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Response to basal resources by stream macroinvertebrates is shaped by watershed urbanization, riparian canopy cover, and season

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Abstract

Riparian reforestation is a common restoration action in urban streams, but relatively little is known about the influence of local riparian vegetation in the face of watershed-scale urban land cover. Allochthonous organic matter and benthic algae are important basal energy resources in streams, but the roles of watershed urbanization vs near-stream vegetation in the availability of these resources are not well understood. Our goal was to understand how the interaction of land cover at 2 spatial scales (watershed vs reach) and seasonal dynamics shape basal resources and their effects on macroinvertebrate communities. We assessed relationships between seasonal patterns in standing stocks of particulate organic matter (POM) and benthic periphyton and macroinvertebrate community composition in open and closed-canopy reaches of 4 urban and 4 reference streams in northern Kentucky, USA. POM standing stocks were not strongly influenced by watershed or riparian condition. Benthic algal biomass was greater in urban than in reference streams in all seasons and in open than in closed riparian canopies in summer when light levels are most affected by a deciduous canopy. Relationships between macroinvertebrate functional feeding group (FFG) biomass and their primary food resources were influenced by watershed land use and season, but riparian canopy effects were minor. The proportion of collectors varied by season, whereas the proportion of shredders was higher in reference than urban streams. Scraper biomass was influenced by benthic algal biomass and varied seasonally, whereas predator biomass was driven by prey-insect biomass. Periphyton density was affected by the interaction of watershed and reach-scale land cover and was the only basal resource strongly related to consumer taxa. Watershed land use influences the stream ecosystem, but local riparian canopy may be important in limiting benthic algal accumulation.

Keywords

urban streams; aquatic macroinvertebrate; trophic interaction; organic matter; periphyton; riparian; watershed

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Watershed urbanization is characterized by an increase in impervious surface cover (IC), which prevents infiltration of rainfall and increases runoff. Urban stormwater delivery drives a collective suite of changes to stream ecosystems including alteration of hydrology, degradation of water quality, and loss of ecosystem function (the urban stream syndrome; Meyer et al. 2005, Walsh et al. 2005). However, the mechanisms and interactions driving specific aquatic ecosystem responses to urbanization, such as the effect of altered organic matter standing stocks on foodweb structure, are poorly understood (Wenger et al. 2009).

The importance of benthic organic matter and algal stocks to macroinvertebrate communities is widely recognized, and the hydrological and physicochemical changes associated with urbanization have the potential to affect basal resource availability strongly. For example, increased stormflow decreases the retention of benthic organic matter (Konrad and Booth 2005). Elevated concentrations of nutrients (Jordan et al. 1997, Vitousek et al. 1997, Carpenter et al. 1998) and gross primary production (Bernot et al. 2010, Alberts et al. 2016) have been observed in urban streams. Thus, urban land cover may alter the basal resources of the stream food web via a combination of decreased allochthonous organic matter retention and elevated autochthonous production.

At the reach scale, riparian vegetation is likely to be an important driver of basal resource availability, but its influence probably is mediated by seasonal variability, particularly where riparian vegetation is predominantly deciduous. For example, low light levels caused by riparian canopy may limit in-stream primary production (Quinn et al. 1997, Hill et al. 2001) during times of year with full leaf cover (i.e. late spring, summer, early autumn). Riparian trees also are an important source of terrestrial organic matter to stream ecosystems (Hession et al. 2003, Sweeney et al. 2004), particularly during leaf senescence in autumn, but the in-stream retention of these inputs is likely to depend on hydrology, which is controlled primarily at the watershed scale.

How local-scale controls on basal resources (i.e., light, leaf-litter inputs) interact with changes associated with urbanization at the watershed-scale (i.e., elevated nutrient loads, flashy hydrology) and season is likely to control basal resource availability (e.g., periphyton biomass, terrestrial organic matter) at the reach scale. Reach-scale differences in standing stock are expected to affect macroinvertebrate biomass and community composition (Fig. 1). For example, reaches with elevated levels of algal production would be expected to support higher biomass of grazer taxa than reaches with lower levels of algal production (Lamberti and Resh 1983). Likewise, reaches that retain coarse particulate (CPOM) or fine benthic (FBOM) organic matter would be expected to support greater biomass of shredders and collectors, respectively, than reaches that retain little organic matter (Cummins et al. 1989). The degree to which reach-scale consumer response might be mediated by watershed land cover and season is unclear.

Knowing the extent to which stream macroinvertebrate communities are shaped by land use and season is important for furthering our understanding of stream trophic interactions and controls on energy-transfer dynamics. Riparian zone management is often used in stream restoration projects (Bernhardt and Palmer 2007), and the importance of terrestrial-to-aquatic subsidies is well known (discussed in Hjältén et al. 2016). However, whether intact

reach-scale riparian canopy can exert local control over basal resource standing stocks and macroinvertebrate community composition in highly altered urban streams remains in question. Reach-scale changes in the trophic base of the food web are likely to exert bottom-up control on aquatic macroinvertebrate communities and potentially extend to other secondary and tertiary consumers (e.g., fish, spiders, bats, swallows) (Baxter et al. 2005, Alberts et al. 2013). Thus, understanding spatial and temporal patterns is critical for conserving aquatic and riparian ecosystems, particularly in the face of increasing urbanization.

The objective of our study was to assess how basal resources in stream ecosystems are shaped by the interaction of reach and watershed-scale land cover and seasonal dynamics, and how aquatic macroinvertebrate community response to food resources is mediated by land cover and season. We assessed benthic organic matter standing stocks and associated macroinvertebrate communities in paired open and closed-canopy reaches in streams draining forested (reference) and urbanized watersheds. We hypothesized that: 1) basal resource standing stock (benthic algae, CPOM, FBOM) would be influenced by both watershed and riparian land cover, with the strongest influence of the riparian cover occurring during the growing season, and 2) biomass of major benthic macroinvertebrate functional feeding groups (FFGs) would be related to benthic food resource availability at the reach scale, but such relationships would be mediated by watershed land cover and seasonality of macroinvertebrate community biodiversity.

We predicted that urban reaches lacking an intact riparian canopy would exhibit low standing stocks of terrestrially derived organic matter (CPOM and FBOM) and higher biomass of benthic algae, but we expected this relationship to vary by season. We anticipated that both total biomass and proportional biomass of scrapers would be positively related to algal standing stock, whereas total and proportional biomass of shredder and collector taxa would be positively related to quantities of CPOM and FBOM, respectively. We also expected that total and proportional biomass of macroinvertebrate predators would be driven by prey availability. Last, we anticipated that macroinvertebrate taxonomic richness would be higher in reference than urban streams and that, as a result, reach-scale community response to basal resources would be muted in urban watersheds.

METHODS

Study area

Our study took place in 8 streams in the Outer Bluegrass Physiographic Region underlain primarily with Ordovician limestone and shale (Ray et al. 1994) in northern Kentucky, USA. This area was characterized by open savannah deciduous woodlands before human habitation (Bailey 1995). Average precipitation is 104.6 cm annually, with the wettest months occurring in spring and early summer. The hottest and coldest months are July and January, with mean temperatures of 30.47C and 4.07C, respectively (NCDC 2008). Riparian vegetation was dominated by deciduous trees and woody shrubs. The dominant riparian trees in the reference streams were American sycamore (*Plantanus occidentalis*), red maple (*Acer rubrum*), pin oak (*Quercus palustris*), white oak (*Quercus alba*), and eastern cottonwood (*Populus deltoids*). Urban stream riparian zones tended to have higher proportions of

invasive Amur honeysuckle (*Lonicera mackii*) and Callery pear (*Pyrus calleryana*) than did reference streams.

Watersheds ranged in size from 5.7 to 11.4 km² (Table 1). To capture seasonal variation, streams were sampled in October 2013 and February, May, and July 2014 (autumn, winter, spring, and summer, respectively). Four streams were classified as urban, based on high watershed IC ($26.5 \pm 5.3\%$), whereas 4 were classified as forested reference ($1.9 \pm 0.3\%$). All watersheds had agricultural land use, consisting mostly of pasture, that ranged from 8.5 to 27.8% of the catchment area, levels generally considered to be below the 30 to 50% threshold at which negative effects on the stream might be expected (Allan 2004). Watershed-scale land cover was estimated based on the 2011 National Land Cover Dataset (NLCD; Homer et al. 2015).

At each stream, adjacent paired reaches (~100 m) with open (summer canopy cover $14.5 \pm 4.2\%$) or closed (summer canopy cover $86.9 \pm 3.6\%$) riparian canopies were selected. Canopy cover was estimated in each season with a spherical convex densiometer (Forestry Suppliers, Jackson, Mississippi) following Riley and Dodds (2012). The percentages of canopy cover visible in the densiometer when facing upstream, downstream, right bank, and left bank were recorded every 10 m, and the mean value was used to represent reach-level canopy cover. The paired reaches were separated by ~100 m, had similar in-stream habitat (i.e., substrate type, embeddedness) as assessed based on protocols described by Kentucky Division of Water (KDW 2008), and no tributary confluences or significant groundwater inputs occurred between the paired reaches.

Water quality

Grab samples of stream water were collected from all stream reaches during periods of base and storm flow each season, for a total of 128 samples (8 streams $\times$ 2 canopy treatments $\times$ 4 seasons $\times$ 2 flow regimes). Samples were transported to the laboratory on ice where they were stored at 4°C until additional processing within 48 h of collection. Stream water samples were analyzed for pH (Orion Ross Ultra Combination pH, Thermo Fisher Scientific, Waltham, Massachusetts) and conductivity (Orion Conductivity Cell). Further chemical analyses including nutrient concentrations were carried out as a part of a companion study on stream metabolism (Alberts et al. 2016).

Basal resources

Benthic organic matter, including leaves, seeds, woody debris, and filamentous algae, was collected with a Surber sampler (500- μ m mesh; 0.09-m² sampling area; Wildlife Supply Company, Buffalo, New York). Three replicate riffle samples were collected in each reach in each season. Benthic macroinvertebrates were removed from the samples and organic matter was sieved into CPOM (>1 mm) and FBOM (0.5–1 mm) fractions (Brown et al. 2013), dried at 60°C for 48 h, and combusted at 500°C to determine loss on ignition and ash-free dry mass (AFDM) (Gulis and Suberkropp 2003). Mean biomass of CPOM and FBOM from the 3 replicate samples was converted to areal estimates by season for each study reach (g AFDM/m²). We assumed that the quantity of FBOM in the 0.5 to 1.0-mm range is a reasonable proxy for the relative amount of food resource available to collectors in a given

stream reach. Our measurement differs from the traditional delineation of FPOM, which includes finer materials down to 0.45 μm , and should not be compared directly to concentrations of FPOM measured in other studies.

Algal biomass was quantified as the amount of chloro-phyll *a* (Chl *a*) from periphyton (Reavie et al. 2010). Periphy-ton was scraped from 5 randomly selected rocks collected in riffles that were separated by 10 m and composited into a single reach sample. Two subsamples of the reach composite were filtered on 47-mm glass fiber filters (GF/F), extracted for 24 h in 95% ethanol, and used for spectrophotometric Chl *a* analyses in the laboratory (SM 10200H; APHA 2005). Chl *a* estimates were converted to areal estimates (mg/m^2) by season for each study reach.

Macroinvertebrate communities and biomass

After removal from Surber samples, macroinvertebrates were stored in 70% ethanol until analysis. Individuals were identified to the lowest possible taxonomic level, usually genus, and length was measured to the nearest millimeter and used to estimate biomass (mg/m^2) (Benke et al. 1999). FFG designations (Merritt et al. 2008) were used to examine community response to food resource availability (Moore and Palmer 2005). Total FFG biomass was used to assess the strength of the relationship between basal resource and consumer biomass. Proportional biomass was used to examine relative changes in community composition in response to environmental predictor variables, i.e., watershed urbanization and riparian shading. Prey-insect biomass was estimated with methods modified from those used by Johnson et al. (2013) and was calculated by excluding predators and taxa expected to be resistant to predation (mollusks, *Gammarus* sp., *Lirceus* sp., *Cambaridae*) from overall macro-invertebrate biomass.

Statistical approach

Linear mixed-effects (LME) models were used to assess physicochemical and basal resource relationships with season, canopy, and watershed land use in R (version 3.2.3; R Project for Statistical Computing, Vienna, Austria; Plummer et al. 2006). LME models also were used to analyze how taxonomic richness and total macroinvertebrate community biomass were influenced by season, canopy, and watershed land use. Last, LME models were used to evaluate the response of total and proportional biomass of each macroinvertebrate FFG to their primary food resource (i.e., scrapers: Chl *a*, shredders: CPOM, collectors: FBOM, predators: prey-insect biomass), watershed land use, and season. This approach allowed us to assess how basal food resources influenced the biomass of each FFG and how resource availability shaped community composition (i.e., the proportional composition of community biomass by FFG). The models used the fixed effect, season, nested within the random effect, stream. The models were constructed using the *lme4* package (Bates and Maechler 2010) in R and the full models took the following forms:

Physicochemical property $\sim$ canopy $\times$ season $\times$ watershed land use, random = canopy | stream,

(Eq. 1)

TR or TMB $\sim$ canopy $\times$ season $\times$ watershed land use, random = canopy | stream, (Eq. 2)

Taxa(FFG) biomass $\sim$ food resource $\times$ season $\times$ watershed land use, random = canopy | stream, (Eq. 3)

where TR is taxonomic richness and TMB is total macro-invertebrate biomass.

This structure allowed the seasonal influence to vary across streams as a random effect. All possible models, including the null, were assessed using Akaike Information Criteria (AIC) model selection (Burnham and Anderson 2002). Model diagnostics included assessment of residual variance and residual distribution, and if any models were within 2 AIC units of one another, they were considered equivalent. Full model results are provided in Table S1.

RESULTS

Site characterization

Physicochemical properties varied across watershed landuse categories and season (Table 2). Conductivity was elevated in the urban streams relative to reference streams and exhibited seasonal patterns (Tables 2, 3). pH was lower in reference streams than in urban streams during summer, but did not differ during other seasons (Tables 2, 3). Mean daily temperature was lower in reference than urban streams in summer, higher in reference than urban streams in autumn, and strongly driven by season (Tables 2, 3). Canopy cover did not influence conductivity or pH, but mean daily temperature was lower in closed than open reaches in summer only (Tables 2, 3).

Basal resources

The standing stocks of CPOM and FBOM were higher in autumn than in other seasons, regardless of reach or watershed treatment (Table 2), but season was the only significant predictor of CPOM (Table 3). CPOM standing stocks were significantly higher in urban than reference streams in winter (Table 3, Fig. 2). FBOM standing stock did not differ among reaches or watershed treatments (Table 3, Fig. 3). Benthic Chl *a* concentration was higher in urban than reference streams throughout the year, in open than closed reaches in summer, and was driven most strongly by watershed and canopy cover (Tables 2, 3, Fig. 4). Benthic Chl *a* concentration showed no overall seasonal effect, but the influence of canopy cover varied by season (Table 3).

Aquatic macroinvertebrate taxonomic richness and total biomass

Taxonomic richness was best predicted by watershed land use as a main effect and by the watershed $\times$ season interaction (Tables 4, 5). Taxonomic richness was higher in reference than urban streams, but only during winter and spring (Fig. 5). Richness in reference streams was greatest in spring, followed by winter, autumn, and summer. Urban streams exhibited higher diversity in autumn and summer than in winter and spring. Taxonomic richness was not affected by canopy cover.

Total macroinvertebrate biomass varied among seasons (Table 5). Neither watershed land use nor canopy treatment were strong predictors of total community biomass. Total macroinvertebrate biomass was highest in spring and lowest in summer.

Dominant taxa in the collector FFG were relatively consistent across seasons and treatments (Tables S2, S3). Ephemeroptera (e.g., *Baetis* sp.) and Coleoptera (e.g., *Psephenus* sp., *Stenelmis* sp.) tended to be the most abundant scraper taxa, and accounted for the greatest proportion of scraper biomass. Shredder composition varied by season and watershed land use. Plecopteran abundance was higher in reference than urban streams in winter and spring. The predator FFG in urban streams was dominated by Tanypodinae and *Dugesia* sp. in all seasons, whereas reference streams had higher proportions of *Nigronia* sp. (Megaloptera) and predatory Plecoptera, particularly in winter and spring.

Macroinvertebrate response to basal resources

Macroinvertebrate FFG biomass varied widely across treatments and by season (Tables 4, 6). Total scraper biomass was best predicted by a model including Chl *a*, season, and the Chl *a* $\times$ season interaction. Total scraper biomass and Chl *a* concentration were negatively related in spring and winter in both watershed types. In reference streams, this period corresponded with the highest total scraper biomass in spring and the lowest in winter. In urban streams, no significant seasonal pattern was apparent in total scraper biomass. Scraper proportional biomass was best predicted by Chl *a* concentration, season, and the Chl *a* $\times$ season interaction. Scraper proportional biomass was negatively related to Chl *a* concentration in spring and was greatest in summer and lowest in winter for both watershed types.

Total shredder biomass was not significantly related to CPOM, watershed land use, or season (Table 6). Shredder proportional biomass varied with watershed land use and was higher in reference than urban streams in all seasons.

Total collector biomass was not related to FBOM (Table 6), but was lowest in summer in both urban and reference streams (Table 4). Collector proportional biomass was best predicted by a model with season and the FBOM $\times$ season interaction. For both reference and urban watersheds, the proportional collector biomass was lowest in summer and was negatively related to FBOM standing stock in winter.

Total predator biomass varied with prey-insect biomass but did so differently depending upon watershed type (Table 6). In reference streams, total predator biomass and prey-insect biomass were strongly positively related in spring; proportional biomass did not vary by season or with watershed land use.

DISCUSSION

Organic matter standing stock

The influence of factors controlled by watershed land cover and riparian canopy on reach-scale standing stock of basal resources varied by season in our study streams. Seasonal patterns were evident in CPOM standing stock but not for FBOM or benthic algae. Benthic algal biomass responded to land cover at both spatial scales, but neither watershed land cover nor riparian canopy exerted strong control over POM standing stock.

Riparian canopy is likely to serve as the primary source of terrestrial organic matter to aquatic ecosystems (Cummins et al. 1989), but its influence was not reflected in our estimates of reach-scale organic matter standing stocks. Benthic organic matter (BOM) retention in streams is influenced by hydrological forces (Quinn et al. 2007, Imberger et al. 2014), which can result in physical breakdown and downstream transport of terrestrial inputs. Differential rates in decay or consumption by stream detritivores also could obscure local canopy effects on standing stocks of BOM (Imberger et al. 2008). Our results suggest that leaf-litter in-puts from riparian trees may be an important source of organic matter in stream ecosystems, but CPOM and FBOM standing stocks are not necessarily closely related to canopy cover at the reach-scale, and organic matter flow may be difficult to estimate with intermittent sampling. Additional studies with more frequent intensive measurements of organic matter may be useful in improving our understanding of this relationship.

The observation that urban streams retained greater amounts of CPOM than reference streams during winter was in contrast to our expectations. Previous studies suggested that the frequency and magnitude of scouring events are likely to be elevated in urban streams because of hydro-logical alteration, which should shorten the duration of terrestrial organic matter residence time (Allan et al. 1997, Walsh et al. 2005). However, our findings do correspond with those of Miller and Boulton (2005), who observed significantly higher biomass of CPOM in urban than in reference streams, and suggested that, at least in part, this difference could be attributed to additional organic matter washed into the urban streams via stormwater drainage networks.

Despite an anticipated decrease in overall BOM associated with watershed urbanization, we expected that reaches with dense canopy cover would have more CPOM and FBOM standing stocks relative to reaches without canopy cover because of greater reach-scale organic matter inputs. For example, evidence from a forested stream suggests that CPOM retention may be closely related to local-scale riparian canopy cover, and that increased canopy cover can result in increased CPOM standing stock (Roberts et al. 2007). However, in our study system, we found no such riparian canopy influence over either CPOM or FBOM standing stock, regardless of watershed land use. This result implies that organic matter standing stocks may be more closely tied to in-stream characteristics that influence retention distance and storage, such as hydrology or bed morphology (Carroll and Jackson 2008, Imberger et al. 2011), than to canopy cover. However, we found no relationships between in-stream habitat assessment scores and basal re-source quantity (data not shown),

suggesting that the Kentucky Division of Water assessment protocol is not well-suited for characterizing factors affecting organic matter retention.

As expected, CPOM standing stock was greatest in autumn, corresponding with elevated leaf-litter inputs, regardless of watershed type. Nevertheless, we found no strong canopy influence, which further strengthens the argument that factors controlling retention and storage of organic matter wield stronger influence than local-scale inputs in determining standing stock. Furthermore, winter CPOM biomass did not differ from that in spring or summer, which suggests that by the onset of the winter sampling season, much of the allochthonous matter inputs from autumn either were flushed from the system or were consumed by microbial (Imberger et al. 2008) or macroinvertebrate processing (Hagen et al. 2006, Cook and Hoellein 2016).

Benthic algal standing stock

Benthic algal standing stock was most strongly associated with watershed land use and was consistently elevated in urban streams. This observation aligns with those of previous investigators, who found greater gross primary production (GPP) in urban than in forested streams across multiple regions of North America (e.g., Bernot et al. 2010) and in our study streams specifically (Alberts et al. 2016). This result probably can be attributed to elevated nutrient levels in the urban study streams. In the absence of scouring events or grazing, elevated GPP may result in elevated benthic algal biomass.

Riparian canopy was an important control on algal biomass during summer when cover from stream-side trees was most dense in closed-canopy reaches but remained sparse in open-canopy reaches. Light limitation is an important regulator of in-stream primary production (Van-note et al. 1980, Hill et al. 1995), and shading during summer resulted in lower algal standing stock in closed than in open-canopy reaches. Urban open-canopy reaches had particularly high algal biomass, possibly because of synergy between elevated nutrient levels and light availability (Hill et al. 2011, Alberts et al. 2016), whereas closed-canopy reference reaches had the lowest algal biomass and may have been limited by both light and nutrients. Benthic algal biomass was similar between urban closed-and reference open-canopy reaches during the summer. This result suggests that the light level associated with riparian canopy was periodically important in shaping benthic algal standing stock at the reach-scale, but watershed land use was highly influential because it affected nutrient availability, and shading by riparian canopy was not enough to restrict algal biomass to reference levels in urban watersheds.

Urban streams are often characterized by high proportions of green algae that thrive in nutrient-rich environments (Allan 2004) and under high light conditions (Carpenter et al. 1998). Our study streams showed similar patterns in summer (Alberts 2016). Urban streams had high proportions of green algae, whereas reference streams were dominated by diatom taxa that may be comparatively more efficient than green algae at lower nutrient levels (Bothwell 1989). At the local scale, lack of shading from riparian vegetation resulted in high proportions of green algae in open-canopy reaches. The combination of elevated light and nutrient availability in urban open-canopy reaches resulted in significantly higher proportions of green algae than in reference open-or urban closed-canopy reaches. Thus, the

interplay of watershed-and reach-scale land cover may be important drivers of benthic periphyton biomass and community composition, which, in turn, may influence higher trophic levels.

Macroinvertebrate taxonomic richness

Macroinvertebrate taxonomic richness was negatively affected by catchment urbanization, in alignment with results from other studies (e.g., Lenat and Crawford 1994, Roy et al. 2003), but taxonomic richness differed between urban and reference streams only in winter and spring. Similar interactions between season and watershed land use exist between urban and rural streams, such that richness tended to increase from June to October in rural streams, but decreased over those months in urban streams (John-son et al. 2012). In some cases, taxonomic richness may be lower in urban than reference streams in all seasons (Helms et al. 2009), but this trend may be highly variable depending on antecedent environmental conditions, including hydrology (Hawley et al. 2016). In our study, reference streams had lower taxonomic richness in summer and autumn than in spring and winter, whereas urban streams had higher richness in summer and autumn and lower richness in spring and winter. The lack of significant reach-scale pat-terns suggests that the influence of riparian canopy on macroinvertebrate diversity was overwhelmed by watershed land use, corroborating previous findings (e.g., Lenat and Crawford 1994, Kjeldsen 1996, Roy et al. 2003). In part, this may be a result of the inability of relatively sensitive taxa, such as Plecoptera, to persist under the impaired water quality often observed in urban stream systems (Urban et al. 2006).

Scrapers

Negative relationships between total and proportional scraper biomass and benthic algal standing stock in spring in both watershed types and in winter in reference streams were contrary to our expectations. This result suggests that grazing by macroinvertebrates might result in relatively strong top-down control of this resource (Kjeldsen 1996), at least during some times of year. In reference streams, the highest and lowest total scraper biomass occurred in spring and winter, respectively, but benthic algal biomass did not vary between winter and spring, suggesting instead that the relationship between scrapers and their primary food resource differs by season. In urban streams, total and proportional scraper biomass were highest in summer, which corresponds with the highest algal standing stock in urban open-canopy reaches, but lowest in urban closed-canopy reaches. Light availability can alter algal biomass and com-munity composition (Hill et al. 1995), and the lack of a reach-scale scraper response to our observed differences in algal biomass might be attributable to a consumer preference for particular algal taxa that are favored by either shaded or sunlit conditions (Feminella et al. 1989).

Shredders

Neither total nor proportional shredder biomass was related to basal resource (CPOM) standing stock, but proportional shredder biomass was closely related to watershed land use. Proportional shredder biomass during winter and spring was higher in reference than in urban streams. Al-though highly variable, total shredder biomass also was higher in reference than urban streams during these sea-sons. In reference streams in winter and spring, shredders were predominantly Plecoptera, taxa that were mostly ab-sent from our

urban streams. Hydrological dynamics in our study streams may have resulted in relatively short CPOM residence times and rapid changes in standing stocks that confounded our ability to detect a shredder bio-mass response to resource availability (K. T. Belt, US Forest Service; S. S. Kaushal, University of Maryland; C. M. Swan, University of Maryland, Baltimore County; R. V. Pouyat, US Forest Service; P. M. Groffman, Cary Institute of Ecosystem Studies; I. Turcsanyi, Dynamac Corporation; J. L. Greenwood, University of Tennessee at Martin; unpublished data). On the other hand, greater total and proportional shredder biomass were evident in reference streams in winter when CPOM stocks were higher in urban than in reference streams, suggesting that different degrees of processing by shredders can lead to similar levels of CPOM among streams with different watershed land uses.

Collectors

Collector taxa dominated the overall macroinvertebrate community biomass in our study streams, and we observed a negative relationship between proportional collector bio-mass and FBOM during winter, again suggesting the potential of top-down resource control. Collector biomass was driven largely by generalist taxa (i.e., *Lirceus* sp., nonTany-podinae chironomids, and *Gammarus* sp.), which are more likely than specialists to incorporate various food sources into their diet and, thus, are inherently less likely to exhibit a close relationship with any particular resource (Mihuc 1997), which may account for the lack of relationships during most of the year. On the other hand, differential rates of FBOM processing may lead to difficulty relating standing stocks to consumer biomass during relatively short sampling periods (Wallace et al. 1982).

Predators

Predator biomass in urban streams was dominated by small-bodied, tolerant organisms, such as predaceous midges, whereas larger-bodied Plecoptera and Megaloptera were the dominant predators in reference streams. Insect-prey bio-mass was greatest in reference streams in spring, followed by winter, and the relationship between predator and prey biomass was strongest and predatory Plecoptera were most abundant in these seasons. In urban streams, the relationship between predator and prey biomass was significant only in spring, when prey biomass was greatest.

Conclusion

Our work highlights the complexity of the interactions among seasonal variation in organic matter standing stocks, riparian canopy cover, and macroinvertebrate phenology that shape aquatic ecosystems. It also provides insight into how responses to this variation may be affected by water-shed development, and supports previous work documenting the overwhelming influence of watershed urbanization on organic matter standing stocks (e.g., Imberger et al. 2008) and aquatic macroinvertebrate communities (e.g., Roy et al. 2005). However, our study also provides evidence that reach-scale riparian canopy cover can be an important driver of basal resource standing stock during certain times of year, particularly via regulation of light, in-stream primary productivity (Alberts et al. 2016), and algal

biomass. The importance of riparian canopy cover as a control of primary production and algal biomass may be greater in regions without seasonal patterns of leaf-out and leaf-fall.

As urban centers proliferate, conservation and restoration of urban aquatic resources will remain an important goal of planners and environmental managers. Our study provides evidence that elements of stream ecosystem function are shaped by factors at both the watershed- and reach-scale, but that these influences vary with season. Strong watershed-scale control over basal resources and macroinvertebrate dynamics were evident, but at times, the riparian canopy played an important role in controlling some aspects of stream functional structure, even in very urbanized watersheds.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Conceptual diagram of expected influences of watershed, riparian canopy, and season on stream benthic basal resource availability and benthic macroinvertebrate functional feeding group (FFG) biomass. CPOM = coarse particulate organic matter, FBOM = fine benthic organic matter.

Figure 2.

Scatterplots of coarse particulate organic matter (CPOM) standing stock by watershed, canopy, and season. Dots represent benthic CPOM dry mass for individual study reaches during the specific sampling season. Lines connect the mean value for each canopy treatment by watershed type. Fall 5 autumn, Ref 5 reference, Urb 5 urban.

Figure 3. Scatterplots of fine benthic organic matter (FBOM) standing stock by watershed, canopy, and season. Dots represent FBOM dry mass for individual study reaches during the specific sampling season. Lines connect the mean value for each canopy treatment by watershed type. Fall 5 autumn, Ref 5 reference, Urb 5 urban.

Figure 4.

Scatterplots of benthic chlorophyll *a* (Chl *a*) stand-ing stock by watershed, canopy, and season. Dots represent Chl *a* dry mass for individual study reaches during the specific sampling season. Lines connect the mean value for each canopy treatment by watershed type. Fall 5 autumn, Ref 5 reference, Urb 5 urban.

Figure 5. Scatterplots of macroinvertebrate taxonomic richness by watershed, canopy, and season. Dots represent taxonomic richness for individual study reaches during the specific sampling season. Lines connect the mean value for each canopy treatment by watershed type. Fall 5 autumn, Ref 5 reference, Urb 5 urban.

Table 1.

Study stream watershed, drainage area, and 100-m riparian buffer % coverage of impervious surface and major land-cover types. Fk 5 fork, Ck 5 creek.

Stream	Watershed	Drainage area (km ²)	Watershed impervious surface cover (%)	Riparian impervious surface cover (%)	Watershed forest cover (%)	Riparian forest cover (%)	Watershed agriculture cover (%)	Riparian agriculture cover (%)
Ashby Fk	Reference	11.4	2.2	4.9	69.1	81.4	23.1	13.7
Cruise Ck	Reference	11.1	1.7	5.6	67.2	70.8	27.8	23.6
Middle Ck	Reference	8.5	2.1	3.1	73.5	83	22.1	13.9
Steep Ck	Reference	9.6	1.7	4.3	66.4	73.2	25.3	22.5
Elijah Ck	Urban	10.1	31.6	28.3	22.3	58.1	16.7	13.6
Oakbrook	Urban	10.1	26.5	29.4	18.2	58.2	26.7	12.4
Sunnybrook	Urban	5.7	27.3	42.1	13.4	51.5	13.3	6.4
Threemile Ck	Urban	8.2	18.8	33.6	28.6	62.3	8.5	4.1

Table 2.

Mean (SD, *n* 5 4) stream physicochemical properties and basal resource estimates by watershed type, reach-scale canopy, and season. CPOM 5 coarse particulate organic matter, FBOM 5 fine benthic organic matter, AFDM 5 ash-free dry mass, Chl *a* 5 chlorophyll *a*.

Watershed	Reach	Season	Specific conductivity (IS/cm)	pH	NH ₄ ¹ (mg/L)	NO ₃ ² (mg/L)	PO ₄ ³² (mg/L)	Temperature (7C)	Benthic Chl <i>a</i> (mg/m ²)	CPOM (gAFDM/m ²)	FBOM (g AFDM/m ²)
Reference	Open	Autumn	487 (117)	8.1 (0.5)	0.02 (0.01)	0.12 (0.07)	0.06 (0.04)	4.2 (1.1)	72 (62)	4.4 (2.8)	0.6 (0.4)
		Winter	498 (112)	8.2 (0.2)	0.04 (0.03)	0.33 (0.12)	0.06 (0.02)	1.6 (0.1)	58 (21)	1.4 (0.6)	0.4 (0.2)
		Spring	344 (163)	8.8 (0.4)	0.05 (0.03)	0.36 (0.17)	0.07 (0.05)	17.9 (1.7)	63 (28)	1.5 (0.6)	0.4 (0.1)
		Summer	504 (57)	8.0 (0.3)	0.06 (0.04)	0.10 (0.04)	0.07 (0.04)	22.5 (1.6)	61 (39)	1.4 (0.9)	0.4 (0.2)
	Closed	Autumn	487 (116)	8.1 (0.4)	0.03 (0.01)	0.13 (0.07)	0.07 (0.04)	4.2 (1.1)	21 (14)	5.4 (0.5)	0.8 (0.6)
		Winter	494 (101)	8.2 (0.3)	0.04 (0.01)	0.30 (0.08)	0.05 (0.02)	1.5 (0.1)	47 (37)	1.1 (0.4)	0.3 (0.1)
		Spring	333 (164)	8.8 (0.3)	0.05 (0.04)	0.37 (0.16)	0.08 (0.05)	17.8 (1.7)	48 (18)	1.7 (0.7)	0.5 (0.2)
		Summer	508 (61)	7.9 (0.4)	0.08 (0.09)	0.10 (0.05)	0.06 (0.04)	20.8 (0.9)	20 (6)	2.3 (3.0)	0.4 (0.3)
Urban	Open	Autumn	682 (237)	8.0 (0.5)	0.03 (0.01)	0.15 (0.06)	0.14 (0.11)	2.6 (0.5)	172 (50)	4.7 (1.4)	0.7 (0.2)
		Winter	1126 (266)	8.1 (0.4)	0.07 (0.05)	0.48 (0.13)	0.03 (0.02)	1.8 (1.3)	125 (43)	2.6 (0.4)	0.5 (0.1)
		Spring	757(348)	8.5 (0.1)	0.16 (0.18)	0.37 (0.20)	0.06 (0.05)	17.7 (3.2)	166 (54)	2.0 (0.7)	0.5 (0.2)
		Summer	784 (119)	8.1 (0.2)	0.14 (0.06)	0.26 (0.37)	0.19 (0.11)	23.9 (0.3)	246 (111)	2.5 (2.5)	0.5 (0.4)
	Closed	Autumn	683 (238)	8.0 (0.5)	0.02 (0.01)	0.15 (0.06)	0.15 (0.11)	2.7(0.5)	189 (85)	3.9 (1.3)	0.6 (0.2)
		Winter	1116 (274)	8.1 (0.4)	0.06 (0.05)	0.49 (0.13)	0.02 (0.02)	1.9 (1.3)	158 (29)	2.9 (1.0)	0.6 (0.2)
		Spring	738 (333)	8.5 (0.2)	0.14 (0.17)	0.37 (0.22)	0.07 (0.05)	17.6 (3.2)	172 (69)	1.7(0.5)	0.4 (0.2)
		Summer	773(122)	8.0 (0.1)	0.12 (0.03)	0.12 (0.06)	0.20 (0.10)	23.3 (0.6)	55 (16)	0.9 (0.3)	0.3 (0.1)

Table 3.

Best-fit linear mixed models for physicochemical properties and basal resource standing stock. For each model, the table shows predictors, marginal R^2 (variance explained by fixed factors) and conditional R^2 (variance explained by both fixed and random factors). For all models, season was treated as a fixed effect nested within the random effect of stream. CPOM 5 coarse particulate organic matter, FBOM 5 fine benthic organic matter, Chl *a* 5 chlorophyll *a*.

Response	Main effects	Interactions	Marginal R^2	Conditional R^2
Conductivity	Season, watershed	Season $\times$ watershed	0.84	0.90
pH	None	None	NA	NA
Mean temperature	Season	None	0.67	0.81
CPOM	Season	None	0.34	0.48
FBOM	None	None	NA	NA
Chl <i>a</i>	Canopy, watershed	Canopy $\times$ season, canopy $\times$ season $\times$ watershed	0.61	0.68

Table 4.

Mean (SD, $n = 4$) macroinvertebrate taxonomic richness and biomass estimates by watershed type, reach-scale canopy, and season. AFDM 5 ash-free dry mass.

Watershed	Reach	Season	Richness	Biomass (g AFDM/m ²)				
				Insect-prey	Predator	Shredder	Scraper	Collector
Reference	Open	Autumn	15.0 (1.4)	7.3 (1.9)	0.6 (0.7)	0.3 (0.4)	3.7 (2.2)	12.0 (9.7)
		Winter	17.0 (3.9)	7.2 (6.5)	0.9 (0.6)	1.7 (1.6)	1.5 (1.6)	8.7 (3.2)
		Spring	21.0 (3.2)	11.7 (2.7)	1.1 (0.4)	2.7 (0.8)	4.4 (3.2)	10.4 (3.1)
		Summer	10.3 (2.2)	4.0 (3.5)	0.1 (0.0)	0.1 (0.1)	2.2 (0.9)	2.3 (3.4)
	Closed	Autumn	15.5 (2.4)	7.2 (2.5)	0.6 (0.8)	0.2 (0.2)	3.4 (1.1)	9.0 (4.0)
		Winter	14.7 (3.0)	5.9 (4.5)	0.9 (1.1)	1.7 (1.2)	0.8 (1.1)	8.2 (5.1)
		Spring	20.3 (5.4)	18.3 (12.5)	2.0 (1.0)	5.0 (5.6)	6.4 (3.1)	8.5 (2.4)
		Summer	13.5 (2.6)	5.2 (4.0)	0.4 (0.5)	0.2 (0.2)	2.1 (0.3)	3.9 (3.2)
Urban	Open	Autumn	13.0 (2.2)	8.5 (6.9)	0.6 (0.3)	0.2 (0.4)	5.3 (5.2)	24.8 (35.6)
		Winter	10.7 (5.2)	5.6 (6.8)	0.4 (0.4)	0.2 (0.4)	3.1 (4.7)	12.8 (14.1)
		Spring	11.0 (2.9)	14.3 (11.0)	0.9 (0.5)	0.1 (0.3)	4.6 (6.2)	19.7 (11.0)
		Summer	13.5 (2.4)	10.0 (5.0)	0.2 (0.1)	0.2 (0.2)	7.3 (3.8)	5.0 (3.9)
	Closed	Autumn	14.7 (2.9)	6.3 (4.7)	0.5 (0.3)	0.1 (0.2)	4.2 (3.9)	13.9 (20.7)
		Winter	8.0 (5.5)	4.0 (4.3)	0.8 (1.0)	0.5 (0.6)	1.4 (1.5)	7.9 (7.4)
		Spring	9.2 (2.1)	15.6 (11.7)	0.8 (0.8)	0.0 (0.0)	5.3 (5.5)	16.3 (9.6)
		Summer	14.3 (5.0)	10.2 (9.3)	0.2 (0.1)	0.1 (0.2)	8.4 (7.8)	2.2 (2.1)

Table 5.

Best-fit linear mixed models for macroinvertebrate taxonomic richness and total community biomass. For each model, the table shows predictors, marginal R^2 (variance explained by fixed factors) and conditional R^2 (variance explained by both fixed and random factors). For all models, season was treated as a fixed effect nested within the random effect of stream. Predictors for macroinvertebrate taxa richness and total community biomass included watershed-and reach-scale canopy cover and season. Each best-fit model explained significantly more variation in response than the null model.

Response	Main effect	Interaction	Marginal R^2	Conditional R^2
Taxonomic richness	Watershed	Watershed $\times$ season	0.47	0.79
Total macroinvertebrate biomass	Season	None	0.14	0.78

Table 6.

Best-fit linear mixed models for functional feeding group (FFG) biomass, expressed as total biomass and as a proportion of the total macroinvertebrate biomass for that site and season. For each model, the table shows predictors, marginal R^2 (variance explained by fixed factors) and conditional R^2 (variance explained by both fixed and random factors). For all models, season was treated as a fixed effect nested within the random effect of stream. Predictors for FFG responses included primary food resource, watershed-scale land cover, canopy cover, and season. Each best-fit model explained significantly more variation in response than the null model. Poisson distributions were used for each total biomass model. FBOM 5 fine benthic organic matter, NA 5 not applicable.

Response	FFG	Main effect	Interaction	Marginal R^2	Conditional R^2
Total biomass	Scraper	Chlorophyll <i>a</i> , season	Chlorophyll <i>a</i> × season	0.22	0.81
	Shredder	None	None	NA	NA
	Collector	None	None	NA	NA
	Predator	Prey-insect biomass	Prey-insect biomass × watershed	0.53	0.82
Proportional biomass	Scraper	Chlorophyll <i>a</i> , season	Chlorophyll <i>a</i> × season	0.62	0.84
	Shredder	Watershed	None	0.55	0.88
	Collector	Season	FBOM × season	0.33	0.81
	Predator	None	None	NA	NA