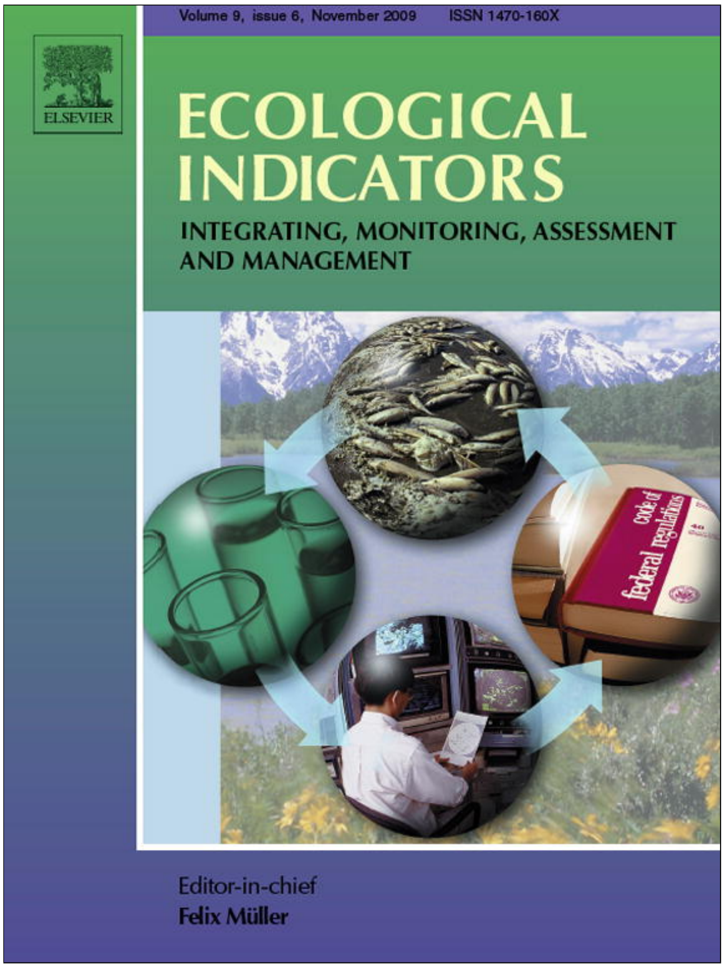
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Multi-scale mechanistic indicators of Midwestern USA stream macroinvertebrates

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ABSTRACT

We developed ecological indicators of stream macroinvertebrates in two regions of the Midwestern USA dominated by row-crop agriculture. Indicators were identified in a hierarchical fashion. Reach-scale variables related to macroinvertebrate attributes were first identified, and then catchment-scale variables related to those reach-scale variables were identified. Reach-scale indicators common to both regions were % fine sediments, number of habitats, and width:depth ratio. SD of elevation and % commercial land use were selected as catchment-scale indicators in both regions. Our analyses revealed a multi-scale mechanistic relationship between macroinvertebrate attributes associated with degraded conditions (i.e., fewer taxa of Plecoptera and Trichoptera, and a higher proportion of chironomids, burrowers, and depositional taxa) and % fine sediments in stream reaches, which, in turn, was negatively related to catchment characteristics (i.e., SD of elevation) in one region. Understanding how natural variables such as topography influence channel shape and within-channel structure can help guide management options and expectations for different regions. We suggest that developing multi-scale indicators in a mechanistic fashion will be more effective than developing indicators at only one spatial scale for protecting and restoring stream structure and function.

1. Introduction

Creating effective management and restoration plans for running waters requires an understanding of the fundamental processes and the appropriate spatial and temporal scales of observation. Ecologists have often turned to hierarchy theory to assist in the conceptual understanding of scales and ecosystem processes (Allen and Starr, 1982; O'Neill et al., 1986). These approaches have been useful in developing an understanding of the relative importance of multiple dimensions of stream ecosystems (e.g., Frissell et al., 1986; Hunsaker and Levine, 1995; Richards et al., 1996, 1997; Allan et al., 1997; Wang et al., 2003; Weigel et al., 2003; Mykrä et al., 2004), and how key features affect various constituents of stream communities. Identification of influential variables without a strong, scientifically-sound knowledge of the mechanisms driving ecosystem function does not address the underlying causes of impairment, and therefore precludes the development of ecologically-based management and restoration strategies.

Development of ecological indicators has been a priority for many government agencies with responsibility for managing public lands and ensuring clean water and air (NRC, 2000; Niemi and McDonald, 2004). Indicators provide information about the status or condition of some characteristics of interest, and can reveal causal relationships with influential variables. Indicators can operate at multiple spatial and temporal scales depending on the needs of the end-user as well as the dynamics of the focal system. Consideration of landscape-scale processes (Gergel et al., 2002) and conceptual models of stream ecosystem function (Lorenz et al., 1997) have enhanced development of indicators for lotic ecosystems. Because of legislation aimed at both identifying sources of impairment and developing restoration and mitigation plans (e.g., Clean Water Act in the U.S., Protocol on Water and Health in the WHO European Region), aquatic systems draining agricultural landscapes are especially in need of ecological indicators to determine causes of impairment and develop options and endpoints for rehabilitation (Watzin and McIntosh, 1999).

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Our approach to developing ecological indicators is to identify landscape- and habitat-scale features that strongly influence stream biota, but which are grounded in a mechanistic understanding of these relationships. Variables at the scale of catchments (e.g., land use and geology) influence biota through processes operating primarily at local, reach-level scales (e.g., habitat) mainly via hydrologic connections and geomorphic processes (Allan, 2004; Burcher et al., 2007). For example, row-crop agriculture does not typically alter the stream macroinvertebrate assemblage directly; instead, sediment, nutrient, and pesticide runoff from agricultural fields alters stream hydrology, habitat, and water chemistry, which, results in a shift in the macroinvertebrate assemblage (e.g., Richards et al., 1996, 1997; Burcher et al., 2007). Our analytical framework consists of a linked two-step process (reach-to-biota and then catchment-to-reach), which aims to incorporate the hierarchical mechanisms operating across landscapes. Given this framework, our goal is to develop indicators using stream macroinvertebrates based on hierarchical relationships across landscapes and to examine consistency of indicators across a large region. Macroinvertebrates are useful as indicators of stream condition because: (1) they are ubiquitous in aquatic habitats; (2) the large number of species show a range of responses to disturbance; (3) they are relatively sedentary as larvae; and (4) their life cycles are long enough to allow changes in population characteristics such as abundance and age structure to be assessed (Rosenberg and Resh, 1993).

Previously, we have reported a suite of catchment and local variables affecting macroinvertebrate assemblages and species traits in east-central Michigan streams, many of which are impacted by agriculture (Richards et al., 1993, 1996, 1997). Our overall goal in this study is to develop mechanistic indicators of macroinvertebrate assemblages in contrasting agricultural regions of the Midwestern USA. To do this we will first identify robust relationships between macroinvertebrate attributes and their local habitat conditions, and subsequently, interpret these relationships in the context of the underlying factors that control the variation in reach-scale variables: landscape structure and the stressor regime in a region. Finally, we are interested in identifying those environmental data that are most predictive of biotic attributes, in addition to discovering the underlying mechanisms for the relationships.

2. Materials and methods

2.1. Study area

We conducted this study in two agricultural regions in the Upper Midwestern USA. These regions differ with respect to climate and geomorphology, but are relatively similar in terms of land use and the types of stressors acting on aquatic systems. In southeastern Minnesota, two geologically distinct areas were chosen to represent the gradient of land use and of hydrologic conditions (Fig. 1A). Quaternary geology is dominated by glacial remnants in one area, and loess geology in the Driftless Plains region (Hobbs and Goebel, 1982). Major streams in the morainal landform include the Cannon (3777 km^2) and LeSeur (2892 km^2) basins. Study streams in the Driftless Plains include the Zumbro (3697 km^2), Root (4313 km^2), and Whitewater (829 km^2) basins. Some streams in the loess geology are also influenced by karst topography, which increases the interactions with groundwater. Agricultural land use across the study catchments in Minnesota ranged from 49 to 92% and averaged 73% (Table 1). Land use patch density was small, indicating that patches were large (Table 1). The larger patches in this region were mostly contiguous agricultural fields.

The Michigan study sites are in the Saginaw Bay basin of Lake Huron in east-central Michigan (Fig. 1B). Quaternary geology is also dominated by glacial remnants (Farrand and Bell, 1982). Drainages within the Saginaw basin range from heavily impacted agricultural land to relatively undisturbed second-growth forested areas. Agricultural land in the Michigan study region was somewhat less pervasive than in Minnesota, averaging 54% and ranging from 20 to 86% of the catchment (Table 1). Land use patch density was almost twice as high as in Minnesota (Table 1), indicating a more heterogeneous landscape with a larger number of small patches, generally in the form of forest and wetland remnants. Richards et al. (1997) provide detailed descriptions of the Michigan study region.

2.2. Study design

In order to develop mechanistic indicators for streams draining the agriculture-dominated Midwest, we applied a common analytical approach to two separate studies of large regions in Michigan and Minnesota. As a result, we were able to identify indicators within and across the two regions. Study sites were selected to reflect the gradient of land-use and physiographic conditions in each region (Table 1). We studied 36 reaches on 36 second- to third-order streams in Minnesota and 36 reaches on 12 second- to third-order streams in Michigan. Study sites in Michigan corresponded to three reaches separated by 2–10 km in each of 12 streams. Although Michigan reaches on the same stream do not represent independent streams as in Minnesota, we believe they correspond to reasonably unique conditions because of the distance separating sites. Nevertheless, we chose to be conservative in our overall analysis by statistically analyzing the two regions separately, and drawing our conclusions for cross-regional indicators based on concordant results for each region. Half of the catchments in both states occurred on predominantly morainal landforms. The remaining streams were in either loess (Minnesota) or lacustrine (Michigan) geology. Databases for land-use/land-cover, hydrography, soil characteristics, elevation, and human population were used to quantify landscape structure. Reaches for biological and physical sampling at each site were 100–250 m in length depending on channel width. Specific analytical methods for each set of variables are described below.

2.3. Macroinvertebrate sampling methods

We used a multi-habitat sampling approach to collecting macroinvertebrates (Lenat, 1988). Quantitative and qualitative benthic samples were collected in Minnesota during 8–17 September 1998 in baseflow conditions. Quantitative samples in run, riffle, and pool habitats were collected using either Hess (all riffles and some runs) or Ekman grab (all pools and some runs) samplers. Three samples were collected in each habitat type present in the reach. If available, wood was also quantitatively sampled by scraping the surface of a known area of a log into a net. Qualitative samples were collected in bank and wood dam habitats for 1 min each using a D-frame kick net (mesh size: 500 μm) to collect more resident taxa. Banks with extensive herbaceous vegetation (primarily grasses) were swept, while wood dams were jabbed (*sensu* Barbour et al., 1999) to dislodge invertebrates. Quantitative sampling devices had a 354-μm mesh net or sieve. All invertebrates from each sample type were frozen in the field using dry ice and returned to the laboratory for processing and identification.

Quantitative and qualitative samples were collected in Michigan during 14–26 September 1994 under baseflow conditions. Wood dams and banks were sampled as described for Minnesota. Run, pool, and macrophyte-dominated habitats were sampled with an Ekman sampler while riffles were sampled with a D-frame kick net. All sampling devices had a 500-μm mesh net or sieve. Samples were preserved with 70% ethanol in the field and returned to the

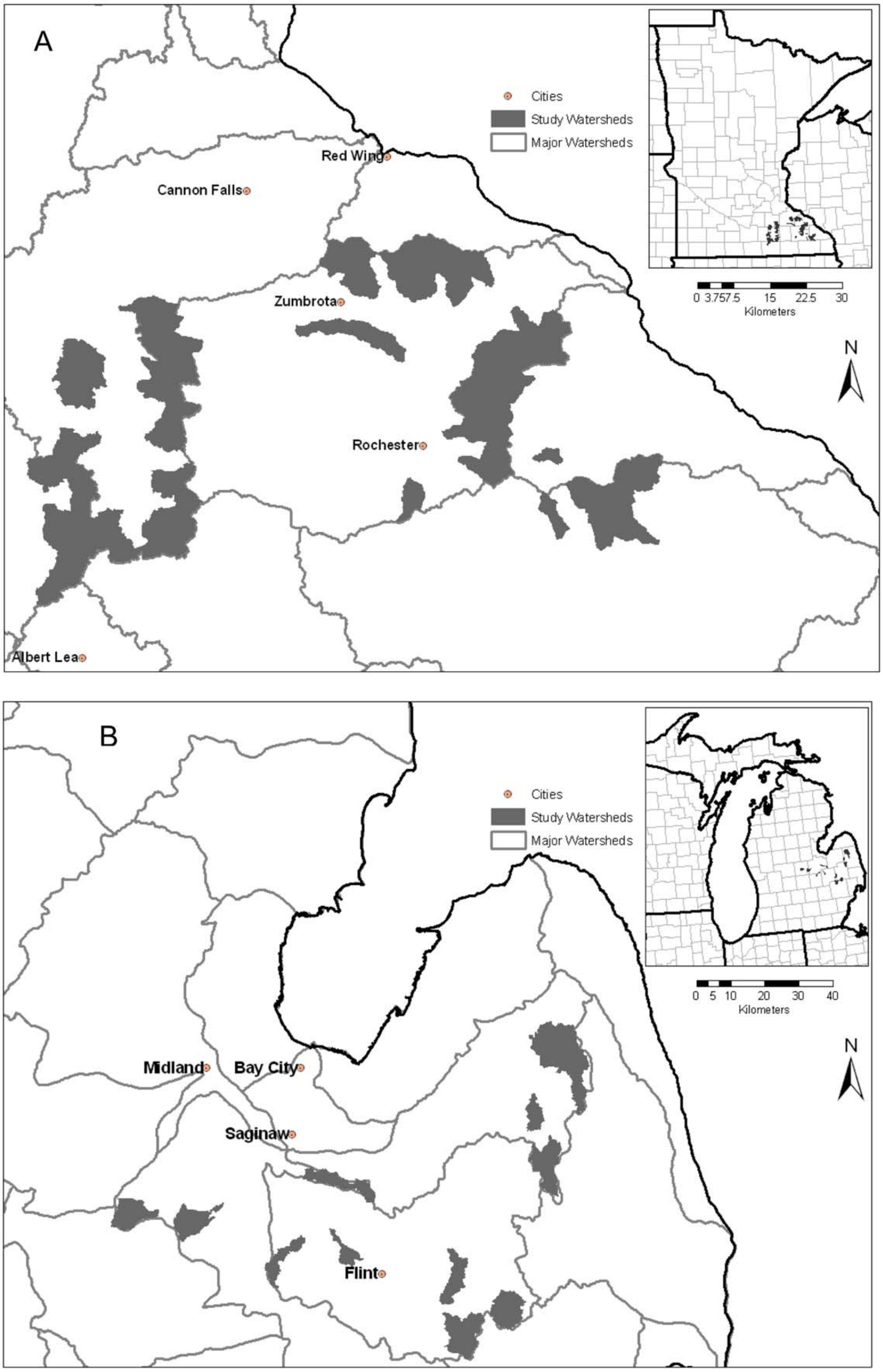

Fig. 1. Map of the two study regions in southeastern Minnesota (A) and central Michigan (B).

Table 1
Descriptive statistics for catchment-scale variables for Michigan ($n = 35$) and Minnesota ($n = 36$). Values represent means (minimum, maximum).

Variable	Michigan	Minnesota
Geomorphology		
Catchment area (km^2)	58.0 (7.1, 218.9)	54.5 (13.8, 146.5)
Elevation (m asl)	243 (194, 331)	359 (320, 387)
SD of elevation	7.5 (1.9, 19.0)	13.0 (3.1. 26.2)
Catchment slope (deg)	0.9 (0.3, 2.5)	2.2 (0.5, 4.7)
Total number of links	19 (1, 164)	24 (3, 100)
Drainage density (km/km^2)	0.9 (0.1, 1.3)	1.1 (0.4, 1.6)
Land use/Land cover		
% Open water	0.7 (0, 4.2)	0.1 (0, 1.6)
% Residential	2.2 (0, 19.5)	3.7 (2.4, 8.7)
% Commercial	0.3 (0, 1.4)	1.1 (0, 4.5)
% Forest	20.2 (2.7, 38.7)	4.4 (0.2, 16.4)
% Grassland	0 (0, 0)	0.1 (0, 0.5)
% Hay pasture	12.3 (1.9, 28.1)	16.4 (2.8, 35.6)
% Row crop	53.8 (20.3, 86.4)	73.0 (49.2, 92.1)
% Wetland	9.9 (0.6, 35.2)	1.0 (0.1, 5.1)
Patch density (no. land use patches/km^2)	48.4 (22.7, 82.9)	25.2 (9.4, 45.1)
Soils		
Depth to bedrock (cm)	152 (151, 152)	146 (109, 152)
Water capacity (cm/cm)	23 (13, 34)	29 (20, 37)
Permeability (cm/h)	11 (3, 29)	5 (2, 12)
K-factor	0.24 (0.18, 0.32)	0.32 (0.24, 0.38)
% Organic matter	5.1 (0.8, 19.4)	2.3 (0.7, 8.2)
% Sand	36.9 (21.8, 68.1)	19.2 (5.0, 36.5)
% Clay	17.6 (8.8, 23.2)	22.8 (17.4, 31.0)
Other		
Population density (no./km^2)	40.7 (8.5, 204.2)	8.8 (3.0, 32.4)
Road density (km/km^2)	1.6 (1.1, 2.3)	1.3 (1.0, 1.6)

laboratory for processing and identification. All invertebrates from the Ekman sampler were collected and 100-count subsampling procedures were used on all qualitative techniques (Lenat, 1988; Richards et al., 1997).

Macroinvertebrates were sorted from debris under 2× magnification and preserved with 70% ethanol. All macroinvertebrates were identified to genus if possible using appropriate keys (Hilsenhoff, 1981; Brinkhurst, 1986; Thorp and Covich, 1991; Merritt and Cummins, 1996). A subsample of chironomid larvae from each sample was permanently mounted and identified according to Wiederholm (1983).

2.4. Local site characterization

We assessed a broad suite of physical, chemical, and ecological characteristics in each sampling reach (Table 2). Physical assessments in Minnesota were conducted from June to October 1999 under baseflow conditions; similar standard parameters were measured in Michigan during August and September 1994. In addition to channel morphology measurements (Table 2), we visually inspected each reach for evidence of past channelization.

Mean nutrient (soluble reactive phosphorus [SRP] and dissolved inorganic nitrogen [DIN; nitrate-N, nitrite-N, and ammonium-N]) concentrations were measured from samples collected in August 1999, which corresponded to the beginning and end of chlorophyll *a* accrual experiments (see below). DIN and SRP were measured on a Lachat QuikChem Automated Flow Injection Ion Analyzer using standard methods (Ameel et al., 1998). Chlorophyll *a* accrual was measured on nutrient-diffusing substrata after 3 weeks of colonization in August 1999 in all reaches using the method of Gibeau and Miller (1989). Coarse particulate organic matter (CPOM) standing stocks were measured using the samples collected for benthic macroinvertebrates in Minnesota and separate benthic samples in run, riffle, and pool habitats in Michigan. Ash-free dry mass (AFDM) of sorted material >1 mm was determined by placing samples in a muffle furnace at 500 °C for 2 h. Filamentous green algae were removed before burning.

2.5. Catchment characterization

Spatial data for land use, hydrography, soils, elevation, roads, and population density were summarized for each catchment. A unique catchment above each site was delineated manually and digitized from USGS 1:24,000 topographic maps.

Land use and land cover (LU/LC) for the study region were derived from the National Land Cover Data Set (NLCD) obtained from the USGS EROS Data Center. LU/LC data were based on 1992 Landsat Thematic Mapper imagery with a 28.5-m resolution. Classification of LU/LC types follows that being used in the Multi-Resolution Land Characteristics Consortium program (Loveland and Shaw, 1996). Patch density was calculated from LU/LC data using FRAGSTATS (McGarigal and Marks, 1995).

Soil characteristics for the study region were summarized from the STATSGO database obtained from the Natural Resources Conservation Service. We selected soil characteristics that influence catchment hydrology (i.e., depth to bedrock, water capacity, permeability, and proportion of sand and clay), erosion potential (K-factor from the Universal Soil Loss Equation), and productivity (proportion of organic matter). Values were averaged by depth for different soil layers and by area.

Mean slope and elevation for the entire catchment were obtained from 1° digital elevation models (USGS) at a scale of 1:250,000. We used SD in elevation within the catchment to represent topographic heterogeneity. Valley slope was derived from elevation data using ARC/INFO algorithms. The number of first-order stream links in each catchment was counted manually from the digitized 1:24,000 topographic maps. Stream length was estimated using TIGER (U.S. Census Bureau) data and converted to drainage density (km/km^2). Population and road density were also estimated using TIGER data.

2.6. Statistical analyses

Macroinvertebrate assemblages were described using biotic attributes, which are measurable parts of biological systems (Karr and Chu, 1999). We chose attributes commonly used to describe ecological condition of streams (e.g., number of sensitive taxa, proportion of functional feeding groups, and biological traits; Table 3) (Barbour et al., 1999). Statistical analyses for genus-level taxonomic data are not presented here because we found similar results for these data as for the attributes. Further, attributes are somewhat more independent of geography and therefore can be generalized across larger regions. Proportional attributes were calculated as percent of total abundance from all habitats regardless of sampling method to ensure a representative reach-scale value. Habitat-weighted total abundance was only calculated for Minnesota because of sub-sampling methods used in Michigan.

Separate matrices of reach- and catchment-scale characteristics by site were constructed for each region. Data were transformed to eliminate problems with heteroscedasticity and non-normality using $\log_{10}(x + 1)$ transformations for count or abundance attributes, and arcsine-square root transformations for proportional attributes. We used dummy variables to designate the type of geology (loess vs. morainal in Minnesota; lacustrine vs. morainal in Michigan) present for each study catchment, and whether the study reach was channelized. One sampling site in Michigan was eliminated because of flooding by beaver, resulting in 35 stream reaches in Michigan versus 36 in Minnesota.

A series of analyses were used to identify important reach- and catchment-scale variables influencing biotic attributes in each region. These analyses were linked (i.e., reach-to-biota and then

Table 2
Description of reach-scale habitat variables measured at, or calculated for, each study site. Descriptive statistics represent means (minimum, maximum) for Michigan (n = 35) and Minnesota (n = 36).

Variable	Description/method	Michigan	Minnesota
Channel morphology			
Mean width (m)	Mean width of stream channel calculated from ten transects	5.2 (1.9, 10.2)	5.4 (2.9, 11.2)
Bankfull width (m)	Mean width of stream channel at bank full discharge calculated from three transects	6.3 (3.7, 12.1)	6.8 (3.5, 13.4)
Flood height (m)	Mean height of highest point that water enters floodplain calculated from three transects	2.1 (0.5, 5.0)	1.7 (0.3, 4.6)
Maximum depth (m)	Depth of deepest part of stream reach	0.6 (0.2, 1.1)	0.7 (0.3, 1.3)
Width:depth	Mean ratio of mean width to mean depth calculated from ten transects	15.2 (7.7, 55.8)	17.0 (5.9, 43.1)
Channel unit			
% Riffle	Proportion of stream reach comprised of riffle habitat from length measurements	11 (0, 50)	15 (0, 83)
% Run	Proportion of stream reach comprising run habitat	38 (0, 100)	63 (0, 100)
% Pool	Proportion of stream reach comprising pool habitat	42 (0, 99)	17 (0, 81)
% Wood[a]	Proportion of stream reach comprising wood habitat	9 (0, 32)	3 (0, 12)
Substratum			
% Boulder	Proportion of stream reach comprised of boulder calculated from visual estimates at five points across each of ten transects	1 (0, 14)	2 (0, 20.0)
% Cobble	Proportion of stream reach comprising cobble	11 (0, 64)	26 (0, 80)
% Gravel	Proportion of stream reach comprising gravel	9 (0, 65)	14 (0, 74)
% Sand	Proportion of stream reach comprising sand	43 (0, 100)	27 (0, 100)
% Fines	Proportion of stream reach comprising fines	34 (0, 100)	31 (0, 100)
Manning's n	Calculated using discharge and channel measurements (Dingman and Sharma, 1997)	0.48 (0.05, 2.87)	0.22 (0.03, 1.23)
Chemistry			
DIN (mg/L)	Mean concentrations calculated from two dates	0.598 (0.045, 4.446)	5.388 (1.440, 10.854)
SRP (mg/L)	Mean concentrations calculated from two dates	0.012 (0, 0.053)	0.083 (0.011, 0.372)
Specific conductivity (μs/cm)	YSI Model 33 conductivity meter	629 (210, 1100)	296 (215, 483)
Total alkalinity (mg/L)	Concentration measured once using standard methods (Ameel et al., 1998)	236 (98, 340)	–
Wood			
Volume (m^3/m^2)	Mean volume of wood ≥ 0.05 m diameter and ≥ 0.5 m length estimated using line-intersect technique (Wallace and Benke,1984) for ten transects in each reach	0.0023 (0, 0.0312)	0.0017 (0, 0.0117)
Total length (m/m^2)	Total length of wood (≥0.05 m diameter and > 1 m length) per 100 m stream channel	0.25 (0.45, 5.03)	0.07 (0, 0.27)
Wood dams (no./100 m)	Total number of wood dams per 100 m stream channel	6 (0, 18)	8 (0, 24)
Wood dam area (m^2/100 m)	Total area of wood dams calculated from length and width estimates per 100 m stream channel	72.9 (0, 306.6)	185.0 (0, 1184.0)
Other			
CPOM (g AFDM/m^2)	Habitat-weighted mean ash-free dry mass of detritus >1 cm diameter collected during macroinvertebrate[b] or separate[c] sampling	193.3 (4.0, 1254.3)	93.8 (3.1, 384.6)
Chlorophyll a accrual (mg/m^2)	Estimate of primary production using the method of Gibeau and Miller (1989)	48.7 (2.0, 139.3)	46.0 (11.6, 130.5)
% Open canopy	Mean calculated from ten transects using spherical densiometer	65.2 (2.4, 100)	71.6 (8.4, 100)
Riparian vegetation width (m)	Mean width of non-agricultural riparian vegetation in 40-m buffer estimated from three transects	24 (2, 40)	23 (2, 40)
Riparian vegetation height (m)	Mean height of non-agricultural riparian vegetation estimated from three transects	5.2 (0.5, 10.0)	3.9 (0.5, 10.0)
Number of habitats	Total number of available habitats (i.e., riffle, run, pool, grassy bank, wood)	3 (2, 4)	3 (2, 4)
Maximum temperature (°C)	Measured using max–min thermometers from spring to fall	29.1 (23.9, 35.6)	20.9 (13.3, 27.8)

[a] % Wood dam area for Michigan.
[b] Minnesota.
[c] Michigan.

catchment-to-reach) to incorporate the hierarchical mechanisms operating across landscapes. We performed separate analyses for each region because collection methods and study design differed somewhat between regions, and data were collected in different years. First, we examined the direct relationship between all reach-scale environmental variables and all macroinvertebrate attributes for each region using redundancy analysis (RDA; Rao, 1964; Van den Wollenberg, 1977). Second, we used RDA to examine the direct relationship between the reach-scale variables identified as having a significant influence on biota from the first step and all of the catchment-scale variables. Third, we assessed the relative importance of the selected variables for each dependent variable by performing separate multiple linear regressions and examining the standard partial regression coefficients.

RDA is a canonical ordination method that assumes a linear relationship between matrices. RDA is essentially a two-step process, in which multivariate response data (e.g., macroinvertebrate attributes) are regressed on multivariate explanatory data (e.g., reach-scale variables), and then the fitted values from the multiple regressions are decomposed using principal component analysis (Legendre and Legendre, 1998). We tested for linearity between matrices by examining the gradient length calculated from detrended correspondence analysis. Short gradient lengths (<3 SD) indicate a linear relationship whereas long gradient lengths (>4 SD) indicate a unimodal relationship (ter Braak and Smilauer, 1998).

All ordinations were run with CANOCO 4.0 (ter Braak and Smilauer, 1998). To quantify macroinvertebrate–reach relationships, we selected the most important reach-scale variables for each ordination using the manual forward-selection procedure provided in CANOCO (α = 0.10). The selection procedure is based on a Monte Carlo randomization procedure (1000 iterations). We reduced collinearity in the data set by only retaining those variables with variance inflation factors <10. Next, the RDA was performed with only the selected reach-scale variables to test for the significance of the first RDA axis and all axes combined using a Monte Carlo randomization procedure.

The second step examined the direct relationship between the selected reach-scale variables and all of the catchment-scale

Table 3
Description of biotic attributes used to describe macroinvertebrate assemblages at all sites. Expected response refers to hypothesized direction of response of each attribute to an anthropogenic disturbance based primarily on Barbour et al. (1999). Attributes derived mainly from Merritt and Cummins (1996) and primary literature. Values represent means (minimum, maximum) for Michigan ($n = 35$) and Minnesota ($n = 36$).

Attribute	Description	Expected response	Michigan	Minnesota
Total abundance[a] (no./m^2)	Total habitat-weighted abundance of riffle, run, pool, and wood habitats	Variable	–	14354 (2051, 47077)
Taxa richness	Total number of macroinvertebrate taxa	Decrease	39 (17, 60)	61 (40, 85)
EPT richness	Total number of Ephemeroptera, Plecoptera, and Trichoptera taxa	Decrease	7 (2, 17)	8 (2, 16)
Ephemeroptera richness	Total number of Ephemeroptera taxa	Decrease	3 (1, 7)	3 (1, 8)
Plecoptera richness	Total number Plecoptera taxa	Decrease	<1 (0, 3)	<1 (0, 2)
Trichoptera richness	Total number or Trichoptera taxa	Decrease	4 (0, 9)	4 (0, 9)
% Dominant	Proportion of the total abundance accounted for by the most abundant taxa at a site	Increase	25.0 (11.1, 71.2)	24.2 (11.9, 69.5)
% Chironomidae	Proportion of the total abundance that are Chironomidae	Increase	43.3 (7.6, 88.7)	61.3 (34.4, 92.7)
% Multivoltine	Proportion of the total abundance that are multivoltine	Increase	29.4 (10.2, 62.7)	64.2 (32.7, 91.1)
% Univoltine	Proportion of the total abundance that are univoltine	Decrease	41.4 (12.3, 84.0)	14.9 (0.5, 60.1)
% Burrowers	Proportion of the total abundance that are exclusively burrowers	Increase	21.3 (3.2, 82.1)	12.0 (0.7, 72.2)
% Clingers	Proportion of the total abundance that are exclusively clingers	Decrease	36.0 (5.7, 89.6)	30.4 (3.1, 58.7)
% Depositional	Proportion of the total abundance that are exclusively found in depositional habitats	Increase	15.9 (1.5, 75.0)	5.9 (<0.1, 70.0)
% Erosional	Proportion of the total abundance that are exclusively found in erosional habitats	Decrease	30.8 (8.9, 65.0)	32.9 (6.3, 74.1)
% Shredder	Proportion of the total abundance that are shredders	Decrease	5.8 (0, 37.5)	9.1 (0.2, 24.3)
% Scraper	Proportion of the total abundance that are scrapers	Decrease	3.2 (0, 14.5)	4.1 (0.1, 18.6)
% Gatherer	Proportion of the total abundance that are collector-gatherers	Increase	44.5 (23.3, 90.1)	50.6 (11.4, 79.2)
% Filterer	Proportion of the total abundance that are collector-filterers	Variable	15.5 (0.5, 33.4)	15.1 (1.6, 61.0)
% Predator	Proportion of the total abundance that are predators	Variable	17.7 (3.6, 47.2)	12.9 (2.7, 32.1)
% Detritivore	Proportion of the total abundance that are detritivores	Variable	61.1 (18.4, 89.5)	62.9 (40.6, 83.3)
% Omnivore	Proportion of the total abundance that are omnivores	Increase	8.5 (1.2, 36.1)	13.1 (3.7, 24.3)

[a] See collection and processing methods in text.

variables using RDA. The most important catchment-scale variables explaining the reach-scale variables were selected using the forward selection procedure described above.

To assess the relative importance of the variables selected by RDA for each dependent variable, we performed multiple linear regressions for each dependent variable and examined the standard partial regression coefficients. Standard partial regression coefficients are free of the original measurement scale; thus, their magnitudes can be compared directly to show the relative strength of the effects of several independent variables on the same dependent variable (Sokal and Rohlf, 1995). It should be noted that this additional analytical step (i.e., calculating standard partial regression coefficients) was conducted solely to improve our interpretation of the significant variables identified using RDA, and did not represent a separate "independent" analysis.

3. Results

3.1. Reach-scale characteristics

There were few pronounced differences in reach-scale characteristics between sites in Michigan and Minnesota. Perhaps the most striking differences between regions were in-stream nutrient concentrations: on average, DIN was ca. 10× higher and SRP was ca. 7× higher in Minnesota (Table 2). In fact, the minimum DIN concentration in Minnesota was >2× higher than the mean in Michigan. In contrast, specific conductivity was higher in Michigan. Another large difference between regions was maximum stream temperature. Streams averaged 8.2 °C cooler in Minnesota, which was presumably a result of cooler groundwater in the streams affected by karst topography.

Most reach-scale variables, such as stream size and canopy cover, were similar between regions (Table 2). Sand and fines dominated substrates in both regions. Run and pool channel units dominated in Michigan, whereas runs alone comprised the majority of the channel in Minnesota. Although standing crops of CPOM were ca. 2× higher in Michigan, chlorophyll *a* accrual was similar in both regions. Wood volume and total wood length were relatively similar between regions, but Minnesota tended to have larger wood dams.

3.2. Catchment-scale characteristics

Soil characteristics were very similar between regions (Table 1). Higher proportions of sand in Michigan catchments were associated with lacustrine geology. Catchment geomorphology differed between regions, as Minnesota catchments were steeper, more topographically diverse (i.e., more variation in elevation), and more dissected with first-order streams than Michigan (Table 1).

LU/LC was dominated by agriculture in both regions, especially in Minnesota (Table 1). Forests covered, on average, ca. 20% of Michigan catchments. Because of the homogeneity in LU/LC in Minnesota, patch density was half that of Michigan. Although population density was low in these predominantly rural areas, study catchments in Michigan had a population density 5× higher than Minnesota.

3.3. Biotic attributes

Mean taxa richness per stream was 56% higher in Minnesota (Table 3). Taxa richness in both regions was dominated by dipterans and especially by chironomid taxa. Chironomids also dominated total abundance, comprising 43 and 61% of total abundance in Michigan and Minnesota, respectively. In general, the two regions were similar in terms of functional feeding groups, as total abundance was always dominated by collector-gatherers. Patterns of voltinism differed between regions; the relative abundance of multivoltine taxa was higher in Minnesota, whereas univoltine taxa were higher in Michigan (Table 3).

3.4. Reach-scale variables and biotic attribute relationships

Reach-scale variables were significantly related to attributes of the macroinvertebrate assemblage in both regions, although there was a stronger relationship in the Minnesota study region

(Table 4). In Michigan, % fines, % open canopy, and number of habitats were correlated at $|r| > 0.3$ with the first RDA axis (Fig. 2A). The second axis was correlated with DIN. Width:depth was also identified as an important reach-scale variable in Michigan, but it was correlated at $|r| > 0.3$ with the fourth RDA axis (axis not shown). In Minnesota, number of habitats, width:depth, wood dam area, channelization history, bankfull width, and flood height were correlated at $|r| > 0.3$ with the first RDA axis (Fig. 2B). The second axis was highly correlated with maximum temperature, number of habitats, width:depth, channelization history, and % sand. Percent fines was also identified as an important reach-scale variable in Minnesota; it was correlated at $|r| > 0.3$ with the third RDA axis (axis not shown). Three reach-scale variables were found in common across regions: number of habitats, width:depth, and % fines.

Specific relationships between individual macroinvertebrate attributes and the reach-scale variables identified as being important by the RDA are shown using standardized partial regression coefficients (Table 5). Coefficients of determination for individual reach–attribute relationships in Michigan ranged from 26.5 to 57.5%, and from 43.7 to 72.2% in Minnesota. Macroinvertebrate attributes that were best explained (based on R^2) by reach-scale variables in Minnesota were: % predators, % gatherers, Ephemeroptera richness, % univoltine, % erosional, and % clingers. The latter two attributes also were well explained by reach-scale variables in Michigan, in addition to % shredders, taxa richness, % scrapers, and % detritivores.

Certain reach-scale variables were found to have relatively strong effects on a range of biotic attributes (Table 5). The number of habitats influenced the largest number (9) of biotic attributes in the Minnesota study streams, while maximum temperature, % fines, and width:depth each strongly influenced between 5 and 7 attributes each. Percent fines and % open canopy influenced ten and nine biotic attributes in Michigan, while DIN and number of habitats strongly influenced six and five attributes, respectively, in the Michigan streams.

3.5. Catchment- and reach-scale variable relationships

Stronger relationships between reach- and catchment-scale variables were found in Minnesota compared to Michigan. The selected catchment-scale variables explained 14% more variation in reach-scale variables in Minnesota study streams than those in Michigan (Table 6). In Michigan, SD of elevation was correlated with the first and second RDA axis (Fig. 3A). The second axis was also correlated with % open water. Road density and % commercial

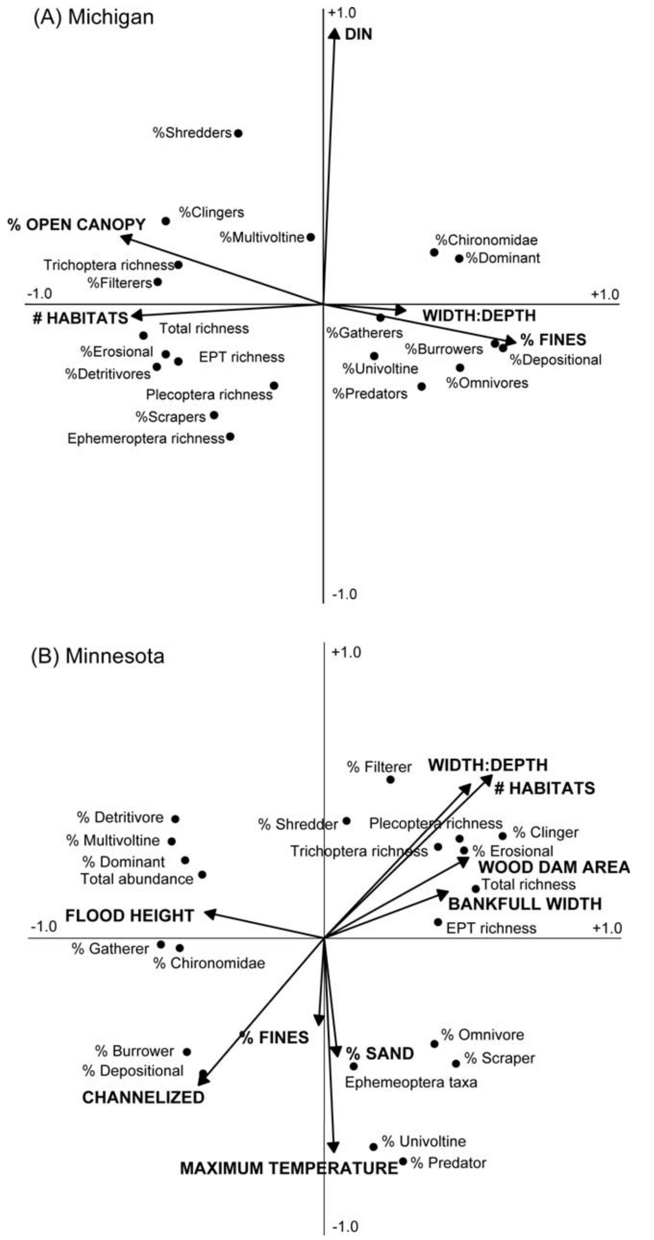

Fig. 2. A biplot showing results of redundancy analysis (RDA) relating reach-scale variables (arrows) to macroinvertebrate attributes (points) in (A) Michigan and (B) Minnesota. The 1st axis explained 19.2 and 17.6% of variation in Michigan and Minnesota, respectively. The 2nd axis explained 6.4 and 15.2% of variation in Michigan and Minnesota, respectively.

were identified as important catchment-scale variables in Michigan, but they were correlated at $|r| > 0.3$ with the third RDA axis (axis not shown). In Minnesota, all selected variables, except for % commercial ($r = -0.28$), were correlated ($|r| > 0.3$) with the first RDA axis (Fig. 3B). The second axis was highly correlated with K-factor. Two catchment-scale variables identified by the RDAs, SD of elevation and % commercial, were common to both regions (Table 6). Variables related to catchment hydrology (i.e., % open water in Michigan; % wetland, water capacity, link # in Minnesota) were also selected in both regions.

Coefficients of determination for catchment-reach regressions in Michigan ranged from 31.2 to 52.2%, and from 35.3 to 64.4% in Minnesota (Table 7). The best explained (based on R^2) reach-scale variables in Minnesota were: number of habitats, maximum temperature, % sand, wood dam area, and width:depth. DIN was best explained in Michigan. Overall, the number of links, SD of

Table 4
Results of redundancy analyses (RDA) for macroinvertebrate biotic attributes explained by reach-scale variables in Michigan and Minnesota.

	Michigan	Minnesota
Attributes explained by reach		
Variance explained by 1st axis (%)	19.2	17.6
F-value of 1st axis	6.904**	5.535**
Variance explained by all axes (%)	34.8	52.0
F-value of all axes	3.095**	3.132**
Selected variables	Number of habitats	Number of habitats
	% Fines	% Fines
	Width:depth	Width:depth
	% Open canopy	Bankfull width
	DIN	Flood height
		Channelization
		% Sand
		Maximum temperature
		Wood dam area

** $P < 0.005$.

Table 5
Standard partial regression coefficients of multiple regressions for each macroinvertebrate attribute that had a strong relationship ($P \leq 0.10$) with the selected reach-scale variables in Michigan and Minnesota. The variables with the highest two coefficients (absolute value) are denoted in bold.

Michigan

Attribute	R^2	Reach variables				
		No. habitats	% Fines	Width:depth	DIN	% Open canopy
Taxa richness	54.6	**0.43**	−0.07	0.07	−0.21	**0.43**
EPT taxa richness	36.7	**0.41**	**−0.29**	0.08	−0.25	0.07
Ephemeroptera richness	35.1	**0.40**	−0.09	−0.23	**−0.45**	−0.13
Plecoptera richness	39.2	0.15	**−0.42**	**0.33**	−0.29	−0.18
Trichoptera richness	33.1	0.25	**−0.27**	0.11	0.05	**0.27**
% Chironomidae	35.2	0.27	**0.45**	0.01	0.35	**−0.36**
% Burrowers	37.3	−0.08	**0.43**	0.05	<0.00	**−0.35**
% Clingers	41.7	0.20	**−0.35**	**−0.21**	**0.21**	0.18
% Shredders	57.5	−0.24	**−0.54**	−0.02	**0.50**	0.16
% Filterers	34.9	**0.28**	−0.19	−0.25	−0.01	**0.27**
% Scrapers	51.1	0.02	**−0.52**	−0.33	**−0.45**	−0.15
% Detritivores	47.0	0.08	−0.15	−0.19	**−0.37**	**0.50**
% Omnivores	35.8	0.20	**0.26**	0.18	−0.05	**−0.56**
% Depositional	40.7	−0.22	**0.24**	0.16	−0.03	**−0.39**
% Erosional	42.8	**0.34**	−0.21	**−0.44**	−0.22	0.07
% Dominant	26.5	−0.07	0.22	0.17	**0.28**	**−0.32**

Minnesota

Attribute	R^2	Reach variables							
		No. habitats	% Fines	Width:depth	Channelization	Bankfull width	Flood height	Debris-dam area	% Sand	Max. temp.
Total abundance	43.7	−0.01	**−0.51**	−0.26	−0.23	0.34	0.50	**−0.65**	−0.18	−0.13
Taxa richness	45.1	**0.64**	0.21	−0.01	0.06	−0.07	**−0.27**	0.20	0.08	0.12
EPT taxa richness	52.5	**0.33**	−0.22	0.15	−0.32	−0.10	−0.32	−0.23	0.07	**0.40**
Ephemeroptera richness	61.5	0.07	−0.17	−0.13	−0.22	0.34	−0.22	**−0.47**	0.18	**0.55**
Plecoptera richness	50.6	**0.84**	−0.01	0.38	−0.16	−0.06	−0.08	**−0.60**	0.07	0.28
Trichoptera richness	47.5	**0.31**	−0.18	0.22	−0.23	**−0.40**	−0.28	0.10	>0.00	0.12
% Multivoltine	46.1	**−0.86**	**−0.77**	−0.28	−0.26	0.14	0.35	0.21	−0.35	−0.47
% Univoltine	60.6	0.23	**0.58**	−0.08	0.16	0.09	0.02	0.17	0.48	**0.57**
% Burrowers	52.5	−0.21	−0.13	**−0.59**	0.12	**0.61**	0.40	−0.22	0.23	−0.11
% Clingers	58.2	**1.10**	0.39	**0.73**	0.37	−0.57	−0.40	−0.31	<0.00	0.19
% Shredders	39.5	0.21	−0.14	0.38	**0.52**	0.04	−0.17	−0.15	−0.04	**−0.47**
% Predators	72.2	−0.14	**0.56**	0.15	0.28	−0.07	−0.36	0.51	0.20	**0.66**
% Gatherers	63.3	−0.39	**−0.87**	**−0.78**	−0.09	0.40	0.62	0.19	−0.18	−0.09
% Filterers	47.8	**0.44**	0.19	0.37	−0.42	−0.33	0.06	**−0.43**	−0.24	−0.03
% Scrapers	55.0	0.52	0.43	**0.54**	**0.80**	−0.11	−0.53	0.08	0.37	0.38
% Detritivores	54.1	−0.42	**−0.77**	−0.59	**−0.74**	0.05	0.27	−0.36	−0.39	−0.37
% Omnivores	52.2	−0.05	**0.60**	0.49	0.11	0.01	0.01	0.40	0.07	**0.60**
% Depositional	51.0	−0.27	−0.29	**−0.48**	0.10	**0.37**	0.02	−0.27	0.16	−0.01
% Erosional	59.6	**0.89**	−0.03	0.30	0.13	−0.20	0.13	0.01	−0.07	**0.42**
% Dominant	47.3	**−0.90**	−0.44	−0.21	**−0.70**	0.02	0.22	−0.11	−0.37	−0.35

elevation, and K-factor influenced the largest number of reach-scale variables in the Minnesota study region, while SD of elevation and road density affected the most reach-scale variables in Michigan (Table 7).

4. Discussion

4.1. Cross-regional indicators

Hierarchical control of stream benthic assemblages has been demonstrated for individual regions (e.g., Roth et al., 1996; Richards et al., 1996, 1997; Allan et al., 1997; Wiley et al., 1997; Dovciak and Perry, 2002; Brosse et al., 2003; Weigel et al., 2003; Black et al., 2004; McRae et al., 2004; Burcher et al., 2007), but it has not yet been well demonstrated across regions (Johnson et al., 2007). We found three cross-regional properties of stream reaches that affected stream macroinvertebrate attributes across our Michigan and Minnesota study areas: percent of fine sediments, habitat complexity, and width–depth ratio. We also identified two catchment-scale indicators, topographic heterogeneity (i.e., SD of elevation) and % commercial land use, which influenced the reach-scale indicators of macroinvertebrate attributes across the two study regions.

The proportion of fine sediment in stream substrates was the most common reach-scale indicator influencing stream invertebrate attributes across both regions. Sediment characteristics are fundamental to understanding macroinvertebrate distributions in streams (Minshall, 1984; Reice and Wohlenberg, 1993), and the addition of fine sediment to streams can have profound impacts on stream macroinvertebrates and ecosystem processes (Cordone and Kelly, 1961; Waters, 1995; Wood and Armitage, 1997). This was especially evident in Michigan, where streams containing a higher proportion of fines appeared to have more degraded macroinvertebrate assemblages. For example, higher levels of fines were positively associated with burrowing invertebrates and chironomids, and negatively associated with caddisfly and stonefly taxa, clingers, and scraper and shredder functional groups. Other studies in streams draining predominantly agricultural regions have found resident macroinvertebrate assemblages to be tolerant to high levels of fine sediments (Richards et al., 1993, 1996, 1997; Barton and Farmer, 1997; Collier et al., 1998; Harding et al., 1999; Poole and Downing, 2004; McRae et al., 2004; Stone et al., 2005; Burcher et al., 2007; Niyogi et al., 2007). Controlling erosion in agricultural streams is, therefore, essential to protect their biotic quality. Successful erosion-management techniques include protecting or

Table 6
Results of redundancy analyses (RDA) for selected reach-scale variables explained by catchment-scale variables in Michigan and Minnesota.

	Michigan	Minnesota
Reach explained by catchment		
Variance explained by 1st axis (%)	16.6	28.1
F-value of 1st axis	6.158**	11.340**
Variance explained by all axes (%)	33.0	47.4
F-value of all axes	3.818**	4.356**
Selected variables	SD Elevation % Commercial % Water Road density	SD Elevation % Commercial % Wetland Link # Water capacity K-factor

** $P < 0.005$

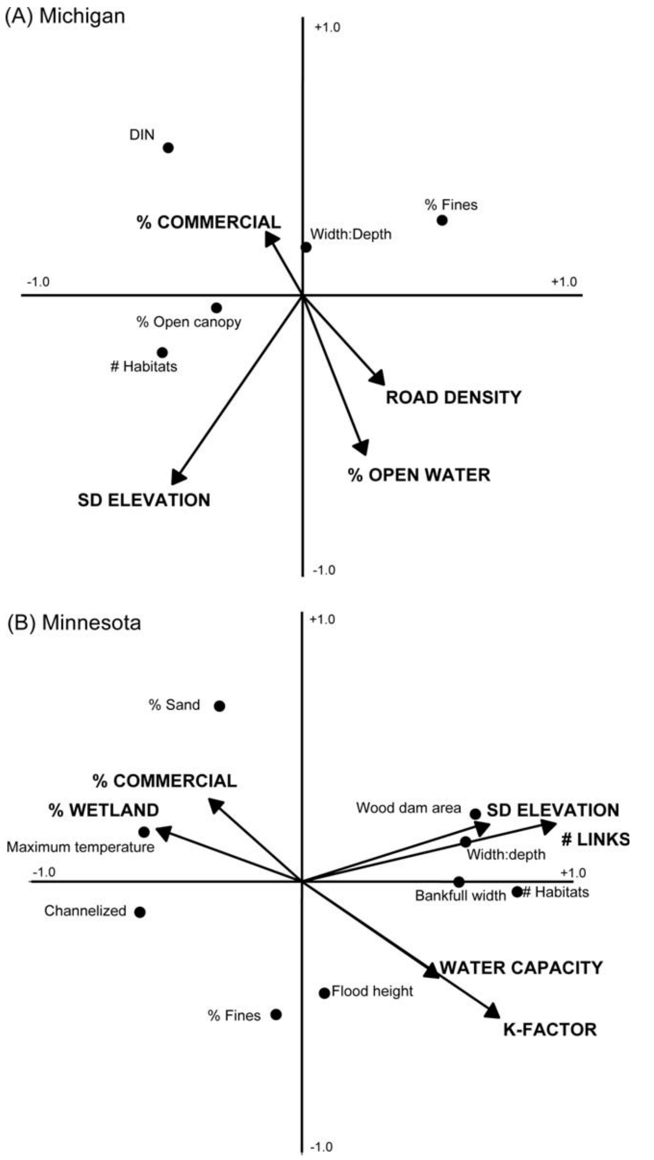

Fig. 3. A biplot showing results of redundancy analysis (RDA) relating catchment-scale variables (arrows) to reach-scale variables (points) that had significant influence on macroinvertebrate attributes in (A) Michigan and (B) Minnesota. The 1st axis explained 16.6 and 28.1% of variation in Michigan and Minnesota, respectively. The 2nd axis explained 8.6 and 10.8% of variation in Michigan and Minnesota, respectively.

restoring riparian vegetation (Osborne and Kovacic, 1993; Lyons et al., 2000; Sponseller et al., 2001; Dosskey, 2002; Meador and Goldstein, 2003), and conservation tillage or other Best Management Practices (BMPs; Barton and Farmer, 1997; Nerbonne and Vondracek, 2001).

A relatively simple measure of habitat complexity, the number of in-channel habitat types in a reach, was the second most common variable influencing invertebrate taxonomic richness across both regions. The relationship between the number of different taxa in a stream reach and habitat complexity is intuitive, yet not supported consistently, perhaps because of differences in the way that complexity is measured among studies (Vinson and Hawkins, 1998). In Michigan, increased habitat complexity was associated with increased total macroinvertebrate and pollution-sensitive EPT taxa richness. In Minnesota, habitat complexity was, by far, the most common variable included in the regression models and influenced several biotic attributes, including total taxa richness (as well as Plecoptera richness and Trichoptera richness), functional feeding groups, and habitat preferences. Declines in habitat heterogeneity in other Midwestern USA regions dominated by agriculture have been associated with declines in mussel biodiversity (Poole and Downing, 2004) and pollution-sensitive macroinvertebrates (Dovciak and Perry, 2002). Simplification and homogenization of stream habitats associated with agricultural activities clearly has strong negative implications for biota and community structure (e.g., Karr and Schlosser, 1978). Given its importance, we recommend researchers devote more attention to accurately and consistently quantifiying habitat complexity.

The width:depth ratio was the third reach-scale indicator identified as important in both regions, but it had inconsistent relationships within each region which limits its usefulness as an indicator. In Michigan a higher width:depth ratio was associated with degraded streams with a high proportion of fine sediments (and thus a preponderance of depositional habitats with burrowing taxa), and assemblages dominated by chironomids. In Minnesota, wider, shallower streams contained more taxa associated with erosional habitats (esp. Plecoptera and Trichoptera), which were primarily shredders and filterers. Thus, this indicator appears to behave differently between the two regions. Width:depth ratios also vary according to the taxonomic composition of riparian zones in the Midwest; wooded riparian buffers have higher ratios than grass buffers (Sweeney, 1993; Lyons et al., 2000; Sweeney et al., 2004). An additional complication is the influence of previous channelization activity. A detailed study of the geomorphology of a channelized headwater stream in Illinois found that construction of a wide ditch relative to the original stream allowed the formation of a meandering stream and a stable floodplain within the ditch (Landwehr and Rhoads, 2003). This stream also contained an abundant and diverse fish assemblage relative to other local channelized streams that were not as wide (Landwehr and Rhoads, 2003). We suggest that researchers and managers give close attention to channel cross-sectional morphology, especially in these highly manipulated streams, because of its importance for stream biota. However, a clear understanding of how channel shape affects stream biota will likely require detailed study at a given site.

Topographic heterogeneity of the landscape (i.e., SD of elevation) was highly related to physical variables at the reach scale in both regions, which agrees with previous findings in Michigan (Richards et al., 1996). For example, both studies found this measure of landform influenced bankfull width. An analogous measure of catchment topography, relief ratio, was one of eight catchment-scale variables identified as important predictors of stream habitat in Australia (Davies et al., 2000). These results provide evidence for the important role that landscape characteristics, such as geology and topography, play in shaping channels. Although good conceptual

Table 7
Standard partial regression coefficients of multiple regressions for each selected reach-scale variable that had a strong relationship ($P \leq 0.10$) with the selected catchment-scale variables in Michigan and Minnesota. The variables with the highest two coefficients (absolute value) are denoted in bold.

Michigan

Reach-scale variable	R^2	Catchment variables			
		SD Elev.	% Comm.	% Water	Road density
No. of habitats	34.4	**0.76**	<0.00	**−0.47**	−0.14
% Fines	38.8	**−0.61**	−0.30	−0.20	**0.72**
DIN	52.2	0.12	**0.85**	−0.45	**−0.62**
% Open canopy	31.2	**0.46**	−0.20	−0.13	**−0.45**

Minnesota

Reach-scale variable	R^2	Catchment variables					
		SD Elev.	% Comm.	% Wetland	Link #	Water capacity	K-factor
No. of habitats	64.4	−0.12	−0.12	−0.16	**0.67**	−0.07	**0.22**
% Fines	35.3	−0.33	−0.14	0.30	−0.32	**−0.70**	**1.22**
Width:depth	50.4	−0.11	−0.26	**−0.51**	**0.67**	−0.44	−0.13
Channelization history	44.5	−0.12	**0.40**	0.05	**−0.54**	0.31	−0.02
Bankfull width	43.4	**−0.45**	−0.30	−0.26	**0.80**	−0.37	0.11
Wood-dam area	51.5	**0.24**	−0.14	0.09	**0.66**	−0.04	−0.15
% Sand	53.7	**0.70**	0.12	0.03	−0.03	0.57	**−1.36**
Maximum temperature	58.5	**−0.20**	−0.07	−0.09	−0.11	−0.03	**−0.59**

models of how geology and topography control stream characteristics exist (e.g., Frissell et al., 1986), the current study provides empirical data in support of these landscape-stream connections. We hypothesize that SD of elevation serves as a functional indicator of these landscape controls.

Percent commercial land use was a catchment-scale indicator in both regions even though it comprised <5% of each catchment in our agriculturally-dominated study regions. These results parallel a separate study conducted in the same streams, in which landscape characteristics were evaluated with respect to large wood in these steams. Percent urban landuse was a strong predictor of large wood density based on regression analyses (Johnson et al., 2006). The detrimental effects of urbanization on stream ecosystems have received much attention (see reviews by Paul and Meyer, 2001 and Allan, 2004), including in the upper Midwest U.S. (Wang et al., 1997, 2000, 2001). Both linear (Moore and Palmer, 2005) and threshold responses to urban land use have been identified, with negative effects becoming apparent when the catchment reaches 10–15% urbanization (measured as impervious surface area; Paul and Meyer, 2001), although even lower levels of impervious surface area (e.g., 6%) can be problematic for stream insects (Morse et al., 2003). We hypothesize that the effects of urbanization can be detected at relatively low levels because most of our study streams are already impacted by agriculture. The effects of a relatively small amount of development may be more pronounced in these disturbed streams, unlike other studies in catchments containing urbanization in a forested matrix. Similarly, Wang et al. (2000) and Snyder et al. (2003) found that urbanization had more deleterious effects on fish communities compared to the effects of agriculture in the same catchments. Osborne and Wiley (1988) reported that urbanization rather than agriculture controlled SRP and nitrate-N concentrations in an Illinois catchment. This was despite urban land use accounting for only ca. 5% of the catchment, and agricultural activity accounted for ca. 90% (Osborne and Wiley, 1988). The results from these studies show that urbanization can have a pronounced effect on stream integrity, even in landscapes that are dominated by other human activity. Recent studies have shown that methods for summarizing nutrient source areas within a watershed (Baker et al., 2006) and the resolution of both landscape and hydrography data (Hollenhorst et al., 2006; Baker et al., 2007) can have a large impact on the relationship between land use and in-stream nutrient concentrations.

4.2. Within-region indicators

Some indicators were specific to a single study region. In Michigan, DIN was an important reach-scale indicator for some invertebrate attributes and DIN concentrations were highly correlated with the proportion of row-crop agriculture in the catchment. The macroinvertebrate assemblage in the higher DIN streams had fewer mayfly taxa, scrapers, and detritivores, but higher proportions of shredders and the dominant taxon. There were no DIN relationships with macroinvertebrate assemblage characteristics in Minnesota streams, presumably because DIN concentrations were so high across all these catchments that nitrogen was above a limiting threshold. It also was likely that our one-time sampling of nutrients was inadequate to capture the range of concentrations that may be present in these streams through natural variations in stream flow and biological activity as well as periodic fertilizer application.

In Minnesota, maximum stream temperature was an important predictor of a variety of invertebrate attributes. Temperature variation was enhanced in the topographically diverse karst regions of Minnesota, which had lower stream temperatures than other agriculturally dominated catchments, presumably because of greater groundwater inputs. The macroinvertebrate assemblage in Minnesota also appeared to respond to structural aspects of streams such as the presence of large wood jams (also see Johnson et al., 2003) and channel morphology.

In Michigan, % open canopy was the second most common predictor of macroinvertebrate assemblage structure. This variable was positively related to total taxa and Trichoptera richness, % filterers, and % detritivores, and negatively related to chironomid richness, % dominant taxon, % burrowers, % depositional, and % omnivores. Our Michigan study streams with little canopy cover contained little wood or CPOM, but still had several habitat types for macroinvertebrates, including macrophytes. The lack of riparian vegetation in these streams likely allowed abundant macrophyte growth, which also provided attachment sites for filterers. Macrophytes can be major components of low-gradient streams (Sand-Jensen, 1998), providing habitat and food for macroinvertebrates (Jacobsen and Sand-Jensen, 1992).

Each region had unique catchment-scale indicators related to hydrology. In Michigan, % surface water was identified, while in Minnesota % wetland, number of links, and soil water holding capacity were identified. Clearly, the ability of the landscape to store and move water has strong controls on the reach-scale indicators in the upper Midwest. Previous studies in Michigan have reported strong effects of catchment hydrology on macroinvertebrates and their habitat (Richards et al., 1996). Riseng et al. (2004) showed that the relationship between algal and herbivore biomass in several Midwestern streams depends on both nutrient concentrations and hydrologic regime. Landscape position also influences freshwater ecosystems in Wisconsin through its controls on the relative importance of groundwater versus precipitation as sources of water and elements (Kratz et al., 1997).

4.3. Multi-scale mechanistic indicators

Our analyses were based on a two-stage process of identifying reach-scale attributes that were mechanistically related to macroinvertebrate attributes, and secondarily selecting catchment-scale variables that influenced the selected reach attributes. Poff (1997) argued that a hierarchical approach incorporating mechanistic relationships between spatial scales would improve our ability to predict how landscape features act as constraints or filters on the characteristics displayed by stream biota. This hierarchical sequence of effects was evident in some of the relationships displayed in this study. For example, key macroinvertebrate attributes, % fine sediments, and catchment characteristics were mechanistically connected in our study regions. In Michigan, a degraded assemblage (i.e., fewer taxa of Plecoptera and Trichoptera, and a higher proportion of chironomids, burrowers, and depositional taxa) was found in streams with a high proportion of fine sediments. Fine sediments were, in turn, linked to SD of elevation–landscapes with less topographic variation had more fine sediments. These relatively flat landscapes probably contain streams with lower stream power to move fine sediments. This landscape-to-reach relationship was also seen in Minnesota, but the positive association between catchment soil erosivity (i.e., K-factor) and fines also indicated the source of sediments. An additional consideration is that human activity may confound these connections across spatial scales. For example, more agricultural activity with its accompanying effects on stream ecosystems is likely to occur in flatter landscapes simply because it is easier to farm these systems. This interaction was suggested in Minnesota, where SD of elevation was negatively related to drainage improvements for agriculture (i.e., channelization; Fig. 3B).

Habitat complexity was a good predictor of macroinvertebrate taxa richness. This indicator was strongly influenced by catchment-scale variables, which differed between the regions. In Michigan, habitat richness was positively related to SD of elevation, and negatively related to % water, whereas the number of links and K-factor were positively related to habitat number in Minnesota. Link number and SD of elevation were probably expressing similar qualities in both regions because both catchment-scale variables were located close together in the RDA bi-plot for Minnesota (Fig. 3B). A high number of links could be related to increased stream size, but greater variation in elevation also could increase the number of first-order streams. This study supports the idea that landscape characteristics (e.g., SD of elevation) have connections to attributes of macroinvertebrate assemblages via their effect on local-scale characteristics of streams.

Although our two-step method successfully developed mechanistic indicators across spatial scales, we recognize some limitations to our analytical framework. Sampling errors at one spatial scale (i.e., sampling biota in the stream) can influence the identification of relationships with other spatial scales (i.e., the reach), which then can affect the second step of connecting the reach to the catchment. Also, it may be more difficult to convey to managers or the public the value of indicators identified using a two-step process compared to using a one-step process relating land use change directly to biota as is often done. However, using an analytical process that identifies mechanisms underlying changes to biota that are driven by landscape-level variables should provide more effective management options.

4.4. Management implications

The successful implementation of indicators varies according to many factors, including: cost, ease of measurement, geographic applicability, precision, accuracy, and goals of the project (NRC, 2000). For example, some of the indicators we identified were relatively inexpensive and simple to measure (e.g., % fines, number of habitats, width:depth ratio), which would allow for rapid implementation. Furthermore, enhancing in-stream conditions by creating additional habitats (e.g., adding wood dams) would likely be very cost effective for improving the structure and function of macroinvertebrate assemblages. For example, the number of habitats was positively associated with richness of sensitive EPT taxa (=structure) and % filterers (=function). Some indicators, however, cannot be manipulated easily; altering the variation of elevations across an entire catchment is an unlikely management option. Yet, understanding how natural factors such as topography influence channel shape and within-channel structure can guide management options and expectations for regions differing in topography. Hawkins et al. (2000) reviewed several studies examining the effectiveness of landscape classifications for describing variation in freshwater biota in a bioassessment context. Based on these studies, Hawkins et al. (2000) recommended a tiered approach to applying landscape classifications to freshwater bioassessment, which relied on considering both reach- and landscape-level approaches in a hierarchical fashion. Our study supports this recommendation as a way to incorporate meaningful variation at multiple, appropriate spatial scales in order to assess biotic communities and suggest remediation actions.

This study also illustrates the difficulties of identifying and developing mechanistic indicators of stream integrity in a highly modified landscape. All of the catchments in this study are dominated by row-crop agriculture. As a result, hydrologic connections have been altered by anthropogenic structures (i.e., channelized streams, drain tile), and considerable seasonal variation in hydrologic processes such as infiltration and evapotranspiration has likely been introduced. That variability in macroinvertebrate assemblages was better explained by variation in non-anthropogenic variables related to geomorphology suggests that some natural hydrologic connections remain intact and that a better understanding of the differential impacts of agricultural landuse on hydrology is needed.

One omission in our study of indicators in agricultural landscapes is how pesticide application on crops affects stream macroinvertebrates. Agricultural pesticides can cause direct mortality of stream macroinvertebrates (e.g., Leonard et al., 1999). Furthermore, many taxa in agricultural streams display ecological traits related to insensitivity to pesticides, unless unimpacted areas upstream provide pesticide-sensitive taxa (Liess and von der Ohe, 2005). Unfortunately, sampling for pesticides in the water, in stream sediments, and those attached to suspended sediments was beyond the scope of our study. Pesticides, like many other chemical constituents, are difficult to quantify because their concentrations vary temporally with storm flow (Liess et al., 1999). Nevertheless, explicitly incorporating pesticide impacts on macroinvertebrates would be a valuable addition to developing mechanistic indicators for agriculture-impacted streams.

Identifying indicators at multiple spatial scales has important implications for the practical implementation of indicators at either the reach or the catchment scale. Historical management of streams has been conducted primarily at the reach scale (e.g., restoration of appropriate channel shape, addition of in-stream habitat structures such as logs). As a result, we expect the reach-scale indicators we have identified to have the highest probability of use by managers. Solely enacting reach-scale (e.g., in-stream habitat) improvements, however, without recognizing the catchment-scale controls (e.g., topography, geomorphology) is analogous to treating the symptom of a problem, but not the cause. Unfortunately, catchment-scale indicators pose a greater challenge to implement successfully. For example, reducing the extent or placement of commercial land use would have considerable positive impact on stream integrity (even in this predominantly agricultural region), but would require action by individuals and governments at many levels (e.g., township, county, and state) to effect change (Allan et al., 1997). Alternatively, BMPs that mitigate the impacts of these activities can be implemented at a local scale, in conjunction with regional planning and management efforts. Despite these challenges, long-term improvement in stream structure and function is likely to be effective only if actions are taken at both local and regional scales.

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