The urban watershed continuum: evolving spatial and temporal dimensions

Sujav S. Kaushal · Kenneth T. Belt

Published online: 1 March 2012

© Springer Science+Business Media, LLC 2012

Abstract Urban ecosystems are constantly evolving, and they are expected to change in both space and time with active management or degradation. An urban watershed continuum framework recognizes a continuum of engineered and natural hydrologic flowpaths that expands hydrologic networks in ways that are seldom considered. It recognizes that the nature of hydrologic connectivity influences downstream fluxes and transformations of carbon, contaminants, energy, and nutrients across 4 space and time dimensions. Specifically, it proposes that (1) first order streams are largely replaced by urban infrastructure (e.g. storm drains, ditches, gutters, pipes) longitudinally and laterally within watersheds, (2) there is extensive longitudinal and lateral modification of organic carbon and nutrient retention in engineered headwaters (3) there are longitudinal downstream pulses in material and energy exports that are amplified by interactive land-use and hydrologic variability, (4) there are vertical interactions between leaky pipes and ground water that influence stream solute transport, (5) the urban watershed continuum is a transformer and transporter of materials and energy based on hydrologic residence times, and (6) temporally, there is an evolution of biogeochemical cycles and ecosystem functions as land use and urban infrastructure change over time. We provide examples from the Baltimore Ecosystem Study Long-Term Ecological (LTER) site along 4 spatiotemporal dimensions. Long-term monitoring indicates that engineered headwaters increase downstream subsidies of nitrate, phosphate, sulfate, carbon, and metals compared with undeveloped headwaters. There are increased longitudinal transformations of carbon and nitrogen from suburban headwaters to more urbanized receiving waters. Hydrologic connectivity along the vertical dimension between ground water and leaky pipes from Baltimore's aging infrastructure elevates stream solute concentrations. Across time, there has been increased headwater stream burial, evolving stormwater management, and long-term salinization of Baltimore's drinking water supply. Overall, an urban

Department of Geology & Earth System Science Interdisciplinary Center, University of Maryland, College Park, College Park, MD 20740, USA

e-mail: skaushal@umd.edu

K. T. Belt

USDA Forest Service, Northern Research Station, Baltimore Field Station at University of Maryland Baltimore County, Baltimore, MD 21227, USA



S. S. Kaushal (🖂)

watershed continuum framework proposes testable hypotheses of how transport/transformation of materials and energy vary along a continuum of engineered and natural hydrologic flowpaths in space and time. Given interest in transitioning from sanitary to sustainable cities, it is necessary to recognize the evolving relationship between infrastructure and ecosystem function along the urban watershed continuum.

Keywords Land use change · Sanitary city · Urban sustainability · Organic carbon · Nitrogen · Phosphorus · Copper · Lead · Zinc · Road salt · Emerging contaminants · Stream restoration · Stormwater management · Aging infrastructure

Introduction

Within two decades, 60% of the world's population will live in cities, and coping with urban drinking water and sanitation issues is one of the greatest challenges of this century (United Nations 2010). New patterns and rates of urban development have led to extensive regional headwater alteration, increased inputs of contaminants, and increased hydrologic connectivity between watersheds and streams (Paul and Meyer 2001; Foley et al. 2005; Grimm et al. 2008; Lookingbill et al. 2009; Kaushal et al. 2011). Urban development increases hydrologic connectivity through the installation of pipe networks, gutters, swales, and ditches (e.g. Elmore and Kaushal 2008; Roy et al. 2009). The sheer magnitude of increased flows and altered subsidies and fluxes of organic matter, organisms, energy, and nutrients creates a complex suite of impacts and stressors that distinguishes urban stream networks from stream networks draining rural landscapes. Moreover, the increased magnitude of these linkages suggests that elucidating the structure and function of urban watersheds and associated changes in downstream processes have important ecosystem and public health implications. Given our expanding knowledge of hydrologic connectivity and growing efforts to transition from sanitary to sustainable cities, we must now consider a dynamic continuum of engineered and natural hydrologic flowpaths that expands hydrologic networks in ways that have been seldom considered across 4 dimensions of space and time. The coupling of watersheds with stream networks as integrated units that act as both "transporters" and "transformers" of material and energy fluxes should now be considered across evolving spatial (meters to kilometers) and temporal scales (minutes to centuries).

Our work builds on a previous landmark concept that describes the consistently observed ecological degradation at the urban stream reach scale known as the "urban stream syndrome" (Walsh et al. 2005a). The urban watershed continuum that we propose here is complementary, yet differs because it considers both transport and transformation processes along dynamic hydrologic flowpaths of the whole watershed (engineered headwaters, natural/engineered riparian zones, ground water, streams) along 4 spatial and temporal dimensions. The urban watershed continuum framework includes a continuum of hydrologic flowpaths that are not considered by the urban stream syndrome, such as vertical groundwater-stream interactions and evolving biogeochemical cycles over time. The urban watershed continuum framework also considers hydrologic flowpaths along watersheds draining all forms of urban development from low-residential development to cities; for example, even at fairly low proportions, impervious surfaces can have significant impacts on streams that range to larger impacts in watersheds that are almost entirely covered by impervious surfaces.

Previous concepts have emphasized important water quality impacts along urban-rural gradients and across a range of watershed impervious surface coverage with great practical



applications to managing water quality (Walsh et al. 2005b; Schueler et al. 2009). For example, small watershed studies have compared hydrologic and biogeochemical impacts of individual land use/cover types or ranges in land use/cover (e.g. forested to entirely urban watersheds) on material and energy fluxes. These are "natural experiments" that mimic the small watershed approach to estimate hydrologic and material budgets (Pouyat et al. 2007, 2010), which has been successfully used for decades at Hubbard Brook and elsewhere (e.g. Likens 2001; Baker et al. 2001; Groffman et al. 2004; Wollheim et al. 2005; Kaushal et al. 2008a). Clearly, small watershed comparisons of the Baltimore LTER and Phoenix CAP LTER sites and other small urban watersheds have advanced our understanding of urban land use changes on watershed ecosystems and have generated many questions and hypotheses (Baker et al. 2001; Kaushal et al. 2011). Although the small watershed approach is useful, this can be a relatively coarse scale that does not always allow for delineating complex mechanisms within urban watersheds along dynamic hydrologic flowpaths. The urban watershed continuum provides a different finer-scale approach that considers mechanisms across varying temporal and spatial scales. There is a need for an expanded concept tracking the spatial transport/transformation and evolution of materials/energy cycles across time along a continuum of engineered and natural hydrologic flow paths to larger receiving waters (e.g. Pouvat et al. 2007).

An urban watershed continuum across space and time represents a new dynamic conceptual framework for investigating several research questions relevant to: how nutrient and hydrologic retention change along flow paths in urban watersheds across space and time (e.g. Baker et al. 2001), how the ecological stoichiometry of carbon, nutrients and metals change along hydrologic flow paths in urban watersheds (e.g. Sterner et al. 2008), how biodiversity and ecosystem functions may change along hydrologic flow paths and watershed environmental gradients (e.g. Warren et al. 2011), and how patterns in ecological community succession and biogeochemical functions can be coupled or decoupled following storms and other disturbances (e.g. Alberti 2005). Given increasing interest in the transition from sanitary to sustainable cities (Pickett et al. 2011a,b), it will be necessary to advance concepts integrating infrastructure and ecosystem function along space and time.

From a spatial perspective, drainage networks and eco-hydrologic processes occur in engineered headwaters (storm drains, swales, ditches, etc.) upstream of what we normally think of as urban streams. These extensive engineered headwaters are emerging ecosystems, and have not fully been considered as functional units involved in both material transport and transformation. Although engineered headwaters should not be ignored as part of drainage networks, there are no concepts comparing ecological and biogeochemical functions in engineered headwaters vs. what we consider as traditional headwater stream ecosystems. From a temporal perspective, there has been evolution of the structure and function of watersheds and engineered headwaters as cities developed over time (e.g. storm drains, stormwater detention basins, bioretention, and other best management practices or BMPs). Although city infrastructures vary in age globally (in some cases by centuries), there are no conceptual frameworks that incorporate the evolving relationship between infrastructure and ecosystem function over time. We propose that urban watershed research needs to more explicitly incorporate material and energy flows along a continuum of engineered and natural hydrologic flowpaths via: 1) engineered headwaters, which play an important and underappreciated ecological role along stream networks; 2) the influence of urban infrastructure on hydrological connectivity, which influences downstream fluxes and transformations; 3) the evolving relationship between urban infrastructure (stormwater, sanitary, and transportation) and ecosystem function; and 4) how urban design and the inevitable degradation of infrastructure influence the relationship between urban infrastructure and ecosystems.



Comparisons with traditional watershed and stream ecological frameworks for natural and forest ecosystems are likely useful in building an urban watershed conceptual model that will incorporate a more complete understanding of fluxes, transformations and network linkages between urbanized watersheds and their stream networks.

There are many conceptual models posing hypotheses of how materials and energy change along hydrologic flowpaths in minimally disturbed and forest watersheds. For example, in natural and forest ecosystems, the River Continuum Concept was an important advancement that proposed the physical variables within a river system present a continuous gradient of physical conditions from headwaters to mouth (Vannote et al. 1980). Furthermore, Vannote et al. (1980) proposed that this gradient should elicit a series of responses resulting in a continuum of biotic adjustments and consistent patterns of loading, transport, utilization, and storage of organic matter along the length of a natural river. A key question is whether existing conceptual models for minimally disturbed watersheds such as the River Continuum Concept can be applied and/or modified to predict transport and transformation processes in suburban and urban watersheds that vary in their impervious surface coverage and their form of urban development. Another key question is to what extent there is a distinct and "unique" urban biogeochemistry because of the role of people as part of ecosystems and large variability in constitutent concentrations, hydrology, and temperatures compared to natural ecosystems (Kaye et al. 2006). Patterns and processes as water flows through watersheds draining forest vs. urbanized watersheds can be similar in some respects but different in others. We include a table to illustrate how the urban watershed continuum can be used to formulate research questions and organize key concepts along flow paths (Table 1). We use the term "continuum" because we propose a conceptual framework that incorporates a continuum of engineered and natural flowpaths from urbanized watersheds through stream networks across 4 dimensions of a space-time continuum, and we also explore the applicability of previous concepts for natural systems (e.g. Vannote et al. 1980). Thus, the urban watershed continuum encompasses a dual discussion of the older classic upstream-downstream continuum. It also proposes the new concept of a dynamic continuum of engineered and natural flowpaths, including the more subtle ways urban landscapes alter ecosystem processes along spatial and temporal dimensions seldom considered.

Previous conceptual frameworks in forest watersheds and streams

There has been an increasing appreciation for the importance of understanding the structure and function of watersheds and streams from a landscape perspective (e.g. through smaller scale ecological linkages between land and water and within the channel and floodplains). The watershed concept has been central in understanding inputs, outputs, and transformations of materials and energy within forest watersheds (Likens 2001). Early work in streams displayed a growing realization that watershed characteristics are an important component of stream ecosystems (Hynes 1970). The study of large rivers led to increased awareness of longitudinal patterns and it stimulated development of the River Continuum Concept (Vannote et al. 1980), as well as concepts regarding the three dimensional interconnectedness of ecohydrologic realms (Stanford 1998). Other concepts and frameworks have advanced our understanding of organic matter dynamics and fauna at individual sites, ecosystem functions at stream reach scales, recognition of parafluvial systems and riparian interactions, and the importance of larger watershed scale and stream network scale processes (e.g. Fisher and Likens 1973; Minshall et al. 1983; Naiman et al. 1987; Fisher et al. 1998). The River Continuum Concept and these other concepts and frameworks have drastically changed our



Table 1 Inputs, pools, processing, and outputs along 4 spatial and temporal dimensions of the Urban Watershed Continuum. V is shorthand for "very" and ? denotes unknown areas requiring further research.

Ecosystem Characteristic, Examples	eristic, Examples	Watershed Land Use/Cover	nd Use/Cover	Examples of Hydrologic Connectivity
		Urban	Forested	
I. The First, Longit Inputs	I. The First, Longitudinal Dimension (Upstream-Downstream) Inputs Runoff and loads (nutrients, organic matter, contaminants, etc.)	V V High	V Low	Ia. ZERO ORDER: Storm drains extend the contributing area of the "zero order" (unchannelized) upper part of the headwater cachment, with engineered channels (pipes, gutters, etc) insuring frequent and large flows of surface water and loads from an area that contributed little of these in the forested state
Pools	Novel storage by altered drainage features (e.g., stormwater facilities) & water/sewage systems	High?	Low	Ib. BURIED BASEFLOW: These "buried" streams (in pipes) carry stormwater transft, but may well also convey much baseflow, which sceps into storm drains at frequent intervals through joints, neither of which are found in forested catchments.
Processing Rates	Metabolism, denitrification in storm drains & facilities	Low?	High	Ic. NEW STORAGE: The storm drainage system also contains many points where water and loads may be stored and processed and exported such as stormwater facilities, gutters, street inlets, and extensive pipe netowrks.
Outputs II. The Second, Lat	Outputs Modified, but great magnitudes may carry loads further downstream & into receiving waters II. The Second, Lateral Dimension (Across the Watershed)	High	V Low	*See also section II below as these properties also apply to piped lateral tributaries.
Inputs	POC and DOC loads from urban litterfall and washoff; ferrel animal waste, etc	V V High	V V Low	IIa. DRAINAGE DENSITY: Storm drain networks increase the "drainage density" by orders of magnitude
Pools	Debris dams in gutters and swales; PAHs in soils in stormwater management facilities	V V High	High	IIb. DRAINAGE NETWORK: The storm drainage network
Processing Rates	Comminution of urban vegetation litter by traffic, changes in heavy metal bioavailability in stormwater basin soils (cation exchange).	High ?	V High	IIc. GUTTER SUBSIDY: The storm drainage network creates a "gutter subsidy"



ranie i (continued)	(pa			
Ecosystem Characteristic, Examples	eristic, Examples	Watershed Land Use/Cover	nd Use/Cover	Examples of Hydrologic Connectivity
		Urban	Forested	
Outputs	Surface waters are highly modified by humans at large, regional scales, creating novel combinations of constituents and residence times	High	V Low	*See also section I as these properties also apply to piped headwater tributaries (i.e.
III. The Third, Vert	III. The Third, Vertical Dimension (The Groundwater Matrix)			
Inputs	Interbasin transfers of urban water; bacteria and exotic compounds in sewage leaks and effluents	V High ?	V V Low	IIIa. MORE PIPES: A labyrinth or matrix of water and sanitary sewage pipes exist both across the watershed and in riparian areas and these can be very leaky (in and out.) Also a novel "groundwater matrix" of potable water
Pools	Salt in groundwater beneath stormwater management basins; sewage & water leaks in upland and riparian settings	V V High	High	IIIb. ENGINEERED WATER: Potable water leaks may dilute contaminant fluxes to streams
Processing Rates	Filtering of sewage particulates in sewage; changes in nutrient, DOC, and sulfur transformations in sewers	High?	Low	IIIc. IRRIGATION & DISPOSAL: Human activities like water harvesting
Outputs	Engineered urban waters create novel groundwater matrices that can leak into cracks in piped infrastructure or seep into streams	V High?	V Low	
IV. The Fourth, Dit	IV. The Fourth, Dimension of Time (Temporal Changes in Landscapes, Behaviors & Channels)	inels)		
Inputs	The process of urbanization can be rapid, drastically increasing flows and loads; changing these (restoration, afforestation) however are likely to be long-term, intensive endeavors	High ?	Low	IVa. LANDSCAPES: The onset of urbanization is often relatively rapid, but even established urban landsapes are in a continuing state of change, with deliberate changes in land use, building practices and vegetation preferences, as well as unintended changes related to the "aging" and degradation of landscape elements and urban infrastructure (roads, waste management, traffic, maintenance, etc). These changes dwarf those seen in the evolution of ecosystem patterns and processes as forests age and carry great implications for changes in urban stream ecosystems.



Table 1 (continued)	zd)			
Ecosystem Characteristic, Examples	ristic, Examples	Watershed Land Use/Cover	l Use/Cover	Examples of Hydrologic Connectivity
		Urban	Forested	
Pools	Stored waters may change greatly, e.g., when stormwater runoff ceases to be "wasted" and is harvested in sustainability movements	High ?	Low	IVb. PIPES/CHANNELS: Urban water networks also age, from the time they are introduced to the landscape to their rehabilitation or replacement with either similar systems or by innovative designs. Moreover, these changes may be dirvue by economics or sustainabilty paradigms, for example, a movement to a distributed rather than centralized urban water system might harvest water for on-site use and minimize storm and wastewater exports from urban catchments.
Processing Rates	Hydrologic impacts on urban stream channels are great, and it may take many decades for disturbed fluvial systems to stabilize.	High ?	Low	IVc. PEOPLE: Both landscapes and urban water systems undergo transformations related to sociological, ecological, economic or philosophical changes. For example, a shift from the sanitary city to the sustainable city model might bring wide-ranging changes in the landscape and in how infrastructure functions (e.g., greening, reconstruction, restoration), resulting in hydrologic as well as in biogeochemical processing and the way water and loads are moved along the landscape.
Outputs	Aging infrastructure of all types can greatly change flows and loads	High ?	Low	*All of these changes dwarf those seen in the evolution of ecosystem patterns and processes as forests age and carry great implications for changes in urban streams.



thinking regarding the structure and function of streams by connecting headwaters with larger order streams. Specifically, the original River Continuum Concept and subsequent work provided a foundation for developing concepts describing longitudinal in-channel processes along natural stream networks (Vannote et al. 1980), lateral connectivity between stream and floodplains (Junk et al. 1989; Stanford and Ward 1993), and importance of dams (Ward and Stanford 1995). However in the case of urban watersheds, comparing and contrasting these and other landmark concepts will not always be useful in the field of urban ecology because of increased hydrologic connectivity and the loss of distinctions across traditional ecological boundaries (Lookingbill et al. 2009).

Hydrologic connectivity: Linking urbanized watersheds with larger order streams

Traditional attempts to understand urban watersheds and streams have dealt with highly complex, dynamic environments, even though they represent much smaller spatial scales than the large, complex river and floodplain systems which the previously mentioned studies focused on. Recent work has focused on the importance of impervious surfaces and altered hydrology on downstream water quality, biotic communities and geomorphic conditions (e.g. Paul and Meyer 2001; Walsh et al. 2005a). As previously mentioned, the "urban stream syndrome" provides an important conceptual advancement for describing the suite of water quality effects of urbanization on streams draining urban landscapes (Walsh et al. 2005a, Wenger et al. 2009a). In addition, a growing body of empirical research in urban stream reaches has focused on characterizing in-stream processes such as metabolism, nutrient uptake, denitrification and effects on degradation and management practices at the stream reach scale (e.g. Meyer et al. 2005). Due to a growing awareness in the nature of hydrologic connectivity within urban watersheds, there has been recognition of the effects of hydrologic connectivity increasing and/or amplifying material and energy flows within and across watersheds (Grimm et al. 2008; Lookingbill et al. 2009). Thus, there is need for a unifying conceptual framework for integrating how materials and energy are transported along and within urban watersheds and transformed through larger order streams along a space and time continuum.

We use the paired terms "transporter" and "transformer" to describe the fate and transport of carbon, nutrients, metals, contaminants, and energy as they travel along urbanized watersheds. This approach can also be used to describe the fate and transport for other novel and exotic materials and substances that humans have added along the urban watershed continuum and urban groundwater matrix such as pharmaceuticals, pesticides, pathogens, or other compounds (e.g. solvents, fuels, building materials.) Although urban ecosystems are known to be flashy, the degree of flashiness will vary along the continuum of engineered and natural flowpaths. We therefore propose that there are unique opportunities for material retention and/or changes in material forms during periods of sufficient hydrologic residence times between storms, and these opportunities will vary along the urban watershed continuum.

In cities and surrounding metropolitan areas, hydrologic flowpaths can be highly correlated with urban landscape attributes such as impervious cover, and these attributes often form a continuum from a highly urban core to suburban and exurban areas. Broadly, we use the continuum of engineered and natural flow paths through a hierarchy of increasing watershed size as water flows to receiving waters to conceptualize the effects of urban land uses on stream and river ecosystems. An urban watershed continuum provides a novel, useful approach to conducting research in urban ecosystems. Researchers have typically emphasized land surface hydrology in their investigations of urban ecosystems, and so have missed key measures or approaches with respect to the 4 dimensions of the urban watershed continuum. In addition, the original River Continuum Concept for natural and forest



ecosystems falls short spatially in urban ecosystems for several reasons. For instance, urban streams should be considered 2nd or 3rd order because of storm drains and engineered drainage representing greatly expanded (and sometimes underappreciated) headwater drainage areas (Elmore and Kaushal 2008). Primary productivity and organic matter quality may be high in urban headwaters and comparable to what is predicted for larger order streams in the original River Continuum (Finlay 2011). In addition, earlier concepts such as the original River Continuum do not account for processes that occur at finer spatiotemporal scales, which is important in explaining short-term diurnal variations and/or "hot spot" and "hot moment" dynamics in urban ecosystems.

In this paper we present a new conceptual framework that addresses characteristics of watersheds that are affected by urban land uses including the (1) hydrologic connectivity between aquatic and terrestrial ecosystems that alters transport and transformation within watersheds at multiple spatial and temporal dimensions, (2) unique characteristics and challenges of recognizing engineered headwaters (zero to third order streams) as part of ecosystems and linkages to impacts in larger order streams and receiving waters, and (3) changes in the relationship between urban infrastructure and watershed material transport and transformation over time. We also examine how the urban watershed continuum framework is useful in structuring research and management questions related to fluxes, flowpaths, and ecosystem functions along engineered and natural headwaters to receiving waters.

We provide examples from collaborative projects from the National Science Foundation supported Baltimore Long-term Ecological Research site and U.S. Forest Service Baltimore Field Station. It is also important to note that the Baltimore wastewater system does not have large combined sewer overflows (CSO's) and instead relies on separate systems for storm drains and sanitary sewer lines. This was part of the popular Sanitary City design of the 20th Century that encompassed civil infrastructure for rapid stormwater conveyance, chlorination/treatment of drinking water, and separate sewer lines to protect public health (Melosi 2000). This paper is not intended to be a review of the urban stream literature and is primarily a conceptual paper based on long-term observations from the Baltimore LTER site. Although our examples draw heavily from urbanized watersheds and stream networks of the Baltimore LTER site, these concepts and questions can be applied to urban watersheds in other regions facing emerging challenges from engineered headwaters, aging infrastructure, stormwater management issues, and protection of downstream receiving waters.

The 4 dimensions of an urban watershed continuum

The patterns, pathways, and processes by which urban watersheds store and transport runoff, groundwater, baseflow, organic matter, contaminants and thermal energy have large implications for the structure and function of downstream stream networks and rivers. These patterns and processes operate at both short and long-term scales in a strongly linked multidimensional hydro-ecological system. Because of variability across space and time, a functional urban watershed continuum concept requires a 4 dimensional approach reminiscent of Ward (1989) but tailored to connecting people and engineered watersheds with their streams. This includes the 3 obvious spatial dimensions: longitudinal, lateral, and vertical; it also involves time as a 4th dimension that includes landscape development patterns and/or the upgrading and degradation of urban infrastructure over time as well as the changes in the social ecological system.

The importance of considering dimensions along watershed ecosystems is not new. For example, the variable source area concept has been useful in forested watersheds when dealing with the role of temporal and spatial dimensions and explaining how contributing



source areas change around the stream (Dunne and Black 1970). Similar to natural watersheds, suburban and urban watersheds can also be considered in topographic and geomorphic units that function across the temporal and spatial dimensions (Dunne and Black 1970; Gomi et al. 2002). However, these can include unique features such as engineered headwaters, modified riparian zones, groundwater exchange between streams and urban infrastructure, and downstream reaches as transporters and transformers of materials and energy delivered from upstream. The importance of these topographic and geomorphic units as variable source areas and linkages with ground water and infrastructure can vary across space and time dimensions (Paul and Meyer 2001; Sivirichi et al. 2011).

The 1st, longitudinal dimension: Storm drains as streams

Forested headwaters serve as primary sources of organic matter such as leaves, wood, debris to downstream food webs and have occupied a particularly important position in stream ecological theory (Vannote et al. 1980). However, urbanized headwaters and stream channels are greatly altered from their natural state via engineering of human-made drainage networks and channelization (Elmore and Kaushal 2008; Roy et al. 2009) (Fig. 1). For example, over the 20th Century many headwater streams in Baltimore City were put into underground stormdrains and buried during urban development (Fig. 1). Upland drainage features are, however, still important sources of organic matter (e.g. contributions from leaves and eroded soils in gutters, curbs, and swales, although there are also coinciding losses of organic matter processing/retention in engineered headwaters due to flashy hydrology, decreased residence times, and losses of channel complexity and losses of natural riparian areas) (Pouyat et al. 2007). Thus, small urbanized headwaters are likely important transporters of organic matter and energy from landscapes during storm events. Moreover, frequent and small storms may be important in providing a steady supply of organic matter during low to moderate flows whereas larger storms may scour organic matter from the stream ecosystem.

Increases in organic carbon loads from storm drains, swales, ditches, and leaky sewers can result in downstream tributaries which are more heterotrophic, more polluted (e.g., metals, pesticides, contaminants, hydrocarbons, biochemical oxygen demand) and more physically disturbed (scour, erosion, and sediment from high flow) than natural forest streams (Paul and Meyer 2001). Increases in organic carbon availability can also impact coupled biogeochemical cycles of nitrogen in urban streams and microbial transformations such as uptake and denitrification (Mayer et al. 2010; Sivirichi et al. 2011) (Fig. 2). For example, there are longitudinal declines in nitrate concentrations from headwaters of the Gwynns Falls (the focal study watershed of the Baltimore LTER site) and relationships between dissolved organic carbon and nitrate along the urban watershed continuum (Delaney 2009). This may be due to increased inputs of organic carbon along the urban watershed continuum from algal and/or sewage sources and decreases in nonpoint nitrate sources in more urbanized reaches. Another mechanism is that increased carbon enhances uptake and denitrification of nitrogen along the urban watershed continuum (Delaney 2009; Sivirichi et al. 2011; Kaushal et al. 2011). Overall, this research at the Baltimore LTER site has also shown that there may be shifts in ecological stoichiometry of carbon and nitrogen dynamics along an urban watershed continuum, although elucidating mechanisms requires further research (Sivirichi et al. 2011; Kaushal et al. 2011).

The 2nd, lateral dimension: Upland riparian zones and urban gutter subsidies

Streets and gutters serve as collectors of organic carbon, nutrients, and heavy metals, which is a unique feature of urban landscapes. The storage, transport, and transformation processes



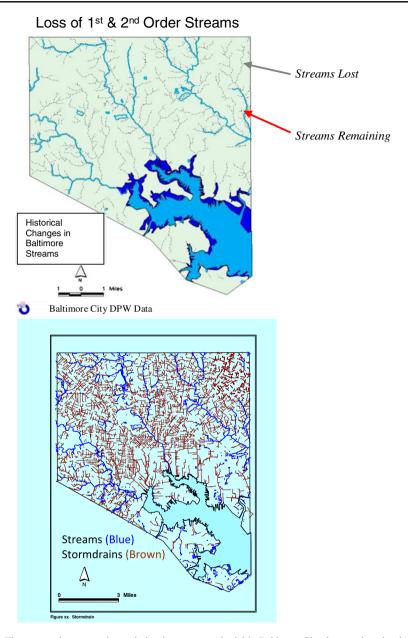
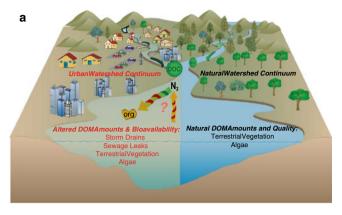
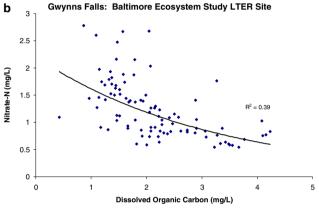


Fig. 1 There was a long-term change in headwater stream burial in Baltimore City due to urban development over the 20th Century (Data Courtesy of Maryland Geological Survey and Baltimore City Department of Public Works). Many streams were placed underground and there was a vast expansion of storm drain networks (Data Courtesy of Baltimore City Department of Public Works). Thus, storm drains as engineered and human-made headwaters now comprise a substantial proportion of urbanized drainage networks in modern Baltimore City

that occur in response to these subsidies of accumulated materials and thermal energy (due to decreased shading and heating of runoff from impervious surfaces) can be substantial at the watershed scale. Lateral connectivity between streams and rivers and adjacent floodplains







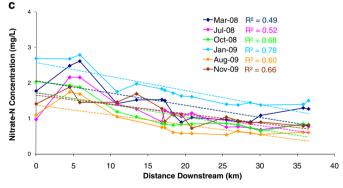


Fig. 2 a Conceptually, there are alterations in the amounts and quality of organic carbon along the urbanizing watershed continuum compared to forested watersheds. There are increases in organic carbon as water flows from low-residential areas in headwaters through progressively urbanizing areas with storm drains, sewage leaks, and algal blooms. Changes in quantity and quality of organic carbon along the urban watershed continuum can increase organic carbon exports downstream and have potential effects on ecosystem functions. Although this presents a specific case study for organic carbon, similar conceptual pathways can be described for nutrients, metals, organic contaminants, pathogens etc. **b** Longitudinal changes in nitrate concentrations along a 36 km transect of the Gwynns Falls during 6 times from spring 2008 to winter 2009. Dashed lines indicate significant linear relationships between distance downstream and nitrate concentrations (p<0.05). **c** Relationship between dissolved organic carbon and nitrate concentrations along longitudinal sampling of the Gwynns Falls watershed during 6 sampling times from spring 2008 to winter 2009



are critical to the understanding of ecological subsidies and ecosystem function (Ward and Stanford 1995). In natural watersheds, there can be enhanced hydrologic connectivity between riparian areas directly adjacent to streams through flood pulses and contributions of vegetation (Junk et al. 1989; Gregory et al. 1991). By contrast, streams in urbanized watersheds may be hydrologically disconnected from adjacent riparian and floodplains through channelization and streambank protection of property from flooding. There may also be decreased localized hydrologic connectivity between streams and riparian zones due to channel incision and decreased groundwater tables (Groffman et al. 2002). However, there is greater hydrologic connectivity at larger spatial scales between urban watersheds and their streams because of upland stormdrain networks (Walsh et al. 2005a; Elmore and Kaushal 2008).

The net effect of both enhanced and reduced hydrologic connectivity is that drainage densities (i.e., stream length per unit watershed area) of natural watersheds are dwarfed by those in urban watersheds (Walsh et al. 2005a). This greatly increased lateral hydrologic connectivity at the watershed scale increases organic carbon loads and other constituent loads to streams. It also magnifies most aspects of the urban stream syndrome and substantially impacts stream ecological structure and function (Walsh et al. 2005a). In forested headwater streams, ecological functions are defined by adjacent riparian forested areas, which regulate heat budgets through shading in the summer and supply organic matter to local aquatic food webs and downstream rivers ecosystems. In urbanized watersheds, headwater stream and riparian areas are vastly expanded via connectivity with impervious surfaces (Paul and Meyer 2001; Walsh et al. 2005a). This greatly increases the surface area for accumulation, storage, and transport of materials and energy from impervious surfaces and contributing areas in watersheds far from streams, beyond the traditional local riparian zones. Therefore, areas around gutters, swales, and other drainage features may act as increased source areas and "artificially extended riparian zones," increasing source areas from watersheds, and facilitating the lateral and longitudinal funneling of organic matter and other subsidies to downstream reaches.

At the Baltimore LTER site, there has been long-term monitoring of small watersheds with storm drains (no natural drainage networks) that receive substantial material inputs from streets and gutter subsidies. Stormdrains that are directly connected to streets and gutters can increase nitrate, phosphate, sulfate, and carbon inputs along lateral dimensions (Fig. 3a). Storm drains can also contribute elevated concentrations of heavy metals (copper, lead, and zinc) from the urban landscape, with concentrations that are above water quality standards of the U.S. Environmental Protection Agency. These concentrations of heavy metals can be elevated during both storm events and dry weather baseflow (Fig. 3b). There are also strong relationships between concentrations of total suspended solids and copper, lead, and zinc in storm drains during storm events suggesting the importance of storm events in mobilizing lateral inputs and gutter subsidies of particulates along the urban watershed continuum (Fig. 3c). Not much is known about empirical relationships between drainage density, quantifying distances of contributing areas in watersheds to streams, and related impacts on amounts and character of organic matter, nutrients, metals, and other contaminants delivered to urban streams (Walsh et al. 2005a; Roy et al. 2009). Supporting work has also shown increasing concentrations of metals and calcium in riparian soils from suburban headwaters to larger order urban streams of the Gwynns Falls at the Baltimore LTER site, and this may be an additional example of how biogeochemical patterns can vary longitudinally along riparian zones of the urban watershed continuum (Bain et al. 2011).



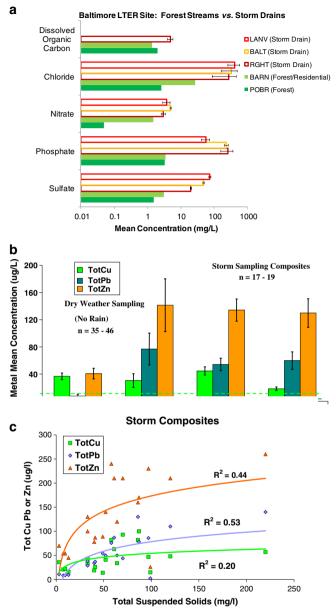


Fig. 3 a Mean concentrations of sulfate, phosphate, nitrate, chloride, and dissolved organic carbon can be substantially elevated in storm drains compared to forest streams. Samples were collected weekly during 2005–2006 and error bars represent standard errors. Routine water chemistry includes data from long-term monitoring stations at the Baltimore LTER site (Groffman 2010). b Long-term monitoring of metals (copper, lead, and zinc) in Watershed 263 of the Baltimore LTER site (2 small watersheds in the inner city of Baltimore with stormdrains and no natural drainage) show that copper and lead concentrations exceed limits set by the U.S. Environmental Protection Agency (dashed lines indicate limits). Metals concentrations can be elevated during stormflow and baseflow in both stormdrains (Data Courtesy of Baltimore City Department of Public Works). c Strong relationships between concentrations of total suspended solids and copper, lead, and zinc during storm events in Watershed 263 stormdrains (Data Courtesy of Baltimore City Department of Public Works)



The 3rd, vertical dimension: Urban groundwater and surface water interactions

Much work has been done on groundwater connectivity in small forested watersheds and streams (e.g., Jones and Mulholland 2000) and larger watersheds and floodplains (e.g., Stanford 1998). This work has been critical to the understanding of ecological subsidies and ecosystem function in those streams that are not greatly impacted by urbanization. However, urbanization changes shallow groundwater flows to streams in a number of ways. For example, at the urban–rural interface, septic systems are commonly used in lieu of sanitary sewers and can release nitrogen below the rooting zone where it can be transmitted to ground water and headwater stream networks (Kaushal et al. 2006, 2011). The role of septic systems and groundwater contamination can be an important consideration in planning decisions at the urban to rural interface of the urban watershed continuum because zoning for larger housing lots makes sanitary sewers expensive. Moreover, septic systems and their drainage fields may deteriorate over time (e.g. through clogging) at different rates than sanitary sewer pipes; septic systems are not always tracked well in a regulatory sense and contaminate groundwater and flowpaths along the rural interface of the urban watershed continuum.

The ecological and biogeochemical roles of groundwater in urban watersheds have been seldom addressed and often underappreciated. Indeed, in many respects we are only now beginning to understand the urban water budget and associated urban groundwater and interactions with civil infrastructure and streams (e.g. Welty et al 2007). It is now becoming apparent that urban watersheds and their streams can be complex, multidimensional, catchment-wide hydrologic ecosystems with strong groundwater interactions (e.g. Rose 2007; Mayer et al. 2010; Sivirichi et al. 2011).

Groundwater interactions related to function and safety of drinking water and wastewater conveyance infrastructure are well known in civil engineering (e.g., Ellis and Bertrand-Krajewski 2010). The three main urban water conveyance networks (drinking water, sanitary sewage, and stormwater) are complex dynamic hydraulic systems and are very different in terms of their leakage patterns and influence on urban ecosystem functions. Firstly, drinking water distribution networks are under high pressure and so have typical leakage rates of ca. 20–30% (Garcia-Fresca 2007). The resulting volumes that are lost can be large, even to the point of offsetting the loss of groundwater recharge due to decreased infiltration capacity due to impervious surface cover (Garcia-Fresca 2007). Secondly, sanitary sewage networks are often composed of numerous pipe segments that are easily disturbed and have poor seals. Sewer pipes mostly flow by gravity and so travel beneath and along stream channels in many cities in the U.S. Even for separated sewage and stormwater networks such as in Baltimore (i.e., no CSOs), small local leakage rates from larger sewage interceptor pipes can exert large effects on downstream ecosystems because proximity to stream channels and the very high nutrient concentrations in raw sewage (e.g., typical domestic sewage has total nitrogen and total phosphorus concentrations of ca. 35 and 7 mg/l, respectively) (Viessman and Hammer 1998). Because sanitary sewer pipes are widespread, small but numerous leaks throughout the urban watershed continuum can greatly influence the nutrient budget of streams. For example, it is estimated by a U.S. Army Corp of Engineers study that an average of ca. 1.7 m³/s of sewage flows through the Gwynns Falls sewershed, which is equivalent to 65% of the average flow in the Gwynns Falls stream. Thirdly, groundwater can also interact with storm drain infrastructure at numerous unsealed pipe joints and inlet boxes, seep through soils, and also infiltrate into stormwater management facilities (e.g., detention basins, bioretention facilities). Storm drains may function analogously to tile drains in agricultural drainage networks during baseflow, providing a route for groundwater seeking lower elevations mixed with leaked drinking water and sewage leaks. The stormdrain network,



which is juxtaposed over the drinking water and sewer pipe networks in the watershed, likely provides a direct connection between upland engineered water systems, shallow groundwater, and urban streams (e.g. Fig. 4a).

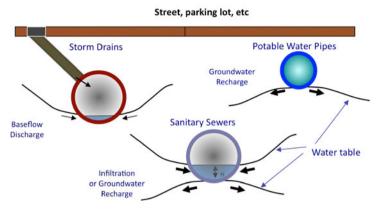
Although land surface hydrology is obviously influenced by urban runoff from impervious surfaces, the role and complexity of civil infrastructure-facilitated groundwater flows on stream baseflows in urban watershed and stream ecosystems is seldom addressed (Rose 2007). For example, a study by the Baltimore City Department of Public Works indicates that the majority of storm drain outfalls in there have dry weather baseflows. Fluxes of pollutants can be great, as seen in the elevated concentrations of copper, lead, and zinc during baseflow in a headwater stormdrain of Watershed 263 at the Baltimore LTER site (Fig. 3b). It is noteworthy that while some urban streams may have been lost through deliberate burial, many more may be functioning as "novel" conduits of groundwater flow during dry weather. Given the density and variety of pipes in urban landscapes, it is quite plausible that drinking water and sanitary sewage pipes can through illicit connections and indirectly via contaminated groundwater, transmit baseflows to storm drainage networks in significant volumes. A key feature of urban catchments is that these dense and overlapping pipe networks cover virtually the entire catchment (e.g., house connections, street gutter drainage) from upland watershed ridges to the stream channels, with additional interactions with riparian stormwater outfalls and sanitary sewage interceptors (Fig. 4a). Fluoride is often added to drinking water in the U.S. and can be used to identify and illustrate the importance of leaks from wastewater and potable drinking water pipes. Along suburban headwaters to progressively more urban downstream reaches of the Gwynns Falls at the Baltimore LTER site, there are increases in fluoride concentrations from leaking sewer and drinking water pipes illustrating the importance of groundwater-surface water interactions (Fig. 4b). These engineered pipe networks, by virtue of their leakiness and density, can therefore impart an "urban karst" structure to urban hydrogeology systems. This urban karst structure is formed because of groundwater influenced pipe flows themselves, as well as via secondary effects due to trenching and soil disturbance around each pipe creating additional complex hydrologic flow paths (Sharp et al. 2003) (Fig. 4a).

The 4th dimension, time: Landscape change & transitioning from sanitary to sustainable city

The influence of time on drainage network structure, material fluxes, and transformation and retention of nutrients in urban catchments is potentially greater and more complex than in natural systems because of human interactions and greatly altered surface and subsurface ecohydrologic processes. In understanding these processes and their fluxes, it may be useful to consider the temporal dimension across engineered headwaters, urban stream networks, and downstream receiving waters. Temporal processes can occur as both short-term "pulses" and long-term "presses" (Collins et al. 2011). Examples of fast processes or pulses (minutes-days) include urban runoff generation, shallow streamriparian biogeochemical interactions, sanitary sewer surcharges from storms, floods, catastrophic loss of infrastructure and pollutant spills. Importantly, longer-term versions of these include press disturbances that reflect spatial changes in development, redevelopment, and the aging of infrastructure. Some of these slower processes (0.1–10 yrs), however, are seldom considered because they operate in unseen engineered water and sanitary sewage drainage systems, which are hydrologically connected via multiple hydrologic pathways to urban streams (described earlier). They are complex both spatially and with respect to flow paths and can include pipe-groundwater (sewer, storm drain, water) interactions, stream-groundwater interactions, and trends in local infrastructure failure, repair and network extensions.



The Matrix: A dense, landscape-wide system of pipes... an urban "Karst"



Gwynns Falls: Baltimore Ecosystem Study LTER Site

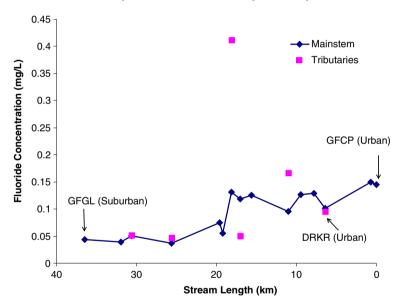


Fig. 4 a The stormdrain network, which is juxtaposed over the drinking water and sewer pipe networks in the watershed, likely provides a direct connection between upland engineered water systems and urban streams. Dense and overlapping pipe networks cover virtually the entire catchment, from upland ridges to stream channels (stormwater outfalls, sanitary sewage interceptors). Storm drains and other leaky sanitary sewer pipes therefore can impart an "urban karst" structure to urban hydrogeology systems, because of groundwater influenced pipe flows and secondary effects due to trenching and soil disturbance around each pipe creating preferential and complex hydrologic flow paths **b** Longitudinal increases in fluoride concentrations along suburban to progressively more urban reaches of Gwynns Falls stream network at the Baltimore LTER site due to leaks in both sewer and drinking water pipes and groundwater-surface water interactions

Considering even longer time scales (10–100 syrs) reveal urban ecosystems that are even more temporally dynamic because of the effects of long-term human and physical processes that are not considered in stream models and study designs. These longer temporal processes



include headwater stream burial, long-term groundwater contamination, aging infrastructure from previous decades/centuries, legacy impacts resulting from prior land use history, evolving stormwater management policies, social behavior trends, and changes in watershed carbon budgets from tree canopy development in older neighborhoods. For example, percent impervious area is often used as a simple explanatory variable in comparative studies, but the components of those impervious surfaces also degrade with age, and likely contribute to novel biogeochemical inputs and ecological stoichiometries of materials to urban waterways (e.g., from pavement (Sansalone and Kim 2008) and from roofing materials (Clark et al. 2008)). In addition, drinking water and sewer infrastructure leaks may increasingly influence groundwater dynamics over time (Kaushal et al. 2011). For example, there are 100–200 water main breaks that currently occur monthly in Baltimore City's aged system. The ecosystem scale impacts from degradation of aging infrastructure and maintenance of roadways, pipes, etc. will become more important over time, especially in an era where traditional civil infrastructure maintenance and replacement is becoming financially untenable (Doyle et al. 2008). Therefore, human factors and social ecological aspects can play a role along the urban watershed continuum, where reinvestment in infrastructure in affluent communities will maintain water quality compared to those urban communities that do not reinvest.

Long-term research is crucial for tracking these kinds of changes, an example of which is the evolution of stream channel geomorphic processes and related impacts on ecosystem functions. Long-term changes in hydrologic characteristics and sediment yields due to urbanization in Watts Branch (Maryland) were not apparent until after 20 years, and may not achieve stable conditions even after 41 yrs of observations (Leopold et al. 2005). Related long-term urbanization induced changes in hydrologic and geomorphic cycles would also include the grading of soil, removal of vegetation, compaction of soils and reduced infiltration, increases in runoff, stormflow, and erosion, and encroachment of floodplains and confinement of the stream channel. There may be coinciding long-term changes in biogeochemical fluxes and ecosystem functions in watersheds and streams following urbanization, but less is known regarding the evolution of biogeochemical cycles in response to urban development.

A long-term research perspective is also needed for investigating the links between urban infrastructure maintenance, ecosystem restoration activities and long-term changes in biogeochemical cycles. For example, rural areas outside of Baltimore, Maryland, have urbanized over time and we see corresponding long-term increases in sodium, chloride, and total solids in drinking water supplies (Fig. 5). These biogeochemical changes indicate increases in watershed inputs from roadway deicers, solutes, and sediments (Kaushal et al. 2005). Furthermore, the sodium and chloride concentrations remain elevated in summer months (even when no road salt deicer is applied) suggesting the accumulation of road salt in ground water and delivery to streams during baseflow (Fig. 5) (Kaushal et al. 2005) (also see preceding section, "The 3rd, Vertical Dimension..."). The increase in total solids may arise from increasing patterns in other solutes such as nutrients and particulate materials from erosion associated with urban development in watersheds (Fig. 5). Overall, this research at the Baltimore LTER site illustrates that there are substantial long-term impacts of urban development on water quality including drinking water (Kaushal et al. 2005). Work in other urbanized regions shows similar deterioration in water quality in watersheds regionally and globally (e.g. Walsh et al. 2005a; Kelly et al. 2008, 2010), and there is a need to understand urbanization driven long-term changes in hydrologic and biogeochemical cycles over time.

Although past land use legacies may influence the trajectory of hydrologic and biogeochemical pathways in urban ecosystem dynamics, there may be opportunities for altering the



temporal changes and evolution of urban ecosystems with management, restoration, and conservation decisions. For example, in many areas of the Northeastern U.S., the "Sanitary City" model for urban development and design of the 20th Century (that facilitated rapid drainage of water) is being replaced by the Sustainable City model (focused on infiltration of stormwater) (Melosi 2000; Pickett et al. 2011a,b). As part of new urban tree canopy goals in cities, the planting and regrowth of urban forests and woodlands in riparian areas can serve as active sites for stormwater management and nutrient retention. Across time, this effect will be modulated through changes in urban forestry budgets, biomass, and mortality of urban tree canopies over periods of decades. Similarly, present decisions regarding upgrades to aging sewer infrastructure may influence future changes in urban groundwater and stream biogeochemistry. As sewer networks degrade over time, new technologies like pipe-lining, driven by the regulatory environment (e.g., Baltimore City's consent decree to spend \$0.9 B on sewer rehabilitation) address leakage issues without the need for pipe excavation and replacement. The ability to understand the present urban water system as well as our ability to predict the future will require an adequate understanding of the past (Bain et al. 2011).

The urban watershed continuum as a research tool

Although we have learned much about urban watersheds in the last decade or so (Paul and Meyer 2001; Walsh et al. 2005a; Wenger et al. 2009b), the four dimensional view of the urban watershed continuum discussed earlier suggests that such an expanded, network-based view of urban watersheds is especially crucial to understanding the structure and function of urban ecohydrologic systems. Here, we discuss how to use this conceptual framework to further advance our understanding of urban development impacts on watershed functions. The urban watershed continuum can play an important role in human-dominated ecosystem inquiry.

In small forested watersheds, the usefulness of studying long-term changes in material and hydrologic export and retention in response to deforestation, acid rain, etc. has been revealed (e.g., Likens 2001). This is also true for urban catchments, and the urban watershed continuum considers long-term changes and gradual increases in urban development on material and hydrologic exports and retention and explicitly includes urban infrastructure (e.g. sewers, drainage, transportation networks) as part of the ecosystem. The urban watershed continuum can help address the many factors/processes that come into play as watersheds urbanize across different temporal stages in a spatially explicit way. This framework can be used as as a research tool, similar to the urban-rural gradient approach (McDonnell and Pickett 1990). This approach can facilitate the comparison of small watersheds on the basis of land use at broad scales (e.g., forested vs. suburban vs. entirely urban), but can also be useful at finer scales, in the stream channel, riparian zone, and engineered "upland" hydrosystems. Since urban landscapes are highly patchy, this conceptual framework not only opens new frontiers of study, but could also encourage a new level of interdisciplinary collaborations born of the necessity to address linkages between aquatic and terrestrial ecosystems (Lookingbill et al. 2009). This may be particularly important where the water cycle is dominated by engineered infrastructure and hydrologic alterations influenced by socioeconomic systems (Lookingbill et al. 2009).

Evaluating ecological processes in natural, degraded urban, and engineered headwaters

Evaluating ecological functions in engineered headwaters vs. degraded downstream reaches vs. natural streams may be helpful in assessing losses/changes of ecosystem functions at the



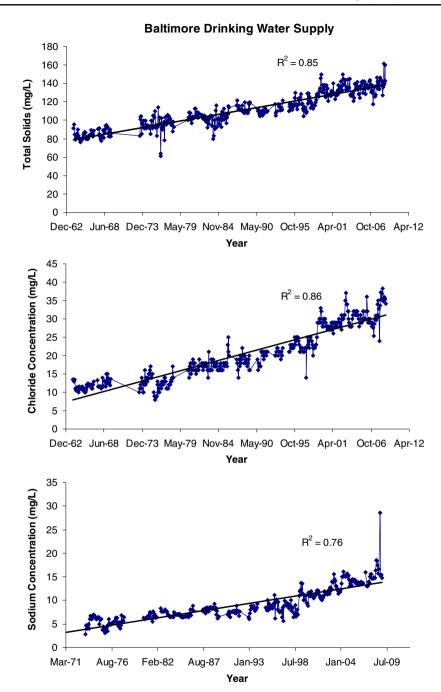


Fig. 5 Over decades, there have been significant long-term linear increases in concentrations of total solids, sodium, and chloride in the Baltimore City drinking water supply due to surrounding watershed urbanization and land-use change outside Baltimore City in formerly rural watersheds (p<0.05) (Data Courtesy of Baltimore City Department of Public Works) (e.g. Kaushal et al. 2005)



larger stream network scale and optimizing stream restoration and stormwater management strategies. Stormdrains can serve as functional tributaries in urban streams, both in terms of the large water volumes and the material and energy fluxes emanating from them. Research is needed comparing the presence or absence of ecological processes in engineered headwaters and streams, differences in ecological functions between buried streams vs. natural streams, and how this may impact downstream ecosystem functions and aquatic foodwebs. Engineered headwaters can take on some roles of natural systems or be relatively ecologically nonfunctional. For example, there may be debris dams in engineered headwaters with high levels of dissolved organic carbon and particulate organic carbon that may stimulate N transformations in stormdrains during baseflow (Kaushal et al. 2011). Because buried streams are underground, there may be less primary production vs. heterotrophic activity due to light availability, but the relative importance of ecological functions such as organic matter decomposition, microbial respiration, and denitrification in buried streams remains to be studied. For example, stormdrains and buried streams may be important hotspots for production of greenhouse gases such as methane or "sewer gas" in urban stream networks. There are lingering questions as to how headwater stream burial and extension of the drainage network by engineered headwaters can impact metabolism and nitrogen uptake at the larger stream network scale (Elmore and Kaushal 2008). Biogeochemical models at the stream network scale will be necessary to predict regional impacts in watersheds experiencing high levels of stream burial and human-made headwater extension due to construction and urbanization (Table 1).

Characterizing the quantity and quality of lateral organic carbon fluxes and urban subsidies

Key research questions will also be related to the sources and quality of organic carbon, and how this might impact biological processes in streams along the urbanizing watershed continuum. Storm drain networks exert large impacts on the processing, storage and transport of organic carbon, both particulate and dissolved organic carbon. Gutters, belowground catchbasins and pipes have analogues in zero order streams and thus become the sources and storage pools of leaf litter (and other) organic carbon, functioning as greatly expanded versions of headwater riparian areas. Extensive processing of this organic matter takes place here via fragmentation, wetting-drying facilitated leaching, and hydraulic abrasion such that there is a great deal of "pre-processing" before arrival at the traditional stream channel. Delivery of organic carbon from urban watersheds therefore may be of high quality in terms of bioavailability for microbial processing. The potentially large fluxes of organic carbon not only raise water quality issues such as increased biochemical oxygen demand (BOD), but there are also questions regarding how the associated nutrients and contaminants will facilitate or impair microbial and ecosystem processes in drainage networks and receiving streams.

The urban watershed continuum as a transporter and transformer of watershed exports

Answers to questions regarding the role of the urban watershed continuum in the transport vs. transformation process may depend greatly on hydrologic residence time. The interplay of transporter vs. transformer functions change along the urban watershed continuum with hydrologic residence time. Obviously, with flashy urban hydrology, transport processes dominate during storms but the "transformer" role may still be important during baseflow with longer hydrologic residence times when organic substrate concentrations and temperatures are elevated (Kaushal et al. 2008a, 2010). During baseflow, biogeochemical



transformations can occur in engineered headwaters (Kaushal et al. 2011), and there can be increased autotrophic production in small "daylighted" streams along the urban watershed continuum (Finlay 2011). This is because of the great expansion of the upstream drainage network by engineered headwaters (Walsh et al. 2005a; Elmore and Kaushal 2008) and elevated temperatures, nutrients, and substrates for biogeochemical reactions (Figs. 1 and 3a). The question of how quickly and in what forms nutrients and carbon propagate downstream to receiving waters is important with respect to material processing along the urban watershed continuum. Furthermore, there are questions regarding how different watershed management strategies may dampen pulses of carbon and nutrients propagated through stream networks via transformations. During storms, transport processes may be more important in engineered headwaters of the urban watershed continuum compared to downstream reaches. Because current methods for estimating fluxes and in-stream retention and transformation can be constrained in unsteady and high flow environments, the introduction of stormflows would constitute a new challenge to developing new methodologies. These could include deployment of automated samplers and sensors for characterizing highresolution changes in carbon quality and nutrient retention and transformation across runoff variability. The transporter and transformer roles along the urban watershed continuum would also be expected to greatly influence ecological communities as well as downstream water quality. For example, there may be scouring of biological communities during high flow (transporter functions) and ecological succession and development of autotrophic and heterotrophic biomass (transformer functions) during periods of baseflow between storms, but this warrants further investigation.

Unrayeling the urban karst: Hydrologic and material exchanges between streams and pipes

The interaction between leaky subsurface pipes and groundwater can have important implications for local and downstream ecological processes and determine the transporter vs. transformer roles along the urban watershed continuum. There can be changes in transporter and transformer roles along upland and engineered pathways and along stormdrain pathways (Kaushal et al. 2011). Crucial questions are related to how extensively an infrastructure facilitated groundwater matrix impacts sources, fluxes, transformations, and flowpaths of nutrients, carbon, metals, and other contaminants. Further questions are related to how this interaction might change over shorter and longer time scales. Surprisingly, stormdrains can play an important role in urban streams during baseflow as part of urban karst-like flowpaths that exist belowground (Elmore and Kaushal 2008; Pouyat et al. 2007). It is quite plausible that the non-stormwater runoff portion of the engineered water networks operating on base flows have effects on urbanizing watershed systems that rival those of urban runoff (Nilsson et al. 2003). A significant portion of urban stream baseflow may arrive via storm drains, but may be very different in terms of chemistry, ecological stoichiometry, and stream temperature from stream channel baseflows (observations from the Baltimore LTER site, e.g. Pouyat et al. 2009; Kaushal et al. 2010; Kaushal et al. 2011). Similarly, sanitary sewer pipes embedded in riparian zones or within urban stream channels can exchange material and energy flows with the stream water and may therefore contribute to, or extract flows and constituents from the stream, depending on local groundwater contexts (Rose 2007). Work is needed to further quantify groundwater-pipe-surface water interactions at the landscape scale, given that sanitary pipeflows are highly complex. There may be unexpected inter-basin transfers as material from infrastructure leaks can originate outside a given stream's watershed, and can easily be magnified by the massive flows of water and sewage. Unlike storms, which largely follow watershed boundaries, baseflow and



sewage can originate from and/or travel through a larger regional drainage catchment. In addition, work is necessary to characterize flows and fluxes at different times (diurnal, seasonal, interannual), across storm drain size/age, and in response to rainfall events, vegetation, geomorphic drivers. Further work is also necessary regarding material transformations during baseflow and the importance of internal storage, sediment accumulation, and biofilm functions. These novel infrastructure-ecosystem fluxes may not be confined to pipes and streams. For example, a study in Baltimore shows that leaky pipes and aging infrastructure provide important water and nutrient subsidies to trees along roads and these leaks provide potential interactions between "riparian" vegetation rooting zones, aging pipes, and stream channels (T. Whitlow et al. unpublished data).

The urban watershed continuum as a management and planning tool

From sanitary city to sustainable city: Past, present, and future of material cycles

With time as a 4th dimension, there will be alterations and changes in watershed development patterns and long-term changes and evolution in biogeochemical and hydrologic cycles over time. A key question will be how upgrades or degradation in urban infrastructure practices and designs will impact headwater streams and downstream rivers over decades and centuries. For example, cities in developed nations were designed for sanitation and runoff conveyance before the 21st century, i.e., the Sanitary City model (Melosi 2000, Pickett et al. 2011a,b), and as these cities and their infrastructure age their intended function will also degrade and their ability to handle emerging contaminants with old technology is questionable (e.g., pharmaceuticals in wastewater). Currently, there is an important recognition of the need to infiltrate and retain water on the landscape with innovative stormwater management practices to provide irrigation for plants and urban blue space for recreation/ habitat in the form of wetlands, lakes, and ponds but questions remain about contaminant fates and water resources should these practices become ubiquitous. A key question will be how characteristics of the urban water matrix will change because of the collapse of aging sanitary city infrastructure, and how upgrades and urban design may offer new opportunities and challenges for improving stormwater management and biogeochemical functions such as N retention (e.g. Walsh et al. 2005b; Kaushal et al. 2008b; Collins et al. 2011).

Urban ecosystems are maintained in a state of dynamic equilibrium that in a long-term sense would be expected to change over time. There is a constant cycle of degradation, abandonment, renovation and redesign in urban built environments. Previous choices in urban infrastructure and development practices have altered the hydrology, temperature, and salinization of urbanized streams over decades and centuries (e.g. Kaushal et al. 2005, 2010). There have also been widespread losses of natural headwaters and replacement with engineered structures as a result of previous development (Elmore and Kaushal 2008; Roy et al. 2009). There are now choices to introduce innovative stormwater management practices and disconnect watershed impervious surfaces to reduce stream impairments (Walsh et al. 2005a). Linking stream research with urban design/planning across time is important for guiding management and the progression of restoration designs and decisions. Monitoring of ecosystem functions and material fluxes across different urban designs and features may serve as "natural experiments" for long-term studies and information for future management decisions (Pouyat et al. 2007).



Tracking downstream impacts of the urban watershed continuum on receiving waters

Even though urban watersheds vary in size, they will still have important downstream effects on larger "river" systems in ways beyond their traditional wastewater point sources, both because of their "hot spot" characteristic as well as their rapidly expanding nature. Further research to characterize the longitudinal transport and transformation of urban biogeochemical signals (carbon, nutrients, metals) into downstream ecosystems such as drinking water reservoirs and estuaries such as Chesapeake Bay is needed because urban pollutant loads are increasingly dominating large parts of the landscape. In fact, stormwater from urban runoff is now the fastest growing source of pollution to its streams and rivers of the Chesapeake Bay (FLCCB 2009). There are growing areas of coastal hypoxia or "dead zones" downstream of urban areas due to nutrients and biochemical oxygen demand from organic matter (Mallin et al. 2006). Sampling designs incorporating the urban watershed continuum approach will help evaluate longitudinal patterns and identify "hot spots" of nutrient inputs and transformations to receiving waters.

From the perspective of real world applications, predicting how interactions between urban streams, land-use decisions, and urban infrastructure change with future development and re-development choices will be as important for these larger scale perspectives as it is for the smaller scale processes and interventions. Large scales imply long-term processes, and there is a real need to understand the transport and transformation of biogeochemical signals, from their initation in cities to larger receiving waters. A better understanding of larger scale watershed processes depends on better understanding of what goes on across the continuum of flowpaths at multiple terrestrial-aquatic interfaces. Knowledge gained here will greatly facilitate management and mitigation of contaminant "pulses" with respect to surface runoff, stream degradation, and their amplification (e.g. Walsh et al. 2005b; Kaushal et al. 2008a; Lookingbill et al. 2009). Elucidating the processes and drivers governing the timing and forms of nutrient, carbon, metals, and contaminants exported to these downstream portions and receiving waters are as important as estimating the fluxes themselves. These changes as well as their associated ecology can be characterized as they reach different aquatic systems by employing modern analytical approaches, geochemical tracers, and sensor methodologies in conjunction with modeling.

Conclusion

We recognize that expansion of urban development into rural areas is taking place at the same time that existing urban infrastructure is aging. Cities are no longer free standing points in the landscape, but are parts of increasingly hydrologically connected ecosystems that encompass large areas of the landscape. Therefore, understanding the impacts of urban landuse change in rural areas will be equally as important as predicting the impacts of urban redevelopment and ecosystem restoration. An urban watershed continuum perspective across 4 spatiotemporal dimensions will be critical as a research tool for investigating alterations in watershed sources, fluxes, and flowpaths of materials and energy and improving downstream ecosystem functions and linking headwater impacts to receiving waters.

Acknowledgements Kaushal and Belt contributed equally to writing, conceptual design, and analysis of data. Research was supported by NSF Awards DBI 0640300, CBET 1058502, Baltimore Ecosystem Study LTER project (NSF DEB-0423476), ULTRA-EX Long-term Research 0948947, and Maryland Sea Grant Awards SA7528085-U, NA05OAR4171042, R/WS-2 and the U.S. Forest Service. This paper would not have



been possible without the encouragement, support, and comments of Richard Pouyat. Steward Pickett provided helpful discussions and Peter Groffman, Paul Mayer, Claire Welty, and Andy Miller provided data and/or long-term collaborations over years. Chris Tripler provided valuable ideas and comments on a previous version of the manuscript. We are indebted to Bill Stack, Robert MaCauley, and Baltimore City Department of Public Works for sharing data, insights, and ideas. Katie Delaney-Newcomb provided synoptic data for 3 sampling dates along the Gwynns Falls. Dan Dillon and Melissa Grese assisted with field work.

References

- Alberti M (2005) The effects of urban patterns on ecosystem function. International Regional Science Review 28:168–192
- Bain DJ, Pouyat RV, Yesilonis ID (2011) Metal concentrations in urban riparian sediments along an urbanization gradient. Biogeochemistry. doi:10.1007/s10533-010-9532-4
- Baker LA, Hope D, Xu Y, Edmonds J, Lauver L (2001) Nitrogen balance for the central Arizona–Phoenix (CAP) ecosystem. Ecosystems 4:582–602
- Clark SE, Steele KA, Spicher J, Siu CYS, Lalor MM, Pitt R, Kirby JT (2008) Roofing materials' contributions to storm-water runoff pollution. J Irrigat Drain Eng-ASCE 134:638–645
- Collins SL, Carpenter SR, Swinton SM, Orenstein DE, Childers DL, Gragson TL, Grimm NB, Grove M, Harlan SL, Kaye JP, Knapp AK, Kofinas GP, Magnuson JJ, McDowell WH, Melack JM, Ogden LA, Robertson GP, Smith MD, Whitmer AC (2011) An integrated conceptual framework for long-term social-ecological research. Front Ecol Environ 9:351–357
- Delaney KM (2009) Organic nitrogen and carbon transformations in a stream network of Chesapeake Bay watershed. M.S. Thesis. University of Maryland, College Park
- Doyle MW, Stanley EH, Havlick DG, Kaiser MJ, Steinbach G, Graf WL, Galloway GE, Riggsbee JA (2008) Environmental science—Aging infrastructure and ecosystem restoration. Science 319:286–287
- Dunne T, Black RD (1970) Partial area contributions to storm runoff in a small New England watershed. Water Resour Res 6:1296–1311. doi:10.1029/WR006i005p01296
- Ellis JB, Bertrand-Krajewski JL (2010) Assessing infiltration and exfiltration on the Performance of Urban Sewer Systems (APUSS). IWA, London
- Elmore AJ, Kaushal SS (2008) Disappearing headwaters: patterns of stream burial due to urbanization. Front Ecol Environ 6:308–312
- Finlay JC (2011) Stream size and human influences on ecosystem production in river networks. Ecosphere 2 (8):srt87. doi:10.1890/ES11-00071.1
- Fisher SG, Likens GE (1973) Energy flow in Bear Brook, New Hampshire—Integrative approach to stream ecosystem metabolism. Ecol Monogr 43:421–439
- Fisher SG, Grimm NB, Marti E, Holmes RM, Jones JB (1998) Material spiraling in stream corridors: a telescoping ecosystem model. Ecosystems 19–34.
- Federal Leadership Committee for the Chesapeake Bay (2009) Executive Order 13508, Draft strategy for protecting and restoring the Chesapeake bay
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574
- Garcia-Fresca (2007) Urban-enhanced groudnwater recharge: review and case study of Austin, Texas, USA. Urban groundwater—meeting the challenge, Selected papers from the 32nd International Geological Congress (IGC), Florence, Italy, August 2004. Howard KW (ed). Taylor & Francis/Balkema, Netherlands, pp. 3–18.
- Gomi T, Sidle RC, Richardson JS (2002) Understanding processes and downstream linkages of headwater systems. Bioscience 52:905–916
- Gregory SV, Swanson FJ, McKee WA, Cummins KW (1991) An ecosystem perspective of riparian zones. Bioscience 41:540–551
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu JG, Bai XM, Briggs JM (2008) Global change and the ecology of cities. Science 319:756–760
- Groffman PM, Boulware NJ, Zipperer WC, Pouyat RV, Band LE, Colosimo MF (2002) Soil nitrogen cycle processes in urban riparian zones. Environ Sci Technol 36:4547–4552
- Groffman PM, Law NL, Belt KT, Band LE, Fisher GT (2004) Nitrogen fluxes and retention in urban watershed ecosystems. Ecosystems 7:393-403



Groffman PM. Long-term Stream Water Chemistry (2010) Baltimore Ecosystem Study LTER Site, Maryland. Cary Institute of Ecosystem Studies. www.beslter.org.

Hynes HBN (1970) The ecology of running waters. University Press, Liverpool

Jones JB, Mulholland PJ (2000) Streams and ground waters. Academic, San Diego, p 425

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) Proceedings of the International Large River Symposium. Can. Spec. Publs. Fish. Aquat. Sci. 106, pp. 110–127.

Kaushal SS, Groffman PM, Likens GE, Belt KT, Stack WP, Kelly VR, Band LE, Fisher GT (2005) Increased salinization of fresh water in the northeastern U.S. Proc Natl Acad Sci 102:13517–13520

Kaushal SS, Lewis WM Jr, McCutchan JH Jr (2006) Land use change and nitrogen enrichment of a Rocky Mountain watershed. Ecol Appl 16:299–312

Kaushal SS, Groffman PM, Band LE, Shields CA, Morgan RP, Palmer MA, Belt KT, Fisher GT, Swan CM, Findlay SEG (2008a) Interaction between urbanization and climate variability amplifies watershed nitrate export in Maryland. Environ Sci Tech 42:5872–5878. doi:10.1021/es800264f

Kaushal SS, Groffman PM, Mayer PM, Striz E, Doheny EJ, Gold AJ (2008b) Effects of stream restoration on denitrification in an urbanizing watershed. Ecol Appl 18:789–804

Kaushal SS, Likens GE, Jaworski NA, Pace ML, Sides AM, Belt KT, Secor D, Seekell D, Wingate R (2010) Rising stream and river temperatures in the United States. Front Ecol Environ 100323112848094. doi:10.1890/090037

Kaushal SS, Groffman PM, Band LE, Elliott E, Kendall CA (2011) Tracking nonpoint nitrogen pollution in human-impacted watersheds. Environ Sci Technol. doi:10.1021/es200779e

Kaye JP, Groffman PM, Grimm NB, Baker LA, Pouyat RV (2006) A distinct urban biogeochemistry? Trends Ecol Evol 21:192–199

Kelly VR, Lovett GM, Weathers KC, Findlay SEG, Strayer DL, Burns DJ, Likens GE (2008) Long-term sodium chloride retention in a rural watershed: legacy effects of road salt on streamater concentration. Environ Sci Technol 42:410–415

Kelly WR, Panno SV, Hackley KC, Hwang HH, Martinsek AT, Markus M (2010) Using chloride and other ions to trace sewage and road salt in the Illinois Waterway. Appl Geochem 25:661–673

Leopold LB, Huppman R, Miller A (2005) Geomorphic effects of urbanization in forty-one years of observation. Proc Am Philos Soc 149:349–371

Likens GE (2001) Biogeochemistry, the watershed approach: some uses and limitations. Mar Freshw Res 52:5–12 Lookingbill TR, Kaushal SS, Elmore AJ, Gardner R, Eshleman KN, Hilderbrand RH, Morgan RP, Boynton WR, Palmer MA, Dennison WC (2009) Altered ecological flows blur boundaries in urbanizing watersheds. Ecol Soc 14.

Mallin MA, Johnson VL, Ensign SH, MacPherson TA (2006) Factors contributing to hypoxia in rivers, lakes, and streams. Limnol Oceanogr 51:690–701

Mayer PM, Groffman PM, Striz EA, Kaushal SS (2010) Nitrogen dynamics at the groundwater-surface water interface of a degraded urban stream. J Environ Qual 39:810–823

McDonnell MJ, Pickett STA (1990) Ecosystem structure and function along urban rural gradients—an unexpoited opportunity for ecology. Ecology 71:1232–1237

Melosi MV (2000) The sanitary city: urban infrastructure in America from colonial times to the present. Johns Hopkins University Press, Baltimore. ISBN 978-0-8018-6152-9

Meyer JL, Paul MJ, Taulbee WK (2005) Stream ecosystem function in urbanizing landscapes. J N Am Benthol Soc 24:602–612

Minshall GW, Petersen RC, Cummins KW, Bott TL, Sedell JR, Cushing CE, Vannote RL (1983) Interbiome comparison of stream ecosystem dynamics. Ecol Monogr 53:2–25

Naiman RJ, Melillo JM, Lock MA, Ford TE, Reice SR (1987) Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68:1139–1156

Nilsson C, Pizzuto JE, Moglen GE, Palmer MA, Stanley EH, Bockstael NE, Thompson LC (2003) Ecological forecasting and the urbanization of stream ecosystems: challenges for economists, hydrologists, geomorphologists, and ecologists. Ecosystems 6:659–674

Paul MJ, Meyer JL (2001) Streams in the urban landscape. Annu Rev Ecol Systemat 32:333-365

Pickett STA, Cadanasso ML, Grove JM, Band LE, Boone CG, Irwin E, Groffman PM, Kaushal SS, Marshall V, McGrath B, Nilon CH, Pouyat RV, Szlavecz K, Troy A, Warren P (2011a) Urban ecological systems: foundations and a decade of progress. J Environ Manage 92:331–362

Pickett STA, Buckley GL, Kaushal SS, Williams Y (2011b) Ecological science in the humane metropolis. Urban Ecosyst. doi:10.1007/s11252-011-0166-7

Pouyat RV, Pataki D, Belt K, Groffman PM, Hom J, Band L (2007) Urban land-use change effects on biogeochemical cycles. In: Canadell P, Pataki D, Pitelka L (eds) Terrestrial ecosystems in a changing world. Springer, Berlin Heidelberg-New York, pp 45–58



- Pouyat RV, Yesilonis ID, Golubiewski NE (2009) A comparison of soil organic carbon stocks between residential turf grass and native soil. Urban Ecosyst 12:45–62
- Pouyat RV, Szlavecz K, Yesilonis ID, Groffman PM, Schwarz K (2010) Chemical, physical, and biological characteristics of urban soils. Chapter 7. In: Aitkenhead-Peterson J, Volder A (eds) Urban ecosystem ecology. Agronomy Monograph 55. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, pp 119–152
- Rose S (2007) The effects of urbanization on the hydrochemistry of base flow within the Chattahoochee River Basin (Georgia, USA). J Hydrol 341:42–54
- Roy AH, Dybas AL, Fritz KM, Lubbers HR (2009) Urbanization affects the extent and hydrologic permanence of headwater streams in a Midwestern US metropolitan area. J N Am Benthol Soc 28:911–928
- Sansalone JJ, Kim JY (2008) Transport of particulate matter fractions in urban source area pavement surface runoff. J Environ Oual 37:1883–1893
- Schueler TR, Fraley-McNeal L, Cappiella K (2009) Is impervious cover still important? Review of recent research. J Hydrolog Eng 14:309–315
- Sharp JM Jr, Krothe JN, Mather JD, Garcia-Fresca B, Stewart CA (2003) Effects of urbanization on groundwater systems. In: Heiken G, Fakundiny R, Sutter J (eds) Earth science in the city: a reader. American Geophysical Union, Washington, pp 257–278
- Sivirichi G, Kaushal SS, Mayer PM, Welty C, Belt KT, Delaney KA, Newcomer TA, Grese M (2011) Longitudinal variability in streamwater chemistry and carbon and nitrogen fluxes in restored and unrestored stream networks. J Environ Monit. doi:10.1039/c0em00055h
- Stanford JA (1998) Rivers in the landscape: introduction to the special issue on riparian and groundwater ecology. Freshwat Biol 40:402–406
- Stanford JA, Ward JV (1993) An ecosystem perspective of alluvial rivers—connectivity and the hyporheic corridor. J N Am Benthol Soc 12:48
- Sterner RW, Andersen T, Elser JJ, Hessen DO, Hood JM, McCauley E, Urabe J (2008) Scale-dependent carbon:nitrogen:phosphorus seston stoichiometry in marine and freshwaters. Limnol Oceanogr 53:1169– 1180
- United Nations World Water Assessment Programme (WWAP) (2010) Water for sustainable urban human settlements. Briefing note. United Nations Human Settlements Programme (UN-HABITAT)
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) River continuum concept. Can J Fish Aquat Sci 37:130–137
- Viessman W, Hammer MJ (1998) Water supply and pollution control. Addison Wesley, Menlo Park
- Walsh CJ, Roy AH, Feminella JW, Cottingham PD, Groffman PM, Morgan RP (2005a) The urban stream syndrome: current knowledge and the search for a cure. J N Am Benthol Soc 24:706–723
- Walsh CJ, Fletcher TD, Ladson AR (2005b) Stream restoration in urban catchments through redesigning stormwater systems: looking to the catchment to save the stream. J N Am Benthol Soc 24:690–705
- Ward JV (1989) The four-dimensional nature of lotic ecosystems. J N Am Benthol Soc 8:2-8
- Ward JV, Stanford JA (1995) The serial discontinuity concept—extending the model to floodplain rivers. Regul Rivers: Res Manage 10:159–168
- Warren PS, Ryan RL, Lerman SB, Tooke KA (2011) Social and institutional factors associated with land use and forest conservation along two urban gradients in Massachusetts. Landsc Urban Plann 102:82–92
- Welty C, Miller AJ, Belt K, Smith J, Band L, Groffman P, Scanlon T, Warner J, Ryan RJ, Shedlock R, McGuire M (2007) Design of an environmental field observatory for quantifying the urban water budget. In: Novotny V, Brown P (eds) Cities of the future towards integrated sustanable water and landscape management. IWA Publishing, London, pp 74–91
- Wenger SJ, Roy AH, Jackson CR, Bernhardt ES, Carter TL, Filoso S, Gibson CA, Hession WC, Kaushal SS, Marti E, Meyer JL, Palmer MA, Paul MJ, Purcell AH, Ramirez A, Rosemond AD, Schofield KA, Sudduth EB, Walsh CJ (2009a) Twenty-six key research questions in urban stream ecology: an assessment of the state of the science. J N Am Benthol Soc 28:1080–1098
- Wenger SJ, Roy AH, Jackson CR, Bernhardt ES, Carter TL, Filoso S, Gibson CA, Grimm NB, Hession WC, Kaushal SS, Martí E, Meyer JL, Palmer MA, Paul MJ, Purcell AH, Ramirez A, Rosemond AD, Schofield KA, Schueler TR, Sudduth E, Walsh CJ (2009b) Top urban stream ecology research questions: what we know, what we don't know, and what we need to know to better manage urban streams. J N Am Benthol Soc 28:1080–1098
- Wollheim WM, Pellerin BA, Vorosmarty CJ, Hopkinson CS (2005) N retention in urbanizing headwater catchments. Ecosystems 8:871–884

