be considered replacements for rigorous demographic assessments, the catalogue may form a useful starting point for management and conservation of a group of organisms often overlooked by mainstream conservation efforts (Master et al., 2000; Strayer, 2006). Additionally, the catalog may be used to identify exceptional streams: if an urbanized stream continues to contain multiple sensitive taxa, the stream may be especially resilient to landscape change and would merit special attention.

Our analytical approach did not address certain factors that may complicate how land use change affects stream ecosystems. We tested land use classes independently though multiple landscape stressors may simultaneously impact streams. While our analysis did not account for interactions between land uses, we believe the effect was not substantial given that agriculture and urban land uses in the Piedmont and Coastal Plain were negatively correlated with one another, and only a weak positive correlation existed in the Highlands (Table 1). Another source of uncertainty comes from the 9-year observation period for the invertebrate data (1995–2004) applied to the land use data for only 2001. The land use present during a given collection may not be exactly congruous to what was assessed for what is likely a small number of watersheds. We were limited to the availability of the 2001 data and must assume that it approximates the actual land uses during the year of collection. In addition, local attributes such as instream habitat and riparian condition undoubtedly influence taxa occurrences (Sponseller et al., 2001; Sandin, 2003; Barker et al., 2006) and will introduce some noise into the results. Such uncertainties should make the listed sensitivities more conservative (more difficult to detect an effect) because some sites with low amounts of urban or agriculture will not have taxa due to unfavorable local conditions.

In summary, our approach was able to identify ecological thresholds and order taxa sensitivity across a range of land uses. While specifically targeted to benthic macroinvertebrates here, the technique may be applied to any organism distributed along a stressor gradient provided that a large enough sample size and range of stressor values are available. We found substantial differences in sensitivity of benthos to landscape change between streams located in adjacent regions, highlighting the importance of choosing the appropriate scale when assessing ecological responses to land use change. The findings also point to the possibility that benthic macroinvertebrates are generally more sensitive to urban land uses in Piedmont compared to Coastal Plain streams. Given the ongoing human population growth and land conversion throughout the mid-Atlantic region, our results cataloging taxa sensitivities should prove useful for future development of assessment metrics and land use planning to help minimize biodiversity loss and ecosystem degradation.

## Acknowledgements

We thank the Maryland Biological Stream Survey for their cooperation and for sharing their dataset with us. Funding was

provided by EPA STAR award RD-83244401 to RH and by the National Park Service through cooperative agreement T-3097-03-103 to RH. Comments provided by Margaret Palmer, Todd Lookingbill, and two anonymous referees improved the manuscript. This is Appalachian Laboratory scientific series contribution number 4218.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2008.08.008.

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