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Determining hydrologic factors that influence stream macroinvertebrate assemblages in the northeastern US†

Jonathan G. Kennen,[1]* Karen Riva-Murray[2] and Karen M. Beaulieu[3]

[1] *US Geological Survey, 810 Bear Tavern Road, Suite 206, West Trenton, NJ 08628, USA*
[2] *US Geological Survey, 425 Jordan Road, Troy, NY 12180, USA*
[3] *US Geological Survey, 101 Pitkin Street, East Hartford, CT 06108, USA*

ABSTRACT

The effects of changes in the landscape and alteration of natural flow process on aquatic macroinvertebrate assemblages were investigated in 67 small-to-medium sized (15–526 km^2) upland streams in the northeastern United States. Environmental characteristics that were found to be important in determining macroinvertebrate-assemblage composition include urbanization and concomitant changes in natural streamflow patterns. In particular, hydrologic attributes accounted for a significant proportion of the variability and were important in driving modifications to assemblage structure after natural environmental variability was extracted. For example, mean April flow accounted for the greatest amount of assemblage variability in any single multiple linear regression (MLR) model (65%) and duration of high flows accounted for a significant portion of the assemblage variability in the five, four and one-variable models (25, 26, and 23%, respectively). Seasonal predictability of low flow consistently accounted for a significant proportion of the assemblage variability in all but the two-variable (MLR) model. Significant ($p < 0{\cdot}05$) bivariate flow–ecology response relations were established, especially for hydrologic measures that account for the frequency, duration, and magnitude of flow events, and these relations generally followed increasing or decreasing trends that would be expected given changes in stream hydrology. This study demonstrates that there are likely specific negative consequences to stream biotic integrity in northeastern streams as the result of hydrologic alteration associated with basin urbanization. Understanding the relations between hydrologic modification and aquatic assemblages will help efforts to set sustainable flow standards for protection of aquatic assemblages while providing water for human needs. Published in 2009 by John Wiley & Sons, Ltd.

KEY WORDS hydroecology; macroinvertebrates; flow–ecology response relations; multiple regression; disturbance gradient; multivariate; landscape fragmentation

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INTRODUCTION

The body of scientific knowledge concerning hydroecological relations has expanded greatly over the last decade, and many studies have identified hydrologic alteration as one of the most serious threats to the ecological sustainability of the world's streams and rivers (Ward and Stanford, 1989; Poff *et al*., 1997; Arthington *et al*., 2006). This is exemplified by the strong linkages frequently established between modification of hydrologic processes and ecosystem function (Ward and Stanford, 1989; Richter *et al*., 1996; Townsend *et al*., 1997; Bunn and Arthington, 2002). The cumulative impacts of such hydrologic alterations markedly affect the composition and structure of stream assemblages (e.g. Poff and Allan, 1995; Clausen and Biggs, 1997; Pusey *et al*., 2000; Konrad and Booth, 2005), often by modifying natural complexity and simplifying intact systems by pushing them to a point beyond resiliency or sustainability (Baron *et al*., 2002). Many authors have stressed that to sustain biotic integrity, natural stream flow patterns need to be protected (Arthington *et al*., 1992; Sparks, 1992; Richter *et al*., 1996, 1997; Stanford *et al*., 1996). The natural flow regime paradigm (Poff *et al*., 1997) further emphasizes these hydroecological linkages and suggests that maintenance of inter- and intra-annual hydrologic variation is essential for sustaining the native biodiversity of aquatic ecosystems.

Structural and functional dynamics of stream assemblages are strongly influenced by temporal variation in flow processes (Biggs *et al*., 2005), and many aquatic species have evolved specific life-history traits that allow them to take advantage of different aspects of the flow regime (Poff *et al*., 1997, 2006; Vieira *et al*., 2006). Some species may be particularly sensitive to hydrologic alteration because of the requirements for particular flow regimes to trigger reproductive behaviours and support crucial life states (Grossman, 1982; Poff and Ward, 1989), or because of relatively narrow tolerances for thermal and/or chemical conditions that are affected by flow regimes. Flow components including low flows (sustained baseflow), annual high-flow pulses, seasonality of flows, annual variability, and flood events provide the conditions necessary to support natural assemblage complexity (Stanford *et al*., 1996; Poff *et al*., 1997; Richter

* Correspondence to: Jonathan G. Kennen, US Geological Survey, 810 Bear Tavern Road, Suite 206, West Trenton, NJ 08628, USA.
E-mail: jgkennen@usgs.gov
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et al., 1997; Mathews, 2005). Conversely, alterations in timing, duration, and magnitude of many of these flow processes can substantially affect sensitive aquatic fauna that embody less resilient or robust traits or life histories.

Landscape alteration has been linked to various hydrologic disturbances that disrupt ecological processes and reduce species diversity by selectively eliminating intolerant species, leaving only the most mobile and tolerant (Resh *et al*., 1988; Poff, 2002). Landscape modification associated with urbanization, such as increasing impervious surface, loss of riparian buffers, soil compaction, and forest fragmentation, can result in hydrologic disturbance (e.g. Coles *et al*., 2004; Kennen *et al*., 2008). The resulting hydrologic alterations can be characterized through changes in the five major flow components: frequency, duration, magnitude, timing, and rate of change of flow. For example, linkages have been established between surface runoff processes, due to landscape alteration and channel erosion, that result in hydrogeomorphic changes such as altered channel morphology and channel instability (Trimble, 1997; Doyle *et al*., 2000; Pizzuto *et al*., 2000). Specifically, stream communities were found to be affected negatively by increases in peak discharge, streamflow variability (flashiness), impervious surfaces, point and non-point sources of contamination (Kennen and Ayers, 2002; Coles *et al*., 2004; Konrad *et al*., 2008), and fragmentation of the riparian corridor (Kennen *et al*., 2005). In addition, increased periodicity of flood flows can lower aquatic assemblage biomass and production through direct dislodgement and, indirectly, through bed movement and scour (Biggs *et al*., 2001, 2005). Such physical disturbances can significantly reduce benthic invertebrate density (McCabe and Gotelli, 2000); however, lotic assemblages are known to recover fairly quickly after individual periods of extremely high or no flow (Power and Stewart, 1987; Scrimgeour and Winterbourn, 1989; Boulton *et al*., 1992; Suren and Jowett, 2006; James *et al*., 2008). Depending on the resistance and resilience of stream assemblages, frequent high-energy flow events, coupled with prolonged periods of low or no flow, can dramatically affect lotic ecosystem structure and function (Biggs *et al*., 2005), often resulting in a highly simplified trophic structure with low-taxonomic diversity and a dominance of relatively few tolerant taxa (Schlosser, 1985; Robinson and Minshall, 1986; Power and Stewart, 1987). Conversely, moderate-to-low magnitude flow events (natural flow patterns) appear to strongly influence processes that act at the population level of ecosystem organization, and may ultimately be responsible for maintaining healthy and diverse lotic ecosystems (Collins and Glenn, 1997; Biggs *et al*., 2005). Streams and rivers that historically experience relatively few such disturbances are likely to be most susceptible to changes in the major components of flow (Richter *et al*., 1996).

Despite the recent advances in understanding how modification of the landscape (e.g. urbanization) alters natural hydrological regimes, and how this hydrologic alteration affects ecological processes, there remains a need to examine hydroecological linkages across the kinds of broad spatial scales at which management strategies and guidelines are often developed (e.g. Krezek *et al*., 2008) and across which other relevant processes (such as climate change) operate (e.g. Rogers and McCarty, 2000). Few previous studies have attempted to derive these linkages at as broad a spatial scale as the northeastern United States. This is, presumably, because of the increased variability in background conditions with increase in spatial extent, and because there are few state, provincial, or governmental agencies with programs specifically designed to collect co-located invertebrate and continuous hydrologic data at a broad spatial scale [e.g. the Environmental Protection Agency's Environmental Monitoring and Assessment Program uses randomly selected stream sites that rarely have associated stream gages; but also see Knight *et al*., 2008 (southeast US) and Kennard *et al*., 2009 (Australia)].

In this paper, we characterize hydrologic disturbance associated with changes in landscape and environmental processes at the regional scale and evaluate the response of aquatic macroinvertebrate assemblages to these observed hydrologic (and associated) modifications. We postulate that (1) variation in the landscape associated with urbanization will have a measurable negative effect on the aquatic macroinvertebrate assemblage and (2) a decline in biotic integrity will be related to the observed variation in at least one of the five major components of the flow regime—magnitude, frequency, duration, timing, and rate of change. We test these hypotheses by identifying a gradient of variation in aquatic macroinvertebrate assemblage structure among stream sites and by determining the hydrologic and landscape attributes that account for this variation, while simultaneously accounting for natural environmental variability. Lastly, we derive bivariate regional flow–ecology response relations between a subset of hydrologic indicators and variation in aquatic macroinvertebrate-assemblage metrics.

STUDY AREA

The study area is located in the northeastern United States and includes all or parts of 13 states (Figure 1). This region of the US has an elaborate network of urban corridors connecting all major cities (e.g. Boston, MA, New York, NY, and Washington, D.C.). The study area is about 339,290 km^2 and total population has increased approximately 7·7% from 1990 to 2000. In some rapidly growing areas, population increased by over 20% in 5 years (2000–2005); US. Census Bureau, http://www.census.gov/popest/cities/SUB-EST2005.html, accessed July 20, 2006). Although the study area boundary includes the northern Atlantic Seaboard, all sites represented are upland northeast streams; coastal streams are not considered due to known differences in aquatic assemblage structure (Kennen, 1999; Kennen and Ayers, 2002). In some parts of the study area, water supply systems are connected, and transfer of water across drainage

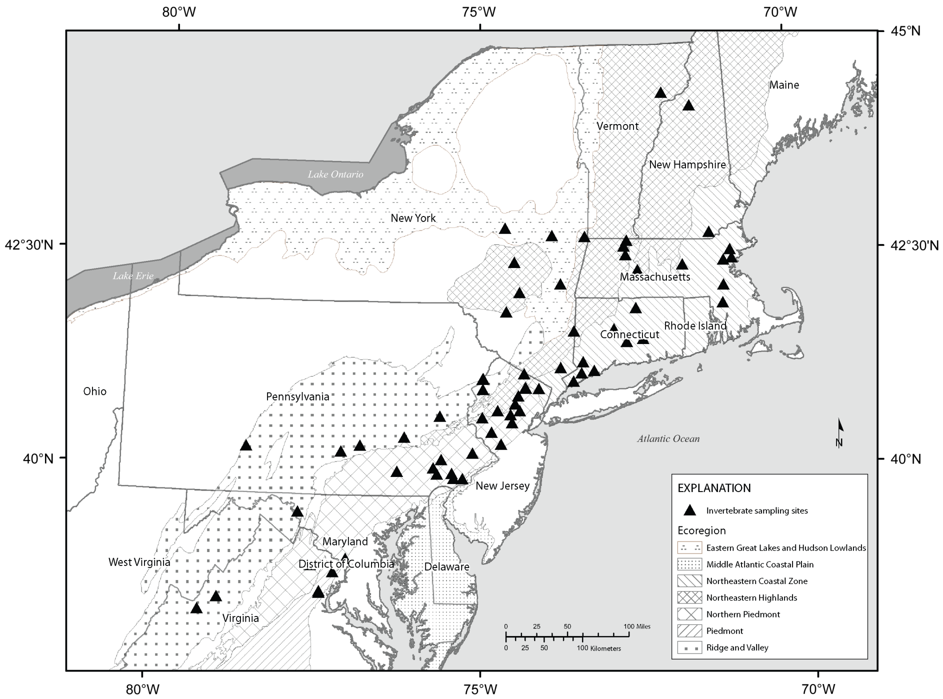

Figure 1. Spatial distribution of invertebrate sampling sites among northeast Level III Ecoregions.

divides and among basins is common, as are water management features (e.g. water diversions, wastewater discharges, dams, and reservoirs). Annual precipitation over the last 20 years in the northeast US has averaged between 20·3 and 44·5 cm year^{-1}; National Climatic Data Center, http://www.ncdc.noaa.gov/oa/climate/research/2006/ann/us-summary.html#precip, accessed September 15, 2009).

Land use and land cover vary widely, and these characteristics are closely linked to geology, terrain, and transportation routes. The study area contains large, highly forested areas (some of the largest connected wilderness areas in the lower 48 states) as well as many of the Nation's most densely populated cities, rapidly urbanizing areas, and important agricultural regions. Most of the major cities are located along the area's largest rivers because waterways represent primary shipping routes. Agriculture is still a major land use in valleys and throughout the many broad floodplains that parallel northeastern rivers. Large areas of contiguous forest areas still exist at higher elevations (e.g. Adirondack, Catskill, White, Green, Kittatinny, Allegheny and Berkshire Mountains). While older cities are losing population (e.g. Boston, MA, down 5·1% 2000–2005), the study area is experiencing rapid conversion of agricultural and forest lands to residential and commercial uses. This is occurring especially in many formerly rural areas within commutable distances of expanding commercial centres.

STUDY DESIGN

This study focuses on hydroecological disturbance of small-to-medium sized upland watersheds in areas that are transitioning from forest or low agriculture to urban in the northeastern US. Data aggregated for this study cover a time period from 1993 to 2003 and encapsulate seven US Geological Survey (USGS) National Water Quality Assessment (NAWQA) Program study units and six level III ecoregions (Figure 1). The largest river basins within the study area are the Connecticut, Charles, Hudson, Delaware, Raritan, Potomac, and Susquehanna.

Site selection

Seventy-six sites were initially selected from over 335 invertebrate sampling sites on the basis of a stratified approach designed to provide at least 3 years of hydrologic data and to control for natural environmental differences. Sites were selected to exhibit a range of urbanization and to minimize nested catchments (i.e. spatial autocorrelation). Sampling sites with a minimum of 3 years of hydrologic data prior to and encompassing the aquatic macroinvertebrate sampling period were targeted. In addition to constraining the study area to upland ecoregions, natural variability was minimized by (1) limiting drainage area to less than 530 km^2, (2) selecting sites in which the richest targeted habitat was rocky substrates of riffle zones, and (3) accounting for the effects of dams upstream of the sampling site and for natural fluctuation in annual precipitation. The number of sites for analysis was maximized by including a few 'surrogate' USGS continuous discharge stations for some invertebrate-collection sites lacking site specific flow data. The following criteria were required for a site to be included as a surrogate discharge station for a given invertebrate site: (1) location was within a 50-km radius of the invertebrate sampling site, and within the same ecoregion, (2) similar land use, and (3) drainage area within 5% of the drainage area of smaller catchments (15–279 km^2) or within 20% of the drainage area of larger catchments (280–526 km^2). Suitable surrogate continuous discharge stations were located for 12 invertebrate-collection sites.

We also attempted to hydroecologically classify these sites following the protocol outlined in Kennen *et al.* (2007), however, this process resulted in just three primary subgroups, two of which contained less than 15 sites. One subgroup consisted of large river sites (some >700 km^2), which were eliminated from further analyses ($N = 5$), the second represented too few sites ($N = 14$) to provide adequate statistical power for a direct comparison with the larger subgroup containing the remaining sampling sites. These two subgroups were subsequently combined because they were located within the same higher cluster (i.e. they were much more similar hydrologically to each other than to the eliminated group). Results of clustering appeared to support our conservative approach to site selection and demonstrate, at least for this study, that small-to-medium sized upland sites in the northeast US tend to respond similarly hydrologically (Poff and Ward, 1989; Olden and Poff, 2003). Four additional sites within close proximity of dams (<1500 m) were dropped leaving a final subset of 67 sites (Figure 1, Table I).

Data aggregation

Invertebrate-assemblage data. Aquatic macroinvertebrate data were assembled from samples collected during stable-flow periods in 1993–2002. Samples were collected during June–October; a large majority of samples (>90%) were collected during July–September. Some sites were visited during multiple years; in these cases, the primary sample for analysis was considered to be that providing the longest antecedent period of hydrologic data, while avoiding years encompassing highly unusual hydrologic events (i.e. severe drought or flooding). Sample collection followed the protocols of Cuffney *et al.* (1993) and Moulton *et al.* (2002). Samples were collected using an integrated sampling approach that incorporates areas of similar substrate composition, current velocity, water depth, and canopy cover. Aquatic macroinvertebrate samples were collected with a Slack sampler (0·5-m wide by 0·25-m high, 500-μm mesh) in five cobble-riffle sections of the stream. The five samples were composited for a total sample area of 1·25 m^2. The sample material was preserved with 10% buffered formalin, and shipped to the USGS National Water Quality Laboratory in Arvada, Colorado, for analysis. In the laboratory, a quantitative fixed-count processing method was used to estimate the abundance of each taxon. Aquatic macroinvertebrates were identified to the lowest possible taxonomic level (usually genus). A complete explanation of aquatic macroinvertebrate processing, identification, and quality control methods is provided in Moulton *et al.* (2000).

Hydrologic data. Data for daily average flows and peak annual flows were acquired from the USGS National Water Inventory System (NWIS; http://waterdata.usgs.gov/nwis). The files were imported into the National Hydrologic Assessment Tool [NAHAT (Henriksen *et al.*, 2006) and 171 ecologically relevant hydrologic Indices (ERHIs) were generated. NAHAT is one of a suite of tools within the Hydroecological Integrity Assessment Process (HIP) Software package. The HIP package was developed to assist water resource professionals who have a role in management and/or regulation of streams with a focus on ecological integrity by utilizing ERHIs that characterize the five major components of the flow regime (magnitude, frequency, duration, timing, and rate of change; Olden and Poff, 2003; Henriksen *et al.*, 2006; Kennen *et al.*, 2007). The following steps were taken in NAHAT for each site: perennial runoff was selected for stream class to best represent the clustered upland northeast stream types (e.g. Poff and Ward, 1989; Olden and Poff, 2003) prior to importing NWIS daily average and peak annual flow data. If the imported files contained years where there were missing values, a conservative approach was taken by excluding years with missing data. Three time periods for analysis were established for each site: (1) the entire period of record; (2) a 3-year time period inclusive of the invertebrate sample date; and (3) a 1-year time period inclusive of the invertebrate sample date. Sensitivity analysis of the three different hydrologic time periods indicated that 3 years of hydrologic data was the minimum period of record needed to adequately represent temporal variation while maximizing the number of possible sampling sites. The 3-year data set was used for all subsequent analytical procedures, and all ERHIs found to be significantly correlated (Spearman's *rho* >0·60) with drainage area

Table I. General watershed characteristics of streams used in regional analysis of aquatic invertebrate assemblages.

Station name	Station abbreviation	Drainage area (km^2)	Land use (%)			
			Urb	For	Agr	Other
Rooster River near Fairfield, CT[a]	roos	21·0	93·0	5·7	0·0	1·3
Saddle River at Ridgewood, NJ	sadd	55·9	86·1	13·3	0·4	0·3
Accotink Creek near Annandale, VA	acco	60·9	83·0	14·4	2·0	0·6
Aberjona River at Winchester, MA	aber	64·0	79·4	16·0	0·0	4·6
Bound Brook at Middlesex, NJ	boun	125·4	75·1	23·2	0·6	1·1
Paxton Creek near Penbrook, PA	paxt	29·0	73·9	9·3	13·6	3·3
Darby Creek near Darby, PA	dard	96·9	71·9	22·3	5·4	0·4

Table I. (*Continued*).

Station name	Station abbreviation	Drainage area (km^2)	Land use (%)			
			Urb	For	Agr	Other
Rock Creek at Sherrill Drive Washington, DC	rocc	161·1	70·0	15·7	13·1	1·3
Saugus R at Saugus Iron Works at Saugus, MA	sauu	53·9	68·7	24·2	0·0	7·1
Lisha Kill Northwest of Niskayuna, NY	lish	40·4	61·0	30·9	6·4	1·7
Little Neshaminy Creek at Valley Road nr Neshaminy, PA	lnes	69·4	50·0	26·4	22·6	1·1
EB Neponset at Canton Junction, MA[a]	ebne	72·9	49·8	43·0	0·2	7·1
Whippany River at Morristown, NJ	whip	76·1	44·8	51·0	3·3	0·9
Valley Creek near Altor, PA[a]	vall	41·4	43·0	34·0	19·4	3·6
Beaver Brook at North Pelham, NH	beav	123·8	40·5	51·2	5·8	2·5
Rippowam River at Stamford, CT	ripp	88·1	41·2	54·0	0·7	4·2
Neponset River at Norwood, MA	nepo	89·9	40·5	51·6	2·2	5·7
Passaic River near Chatham, NJ	pasc	259·0	39·0	50·9	8·6	1·5
Kisco River below Mount Kisco, NY	kisc	45·6	33·4	61·0	5·0	0·6
Letort Spring Run at Carlisle, PA	leto	56·5	32·5	6·6	59·9	1·0
Norwalk River At South Wilton, CT[a]	norw	77·7	29·6	65·1	3·0	2·4
Crum Creek at Goshen Road near Whitehorse, PA[a]	crum	32·4	29·3	51·9	18·4	0·3
Rockaway River above Reservoir at Boonton, NJ	rocw	300·4	27·4	65·6	2·3	4·7
Passaic River near Millington, NJ	pasm	143·5	27·2	60·1	10·4	2·3
Ridley Creek near Media, PA[a]	ridl	70·7	27·0	50·2	22·5	0·3
Wading River near Norton, MA	wadi	112·1	26·2	64·5	3·9	5·4
Wanaque River near Awosting, NJ[a]	wanw	72·0	21·4	66·5	0·7	11·4
Lamington River near Pottersville, NJ	lami	85·0	19·7	62·8	14·6	2·8
Coginchaug River at Middlefield, CT	cogi	77·2	19·7	56·0	21·5	2·8
Wanaque River at Pompton Lakes, NJ[a]	wanp	277·1	15·2	74·7	0·7	9·4
Saugatuck River near Redding, CT	saua	54·4	14·4	78·0	4·3	3·4
Stony Brook at Princeton, NJ	ston	115·3	14·1	52·8	32·5	0·7
Broad Brook at Broad Brook, CT	broa	40·1	14·0	46·2	37·8	2·0
Fort River near Amherst, MA	fort	107·5	13·7	76·4	7·2	2·7
Mill Creek at Eshelman Mill Road near Lyndon, PA	mill	140·4	13·5	10·0	76·1	0·3
Pequannock River at Riverdale, NJ	peqr	217·3	12·5	81·2	0·7	5·6
Salmon River near East Hampton, CT	salm	259·0	11·8	72·0	11·4	4·9
Neshanic River at Reaville, NJ	nesh	66·6	11·62	31·3	57·0	0·2
Marsh Run at Grimes, MD	mars	49·0	11·14	11·5	76·5	0·8
Claverack Creek at Claverack, NY	clav	157·0	9·44	65·7	24·2	0·7
Paulins Kill ds Blair Ck At Blairstown, NJ[a]	paul	364·1	9·05	68·9	17·7	4·3
Tulpehocken Creek near Bernville, PA	tulp	172·2	8·89	11·9	78·2	1·0
Mulhockaway Creek at Van Syckel, NJ	mulh	30·6	8·75	67·4	23·6	0·2
Jordan Creek near Schnecksville, PA	jord	137·3	7·01	31·4	61·2	0·4
French Creek near Phoenixville, PA	fren	153·1	6·87	60·5	32·0	0·7
EB Brandywine Creek near Dorlan, PA[a]	ebbr	86·5	6·55	42·5	49·7	1·3
Stillwater River near Sterling, MA	stil	81·8	6·31	81·1	8·2	4·4
Tenmile River near Gaylordsville, CT	tenm	525·8	6·14	66·9	24·8	2·2
South River near Conway, MA	sout	62·4	5·87	83·4	9·0	1·8
Monocacy River at Bridgeport, MD	mono	448·1	5·55	28·5	64·6	1·3
Muddy Creek at Mount Clinton, VA	mudd	36·8	4·70	26·1	69·0	0·2
Little Hoosic River at Petersburg, NY	lhoo	145·3	3·34	90·6	6·0	0·1
Bull Run near Catharpin, VA	bull	66·6	3·28	48·0	48·3	0·4
North River 61 m ab Fox Brook at Griswoldville, MA	norg	228·2	3·04	87·0	8·4	1·6
SF Quantico Creek near Independent Hill, VA	sfqu	19·8	2·30	93·0	3·0	1·7
Esopus Creek at Allaben, NY	esop	165·0	2·26	96·9	0·8	0·0
Bobs Creek near Pavia, PA	bobs	43·0	2·19	89·1	8·5	0·2
Flat Brook near Flatbrookville, NJ	flat	165·8	2·06	89·8	6·7	1·4
Sleepers River (Site W-5) near St. Johnsbury, VT	slee	111·1	2·02	78·8	16·3	2·8
Canajoharie Creek near Canajoharie, NY	cana	154·6	1·73	37·3	60·8	0·2
NB Chopawamsic Creek near Independent Hill, VA	ncho	15·0	1·57	92·6	4·1	1·8
Ammonoosuc River near Twin Mountain, NH[a]	ammo	216·8	1·56	91·5	0·3	6·7
West Kill Northwest of North Blenheim, NY	wesk	97·9	1·56	88·2	9·9	0·4
Green River at Stewartville, MA[a]	gree	105·7	1·31	92·1	5·5	1·1
East Mahantango Creek at Klingerstown, PA	emah	115·8	1·28	43·3	54·5	0·9
Neversink River near Claryville, NY	neve	172·5	0·91	98·6	0·4	0·1
North River near Stokesville, VA	nors	44·5	0·05	99·6	0·09	0·3

Stations are listed in order of decreasing percentage of urban land; Urb, urban; For, forest; Agr, agriculture; other includes water, natural, non-forest, and barren; SF, South Fork; NB, North Branch; EB, East Branch; ab, above; ds, downstream; nr, near.
[a] Sampling sites where surrogate hydrologic records were used.

were standardized by drainage area. The entire suite of 171 ERHIs was calculated for all stations except two for which peak annual flow data were unavailable.

Digital data used in watershed assessment. Landscape characteristics were derived by using a road-density correction of 1992 enhanced National Land Cover Data (NLCDe) using Tagged Image File Format (TIFF) images. The road-density correction was done because satellite imagery can miss urban areas where there is high tree cover, and recent analyses in portions of the study area demonstrate a favourable comparison between selected variables based on road-density corrected NLCDe coverages with those based on photointerpretation of digital orthophotography (Lister *et al.*, 2003). Land use and fragmentation variables known to achieve reasonable correction were derived from the road-corrected NLCDe coverage for this study.

Road correction of NLCDe was based on a technique developed by the US Forest Service for use in the Delaware River Basin (Lister *et al.*, 2003). The raw TIFF NLCDe statewide images were converted to an Environmental Systems Research Institute grid format and merged. Tiger/line files representing road features from the year 2000 were acquired from the US Bureau of the Census website (U.S. Census Bureau, 2001). This road layer was then converted to a raster grid with a 30-m cell size to match the NLCDe. Using the ArcGIS Spatial Analyst module (Environmental Systems Research Institute, 2001), a neighbourhood statistics analysis was computed on the rasterized road layer using a circle with a radius of 7 pixels. The output cell size was maintained at 30-m pixels. This product was then classified into a binary grid where cell values from the neighborhood analysis greater than 35 pixels were retained and given a value of 100; all other values were assigned No Data. This road layer was then added to the merged NLCDe product to create a new grid where NLCDe values that overlapped the 100 valued cells from reprocessed road layer now possess a value of their land use class plus 100. The entire NLCDe grid was then reclassified to create three new land use classes of 27, 28, and 29. This land use class represents areas that have a high-road density and now are to be classified as residential or urban. Land uses were aggregated into percent residential, percent urban, percent agricultural, percent developed, and percent forested. Percent urban is residential plus two additional classes, and percent developed is percent urban plus percent agricultural.

Selected fragmentation statistics were calculated using the raster image analysis software program (IAN) from the University of Wisconsin's Forest Ecology Laboratory (downloaded from http://landscape.forest.wisc.edu/projects/ian/, DeZonia and Mladenoff, 2004). IAN was run to compute the following variables, using an 8-cell neighbourhood: adjacency matrix, aggregation index, area, and core area. These values were used to compute core forest area per unit catchment area, core forest area as percentage of total forest area, core urban area per unit basin area, and core urban area as percentage of total urban area. FRAGSTATS (McGarigal *et al.*, 2002), a spatial pattern analysis program (downloaded from www.umass.edu/landeco/research/fragstats/fragstats.html) was used to provide forest patch size data with which percentages of forest patches less than 50 acres in size and less than 100 acres in size. Selected basin characteristics were also aggregated from the NAWQA data warehouse, based on NLCDe coverages (Vogelmann *et al.*, 2001; U.S. Geological Survey, 2006).

Chemical data. Data on selected physical and chemical characteristics were retrieved from the NAWQA Data Warehouse (http://infotrek.er.usgs.gov/nawqa_queries/biomaster/index.jsp), as ancillary characteristics for use in interpreting the aquatic macroinvertebrate assemblage patterns. Chemical variables retrieved were specific conductance and concentrations of chloride, silica, dissolved organic carbon, total phosphorous, and total nitrogen (obtained by summing nitrate plus nitrite, with ammonia plus total organic nitrogen). Where multiple samples had been collected, we included only the chemical sample collected nearest the date of the invertebrate sample; however, chemical data meeting this criterion were not available for all sites. Methods of chemical sample collection and laboratory analysis are detailed in Shelton (1994).

Data analysis

Variation in hydrologic, land use, and environmental attributes and aquatic macroinvertebrate-assemblage structure was assessed using a combination of partial correlation, regression, and conditional multivariate analyses to identify potential linkages among these attributes. Partial and conditional analyses were applied to eliminate the variability associated with proximity to dams and natural climatic variability (annual precipitation). Aquatic macroinvertebrate assemblages were analysed on the basis of the relative abundance of various taxa, which provides detailed information on species tolerance of environmental conditions and is useful in identifying environmental determinants of assemblage structure (Poff and Allan, 1995). Aquatic macroinvertebrate site by species matrices were censured by eliminating rare species that accounted for less than 0·01% of overall abundance and that were present in less than 2% of the samples. Ambiguities in the taxonomic assemblage (i.e. organisms that are not completely identified because of small size, incomplete development, damage, or poor preservation) were resolved by distributing the abundance of the ambiguous parents among their children in accordance with the relative abundance of each child using the Invertebrate Data Analysis System (IDAS; Cuffney, 2003). This approach represents a compromise between removing redundant taxonomic information and conserving quantitative information on taxa richness and abundance (Taylor, 1997) and is one of the methods suggested by Cuffney *et al.* (2007).

Patterns in macroinvertebrate-assemblage structure among sampling sites were examined using non-metric multidimensional scaling (NMDS). Macroinvertebrate data were first standardized by total abundance, and then square root transformed. The distance measure used was Bray Curtis, and NMDS procedures (Kruskal, 1964a,b) were performed using PRIMER software (Clarke and Warwick, 2001; Clarke and Gorley, 2006). The NMDS analysis was used to establish which environmental variables accounted for the highest proportion of the variability in the distribution of macroinvertebrate taxa in ordination space (e.g. Roy *et al.*, 2003; Walters *et al.*, 2003; Kennen *et al.*, 2005). Identification of a synthetic factor (axis scores) that could be interpreted as a disturbance gradient was accomplished through regressions and correlations with environmental variables, land use and land cover variables, proportional abundance of sensitive and tolerant taxa, selected macroinvertebrate metrics and indices, and other visual and analytical exploratory techniques (e.g. bubble plots, draftsman plots).

A total of 527 environmental variables (i.e. hydrologic, landscape, chemical and physical variables associated with each site) were evaluated for this study. Principal component analysis (PCA; SAS Institute Inc., 1989) in combination with partial collinearity assessment was used to isolate a subset of variables that accounted for the greatest proportion of variance, while minimizing redundancy and reducing the effects of natural variation. Distributions of all variables used in the PCA were evaluated for normality and were appropriately transformed when necessary. Variables based on amount of land use in a basin were standardized by basin area and arcsine square root transformed (Zar, 1984). We conducted PCA on the correlation matrix and evaluated the significance of principal components using the broken stick method (Jackson, 1993; McCune and Grace, 2002). By using the correlation matrix, we ensured that all the environmental variables contributed equally to the PCA and that the contributions were scale-independent (Legendre and Legendre, 1998). Loadings of the environmental variables on each significant principle component were used to identify variables that extracted dominant patterns of variation. A partial Spearman rank correlation matrix (SAS Institute Inc., 1989) of the reduced set of environmental variables was then examined to eliminate any remaining redundant variables with a Spearman's *rho* $>0{\cdot}75$. This conservative data reduction approach helped avoid the common pitfalls associated with establishing significant ($p \leq 0{\cdot}05$) correlations among a large suite of environmental variables simply by chance and introducing interdependencies among multiple explanatory variables (Van Sickle, 2003; King *et al.*, 2005). This approach does not strive to eliminate all forms of redundancy, rather, it attempts to minimize strong interdependencies and identify a subset of parsimonious variables for use in the development of multivariate models. The data reduction approach used in this paper helped reduce the number of explanatory environmental (e.g. land use, chemical, hydrological) and ecological metric (e.g. EPTR (richness of Ephemeroptera, Plecoptera and Trichoptera taxa), RICH (total taxa richness) variables available for modelling from 527 to 52.

Conditional multiple linear regression (MLR) analysis of study basin characteristics and hydrologic attributes was used to develop a series of equations defining the probability of assemblage alteration across a gradient of disturbance. MLR analysis is often used to predict or model a response variable (e.g. ordination axis scores) from one or more continuous explanatory variables (e.g. land use, hydrology, and catchment characteristics). The result is a regression equation that describes the relation among the variables being modelled. Variance associated with the influence of dams (proximity to dams) and natural climatic variability (annual precipitation) was extracted prior to fitting all MLR equations. That is, these variables are fitted in the model and the overlap in variability that they explain is eliminated from the data cloud prior to fitting any other explanatory variable (this is known as a conditional or partial test).

Ordination results were incorporated into conditional MLR analysis by using the NMDS axis I scores as the response variable. MLR analysis was then used to identify the minimum set of explanatory variables needed to account for the observed variation in the response variables—that is, a series of conditional MLR models were constructed that describe the relation between the environmental and hydrologic data and the distribution of sites along the disturbance gradient. By using multiple explanatory variables to estimate values of a response variable (e.g. NMDS axis scores), errors in prediction were limited while still accounting for a large proportion of the variance in the response variable. In addition, this approach provides diagnostic tools that allow us to explicitly confront the dependencies between multiple candidate explanatory variables (Van Sickle, 2003). Screening variables prior to MLR modelling can improve predictive power; however, care was taken (i.e. a parsimonious approach was used) to prevent elimination of variables that are important in providing a complete description of the relations between explanatory and response variables. Best fit conditional MLR models were derived from the reduced set of explanatory variables. Two measures of goodness of fit were used to assess the relations indicated by the resulting conditional MLR equations: (1) coefficient of determination (R-squared statistic) which is the percentage of the variability of the dependent variable that is explained by the variation on the independent variables. The R-squared value ranges from 0 to 1, with 1 being a perfect fit and most conditional MLR modelling procedures attempt to maximize this value; and (2) Akaike's Information Criteria (AIC) which is a function of the number of observations and the sum of squared errors. This criterion measures the lack of model fit relative to the number of explanatory variables in the model. As the number of variables in the model increases, the lack of fit decreases and the penalty for having too many variables increases.

In this analysis, the model with the smallest AIC and highest *R*-squared value was considered the 'best', that is, most parsimonious model. Models were also evaluated on the basis of Variance Inflation Factor (VIF) of the component variables. Higher VIF indicates that a variable is more closely related to one or more other variables in the model than to the model itself. A standard VIF cutoff criterion of 10 was used for evaluating whether there was any undue influence of one independent variable on another, however, this value is considered somewhat arbitrary as there are no formal criteria for determining at what magnitude an inflation factor actually results in poorly estimated regression coefficients (SAS Institute Inc., 1989).

RESULTS

Linking invertebrate-assemblage composition and environmental alteration

Initial compilation of macroinvertebrate assemblage data among the 67 sites yielded 425 taxa. Processing through IDAS reduced the number of taxa in the final analysis data set to 198. Number of taxa at a site ranged from 12 to 46 (median 30), and total abundance ranged over several orders of magnitude, from 134 to 35,000 (median 4542). Macroinvertebrate metrics exhibited a broad range and included values normally associated with very poor conditions to very good or excellent conditions. For example, EPT richness (EPTR) ranged from 2 to 26 (median 10), and percent richness as non-insects (NONINSRP) ranged from 2·7 to 47 (median 12·1). Percent abundance of EPT (EPTp) ranged from 4 to 82 (median 52), and percent abundance of non-insects (NONINSp) ranged from 0·7 to 55 (median 7·9).

Twenty-five NMDS iterations were completed, which indicated the three-dimensional solution was the best solution with a final stress (a measure of the 'goodness of fit' of the data that attempts to maximize the rank correlation between the calculated Bray Curtis distances and the plotted distances; McCune and Grace, 2002) of 17·0. Higher dimensions did little to improve the model. Together, the three axes accounted for 78% of the variance in the analytical data set. The first NMDS axis accounted for the majority (40%) of the invertebrate-assemblage variation. The second and third axes accounted for significant but generally smaller proportions of the overall variance (15 and 23%, respectively) and were not considered for further analysis. Macroinvertebrate assemblages were distributed across the first ordination axis such that sensitive taxa were more common and abundant nearer the left portion of the axis, and tolerant taxa were more common and abundant nearer

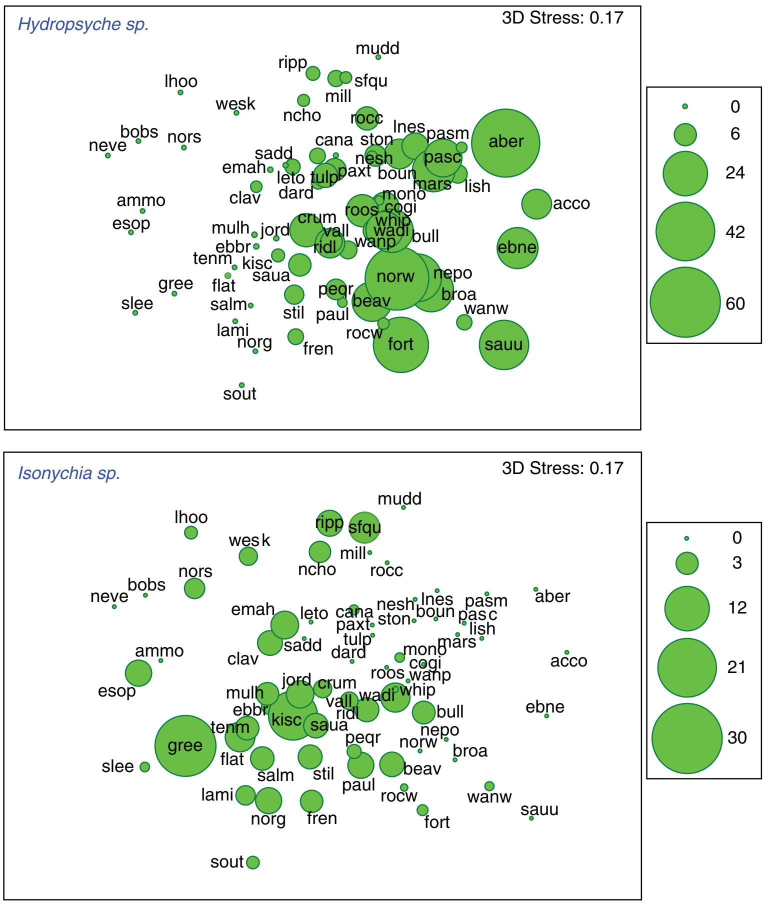

Figure 2. NMDS ordinations plots of primary (x) axis and secondary (y) axis, with bubble sizes representing raw abundance of *Hydropsyche* sp (top), a relatively tolerant macroinvertebrate taxon, and *Isonychia* sp (bottom), a relatively sensitive macroinvertebrate taxon. Station names for abbreviations are provided in Table 1.

Table II. Significant partial correlations (Spearman's rho) between relative abundance of selected macroinvertebrate taxa and NMDS ordination axis I scores (the derived disturbance gradient).

Order	Family	Species	*rho*	p-Value
Ephemeroptera	Baetidae	*Acentrella* sp.	−0·6344	<0·0001
		Plauditus sp.	−0·4201	0·0004
	Isonychiidae	*Isonychia* sp.	−0·5241	<0·0001
	Ephemerellidae	*Serratella* sp.	−0·5111	<0·0001
		Ephemerella sp.	−0·3225	0·0083
	Leptophlebiidae	*Paral eptophlebia* sp.	−0·4591	0·0001
	Heptageniidae	*Rhithrogena* sp.	−0·3159	0·0098
Plecoptera	Leuctridae	*Leuctra* sp.	−0·5440	<0·0001
	Perlidae	*Agnetina* sp.	−0·4162	0·0005
		Acroneuria sp.	−0·2433	0·0490
	Perlodidae	*Sweltsa* sp.	−0·3405	0·0052
Trichoptera	Hydropsychidae	*Hydropsyche* sp.	0·7813	<0·0001
		Ceratops yche sp.	−0·4971	<0·0001
	Lepidostomatidae	*Lepidostoma* sp.	−0·4508	0·0001
	Rhyacophilidae	*Rhyacophila* sp.	−0·3582	0·0031
	Helocopsychidae	*Helicopsyche* sp.	−0·4415	0·0002
	Philopotamidae	*Dolophilodes* sp.	−0·4678	<0·0001
	Brachycentridae	*Brachycentrus* sp.	−0·3649	0·0026
	Glossosomatidae	*Glossosoma* sp.	−0·4007	0·0003
Coleoptera	Elmidae	*Optioservus* sp.	−0·4898	<0·0001
	Psephenidae	*Psephenus* sp.	−0·3472	0·0043
Diptera	Tipulidae	*Hexatoma* sp.	−0·5191	<0·0001
	Athericidae	*Atherix* sp.	−0·3798	0·0017
	Chironomidae	*Potthastia* sp.	−0·4301	0·0003
Amphipoda	Gammaridae	*Gammarus* sp.	0·4617	<0·0001
Isopoda	Asellidae	*Caecidotea* sp.	0·3098	0·0114
Haplotaxida	Tubificidae	Tubificidae[1]	0·3720	0·0021

[1] Lowest possible taxonomic identification for this organism was family-level.

the right portion of the axis (Figure 2) reflecting a gradient of assemblage response to stress. Partial correlation coefficients (Spearman's *rho*) of selected taxa relative abundances with primary axis score (Table II) consistently reflect this response pattern. For example, the proportion of taxa richness composed of sensitive macroinvertebrates such as *Acentrella* sp., *Isonychia* sp., *Leuctra* sp., *Sweltsa* sp., *Ceratopsyche* sp., and *Lepidostoma* sp. was negatively correlated with the disturbance gradient (Table II). Conversely, relative abundance of highly tolerant omnivorous taxa such as *Gammarus* sp. increases, as does the relative abundance of taxa with moderate tolerance, such as the caddisfly taxon *Hydropsyche* sp. (Figure 2). Results of partial Spearman rank correlation of invertebrate metrics with axis I (Table III) generally show that larger axis scores are related to lower total taxa richness and fewer sensitive taxa, and higher dominance, assemblage tolerance, and replacement of insect taxa with non-insects. In addition, the underlying environmental gradient across which the macroinvertebrate-assemblage pattern changes is highly associated with anthropogenic disturbance, as indicated by correlation results showing increasing concentrations of chloride, nutrients, dissolved organic carbon, and specific conductance (Table III).

Changes in basin characteristics associated with human activity and with natural factors were also evident in partial correlation results (Table IV). NMDS axis I score was more highly correlated with catchment characteristics associated with human activity than with any other explanatory variable except basin elevation. Axis I score was positively correlated with population density (0·6798; $p < 0·0001$), urban-developed land use (0·7008; $p < 0·0001$), and road density (0·6170; $p < 0·0001$), and negatively correlated with percent of buffer as forest land (−0·6096; $p < 0·0001$), mean basin elevation (−0·7087; $p < 0·0001$) and slope (−0·6915; $p < 0·0001$). Elevation and basin slope were the only natural characteristics with relatively high-partial correlations with axis I scores; these are also highly (inversely) correlated with urban indicators. In many regions of the northeast US, these attributes do not vary independently because steep slopes often deter development. An absence of latitudinal effect was indicated by lack of significant correlation between NMDS axis 1 score and latitude ($R = 0·1748$, $p = 0·1310$). Significant partial correlations with runoff/soil wetness and infiltration properties were also found (Table IV).

Results of conditional MLR analysis indicate that many environmental variables contribute independent information to the synthetic factor represented by the primary NMDS axis score, and that the MLR models describing these relations were highly significant. Four highly parsimonious two-variable conditional MLR models were derived based on landscape configuration that accounted for up to 48% of the overall variability in axis I scores (Table V). In particular, these MLR models demonstrate how increasing invertebrate-assemblage impairment is directly related to urban development, and

Table III. Significant partial correlations (Spearman's *rho*) between the primary NMDS axis scores and reduced set of macroinvertebrate indices and chemical concentrations.

Metric abbreviation	Metric description	*rho*	*p*-Value
Macroinvertebrate metrics and indices ($n = 67$)			
NONINSRp	Percent of total richness as non-insect taxa	0·80	<0·0001
RichTOL	Average USEPA tolerance values based on richness	0·78	<0·0001
EPTR	EPT taxa richness	−0·72	<0·0001
ODIPNIRp	Percent richness as non-chironomid dipterans and non-insects	0·71	<0·0001
AbundTOL	Abundance-weighted USEPA tolerance value	0·70	<0·0001
NONINSR	Non-insect taxa richness	0·67	<0·0001
Dom5	Percent dominance top five taxa	0·66	<0·0001
ShanDiv	Shannon diversity	−0·65	<0·0001
RICH	Total taxa richness	−0·63	<0·0001
EPTRp	Percent richness as EPT taxa	−0·62	<0·0001
Dom3	Percent dominance of top three taxa	0·61	<0·0001
TRICHR	Trichoptera taxa richness	−0·51	<0·0001
pSC_Rich	Percent richness composed of shredder taxa	−0·41	0·0005
Chemical characteristics (units)			
DOC ($n = 33$)	Organic carbon, water, filtered (mg l^{-1})	0·67	<0·0001
NH4OD ($n = 45$)	Ammonia plus organic nitrogen, water, filtered (mg l^{-1} as nitrogen)	0·66	<0·0001
NH4OT ($n = 45$)	Ammonia plus organic nitrogen, water, unfiltered (mg l^{-1} as nitrogen)	0·63	<0·0001
Cl ($n = 42$)	Chloride, water, filtered (mg l^{-1})	0·52	0·0005
Sc ($n = 57$)	Specific conductance (uS cm^{-1})	0·43	0·0007
Ntot ($n = 45$)	Total nitrogen (mg l^{-1}; calculated as sum of NH4OT and NO_2NO_3)	0·42	0·0042
Ptot ($n = 45$)	Phosphorus, water, unfiltered (mg l^{-1})	0·37	0·0111

Macroinvertebrate and chemical metrics are listed in order of decreasing |*rho*|; USEPA, United States Environmental Protection Agency; EPT, Ephemeroptera, Plecoptera and Trichoptera.

is further affected by increasing levels of forest patchiness, road density, and the percent of overland flow (PERDUN, an indicator of low soil permeability). Attempts to generate higher order models resulted in undesirable collinearity among explanatory variables, as indicated by elevated VIFs. Figure 3 represents the observed versus predicted fitted regression relation for the best (i.e. model with highest AIC score) of these two-variable models. The best two-variable MLR models (Table V) combined an indicator of urban intensity, such as percent urban land use or road density, with an indicator of forest patchiness or overland flow, either on a whole-catchment scale or in the riparian corridor. The significance of these factors in an area as large as the Northeast US emphasizes the level of influence anthropogenic changes in the landscape have on stream systems and stream biotic integrity, even at a broad spatial scale.

Relating hydrologic disturbance to changes in invertebrate-assemblage composition

The selected hydrologic variables and their individual correlations with NMDS axis I scores are listed in Table VI. Increasing axis I score was associated with declines in factors such as magnitude of spring and fall flows, high-flow duration, and seasonal predictability of low flows, and with increases in factors such as variation in magnitude of summer flows, and frequency of high and low flows. A series of two- through five-variable conditional MLR models were derived on the basis of hydrologic attributes that explained between 35 and 60% of the variability in axis I scores (Table VII). Eight hydrological variables were significantly ($p < 0{\cdot}05$) related to the extracted NMDS axis I scores for the aquatic invertebrate assemblage, and all these variables had low VIFs. Combined, these hydrologic measures accounted for all five major components of the flow regime (i.e. magnitude, frequency, duration, timing, and rate of change). The seasonal predictability of low flows (TL4), mean monthly April flow (MA15), and high-flow duration (DH17) appeared in three out of the four models and accounted for between 19–58%, 21–65%, and 23–25% of the overall variability, respectively. High-flow frequency (FH9) only appeared in 1 out of 4 of the multiple regression models. Mean monthly flow for April (MA15) accounted for the greatest amount of variability in any single model (65% in the two-variable model). Mean minimum flow for April across all years (ML4) accounted for 21% of the variability in the disturbance gradient in the five-variable model. TL4, RA4 and FH9 were positively related to the disturbance gradient; all other hydrologic variables were negatively related (Table VII). Figure 4 represents the observed versus predicted fitted regression relation of axis I score and hydrologic metrics for the five-variable model.

Flow-ecology response relations

Regional flow–ecology response relations between a reduced set of individual flow measures and ecological metrics were evaluated using partial Spearman's correlation (Table VIII). Many hydrologic measures accounting for the frequency, duration and magnitude of flow events were significantly correlated with

Table IV. Reduced set of catchment characteristics that are significantly correlated (partial Spearman rank correlation, $p < 0.01$) with macroinvertebrate ordination axis I scores.

Variable (abbrev.)	Variable (units)	*rho*	p-Value	*Mean*	Min	*Max*	SD
PER_URB	Percentage of catchment as urban land use	0·7008	<0·0001	24·1	0·0	93·0	26·4
PDENS00	Population density 2000 (people per km^2)	0·6798	<0·0001	321	4	1597	405
RD_DEN	Road density (km km^{-2})	0·6170	<0·0001	3·4	0·6	9·2	2·2
PERBUF_URB	Percentage of buffer as urban land	0·6162	<0·0001	19·6	0·0	88·0	22·0
PERBUF_FOR	Percentage of buffer as forest land	−0·6096	<0·0001	52·1	9·3	99·1	23·9
PERPAT_FOR	Percentage of forest patches that are less than 100 acres in size	−0·5377	<0·0001	16·6	0·0	100·0	24·8
ADJ_FOR	Probability that forest patch is adjacent to another forest patch	−0·4874	<0·0001	0·2	0·0	0·6	0·2
RD_STR_INT	Number of road–stream intersections	0·5022	<0·0001	1·2	0·2	3·1	0·6
PERDUN	Percent Dunne overland flow from TOPMODEL (percent of total streamflow)	0·5433	<0·0001	3·0	1·3	4·8	0·7
POT_EVAP	Potential evapotranspiration (mm year^{-1})	0·4646	<0·0001	660·4	492·1	784·1	66·6
TOPWET	Hydrologic Topographic Wetness Index, $\ln(a/S)$; where 'ln' is the natural log, 'a' is the upslope area per unit contour length and 'S' is the slope at that point (See http://ks.water.usgs.gov/Kansas/pubs/reports/wrir.99–4242.html and Wolock and McCabe (1995) for more details)	0·4409	0·0002	10·5	7·5	49·8	5·8
RUNOFF96	RUNOFF, 1996 (mm year^{-1}); Estimated basin mean annual runoff	−0·4351	<0·0001	710·6	504·8	1131·0	131·5
BAS_ELEV	Mean basin elevation (m)	−0·7087	<0·0001	225·3	30·9	961·7	194·3
BAS_SLOPE	Mean basin slope (%)	−0·6915	<0·0001	7·3	1·3	28·0	5·4
TEMP_ANN	Mean annual temperature (°C)	0·4335	0·0003	9·7	3·5	12·9	1·9
SEG_GRAD	Segment gradient (m km^{-1})	−0·3727	0·0022	5·4	0·0	43·1	6·0
HSGC	HSGC Soils from STATSGO: percent soils in hydrologic soil group C (see http://soils.usda.gov/technical/handbook/contents/part618.html for more detail on Hydrologic Groups)	−0·3228	0·0082	37·3	1·0	83·9	19·1

DAYMET, daily surface weather and climatological summaries; TOPMODEL, a physically based rainfall runoff model (Beven and Kirkby, 1979; Wolock, 1993); STATSGO, State Soil Geographic Database.

Table V. Best two-variable conditional multiple regression models relating NMDS axis I scores to catchment characteristics.

Number in model	AIC	Model R^2	Model p	Partial R^2	p-Value	Variable influence	Variable (abbrev.)	VIF
2	−107·3	0·4709	<0·0001	0·3818	<0·0001	+	PER_URB[a]	1·18
				0·0891	0·0017	+	PERDUN	1·18
2	−107·1	0·4848	<0·0001	0·2675	0·0015	+	PERDUN	1·17
				0·2174	<0·0001	+	RD_DEN[b]	1·17
2	−102·7	0·4564	<0·0001	0·3053	<0·0001	−	ADJ_FOR	1·07
				0·1511	<0·0001	+	PERDUN	1·07
2	−100·5	0·4127	<0·0001	0·2884	0·0002	+	PERBUF_URB[a]	1·13
				0·1243	0·0005	+	PERDUN	1·13

Models are ordered from lowest to highest AIC. All model intercepts were significant at the $p < 0.05$ level. Variable definitions can be found in Table IV.
[a] Square root transformed.
[b] Fourth-root transformed.

ecological response. Many invertebrate-assemblage metrics ($n = 183$) accounting for richness, abundance, and function of the aquatic assemblage were computed; however, we found that the subset of metrics showing the greatest relation with hydrologic attributes was often richness-based metrics (Table VIII). The percentage of total richness composed of non-midge Diptera and non-insects (ODIPNIRp) as well as the richness of tolerant taxa (RichTOL) were some of the metrics most highly correlated with flow processes. Even though most of the regional flow–ecology response relations between ecological metrics and flow measures had correlation coefficients less than 0·5, all were significant and generally followed increasing or decreasing trends that would be expected given anthropogenic changes in upland basins and concomitant changes in

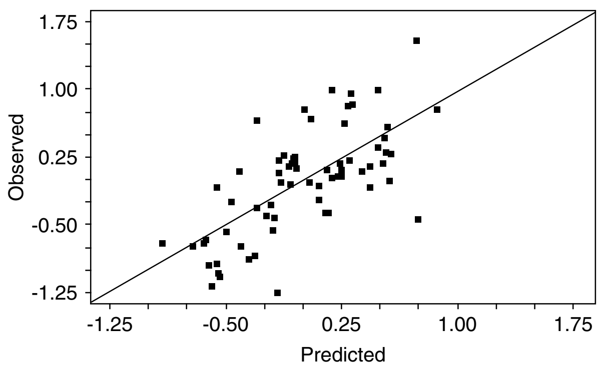

Figure 3. Fitted best two-variable conditional multiple regression model of the observed versus predicted NMDS axis I score using percent urban land use (square root transformed) and Dunne overland flow (Model $R^2 = 0{\cdot}48$, $p < 0{\cdot}0001$, $n = 67$). Regression line follows the 1 : 1 line shown, and model specifications are presented in Table V.

stream hydrology. For example, as the average frequency of high-flow events above the 75% exceedance value (i.e. FH9) increased, RichTOL and ODIPNIRp increased (Table VIII). Figure 5 represents an example of a significant linear bivariate flow–ecology relation between FH9 and RichTOL. The moderate regression slope depicted appears to reflect nearly a twofold increase in the number of tolerant taxa with a sixfold increase in the number of high-flow events. This may indicate that as upland streams become flashier as the result of increases in impervious cover and shifts from forested to urban basins, there is a general increase in tolerant taxa such as *Gammarus* sp, non-midge Diptera and non-insects (e.g. Table II). A highly similar linear response was also seen for RichTOL and variability of mean monthly July flow values (MA30), indicating that changes in streamflow variability may also have an appreciable effect on assemblage integrity. Declines in the richness of EPT taxa were noted with increasing frequency of low flows (FL1). Additionally, duration and magnitude of flows were directly related to changes in the percent richness composed of scraper taxa (pSC_Rich). Alterations in many, rather than just one, flow components were apparent and these alterations were directly related to changes in invertebrate-assemblage complexity and richness (Table VIII).

Table VI. Reduced set of hydrological variables listed in descending order of partial correlation (Spearman's *rho*) with NMDS ordination axis I scores.

Variable name	Description (unit of measurement)	*rho*	*p*-Value	Mean	SD	Min	Max
MA15	The mean of all April flow values over the entire record (CFS).	−0·3923	0·0013	149·2	164·6	6·6	802·2
FL1	Low flood pulse count. Computed as the average number of flow events with flows below a threshold equal to the 25th% value for the entire flow record (number of events/year).	0·3818	0·0018	10·9	3·8	3·0	20·0
FH9	High-flow frequency. Computed as the average number of flow events with flows above a threshold equal to 75% exceedance value for the entire flow record (number of events/year).	0·3645	0·0031	11·1	4·0	3·0	20·0
ML4	The mean of the minimums of all April flow values over the entire record (CFS)	−0·3456	0·0052	64·2	69·5	2·4	413·0
DH21	High-flow duration (days).	−0·3446	0·0053	36·9	26·3	13·7	159·6
MA30	Coefficient of variation of mean monthly July flow values (%).	0·3317	0·0074	89·5	44·9	15·8	231·1
MA42	Variability across annual flows. MA42 is the maximum annual flow minus the minimum annual flow divided by the median annual flow (D)	0·3185	0·0103	0·5	0·3	0·0	2·4
MH18	Variability across annual maximum flows (D)	0·2863	0·0218	8·0	4·4	1·8	21·4
RA7	Change of flow (negative) for entire flow record (CFS/day)	−0·2853	0·0223	−0·1	0·0	−0·2	0·0
DL17	Variability in low-flow duration (%)	−0·2843	0·0228	42·6	20·3	0·3	85·6
FH5	Flood frequency. Computed as the average number of flow events with flows above a threshold equal to the median flow value for the entire flow record (number of events/year)	0·2713	0·0301	15·7	6·2	5·0	34·0
ML10	The mean of the minimums of all October flow values over the entire record (CFS)	−0·2380	0·0580	14·1	15·7	0·3	86·0
MH4	The mean of the maximums of all April flow values over the entire record (CFS)	−0·2337	0·0058	420·2	464·9	22·3	2497·0
MH13	Variability (coefficient of variation) across maximum monthly flow values (%)	−0·2079	0·0991	109·0	34·3	55·7	251·8
DH4	Annual maximum of 30-day moving average flows (CFS)	0·1982	0·1165	233·6	209·8	14·1	1123·0

All five major components of streamflow are represented—magnitude, duration, frequency, rate of change, and timing. CFS, cubic feet per second; D, dimensionless; SD, standard deviation; min, minimum; max, maximum.

Table VII. Best two, three, four, and five-variable conditional multiple regression models relating axis I scores to hydrologic variables.

Number in model	AIC	Model R^2	Model p	Partial R^2	p-Value	Variable influence	Variable (abbrev.)	VIF
5	−119·4	0·6005	<0·0001	0·14824	<0·0001	−	DH17	1·44
				0·12866	0·0004	−	DL4[a]	1·49
				0·12554	0·0012	−	MA15[ad]	1·26
				0·11186	0·0001	+	TL4[a]	1·44
				0·08624	0·0344	+	RA4[c]	1·29
4	−115·3	0·5613	<0·0001	0·22358	<0·0001	−	MA15[ad]	1·10
				0·18001	<0·0001	+	TL4[a]	1·44
				0·14824	<0·0001	−	DH17[a]	1·27
				0·00952	0·0044	−	RA7[b]	1·36
3	−106·9	0·4848	<0·0001	0·28333	<0·0001	+	TL4[a]	1·25
				0·11126	<0·0001	−	DH17[a]	1·24
				0·10372	<0·0001	−	ML4[a]	1·05
2	−92·7	0·3497	<0·0001	0·22860	<0·0001	−	MA15[ad]	1·00
				0·12113	<0·0022	+	FH9	1·00

All model intercepts were significant at the $p < 0{\cdot}001$ level. Hydrologic variable definitions can be found in Table VI and Kennen *et al*. (2007).
[a] Square root transformed.
[b] log transformed.
[c] Rank transformed.
[d] Standardized by drainage area.

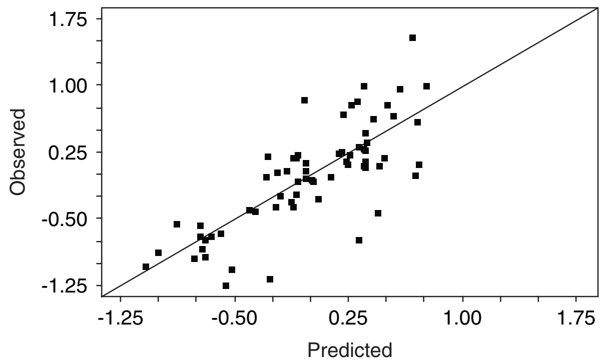

Figure 4. Fitted best five-variable conditional MLR model of the observed versus predicted NMDS Axis I score using hydrologic metrics (Model $R^2 = 0{\cdot}60$, $p < 0{\cdot}0001$, $n = 67$). Regression line follows the 1 : 1 line shown and model specifications are presented in Table VII.

DISCUSSION

In this study we identified landscape and hydrologic factors that were directly related to differences in aquatic invertebrate-assemblage structure across a defined disturbance gradient at the regional level, in the absence of a natural factor that is known to drive hydrologic variability (i.e. annual precipitation). We postulated that variation in the landscape associated with urbanization will have a measurable negative effect on the aquatic macroinvertebrate assemblage. We also postulated that a decline in biotic integrity will be related to the observed variation in at least one of the five major components of the flow regime. Our findings indicate that landscape alteration has a direct effect on the macroinvertebrate assemblage and that biotic decline is related to all

Table VIII. Flow–ecology response relations of selected invertebrate-assemblage metrics significantly correlated (partial Spearman's *rho*) with the reduced set of hydrologic measures.

Metric abbreviation	Metric description	Hydrologic variable	*rho*	p-Value
ODIPNIRp	Percent of total richness as non-chironomid dipterans and non-insects	MA15	−0·4058	0·0007
		FH9	0·3691	0·0023
		FL1	0·3666	0·0025
EPTR	Richness of EPT taxa	FH9	−0·4321	0·0003
		FL1	−0·4342	0·0003
NONINSRp	Percent of total richness as non-insect taxa	FH9	0·3945	0·0005
		MH4	−0·3678	0·0024
		DH4	−0·3058	0·0125
RichTOL	Average USEPA tolerance values based on richness	FH9	0·4149	0·0005
		FL1	0·4297	0·0003
		MA30	0·4021	0·0008
PSC_Rich	Percent richness composed of scraper taxa	DL17	0·3332	0·0071
		MH4	0·3175	0·0094
TRICHR	Trichoptera taxa richness	DL17	0·3475	0·0049
		ML4	−0·3249	0·0078

Hydrologic variable definitions can be found in table VII and Kennen *et al*. (2007). EPT, Ephemeroptera, Plecoptera and Trichoptera.

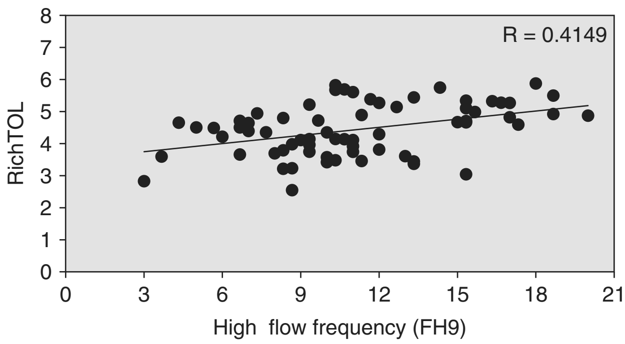

Figure 5. Example of a bivariate flow–ecology response relation between average Environmental Protection Agency tolerance values for a sample based on richness (RichTOL) and high-flow frequency (FH9). In general, this relation reflects a significant increase in the amount of tolerant taxa with increasing frequency of high-flow events (i.e. stream flashiness).

five components—magnitude, frequency, duration, timing, and rate of change. Additionally, many of the MLR models and flow–ecology response relations developed in this study clearly support these hypotheses. Few previous studies have empirically established hydroecological linkages at such a broad spatial scale. This is presumably because as one moves up in scale, data tend to gain variability (i.e. the amount of 'scatter' increases), and because there are few programs in the US or elsewhere that collect co-located invertebrate and continuous hydrologic data at such a broad spatial scale (e.g. the Environmental Protection Agency's Environmental Monitoring and Assessment Program uses randomly selected stream sites that rarely have associated stream gages; but also see Knight *et al*., 2008 [southeast US] and Kennard *et al*., 2009 [Australia]).

Results of this study indicate that a clear disturbance gradient exists across the study region, and that this disturbance gradient is associated with catchment development, particularly urban development. The disturbance gradient, established on the basis of ordination of macroinvertebrate relative abundances, was directly associated with changes in taxa and biological metrics. Partial correlation results, with axis scores as dependent variables and macroinvertebrate taxa and biological metrics as independent variables (Tables II and III, respectively), showed changes in several aspects of the macroinvertebrate assemblage across the disturbance gradient; these include reduction in number of sensitive taxa and the replacement of taxa and individuals that are more specialized feeders with more generalist taxa. These types of response patterns have been seen in numerous studies relating urbanization to aquatic assemblage impairment (Roy *et al*., 2003; Coles *et al*., 2004; Cuffney *et al*., 2005; Meyer *et al*., 2005; Wang *et al*., 2008, and many more). Some investigators (e.g. Armstrong *et al*., 2001; Roy *et al*., 2005; Freeman and Marcinek, 2006) have successfully linked hydrologic alteration indicators to changes in assemblage structure; however, these studies have been done at a limited spatial scale.

Many of the hydrologic variables in this study accounted for a significant proportion of the variability and were highly important in driving modifications to invertebrate-assemblage structure, including reduction in diversity, simplification of trophic structure, and replacement of sensitive taxa by tolerant taxa. Predictive conditional MLR models were derived by linking changes in assemblage structure with changes in hydrology, indicating that hydrologic alteration resulting from landscape change has modified stream biotic integrity. In addition, a number of significant bivariate flow–ecology response relations were established that directly and linearly link alterations in the natural flow regime (i.e. hydrologic stress) with changes in invertebrate-assemblage structure and function. Most prominent were changes in high- and low-flow processes that individually and cumulatively had the greatest effect on the aquatic assemblage. Most susceptible were structural attributes such as those based on invertebrate richness. Other assemblage components (e.g. behavioural, habitat, or functional) appeared to be a little less responsive to changes in flow processes at the regional level. One functional measure (i.e. percent scraper richness) did, however, respond significantly to changes in the duration and magnitude of low and high flows, respectively (Table VIII). All of these changes in the biotic assemblage may be a direct result of hydrologic alteration, or a result of landscape factors associated with hydrologic alteration (Lytle and Poff, 2004).

Magnitude of low flows and duration and timing of high flows were identified as important hydrologic variables in our analysis. For example, magnitude of low flow accounted for significant amount of the variability in invertebrate-assemblage structure in the three-variable MLR model (Table VII). Periods of low flow tend to favour taxa that prefer slower velocities (Jowett, 1997) or those taxa that are more tolerant of stressors (e.g. oxygen depletion and higher water temperatures) associated with slower flowing water. In particular, minimum flows appeared to be highly important in maintaining invertebrate-assemblage integrity, and spring low flow (i.e. ML4), was one of the hydrologic variables most strongly correlated with NMDS axis I scores (Table VI). The maintenance of spring flow magnitude is known to be important for aquatic species that are adapted to particular flow regimes, especially those species that rely on flow cues for reproduction and support of crucial life cycle stages (Grossman, 1982; Poff and Ward, 1989). Similarly, maintenance of spring flows may be essential for oviposition behaviour and dispersal of some ephemeropterans (e.g. *Baetis* sp; Peckarsky *et al*., 2000). In general, the duration of high flow and the magnitude of low flows are decreasing with increasing assemblage impairment, indicating that upland streams are becoming flashier and tend to have high flows of shorter duration and lower low-flows. Streams with more unpredictable high-flow events in combination with extreme low flows are indicative of catchments that are affected by changes in the landscape associated with urbanization (Konrad and Booth, 2005; Walsh *et al*., 2005). Such changes in runoff and streamflow patterns alter the natural flow regime and greatly affect native and endemic species.

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Annual streamflow variability has been identified as important to support native stream communities (Poff *et al*., 1997), and adaptation to a specific flow regime typically occurs as a response to the interaction between predictability, frequency, and magnitude of mortality-causing flow events (Lytle and Poff, 2004). Timing of flow events is particularly relevant for synchronization of life-history processes; Lytle and Poff (2004) suggest that even though it is difficult to forecast individual flow events, it is likely that aquatic organisms adapt to the long-term average timing, especially if such occurrences are in regions where there is some level of flow predictability (e.g. high-spring flows or summer low flows in the Northeastern US). Synchronizing reproductive processes with high- or low-flow periods likely optimizes reproductive success and helps avoid high-mortality rates during extreme events such as floods or droughts (Lytle, 2002; Boulton, 2003). In this study, flow variability appeared to be important for the aquatic invertebrate assemblage, especially variability across maximum monthly and average monthly flows, annual variability of stream flow, and annual maximum monthly flow, which were found to be significantly correlated to the hydrologic disturbance gradient (Table VI). This result may indicate that as high- and annual-flow variability are altered, invertebrate species with life-history and behavioural constraints that rely on the timing and predictability of annual flow processes for emergence and reproduction may become less abundant. For example, life cycle processes of more sensitive taxa (those taxa with a less plastic life histories) like *Isonychia* sp., *Ephemerella* sp., and *Leuctra* sp. may be affected by alterations in annual flow variability, whereas aquatic macroinvertebrate taxa that are more tolerant to changes in natural stream flow variability reflect an increase in abundance along the disturbance gradient (e.g. *Hydropsyche* sp and *Gammarus* sp.; Table II). A similar pattern was also found for some bivariate flow–ecology response relations using assemblage metrics (Table VIII). Many of these metrics indicated that changes in flow variability appeared to have a direct effect on assemblage structure and function. For example, as variability in maximum monthly flows (MA30) increased (i.e. an indicator of stream flashiness), the total richness of tolerant taxa (RichTOL) increased. Similarly, as the frequency of high flows (FH9) increased, the richness of tolerant taxa and percent of total richness of non-chironomid dipterans and non-insects (ODIPNIRp) increased. In general, the taxa that comprise these two metrics tend to be more tolerant to changes in monthly and annual flow variability. Conversely, the richness of intolerant EPT taxa (EPTR) decreased with increasing frequency of high flows. High-flow stability is likely essential in maintaining and supporting the life-history requirements of many stream species, especially those taxa that rely on the timing and predictability of annual flow processes for emergence and reproduction. A reduction in the richness of EPT taxa was also found with increasing number of low-flow events (FL1) indicating that as the periodicity of low-flow events increases there may be a decline in sensitive taxa.

Establishing empirically based regional flow–ecology response relations (e.g. Table VIII) provides insight into understanding those aspects of flow that help to maintain stream biotic integrity and can be used by managers for targeting the maintenance, restoration or remediation of natural streamflow processes. Generally, all bivariate ecological response relations developed during this study represented a linear response (e.g. Figure 5); no discrete 'thresholds' were found. The high amount of implicit variability for hydrological and ecological data at the regional level, however, may have obscured our ability to identify distinct non-linear or threshold-type response relations. This is clearly a limitation of studies such as this one that attempts to derive relations at such a broad regional level. Improvement in the fit between flow variables and assemblage metrics would likely require a smaller study area, a less heterogeneous setting, or a larger number of sites having both aquatic macroinvertebrates and long-term hydrological data (see Poff *et al*., 2009). Incorporating multiple aquatic assemblages, particularly fish, may also be useful due to their longer life span and greater sensitivity to physical disturbances and habitat change. Other limitations of this paper include our inability to specifically account for the effects of ongoing human-induced impacts on water availability (e.g. interbasin transfers, groundwater withdrawals) that reduce the amount of water in the streams and likely accentuate the high and low flows at specific times of the year. These types of hydrologic alterations no doubt have a cumulative effect on the aquatic assemblage, however, their impact is extremely difficult to separate from variability in yearly precipitation and concomitant anthropogenic affects because the records for such data are often scarce, lacking, or unregulated for movement of water or direct withdrawals under a specific amount. This is especially true in some transitional areas in the northeast where agricultural withdrawals are not regulated as long as they fall below a preset withdrawal rate.

Although hydrologic disturbance is an inherent feature of urbanizing lotic systems across our study area, our results indicate the magnitude and predictability of low and high flows may be altered to a degree that many taxa cannot tolerate (see Table II). Aquatic macroinvertebrates appear to be resilient to stress associated with short-term reductions in streamflow (Miller *et al*., 2007; James *et al*., 2008) and discrete high-flow events (Suren and Jowett, 2006) possibly by utilizing the hyporheic zone as refugia (Dewson *et al*., 2007). However, our results indicate that urban-related landscape change in the Northeastern US can push the hydroecological system beyond the assemblage's capacity for recovery. This has important management implications for future growth and development in upland streams. If the goal is to protect healthy aquatic assemblages while simultaneously allowing for further development, the duration of high flows and even more so, the magnitude of low flows, will need to be promoted to ensure continued success of important, and in some cases, threatened and endangered aquatic species. Dampening the effect of urban runoff through greater infiltration is one way to offset high-flow magnitude. Best management approaches that allow more water to infiltrate and slowly release precipitation will likely reduce the intensity and duration of floods and flood peaks, respectively. This can often be accomplished with minimal efforts designed to protect groundwater recharge areas, reduce the extent of impervious surface cover in the watershed, and protect and enhance the amount of forested riparian buffers, especially in those areas where buffers are not directly bypassed by existing storm drains. Appropriately designed water detention basins and biofiltration systems including grassed waterways and filter strips are some examples that have been suggested as measures to reduce surface runoff and increase groundwater infiltration (e.g. Walsh *et al*., 2005).

Aquatic invertebrate assemblages represent or reflect the cumulative effects of hydrologic changes over time (Poff *et al*., 1997), therefore, long-term studies are necessary to evaluate whether such hydrologic events result in a negative cumulative impact on aquatic assemblages, especially when the periodicity of such events often increases with increasing anthropogenic disturbance such as with urbanization and climate change (e.g. Rogers and McCarty, 2000). Such long-term studies, however, are often impractical and difficult to implement under typical funding cycles. Although rare, some exceptions do exist (see Daufresne *et al*., 2003; Humphries *et al*., 2008). The spatially distributed sampling network evaluated in this study, however, was chosen to evaluate changes in hydrologic processes through time (i.e. substitute space for time) and represents a viable method of examining possible long-term effects of hydrologic alteration in a relatively short timeframe. The findings of this study indicate that ongoing urbanization and associated hydrologic alteration may result in significant changes in stream biologic integrity in upland northeastern streams. The USGS continues to monitor a subset of the sites assessed in this study on an annual or biannual basis as part of NAWQA's ecological trends network. Many of these sites have been studied since 1991. These data will be highly valuable to compare against the patterns and interpretations generated when using spatial variation as a surrogate for temporal variation. It will also be valuable to document the trajectory of hydrologic and biological responses under different land use change scenarios and starting points. We were able to quantify ecological and hydrologic responses to a disturbance gradient across a broad regional area while simultaneously accounting for natural variability in hydrologic fluctuation and reducing the effects of some human-induced hydrologic alterations (dams, impoundments, and so on). This study indicates that continued monitoring of biological and hydrologic conditions in streams will prove valuable in being able to document patterns of change over time at hydrologically transitional sites in the Northeastern US and elsewhere and underscores the need for state and provincial resource agencies to fully account for changes in water use.

A recent multi-authored paper by Poff *et al*. (2009) has been instrumental in outlining a unified framework for developing regional environmental flow standards called the Ecological Limits of Hydrologic Alteration (ELOHA). ELOHA builds directly upon the work of Arthington *et al*. (2006) who challenged water scientists to establish and validate thresholds for flow measures using empirical biological data from natural or 'reference' streams and flow-altered streams. The authors suggest that flow–ecological response relations should be developed for a suite of ecological metrics across a gradient from reference flow regimes to modified flow regimes, as was done in this study. ELOHA, however, is designed to support comprehensive regional flow management and strives to synthesize available scientific information into ecologically based and socially acceptable goals and standards for management of environmental flows. A number of key steps are outlined to help environmental flow practitioners develop relations between flow alteration and ecological response. These include (1) building a sound hydrologic foundation of baseline hydrographs for ungaged streams using a flow modelling tool (e.g. Kennen *et al*., 2008); (2) employing a set of ecologically relevant flow attributes to classify streams into distinctive flow regime types (e.g. Olden and Poff, 2003; Kennen *et al*., 2007; Armstrong *et al*., 2008; Kennard *et al*., 2009); determining the deviation of current-condition flows from baseline-condition flows (e.g. Esralew *et al*., 2008); and (4) developing flow–ecological response relations. The approach presented in this paper is highly consistent with ELOHA and directly incorporates most of the major steps. The final step outlined in ELOHA of directly establishing flow–ecology response relations is accomplished at the regional level by using a single class of upland streams that have directly overlapping ambient aquatic assemblage data and are located at or near a USGS continuous record gaging station (in some cases, a surrogate station was used). These flow–ecology response relations can be further used to enhance the utility of flow management strategies by providing stream-type specific empirical results to better guide the implementation of remediation efforts. In addition, these empirical relations can be used to better guide the development of state environmental flow programs whether they are descriptive or based on ecologically relevant flow measures such as the HIP (Kennen *et al*., 2007) or the Indicators of Hydrologic Alteration (Richter *et al*., 1997). Ultimately, such relations will better inform water resource managers, planners, and policy makers on the best suite of hydrologic indices to use for setting environmental flow standards at the state and regional levels.

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