Aquatic insect functional diversity and nutrient content in urban streams in a medium-sized city

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Citation: Lundquist, M. J., and W. Zhu. 2018. Aquatic insect functional diversity and nutrient content in urban streams in a medium-sized city. Ecosphere 9(5):e02284. 10.1002/ecs2.2284

Abstract. Aquatic insects play a large role in the processing of organic matter in headwater streams; however, anthropogenic disturbances associated with watershed urbanization can impact the biodiversity and abundance of these insects. Aquatic insects function on multiple trophic levels (i.e., shredders, collectors, scrapers, and predators) and interact in the nutrient cycling within lotic systems. The degradation or loss of any of these functional groups could disrupt stream biogeochemistry and the flow of energy in stream ecosystems. We used a paired reach site design to assess the insect functional group representation in five streams impacted by urbanization with downstream urban and upstream rural reach sites. We also sampled two non-urban reference streams with rural upstream and rural downstream reach sites. We assessed functional group richness and abundance and measured insect biomass, insect body nitrogen (N) content, phosphorus (P) content, and N:P ratio. We found that collectors were numerically the most abundant and taxonomically the richest insect group in all site types. There were much fewer insects collected from urban sites than rural sites and individual insects were generally smaller in the urban sites. Collectors represented the most insect biomass in urban sites and predators the most insect biomass in rural sites. Insect N and P concentrations were not affected by urban landuse, ranging from 88.45 ± 12.50 to 121.74 ± 15.80 mg/g and 10.60 ± 2.10 to 18.36 ± 7.05 mg/g, respectively; and N:P ratios from 3.48 to 20.97. However, lower total insect biomass, particularly of predators and shredders, led to significantly lower total N and P mass in urban sites. Urbanization had clear effects on the diversity of functional groups, insect biomass, and their nutrient mass in this medium-sized city.

Key words: aquatic insects; functional feeding groups; medium-sized city; nitrogen; phosphorus; urbanization.

Received 18 March 2018; revised 1 May 2018; accepted 3 May 2018. Corresponding Editor: Robert R. Parmenter.

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INTRODUCTION

The urbanization of watersheds negatively impacts stream benthos. The loss of benthic insect taxa from urbanized streams has been widely reported (Paul and Meyer 2001, Walsh et al. 2005). While taxonomic richness can be a reliable indicator of impacts of urbanization, it falls short of describing the interactions between taxa and stream ecosystem function (Walsh et al. 2005). Indeed, restoration of anthropogenically disturbed watersheds should seek the restoration of stream hydrology, recolonization of locally extirpated aquatic fauna, and the restoration of aquatic ecosystem function (Palmer et al. 2005, 2014, Kaushal et al. 2008, Sudduth et al. 2011).

In undisturbed streams, the abundance of each trophic level is associated with the size of the stream and the relative availability of basal food resources (e.g., leaves, algae, prey) along the river continuum (Vannote et al. 1980). Aquatic insects serve a vital role as processors of detritus and other energy inputs in streams at multiple trophic levels (Cummins 1973). In short, shredders...
process allochthonous leaf litter, scrapers feed on benthic algae, collectors filter or gather fine organic particles, and predators feed on the other trophic levels. The diversity of functional group taxa is important for stream ecosystem functioning (Jonsson et al. 2001), and anthropogenic activity has been shown to reduce functional group richness (Moore and Palmer 2005) and abundance (Huryn et al. 2002, Roy et al. 2003). This could have a major impact on ecosystem functioning in urban streams.

Watershed urbanization can also modify the rates at which nutrients enter the stream (Bernhardt et al. 2008, Duan et al. 2014, Wallace et al. 2015) and how quickly they move out of the system (Rosemond et al. 2015). This could affect the availability of these resources for aquatic insects. Ecological stoichiometry, the concentration, and the ratio of nitrogen (N) and phosphorus (P) within body tissue, is related to available nutrients in the environment and is impacted by anthropogenic disturbance (Morse et al. 2012). However, information on the effects of urbanization on insect biomass production and nutrient stoichiometry is still relatively limited (but see Milanovich et al. 2014), particularly in small to medium-sized cities where anthropogenic and natural forces interact more closely. We define medium-sized city as a city with fewer than 500,000 inhabitants (United Nations Population Division 2014). As opposed to large cities, where the biological impacts of urbanization have been well documented (Walsh et al. 2005), there have been few studies in smaller cities. Medium-sized cities have less developed land and closer human–nature connections, potentially affecting the severity of urbanization impacts.

In this study, we investigated the taxonomic diversity of aquatic insect functional groups in urban streams in a medium-sized city, as well as the nutrient content of those insects and their contribution to total insect biomass and nutrient mass. We postulated that (1) there would be fewer taxa within functional groups in urban sites compared to rural sites; (2) there would be fewer insects collected from urban sites than from rural sites; (3) N and P concentrations, and N:P ratios would be different among functional groups; and (4) total insect biomass, N mass, and P mass would be lower in urban sites than in rural sites.

**Methods**

**Study sites**

We conducted this study in the Greater Binghamton metropolitan area, Broome County, New York, USA. The metropolitan area incorporates the city of Binghamton, which has a population of approximately 45,600 people and the surrounding towns, with an additional 210,000 people. Greater Binghamton is on the Susquehanna River Basin within the upper Chesapeake Bay watershed.

Fourteen paired 50-m reach sites were selected in seven low-order cobble-bed streams. Five streams flow from upstream sites surrounded by rural landscape that is primarily agricultural and forested to downstream sites surrounded by more developed urban landscape; paired upstream (rural) and downstream (urban) sites were selected for each stream. We also selected two reference streams with rural upstream sites and rural downstream sites to test for upstream and downstream differences that could confound the measures of urbanization. We delineated the watersheds using QGIS (Quantum GIS Development Team 2016) and digital elevation model data, from the US Geological Survey. We assessed % landuse from the National Land Use Database 2011 land cover map (Homer et al. 2015) and can be found in Appendix S1: Table S1. Data of stream water chemistry from 2014 to 2015 can be found in Appendix S2: Table S1.

**Insect collection and identification**

Aquatic insects were all collected from riffle habitats, the most common habitat type in these streams. Each reach was sampled monthly from April to September in 2014 and 2015. During each sampling time, insects were collected from three points along the 50-m reach by kick-netting for 1 min at each point and then combined. Insects were collected alive and transported on ice to the lab.

In 2014, insects from each family collected that represented the range of body sizes were transferred to glass vials with Nanopure water and incubated at room temperature for 1 d to allow for the clearing of the gut. Insects were then sacrificed, rinsed, and oven-dried at 60°C for 48 h and stored for biomass determination and full-body nutrient concentration measurement. All other
insects collected in 2014 and 2015 were stored in 90% ethanol. Most preserved insects were then identified to the genus level except Chironomidae, Pteronarcyidae, and Ceratopognidae which were identified to family (Appendix S3: Table S1) and were assigned to functional groups using keys from Merritt et al. (2008).

**Insect body mass and nutrient analysis**

Insect biomass, total Kjeldahl nitrogen (TN), and total Kjeldahl phosphorus (TP) were determined from dried insect body tissue collected from 2014. If there were multiple, small individuals collected from particular sites, they were pooled by family, site, and sampling time. Dried insects were weighed to the nearest 0.01 mg, and if the insects were too small to weigh, they were assigned a value of 0.005 mg. The dried insects were then digested in a 6 mL solution containing concentrated H$_2$SO$_4$, H$_2$O$_2$, Li$_2$SO$_4$-H$_2$O, and Se and an additional 3 mL of 30% H$_2$O$_2$ heated at 200°C for 30 min and then at 380°C for an additional 2.5 h (Allen 1989). The digested material was then diluted and analyzed for TN and TP with a Lachat QuickChem 8000 Series Flow-Injection Autoanalyzer.

The detection limit for the nutrient analysis required >2 mg of insect biomass; therefore, individuals <2 mg were pooled when possible or excluded from analysis. Concentration of N and P (mg/g) and N:P ratios were determined for each sample. Mean individual biomass, N concentration, P concentration, and N:P ratios weighted for the number of individuals per sample were calculated for each functional group, site, and sample time for use in statistical analyses. Total N and P mass were calculated for each functional group, site, and sample time using the weighted means.

**Statistical analyses**

All statistical tests were performed in R (R Core Team 2016). Because streams were resampled over time, we accounted for variability among streams by using mixed model analysis in the lme4 package (Bates et al. 2017). We tested the fixed effects of functional group, urban and rural landuse, and sampling time ($n = 12$) on insect richness and abundance. We tested the fixed effects of functional group and landuse on insect N, P, and biomass collected in 2014 ($n = 6$). Both stream ID and percentage developed landuse (Appendix S1: Table S1), with urban/rural landuse type nested within stream ID were included as random intercepts in mixed models to account for among stream variability. Functional group richness was analyzed using generalized linear mixed modeling (GLMM) assuming a Poisson distribution. Insect abundance, biomass, N, and P were analyzed using linear mixed modeling (LMM). Mixed effects models were also used to test the effect of downstream and upstream location and sampling time on stream data collected from the reference sites, with upstream/downstream position nested within stream. Likelihood ratio tests of full models against models without certain explanatory variables (functional group, landuse/location, or sampling time) were performed to calculate $P$-values from Wald $\chi^2$ tests. If significant differences were detected through the GLMM and LMM, paired $t$-tests were used to compare upstream and downstream differences; $P$ values were Holm–Bonferroni adjusted for multiple comparisons (Holm 1979). Functional group richness was Freeman-Tukey transformed using the expandFunctions package (Miller 2016) before performing paired $t$-tests. We also used GLMM regressions to assess correlations between percentage developed land and functional group diversity. We used LMM regressions to assess correlations between percentage developed land on insect biomass, and nutrients and percentage developed landuse x functional group interactions. Stream ID was used as a random intercept in all models. Marginal (without random factor) and conditional (with random factor) $r^2$ of regressions were calculated using piecewiseSEM in R (Lefcheck 2016).

**RESULTS**

**Functional group taxonomic richness and abundance**

A total of 2826 insects were collected from the 10 reach sites in the urban-impacted streams over the 12 sampling months (2014–15). We collected seven shredder taxa, 26 collector taxa, 10 scraper taxa, and 25 predator taxa. A total of 2071 insects were collected from the four reference sites, which included two unique shredder taxa, one collector taxon, and one predator taxon. A full list of taxa collected can be found in Appendix S3: Table S1.
Landuse had a significant effect on the taxonomic richness of both collectors ($\chi^2(1) = 4.65$, $P = 0.031$) and predators ($\chi^2(1) = 10.42$, $P = 0.005$). Richness of collectors and predators was on average 30% and 64% lower in urban reaches (downstream) than in rural reaches (upstream; Fig. 1). There were also significant negative correlations between % developed landuse and collector richness ($\chi^2(1) = 21.82$, $P < 0.001$, marginal $r^2 = 0.25$, conditional $r^2 = 0.40$) and % developed landuse and predator richness ($\chi^2(1) = 51.37$, $P < 0.001$, marginal $r^2 = 0.46$, conditional $r^2 = 0.46$). Scraper richness and shredder richness were low in both urban and rural sites (Fig. 1). The in-stream urban

![Bar chart of taxonomic richness per sampling time of shredder, collector, scraper, and predator aquatic insect functional groups collected from downstream (black, $n = 5$) and upstream (gray, $n = 5$) sites, April–September of 2014 and 2015. The five streams to the left of the dotted line flow from rural upstream sites to urban downstream sites. The two reference streams to the right of the dotted line flow from rural upstream to rural downstream sites. Comparisons between upstream and downstream sites within streams were done with paired t-tests, and $P$ values were Holm-Bonferroni adjusted. See Table 1 for stream abbreviations. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.](image-url)
and rural differences in collector richness were marginally significant in Patterson Creek (Holm–Bonferroni adjusted $P = 0.052$, Fig. 1). Predator richness was significantly lower in the urban sites in every stream except Fuller Hollow Creek (Fig. 1). Only shredder richness was significantly affected by sampling time ($n = 12$) in the urban-impacted streams ($\chi^2(1) = 34.20$, $P < 0.001$), and there was a significant landuse $\times$ time interaction ($\chi^2(11) = 21.46$, $P = 0.029$).

The GLMM revealed no significant upstream/downstream location effects on taxonomic richness of collectors, scrapers, or predators in the reference streams. There were too few shredders found in the reference sites to perform a GLMM. Shredder richness was relatively low, on average, in both downstream (0.08 ± 0.06) and upstream (0.41 ± 0.17) sites.

The total number of predators collected was greatly reduced in the urban stream sites, ranging from 64% to 96% fewer individuals than in the rural sites (Table 1A). Collectors were the most abundant functional group found in all streams and site types and did not differ significantly between urban and rural sites (Table 1A). Scraper abundance was lower in the downstream sites in three of the streams but was higher in the downstream in two streams (Table 1A). Shredders were relatively rare, accounting for $<10\%$ of the total number of insects collected within most reach sites, except in LCU and PTU where they were more abundant (Table 1B). Indeed, the abundance from each functional group from each site per sampling time ($n = 12$) was significantly affected by functional group ($\chi^2(3) = 47.24$, $P < 0.001$), marginally by landuse type ($\chi^2(3) = 3.71$, $P = 0.054$), and significantly by sampling time ($\chi^2(11) = 26.02$, $P = 0.006$). There was also a significant functional group $\times$ landuse ($\chi^2(3) = 13.17$, $P = 0.004$), predators and collectors tended to be more abundant in the rural sites than in the urban sites (Tables 1, 2). There was no significant correlation between % developed landuse and insect abundance ($\chi^2(1) = 0.32$, $P = 0.57$, marginal $r^2 = 0.03$, conditional $r^2 = 0.10$), but there was a significant % developed $\times$ functional group interaction ($\chi^2(3) = 14.63$, $P = 0.002$), similar to the models with urban/rural landuse groups.

In the reference streams, abundance per site and sampling time was also significantly affected by functional group ($\chi^2(3) = 13.23$, $P = 0.004$), but not upstream/downstream location or sampling time. Collectors were the most abundant in both upstream and downstream sites, and shredders were extremely rare (Table 1A,B).

**Functional group biomass**

We estimated biomass from 568 insects collected from the urban and rural stream sites in 2014; 144 additional insects were too small to measure directly and were assigned a biomass of 0.005 mg each. The average number of

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**Table 1.** Number of insects (A) and relative abundance (%; B) collected in 2014 and 2015, arranged by functional groups and sites.

| Functional group | Site          | CCD | CCU | FHD | FHU | LCD | LCU | PCD | PCU | PTD | PTU | LSD | LSU | TBD | TBU |
|------------------|--------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| (A) No. insects  | Shredder     | 2   | 14  | 6   | 5   | 3   | 26  | 18  | 9   | 12  | 3   | 0   | 14  | 2   | 7   |
| Collector        | 319          | 534 | 95  | 44  | 48  | 71  | 117 | 175 | 57  | 194 | 588 | 320 | 212 | 142 |
| Scraper          | 67           | 203 | 5   | 7   | 31  | 2   | 37  | 19  | 1   | 23  | 146 | 80  | 81  | 24  |
| Predator         | 18           | 156 | 32  | 94  | 13  | 37  | 24  | 128 | 7   | 173 | 153 | 81  | 139 | 83  |
| Total            | 406          | 907 | 138 | 150 | 95  | 136 | 196 | 325 | 77  | 470 | 887 | 495 | 434 | 256 |
| (B) Relative abundance (%) | Shredder | 0.5 | 1.5 | 4.3 | 3.3 | 3.2 | 19.1 | 9.2 | 2.7 | 15.6 | 0.8 | 2.5 | 0.8 | 2.7 |
| Collector        | 78.6         | 58.9 | 68.8 | 29.3 | 50.5 | 52.2 | 59.7 | 52.9 | 74.0 | 49.4 | 66.3 | 64.6 | 48.8 | 55.5 |
| Scraper          | 16.5         | 22.4 | 3.6 | 4.7 | 32.6 | 1.5 | 18.9 | 5.7 | 1.3 | 5.9 | 16.5 | 16.2 | 18.7 | 9.4 |
| Predator         | 4.4          | 17.2 | 23.2 | 62.7 | 13.7 | 27.2 | 12.2 | 38.7 | 9.1 | 44.0 | 17.2 | 16.4 | 32.0 | 32.4 |
| Total            | 100          | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |

*Notes: Five streams (CC, FH, LC, and PC) flowed from upstream rural (U) sites to downstream urban (D) sites; while two reference streams (LS and TB) flowed from upstream rural (U) sites to downstream rural (D) sites. See Appendix S1: Table S1 for landuse data.*
individuals collected from each functional group per sampling time in 2014 followed similar patterns to the full twelve-month study (Table 2).

Biomass per individual insect was significantly affected by functional group ($\chi^2(3) = 18.63$, $P < 0.001$) with a marginal functional group × landuse type interaction ($\chi^2(3) = 7.48$, $P = 0.058$). Predators and shredders were the largest in both urban and rural sites, and there was a trend toward smaller shredders and predators in the urban sites, but the difference was not statistically significant (Fig. 2A). Collectors and scrapers had much smaller individuals, and their per capita biomass did not differ between landuse types (Fig. 2A). There was also no significant correlation between % developed land and biomass per individual ($\chi^2(1) = 0.61$, $P = 0.44$, marginal $r^2 = 0.01$, conditional $r^2 = 0.02$). Reference site insect biomass was estimated from 306 insects collected in 2014; among them, 89 insects were assigned a biomass of 0.005 mg. The biomass of individuals in the reference streams was marginally affected by functional group ($\chi^2(3) = 6.91$, $P = 0.075$) and not by the upstream/downstream location.

Total insect biomass in urban streams was significantly affected by functional group ($\chi^2(3) = 12.24$, $P = 0.007$) and marginally affected by landuse type ($\chi^2(1) = 3.25$, $P = 0.071$). There was also a significant functional group × landuse type interaction ($\chi^2(3) = 15.28$, $P = 0.001$). Predators and shredders provided 97% and 86% less insect biomass on average to the urban sites than to the rural sites. Collectors provided a similar amount of the biomass in both site types, but collector biomass accounted for the majority of the insect biomass in the urban sites (Table 2). There was a significant negative correlation between % developed land and total biomass sampled ($\chi^2(1) = 4.90$, $P = 0.027$, marginal $r^2 = 0.02$, and 0.08). There was also a significant interaction between % developed land and functional group ($\chi^2(3) = 11.19$, $P = 0.011$), which is similar to what was seen in the model with landuse type as groups. Total insect biomass in the reference sites was significant affected by functional group ($\chi^2(3) = 10.88$, $P = 0.012$), but not site location.

**Nitrogen and Phosphorus concentrations**

Concentrations of N and P were estimated from 484 insects from the urban-impacted streams. The concentration of N in individual insects was not significantly affected by functional group, or landuse (Fig. 2B). Insect P concentrations were marginally affected by functional group ($\chi^2(3) = 3.14$, $P = 0.076$). Collectors and scrapers tended to have higher P

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**Table 2. Summary table of mean ± SE number of insect individuals collected, total insect biomass, total N mass, and total P mass from 3 m$^2$ area per sampling time in 2014 in urban downstream (n = 30) and reference downstream (n = 29), rural upstream (n = 30) and reference upstream (n = 12) and reference upstream (n = 12) sites.**

| Site type          | Functional group | Individuals†‡ | Total biomass (mg)†‡ | Total N mass (mg)†‡ | Total P mass (mg)†‡ |
|--------------------|------------------|---------------|----------------------|---------------------|---------------------|
| Urban downstream   | Shredder         | 0.66 ± 0.19   | 7.23 ± 3.47          | 0.23 ± 0.08         | 0.03 ± 0.01         |
|                    | Collector        | 8.93 ± 2.89   | 19.19 ± 9.65         | 1.91 ± 0.68         | 0.20 ± 0.06         |
|                    | Scraper          | 2.48 ± 1.10   | 2.15 ± 1.31          | 0.23 ± 0.17         | 0.05 ± 0.04         |
|                    | Predator         | 1.17 ± 0.35   | 5.58 ± 2.74          | 0.56 ± 0.27         | 0.03 ± 0.01         |
| Rural upstream     | Shredder         | 1.20 ± 0.42   | 48.61 ± 25.77        | 3.13 ± 1.50         | 0.16 ± 0.09         |
|                    | Collector        | 15.80 ± 3.01  | 19.01 ± 6.28         | 3.59 ± 1.08         | 0.82 ± 0.33         |
|                    | Scraper          | 4.70 ± 2.26   | 5.24 ± 3.13          | 0.37 ± 0.18         | 0.07 ± 0.04         |
|                    | Predator         | 9.40 ± 1.74   | 146.87 ± 50.68       | 15.46 ± 5.22        | 1.87 ± 0.66         |
| Reference downstream | Shredder     | 0.08 ± 0.08   | –                     | –                   | –                   |
|                    | Collector        | 37.50 ± 16.00 | 30.03 ± 9.52         | 4.85 ± 2.18         | 0.60 ± 0.22         |
|                    | Scraper          | 8.00 ± 2.12   | 14.19 ± 9.35         | 6.04 ± 5.12         | 0.69 ± 0.59         |
|                    | Predator         | 11.75 ± 1.53  | 54.41 ± 11.36        | 5.26 ± 1.14         | 0.59 ± 0.13         |
| Reference upstream | Shredder         | 1.50 ± 0.87   | 19.19 ± 10.69        | 0.83 ± 0.44         | 0.75 ± 0.72         |
|                    | Collector        | 17.25 ± 3.02  | 37.12 ± 17.43        | 3.77 ± 2.00         | 0.53 ± 0.24         |
|                    | Scraper          | 4.67 ± 1.58   | 10.81 ± 4.83         | 0.87 ± 0.36         | 0.07 ± 0.03         |
|                    | Predator         | 5.67 ± 1.23   | 127.63 ± 42.43       | 12.48 ± 4.36        | 2.94 ± 1.32         |

*Note:* Shredders in the reference downstream sites were too small to measure total biomass, total N mass, and total P mass.
† Significant effect of landuse.
‡ Significant effect of functional group membership.
concentrations than either predators or shredders (Fig. 2C). There were no significant correlations between % developed land and insect N or P concentrations.

Urban landuse had a significant effect on insect N:P ratios ($\chi^2(1) = 4.40, P = 0.036$). Average N:P ratios tended to be higher in rural insects than those in urban insects (Fig. 2D). There was also a marginal functional group $\times$ landuse interaction ($\chi^2(3) = 6.41, P = 0.093$). Larger differences in N:P ratios between urban and rural sites were observed in collectors and shredders (Fig. 2D). There was no significant correlation between % developed landuse and insect N:P ratios.

Concentrations of N and P were estimated from 216 individuals from the reference streams. There was a significant effect of location on insect N concentrations ($\chi^2(1) = 4.14, P = 0.042$) and a
significant functional group \times location interaction ($\chi^2(2) = 8.31, P = 0.016$). However, scraper N concentrations were approximately 45% higher and predator N concentrations were 33% higher, on average, in the downstream sites than in the upstream sites. This was the opposite of what was observed in the urban streams (Fig. 2B). There were no functional group or landuse effects on P concentrations or N:P ratios in the reference streams.

**Total nitrogen and phosphorus mass**

Total insect N mass followed the pattern of biomass and was significantly affected by functional group ($\chi^2(3) = 12.18, P = 0.007$), marginally affected by landuse type ($\chi^2(1) = 3.14, P = 0.058$), and had a significant functional group \times landuse type interaction ($\chi^2(3) = 16.00, P = 0.001$). There was a significant negative correlation between % development and total N per sampling ($\chi^2(1) = 7.56, P = 0.006$, marginal $r^2 = 0.04$, conditional $r^2 = 0.11$) as well as a significant % development \times functional group interaction ($\chi^2(3) = 14.79, P = 0.002$). Each functional group provided more total N mass in the rural sites than in the urban sites (Table 2). However, predators and shredders provided nearly twice as much N mass to the rural sites than to the urban sites (Table 2).

Total insect P mass was also significantly affected by functional group ($\chi^2(3) = 11.32, P = 0.010$) and by landuse type ($\chi^2(1) = 6.15, P = 0.013$). Like N mass, there was also a significant functional group \times landuse type interaction ($\chi^2(3) = 15.21, P = 0.002$). More total P mass was provided by each functional group in the rural sites, but the greatest differences in contributions were observed between predators in the urban and rural sites (Table 2). This also follows a similar significant negative correlation between % development and total P ($\chi^2(1) = 4.30, P = 0.038$, marginal $r^2 = 0.040$, conditional $r^2 = 0.040$) with a significant % development \times functional group interaction ($\chi^2(3) = 9.48, P = 0.023$).

Total insect N mass in the reference streams was significantly affected by functional group ($\chi^2(3) = 8.26, P = 0.041$), but not location. There was also a significant functional group \times location interaction ($\chi^2(3) = 7.38, P = 0.061$). Total insect P mass in the reference sites was not affected by functional group or location, but there was a marginal functional group \times location interaction ($\chi^2(3) = 7.45, P = 0.059$). Collectors and scrapers provided more total N and P mass in the downstream reference sites than the upstream reference sites, but at levels similar to the rural upstream sites (Table 2). Predators provided more in the upstream sites, but their contribution of N mass to the reference downstream sites was nearly 10x higher to the urban downstream urban and the P contribution was nearly 20x higher (Table 2).

**Discussion**

Urbanization had a clear impact on stream insect functional groups in this study. Lower richness and abundance within functional groups in the urban sites also resulted in less total insect biomass in the urban sites. Insect nutrient concentrations were relatively similar between urban and rural sites; however, lower total insect biomass also resulted in lower total N mass and total P mass in urban sites. Significant functional group \times landuse interactions for total insect biomass, total N mass, and total P mass in the urban streams revealed important differences in the reactions of each functional group to urbanization. Predators contributed the most biomass in rural sites but were much less abundant in urban sites and represented much less of the total insect biomass and nutrients. Instead, collectors contributed a higher proportion of total biomass to urban sites, although their size and abundance were not significantly different between the site types.

No significant effects of downstream or upstream location on functional group taxonomic richness, abundance, biomass, and most nutrient measures were found in our reference streams. Significant location differences in total N and P mass were caused by higher downstream mass, which is the opposite of what was observed in the urban streams. Therefore, the differences we observed between urban and rural sites were likely not due simply to longitudinal, upstream/downstream differences, rather they reflected the impact of urbanization. Furthermore, the much higher insect abundance, total biomass, and N and P mass observed in the reference sites than in the urban sites indicated clearly that urbanization had an important impact on streams in this medium-sized city.
Aquatic insects are important components of stream ecosystems (Vannote et al. 1980, Grimm 1988, Huryn et al. 2002, Bernhardt et al. 2005) and the loss of insect functional group richness and abundance can impair stream function (Jonsson et al. 2001). Our observations of lower overall insect richness and abundance in the urban sites are similar to other studies of urbanization (see reviews by Paul and Meyer 2001, Walsh et al. 2005). However, functional groups reacted differently to urbanization in our study.

Predator richness and abundance were much lower in the urban sites than the rural sites in this study. Previously, Moore and Palmer (2005) found a 50% loss of predator taxa and up to 70% loss of collector taxa in urban streams in northern Maryland, USA. While we observed similar losses in predators (Fig. 1), collectors fared relatively better. Indeed, collector abundance was similar in both urban and rural sites and while collector richness was significantly affected by urban/rural landuse, richness was not significantly lower between sites in most streams (Fig. 1). It is possible that members of the Chironomidae represented multiple genera, but even after excluding Chironomidae from analyses, there was still a significant urban/rural landuse effect ($\chi^2(1) = 4.29, P = 0.038$). Collector relative abundance was also much higher in the urban sites. Higher abundance of collectors, relative to other functional groups, in urban streams has been widely reported (Moore and Palmer 2005, Smith and Lamp 2008, Fu et al. 2016, Sterling et al. 2016).

Low scraper richness in urban streams has been previously reported (Moore and Palmer 2005). While we collected few scraper taxa, there were slightly more scraper taxa in two of our five urban streams (Fig. 1). Shredder richness and abundance was low in most of our study sites. Similarly, low shredder diversity has been observed in streams in watersheds with urban and agricultural landuse (Purcell et al. 2002, Nedeau et al. 2003, Moore and Palmer 2005, Smith and Lamp 2008, Sterling et al. 2016). Tipula sp. (Diptera: Tipulidae) has been reported in multiple studies as the dominant shredder taxa in urban streams (Huryn et al. 2002, Purcell et al. 2002). Indeed, it was also the most abundant in our urban sites (Appendix S3: Table S1). Shredder diversity is positively correlated to the amount of watershed forested land cover (Fu et al. 2016); however, while most of our watersheds have a high proportion of urban and agricultural landuse, they also have at least 50% forested landuse (Appendix S1: Table S1). There are likely other factors contributing to shredder richness and abundance in our streams beyond landuse.

Individual insect biomass and N and P concentrations were not affected by urban landuse in our study. This is similar to other findings that urbanization does not significantly impact individual insect stoichiometry (Milanovich et al. 2014). However, urbanization did act at the community level by reducing the abundance of large predators and shredders. Indeed, while predator biomass in reference streams was also lower in the downstream sites than the upstream sites, that biomass was nevertheless almost 10× of those in the urban downstream sites (Table 2). Urbanization has been previously shown to reduce total insect biomass (Johnson et al. 2013, Sterling et al. 2016) by as much as 7% per 1% increase in urbanization (Sterling et al. 2016). This is also supported by the significant negative correlations between percent-age developed land on insect diversity and biomass found in this study. We have gone further to show that this shift in total biomass also reduces the total insect N and P mass in urban sites. While not the focus of our study, stream water specific conductivity, but not dissolved nitrogen, was elevated in urban sites (Appendix S2: Table S1).

However, no measures of stream water chemistry were significantly correlated with insect richness (data not shown). The mechanism for the shift in relative abundance of the four functional groups in our urban sites is unclear but may be related to the availability and quality of basal resources. Loss of riparian cover along urban stream channels can reduce shredder abundance by decreasing leaf litter inputs (Wallace et al. 2015). Our study streams drained primarily forested watersheds, but further work is needed to assess riparian cover and leaf litter flux in these streams. Fewer prey in the urban sites could also have led to the low predator abundance we observed (Johnson et al. 2013).

In this study in a medium-sized city, we found that urbanization impacted functional group taxonomic richness and abundance, which is similar to what has been found in other large cities (Moore and Palmer 2005, Smith and Lamp 2008, Fu et al. 2016) and a medium-sized city (Sterling...
et al. 2016). We have also demonstrated that as urbanization changes the abundance of aquatic insects, particularly of larger predators and shredders, it also changes the total insect biomass, N mass, and P mass in those streams. The loss of the taxonomic richness, abundance, and biomass of functional groups, especially predators and shredders, could reduce the capability of urban streams to deal with increased nutrient inputs and habitat modification in urban watersheds (Huryn et al. 2002). We have also shown large heterogeneity in developed landuse intensity functional group diversity among stream sites within the Greater Binghamton, New York, urban area, a phenomenon that likely occurs commonly in the process of urbanization. Degraded insect communities also undermine the resilience of these urban ecosystems to disturbances (Elmqvist et al. 2003), which are expected to rise with increased urbanization and climate change (Grimm et al. 2008).

ACKNOWLEDGMENTS

We would like to thank the support from the Center for Watershed Studies (CIWS) and the Sustainable Communities Transdisciplinary Areas of Excellence (TAE) of Binghamton University, State University of New York. We would also like to thank the reviewers and the editor for their thoughtful inputs which greatly improved the quality of this paper.

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