

Flow and impervious cover thresholds in aquatic communities in Austin, Texas.

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Ryan King, Ph.D, Baylor University
Abel Porras, P.E., City of Austin, Watershed Protection Department
Mateo Scoggins, City of Austin, Watershed Protection Department

Abstract

Climate change is predicted to increase the frequency and magnitude of extreme weather events. Such events coupled with demand for freshwater to support rapidly growing cities may reduce stream flow permanence and threaten stream biodiversity. Here, we examined the role that flow permanence and urbanization play in limiting stream biodiversity in the Austin, Texas, USA metropolitan area. We contrasted responses of macroinvertebrate communities to impervious cover (IC) among streams spanning a wide range of flow permanence using long-term biomonitoring and discharge data collected across 104 sites. The number of Ephemeroptera, Plecoptera and Trichoptera taxa significantly and independently declined with increasing IC and decreasing flow permanence. However, the decline in the number of all taxa as flow permanence decreased depended on the level of IC; higher IC levels were associated with disproportionately greater declines in taxon richness. Threshold Indicator Taxa ANalysis (TITAN) further parsed the community response by identifying 49 taxa that sharply declined in density and frequency of occurrence primarily between 3.7 and 24% IC. However, when the analysis was repeated after splitting the data into 2 groups of high and low flow permanence, the range of IC resulting in sharp density declines was lower for the low flow permanence group (3-11% IC, greatest change at 9% IC) compared with the high flow permanence group (7.7-28% IC, greatest change at 23% IC). Despite being composed of taxa largely regarded as pollution-tolerant, the low-flow permanence group of streams was characterized by taxa that evolved in habitats with intermittent flow and are integral components of their biological integrity. These results imply that future urban growth may have disproportionately negative effects on streams forecasted to become increasingly intermittent due to climate change.

Introduction

The natural flow regime of stream ecosystems constrains all facets of their physical, chemical, and biological condition (Poff et al. 1997). Flow permanence is one component of the natural flow regime and plays a critical role in shaping biological communities of streams (Feminella

1996). Many stream-dwelling taxa have evolved with life-histories requiring permanent flow to complete their life cycles (Hynes 1970, Allan and Castillo 2007, Merritt et al. 2008, Thorp and Covich 2009). Others have evolved to cope with intermittent flow, possessing traits or using mechanisms, e.g. diapause, that allow them to persist in still-water and dry-stream habitats (Boulton and Lake 1992, Williams 1996). Thus, coevolved communities of aquatic organisms may be as diverse and ecologically significant in streams with intermittent flow when compared to those with perennial flow (Lake 2000, Boulton 2003, Bonada et al. 2007, Meyer et al. 2007).

Urban streams in Austin, Texas, USA, a rapidly growing metropolitan area on the eastern edge of the semi-arid southwestern region of North America, have the typical hydrological problems encountered in densely developed areas. Impervious cover can reduce or increase baseflow by limiting the amount of water infiltrating into catchment soils or contributing water from irrigation runoff, leaky pipes, and point-source discharges, respectively (Bhaskar et al. 2016). Further, flow volumes and velocities often increase during storms due to the high quantities of water that run off impervious surfaces into stream channels. This creates unstable systems that can alternate between flood and dewatered conditions within very short time periods and stressful environments for the biological inhabitants. Due to the short duration, high intensity nature of rainfall events in central Texas, hydrologic regimes of streams tend to be more variable and dramatic than in more temperate regions of North America where most bioassessment protocols were developed (e.g., Fritz and Dodds 2005). Consequently, understanding the effects of hydrology on the biological communities of streams in this region is critical to the interpretation of benthic macroinvertebrate data.

Here we examined the independent and combined effects of flow permanence and catchment impervious cover on stream biodiversity using a 13-y benthic macroinvertebrate data set collected by the City of Austin. Because previous efforts conducted by the city have indicated relatively weak relationships between single-year estimates of biological condition in Austin streams and urbanization (Scoggins 2000, Richter et al. 2011), we took advantage of the repeated monitoring of individual sites to generate temporally integrated estimates of biodiversity and community structure to increase detection of individual taxa that may be influenced by the substantial temporal variability in precipitation and stream flow. We hypothesized that accounting for flow permanence using an empirical index developed from numerous stream-flow measurements at each site would reveal relationships between biodiversity and impervious cover otherwise masked in previous single-year analyses by the City of Austin due to differences in flow permanence among streams.

Methods

Study Area

The studied streams are located in and around the city of Austin, Travis County, Texas, (30° 16' 0" N, 97° 44' 34" W). Austin is a rapidly growing metropolitan area, with a population of 900,700 (city) and 1,990,600 (metropolitan area) in 2015. The climate is semi-arid with an average annual precipitation of 810 mm, spread relatively evenly throughout the year, but is characterized by high-intensity, short-duration precipitation events and a high average rate of pan evaporation (1,956 mm/y). Austin is in the transitional area between the Central Texas Plateau and Blackland Prairie ecoregions (Omernik 1987); this transition is often referred to as the

Balcones Escarpment, due to the contrasting topography and geology that is separated by a wide fault zone. Streams to the west are characterized by moderate gradients, limestone bedrock and karst hydrology, while streams to the east tend to be lower gradient with deep clay and alluvial soils (Fig. 1). The karst nature of the geology in many streams strongly drives hydrology, providing baseflow where springs are present, and removing flow where faults and features carry surface flow directly into aquifers (Passarello et al. 2012). Headwater streams can have stable baseflow due to high levels of groundwater contact, and larger order streams can lose 90% of flow into fault zones. Blackland Prairie streams often maintain perennial pools due to the thick clay character of the base material, but can lose connecting flow and have large dry reaches for much of the year, due to lack of groundwater contact and long periods with no rain. All these factors contribute to generally unpredictable flow permanence in streams in either ecoregion, not aligning with drainage area or stream order.

Biological Data

The City of Austin maintains a biological monitoring program that has been active for > 20 years. The program uses a fixed reach, repeated measures approach such that > 100 sites typically are sampled for benthic macroinvertebrates once every 2-3 years (City of Austin 2002). Most samples were collected during April, May, or June, although some samples were collected in February and March. Depending upon year, streams may have lost surface-water connections between riffles and glides/pools. Streams were otherwise sampled during baseflow conditions. At each site, at least 3 Surber samplers (total area $\geq 0.276 \text{ m}^2$) are collected from riffle or erosional habitat immediately at the base of riffles when riffles lack sufficient flow. The samples are composited and macroinvertebrates are sorted from debris in the field using a gridded pan with a target of 200 organisms; typically up to 250 are retained for identification, fewer if the entire sample contained fewer than 200 individuals. The proportion of the total sample (number of grid cells in the pan) picked is also documented so that counts can be converted to densities. Individuals are identified to the lowest practical taxonomic unit, which ranges from family to, more typically, genus and species.

Data collected at the initiation of the monitoring program were used to develop a multimetric Environmental Integrity Index used to benchmark and track the biological condition of reaches over time. The index is weighted by metrics of taxonomic richness, trophic structure, and tolerance to organic pollution (i.e., Hilsenhoff Biotic Index; Hilsenhoff 1987). However, as data was accumulated, the multimetric index was shown to be relatively insensitive to increasing levels of impervious cover but not to interannual and among-stream variation in flow (Glick et al. 2010). Such variability within streams over time strongly affects seasonal and annual macroinvertebrate community structure as well as other taxa such as periphyton (Muscio 2002), and fish (Pease et al. 2011, Stanley et al. 2012).

Therefore, we elected to integrate samples from each site across years sampled between 2000 and 2012, a period which ensured that each site had at least 3 years of sampling data. There were 104 sites with 3 or more years of sampling (Number of Years of Sampling, NYS); most had 4-5 NYS and the maximum NYS was 6 (Table 1). Preliminary diagnostics indicated that NYS was not likely to be an important confounding factor in subsequent analyses (see Data Analysis). From the temporally integrated samples, we calculated for each site 2 biodiversity metrics: the cumulative number of Ephemeroptera, Plecoptera, and Trichoptera taxa (EPT), a metric expected

to be dominated by flow-dependent taxa, and the total number of taxa (NTAXA), both using the cumulative number (not annual means) detected at each site over the study period. Community composition was also characterized at each site based on mean density (no/m²) of each taxon over time. Integrating samples over multiple years was also critical for evaluating to what degree flow permanence limited biodiversity and community structure and whether it masked effects of impervious cover.

Table 1. Quantiles of variables that may confound GLM models relating impervious cover and flow permanence to biological responses in the Austin data set (n=104).

| Variable | Quantiles | | | | |
|--|-----------|------|------|------|-------|
| | 0 | 0.25 | 0.5 | 0.75 | 1.0 |
| Impervious cover, %, catchment | 0.0 | 5.7 | 21.8 | 37.0 | 60.6 |
| Flow permanence index | 13.3 | 54.9 | 74.9 | 87.4 | 97.0 |
| Number of years benthic samples collected, 2000-2012 | 3 | 4 | 5 | 5 | 6 |
| Catchment area, km ² | 1.4 | 4.6 | 11.3 | 35.8 | 889.7 |
| Catchment slope, %, mean | 2.2 | 4.3 | 5.3 | 8.0 | 23.7 |
| Reach slope, %, 500 m | 0.5 | 4.3 | 7.2 | 9.5 | 23.6 |
| Natural land cover, %, catchment (forest, wetland, shrubland, grassland) | 0.0 | 11.4 | 42.0 | 77.4 | 97.3 |
| Wetland cover, %, catchment | 0.0 | 0.1 | 0.3 | 1.4 | 5.6 |
| Cropland, %, catchment | 0.0 | 0.0 | 0.0 | 0.1 | 16.2 |
| Pasture, %, catchment | 0.0 | 0.0 | 0.0 | 0.0 | 5.2 |

Flow Permanence Index

Individual observations of instantaneous stream flow (discharge) were used in a probability analysis to establish a gradient of long-term stream flow permanence across the Austin area (Porras and Scoggins 2013). Approximately 9,000 individual observations of stream discharge derived from 126 distinct biological sampling reaches were incorporated into the analysis from long-term City of Austin ambient stream monitoring records from 1991 to 2012. These individual observations occurred consistently throughout the above time frame during quarterly surface-water sampling. Surface flow was observed during base flow conditions at random days within the quarter regardless of antecedent climatic conditions (wet years, dry years) and all locations were visited, regardless of anticipated flow regime (perennial, intermittent, ephemeral). The quarterly frequency provides sufficient time for independence among the observations while sampling base flow mitigates bias from storm events. A sampling reach was classified as having flow or flow permanence at the time of sampling if flow was $> 0.0003 \text{ m}^3/\text{s}$ or there was visually discernible flow if stream discharge was not directly measured. When measured directly, stream discharge was measured using Marsh-McBirney electromagnetic velocity meters and the standard velocity-area method (Holmes et al. 2001).

Each sampling event at each site was partitioned into the binary categories of flowing or not flowing. Confidence intervals were constructed on the true proportion of sampling events with flow for each sampling reach following calculation methods described by Blyth and Still (1983). From these intervals, a Flow Permanence Index (FPI) was developed to estimate the proportion of times a sampling reach will have surface flow. The FPI was then calculated for each sampling reach (equation 1):

$$\text{FPI} = 100 \cdot p_l + 1/[100 \cdot (p_u - p_l)] \quad \text{Eq. 1,}$$

where p_l and p_u are the lower and upper confidence intervals, respectively, on proportion of observations with flow. This formula scores sites higher in the index based on two components: its lower confidence interval and uncertainty. The reach with the smallest uncertainty scored higher than reaches with the same lower confidence intervals and larger uncertainty. Those reaches with the highest total number of site visits had smaller uncertainty and smaller range, and thus, had higher FPI scores. Although higher FPI scores have a higher probability of flow permanence they do not guarantee flow at a site and conversely, low FPI scores do not guarantee dry conditions.

Land Cover and Topographic Data

Terrain analysis, catchment delineation, and impervious-cover estimation were accomplished in ArcGIS 10 (ESRI, Inc., Redlands, California). We used the geographic coordinates of the each stream reach to define a catchment outlet. We determined the contributing area of a catchment draining to each outlet using flow accumulation values derived from a digital elevation model (DEMs) expressed as a 3 m raster (City of Austin 2007).

We estimated land use/land cover in each catchment by performing weighted flow accumulations such that the ratio of the number of flow-accumulated cells of a particular land-cover class to the total flow accumulated cells * 100 was equivalent to the % cover of that land-cover class. This

approach produced a continuous estimate of % cover of each class across every pixel representing the entire stream network. We used the National Land Cover Data (MRLC 2012) raster for all types of land cover that occurred in the study catchments except impervious cover (IC). We used an IC raster developed by the City of Austin (City of Austin 2006) to estimate % IC in each catchment.

We also estimated size and gradient metrics intended to capture first-order controls on water movement in each catchment to characterize physiographic differences that could modulate or confound the unit effect of IC or flow permanence on biological responses. Catchment area (km²) was calculated to estimate the effect of stream size on biota. Topographic metrics included mean catchment slope (%) and mean reach slope (%; 500 m segment). Finally, we classified each reach by its corresponding Level III ecoregion (Omernik et al. 1987), which was either the Central Texas Plateau or Blackland Prairie.

Data Analysis

We conducted a multi-stage analysis of biological responses to IC and FPI using data visualization, generalized linear models (GLM), ordination (nonmetric multidimensional scaling; NMDS), multivariate GLM (Wang et al. 2012), and Threshold Indicator Taxa ANalysis (TITAN; Baker and King 2010). Prior to conducting any analyses, we followed steps recommended by Zuur et al. (2010) to identify potential confounding factors or other problems that could compromise the models. First, we visually screened data by mapping variable-scaled points to assess spatial contagion of predictors and response variables. This step was followed by graphically evaluating pairwise relationships among predictors and response variables with bubble plots that allowed as many as five variables to be screened at once. We further calculated correlation matrices to assess collinearity and variance inflation among predictors, and ultimately modeled the responses as a function of IC and FPI along with variables deemed to be potentially important confounders or covariates.

We used GLM to model EPT and NTAXA in response to IC, FPI, and potential covariates. We specified a Poisson distribution for each model because the response variables were counts but were not overdispersed (Zuur et al. 2009). Models were constructed with IC, FPI, an IC*FPI interaction term, and NYS, ecoregion, and catchment area (log transformed) as covariates. The covariates selected were the only variables that showed any pattern in data visualization that could be viewed as potentially important (Zuur et al. 2010). Covariates were sequentially removed from the full model based on effect size and the simpler model was rerun. This was repeated for all variables. Models were compared using Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002) using standard procedures to identify models with the fewest predictors that captured the most information. We carefully examined residual plots to assess heterogeneity, which was deemed acceptably low for the selected models. We used the `glm` function in R 3.1 (R Core Team 2014) to fit the models.

We used the `predict.glm` function to generate responses of EPT and NTAXA to FPI after iteratively holding IC constant at 0, 5, 10, 20, 30, 40, 50, and 60%. These modeled predictions produced a response surface depicting the effect of FPI given different levels of IC. If any covariates were included in the model, the mean value of that variable was assigned to every site

to hold that effect constant. We plotted the predictions as response surfaces using `ggplot2` in R 3.1.

We visualized dissimilarity in community structure among sites using NMDS ordination. We used Bray-Curtis dissimilarity (%) as the distance metric, 500 random starts to select the best model (lowest stress), and log-transformed taxa densities ($n=179$ taxa) prior to analysis to increase the contribution of taxa that have low densities but may be highly sensitive to IC or FPI. We reduced the number of taxa from 179 to 128 because stress (an indicator of how well distances among sites were represented in the ordination compared to the rank dissimilarities in the data matrix) was reduced and stabilized after eliminating taxa that only occurred 1 or 2 times out of 104 sites. We graphically evaluated gradients in composition using bubble plots that sized symbols in proportion to a variable of interest. We also used rotational vector fitting to identify the direction and magnitude of the correlation between IC and FPI and the configuration of sample units in ordination space. NMDS ordination and vector fitting were conducted using the `vegan` package (Oksanen et al 2015) in R 3.1, whereas graphs were made using `ggplot2`.

Whereas NMDS provided a visual model of gradients in community structure, the `mvabund` package for R 3.1 provided a statistical model for estimating the statistical significance of IC, FPI, and their interaction on community structure (Wang et al. 2012). We used the `manyglm` function to build the multivariate model, a procedure that fits a separate GLM to each species. This model-based approach also allows the specification of the appropriate distribution for fitting the data and conducting hypothesis tests. We used the negative binomial distribution because untransformed taxa densities were overdispersed. One important limitation of the method is that the multivariate test is highly dependent upon the number of taxa modeled; and is particularly degraded by inclusion of numerous taxa with low frequency of occurrence. Therefore, we limited the analysis to taxa with ≥ 20 occurrences (out of 104 sample units; $n=53$ taxa). We limited our interpretation to the multivariate test.

We further parsed community responses to IC and FPI using TITAN, a method that has been shown to reveal sharp, nonlinear declines in simulated and real community data that are otherwise revealed as linear or completely masked by aggregate community metrics such as EPT (King and Baker 2010, 2011). TITAN identifies the value of an environmental variable (in this case, IC or FPI) that maximizes association of a taxon's frequency and abundance on one side of the gradient (Baker and King 2010, 2013). Association is measured by `IndVal`, computed as the product of the percentage of sample units in which a taxon occurs and the percentage of the number of individuals captured by each partition (Duf rene & Legendre 1997). Bootstrapping is used to identify reliable indicator taxa. A taxon is determined to respond positively or negatively to the gradient of interest if 1) the change in frequency and abundance of the taxon is in the same direction for at least 95% of the 1000 bootstrapped runs = "high purity", and 2) at least 95% of 1000 bootstrapped runs are significantly different from a random distribution (at $p < 0.05$) = "high reliability". The sum of `IndVal` z scores is used as an indicator of community- (or assemblage) level thresholds by identifying peaks in sums of all taxa z scores along the gradient associated with the maximum decline in all negative responders (z-) or increase in frequency and abundance of all positive responders (z+).

We performed TITAN in R 3.1 using the package `TITAN2` (Baker and King 2013). We required that the minimum number of observations on either side of any partition was ≥ 3 and retained taxa with ≥ 3 occurrences for analysis. We did not transform taxa densities because King and Baker (2014) deemed transformation unnecessary in most situations in TITAN. We ran TITAN using IC and FPI as predictors in separate models. As a result of a strong effect on community structure at FPI ~ 70 , we split the data set into two groups (≥ 70 , <70 ; $n=60$ and 44 sample units, respectively) and reran TITAN using IC as the predictor to evaluate whether there were differences in the unit effect of IC above and below this FPI threshold.

Results

FPI was not strongly related to any landscape variables, including catchment area (Table 2) despite a large range among catchments (1.4–890 km²; Table 1). IC and FPI also were weakly correlated, and scatterplots confirmed a wide spectrum of FPI values across the full gradient of IC and between ecoregions (Figures 1 and 2).

IC was also widely distributed between ecoregions, although the highest IC values tended to be in the Blackland Prairie (Figures 1 and 2). IC was almost perfectly correlated to percent natural land cover (Table 2), indicating that the absence of natural land cover in this data set was almost exclusively represented by a proportional replacement with IC.

Table 2. Pearson correlation (r) matrix among variables that may confound GLM models relating impervious cover and flow permanence to biological responses in the Austin data set (n=104). Correlations > 0.50 are bold.

| Variable | ic | flowindex | n.years | catkm2 | catslp | rchslp | natural | wetland | crop | pasture |
|--|--------------|-----------|---------|--------|--------|--------|---------|---------|-------------|---------|
| Impervious cover (ic) | 1.00 | | | | | | | | | |
| Flow permanence index (flowindex) | 0.18 | 1.00 | | | | | | | | |
| Number of years benthic samples collected, 2000-2012 (n.years) | -0.17 | 0.33 | 1.00 | | | | | | | |
| Catchment area (catkm2), log-transformed | -0.34 | 0.26 | 0.00 | 1.00 | | | | | | |
| Catchment slope (catslp) | -0.27 | -0.03 | 0.24 | -0.05 | 1.00 | | | | | |
| Reach slope (rchslp) | 0.08 | -0.04 | 0.29 | -0.28 | 0.11 | 1.00 | | | | |
| Natural land cover (natural) | -0.94 | -0.18 | 0.10 | 0.37 | 0.36 | -0.16 | 1.00 | | | |
| Wetland cover (wetland) | -0.07 | 0.23 | 0.04 | 0.01 | -0.20 | 0.08 | -0.05 | 1.00 | | |
| Cropland (crop) | -0.28 | -0.30 | 0.00 | -0.03 | -0.22 | 0.16 | 0.19 | 0.32 | 1.00 | |
| Pasture (pasture) | -0.23 | -0.19 | 0.04 | 0.10 | -0.18 | 0.18 | 0.17 | 0.20 | 0.73 | 1.00 |

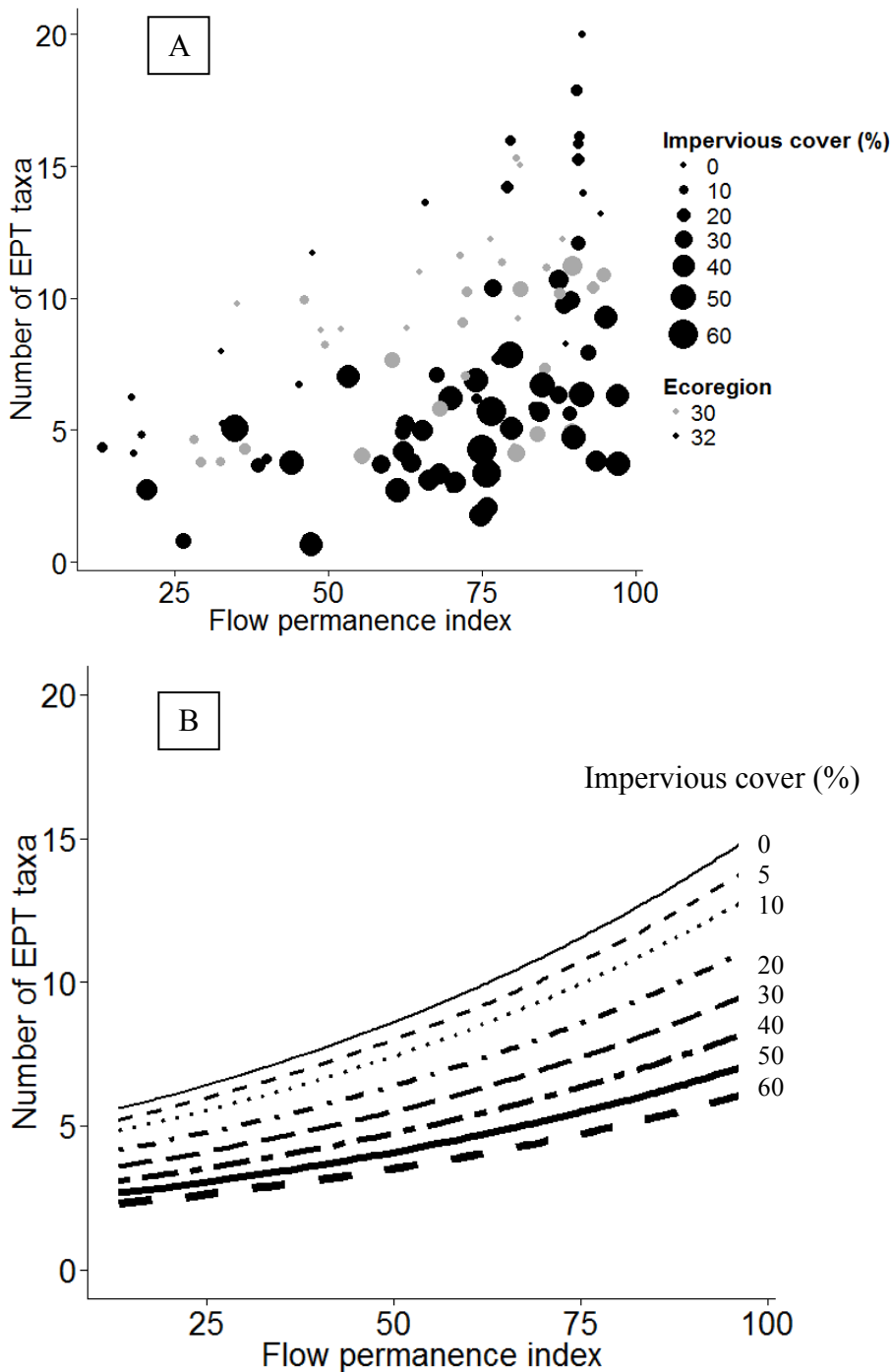


Figure 1. (A) Bubble plot of EPT in response to FPI. Symbols are sized in increments corresponding to IC and colored to correspond to ecoregions. (B) Predicted responses of EPT to FPI at different increments of IC based on GLM (see Table 3; note that the effect of catchment area is removed from the predicted relationships).

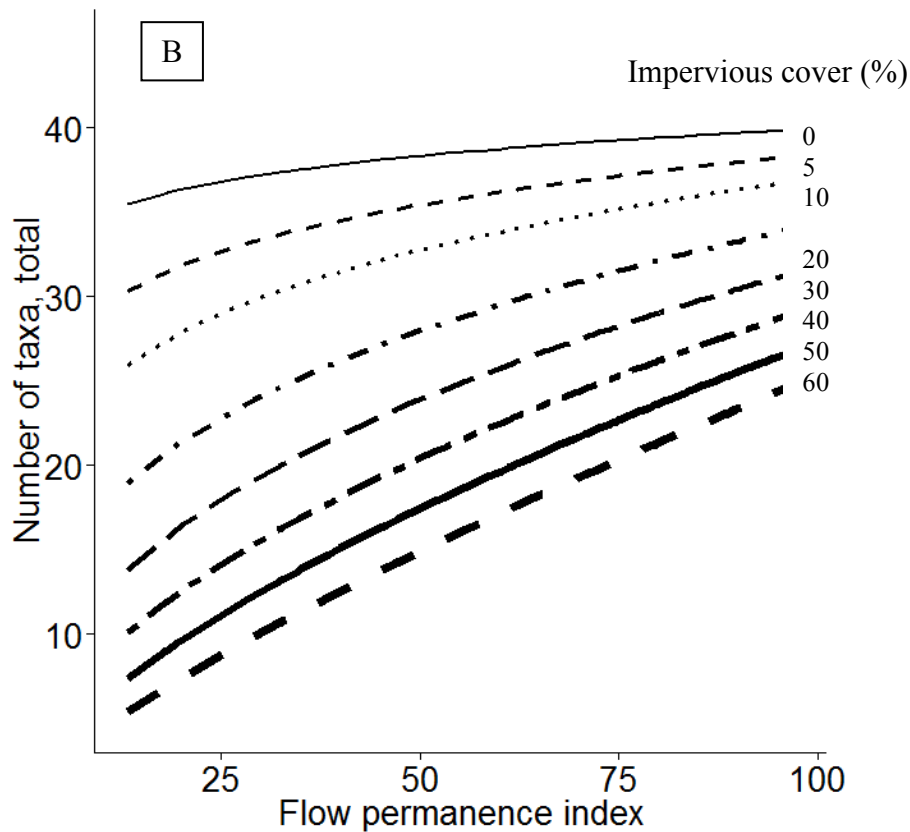
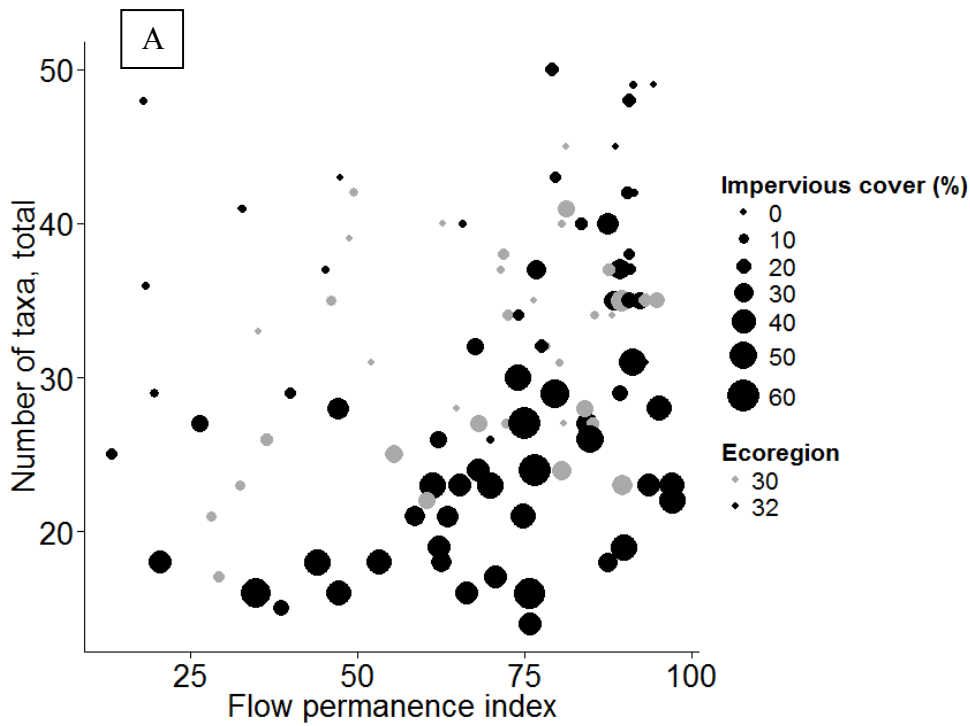


Figure 2. (A) Bubble plot of NTAXA in response to FPI. Symbols are sized in increments corresponding to IC and colored to correspond to ecoregions. (B) Predicted responses of NTAXA to FPI at different increments of IC based on GLM (see Table 3).

The GLM model resulting in the best fit of EPT included IC, FPI, and catchment area as predictors (Table 3). The interaction between IC and FPI was not significant, nor were other covariates. Bubble plots illustrated a positive relationship between FPI and EPT (Figure 1A). Sites with FPI values < 50 supported 1 to 10 EPT taxa with most sites supporting 5 or less, whereas sites with FPI values near the maximum (100) supported as many as 20; the ceiling of this positive, wedge-shaped relationship was approximately linear. IC also appeared to limit EPT in a similar manner such that low or high FPI sites had fewer EPT taxa with increasing IC (Figure 1A). GLM predictions of EPT in response to FPI and IC while holding catchment area constant revealed a relatively proportional, negative effect of IC with decreasing FPI (Figure 1B). EPT decreased rapidly with decreasing FPI until reaching about 70, beyond which EPT decreased more slowly.

The best GLM model of NTAXA included IC and an interaction between IC and FPI (Table 3). No covariates were deemed significant or sufficiently improved information ($\Delta AIC_c < 2$). NTAXA exhibited a non-significant relationship to FPI alone, but instead was reduced disproportionately by increasing IC as FPI declined (Figure 2A). GLM predictions revealed a nearly flat relationship between NTAXA and FPI when IC=0%, but increasingly steeper declines with increases in IC (Figure 2B).

Table 3. Summary of results from generalized linear models (GLMs) of total number of taxa (NTAXA) and number of EPT taxa to impervious cover (IC) and flow permanence index (FPI). See text for details about covariates and model selection and figures 2 and 3 for illustration of the results.

AREA=catchment area, km².

| NTAXA | | | |
|------------------------------------|--|------------------------------|---------|
| Coefficients | Estimate | Std. error | z value |
| Intercept | 3.521 | 0.251 | 13.61 |
| IC | -0.025 | 0.015 | -4.266 |
| FPI | 0.002 | 0.001 | 1.673 |
| IC*FPI | 0.018 | 0.003 | 3.463 |
| Null deviance: 278.59 on 103 df | Residual deviance: 126.75 on 100 df | Deviance explained: 54.5% | |
| ----- | | | |
| EPT | | | |
| Coefficients | Estimate | Std. error | z value |
| Intercept | 1.293 | 0.147 | 8.815 |
| IC | -0.0149 | 0.0027 | -5.353 |
| FPI | 0.0117 | 0.002 | 5.662 |
| log(AREA) | 0.0672 | 0.0279 | 2.411 |
| Null deviance: 220.47 on 103 df | Residual deviance: 95.13 on 100 df | Deviance explained: 56.8% | |

NMDS ordination revealed a pattern in community structure that was consistent with the significant interacting effect of FPI and IC on NTAXA (Figure 3). NMDS 1 was aligned strongly with FPI ($r=0.79$) whereas NMDS 2 represented a strong gradient in IC ($r=0.73$). Sample units along NMDS 1 were widely and quite evenly dispersed when IC was near 0% (negative end of NMDS 2), but converged toward the middle as IC increased (positive end of NMDS 2). Bubble plots revealed that sample units

with moderate levels of IC were also mixed with units with very low IC on the ordination where FPI was highest. However, as NMDS 1 scores decreased (lower FPI), sample units were almost exclusively represented by low-IC sites, reflective of the disproportionate effect of IC on community structure when FPI declined.

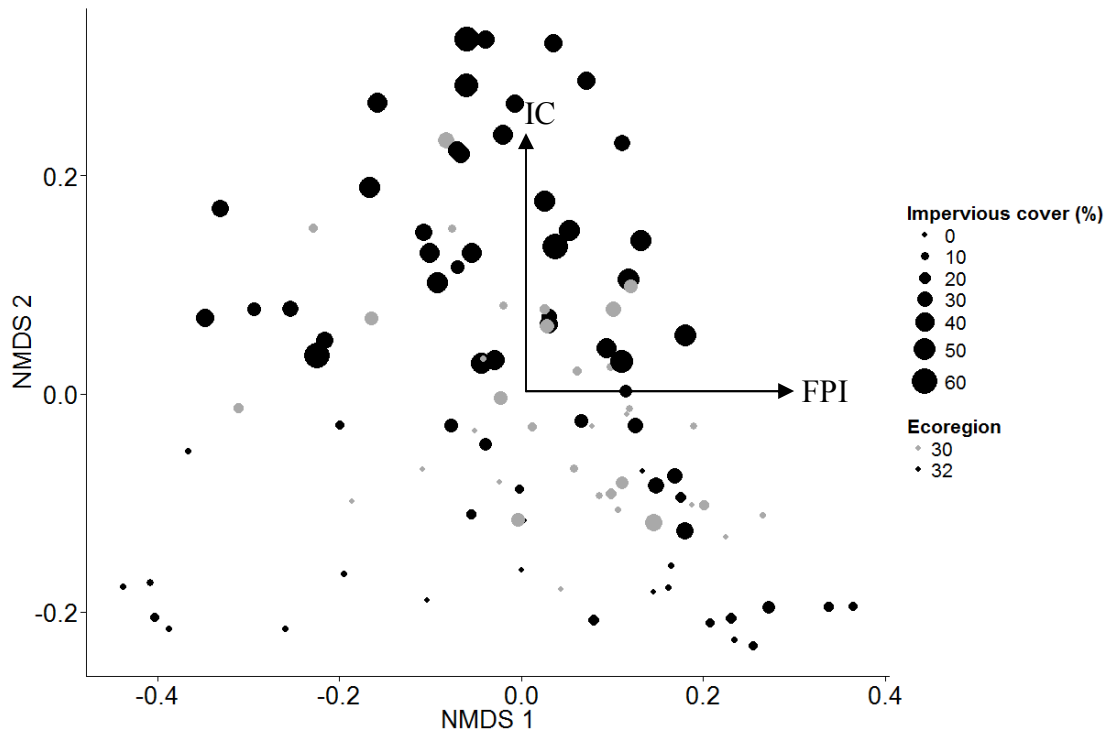


Figure 3. NMDS ordination of community structure. Symbols are sized in increments corresponding to IC and colored to correspond to ecoregions

Multivariate GLM further confirmed the significant interacting effect of IC and FPI on community structure (deviance explained: IC, 267.9 ($p \leq 0.001$); FPI, 337.8 ($p \leq 0.001$), IC*FPI, 104.6 ($p \leq 0.01$)). Thirty-five of the 53 taxa included in the model contributed significantly to the multivariate responses related to IC, FPI, and/or the IC*FPI interaction term (individual taxa results not shown).

TITAN further parsed community responses by identifying 49 (of 128) taxa that sharply declined in response to IC, with most change points observed between 3.7 to 24% IC. Six taxa gradually increased with increasing IC (Figure 4, Table 4). In contrast, a large group of taxa (29 of 34 increasers) coincidentally increased when FPI exceeded ~ 70 . *Brechmorhoga mendax*, an odonate, was the last of a series of coincidental decliners; its change point was 71 with a lower FPI of 68, whereas a slightly smaller group of taxa declined (24) in a more gradual fashion with increasing FPI, with zones of greatest change typically below 70-80 FPI (Figure 5, Table 4).

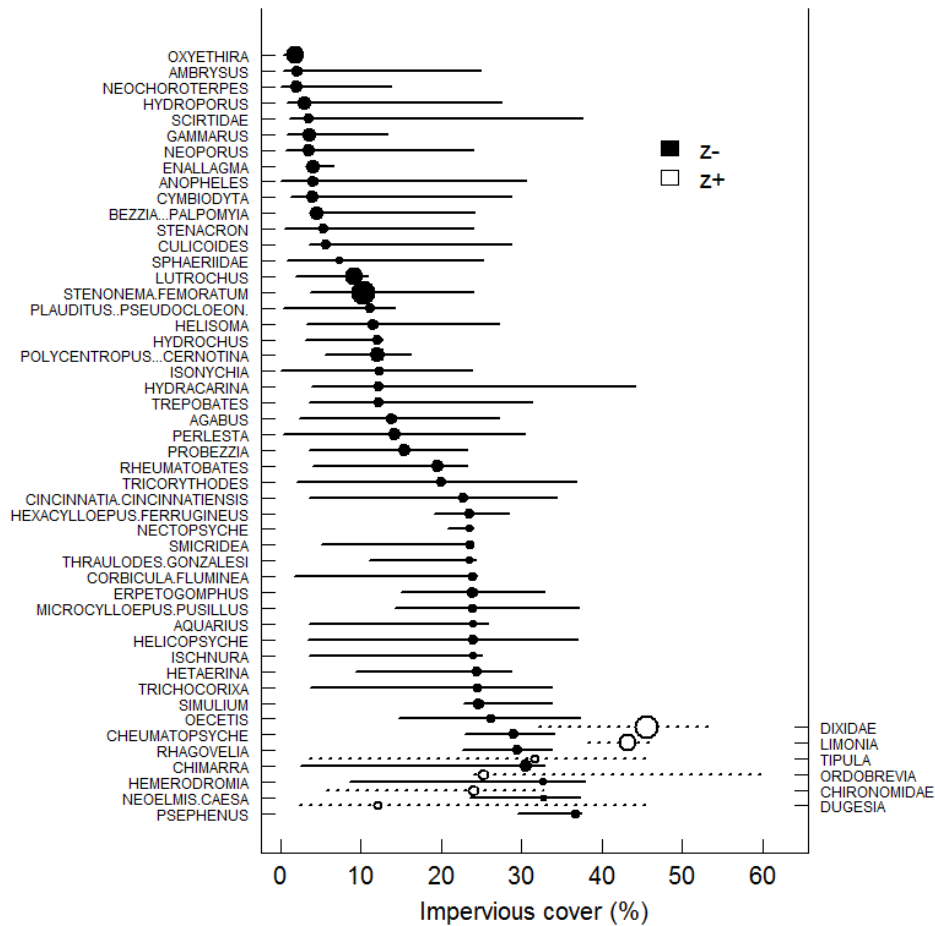


Figure 4. Results from TITAN on individual taxa densities in response to IC. Black symbols correspond to taxa that declined with increasing IC (z-), whereas open symbols correspond to those that increased (z+). Symbols are sized in proportion to the magnitude of the response (z-score). Horizontal lines represent 5th and 95th quantiles of values of IC resulting in the largest change in taxa z-scores among 1000 bootstrap replicates.

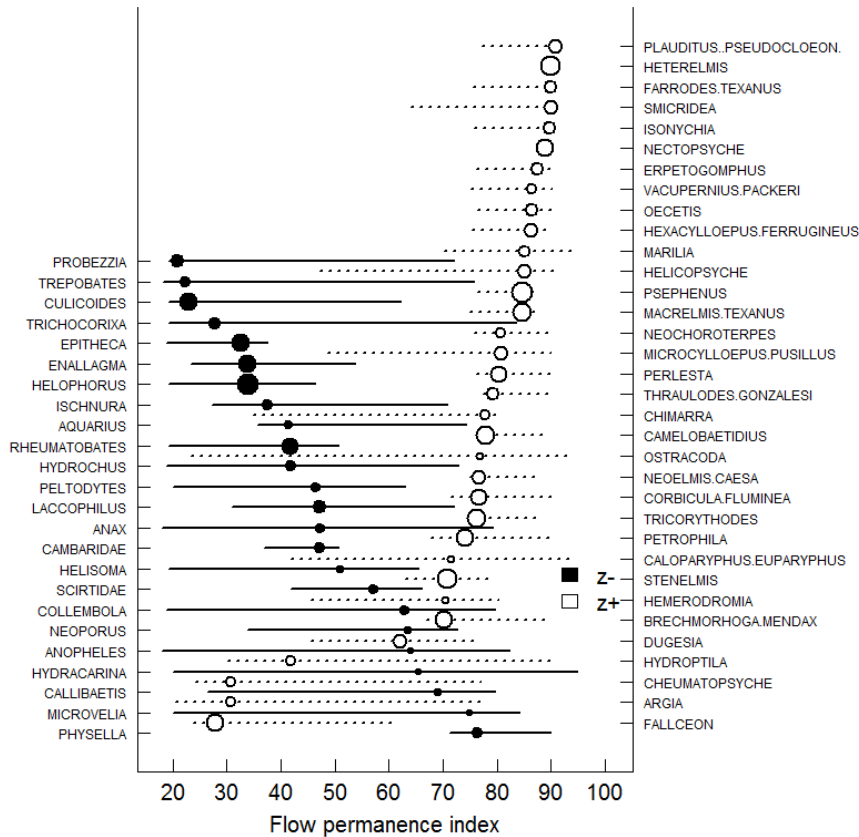


Figure 5. Results from TITAN on individual taxa densities in response to FPI. Black symbols correspond to taxa that declined with increasing FPI (z-), whereas open symbols correspond to those that increased (z+). Symbols are sized in proportion to the magnitude of the response (z-score). Horizontal lines represent 5th and 95th quantiles of values of IC resulting in the largest change in taxa z-scores among 1000 bootstrap replicates.

Table 4. Community-level thresholds of impervious cover and flow permanence index values estimated by Threshold Indicator Taxa ANalysis (TITAN). Observed thresholds correspond to the maximum sum(z) whereas the 5th, 50th and 95th percentiles (in parentheses following the observed value, respectively) correspond to the frequency distribution of thresholds from 1000 bootstrap replicates (see Figures 5-7 for taxon-specific results corresponding to community-level thresholds). Note: sum(z+) represents the subset of the assemblage that responds positively to increasing values of IC or FPI; in the case of IC, these are taxa tolerant of increasing stress related to urbanization, whereas for FPI, these are taxa that are sensitive to the consistency of stream flow (i.e., decline with declining flow permanence).

| Variable | TITAN sum(z-) change point | TITAN sum(z+) change point |
|-----------------------------|----------------------------|----------------------------|
| Impervious cover (IC) | 23.8 (3.76, 23.3, 24.1) | 32.7 (24.2, 36.8, 59.0) |
| Flow permanence index (FPI) | 49.1 (18.9, 46.2, 63.1) | 76.1 (75.0, 76.6, 90.1) |
| IC FPI < 70 (n=44) | 9.34 (3.68, 9.34, 11.13) | 45.5 (24.0, 41.4, 46.3) |
| IC FPI ≥ 70 (n=60) | 23.8 (7.72, 23.6, 28.2) | 43.3 (12.3, 37.2, 59.0) |

When TITAN was repeated after splitting the data into 2 FPI groups (≥ 70 and < 70), the range of IC resulting in sharp taxa declines was lower for the low FPI group (3-11% IC, greatest change at 9% IC; Table 4, Figure 6A) than for the high FPI group (7.7-28% IC, greatest change at 23% IC; Figure 6B, Table 4).

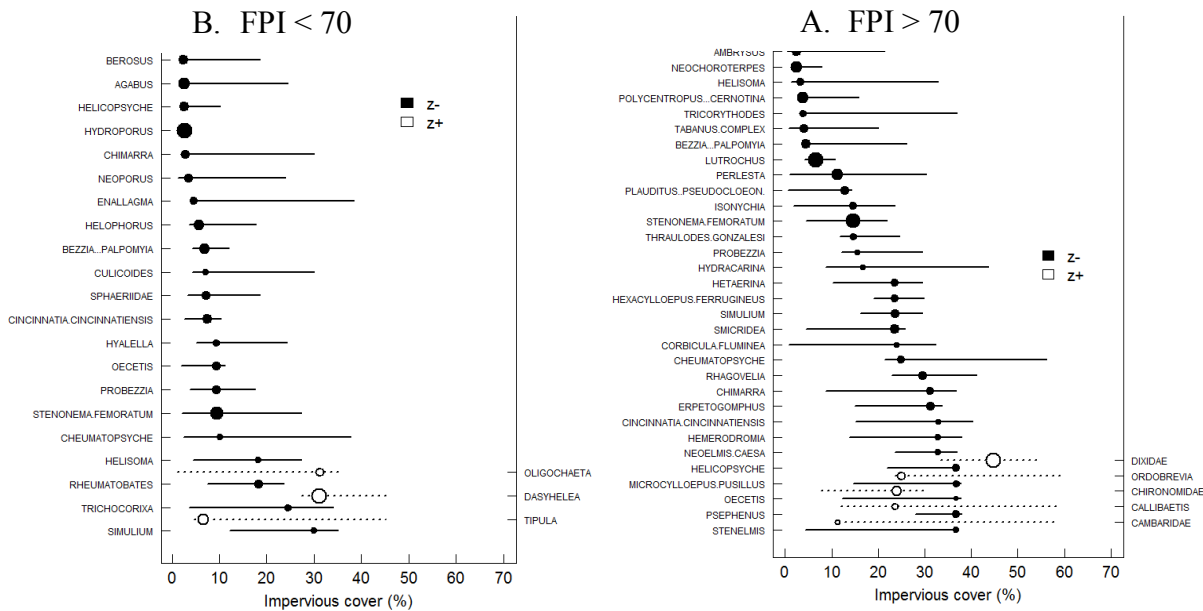


Figure 6. Results from TITAN on individual taxa densities in response to IC when (A) $FPI < 70$ and (B) $FPI \geq 70$. Black symbols correspond to taxa that declined with increasing FPI (z-), whereas open symbols correspond to those that increased (z+). Symbols are sized in proportion to the magnitude of the response (z-score). Horizontal lines represent 5th and 95th quantiles of values of IC resulting in the largest change in taxa z-scores among 1000 bootstrap replicates.

Discussion

An emerging theme among recent studies of urbanization effects on streams is that regional context matters (Hale et al. 2016, Utz et al. 2016). While this idea should not come as a surprise, it is a contrast to the broad generalization of a biological threshold at 10% IC (Schueler 1994) or linear response models implying a gradual degradation of stream biological condition (reviewed by Walsh et al. 2005a). Here, our multi-stage analysis of both univariate metrics and multivariate community structure revealed several results that were somewhat distinct when compared to those from studies of streams in mesic climates with greater flow permanence (e.g., Walsh et al. 2005b, Booth 2005, King et al. 2011) as well as studies conducted in the same ecoregion and climate (Cuffney et al. 2010).

Arguably the most intriguing finding was the disproportionate effect of IC on biodiversity (NTAXA) and community structure as flow permanence declined. We expected flow permanence to play a strong role in limiting and confounding biodiversity response to urbanization. Indeed, flow permanence did limit EPT, a taxonomic aggregation of mostly flow-dependent taxa and widely considered to be one of the best univariate metrics of stream biological integrity (Barbour et al. 1999). EPT was nonlinearly related to FPI, declining rapidly as FPI declined and gradually leveling off once FPI fell below ~ 70 . Further, the effect of IC on EPT was proportional along the FPI gradient, further reducing EPT as IC

increased regardless of FPI. In contrast, NTAXA remained high with minimal declines with decreasing FPI when IC was low, indicative of a continuum of taxa that have evolved in and are characteristic of temporary flowing habitats (Feminella 1996).

We did not expect that the unit effect of IC on the NTAXA would be stronger on low-FPI communities than on those from streams with permanent or near-permanent flow. Mechanisms for this result were not quantitatively addressed in this study but may be related to greater frequency and intensity of disturbance during storm events limiting adequate refugia for taxa in low FPI streams (Lake 2003), such as dense accumulations of terrestrial detritus in pools and glides (Reid et al. 2008). Other factors may include greater contact with persistent chemical pollutants in sediments due to greater dependence upon depositional habitats (Scoggins et al. 2007), and increased organic pollution that may exacerbate dissolved oxygen depletion at night and amplify pH during the day (Valenti et al. 2011).

Bhashkar et al. (2016) emphasized a variety of potential influences of urban land cover on baseflow in streams, including increased baseflow. Although our data did not reveal a pattern consistent with a clear increase or decrease in flow permanence, it is important to acknowledge that, in other regions, the effect of IC could have had a much different effect on stream biodiversity if increased baseflow were the predominant effect. Moreover, alternative stormwater management associated with future urban growth in the Austin metropolitan area could also lead to a different effect of IC on biodiversity across the flow permanence gradient (Walsh et al. 2016). Thus, our results must be interpreted within the context of the climate and physiography of this particular region (e.g. extremely flashy hydrology, karst geology, hot and dry summers) and historical and current urban stormwater management.

Another finding that was distinct from many other regions was the relatively broad zone of IC resulting in biodiversity declines at high FPI. In the TITAN analysis of sites with $FPI \geq 70$, there was a much wider spread in the distribution of change points among taxa that declined significantly in response to IC when compared to ones that declined in the low-FPI group. Levels of IC associated with sharp nonlinear declines in individual taxa and community metrics have been shown to be as low as 1-5% in many other regions (e.g., King et al. 2011a, b; Walsh and Webb 2016). Regional differences in physiography and climate again are likely responsible for higher thresholds for biological degradation in Austin streams with high FPI. In this study area, the natural flow regime (Poff et al. 1997) exhibits very high seasonal and interannual variability. Non-urbanized 2nd to 4th order streams with near-permanent flow may have median summer baseflow as low as $0.001 \text{ m}^3/\text{s}$ yet experience storm-flow events that increase instantaneous discharge to $>1,000 \text{ m}^3/\text{s}$ (catchment areas 5-35 km^2). The slight to moderate increase in magnitude of runoff associated with IC is unlikely to have the same unit effect in these streams as in regions with typically much lower extremes in discharge because biota are naturally adapted to a flashy flow regime (Hawley and Vietz 2016, Walsh and Webb 2016).

Walsh et al. (2005a, b) and Walsh and Webb (2014, 2016) have demonstrated stronger relationships between biota and urbanization when only IC that is connected to stream channels by storm drains is used as a predictor ("effective imperviousness" or EI). Our estimates of IC were not restricted to EI because the data needed to estimate EI were not available. Future analyses based on EI and distance-weighting of land cover (King et al. 2005, Walsh and Webb 2014) may be warranted and could improve predictive models relating IC, FPI and biological condition in Austin area streams.

Research has demonstrated minimal influence of IC on univariate community metrics in metropolitan areas in the USA where antecedent agriculture presumably had degraded streams to the point where IC had no additional effect, including the Dallas-Fort Worth (DFW), TX metropolitan area ~250 km north of Austin (Cuffney et al. 2010). In our study, we found highly significant relationships between IC and all measures of biological condition, especially when we accounted for FPI. Integration of biological data from the same sites over several years may be one factor that allowed us to detect stronger IC signal than did Cuffney et al. (2010) in the DFW area, despite the higher levels of antecedent agriculture in their study catchments. The size of streams sampled in their study could be classified anywhere from low to high FPI because DFW and Austin have similar climates and over half of the data in this study were collected from the same ecoregion as the Cuffney et al. (2010) study (Blackland Prairie). Thus their single-year data probably were affected by antecedent flow status and differences in flow permanence among streams in addition to the antecedent agriculture. Previous analyses using single-year data from the Austin data set showed very weak responses of community metrics to IC (Scoggins 2000, Richter 2011). Thus, the weak linkage between IC and biological condition in streams of DFW and other regions with similar flow regimes to streams in Austin may be at least partially influenced by flow permanence and the absence of multiple years of data from each stream.

The development of the FPI unequivocally enhanced our understanding of factors limiting stream biodiversity in the semi-arid, southwestern region of the USA. An important outcome of this study is the potential for using GLM or similar models for establishing benchmarks for biological condition given the FPI of a stream. For example, sentinel sites could be monitored more frequently to provide a temporally integrated assessment of biodiversity that could be contrasted to the expected mean value (with error) at a test site with a particular FPI when IC is set to 0% or some other benchmark selected by managers. Analogous to the reference condition approach (RCA; Reynoldson et al. 1997), continuous IC benchmark estimates could be used rather than ones based on groups or classes of streams (e.g. Paul et al. 2009). Further study could explore developing an RCA-type model based on expected and observed taxa along a continuum of FPI.

Climate forecasting predicts more extreme weather events in the southwestern USA and in many other parts of the world (Leigh et al. 2014). This fact, coupled with rapid population growth forecasted for the southwestern USA region suggests that streams may become more intermittent while also being situated in catchments with increasing levels of impervious cover. Therefore, the main implication that can be drawn from our results is that future urban growth may have disproportionately negative effects on the biodiversity of streams forecasted to become increasingly intermittent due to global change.

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