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A MULTITAXONOMIC APPROACH TO UNDERSTANDING LOCAL- VERSUS WATERSHED-SCALE INFLUENCES ON STREAM BIOTA IN THE LAKE CHAMPLAIN BASIN, VERMONT, USA

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ABSTRACT

Twenty-one stream reaches in northwestern Vermont were surveyed to assess the relative influence of local- and watershed-scale variables on stream biotic assemblages including fish, aquatic macroinvertebrates and birds. Data were collected during the summers of 2003 and 2004 and included quantitative and qualitative geomorphic and habitat assessments (local-scale) and land-use characterization and modelled annual flow and sediment loading (watershed-scale). Biotic assemblages were surveyed to capture characteristics related to abundance, diversity and composition. Principal components analysis (PCA) was used to generate sets of factors representing unique scenarios of geophysical data derived from various spatial extents within the watershed. These factors were then used as the independent variables in multiple regression models using the biotic data as the dependent variables. Forty significant models were built from the combination of the eight scenarios and 11 dependent variables. Fish assemblage diversity and composition were influenced by a combination of local-scale and watershed-scale variables; however, the qualitative local data were more predictive than the quantitative data. Local-scale data and sediment (model-derived) were important factors in building significant macroinvertebrate models. Bird abundance and species richness were best predicted using local geomorphic characteristics and the qualitative local data. Our results reinforce the concept that whereas both local- and watershed-scale variables affect stream biota, their relative influence depends upon the individual ecology of each taxon. In order to address these issues, comprehensive watershed management, restoration and conservation plans would benefit from assessments at multiple scales and from geomorphological, watershed and multitaxonomic perspectives. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: stream geomorphology; fish; macroinvertebrates; birds; watershed condition

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INTRODUCTION

Watershed management and protection and the restoration of aquatic ecosystem health have been identified as national priorities. Defining aquatic health, condition and integrity have often been controversial because these measures are difficult to quantify and compare (Amir and Hyman, 1993; Frissell *et al*., 2001). Aquatic macroinvertebrates (Karr and Dudley, 1981; Plafkin *et al*., 1989; Resh *et al*., 1996; Barbour *et al*., 1999) and fish (Karr, 1981) have been widely used to identify impaired waters. However, the relative impact of local- versus watershed-level stressors has remained elusive, although an increasing number of studies have begun to address the issue (Schlosser, 1982; Roth *et al*., 1996; Richards *et al*., 1997; Johnson *et al*., 2007; Sullivan *et al*., 2007; Walsh *et al*., 2007; 2009; Pinto *et al*., 2009; Walters *et al*., 2009). Developing sound management programs to address watershed and stream condition requires an understanding of the relative influences of factors at multiple spatial scales and how their potential interaction affects multiple taxa associated with these ecosystems.

Studies have shown how watershed-scale characteristics, including land use and land-use change, affect stream geomorphology (Booth, 1990; Pizzuto *et al*., 2000; Booth *et al*., 2002; Cianfrani *et al*., 2006), fish (Allan and Johnson, 1997; Wiley *et al*., 1997; Sutherland *et al*., 2002; Argent and Carline, 2004; Horwitz *et al*., 2008) and macroinvertebrate communities (Dovciak and Perry, 2002; Roy *et al*., 2003; Walsh *et al*., 2007; Helms *et al*., 2009; Walters *et al*., 2009). Hynes (1975) argued that the 'valley rules the stream' and that watershed characteristics ultimately govern in-stream characteristics. Similarly, landscape-level influences are reflected in the River Continuum Concept (Vannote *et al*., 1980) and more recently in the Networks Dynamic

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Hypothesis (Benda *et al*., 2004) and the Land Cover Cascade (Burcher *et al*., 2007). However, studies have also shown that fish and macroinvertebrates are affected by stream characteristics at the local- (e.g. site or reach) scale (Huryn and Wallace, 1987; Nerbonne and Vondracek, 2001; Sawyer *et al*., 2004; Walters *et al*., 2009). Recent work has shown that stream-riparian bird communities reflect stream habitat characteristics across the riverine landscape (Collier and Wakelin, 1996; Bryce *et al*., 2002; Inman *et al*., 2002; Buckton and Ormerod, 2003; Sullivan *et al*., 2006a; Sullivan *et al*., 2007). However, studies that simultaneously consider multiple taxa and multiple spatial scales are rare, yet represent an important step in understanding the relative influences of local- versus watershed-scale variables on stream biological assemblages. The information derived from such studies is critical both for purely scientific outcomes as well as for the development of comprehensive watershed and stream management, protection and restoration plans. Furthermore, understanding the relative influences across spatial scales would aid in developing time and cost-efficient sampling strategies by identifying the predominant variables impacting stream ecosystem health.

In this study, we used two types of local-scale data (quantitative geomorphic assessments and qualitative geomorphic and habitat surveys) and two types of watershed-scale data (land use and model-derived flow, sediment and nutrient data) to explore their relative influences on fish, aquatic macroinvertebrate and riverine bird assemblages. These taxa, although all tied to the stream ecosystem, rely on different habitat and food resources, and select and interact with their habitats in different ways and at different spatial scales. The goal of the study was to identify the most important factors in predicting assemblage characteristics relating to abundance, diversity and composition of each taxonomic group by considering a suite of scenarios representing local-scale to watershed-scale variables.

METHODS

Study area

We studied 21 3rd through 5th order (based on USGS 1:24 000 maps) stream reaches located in the Lake Champlain Basin in northwestern Vermont (Figure 1). The stream reach watersheds were independent and ranged in size from 16 to 509 km^2 with an average size of about 118 km^2. Streams were dominated by Warm Water Moderate Gradient Streams and Medium-size High Gradient Streams; no Small High Gradient Streams (e.g. coldwater) were

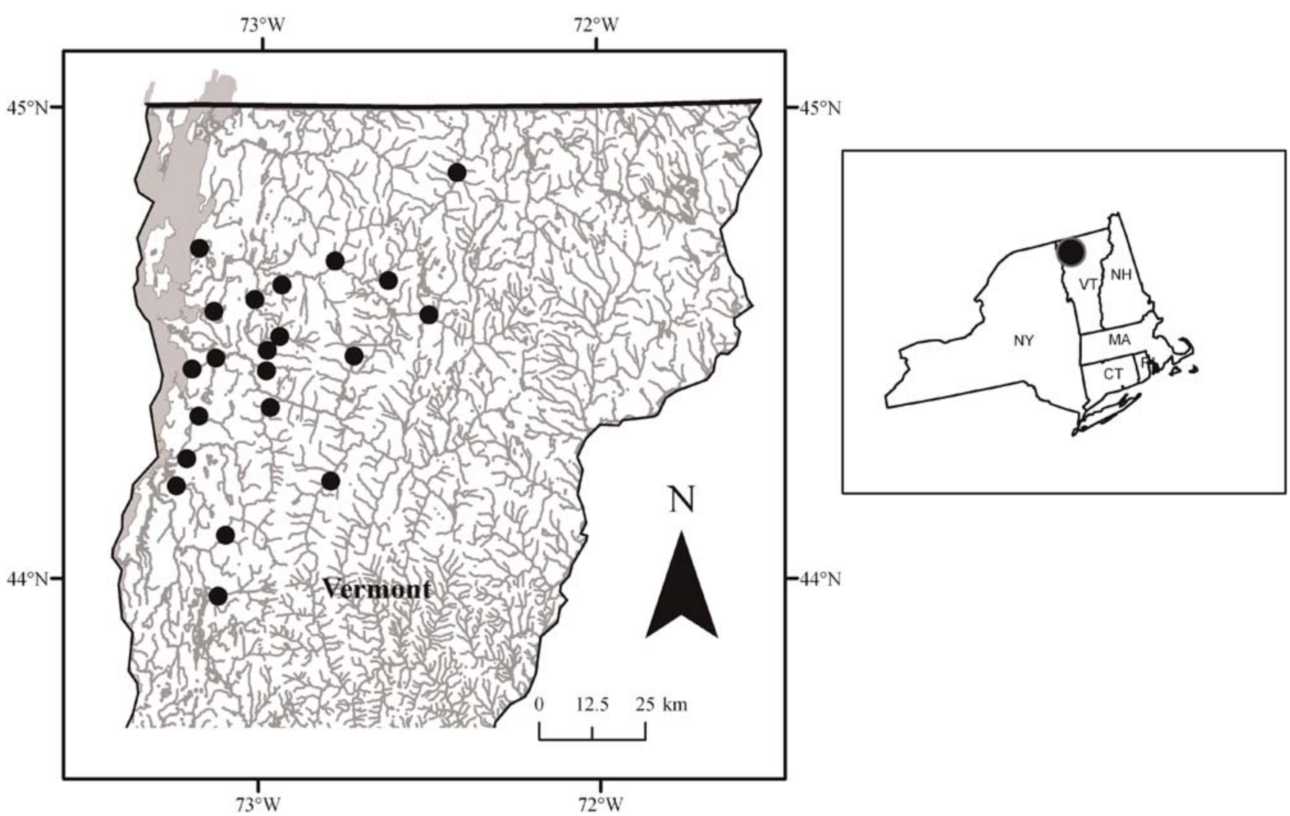

Figure 1. Map of New England showing the location of stream reaches in the Lake Champlain Basin, Vermont, USA.

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included in the study (VTDEC, 2004). Three major physiographic regions dominate the Lake Champlain Basin including the Champlain Lowland, the Vermont Piedmont and the Green Mountains. All watersheds were typical for mixed-use glaciated regions. Watershed land use varied, but the Lake Champlain Basin in general contains mostly forest (64%) and agriculture (16%) with lesser amounts of open water (10%), urban area (6%) and wetlands (4%) (LCBP, 2004).

Quantitative geomorphic assessments

We collected quantitative local-scale geomorphic data during the summers of 2003 and 2004 following procedures detailed in Cianfrani *et al*. (2004). A laser level was used to survey longitudinal and cross-sectional profiles for each stream reach. Stream reach lengths were determined on-site and were at least 10–20 bankfull widths in length (Harrelson *et al*., 1994; Kondolf and Micheli, 1995). Longitudinal profiles were surveyed for the entire length of the stream reach to generate channel slope. Four to six detailed cross-sections were surveyed for each stream reach. Measurements of bankfull cross-sectional area, bankfull width, mean and maximum bankfull depth and bankfull width/depth ratio for the cross-sections were averaged for each stream reach.

Qualitative geomorphic and habitat assessments

The State of Vermont has developed rapid geomorphic and habitat assessments as part of a fluvial geomorphic approach to river and watershed management (VTDEC, 2001, 2002a, 2002b). We used these rapid assessment protocols to assess the geomorphic and habitat condition of each of our 21 stream reaches (VTDEC, 2002a). The rapid geomorphic assessment (RGA) is designed to identify the major mode of adjustment for each stream reach. Each reach is given a score from 1 to 20 (1 = poor, 20 = reference) in four categories: (1) degradation (incision); (2) aggradation; (3) over-widening and (4) change in planform (VTDEC, 2002a). Degrading streams exhibited erosion of bed material resulting in stream incision or lowering of the bed elevation. Aggrading streams exhibited the opposite qualities—increases in the bed elevation due to increased deposition of bed material. Channel widening occurred in confined streams where stream flows became erosive and caused bank failure. Changes in planform occurred as streams adjusted from straightening or other channel modification or in response to aggradation or degradation as the channel attempted to establish a new equilibrium. To obtain the final RGA score, all categories were summed and divided by 80 (the total possible) and then subtracted from 1 to give the deviation from reference (RGA_{dev}). The purpose of the RGA was to determine the overall physical condition of the stream and identify the dominant adjustment process (stage of channel evolution) occurring within the stream (Schumm, 1977).

The rapid habitat assessment (RHA) is derived from the USEPA's Rapid Bioassessment Protocols (Plafkin *et al*., 1989; Barbour *et al*., 1999) and involved scoring each stream reach on a scale of 1–20 in 10 different categories for a total maximum score of 200. Habitat characteristics evaluated include the following: epifaunal substrate and available in-stream cover; degree of embeddedness; representation of a heterogeneous mixture of velocity and depth regimes; amount of sediment deposition; status of channel flow (e.g., wetted width); degree of channel alteration; frequency of riffles; bank stability (e.g., bank erosion, undercut banks); vegetative protection and the width of the riparian vegetative zone. The final score provided an indication of how well the stream reach supported aquatic life (specifically fish and macroinvertebrates) based on the physical habitat present. The RHA did not, however, give any indication of water quality (other than sediment).

Land use

We used the Multi-Resolution Land Characteristics Consortium (MRLC) land-cover data layer based on 1990–1992 Landsat Thematic Mapper (TM) data (Vogelman *et al*., 1998) within a geographic information system (GIS) to calculate land-use area percentages for each watershed. Detailed land-cover categories were summed to produce four major land-use classes: agriculture; forest; urban and other. The 'other' category contained mostly open water and was not used in our analysis.

Watershed modelling

To obtain an understanding of the relative differences in flow, sediment and nutrient loadings among the stream reach watersheds, we used a continuous hydrologic model, the Soil and Water Assessment Tool (SWAT) (Arnold *et al*., 1998). SWAT was developed by the United States Department of Agriculture—Agricultural Research Station (USDA-ARS) and has been described extensively in other studies (Srinivasan and Arnold, 1994; Arnold and Allen, 1996; Arnold *et al*., 1998; Eckhardt and Arnold, 2001; Neitsch *et al*., 2001; Santhi *et al*., 2001; Fontaine *et al*., 2002; Van Liew and Garbrecht, 2003).

SWAT was run using an ArcView GIS (ESRI, Redland, CA) interface (DiLuzio *et al*., 2002). GIS data layers required by the SWAT model were obtained from the Vermont Center for Geographic Information (www.vcgi.org) and included: (1) a digital elevation model (DEM) with 30 m pixel size; (2) MRLC Landsat TM land-use grid (30 m pixel size) and (3) soils data from the STATSGO soil database (USDA NRCS). Stream reach watershed outlet points were determined with a global positioning system (GPS—Geoexplorer

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XT, Trimble, Sunnyvale, CA) in the field and then imported into a GIS.

Basic calibration of the SWAT model was performed following procedures outlined by Neitsch *et al*. (2002). We calibrated SWAT for flow only as sediment and nutrient monitoring data were not available. The calibration and validation watershed (Lewis Creek) was centrally located in our study region (northwestern Vermont), contained one of our stream reaches and is gauged at the outlet. Specific parameters were recommended for adjustment in the SWAT calibration documentation (Neitsch *et al*., 2002) and other relevant studies (Fontaine *et al*., 2002). Parameters, their original values and final calibrated values are listed in Table I. Volume (mm over entire watershed) and flow (cm) were calibrated first on an annual average basis, then on an average monthly basis. Model prediction was evaluated using the following methods: relative error (RE%); root mean square error (RMSE); normalized objective function (NOF); coefficient of determination (R^2) and Nash-Sutcliffe simulation efficiency (E) (Nash and Sutcliffe, 1970; Pennell *et al*., 1990; Van Liew and Garbrecht, 2003). Heddon (1986) recommends the NOF to be within an order of magnitude for screening applications and within a factor of two for site-specific applications. Hession *et al*. (1994) applied this criterion for evaluating the applicability of flow models for screening or site-specific applications. Calibration targets were RE within 15%, $R^2 > 0.60$ and $E > 0.5$ (Santhi *et al*., 2001).

The model was validated by holding all parameters to the values determined during calibration. The model was run using the same watershed (Lewis Creek), but with different years of precipitation and flow (1993–1994).

Biological assemblage data

Fish. Using bag seines (1.22 m × 12.19 m with 3.175 mm mesh weighted with sinkers), we collected fish following a two-pass depletion method (Zippin, 1958) at three to four locations that reflected the flow composition (e.g., pools, riffles, runs) of the reach at large (VTDEC, 2004). The sampling effort at each reach approximated 15% of its wetted area. All streams were wadeable and were successfully sampled by the seine across a range of depths. All fish captured were enumerated. From each sampling location of each reach, we identified a subsample of 150 fish (see Sullivan *et al*., 2006b) and weighed (g), measured (tail length, mm) and identified each of these individuals to species. Young-of-year fish were excluded from the analysis. After fish were surveyed, they were released into the stream at the site of capture.

For each reach, we pooled the data from each of the subsampling locations to calculate statistics relating to fish assemblages. We used species richness (S) (the number of species) and Simpson's index ($1/D$) (a multifactor dominance index) (Simpson, 1949) to represent fish assemblage diversity at each reach. Total fish assemblage biomass ($\mathrm{g\,m^{-3}}$) for each stream reach was estimated using the total number of fish caught per cubic meter and the mean weight of the 150 fish subsampled. In addition, we calculated the Vermont Mixed Waters Index of Biotic Integrity (MWIBI) (VTDEC, 2004), which is a regional adaptation of the Index of Biotic Integrity (Karr, 1981) and represents both assemblage composition and condition. The MWIBI is a composite index with scores below 25 considered poor and those above 33 considered good (VTDEC, 2004).

Aquatic macroinvertebrates. We sampled macroinvertebrates at a subset of 16 stream reaches during early July through August 2003 and 2004, waiting at least 48 h after any significant rainfall event. We collected subsamples at six regularly-spaced intervals along the length of each stream reach using a 500 μm mesh Surber sampler, disturbing the substrate for 90 s intervals per collection effort. In order to

Table I. Inputs used in SWAT model calibration

Variable	Description	Original value	Calibrated value
CN2	Runoff curve number	Default	−10%
SFTMP	Snowfall temp. Mean air temp. at which precip is equally likely to be rain as snow/freezing rain.	1.0°C	1.0°C
SMTMP	Snow melt base temp.	0.5°C	0°C
SMFMX	Melt factor for snow on 21 June	4.5 mm °C^{-1}	6 mm °C^{-1}
SMFMN	Melt factor for snow on 21 December	4.5 mm °C^{-1}	4.5 mm °C^{-1}
TIMP	Snow pack temp. lag factor	1	0.5
SNOCOVMX	Min. snow water content that corresponds to 100% snow cover, SNO_{100}	1 mm	100 mm
SNOCOVMN	Fraction of snow volume represented by SNOCOVMX that corresponds to 50% snow cover	0.5	0.5
RCN	Conc. Of Nitrogen in rainfall ($\mathrm{mg\,N\,L^{-1}}$)	1	1
SURLAG	Surface runoff lag coefficient	4	4

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collect a representative sample of habitat types in the stream channel, we alternated the position of the sampler at each subsample location (i.e., towards mid-channel, towards the left bank or towards the right bank). We preserved all six subsamples from each reach in 70% ethanol and later enumerated and identified all insects in the laboratory, pooling the subsamples to obtain reach-level estimates of the aquatic macroinvertebrates. We used three macroinvertebrate metrics as biological endpoints: (1) per cent insects in the orders Ephemeroptera, Plecoptera and Tricoptera (%EPT); (2) per cent insects in the genus *Chironomidae* (%Chiros) and (3) the mean density of insects per reach (Density, No. 900 cm^{-2}).

Birds. Following Sullivan *et al*. (2007), we surveyed bird assemblages using a modified version of Nichols *et al*.'s (2000) double observer method. Surveys were conducted from mid-May through mid-June 2003 and 2004 during which time we conducted two surveys of each stream reach, at least 10 days apart, with the first occurring in the morning (sunrise to 4 h after sunrise) and the second in the evening (3 h before dusk to dusk) (USFWS, 1990). At each reach, we established fixed-width line transects (250 m parallel transects, established on both sides of the stream at the bankfull width) along which surveys were conducted. We treated groups of birds as a single observation for purposes of distance and location and immature birds were not included in the count.

After the surveys were completed, we removed migrants and upland bird species from the dataset and grouped the remaining birds into: (1) River Corridor Birds (RC)—all species that commonly use river-riparian ecosystems because of habitat and/or food resources and (2) Piscivores (PISC)—species whose primary food source is fish. We calculated abundance (A_{RC}, A_{PISC}) and species richness (S_{RC}, S_{PISC}) for each stream reach.

Numerical and statistical analysis

We completed all statistical analyses using JMP 5.0.1.2 Statistical Discovery Software (SAS Institute, Inc., Cary, NC). We tested variables for normality using the Shapiro–Wilk test and transformed them (ln x or x^2) when necessary (McGarigal *et al*., 2000; Afifi *et al*., 2004). All variables are listed in Table II. We reduced local, rapid assessment, land-use and watershed modelling variables to factors using principal components analysis (PCA) with a varimax rotation (McGarigal *et al*., 2000; Afifi *et al*., 2004). We used PCA with factor rotation to reduce the number of variables for use in multiple regression analysis with the biological data. For this study, the number of principal components (PC) axes explaining at least 80% of the variance were retained and used in the varimax rotation to generate uncorrelated factors (McGarigal *et al*., 2000).

Eight scenarios were developed in the final regression matrix used to evaluate the relative importance of local, rapid assessment, land-use and watershed modelling variables on the 11 biotic variables. Six sets of factors which represented different combinations of variable categories were generated from the PCA analysis and used as scenarios. Individually, land-use data and RGA_{dev} were also used as two separate scenarios. For example, in evaluating the importance of local geomorphic variables, a set of factors was generated from only the seven local variables. In evaluating the importance of the combination of local, land-use and watershed modelling variables, a new set of factors created from all 18 original variables was generated. For each scenario, stepwise multiple regression was used to select the factors most useful in predicting the biological variable. Simple regression was used to test the biological data with the RGA_{dev} scenario. All data were tested at the $\alpha = 0.05$ level (Afifi *et al*., 2004).

RESULTS

Geomorphic, land-use and habitat data

All stream reach geomorphic data are reported in Table III. Watershed size ranged from 16 to 509 km^2. Channel slope was fairly low with only four sites greater than 1%. Depths were also fairly shallow with a maximum bankfull depth of 1.9 m for all sites. While most stream reach watersheds were dominated by forest land cover, four watersheds had greater than 10% urban land, while 11 had greater than 10% agricultural land (Table IV). The stream reaches showed a range of RGA_{dev} and RHA scores (Table IV). High RGA_{dev} scores indicate significant channel adjustment. Eight sites scored in 'fair' condition, 12 sites in 'good' condition and only one site in 'reference' condition. High RHA scores indicate good quality physical habitat. Twelve sites scored between 130 and 169 placing them in the 'good' category. Only one site was considered 'reference'.

Watershed modelling

Model calibration resulted in a slight improvement in the predictive capability of the model (Table V). Pre-calibrated, calibrated and validated volumes all met the $\leq$15% RE criterion for total annual average volume (mm). Using Heddon's (1986) criterion, the NOF should be within an order of magnitude for screening applications and within a factor of two for site specific applications. Model performance at the monthly level improved after calibration so that values for both average annual and monthly volume met the site-specific criterion (NOF < 1). Monthly

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Table II. Stream reach variables used in data analyses

Variable	Description	Units	Transformation
Local			
A_D	Drainage area upstream of stream reach	km^2	ln
S_{Ch}	Channel slope	$m\,m^{-1}$	ln
A_{BF}	Bankfull cross-sectional area	m^2	ln
W_{BF}	Bankfull width	m	ln
D_{MEAN}	Mean bankfull depth	m	ln
D_{MAX}	Maximum bankfull depth	m	ln
WD_{BF}	Bankfull width/depth ratio	$m\,m^{-1}$	ln
Qualitative Assessment			
RGA_{dev}	Deviation from reference rapid geomorphic score	0–1.00	
RHA	Rapid habitat assessment score	0–200	
Land use			
%Urb	% urban land in the watershed	%	ln
%Ag	% agricultural land in the watershed	%	ln
%For	% forested land in the watershed	%	x^2
Watershed Modeling			
SURQ	Surface runoff contribution to streamflow	mm	
GW_Q	Groundwater contribution to streamflow	mm	
ORGN	Organic N yield	$kg\,N\,ha^{-1}$	
ORGP	Organic P yield. Organic P transported with sediment	$kg\,P\,ha^{-1}$	
SYLD	Sediment yield. Sediment from watershed transported to reach	metric tons ha^{-1}	ln
NSURQ	NO3 in surface runoff. Nitrate transported by surface runoff	$kg\,N\,ha^{-1}$	ln
SOLP	Soluble P yield. P that is transported by surface runoff	$kg\,P\,ha^{-1}$	ln
SEDP	Mineral P yield. Mineral P attached to sediment that is transported by surface runoff	$kg\,P\,ha^{-1}$	ln
Fish			
S_{Fish}	Species richness (number of species)	No. of species	
$1/D$	Simpson's index	Unitless	
Biomass	Fish biomass	$g\,m^{-3}$	
VT MWIBI	Vermont mixed-waters index of biotic integrity	Score (17–33)	
Macroinvertebrates			
%EPT	*% Ephemoptera, Plecoptera, and Tricoptera*	%	
%Chiros	*% Chironomidae*	%	
Density	Total density	No. 900 cm^{-2}	ln
Birds			
A_{RC}	River corridor bird abundance	No. of individuals	
S_{RC}	River corridor bird species richness	No. of species	
A_{PISC}	Piscivore abundance	No. of individuals	
S_{PISC}	Piscivore species richness	No. of species	

R^2 approximately doubled after calibration of the model while the monthly E value improved but did not reach the criterion of 0.5. However, since the modelling results were used to assess relative differences between stream reach watersheds, the output was deemed adequate.

Biological assemblage data

Biological data among stream reaches varied significantly (Table VI). Data are reported for the 21 stream reaches sampled for fish and bird assemblages and the 16 stream reaches sampled for aquatic macroinvertebrates.

Numerical and statistical analysis

PCA (with varimax rotation). The number of factors retained for each set of variables varied from two to five (Table VII). Set no. 1 contained land-use and modelling variables—data that did not require site visits. Factor 1 loaded heavily for land use, Factor 2 for sediment and Factor 3 for surface runoff. Set no. 2 included local geomorphic data, watershed land-use variables and variables derived from the modelling (flow, sediment and nutrients). Four factors were retained explaining 87% of the variance. Factor 1 loaded most highly for land-use characteristics as well as the WD_{BF} ratio. Variables associated with sediment

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Table III. Geomorphic stream reach characteristics

Site no.	Site name	Drainage area (km^2)†	Channel slope (%)	Bankfull cross-sectional area (m^2)	Bankfull width (m)	Mean bankfull depth (m)	Max bankfull depth (m)	Bankfull width/depth ratio
1	Beaver Brook	30	0.96	7.2	14.5	0.5	0.9	29.1
2	Rogers Brook	17	0.96	2.6	6.7	0.4	0.5	17.6
3	Browns River	53	0.77	7.1	19.8	0.4	0.6	54.8
4	Lee River	35	1.05	4.5	10.8	0.4	0.6	26.2
5	Malletts Creek	44	0.66	5.5	10.8	0.5	0.8	21.1
6	Huntington River	161	0.66	14.3	22.0	0.7	1.0	33.7
7	Allen Brook	28	0.49	3.7	6.6	0.6	0.8	11.9
8	Mill Brook	33	0.98	4.5	12.2	0.4	0.6	32.7
9	LaPlatte River	81	0.50	7.6	13.8	0.5	0.9	25.1
10	Lewis Creek	196	0.70	15.9	24.5	0.6	0.9	37.8
11	Little Otter Creek	148	0.31	7.4	17.1	0.4	0.7	39.8
12	New Haven River	220	0.51	13.7	20.9	0.7	1.0	31.9
13	Mississiquoi River	174	0.47	10.5	25.8	0.4	0.7	63.4
14	Lamoille River	509	0.30	24.2	35.2	0.7	1.2	51.1
15	North Branch Lamoille River	150	0.42	14.8	26.3	0.6	1.0	46.9
16	Gihon River	139	0.55	16.3	23.7	0.7	1.1	34.3
17	West Branch Waterbury River	59	1.18	8.8	14.6	0.6	1.0	24.1
18	Mad River	240	0.46	39.6	33.2	1.2	1.9	27.8
19	Stone Bridge Brook	23	1.41	3.4	7.8	0.4	0.6	18.1
20	Potash Brook	16	1.05	3.9	8.3	0.5	0.6	17.7
21	Middlebury River	121	0.51	11.9	23.9	0.5	0.8	47.9
	Mean	117.9	0.60	10.8	18.0	0.6	0.9	33.0
	Median	80.9	0.44	7.6	17.1	0.5	0.8	31.9
	Standard deviation	115.3	0.50	8.6	8.4	0.2	0.3	13.7

†Upstream from bottom of reach.

Table IV. RGA_{dev}, RHA and land-use percentages for stream reaches

Site no.	RGA_{dev}	RHA	%Urban	%Agriculture	%Forest
1	0.29	155	10	7	78
2	0.29	156	6	19	67
3	0.44	114	9	6	78
4	0.41	133	9	6	81
5	0.36	127	12	21	60
6	0.08	161	5	7	83
7	0.60	101	29	32	35
8	0.40	149	8	6	81
9	0.38	128	16	31	45
10	0.16	141	5	24	63
11	0.31	147	6	45	40
12	0.40	104	4	8	83
13	0.34	170	5	8	84
14	0.30	159	5	11	78
15	0.53	94	2	4	85
16	0.26	169	4	7	82
17	0.56	82	3	9	82
18	0.50	116	7	9	82
19	0.25	149	9	21	61
20	0.28	158	51	32	11
21	0.34	160	3	1	90
Mean	0.36	137	10	15	69
Median	0.34	147	6	9	78
Standard deviation	0.13	26	11	12	21

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Table V. Annual and monthly SWAT calibration results for 21 stream reach watersheds. Model evaluation methods: relative error (RE%); root mean square error (RMSE); normalized objective function (NOF); coefficient of determination (R^2); and Nash-Sutcliffe simulation efficiency (E)

Variable	Simulated period of record	Average annual rainfall (mm)	Observed average annual volume (mm)	Simulated average annual volume (mm)	RE (%)	RMSE	NOF	R^2	Monthly E
Pre-Calibration	Annual	928	423	423	−0.12	77.99	0.18	0.63	
1/1/98–31/12/02	Monthly				0.08	33.56	1.02	0.17	−0.11
Calibration	Annual	928	423	487	−15.2	110.45	0.26	0.63	
1/1/98–31/12/02	Monthly				8.11	31.56	0.89	0.33	0.18
Validation	Annual	876	414	411	0.89	109.63	0.28	NA	
1/1/93–31/12/94	Monthly				−1.2	25.42	0.73	0.61	0.6

(sediment yield, nutrients attached to sediment) loaded on Factor 2. Surface runoff and nitrogen in surface runoff loaded on Factor 4. Set no. 3 combined all the variables in the study, land-use, modelling, local geomorphic data, RGA_{dev} and RHA—the most intensive 'in-office' and field-collected data effort. Five factors were retained to explain 89% of the variance. Factor 1 loaded heavily for land use and WD_{BF}, Factor 2 for sediment, Factor 3 for local geomorphic variables, Factor 4 for RGA_{dev} and RHA and Factor 5 for surface runoff. Set no. 4 combined land-use, modelling, RGA_{dev} and RHA variables—data requiring a modest amount of field effort. Four factors were retained to explain 91% of the variance. Factor 1 contained the highest loadings for land use, Factor 2 loaded heavily for sediment variables, Factor 3 for RGA_{dev} and RHA and Factor 4 for surface runoff. Set no. 5 contained variables for both local geomorphic data and RGA_{dev} and RHA—all data that must be collected on site. Three factors were retained explaining 87% of the variance. Factor 1 loaded most highly for channel size variables, Factor 2 for RGA_{dev} and RHA and Factor 3 for bankfull channel depths. Finally, set no. 6 comprised only the local geomorphic data. Two factors were retained to explain 85% of the variance in the original data. Factor 1 contained high loadings for the channel size variables while Factor 2 contained high loadings for depths.

Table VI. Mean, median and standard deviation for biological assemblage data

Variable	Mean	Median	Standard deviation
Fish			
S_{Fish}	8	8	3
$1/D$	3.13	3.17	1.13
Biomass (g m^{-3})	12.1	7.1	14.1
VT MWIBI	24.57	25.00	4.82
Macros			
%EPT	36	30	19
%Chiros	46	48	23
Density (No. 900 m^{-2})	549.1	359.5	468.4
Birds			
A_{RC}	19.7	17.0	11.3
S_{RC}	9	9	3
A_{PISC}	0.9	1.0	1.1
S_{PISC}	0.8	1.0	0.8

Multiple regression. Forty significant models were built using the 11 biological assemblage variables and the eight scenarios of local/watershed variables (Table VIII). Fish assemblage diversity and condition were best predicted when using a combination of local-scale and watershed-scale data (scenarios 4 and 5). However, based on the factors used in the models, local stream geomorphology data only improved the model for fish biomass and the MWIBI but not the diversity measures. The RGA_{dev} and RHA did contribute, however, indicating that qualitative indices of geomorphic and habitat condition surveyed at the local-scale were more useful than the actual quantitative field data. Eleven significant models were built for the macroinvertebrate variables; the greatest number of models was built using a combination of watershed-scale and local-scale (scenario 4). The significant factors in building these models, however, were the local-scale data, RGA_{dev} and RHA and sediment. Significant models were also built using the local-scale and RGA_{dev} and RHA (scenario 6) and the RGA_{dev} (scenario 7). Land use as a variable across scenarios was only significant in building one of the macroinvertebrate models. Whereas land use was a significant contributor to models for the fish measures, it was not a significant factor in the majority of macroinvertebrate models and did not predict species richness or abundance of RC or PISC birds. Bird assemblage richness and abundance were best predicted with local geomorphic characteristics and the RGA_{dev} and RHA.

DISCUSSION

Local-scale

The components used in our study to represent local-scale (i.e. geomorphic data, RGA_{dev} and RHA) contributed in

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Table VII. Results of PCA with varimax rotation. Bolded factor scores load highly on a given factor and were used in the interpretation of the factor. Blanks indicate a variable was not used in the generation of factors for that set

Variables	(1) Land use, modeling			(2) Land use, modeling, local				(3) Land use, modeling, local, RGA/RHA				
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
A_D				0.442	0.076	**−0.848**	0.005	−0.350	−0.025	**0.896**	0.105	−0.021
S_{Ch}				−0.186	−0.252	**0.740**	0.358	0.141	0.233	**−0.753**	0.053	−0.368
A_{BF}				0.439	−0.062	**−0.868**	0.064	−0.363	0.084	**0.902**	0.010	−0.079
W_{BF}				0.635	0.087	**−0.742**	0.075	−0.564	−0.054	**0.797**	0.084	−0.088
D_{MEAN}				−0.055	−0.313	**−0.825**	0.023	0.117	0.311	**0.810**	−0.129	−0.034
D_{MAX}				−0.072	−0.362	**−0.688**	−0.011	0.047	0.297	**0.624**	−0.429	0.052
WD_{BF}				**0.791**	0.307	−0.345	0.074	**−0.747**	−0.267	0.420	0.184	−0.080
RGA_{dev}								−0.063	0.229	−0.040	**−0.910**	0.096
RHA								−0.075	−0.127	−0.080	**0.914**	0.150
%Urb	**0.665**	−0.054	0.526	**−0.646**	0.056	0.346	−0.497	**0.593**	−0.085	−0.402	−0.068	0.512
%Ag	**0.907**	−0.192	0.116	**−0.905**	0.288	−0.083	−0.091	**0.921**	−0.267	0.028	0.023	0.100
%For	**−0.882**	0.234	−0.358	**0.856**	−0.300	−0.120	0.342	**−0.840**	0.302	0.177	0.023	−0.354
SURQ	0.215	−0.128	**0.953**	−0.247	0.134	−0.105	**−0.944**	0.245	−0.133	0.094	0.023	**0.942**
GW_Q	**0.793**	−0.189	0.032	**−0.639**	0.302	0.200	−0.119	**0.656**	−0.206	−0.220	0.353	0.149
ORGN	0.291	**−0.928**	0.120	−0.243	**0.939**	0.013	−0.110	0.255	**−0.927**	−0.002	0.158	0.105
ORGP	0.311	**−0.916**	0.138	−0.266	**0.931**	0.002	−0.127	0.278	**−0.918**	0.008	0.154	0.123
SYLD	0.077	**−0.979**	0.101	−0.035	**0.954**	0.055	−0.103	0.031	**−0.962**	−0.034	0.099	0.099
NSURQ	0.241	−0.114	**0.948**	−0.260	0.123	−0.061	**−0.945**	0.261	−0.112	0.053	0.073	**0.941**
SOLP	**0.834**	−0.280	0.371	**−0.772**	0.378	0.314	−0.371	**0.733**	−0.357	−0.370	−0.101	0.380
SEDP	0.151	**−0.952**	0.047	−0.068	**0.931**	0.203	−0.064	0.057	**−0.930**	−0.182	0.152	0.063
Eigenvalue	3.682	3.801	2.409	4.696	4.337	4.183	2.496	4.324	4.255	4.475	2.162	2.569
% Variance	33.471	34.556	21.901	26.088	24.095	23.241	13.866	21.621	21.276	22.372	10.809	12.843
Cum. Var.	33.471	68.027	89.928	26.088	50.183	73.424	87.290	21.621	42.897	65.269	76.078	88.922
Interpretation	Factor 1	Land use		Factor 1	Land use, WD_{BF}			Factor 1	Land use, WD_{BF}			
	Factor 2	Sediment		Factor 2	Sediment			Factor 2	Sediment			
	Factor 3	Runoff		Factor 3	Local			Factor 3	Local			
				Factor 4	Runoff			Factor 4	RGA/RHA			
								Factor 5	Runoff			

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Table VII. (Continued)

Variables	(4) Land use, modeling, RGA/RHA				(5) Local, RGA/RHA			(6) Local	
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2
A_D					**0.784**	−0.087	0.509	**0.800**	0.483
S_{Ch}					**−0.665**	−0.068	−0.432	**−0.651**	−0.457
A_{BF}					**0.681**	0.017	0.694	**0.683**	0.686
W_{BF}					**0.895**	−0.025	0.384	**0.895**	0.386
D_{MEAN}					0.115	0.080	**0.968**	0.120	**0.947**
D_{MAX}					0.226	0.451	**0.686**	0.146	**0.815**
WD_{BF}					**0.946**	−0.086	−0.250	**0.943**	−0.233
RGA_{dev}	0.032	−0.253	**−0.889**	0.056	−0.445	**0.962**	0.028		
RHA	0.012	0.129	**0.942**	0.117	0.067	**−0.895**	−0.154		
%Urb	**−0.670**	0.079	−0.076	0.514					
%Ag	**−0.912**	0.204	−0.012	0.088					
%For	**0.889**	−0.252	0.044	−0.334					
SURQ	−0.234	0.125	0.029	**0.948**					
GW_Q	**−0.790**	0.122	0.376	0.038					
ORGN	−0.290	**0.918**	0.152	0.110					
ORGP	−0.311	**0.907**	0.147	0.128					
SYLD	−0.075	**0.973**	0.108	0.098					
NSURQ	−0.260	0.104	0.078	**0.944**					
SOLP	**−0.841**	0.310	−0.127	0.347					
SEDP	−0.145	**0.937**	0.164	0.047					
Eigenvalue	3.732	3.819	1.932	2.353	3.288	1.956	2.570	3.250	2.680
% Variance	28.711	29.380	14.862	18.098	36.530	21.733	28.557	46.494	38.254
Cum. Var.	28.711	58.090	72.952	91.051	36.530	58.263	86.820	46.494	84.748
Interpretation	Factor 1	Land Use			Factor 1	Channel size		Factor 1	Channel Size
	Factor 2	Sediment			Factor 2	RGA/RHA		Factor 2	Depth
	Factor 3	RGA/RHA			Factor 3	Depth			
	Factor 4	Runoff							

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Table VIII. Matrix of multiple regression equations generated using factors and biological assemblage data. Factors are listed in the order they entered the regression

	Scenario 1		Scenario 2			Scenario 3			Scenario 4		
	Land use		Land use, modeling			Land use, modeling and local			Land use, modeling, local and RGA/RHA		
	R^2	p	Factors	R^2	p	Factors	R^2	p	Factors	R^2	p
Fish											
Species richness									4,1	0.28	0.051
Simpson's index	0.35	<0.001	1,3	0.43	0.007	1	0.24	0.024	1,4	0.40	0.010
Biomass			2,1	0.43	0.006	2	0.43	0.001	2,4,1	0.55	0.003
VT MWIBI									4,3,5	0.59	0.002
Macros											
%EPT									4,2	0.39	0.041
%Chiros						2	0.28	0.037	4,2	0.48	0.014
Density	0.25	0.050							3,4,2	0.57	0.045
Birds											
A_{RC}			2	0.21	0.037						
S_{RC}						3	0.38	0.003	3	0.37	0.003
A_{PISC}											
S_{PISC}									4,2	0.33	0.027
Variables loading on factors	% Ag		Factor 1	Land use		Factor 1	Land use, WD_{BF}		Factor 1	Land use, WD_{BF}	
			Factor 2	Sediment		Factor 2	Sediment		Factor 2	Sediment	
			Factor 3	Runoff		Factor 3	Local		Factor 3	Local	
						Factor4	Runoff		Factor 4	RGA/RHA	
									Factor 5	Runoff	

	Scenario 5			Scenario 6			Scenario 7		Scenario 8		
	Land use, modeling, and RGA/RHA			Local and RGA/RHA			RGA_{dev}		Local		
	Factors	R^2	p	Factors	R^2	p	R^2	p	Factors	R^2	p
Fish											
Species Richness	3,1	0.32	0.032								
Simpson's Index	1,3,4	0.54	0.004								
Biomass	2,3,1	0.54	0.004	2,3	0.30	0.019	0.27	0.008			
VT MWIBI	3	0.48	0.001	2	0.43	<0.001	0.33	0.003			
Macros											
%EPT				2,1	0.38	0.044	0.29	0.032	1	0.24	0.052
%Chiros	3,2	0.44	0.024	2	0.32	0.022	0.33	0.019			
Density											
Birds											
A_{RC}	2	0.20	0.042						2	0.19	0.031
S_{RC}				1,3,2	0.49	0.002			2,1	0.45	0.001
A_{PISC}				2,1	0.26	0.036					
S_{PISC}	3	0.22	0.031	2,1	0.30	0.019			1	0.16	0.045
Variables loading on factors	Factor 1	Land use, WD_{BF}		Factor 1	Channel size				Factor 1	Channel size	
	Factor 2	Sediment		Factor 2	RGA/RHA				Factor 2	Depth	
	Factor 3	RGA/RHA		Factor 3	Depth						
	Factor 4	Runoff									

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different ways in building regression models. Fish diversity and condition appear to be best predicted by a combination of variables, but at the local-scale, geomorphic and habitat condition, as represented by RGA_{dev} and RHA, were more useful for prediction than the more detailed, quantitative geomorphic data. The factor with dominant RGA_{dev} and RHA influences was significant in building all models, and was most significant in the MWIBI model (Table VIII) where it was the first variable to enter in all significant models, explaining between 33 and 50% of the variance. This finding is consistent with previous analyses of fish assemblages in the Lake Champlain Basin using a larger data set (Sullivan *et al*., 2006b). A previous study using data from these same stream reaches has also shown that fish assemblage diversity varies based on local conditions as defined by geomorphic class (Cianfrani *et al*., 2009). Nerbonne and Vondracek (2001) found riparian land use (incorporated into our RHA; e.g. riparian vegetation extent and composition) to be important in determining in-stream habitat which influenced fish communities in Minnesota streams. Creque *et al*. (2005) found local-scale variables (including depth) explained 12–57% of the variance in fish density in regression models. Walters *et al*. (2009) also found fish to be influenced by local-scale variables. Our finding supports the use of field bioassessment protocols as their predictive power relating to fish assemblages was greater than the detailed geomorphic data collected in this study. We recognize, however, that although we used commonly collected geomorphic metrics at the stream reach scale (e.g. slope, bankfull width and depth, etc.) and attempted to balance spatial resolution between the qualitative and quantitative data, a more intensive data collection effort (e.g. higher density of data points, additional variables), may have shown different relationships with the fish data.

Both local-scale components and model-derived sediment were significant in building models for aquatic macroinvertebrates. Many studies have shown that local geomorphic variables (Richards *et al*., 1997; Dovciak and Perry, 2002) and water chemistry (Sawyer *et al*., 2004) affect macroinvertebrate species composition. Others have found that larger-scale variables, such as ecoregion, are also significant (Mykrä *et al*., 2004). Sullivan *et al*. (2004), doing research in the same study area, found in-stream and riparian habitat condition explained 28% of the variance seen in EPT taxa. In our study, the local geomorphic variables, and RGA_{dev} and RHA (scenario 6) explained 38 and 32% of the variation in %EPT and %Chiros, respectively. Although adding the land-use and modelling data improved the amount of variance explained for all three macroinvertebrate measures, the RGA_{dev} and RHA factor was the first variable to enter for the %EPT and %Chiros, and local geomorphic variables entered first for macroinvertebrate density indicating that these local-scale variables are still the most important. Whereas these models were statistically significant, more than 50% of the variance remains unexplained by local characteristics of the reach. In this study we used only %EPT, %Chiros and density. Furthermore, the sample size for macroinvertebrates was smaller than either of the other groups (16 versus 21 stream reaches). Richards *et al*. (1997), Dovciak and Perry (2002) and Sawyer *et al*. (2004) all used additional indices or species in generating their relationships. Richards *et al*. (1997) indicated that multimetric indices, rather than individual taxa, may be more appropriate to use if the underlying mechanisms affecting habitat and conditions within stream ecosystems are unknown. Therefore, whereas we may have observed stronger relationships between macroinvertebrates and local-scale variables if we had increased our sample size or used multimetric indices, our results may also indicate that macroinvertebrates, in some settings, may not always be the most sensitive taxon in reflecting the physical habitat condition (Sullivan *et al*., 2004; Sullivan and Watzin, 2008). Macroinvertebrates may be more sensitive to smaller, patch-scale dynamics, water quality and/or to changes in energy sources than to relatively coarse estimates of physical structure (Wright and Li, 2002).

The variety of patch habitats that comprise stream ecosystems (e.g., riparian, floodplain, in-stream) provides a rich mosaic of habitats for RC birds. This was reflected in our results: both local-scale geomorphic characteristics as well as geomorphic and habitat conditions were important in the regression models for bird abundance and species richness. Birds commonly associated with river corridors included an array of species representing a host of food preferences, foraging strategies and habitat requirements [e.g., alder flycatchers (*Empidonax alnorum*), grey catbirds (*Dumetella carolinensis*), spotted sandpipers (*Actitis macularia*), tree swallows (*Iridoprocne bicolor*), wood ducks (*Aix sponsa*)]. Among the most prevalent PISC were belted kingfishers (*Ceryle alcyon*), great blue herons (*Ardea herodias*) and common mergansers (*Mergus merganser*). Because of their spatial integration of stream-riparian habitat units, many RC are likely released from the strict reliance on solely in-stream attributes so crucial for macroinvertebrates and fish. Because of this, birds might be expected to select stream reaches based on local-conditions of habitat across the riverine landscape, including aquatic, semi-aquatic and terrestrial (i.e., riparian/upland interface) habitat patches. Stream size is expected to exert influence over both the abundance and number of species, and our findings are consistent with this pattern. On the other hand, PISC likely reflect both local- and watershed-level factors because of their direct link to stream fish productivity. However, our results do not support this, suggesting that some PISC are adaptable in their foraging

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strategies being able to sufficiently complement their diets with other food sources, or that none of our reaches exhibited local-level conditions that were sufficiently poor to reduce the biomass of fish below a critical threshold that would translate to fish-feeding birds.

Watershed-scale

At the watershed-scale, we considered land use, annual average flow and annual average sediment loading. Land use was the most significant variable in predicting fish assemblage diversity and condition. Studies have shown that increased watershed urbanization (Booth and Jackson, 1997; Sovern and Washington, 1997; Sawyer *et al*., 2004) and agricultural land use (Allan *et al*., 1997; Argent and Carline, 2004; Sawyer *et al*., 2004) are often associated with decreased fish assemblage diversity and condition. Argent and Carline (2004) cite row crops as particularly disruptive to stream and habitat conditions due to consistent annual perturbations. In this study, however, we observed an increase in fish assemblage diversity and condition as %Ag increased. Upon further analysis of the land-use patterns within our study watersheds, we noted that %Ag was fairly low (mean = 15%, standard deviation = 12%) and an average of 50% of the agricultural land was hay and pasture and not actively managed row crops. Wang *et al*. (1997), based on work in Wisconsin streams, indicated that fish may not respond to low levels of agriculture and that even at high levels it may be possible to find relatively high fish assemblage condition scores. Stepenuck *et al*. (2002) found the same results when using macroinvertebrates. In our study, land use only contributed significantly in building one regression model for macroinvertebrates and none for birds. While Mykrä *et al*. (2004) found ecoregion to be important, our results are consistent with studies that have found watershed land use to be less important in predicting macroinvertebrate populations than local or water chemistry variables (Richards *et al*., 1997; Sawyer *et al*., 2004). Multiple investigations have shown that birds are sensitive to land-use attributes (Croonquist and Brooks, 1993; Bryce *et al*., 2002; Clear *et al*., 2005). Although we did not observe relationships between bird assemblages and land-use variables, we suspect this in part to be an artifact of resolution, and that we could potentially see relationships with land-use metrics derived at the stream reach scale (e.g. riparian zone land use).

Whereas Sawyer *et al*. (2004) found that fish assemblages responded to suspended sediments in Florida and south-eastern Alabama with a decrease in intolerant species, in this study, sediment loading information was only significant in building models for fish biomass. This may, however, be an indication that annual average sediment data are too coarse to provide meaningful information as compared to fine-scale in-stream measurements. The results may also be confounded by differing responses of species to sediment loading as reported by Sullivan and Watzin (2009). Similarly, for macroinvertebrates, other studies have shown a negative correlation between in-stream sediment and sensitive species (e.g. Roy *et al*., 2003). The sediment factor was significant in building five of the 11 macroinvertebrate regression models. Sediment also loaded significantly in three of the bird regressions, one for A_{RC} and two for S_{PISC}. Increased sediment loads may be precipitating widening channels and bank failure, thereby reducing overbank vegetation and in-stream shading. The reduction in vegetation along the active channel boundary may account for reductions in the abundance of many RC, particularly in aerial insectivores and other species that require near-water perching sites. Conversely, our data indicate that increases in sediment increase the number of PISC. This increase may be linked to the increase in fish biomass we observed with increases in stream reach sediment. As sediment increases and homogenizes in-stream habitat (thereby reducing availability of benthic food resources, spawning substrate, and cover; see Sullivan and Watzin, 2009), more common and ubiquitous fish species may become abundant at the expense of more sensitive species, resulting in a potential increase in biomass. This general pattern was also reported in a previous study in the region, where Sullivan *et al*. (2006b) observed greater relative numbers of tolerant, generalist feeders (e.g. creek chubs [*Semotilus atromaculatus*], common shiners [*Luxilis cornutus*] and white suckers [*Catostomus commersoni*]) in reaches undergoing geomorphic adjustment. Since PISC feed largely based on size and position in the water column, a turnover in the fish species composition of a reach would not necessarily be expected to negatively influence PISC. Additionally, the reduction of in-stream cover available to forage fish in sediment-loaded stream reaches may increase the accessibility of fish to foraging PISC. As with the fish data, it appears that annual average sediment and nutrient data, while contributing to some of the regression models, are not as useful as other variables in predicting bird assemblages. Data derived at finer resolutions—either with modelling or in-stream sampling—may reveal stronger relationships.

Despite statistically significant regression models, R^2 values ($\leq$0.59) for our models indicate that a significant proportion of residual variance remained. Wiley *et al*. (1997) found significant variance in fish populations not only over space but also over time. They found after approximately 20 years of sampling variances started to stabilize with approximately half of the variance due to the spatial component and the remaining variance distributed between time and a time *X* site interaction factor (Wiley *et al*., 1997). As our study sampled all biota during one time period, the

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unexplained variance may in part be due to potential temporal rather than spatial differences. The unexplained variance may also be due to a number of other factors known to affect biotic populations. Nerbonne and Vondracek (2001) cite a number of additional considerations including dissolved oxygen, toxins (e.g. pesticides) and other in-stream water quality parameters. Furthermore, because of the extensive data collection required for this study, we were limited to 21 study reaches. However, we predict that we would capture additional variance given a larger number of study reaches.

CONCLUSIONS

Twenty-one stream reaches were studied in northwestern Vermont to determine the relative influence of local-scale and watershed-scale variables on fish, macroinvertebrate and bird assemblages. While our analysis identified a number of key variables in relating stream and watershed characteristics with biological assemblage data, we recognize the existence of significant unexplained residual variance. For example, at the local-scale, coordinated measurements of water quality and quantity alongside physical habitat surveys could further refine our understanding of the influences on aquatic biota. At the watershed-scale, additional research explicitly addressing both direct and indirect influences of the broader riverine landscape is also needed (Passy, 2009). For example, agricultural land-use was most often located within valleys—a human impact that often covaries with an existing environmental gradient. Our analyses did not discern between these two variables and thus may attribute influence incorrectly. More detailed analyses of the structure of ecosystems and the relationships of variables (including environmental gradients, watershed structural characteristics, landscape size and connectivity, etc.) could provide additional insight into the influence of broader-scale characteristics on biological assemblages. Concurrently, considering both food web dynamics and the flow of energy and materials (Baxter *et al*., 2005; Raikow *et al*., 2010) in a spatially-explicit manner would also likely illuminate key biotic-physical relationships in watersheds.

Our results speak directly to the challenge of reconciling ecological and management scales, reinforcing the concept that stream biota respond to their environment over a range of spatial scales. The nature of these responses, in this and other studies, is highly dependent on the life-history traits and habitat requirements of each taxon (Vaughn *et al*., 2007; Walters *et al*., 2009). In order to address these issues, comprehensive watershed management, restoration and conservation plans would benefit from assessments at multiple scales from a geomorphological, watershed and multitaxonomic perspective.

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