How novel is too novel? Stream community thresholds at exceptionally low levels of catchment urbanization

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Abstract. Novel physical and chemical conditions of many modern ecosystems increasingly diverge from the environments known to have existed at any time in the history of Earth. The loss of natural land to urbanization is one of the most prevalent drivers of novel environments in freshwaters. However, current understanding of aquatic community response to urbanization is based heavily upon aggregate indicators of community structure and linear or wedge-shaped community response models that challenge ecological community theory. We applied a new analytical method, threshold indicator taxa analysis (TITAN), to a stream biomonitoring data set from Maryland to explicitly evaluate linear community response models to urbanization that implicitly assume individual taxa decline or increase at incrementally different levels of urbanization. We used TITAN (1) to identify the location and magnitude of greatest change in the frequency and abundance of individual taxa and (2) to assess synchrony in the location of change points as evidence for stream community thresholds in response to percent impervious cover in catchments. We documented clear and synchronous threshold declines of 110 of 238 macroinvertebrate taxa in response to low levels of impervious cover. Approximately 80% of the declining taxa did so between ~0.5% and 2% impervious cover, whereas the last 20% declined sporadically from ~2% to 25% impervious cover. Synchrony of individual responses resulted in distinct community-level thresholds ranging from ≤0.68% (mountains), 1.28% (piedmont), and 0.96% (coastal plain) impervious cover. Upper limits (95% confidence intervals) of community thresholds were <2% cover in all regions. Within distinct physiographic classes, higher-gradient, smaller catchments required less impervious cover than lower gradient, larger catchments to elicit community thresholds. Relatively few taxa showed positive responses to increasing impervious cover, and those that did gradually increased in frequency and abundance, approximating a linear cumulative distribution. The sharp, synchronous declines of numerous taxa established a consistent threshold response at exceptionally low levels of catchment urbanization, and uncertainty regarding the estimation of impervious cover from satellite data was mitigated by several corroborating lines of evidence. We suggest that threshold responses of communities to urban and other novel environmental gradients may be more prevalent than currently recognized.

Key words: aquatic biodiversity conservation; bioassessment; ecological thresholds; indicator species; no-analog ecosystems; novel environmental gradients; species sensitivity distribution; watershed classification.

Introduction

The physical and chemical conditions of many modern ecosystems increasingly diverge from environments known to have existed at any time in the history of Earth (Fox 2007). These "no-analog" or novel environments can lead to wholesale changes in community structure caused by a cascade of intra- and interspecific mechanisms ranging from extirpation of species due to physiological stress, decoupling of positive interactions such as facilitation, relaxation of resource limitations on some while imposing new ones

on others, and altering competition or predation (Hobbs et al. 2006, Williams and Jackson 2007). Novel environmental gradients likely represent a strong selective pressure favoring native taxa that are less specialized, have greater physiological plasticity, or facilitate invasion of adaptive nonnative taxa (Stralberg et al. 2009). Species replacement results in novel biotic communities that may be difficult to manage, afford fewer ecosystem services, and may not respond to habitat restoration efforts (Palmer et al. 2009, Clements et al. 2010). Thus, characterizing taxon-specific responses to novel anthropogenic gradients is important for detecting critical levels of alteration, understanding mechanisms of biodiversity loss, identifying adaptive traits that confer success, assessing

changes to ecosystem function, and shaping restoration strategies.

The conversion of native grasslands, forests, wetlands, and other natural land cover to cultivated and developed land represents one of the most prevalent drivers of novel environments and reduced biodiversity in freshwaters (Allan 2004). Land use change is rivaled only by climate change in global extent and magnitude of influence on biodiversity of freshwater ecosystems, which host a disproportionately high number of endangered species worldwide (Jenkins 2003). The physical and chemical environment of streams is particularly responsive to urban land use (Hansen et al. 2005, Walsh et al. 2005*a*). Increasing amounts of catchment impervious cover increases the magnitude of peak discharges and reduces catchment storage (Poff et al. 2006), alters fluxes of sediment and organic matter that sustain natural stream channel morphology, in-stream habitat, and ecosystem processes (Booth and Jackson 1997, Meyer et al. 2005), and serves as nonpoint sources of urban chemicals that are harmful to biota (Hatt et al. 2004). Accordingly, urbanization has been shown to reduce biodiversity and alter community structure in every type of stream ecosystem studied to date (Wenger et al. 2009). Collectively, the suite of changes has been described as the urban stream syndrome (Walsh et al. 2005*a*).

Current understanding of stream community response to urbanization is based heavily upon aggregations of multiple taxon abundances as summary indicators of community structure or functioning (Wenger et al. 2009). Aggregate community variables, such as the number of taxa or index of biotic integrity (IBI), are often used because most individual taxa exhibit highly variable occurrence and abundance among sample units and a dependence upon univariate statistical techniques for analysis (e.g., Dodds et al. 2010). However, aggregating taxon abundances may dampen or even obscure responses to urbanization because different taxa may respond to different levels of impervious cover or have different forms of response (King and Baker 2010, 2011). Community responses inferred from aggregate metrics may be confounding synchronous, nonlinear declines among taxa with more gradual increases or no changes in others.

Further confounding our understanding, different investigators have reported stream community response models to urbanization that are linear (Moore and Palmer 2005, Cuffney et al. 2010), wedge shaped (Booth 2005, Paul et al. 2009), or sharply linear to gradual in form (Walsh et al. 2005*a*). Each of these response models assumes that any level of urbanization above zero (expressed as, e.g., impervious cover or urban intensity) has an effect on the community, and that this effect is a linear function for most or the entire gradient (King and Baker 2011). Neither assumption is well supported by our understanding of species responses and discrete communities along natural gradients (e.g.,

Whittaker 1956) or experimental data from the toxicology literature, where single-species responses to physiological stressors are characterized as zones of no effect followed by sharp nonlinear responses (e.g., Suter 1993). While some urban-related stressors may indeed elicit community changes at any detectable level beyond a natural range of conditions, this range likely varies across broad regions due to hydrologic differences and distinct patterns of development (Poff et al. 2006, Cuffney et al. 2010). Moreover, if linear community responses are valid, then they would suggest that novel gradients affect each taxon independently and at incrementally different levels of the gradient, regardless of coevolution or interspecific interactions believed to be important in structuring communities (Økland et al. 2009).

Here, we apply a new analytical method, threshold indicator taxa analysis (TITAN), designed specifically to (1) identify the location and magnitude of changes in the frequency and abundance of individual taxa along an environmental gradient and (2) estimate the relative synchrony of those changes as a metric of a community threshold (Baker and King 2010). We apply TITAN to decompose stream community response to catchment urbanization into its basic components—individual taxa—to more explicitly test the linear response models that implicitly assume that individual taxa decline or increase at incrementally different levels of urbanization, from zero to complete conversion to urban land. We use a large and well-studied biomonitoring data set from Maryland, USA because aggregate metrics used by many investigators in other urban stream studies in this region have already been shown to respond in a wedge-shaped, linear manner to impervious cover (Moore and Palmer 2005, Paul et al. 2009, King and Baker 2010).

METHODS

Study area

Maryland is located in the mid-Atlantic region of the eastern United States and spans a topographic and geologic gradient from steep, mountainous terrain in the west to coastal lowlands in the eastern part of the state (Fig. 1). Based on previous descriptions of stream geomorphology, land use patterns, and macroinvertebrate taxon distributions (e.g., Southerland et al. 2005, Baker et al. 2006*a*, Johnson and Fecko 2008) we stratified our study design into three distinct regions that best contrasted dominant broad-scale physiographic patterns in the state: Appalachian Mountains (hereafter, mountain or MT), piedmont (PD), and coastal plain (CP; Fig. 1).

There are important geological and topographic differences among the physiographic regions. The MT region, including portions of the Appalachian Plateau, Valley and Ridge, and Great Valley physiographic provinces are underlain by a folded and faulted mix of sedimentary rocks including siliciclastic (sandstone,
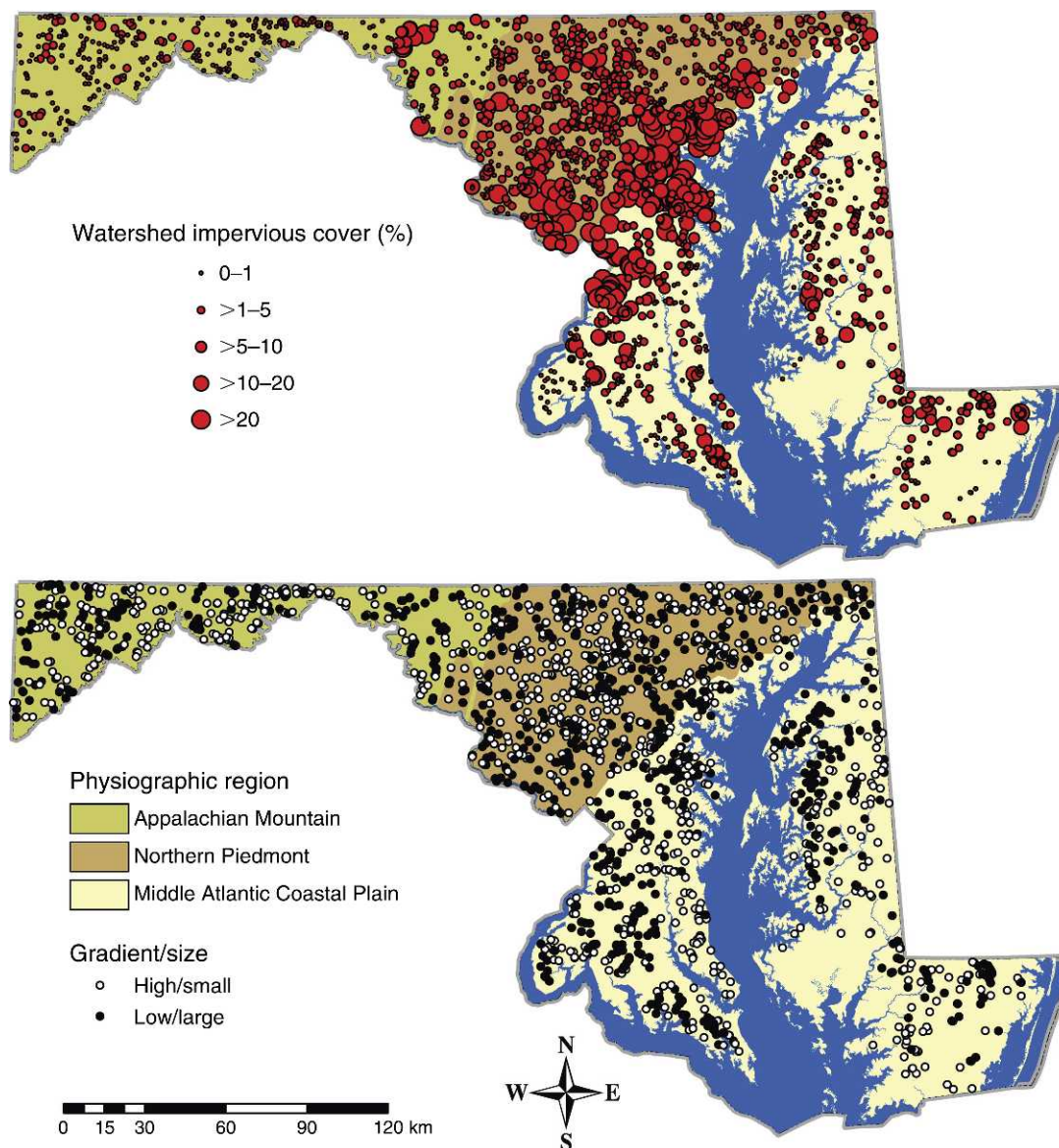
FIG. 1. Maps of Maryland, USA, illustrating the percentage of impervious cover within each of 1939 catchments and the classification of catchments into size-gradient strata within physiographic regions.

siltstone, shale, conglomerates) and carbonate (limestone, dolomite, marble) bedrock (Edwards 1981). Crystalline igneous and metamorphic (schist, granite, quartzite, gneiss) bedrock underlie the Piedmont and Blue Ridge provinces within the PD region, and unconsolidated sediments (gravel, silt, sand, clay) predominate in the CP.

These three physiographic regions also differ in dominant land uses, the degree of urbanization, and the arrangement of land cover types within catchments (Jantz et al. 2005, Baker et al. 2006a; Fig. 1). The PD and CP are both heavily developed around Baltimore and Washington, D.C., where the percentage of impervious cover in first- through fourth-order catch-

ments ranges from zero to over 50%. Both the PD and CP also have patches of relatively high impervious cover scattered throughout their boundaries, so moderate-to-high imperviousness is not confined to the Baltimore–Washington metropolitan areas. The MT region is much less developed than the PD or CP, with relatively few first- through fourth-order catchments exceeding 10% impervious cover (Fig. 1). However, patches of moderately high percentage impervious cover are distributed throughout the MT region. Agricultural activity and impervious cover are more likely to be located near streams in the MT than the PD and CP region (Baker et al. 2006a).

Stream data

We used macroinvertebrate taxon abundance data from 1811 stream reaches sampled by the Maryland Biological Stream Survey (MBSS; Klauda et al. 1998) and 128 stream reaches sampled by the Smithsonian Environmental Research Center (SERC). The MBSS is a stream-monitoring program based on probabilistic sampling stratified by major basins and stream order (first to third order on a 1:250 000 stream map during 1995–1997 and first to fourth order on a 1:100 000 stream map during 2000–2003). Sampling locations were randomly assigned to non-overlapping, 75-m stream segments across the state of Maryland. Within each randomly selected segment, the survey included rapid-assessment metrics of stream physical characteristics, conventional water chemistry, in-stream habitat, discharge, and macroinvertebrate assemblage composition (2-m^2 sample collected with a 500-μm D-framed dip net from favorable habitat, genus-level identification, 100-organism, fixed-count method; Maryland Department of Natural Resources 2000). All of the selected sites were sampled during 1995–2003, a period that overlapped with the 1999–2000 satellite imagery used to classify impervious cover (see *Geographic analyses*). Greater details on data collection methods and quality assurance and quality control are provided in Mercurio et al. (1999) and Roth et al. (2005).

During 2002 and 2003, SERC sampled additional sites throughout the Coastal Plain using MBSS standard operating procedures. SERC macroinvertebrate samples were identified by the Maryland Department of Natural Resources taxonomic staff for consistency in taxonomic quality between MBSS and SERC data sets. MBSS and SERC data sets were combined for analysis. Each of the 1939 stream reaches was assigned to one of the three physiographic regions based on the location of the catchment outlet. A total of 402 reaches were located in the MT region, 737 in the PD, and 800 in the CP (Fig. 1).

We screened macroinvertebrate data for consistency in taxon names and enumerations prior to analysis. We resolved ambiguous taxa following the operational-taxonomic-unit-approach method of Cuffney et al. (2007). Many of the samples contained >100 individuals because the procedure intentionally allows over 100 individuals to be retained during sorting to ensure that at least 100 are in adequate condition for taxonomic identification (Maryland Department of Natural Resources 2000). If more than 100 individuals were enumerated for a stream reach, we used a computer-generated random sampling procedure to select of subsample of 100 individuals (Ostermiller and Hawkins 2004). Standardizing in this way ensured that individual taxa frequencies and abundances were expressed in a consistent manner for all sample units because both attributes depend on the number of individuals enumerated in the subsample (Larsen and Herlihy 1998). Samples with fewer than 100 individuals

were not changed because they represent stream reaches with low densities of individuals possibly due to anthropogenic stressors, including catchment imperviousness.

Geographic analyses

Terrain analysis, catchment delineation, and impervious-cover estimation were accomplished in ArcGIS 9.3 (ESRI, Redlands, California, USA). We used the geographic coordinates of the downstream end of each 75-m stream sampling reach to define a catchment outlet. We delineated the boundary of the catchment draining to each outlet from 1:24 000 digital elevation models (DEMs) expressed as a 30-m raster (U.S. Geological Servey National Elevation Dataset; *available online*).[6] The DEMs were modified by lowering the elevation values of mapped stream channels (1:24 000 National Hydrography Dataset) by normalized excavation (Baker et al. 2006b) to ensure flow lines matched existing stream maps and to improve automated catchment delineation (data set *available online*).[7]

We estimated percent impervious cover in each catchment from a 30-m raster classified from Landsat thematic mapper images taken during 1999–2001 (Regional Earth Sciences Application Center 2003, Goetz et al. 2004). Pixels in the raster are zero (no impervious cover) or have an integer value of percent imperviousness ranging from 10% to 100%. The Regional Earth Sciences Application Center raster was released prior to the National Land Cover Data (NLCD) raster, but used a similar classification approach as the NLCD (Jantz et al. 2005). The pixel-by-pixel accuracy was assessed at 83% (Goetz et al. 2004, Jantz et al. 2005), with slightly higher percentages of omissions (classifying impervious cover as another land cover type, 12%) than commissions (classifying other land cover as impervious cover, 5%). Aggregation of pixels to the scale of our catchments (typically thousands of pixels) neutralizes omissions and commissions due to randomly distributed errors (e.g., Hodgson et al. 2003), so catchment-scale impervious estimates become increasingly precise as a function of increasing spatial scale. Bias due to the absolute accuracy of 30-m data relative to other, high-resolution data sources remains an unresolved issue particularly in suburban landscapes. However, recent estimates suggest that this value is biased low by an average of approximately 5% in catchments with 15–30% impervious cover but by a much lower amount in low impervious areas (<10%) because the relative error varied with the magnitude of the prediction (Chabaeva et al. 2009, Greenfield et al. 2009, Smith et al. 2010).

To characterize physiographic differences that could modulate the unit effect of impervious cover on taxa responses, we estimated a set of size and gradient metrics

intended to capture first-order controls on water movement throughout each catchment. Total catchment area (ha) and median flow distance to the catchment outlet were calculated to capture variation in stream size and shape. Topographic metrics included mean elevation (m), which described the relative topographic positioning of each catchment, average slope (%), and the median flow gradient from each pixel in the catchment to the catchment outlet (m/km). The median topographic index was used to summarize heterogeneity arising from topographic control over runoff generation which forms the basis for TOPMODEL (Beven and Kirkby 1979), whereas the median length-to-gradient ratio (km) was used to characterize topographic controls on mean water residence time (McGuire et al. 2005).

We partitioned catchments into two relatively distinct classes within each physiographic province. Rather than validate a catchment classification system based on physiography, the goal of our study was to contrast taxa responses to impervious cover across classes of catchments representing differences in expected patterns of water routing, residence time, and unit response to storm events. To accomplish this classification, we performed Ward's method of hierarchical agglomerative cluster analysis on the catchment metrics of size, elevation, and topography within each physiographic region (PC-ORD v.5.15; MjM Software, Gleneden Beach, Oregon, USA). We used Euclidean distance to as a metric of cumulative dissimilarity among catchments using the metrics. Prior to analysis, catchment metrics were $\log_{10}$-transformed, if necessary, to achieve skewness $< |1|$ for each variable (McCune and Grace 2002). After transformation, we standardized each metric to a mean of zero and standard deviation of 1 to avoid disproportional variable weighting in the Euclidean distance metric due to differences in magnitude of measurement units. This approach distinguished a numerically balanced pair of high-gradient, small (HS) and low-gradient, large (LL) catchment classes within each physiographic province for testing hypotheses about different unit effects of impervious cover on stream biota (see *Results*). Taxonomic and impervious cover data were subsequently partitioned into one of these six catchment classes (two classes per physiographic region) for analysis.

Analysis of stream community response to urbanization

Taxon-specific change points.—We performed TITAN on macroinvertebrate community data for each of the six catchment classes to identify potential change points in the relative frequency and abundance of individual taxa as a function of percent impervious cover and to estimate the relative synchrony of those changes as a metric of a community threshold (Baker and King 2010). Although TITAN has been described and tested in detail using simulated and real ecological data sets by Baker and King (2010) and King and Baker (2010), here

we provide a brief overview of the method and its applicability to our study.

TITAN uses binary partitioning to find the value of an environmental gradient that produces the greatest change in species abundance and occurrence within a sample population. Although superficially similar to regression trees (De'ath and Fabricius 2000) and change-point analysis (King and Richardson 2003, Qian et al. 2003), TITAN uses indicator species scores (Dufrêne and Legendre 1997) instead of deviance reduction to locate taxon-specific change points. Indicator species scores (IndVals) weight the relative abundance of each taxon across candidate partitions by its within-partition occurrence frequency to provide an unbiased empirical measure of association with each side of an environmental gradient. Taxa indicator scores are scaled from 0–100%, with a score of 100 (perfect association) indicating that a taxon was collected in every sample within a group and not in any other group. Significance (P) of indicator scores is estimated via randomized permutation. Because association is measured for each side of the partition, TITAN empirically distinguishes increasing and decreasing taxa, whereas taxon-specific response magnitudes are normalized (as z scores) by comparison with values obtained from permuted samples in order to facilitate cross-taxon comparisons (Baker and King 2010).

Community-level change points.—In TITAN, community-level change points for increasing and declining taxa are estimated by separately tabulating all $z-$ and $z+$ scores along an environmental continuum for each possible partition, represented as the midpoint between every pair of successive observations with distinct environmental values. The value(s) of the environmental gradient resulting in the largest cumulative z scores for negative (sum[$z-$]) and positive (sum[$z+$]) taxa correspond to the maximum aggregate change in their respective frequency and abundance. These values may be interpreted as observed impervious-cover thresholds if they constitute a clear maximum along the gradient, but especially if they occur as the result of many synchronous taxon-specific change points.

TITAN estimates uncertainty surrounding thresholds using the distribution of environmental values that produce the largest sum($z-$) or sum($z+$) among 500 bootstrap replicates (resampling with replacement). Quantiles (e.g., 0.05, 0.95) of the distribution serve as empirical confidence limits. Important indicator taxa are identified using indices of purity and reliability. Pure indicator taxa are those that respond consistently in the same direction, either positive or negative, during resampling (e.g., purity ≥ 0.95). Reliable indicator taxa are those that show consistently strong changes during resampling (e.g., $P < 0.05$ for >0.9 resamples). Finally, for each pure indicator taxon, TITAN uses the bootstrap replicates to compute quantiles of the distribution of change points, although we discourage strict-interpretation of taxon-specific empirical confi-

dence limits because they are likely to be unreliable for taxa with low occurrence frequencies (Manly 1997). Rather, we recommend them as a relative measure of uncertainty among taxa.

Statistical analysis.—We performed TITAN in R (version 2.9.2; R Development Core Team 2009) using a custom TITAN package written by M. E. Baker and R. S. King (Baker and King 2010). We required that the minimum number of observations on either side of any partition was five or more, which was <1–2.5% of the total sample units per catchment class. All taxa with five or more occurrences per catchment class were retained for analysis. We $\log_{10}(x + 1)$-transformed taxa abundances to downweight the influence of highly variable abundances on taxa indicator score calculations, which was particularly important for taxa with low occurrence frequencies. For each of the six catchment classes, we reran TITAN across 500 bootstrap replicates and used these to compute purity and reliability of individual threshold indicator taxa and uncertainty surrounding thresholds based on the distribution of maximum TITAN z (individual taxa) and TITAN sum(z) values.

RESULTS

Catchment classification

The cluster analyses distinguished relatively balanced groups of higher-gradient, small (HS) and lower-gradient, large catchments (LL) in each physiographic region (MT-HS (225), MT-LL (177), PD-HS (405), PD-LL (332), CP-HS (373), and CP-LL (427; Fig. 1). As regional physiography is strongly correlated with patterns of annual temperature and precipitation in Maryland, the metrics and resulting classification were indicators of more complex hydrologic processes, thus these strata necessarily forced breaks along continua. Groups reflected aggregate differences in catchment area, flow gradient, and length-to-gradient ratio (Fig. 2). Catchment area was similar within size-gradient classes among regions, whereas median flow gradient declined steadily from the MT to the CP. Median length-to-gradient ratio reflected components of both catchment size, shape, and gradient, indicating that, based solely on topography, MT-HS catchments had the lowest expected mean water residence time, whereas CP-LL had the greatest. Elevation declined across physiographic regions from MT to CP but had similar distributions between catchment classes within regions.

Analysis of stream community response to urbanization

Negative indicator taxa (z–).—Numerous taxa exhibited threshold declines in frequency and abundance in response to percent impervious cover (Tables 1–4; Appendix B, C). Most individual negative (z–) indicator taxa synchronously responded between 0.5% and 2% impervious cover (Figs. 3–7, Table 4). Half of the negative indicator taxa declined sharply at or below 0.14–1.32% impervious cover, depending upon catchment class (Fig. 7). Roughly 80% of the z– taxa exhibited threshold declines at or below 0.5–2% impervious cover. The last 20% of z– taxa fell out sporadically from approximately 1% to 25% impervious cover.

Among catchment classes, 110 of 238 taxa with five or more occurrences sharply declined, whereas 63 of these declined in two or more catchment classes (Appendix B, C). In rank order, Diptera (true flies), Plecoptera (stoneflies), Ephemeroptera (mayflies), Trichoptera (caddisflies), and Coleoptera (beetles) had the largest percentage of negative indicator taxa among orders (Tables 3 and 4). Plecoptera and Ephemeroptera had relatively similar numbers of indicator taxa among catchment classes, whereas Trichoptera had proportionally fewer sensitive taxa in the MT than in the PD and CP. Taxa typically associated with low-gradient systems became increasingly important indicators from the MT to the CP, particularly Diptera, which showed a consistent increase in the number of negative indicator taxa moving from the MT to the CP region (Tables 3 and 4).

Numerous taxa exhibited synchronous change points in response to impervious cover, resulting in sharp peaks in the additive response of negative indicator taxa (sum[z–]) (Appendix E, Fig. 7). Community-level change points (sum[z–]) peaked at ~1% or less among all six catchment classes (Table 1). The negative-responding community change point was lowest in the MT-HS class and highest in the PD-LL class. CP-HS and CP-LL community-level change points for negative indicator taxa were slightly lower than PD-HS and PD-LL, respectively. However, HS classes always had lower observed change points than LL classes within the same physiographic region. The pattern of paired differences between HS and LL classes within physiographic regions was also evident at the 5th and 95th percentiles of the bootstrap threshold frequency distributions (Fig. 7, Table 1).

Positive indicator taxa (z+).—Individual positive indicator taxa (z+) were widely distributed along the impervious-cover gradient, spanning most of the range of values in each catchment class and approximating a linear cumulative distribution with increasing cover (Appendix D, E). In contrast to the narrow range of impervious cover among most of the negative taxa thresholds, positive taxa exhibited relatively wide bootstrap threshold frequency distributions consistent with a more gradual increase in relative frequency and abundance with increasing impervious cover. Most positive taxa change points only marginally overlapped with those of negative responding taxa.

Most (>90%) of the positive taxa change points in the PD and CP occurred above 1–2% impervious cover and >50% were observed above 10% (Appendix B, D). A total of 75 different taxa were significant positive indicators across all six catchment classes, but only 25 were indicators in two or more classes (Appendix B). The number of positive indicator taxa was much lower than negative taxa in five of six of the catchment classes
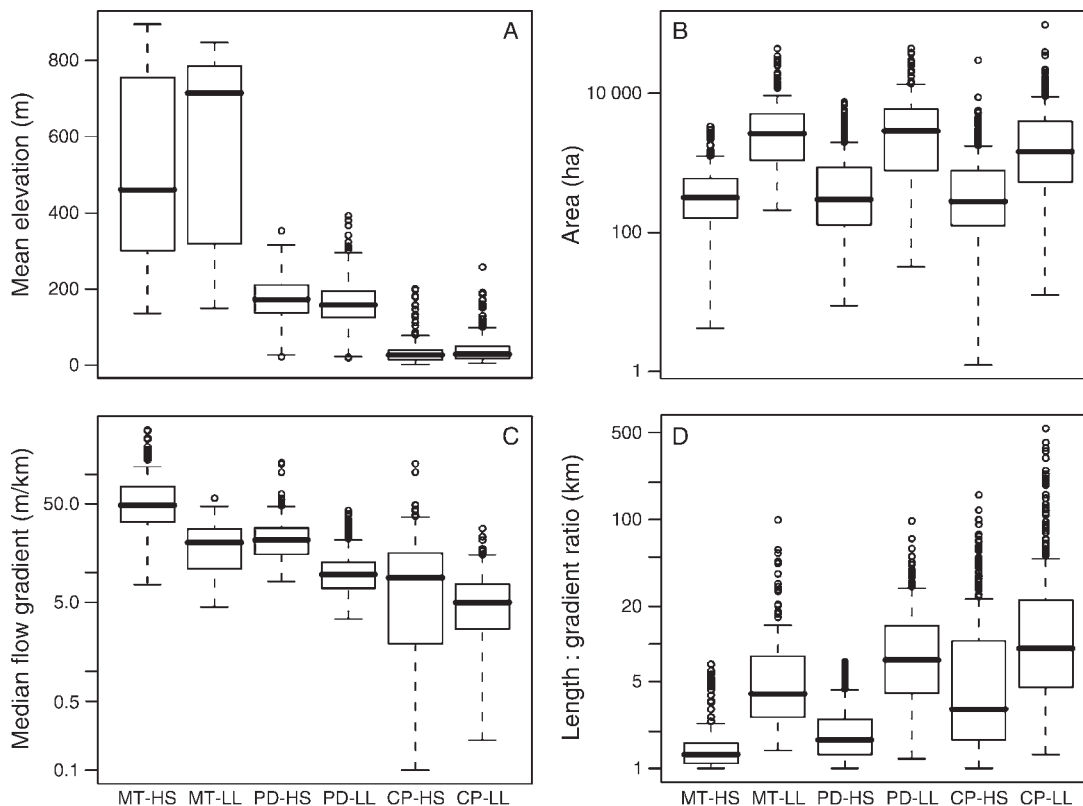
Fig. 2. The distribution of values of four catchment metrics used to classify catchments by physiography: (A) mean elevation, (B) drainage area, (C) median flow gradient, and (D) median flow length-to-gradient ratio. Box plots summarize the median (solid line), interquartile range (IQR, box), 1.5IQR (whiskers), and values outside 1.5IQR (points). Key to other abbreviations: MT, mountain; PD, piedmont; CP, coastal plain; HS, high-gradient, small catchments; LL, low-gradient, large catchments.

(Table 2). Among orders, Diptera (50.4%) had by far the largest number of positive taxa (Table 3).

Community-level responses of positive-responding taxa (sum[$z+$]) were generally lower in magnitude and far less abrupt than those of negative indicator taxa (Appendix E). Change points in sum($z+$) were not evident in most catchment classes, with the only distinct single peak occurring in the MT-LL class at 2.10% impervious cover. Sum($z+$) had distinct peaks at two different levels of impervious cover in the MT-HS class (0.50% and 3.07% impervious cover). PD and CP sum($z+$) rapidly increased between 0 and 5% impervious cover, but plateaued until declining between 25% and 35% cover, resulting in wide bootstrap frequency distributions inconsistent with a sharp, predictable change in composition above any particular level of impervious cover (Table 1, Appendix E).

DISCUSSION

Alarmingly low levels of catchment imperviousness corresponded to sharp, synchronous declines of many taxa across all six catchment classes. The location of greatest effect (~1% impervious cover), shape of response (sharp threshold declines of many taxa followed by gradual increases in fewer taxa) and

magnitude of effect (the majority of taxa declined between 0.5% and 2% cover) are distinct from responses reported previously. However, the large number of catchments, the nature of our analytical method, and the consistency of the signal are powerful arguments in support of this discovery.

TABLE 1. Percentage impervious cover thresholds estimated by TITAN sum($z–$) (negative indicator taxa) and sum($z+$) (positive indicator taxa).

Catchment class	Impervious cover threshold (%)	
	TITAN sum($z–$)	TITAN sum($z+$)
MT-HS	0.02 (0.01, 0.03, 0.17)	0.50 (0.31, 0.67, 3.36)
MT-LL	0.68 (0.17, 0.60, 0.86)	2.10 (0.71, 1.53, 2.62)
PD-HS	0.95 (0.33, 0.55, 1.36)	22.1 (4.68, 12.6, 30.6)
PD-LL	1.28 (0.62, 1.24, 1.88)	14.3 (1.81, 8.99, 21.8)
CP-HS	0.36 (0.19, 0.36, 0.93)	13.8 (2.56, 10.4, 20.5)
CP-LL	0.96 (0.47, 0.99, 1.91)	6.99 (4.48, 8.36, 17.2)

Notes: Observed thresholds are the maximum sum(z). Values in parentheses are the 5th, 50th, and 95th percentiles correspond to the frequency distribution of thresholds from 500 bootstrap replicates (see Figs. 3–5 for cumulative frequency distributions). Catchment classes are: MT, mountain; PD, piedmont; CP, coastal plain; HS, high-gradient, small catchments; LL, low-gradient, large catchments.

TABLE 2. Number and percentage of total taxa identified by TITAN as significant threshold indicator taxa among the six catchment classes.

Catchment class	Total no. taxa	No. threshold indicator taxa	
		Negative ($z-$)	Positive ($z+$)
MT-HS	139	13 (10)	22 (16)
MT-LL	142	32 (23)	16 (11)
PD-HS	197	49 (25)	15 (8)
PD-LL	177	48 (28)	6 (3)
CP-HS	212	47 (22)	24 (11)
CP-LL	216	67 (30)	18 (8)

Note: See Appendix A for details. Values in parentheses are the percentages of total taxa.

Urban streams constitute a novel environment for aquatic organisms, and our results support previous findings of declines in biodiversity and shifts in community structure as a result of increasing catchment urbanization. However, our results do not support the theoretical responses proposed by others that biodiversity or community structure changes in a linear or wedge-shaped manner with increasing urbanization, such that each incremental addition in impervious cover or urban intensity results in a proportional effect on communities. The observed community thresholds imply that the majority of sensitive taxa in these communities begin to decline within a narrow band of exceptionally low levels of impervious cover, and a linear response model does not adequately convey the gravity of degradation to stream biodiversity (King and Baker 2011). Although we were surprised by the threshold level of urbanization, we submit that synchronous declines of stream taxa make sense from an evolutionary perspective and are supported by ecological theory.

High biodiversity in streams is largely a result of subtle, yet critical, differences in stream flow velocities and material transport through time and space (e.g., Poff et al. 1997). Diverse microhabitats have resulted in extensive adaptive radiation of many stream-dwelling taxa (Vinson and Hawkins 1998), whereas moderate frequency and magnitude of hydrological disturbances have maintained high levels of species richness at a local scale (Connell 1978). Facilitation among taxa is also well documented in streams (Cardinale et al. 2002). Consequently, lotic species have coevolved to possess unique morphological, behavioral, and physiological adaptations that correspond to an often narrow range of environmental conditions. Small functional niches undoubtedly render many species intolerant of conditions that fall outside those experienced in evolutionary time (sensu Shelford 1913). Thus, taxa sensitive to the novel environment are selected against, sharply decline and eventually disappear.

TABLE 3. Number of threshold indicator taxa identified by TITAN by order across the six catchment classes.

Order	Catchment class					
	CP-HS	CP-LL	PD-HS	PD-LL	MT-HS	MT-LL
Negative ($z-$)						
Amphipoda	2	1				
Coleoptera	3	5	1	4		
Decapoda			1		1	
Diptera (Chironomidae)	5	14	4	6		3
Diptera (other)	6	10	6	4	2	3
Ephemeroptera	8	7	15	14	5	10
Isopoda	1	1				
Megaloptera	1	1	1			1
Mesogastropoda		2		1		
Odonata	2		1			
Plecoptera	12	16	11	14	5	12
Trichoptera	7	6	8	5	1	2
Positive ($z+$)						
Amphipoda			2			
Basommatophora	1		1		1	1
Coleoptera			1	2	2	2
Diptera (Chironomidae)	12	6	6	2	7	6
Diptera (other)	3	1	1	1	3	1
Gordioidea		1				1
Haplotaxida		2	1		2	
Hoplonemertea	1	1				
Isopoda			1			1
Lumbriculida	1	1	1			
Odonata	1	1	1			
Trichoptera	2	1			3	1
Tricladida		1				1
Tubificida	2	2	1		1	1
Veneroida	1					1

Note: Only orders with two or more threshold indicator taxa are included.

TABLE 4. Mean and maximum (max.) impervious cover thresholds of taxa that were significant threshold indicator in three or more of the six physiographic classes (*n*).

Taxon	Common name	*n*	Impervious cover (%)	
			Mean	Max.
Oulimnius	beetle	4	0.62	1.10
Psephenus	beetle	3	2.87	6.41
Chimarra	caddisfly	3	3.82	8.70
Diplectrona	caddisfly	4	0.55	1.30
Dolophilodes	caddisfly	3	0.17	0.33
Neophylax	caddisfly	3	4.37	10.94
Polycentropus	caddisfly	3	1.73	2.79
Pycnopsyche	caddisfly	3	3.58	5.77
Rhyacophila	caddisfly	4	0.89	1.93
Nigronia	dobsonfly	3	0.76	1.48
Acerpenna	mayfly	4	1.83	4.02
Ameletus	mayfly	4	1.04	2.29
Baetidae	mayfly	3	1.53	2.92
Drunella	mayfly	3	1.04	1.55
Epeorus	mayfly	4	1.40	3.31
Ephemerella	mayfly	5	3.44	12.80
Eurylophella	mayfly	3	3.16	6.19
Heptageniidae	mayfly	6	0.59	1.46
Isonychia	mayfly	3	2.67	5.86
Leptophlebiidae	mayfly	3	0.94	1.52
Paraleptophlebia	mayfly	6	1.10	2.13
Stenonema	mayfly	4	5.96	19.12
Acroneuria	stonefly	3	1.07	1.85
Allocapnia	stonefly	3	1.98	3.73
Amphinemura	stonefly	5	0.98	2.06
Capniidae	stonefly	3	1.05	2.19
Chloroperlidae	stonefly	3	0.82	1.09
Clioperla	stonefly	3	0.58	0.93
Eccoptura	stonefly	3	0.77	1.31
Isoperla	stonefly	5	4.93	21.65
Leuctra	stonefly	6	0.53	1.02
Nemouridae	stonefly	5	0.86	1.82
Oemopteryx	stonefly	3	0.49	1.18
Perlodidae	stonefly	6	0.84	2.23
Prostoia	stonefly	5	0.90	1.62
Sweltsa	stonefly	3	0.19	0.24
Prosimulium	true fly (blackfly)	6	2.76	8.78
Stegopterna	true fly (blackfly)	5	6.87	13.40
Hexatoma	true fly (cranefly)	4	0.59	1.88
Pseudolimnophila	true fly (cranefly)	3	0.75	1.03
Corynoneura	true fly (midge)	4	6.08	14.27
Micropsectra	true fly (midge)	4	1.57	3.35
Parametriocnemus	true fly (midge)	3	0.66	1.08

In contrast to the synchronous declines of sensitive taxa, positive-responding $z+$ taxa were almost exclusively those documented as tolerant, ubiquitous, and opportunistic (Barbour et al. 1999). These taxa did not increase synchronously, but gradually became more frequent and abundant at various levels of urbanization. The lack of synchronous change points at wide confidence bands around change points implied that positive responding taxa did not represent well-organized communities, but rather were comprised of historically native taxa that either directly (resource subsidy) or indirectly (e.g., realized niche expansion, reduced competition or predation) benefited from it. Other, invasive taxa may have been able to cross ecosystem boundaries due to a variety of factors related to the novel environment.

The ability of TITAN to separate responses of negative and positive indicator taxa was critical for understanding community-level thresholds. Linear or wedge-shaped responses of aggregate community metrics can be artifacts of a priori assignments of taxa to sensitivity (tolerant/intolerant), coarse taxonomic (e.g., number of Ephemeroptera, Plecoptera, or Trichoptera taxa), functional (e.g., percentage of grazers), and habit (percentage of clingers) classes and subsequently combining their abundances or occurrences without distinguishing response direction, location, and magnitude (King and Baker 2010). The poorly defined change points and gradual increase in tolerant taxa combined with the synchronous declines of numerous but less frequent taxa in this study provide a quantitative explanation for the linear or wedge-shaped phenomenon. We suggest that future studies of novel environmental gradients consider disaggregating community responses and aggregating only after response direction
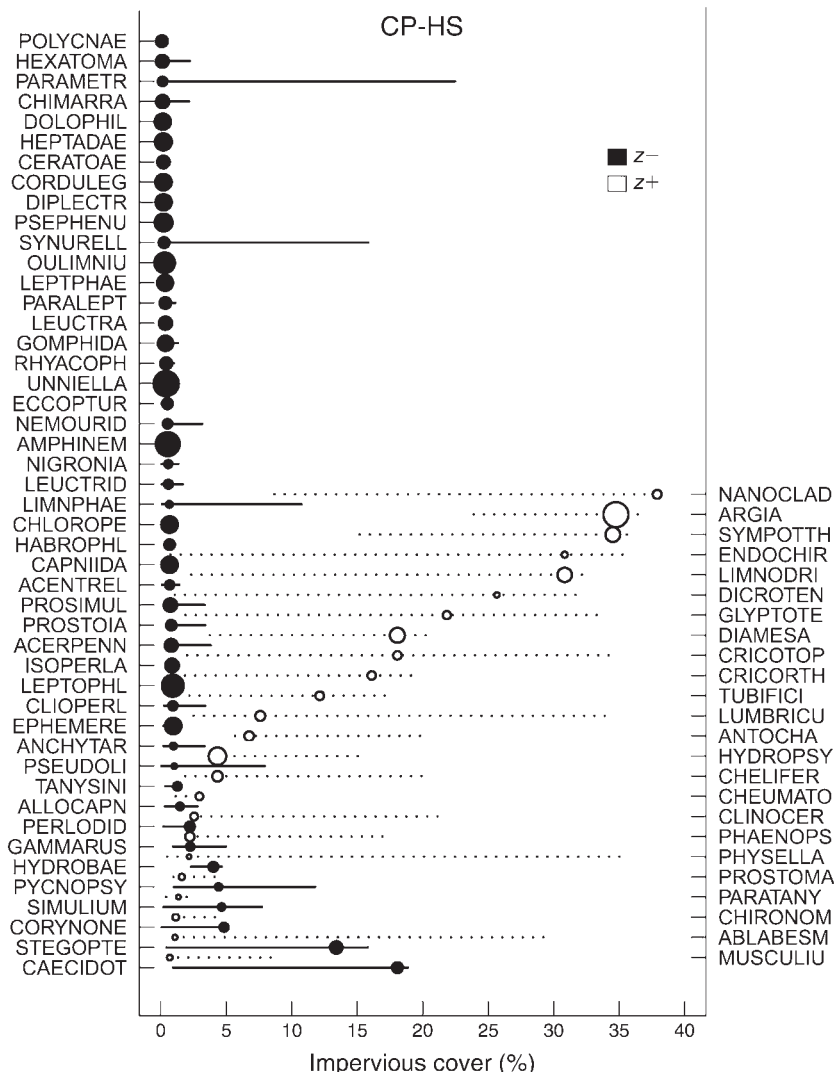
FIG. 3. Threshold indicator taxa analysis (TITAN) of macroinvertebrate community response to percent impervious cover between HS (high-gradient, small) and LL (low-gradient, large) catchments in the Coastal Plain (CP). Significant indicator taxa are plotted in rank order by their impervious cover change point. Solid symbols correspond to negative ($z-$) indicator taxa (taxa codes on left side of axis; see Appendix A), whereas open symbols represent positive ($z+$) indicator taxa (taxa codes on right side of axis). Within panels, symbols are sized in proportion to their z scores. Horizontal lines overlapping each taxon symbol represent the 5th and 95th percentiles of bootstrap threshold frequency distributions. See Appendix E for plots of sum(z) scores and cumulative threshold frequency vs. percent impervious cover.

and magnitude of individual taxa has been empirically estimated.

Did physiography influence community thresholds?

Catchment physiography may be an important factor modulating the magnitude and even the form of the relationship between imperviousness and stream biodiversity. Poff et al. (2006) aptly concluded that a "one size fits all" management target for imperviousness is unrealistic because the effect of impervious cover on stream power and sediment delivery depends upon physiographic context. Therefore, the fact that regional studies report different relationships between urbaniza-

tion and stream biological indicators is unsurprising (e.g., Walsh et al. 2005b, Utz et al. 2009, Cuffney et al. 2010). Physiographic variables such as catchment size, geology, and topography control hydrologic and geomorphic processes that shape stream habitat and structure distinct biological communities. Indeed, threshold responses differed across catchments with distinct physiography.

MT headwaters are predominantly forested, thus impervious surface represents a loss of interception storage on relatively steep terrain with limited storage capacity, a potentially profound hydrologic alteration. In larger MT catchments, development is often concen-
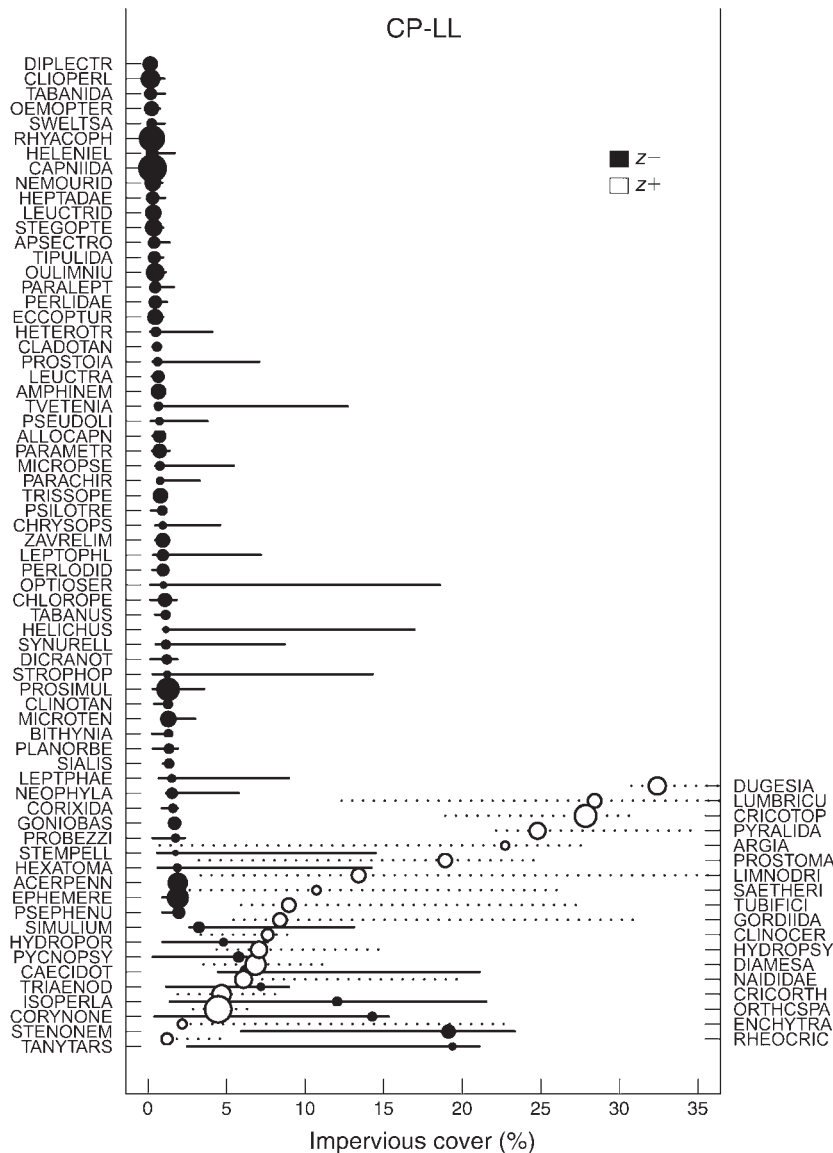
FIG. 3. Continued.

trated in valley bottoms close to streams, interrupting recharge in valleys underlain by highly fractured limestone and dolomite. In each case, impervious surfaces are likely to produce strong signals amplified by high transmission potential, which is expected to increase with gradient or proximity. MT catchments had the smallest range of percentage impervious cover across the data sets, yet consistent taxon-specific responses across the three regions support MT responses as real (e.g., 36 of the sensitive threshold indicators in the MT data sets also were deemed sensitive indicators in the PD or CP; Appendix B). We have found previously that spatial proximity can lower threshold responses (King et al. 2005) and that MT catchments are more likely to concentrate anthropogenic activity near streams (Baker

et al. 2006a), which may have also contributed to lower thresholds than those in other regions.

In contrast, because PD saprolite is capable of relatively poor infiltration, impervious cover may not represent as strong a divergence from predevelopment conditions as in MT catchments, despite moderate topographic gradients. Previous hydrologic comparisons suggest that some PD catchments may have higher base flows than CP streams (Jordan et al. 1997), which may further mitigate and ameliorate the influence of low levels of impervious surface. Likewise, we expected that infiltration differences between impervious cover and unconsolidated CP sediments would be offset to some degree by low gradients, more extensive streamside wetlands, and poor transmission potential, particularly
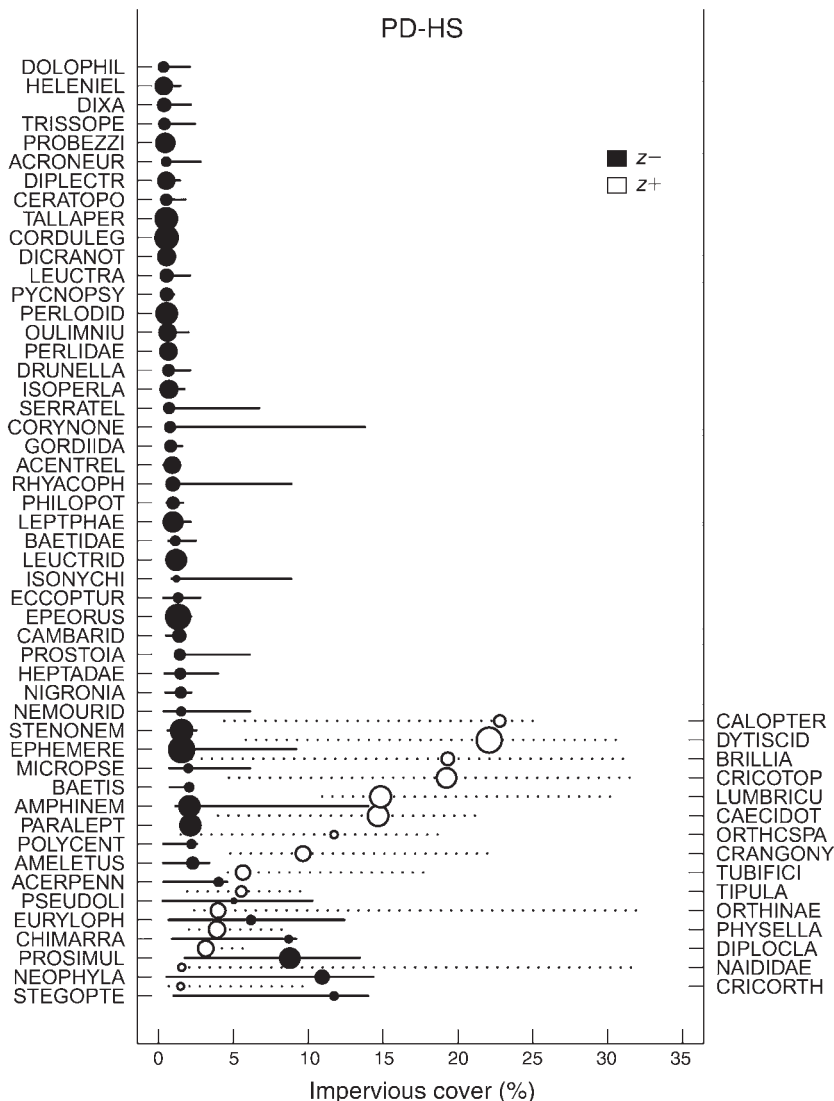
FIG. 4. Threshold indicator taxa analysis (TITAN) of macroinvertebrate community response to percent impervious cover between HS and LL catchments in the Piedmont (PD). See Fig. 3 for details. See Appendix E for plots of sum(z) scores and cumulative threshold frequency vs. percent impervious cover.

in larger catchments. Consistently lower thresholds in the CP than PD, when paired by HS and LL catchment classes, suggests that infiltration and base flow differences between regions may be modulating stream response to impervious cover. Indeed, Utz et al. (2011) quantified high flow event frequency, magnitude and duration and found that they were altered more severely in CP than PD catchments of Maryland, a finding that conflicted with their biological conclusions (Utz et al. 2009) that stream communities were more rapidly degraded in PD than CP streams.

Within regions, impervious cover thresholds were consistently lower in HS than LL classes. Snyder et al. (2003) also reported a greater unit effect of urban land cover on biotic integrity in streams with steeper gradients, a pattern consistent with our findings. This

is consistent with the expectation that the unit effect of impervious cover will be amplified due to greater transmission potential in smaller, higher-gradient catchments. It may also reflect differences in community structure in small vs. large wadeable streams.

What are the abiotic drivers of observed community thresholds?

Because geology and topography are important determinants of the spatial distribution of land use (Allan 2004), it can be difficult to differentiate land use effects from other, unmeasured factors that have similar spatial distributions (King et al. 2005). However, there are several lines of evidence that implicate urbanization and associated patterns of impervious cover over other potential underlying spatial phenomena as the ultimate
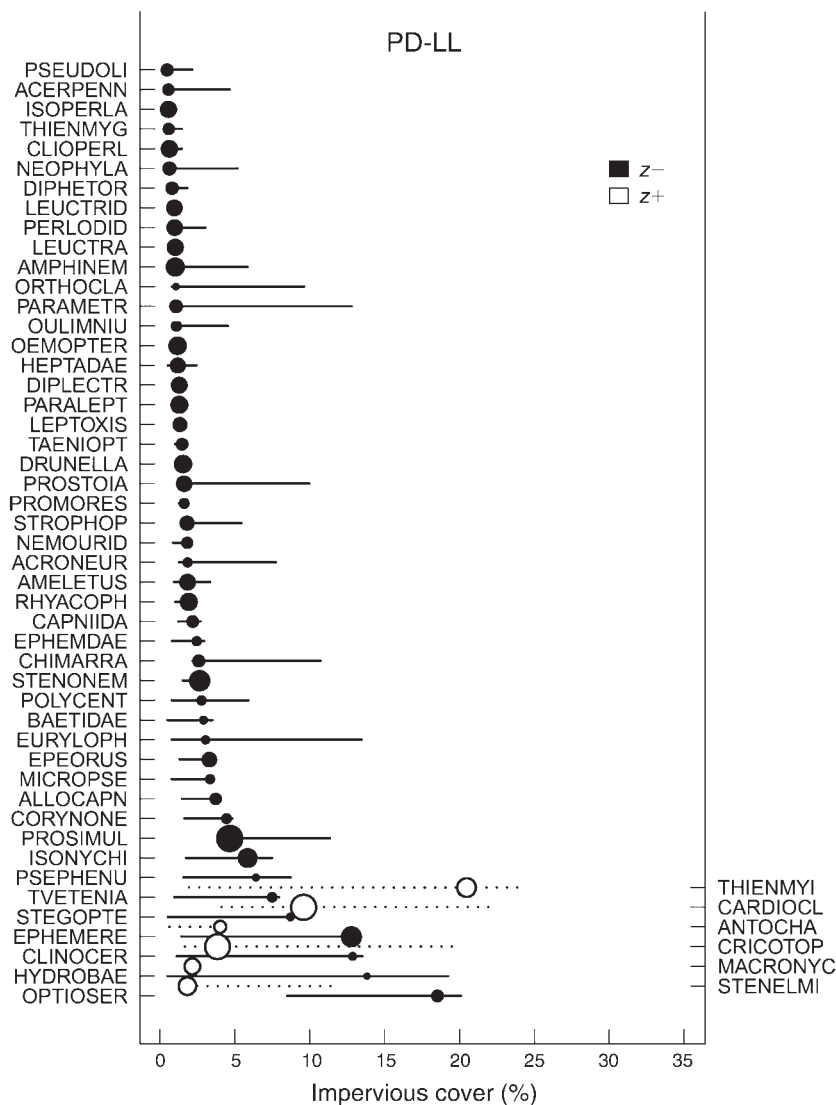
Fig. 4. Continued.

cause for the changes we observed. First, we separated catchments by physiographic region to avoid pooling catchments with characteristically distinct patterns of land use. Second, we further stratified catchments into HS and LL classes to minimize confounding effects of size and gradient on stream communities with impervious cover. Third, low and high impervious catchments were distributed throughout each region such that basin-specific fauna or unique biogeographic patterns correlated with spatial patterns of land use were highly unlikely (Fig. 1). Fourth, many of the same taxa repeatedly responded to very similar levels of impervious cover across regions and geomorphic classes, even between the MT and CP where taxonomic composition differs markedly. Fifth, previous analyses in both the CP (King et al. 2005) and PD (Moore and Palmer 2005, Utz et al. 2009) found that catchment development was a

strong predictor of macroinvertebrate community composition, but agricultural land, which is the other dominant anthropogenic land use in the region, had little to no statistically detectable effect on stream biodiversity. In our previous CP study we demonstrated that catchment developed land accounted for a unique component of variance in stream community composition that was not accounted for by the combined effects of all other land cover, spatial, riparian and in-stream variables in the MBSS (King et al. 2005). Thus, the effects of impervious cover reported in this study are relatively free of hidden spatial effects that may confound interpretations of thresholds relative to current patterns of land use. However, the role of land use legacies (e.g., Harding et al. 1998) in modulating modern responses of stream communities to urbanization needs further investigation.
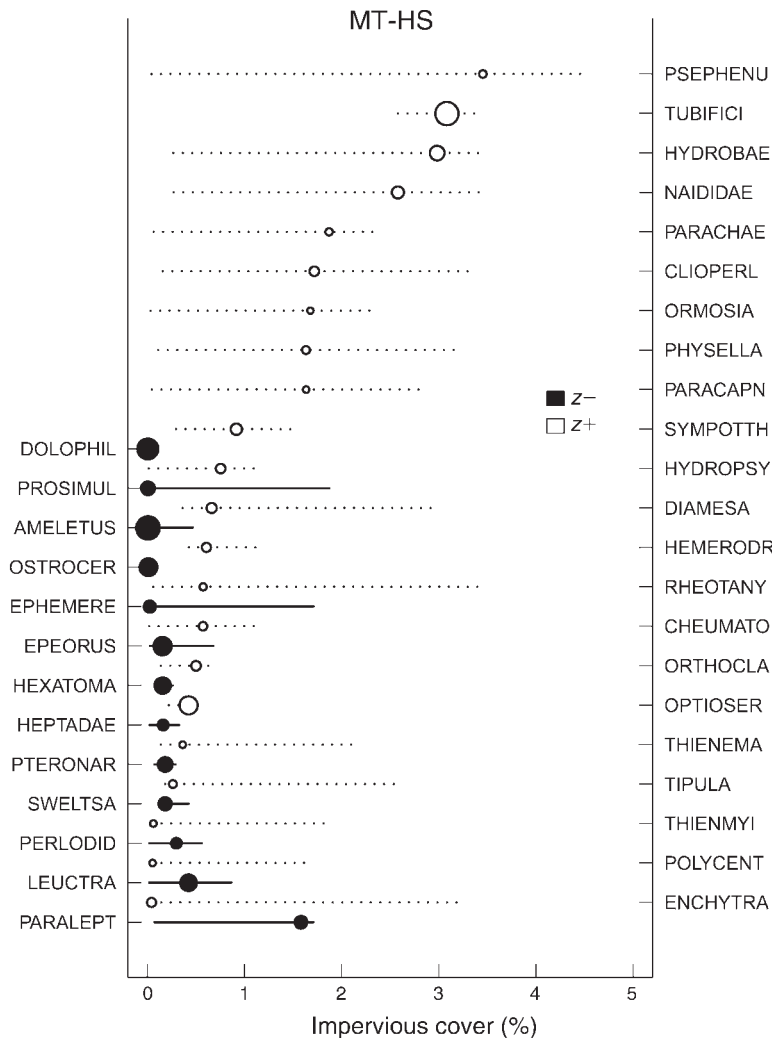
FIG. 5. Threshold indicator taxa analysis (TITAN) of macroinvertebrate community response to percent impervious cover between HS and LL catchments in the Mountains (MT). See Fig. 3 for details. See Appendix E for plots of sum(z) scores and cumulative threshold frequency vs. percent impervious cover.

Accuracy of impervious cover data is source of uncertainty, but because our catchments typically involve thousands of 30-m pixels, the ordinal precision of sites along the impervious gradient is quite high, and thus bias is the primary concern. Misclassification rates for individual 30-m impervious pixels range between 4% and 12% relative to planimetric reference data (Goetz et al. 2004, Jantz et al. 2005, Wickham et al. 2010), whereas comparisons across broader areal units (e.g., municipalities, counties, catchments) result in an RMSE of ~5% (Smith et al. 2010). Because these studies assess error across a large range of urbanization intensity, error estimates of model predictions necessarily result in a wider absolute range of uncertainty than would be observed if error were assessed within our much lower focal range of concern (0–2%). In all cases where authors plot error distributions (Chabaeva et al. 2009, Greenfield et al. 2009, Smith et al. 2010), areas with

<10% impervious cover show much greater accuracy (<5% RMSE) than areas with higher amounts of urbanization. Even if we assume a two- or three-fold underestimate of catchment-scale cover within our focal range of 0–2% cover, our observed thresholds would only increase to a maximum of 2–3%. Finally, the synchronous declines of taxa at low levels of cover are distinctly lower than other studies of macroinvertebrate responses to impervious cover despite our use of land cover data sets derived from the same, widely used satellite imagery (e.g., Paul et al. 2009, Utz et al. 2009, Cuffney et al. 2010). Thus the differences in our results from others are not dependent upon the land cover data but are a product of differences in analytical frameworks. The low threshold levels of imperviousness are, at worst, modest underestimates of catchment-scale cover and, more importantly, can be directly compared
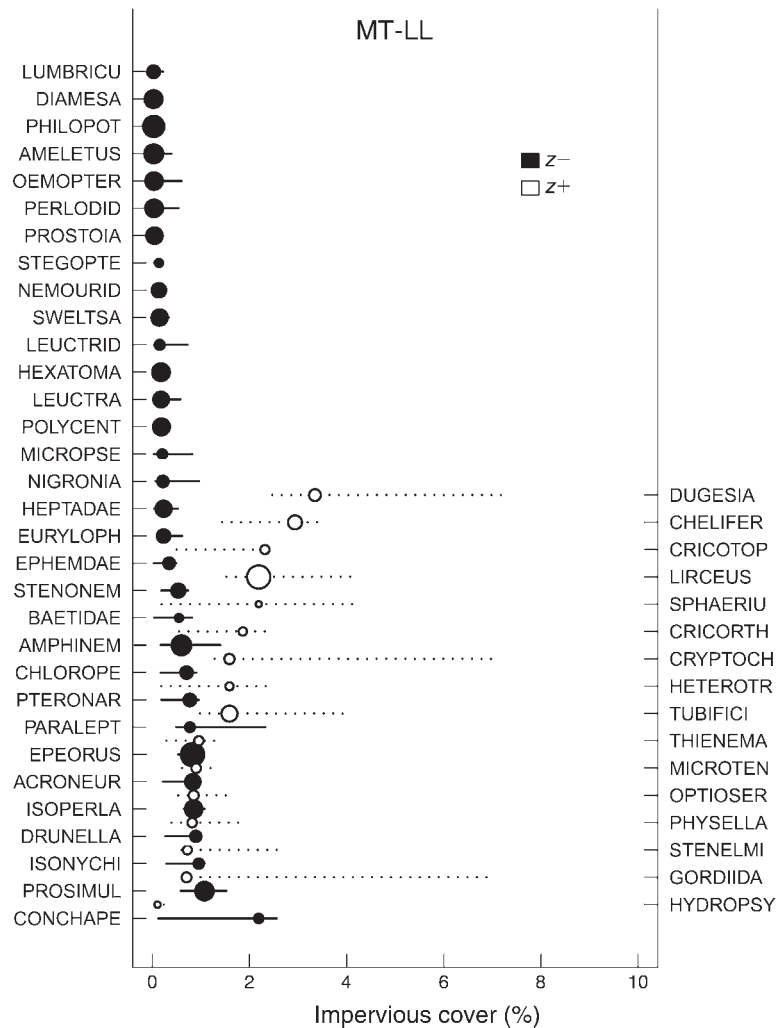
FIG. 5. Continued.

Walsh et al. (2005a) differentiated whole-catchment impervious cover from cover explicitly connected to streams via storm drains (effective impervious cover or EI) and concluded that effective impervious cover was a better correlate of stream degradation. They found that streams in apparently good condition biologically at 8–12% imperviousness were located in catchments with low (1–5%) EI, and threshold responses to total impervious cover became linear declines once adjusted for EI. In contrast, our study reports threshold responses to whole-catchment percentage impervious cover derived solely from satellite imagery. We do not know what proportion of impervious cover was connected to streams via storm water systems or other flow pathways in any of our study catchments. However, the thresholds we observe are so low that adjusting for connectivity could only lower threshold estimates modestly, and certainly would not increase them. In

sum, the high precision of the impervious cover data set coupled with the consistency of thresholds observed in this study suggests that whole-catchment impervious cover is a reliable broad-scale predictor of stream degradation in Maryland, particularly in the context of biodiversity conservation.

Among-region consistency of sharp, negative taxa responses indicates a common stressor or sets of covarying stressors linking impervious cover and stream response. Hydrologic alteration may partly explain these results, but there is relatively weak evidence for detectable changes in stream hydrographs at our observed threshold levels of impervious cover (e.g., Roy et al. 2003, Brown et al. 2009). Runoff of deicing salts from pavement represents a more likely culprit for altering environmental conditions at low levels of impervious cover and inducing community thresholds. Salinization of freshwater in northeastern United States has reached alarming levels in areas with high impervious cover (Kaushal et al. 2005), and there is an
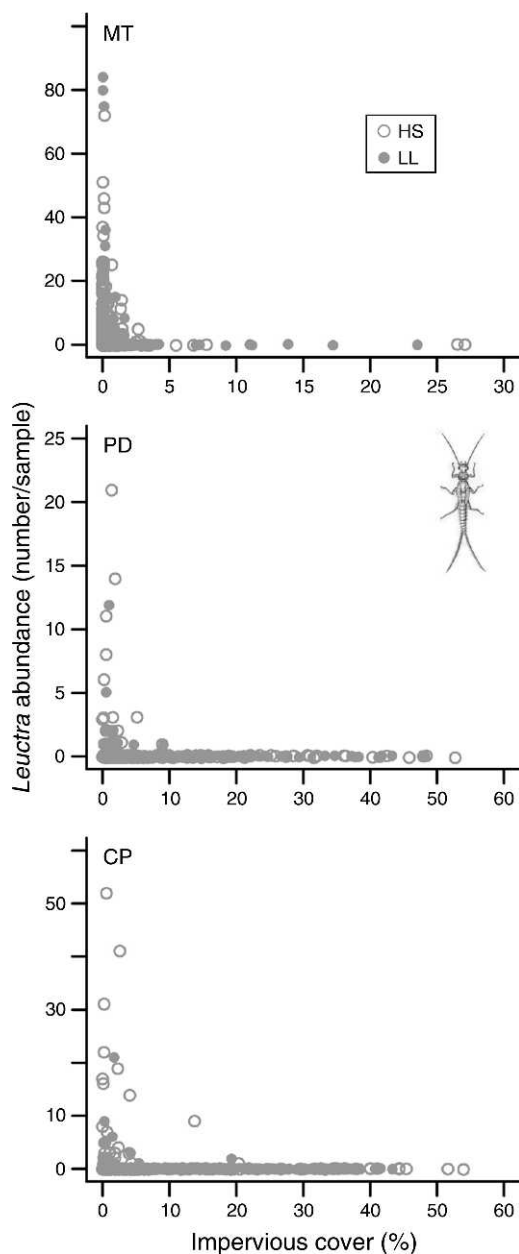
FIG. 6. Abundance of the stonefly, *Leuctra* (Plecoptera: Leuctridae), in response to impervious cover in each of the six catchment classes. *Leuctra* was a significant threshold indicator in all data sets. See Appendices C and D for scatterplots of abundance of all threshold indicator taxa in response to impervious cover. Key to abbreviations: MT, Mountain; PD, Piedmont; CP, Coastal Plain; HS, high-gradient, small catchments; LL, low-gradient, large catchments.

increasing body of evidence of reduced biodiversity caused by road salts in a variety of aquatic habitats (e.g., Karraker et al. 2008). Although the data analyzed in this paper represent a single snapshot in time measured a few months after typical road-salt pulses, our previous analyses (King et al. 2005) identified specific conductance, a very strong indicator of chloride concentrations

(Pellerin et al. 2008, Daley et al. 2009), as the strongest abiotic linkage between developed land and community dissimilarity among catchments. Differences among regions may also be related to the magnitude of road-salt use (presumably higher in the MT than PD and CP) coupled with the proximity of roads to streams (development and thus roads are consistently closer to streams in MT than PD and CP).

Evidence against road salts being the only or primary driver of degraded stream communities is the consistent decline of biodiversity along urban gradients in warmer regions, where road deicing is unnecessary (e.g., Walsh et al. 2005a, Cuffney et al. 2010). This implicates other physical or chemical stressors potentially linked to urbanization, many of which are unknown, unmeasured, or only recently discovered to be prevalent and highly toxic (Scoggins et al. 2007). At a minimum, elevated conductivity or chloride from road salts may serve as a conservative tracer of relative strength of connections between urban runoff and streams.

What are the implications for catchment assessment and management?

The threshold responses we report are alarming and we believe they require serious consideration in the context of global biodiversity losses. Rather than a management directive, the analytical results presented here should be used to inform the value-laden decisions surrounding land use policy and regulatory criteria. We need to know the true costs and environmental consequences of catchment development in order to make appropriate decisions in the face of human population growth. Here we report the strongest and most severe declines in stream invertebrate communities, but they are not the only changes we observe. Further declines in some taxa are apparent at levels of impervious cover approaching 10–15%, and the arrival or increases in still other taxa at higher levels of impervious cover denote additional changes. Management guidelines may also differ in cases of taxon decline vs. imminent extirpation. Explicit knowledge about what taxa change where and why can provide critical insight for future low impact and sustainable urban design.

As urban areas rapidly expand to support a burgeoning world population, biodiversity conservation will become increasingly challenging (Nilsson et al. 2003, Grimm et al. 2008). Our study has revealed that stream biodiversity sharply declines in catchments with levels of urbanization previously considered benign. The weight of evidence presented here demonstrates that relatively low levels of impervious cover drive community-level thresholds, and that catchment physiography modestly modulates this relationship. These results also demonstrate a need for focused research on key physical and chemical intermediaries, such as road-deicing salts, that mechanistically link impervious cover to these alarming taxa thresholds distinguished by TITAN. The implica-
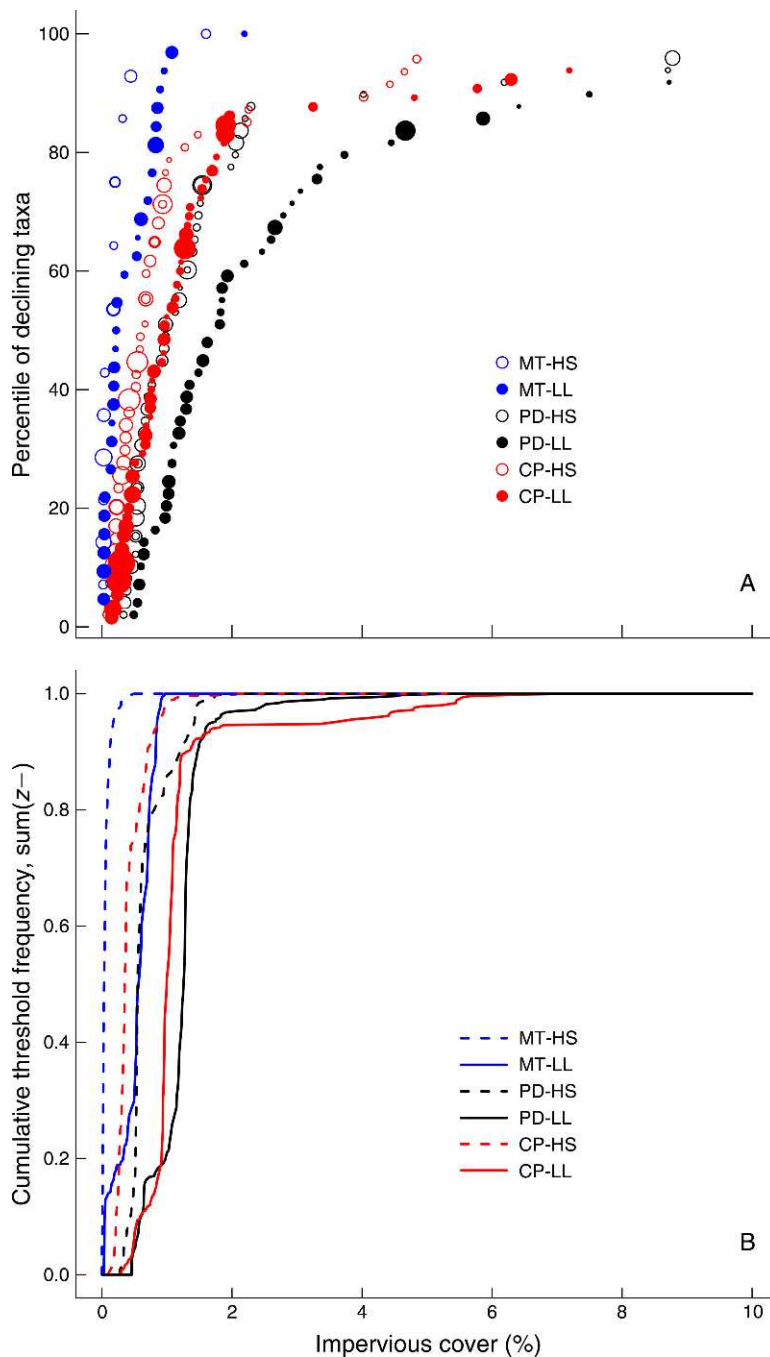
FIG. 7. (A) Percentile of significant negative (declining) threshold indicator taxa plotted against impervious cover by catchment class. Symbols are sized in proportion to taxa z scores. (B) Cumulative frequency distribution of sum(z–) thresholds among 500 bootstraps by catchment class.

tions of these findings are important in several management contexts, including but not limited to stream restoration (what is a realistic goal for biodiversity restoration under current or future levels of catchment imperviousness?), ecological forecasting (how much of our remaining biodiversity will succumb to encroaching development?), regulatory actions (what physical and chemical factors are driving these responses, and how can they be mitigated?), and conservation (where should conservation priorities be placed?). The sensitivity and precision of the TITAN method described in this paper should prove useful for detecting taxa-specific and community-level thresholds in support of similar management applications in other ecosystems.

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APPENDIX A

Taxonomic classification and ecological attributes of threshold indicator taxa (*Ecological Archives* A021-075-A1).

APPENDIX B

Impervious cover change points and indicator scores for significant threshold indicator taxa among catchment classes (*Ecological Archives* A021-075-A2).

APPENDIX C

Scatterplots of abundance in response to impervious cover (%) for every negative (z−) threshold indicator taxon among the six physiographic classes of catchments (*Ecological Archives* A021-075-A3).

APPENDIX D

Scatterplots of abundance in response to impervious cover (%) for every positive (z+) threshold indicator taxon among the six physiographic classes of catchments (*Ecological Archives* A021-075-A4).

APPENDIX E

Threshold indicator taxa analysis (TITAN) of macroinvertebrate community response to percent impervious cover between high-gradient, small (HS) and low-gradient, large (LL) catchments in the Coastal Plain (CP), Piedmont (PD), and Mountains (MT) (*Ecological Archives* A021-075-A5).